

**Determinants of the introduction, naturalisation, and spread
of *Trifolium* species in New Zealand**

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Master of Science

At

Lincoln University

By

Kelly Gravuer

Lincoln University

2004

Abstract of a thesis submitted in partial fulfilment of the
requirements for the Degree of M.Sc.

**Determinants of the introduction, naturalisation, and spread
of *Trifolium* species in New Zealand**

by Kelly Gravuer

Two conceptual approaches which offer promise for improved understanding of biological invasions are conceptualizing the invasion process as a series of distinct stages and explicitly incorporating human actions into analyses. This study explores the utility of these approaches for understanding the invasion of *Trifolium* (true clover) species in New Zealand. From the published literature, I collected a range of *Trifolium* species attributes, including aspects of global transport and use by humans, opportunistic association with humans in New Zealand, native range attributes, habitat characteristics, and biological traits. I also searched historical records to estimate the extent to which each species had been planted in New Zealand, a search facilitated by the enormous importance of *Trifolium* in New Zealand's pastoral agriculture system. Regression analysis and structural equation modelling were then used to relate these variables to success at each invasion stage. Fifty-four of the 228 species in the genus *Trifolium* were intentionally introduced to New Zealand. Species introduced for commercial agriculture were characterised by a large number of economic uses and presence in Britain, while species introduced for horticulture or experimental agriculture were characterised by a large native range area. Nine of these 54 intentionally introduced species subsequently naturalised in New Zealand. The species that successfully naturalised were those that had been planted extensively by humans and that were well-matched to the New Zealand climate. A further 16 species (from the pool of 174 species that were never intentionally introduced) arrived and naturalised in New Zealand without any recorded intentional aid of humans. Several attributes appeared to assist species in unintentional introduction-naturalisation, including a good match to the New Zealand climate, a large native range area, presence in human-influenced habitats, a widespread distribution in

Britain, and self-pollination capability. The 25 total naturalised species varied greatly in their current distributions and in the rates at which they had spread to achieve those distributions. Species that had spread quickly and are currently more widespread had been frequent contaminants in the pasture seed supply and have a long flowering period in New Zealand. Other biological traits and native range attributes played supporting roles in the spread process. Attributes facilitating success clearly varied among invasion stages. Humans played a dominant role at all stages of this invasion, although biological traits had increasing importance as a species moved through the invasion sequence. My findings suggest that incorporation of human actions and the stage-based framework provide valuable insight into the invasion process. I discuss potential avenues by which these approaches might be integrated into predictive invasion models.

Keywords: invasive, alien, exotic, non-indigenous, introduced species, plant, stage, transition, stage-specific framework, experimental trials, introduction, naturalisation, spread, *Trifolium*, clover, human agency, human dispersal, introduction effort, unintentional, deliberate

Contents

	Page
Abstract	ii
Contents	iv
Tables	v
Figures	vii
1 Introduction	1
2a Methods: Rationale	10
2b Methods: Procedures	40
3 Results	74
4 Discussion	101
Acknowledgments	128
References	129
Appendices	
Appendix 1	146
Appendix 2	155
Appendix 3	156

Tables

	Page
1.1 Review of stage-specific studies of invasion in animal taxa: multivariate models of naturalisation and spread	8
1.2 Invasion patterns for the alien flora of the Czech Republic, the closest approximation to a stage-specific analysis of plant invasion currently available	9
2.1 Stages of invasion defined and analysed in this study	68
2.2 Predicted effects of explanatory variables across invasion stages	69
2.3 Variables used in the statistical analyses, including stage(s) at which explanatory variables were evaluated, number of species available for analysis, variable classifications, and transformations for statistical analyses	71
2.4 Climate parameters used in the matching analysis	73
3.1 Simple regressions of intentional introduction on explanatory variables	80
3.2 Multiple regression model explaining intentional introduction	81
3.3 Simple regressions of naturalisation of intentional species on explanatory variables	83
3.4 Multiple regression model explaining naturalisation of intentionally introduced species	85
3.5 Simple regressions of unintentional introduction-naturalisation on explanatory variables	86
3.6 Multiple regression model explaining unintentional introduction-naturalisation	88
3.7 Simple regressions of coarse-scale current distribution on explanatory variables	90
3.8 Multiple regression model explaining coarse-scale current distribution	92
3.9 Simple regressions of fine-scale current distribution on explanatory variables	93

3.10	Multiple regression model explaining fine-scale current distribution	95
3.11	Simple regressions of rate of spread on explanatory variables	96
3.12	Multiple regression model explaining rate of spread	98
3.13	Comparison among stages of simple regression results	99
3.14	Comparison among stages of multivariate models, with highest significance in multiple regression or SEM (direct effect) indicated	100
AP1.1	Transformations and convergence adjustments applied to variables prior to inclusion in confirmatory factor analysis (CFA) or structural equation models (SEM)	146
AP1.2	Trait and habitat confirmatory factor analysis (CFA): Factor loadings and residual covariances	149
AP1.3	Trait and habitat confirmatory factor analysis (CFA): Relationships to covariate	150
AP1.4	Trait and habitat confirmatory factor analysis (CFA): Factor correlation matrix	150
AP1.5	Intentional introduction SEM parameter estimates	151
AP1.6	Intentional introduction for horticulture or experimental agriculture SEM parameter estimates	152
AP1.7	Naturalisation of intentional species SEM parameter estimates	153
AP1.8	Unintentional introduction-naturalisation SEM parameter estimates	154
AP3.1	The 54 intentionally introduced <i>Trifolium</i> species, including reason for introduction, introduction and naturalisation dates, current distribution in New Zealand, and selected explanatory variables	156
AP3.2	The 16 unintentionally introduced-naturalised <i>Trifolium</i> species, including naturalisation date, current distribution in New Zealand, and selected explanatory variables	158

Figures

	Page
2.1 Division of New Zealand into 10 regions (A) and 329 grid cells (B) for the assessment of species spread. Regional divisions correspond to those used by Webb et al. (1988), while grid cells correspond to the NZMS260 topographic map series (2004).	70
3.1 Interaction between global economic uses and presence in Britain in the intentional introduction multiple regression model	81
3.2 Intentional introduction structural equation model (SEM) including all intentionally introduced species	82
3.3 Intentional introduction structural equation model (SEM) including only species introduced for horticulture or experimental agriculture	82
3.4 Naturalisation of intentionally introduced species structural equation model (SEM)	85
3.5 Unintentional introduction-naturalisation structural equation model (SEM)	89
AP1.1 Trait and habitat confirmatory factor analysis (CFA): Illustration of model	148

1 Introduction

“New Zealand is essentially a land of pastures, and the endeavour of its farmers is to grass every type of country from the sea shore to the line of perpetual snow.” (Levy 1923a)

“Humans are now the dominant vector of plant dispersal and any attempt to classify the properties of a plant that increased its susceptibility to long distance dispersal is more likely to be based on the psychology of higher primates than the biology of plants.” (Noble 1989)

Despite at least 45 years of research on biological invasions, very few, if any, invasion biologists would claim to be able to predict with certainty the fate of a particular organism introduced to a new range. Many scientists have expressed pessimism that such flawless prediction will ever be achievable (e.g. Crawley 1986, Williamson 1999). Nonetheless, although we may never be able to predict every invader in every situation, recent years have seen notable progress in the development of predictive models for particular groups of organisms and locations (Richardson et al. 1990, Scott and Panetta 1993, Tucker and Richardson 1995, Reichard and Hamilton 1997, Pheloung et al. 1999, Kolar and Lodge 2002, Daehler et al. 2004). Although these models appear to achieve reasonable percentages of correct retrospective prediction of invaders, further increases in predictive power are needed if more certain benefit is to be gained (Smith et al. 1999).

Because short-term experiments have limited ability to predict long-term invasion potential (Kareiva et al. 1996), long-term predictive power may be best improved by applying new approaches to existing historical datasets. Refining our analyses may give new insight into the invasion process, which can then be applied to predictive model construction. Recently, two approaches have been suggested which offer promise for using historical datasets to gain a better understanding of the invasion process. The first approach suggests that the invasion process be conceptualized as a series of distinct stages through which a species must pass in order to become invasive (Kolar and Lodge 2001). By considering the factors that allow success at each stage separately, we can more precisely define the processes of interest, potentially improving both statistical and conceptual power. The second approach involves the explicit incorporation of human actions throughout the invasion process (McNeely 2001, Mulvaney 2001, Kowarik 2003).

Because humans are key players at all stages of species' invasions, attempting to quantify their role in comparison to that of species and habitat characteristics can allow the invasion process to be understood more fully. This study explores the utility of these approaches for understanding the invasion of *Trifolium* species in New Zealand.

In making the transition from occurrence in its native range to status as a widespread invader in a new range, a species must pass through several distinct stages (Vermeij 1996, Kolar and Lodge 2001, Heger and Trepl 2003). First, the species must be transported to the new range and released from human containment. I consider the combination of these two processes to be the species' *introduction*. Next, the species must survive and reproduce in the new range, generating successful descendents until it achieves a self-sustaining population. At this point, the species has achieved *naturalisation*. Once naturalised, the species may extend its geographic range in the new area, through expansion of existing populations, dispersal and founding of new populations, or, most likely, both. These processes comprise the species' *spread*. Some authors define a fourth stage beyond that of geographical expansion. In this stage, termed *integration* (Vermeij 1996) or *impact* (e.g. Kolar and Lodge 2002), the species becomes more fully incorporated into local food webs and ecosystem processes, which can have negative consequences for native species and ecosystem services. Unfortunately, quantitative study of this stage is difficult (Parker et al. 1999), and I do not address it further in this study.

As a species might be expected to face different challenges at each of these stages, different attributes may enable it to achieve success at each. At the introduction stage, a species must overcome a major geographical barrier through intentional or unintentional human actions (Richardson et al. 2000b). Traits that increase a species' usefulness to humans, or its ability to hitchhike along human transport routes, would therefore be expected to contribute to success at this stage. A range of challenges would then confront the species in its attempt to naturalise. These may include climatic factors, a lack of mating partners, competitors, enemies, and demographic and environmental stochasticity (Mack 1996a, Richardson et al. 2000b, Heger and Trepl 2003). An equally diverse array of attributes may be important for overcoming these challenges, including a match to the new climate, uniparental reproduction, a high population growth rate, large initial population size, competitive ability, and ecological versatility, especially with regard to climate (Heger and Trepl 2003). Finally, once naturalised, the spread of a species may be inhibited by additional barriers. These include a lack of appropriate dispersal

morphology, the absence of effective dispersers or pollinators, inappropriate physiology or behaviour, additional competitors, a lack of suitable habitat, and pest control measures implemented by humans. A species might surmount these challenges by possessing a morphology suited to long-distance abiotic dispersal, a high rate of propagule production, ecological versatility, especially with regard to habitat (Heger and Trepl 2003), and resistance to human control efforts (Esler 1988b, c).

To date, several studies have presented stage-specific analyses of the invasion process for animal taxa. Most of these studies have compared the naturalisation and spread stages, while only a few have included transport or introduction (Lockwood 1999, Cassey et al. 2004b). However, further study of the introduction stage is clearly necessary, as better understanding of processes occurring early in an invasion may lead to better screening methods at the stage when control can be most successful and cost-effective (Kolar and Lodge 2001). Studies comparing naturalisation and spread showed different attributes to be important at each stage and appeared to largely confirm predictions of the relevant stage-specific challenges (Table 1.1). For example, a large initial population size (introduction effort) appeared paramount at the naturalisation stage for most of the groups studied. Large initial populations may help species to avoid the detrimental effects of demographic and environmental stochasticity that can plague smaller populations (Mack 1995).

There do not yet appear to be any stage-specific analyses of the invasion process for a single group of plants. The nearest approximation to such a dataset is the studies of Pyšek and colleagues of the flora of the Czech Republic (Pyšek et al. 1995, Pyšek 2003). These researchers examined factors contributing to the date of first recording for all species ever recorded in the Czech flora (i.e. those successful in transport, introduction, and at least short-term persistence), as well as factors determining naturalised species' success in several habitats (i.e. those successful in spreading and increasing their abundance) (Table 1.2). As in the animal studies, important factors in these analyses also differed between stages and seemed to largely confirm predictions. For example, species that were deliberately introduced and used by humans, and those from nearby areas with similar climates, were more successful in the earlier stages. The later-stage analysis illustrated two important points. First, although factors thought to be important for spread achieved significance in man-made habitats, traits critical in seminatural habitats differed from those in man-made areas. This result emphasizes the importance of considering spread traits in relation to habitat. Second, dispersal mechanism was an important component of spread,

whether by long-distance dispersal adaptations or human planting. In contrast, dispersal did not appear to be an important factor in the animal studies, illustrating the need for stage-specific studies of plants if the process is to be properly understood for these organisms (Bellingham et al. 2004).

In addition to the use of a stage-based approach, greater insight into the invasion process can be gained by explicitly incorporating human actions into invasion analyses (McNeely 2001). Humans interact with the invasion process in several key ways. First, they determine which species will be introduced, by selection of species for intentional introduction and by behaviours which facilitate the unintentional introduction of additional species (Mack and Lonsdale 2001). Second, they bestow different amounts of introduction or control effort upon these introduced species, which may influence the species' subsequent fates. Finally, humans contribute to the spread of naturalised species by intentionally or unintentionally dispersing them to additional locations within the introduced area, and by their control decisions in response to this spread. Incorporating all of these processes into invasion models should make them more accurate and informative.

Human actions at the introduction stage shape the potential group of invaders, which can profoundly impact subsequent invasion dynamics (Mack 1996b, Williamson and Fitter 1996). For example, for global bird introductions, the bird families chosen by humans for purposeful transport were the same families that dominated the pool of naturalised species (Lockwood 1999). Unintentional fish introductions in ship ballast water seem to exhibit a similar pattern, as the families most commonly transported in ballast are also families well-represented among naturalised species (Wonham et al. 2000). Both intentional and unintentional human introduction patterns thus clearly play a role in defining the pool of naturalised species.

Beyond defining which species are introduced and which are not, humans may also influence the pool of potential invaders by conferring different amounts of introduction effort on the introduced species. A wealth of evidence from animal invasions (Newsome and Noble 1986, Griffith et al. 1989, Williamson 1989, Hopper and Roush 1993, Veltman et al. 1996, Duncan 1997, Green 1997, Duncan et al. 2001, Forsyth and Duncan 2001, Forsyth et al. 2004) and some limited evidence from plants (Rejmánek 2000, Mulvaney 2001) suggest that species released or planted in greater numbers have a higher probability of naturalisation. Humans also affect the spatial and temporal extent over which introductions take place, which define the range of conditions within which the species has the chance to naturalise. Finally, humans may choose to

exterminate some species soon after their naturalisation. Such decisions may be affected by the species' perceived usefulness.

Humans may also play a significant role in the spread of naturalised species by intentionally or unintentionally dispersing them to new locations (Falinski 1972, Hodkinson and Thompson 1997, Kowarik 2003). According to 19th century records, deliberate human actions helped to disperse many invasive species rapidly across the North American continent (Mack 1991). In more modern times, a large number of species were shown to be dispersed inadvertently by humans in Britain, indicating that humans may be the dominant dispersal vector in the modern landscape (Hodkinson and Thompson 1997). In Germany, the vast majority of invasive species have been dispersed within the country by humans (Kowarik 2003). Differential human dispersal is also suspected to play a key role in the differing spread patterns observed among closely-related groups of invaders (Perrins et al. 1993, Weber 1998). Habitats that humans create and maintain, such as railway embankments, can also function as key dispersal routes for introduced species (Clapham et al. 1962, P. Bellingham pers. comm.). In addition to establishing new invasion foci, humans may assist potential invaders to disperse from their point of entry into a more appropriate habitat (Pyšek et al. 1995, Mulvaney 2001). Finally, humans can also check the spread of particular naturalised species by their decisions to implement various control measures (Esler 1988c), which may also be affected by species' usefulness.

Given the substantial impacts that human actions may have at every stage of the invasion process, much can be gained by explicitly incorporating these actions into invasion models. Frequently, invasion studies including only biological and habitat attributes have uncovered patterns which may be attributable to either human actions or biological mechanisms (e.g. Williamson and Fitter 1996, Allen et al. *in review*). Uncertainty over the processes generating such results considerably limits the power of these studies to improve understanding of the invasion process. By explicitly including human actions, such uncertainty can be avoided. In addition, Kowarik (2003) argues that identification of key human dispersal pathways for problematic species might provide new opportunities to regulate the spread of these invaders.

Given the promise of these two approaches to increase understanding of the plant invasion process, an appropriate group of species must be selected in order to properly explore their merits. The comparison of congeneric species is a powerful method for elucidating species-level differences which contribute to invasion success (Mack 1996b). Because such species have many attributes in common, the particular traits responsible for differences in invasive behaviour

can be more precisely identified. To date, congener studies have identified such attributes as germination pattern, establishment success, growth rate, biomass allocation, phenology, environmental tolerance, and competitive ability as potentially associated with invasive behaviour (Hulbert 1955, Cumming 1959, Zimmerman 1976, Nilsen and Muller 1980, Martin and Carnahan 1983, Dillon and Forcella 1984, Forcella et al. 1986, Perrins et al. 1993, Thébaud et al. 1996, Lambrinos 2002, Gerlach and Rice 2003). Studies comparing invasive and native congeners have also made progress in identifying factors responsible for the invader's success (e.g. Caldwell et al. 1981, Schierenbeck et al. 1994, Matsuo 1999, Weber and D'Antonio 1999, Radford and Cousens 2000). However, most congener studies are limited by the lack of sufficient species for quantitative hypothesis testing.

Nonetheless, a few studies conducted within relatively large genera have achieved quantitative support for their hypotheses. Several congener studies have reported a significant relationship between native range area or breadth and invasion success (Forcella and Wood 1984, Roy et al. 1991, Rejmánek 1999). In the genus *Medicago*, annual species were more invasive than perennial species in the western Mediterranean (Olivieri et al. 1991). In a thorough investigation of *Oenothera* species in Europe, both climatic pre-adaptation and a biennial life span were features of the most widespread species (Mihulka 2001, Mihulka and Pyšek 2001). Extensive study of the genus *Pinus* has also revealed biological traits, such as seed mass, minimum juvenile period, and mean interval between large seed crops (Rejmánek and Richardson 1996, Grotkopp et al. 2004), and growth features, such as relative growth rate and specific leaf area (Grotkopp et al. 2002, but see Bellingham et al. 2004), that appear to promote invasion. Importantly, Rejmánek and Richardson (1996) argued that insights gleaned from *Pinus* may apply to predictive models for woody species more generally, illustrating the potential for wider application of quantitative findings from congener studies.

Combining the advantages of quantitative congener study, explicit incorporation of human actions, and a stage-based approach, this study explores the factors responsible for invasion success of *Trifolium* species in New Zealand. *Trifolium* was chosen because the large number of species introduced to and naturalised in New Zealand allowed a quantitative analysis to be performed for each stage of invasion. In addition, both New Zealand and Polynesia, from which New Zealand's first human colonists came, lack native *Trifolium* species. All species therefore arrived after the early 1800s, when Europeans first began to colonize New Zealand.

Furthermore, the genus *Trifolium* has tremendous economic importance to New Zealand due to its vital role in the pastoral agriculture system (Saxby 1940). These mean that a remarkably complete historical record of *Trifolium* introductions is available.

Considering a range of biogeographic, habitat, biological, and human use attributes, I address the following questions:

1. What determined which species of the genus *Trifolium* were intentionally introduced to New Zealand?
2. What determined which of these intentionally introduced species naturalised?
3. Of the *Trifolium* species not intentionally introduced, what determined which species were unintentionally introduced-naturalised in New Zealand?
4. What determined the rate of spread and current distribution of New Zealand's naturalised *Trifolium*?
5. What are the implications of these findings for future invasions research and the improvement of predictive models?

The remainder of this thesis is presented in four sections. In Methods: rationale, I present the rationale for the choice of response and explanatory variables. Focusing on previous studies of biological invasions, I also discuss predictions for the effect of each explanatory variable at each invasion stage. In Methods: procedures, I describe how I collected the data to quantify each of these variables and the statistical methods used to analyse these data. In Results, I outline key results from each of the statistical analysis techniques. The Discussion relates these results to the history of *Trifolium* use in New Zealand as well as previous study of biological invasions. A brief conclusion is presented at the end of the Discussion. All tables and figures referenced in each section can be found at the end of that section.

Table 1.1. Stage-specific studies of invasion in animal taxa. Naturalisation and spread models only are compared, as these stages have received the most study thus far. Multivariate modelling results are shown from multiple regression (sources 1-6, 8) and discriminant analysis (source 7). NA = no comparable attribute category in this study. * = control for phylogenetic relationships included in the model construction procedure (source 3: family forced into model before other variables; source 6: generalized estimating equations).

Taxon	Location	<i>Naturalisation</i>		<i>Spread</i>		Source
		<i>Associated attributes</i>	<i>Comparable attribute category in this study</i>	<i>Associated attributes</i>	<i>Comparable attribute category in this study</i>	
Birds	New Zealand	<ul style="list-style-type: none"> · More individuals released · Non-migratory 	<ul style="list-style-type: none"> + Intro. effort NA 	<ul style="list-style-type: none"> · More broods per season · Migratory · More individuals released 	<ul style="list-style-type: none"> - Genetic system - Seed size & disp. NA + Intro. effort 	1,2,3*,4
Birds	Australia	<ul style="list-style-type: none"> · More introduction sites · Not a game bird · Better climate match · Prior invasion success · Large body mass 	<ul style="list-style-type: none"> + Intro. effort NA + Nat. range NA + Genetic system 	<ul style="list-style-type: none"> · Better climate match · Small body mass 	<ul style="list-style-type: none"> + Nat. range - Genetic system 	5
Mammals	Australia	<ul style="list-style-type: none"> · Better climate match · Prior invasion success · More introduction attempts 	<ul style="list-style-type: none"> + Nat. range NA + Intro. effort 	<ul style="list-style-type: none"> · Low body mass · Longer lifespan 	<ul style="list-style-type: none"> - Genetic system + Genetic system 	6*
Fish	Great Lakes, USA	<ul style="list-style-type: none"> · Faster relative growth rate · Wider temperature tolerance · Wider salinity tolerance · Prior invasion success 	<ul style="list-style-type: none"> NA + Nat. range + Nat. range NA 	<ul style="list-style-type: none"> · Less tolerance of high temp. · Wider temperature tolerance · Slower relative growth rate 	<ul style="list-style-type: none"> - Nat. range + Nat. range NA 	7
Fish	California, USA	<ul style="list-style-type: none"> · More individuals released · More parental care · Longer lifespan · High physiological tolerance · Smaller native range · Prior invasion success 	<ul style="list-style-type: none"> + Intro. effort NA + Genetic system + Nat. range - Nat. range 	<ul style="list-style-type: none"> · Moderately long lifespan · From closer location · Non-herbivorous · Prior invasion success 	<ul style="list-style-type: none"> + Genetic system + Nat. range NA NA 	8

Sources: 1.(Veltman et al. 1996), 2.(Green 1997), 3.(Duncan 1997), 4.(Duncan et al. 1999), 5.(Duncan et al. 2001), 6.(Forsyth et al. 2004), 7.(Kolar and Lodge 2002), 8.(Marchetti et al. 2004)

Table 1.2. Invasion patterns for the alien flora of the Czech Republic, from Pyšek and colleagues (Pyšek et al. 1995, Pyšek 2003). These studies represent the closest approximation to a stage-specific analysis of plant invasion currently available. NA = no comparable attribute category in this study.

<u>Year of first flora record (<i>Transport, Introduction</i>, and beginning of <i>Naturalisation</i>)</u>		<u>Frequency (<i>Spread</i> and <i>Abundance</i>)</u>	
<i>Associated attributes</i>	<i>Comparable attribute category in this study</i>	<i>Associated attributes</i>	<i>Comparable attribute category in this study</i>
<i>All species:</i> 1) Deliberate species earlier than accidental 2) Of deliberate species, utilitary species earlier than ornamentals 3) European species earliest; American species earlier than Australian 4) CSR strategists earlier than SR, C, or CR; CS earlier than C or CR 5) Species starting to flower sooner appeared earlier than those starting to flower later <i>American accidental species only:</i> 1) Annuals earlier than biennials and perennials 2) Species starting to flower sooner appeared earlier than those starting to flower later	+ Intro. effort + Intro. effort + Global transport & use by humans NA - Phenology - Genetic system - Phenology	<i>Seminatural habitats:</i> 1) Greater height 2) Hemicryptophyte 3) Planted by humans 4) Prefers more moist sites 5) Can tolerate low-light conditions 6) C-strategist 7) Vegetative reproduction <i>Man-made habitats:</i> 1) Therophyte 2) Can tolerate low-light conditions 3) C- or CR-strategist 4) Animal-dispersed 5) Self-pollinated	+ Morphology + Genetic system + Intro. effort NA - Habitat char. NA + Genetic system - Genetic system - Habitat char. NA - Seed size & disp. - Genetic system

2a Methods: Rationale

Response variables

I identified three distinct stages of the invasion process, which I refer to as “introduction”, “naturalisation”, and “spread”.

I defined an “introduced” species as one with “plants or propagules present outdoors in a location suitable for the reproduction of at least one other vascular plant species”. I excluded plants grown in glasshouse, laboratory, or growth chamber experiments, as well as plants that were not grown to maturity in outdoor field experiments (e.g. Caradus 1995). The definition implies that the species had previously been transported from its native range to New Zealand by some human means. Some authors, primarily in the animal invasions literature, define a “transport” stage as distinct from and preceding an “introduction” stage. For example, Duncan et al. (2003b) note that an alien bird species must “first... be transported from its native geographic range to a new location” (= transport) and that “second, the species must be released or escape into the environment” (= introduction). I did not identify a distinct transport stage for several reasons. First, because of the economic importance of *Trifolium* in New Zealand, at least 199 of the 228 species have been intentionally transported (W. Williams, personal communication; <http://www.agresearch.co.nz/seeds/>). Therefore, there would have been little variation among species to analyse if the transport stage had been considered on its own. Second, because these plants are rather inconspicuous, especially as seeds, data on species which were unintentionally transported to New Zealand but never introduced into suitable outdoor locations for growth were impossible to obtain. For plant invasions, Richardson et al. (2000b) define “introduction” as meaning that “the plant (or its propagule) has overcome, through human agency, a major geographical barrier”. They thus adopt a definition more akin to the “transport” discussed above. However, because many *Trifolium* species were transported to New Zealand without ever receiving the opportunity to grow and reproduce outdoors, these species could not be considered to have failed in naturalising in the same way as species which had received such an opportunity. Therefore, I considered my definition of “introduction” to be the earliest distinction that could clearly and usefully be drawn between species.

I defined a “naturalised” species as one that had been “collected or observed in the reproductive state at a location not suggesting direct intervention by humans”. Essentially, this

includes what Richardson et al. (2000b) refer to as both “casual” (“alien plants that may flourish and even reproduce occasionally in an area, but which do not form self-replacing populations, and which rely on repeated introductions for their persistence”) and “naturalised” plants (“alien plants that reproduce consistently and sustain populations over many life cycles without direct intervention by humans (or in spite of human intervention); they often recruit offspring freely, usually close to adult plants...”). The distinction between their two terms is primarily one of intermittent vs. consistent, self-sustaining reproduction. However, because I based my survey on historical records (herbarium specimens and plot survey presence/absence data) and because many *Trifolium* species can reproduce vegetatively, it was not always possible for me to distinguish the reproductive nature of the populations from which these records had been collected. Therefore, I selected the distinction which I could draw with the greatest confidence: collected/observed as reproductive, or not. Using my definition of naturalisation, I identified essentially the same set of *Trifolium* species as those that New Zealand botanists consider to be naturalised (Webb et al. 1988). A questionable species was *T. ambiguum*, which was not listed by Webb et al.(1988), but was identified as a new casual record by Heenan et al. (2002). However, correspondence with the collector of the specimen which formed the basis for this record (AK219444) indicated that it had almost certainly been taken out of a planted and cultivated plot (A. E. Esler, personal communication to E. Cameron). Therefore, the species did not meet my definition of naturalised and was excluded from the list.

For species I defined as “introduced”, two groups could be distinguished: those that had been intentionally introduced to New Zealand by humans, and those that had arrived unintentionally. For the first group, the recording of these introduction activities was generally good. The short duration of the European colonization of New Zealand, combined with the potential economic incentive for careful record-keeping and reporting of trials, made it possible to generate a reasonably comprehensive list of *Trifolium* species that had been intentionally planted. From this pool of intentionally introduced species, species which had succeeded and failed in meeting my definition for “naturalised” could be identified. In contrast, comprehensive listing of species in the unintentional introduction group was difficult, as the overall recording of these species throughout New Zealand’s history had been incomplete, both spatially and temporally. Therefore, for unintentionally introduced species, the earliest distinction that could be drawn with confidence was between species that had subsequently been recorded as “naturalised” in New Zealand, and those that had not. Although I am aware of the drawbacks of

combining multiple stages of invasion into a single analysis (Cassey et al. 2004a), it seemed most important to identify a breakpoint at which successful and unsuccessful species could be confidently identified with the available data.

All “naturalised” species, whether intentionally or unintentionally introduced, were considered together in the analysis of spread, which examined rate of spread and current distribution. By “spread”, I refer to the overall presence of plants in the landscape (= geographic range size) rather than to the increase in area occupied by particular populations. Current distribution was measured by both a coarse-scale and a fine-scale metric. This allowed for the possibility that different factors were important for coarse-scale distribution (e.g. long-distance dispersal ability) than for fine-scale distribution (e.g. traits associated with population increase). In addition, each metric had its strengths: the coarse scale metric will allow comparison with a study of the spread of all naturalised species in New Zealand (H. Gatehouse, R. Duncan, J. Sullivan, and P. Williams, unpublished data), while the fine-scale metric provided greater ability to differentiate between widespread species that occupy all regions of New Zealand. The rate of spread measure attempted to address biases in the collection and recording of species over time (see below), allowing for a more objective comparison of species. In addition, this measure may be the most relevant for predicting the spread of species not yet in New Zealand. Table 2.1 provides a summary of the invasion stages defined and analysed in this study.

Explanatory variables

The explanatory variables used in this study were chosen based on 1) a review of theoretical and empirical invasion studies, and studies of the genus *Trifolium*, that identified key variables likely to be important at different stages of the invasion process; 2) research concerning New Zealand’s agricultural and economic history, which suggested additional influences on the fates of this economically important species group; and 3) the availability of data to adequately quantify anticipated effects. I grouped the explanatory variables into six broad categories (Global transport and use by humans, Introduction effort, Opportunistic association with humans in New Zealand, Native range attributes, Habitat characteristics, and Biological traits). As there was a large number of biological traits, I further sub-divided this category into several trait groups (Genetic system, Morphology, Seed size and dispersal, Phenology, Other). All variable categories are specified by sub-headings throughout the Methods sections and are indicated in the

Results tables. In addition, predicted effects of all explanatory variables at each invasion stage are summarised in Table 2.2.

Global transport and use by humans

Centre of origin. The three primary diversity centres for the genus *Trifolium* are located approximately in Turkey (Mediterranean centre), Ethiopia (African centre), and northern California, USA (American centre) (Zohary and Heller 1984). Previous studies (e.g. Forcella and Wood 1984, Reichard and Hamilton 1997, Widrlechner and Iles 2002, Pyšek 2003, Allen et al. *in review*) found that plant species originating in particular regions were statistically more successful at several stages of the invasion process than species originating in other regions. One potential reason for this pattern relates to introduction effort, as humans immigrating to new areas often introduce familiar plants from their home regions (Mack 2001, McNeely 2001). This increased introduction effort may facilitate species success in subsequent invasion stages (see below). The fact that some regions better match the climate and vegetation structure of the recipient area also probably contributes to regional differences (Johnston 1924, Curnutt 2000). In addition, species originating in regions with disturbance regimes more similar to those currently experienced by the target region may have increased chances of success, especially if the disturbance regime in question is new to the target region (Baker 1974, Crosby 1986, di Castri 1990, Roy 1990). All of these factors, in addition to the tendency for Mediterranean *Trifolium* species to be more “weedy” and adapted to “secondary habitats” than species from the other two centres (Zohary and Heller 1984), led me to hypothesize that Mediterranean species would be the most successful at all stages of New Zealand invasion.

Presence in Britain and British distribution. Unlike Europe, both New Zealand and Polynesia, from which New Zealand’s first human colonists came, lack native *Trifolium* species. European colonists first began to arrive in New Zealand in significant numbers in 1840 (King 2003). From that time until approximately the close of World War II, Britain held a strong monopoly on both immigration to and trade with New Zealand (King 2003). I expected that immigrants would have purposefully brought to New Zealand those species which were important in the economy and familiar in the landscape of their home countries (Mack 2001, McNeely 2001). In addition, the strong trading relationship allowed Britain to supply the majority of *Trifolium* seed imports to

New Zealand. For example, of grass and clover seed imported by New Zealand between 1868 and 1900, 84.5% was from Britain, 5.8% was from Australia, and 9.7% was from the rest of the world (New Zealand Registrar-General's Office 1868-1900).

I also expected that British presence and a wide British distribution would have assisted *Trifolium* species in hitchhiking to New Zealand, by means such as pasture seed impurities, attachment to imported farm animals, presence in hay attached to or accompanying animals, ballast, packing material, and soil around the roots of imported plants (Healy 1952). Higher introduction effort for both intentional and unintentional introductions from Britain could then translate into higher success at later invasion stages (see below). Indeed, introduction effort is an important mediator of the correlation between British and New Zealand range sizes for birds (Duncan et al. 1999). In summary, I expected that *Trifolium* species that were present in Britain would have a greater probability of success at all invasion stages, and that, among the British species, species that were more widely distributed would be more successful than those that were narrowly distributed.

Economic uses (global). Worldwide, *Trifolium* species are used for a large number of economic purposes, including forage and fodder for animals, bee plants, erosion control, soil improvement, ornamentals, turf and lawns, and medicinal and herbal plants (Wiersema and León 1999). I expected that species with a greater number of economic uses would be more likely to have been intentionally introduced to New Zealand. In addition, a larger number of uses might increase both the introduction effort applied to a species and the diversity of conditions into which it was planted, increasing the chance of encountering a favourable set of conditions for naturalisation in both space and time (Crawley 1989).

Introduction effort

Introduction and naturalisation date. I tested the importance of introduction date in predicting naturalisation success, and the importance of naturalisation date in predicting rate of spread and current distribution.

For introduction date, my predictions depended somewhat on the introduction pattern. For species that were introduced repeatedly (i.e. commercial agriculture species), I expected that earlier introductions would be more likely to naturalise. First, the extended time period of

introduction would have increased the chance of encountering a favourable set of conditions for naturalisation (Crawley 1989). In addition, earlier introduction may translate into greater cumulative introduction effort, which should also increase naturalisation probability (Mulvaney 2001, also see below).

My predictions were less clear for those species introduced only once or a few times (horticultural and experimental agricultural species). Species experiencing an earlier introduction episode would have encountered fewer established *Trifolium* and similar species, which some authors (e.g. Moulton and Pimm 1983) have argued could increase the chance of success via reduced competition. On the other hand, species experiencing a later introduction episode would be more likely to encounter other introduced species that provide them with important mutualistic interactions (e.g. pollinators or grazing mammals) (Crosby 1986, Simberloff and Von Holle 1999, Richardson et al. 2000a), which could render species introduced later more likely to succeed. Also, species introduced later would have encountered a landscape more thoroughly modified by humans (Esler 1988b), which should increase their chance of success (Newsome and Noble 1986). Finally, for both repeated and non-repeated introductions, a positive effect of early introduction could be observed because the species introduced early were those that people felt were more likely to succeed (Simberloff 1989), or because recently introduced species may not yet have expressed their naturalisation potential (Kowarik 1995). Given these conflicting influences and the fact that horticultural and experimental agricultural species formed the majority of the intentionally introduced sample, I did not expect an overall effect of introduction date on naturalisation success.

For current distribution, I expected that *Trifolium* species that had naturalised earlier would be more widespread. Both within New Zealand and elsewhere, a number of plant studies have found that earlier naturalisation allowed species to achieve more widespread distributions (Rejmánek 2000, Mihulka and Pyšek 2001, Williams and Wiser 2004, Allen et al. *in review*) and higher levels of population density (Esler 1988b, Scott and Panetta 1993, Maillet and Lopez-Garcia 2000). Although the link between early naturalisation and widespread distribution has not been observed in New Zealand birds (Duncan et al. 1999), these organisms would likely disperse much more quickly than *Trifolium*. In terms of overall rate of spread, my predictions were less clear, being subject to many of the same uncertainties listed for non-repeated introductions.

Introduced for commercial agriculture? I expected that commercial agricultural *Trifolium* species would be the most successful in both naturalisation and spread. First, these species experience introduction effort orders of magnitude greater than that of horticultural, experimental agricultural or unintentional species, which should give them an advantage in later stages (see below). Second, species of *Trifolium* introduced for commercial agriculture would be more likely to have had compatible strains of mutualist *Rhizobium* bacteria introduced (see below). Third, a number of commercial agricultural *Trifolium* species were planted as cultivars. Prior selection for traits successful in agricultural environments may give these species an advantage in other human-influenced parts of the landscape (e.g. roadsides, lawns) or in natural areas with similar characteristics (e.g. natural grasslands, Lumaret 1990). Additionally, New Zealand undertook its own *Trifolium* cultivar selection programme, starting in the early 1930s (e.g. Levy and Davies 1930, Davies and Levy 1931), from which variously-adapted cultivars of the most important species have been developed (Rumball 1983). This programme may have both accelerated these species' adaptation to New Zealand conditions and increased the range of New Zealand environments in which they could persist. Fourth, introduction into the commercial agricultural system would have brought species into contact with sheep and cattle. Consumption and re-deposit of seeds would have provided them with favourable micro-habitats for growth and a potential means of both short- and long-distance dispersal to additional suitable areas, potentially aiding them in both naturalisation (Malo and Suarez 1997) and spread (Lamont 1939, Healy 1952).

The naturalised *Trifolium* species pool consists predominantly of commercial agricultural and unintentional species. For spread, the commercial agricultural species might have an additional advantage over the unintentional species due to human cultivation. Cultivated populations may provide colonizing propagules to the surrounding landscape, increasing the chance of establishing new invasion foci (Mack 2000). Additional foci could provide a key advantage for spread, as multiple small foci provide a greater rate of spread than a single large focus given the same number of initial individuals (Auld and Coote 1980, Moody and Mack 1988). Human control of spread may also be less likely for commercial agricultural than for unintentional species, potentially increasing the advantage for commercial agricultural introductions. However, control is unlikely for *Trifolium* species, as even unintentional species are generally seen as having some economic value (Guthrie-Smith 1921, Boswell et al. 2003), although they can be detrimental in seed production areas (Dingwall 1969).

Estimated hectares planted. The importance of introduction effort in facilitating invasion success has been referred to as “the most robust... generalization in invasion ecology” (Rejmánek 2000). Theory relates increased initial population size to greater likelihood of persistence in the face of demographic and environmental stochasticity (Shaffer 1981, Lande 1993). Furthermore, increased introduction effort may relate to release at a larger number of sites (e.g. Veltman et al. 1996), which could facilitate the formation of multiple invasion foci, increasing rate of spread (Auld and Coote 1980, Moody and Mack 1988). In addition, greater introduction effort would increase the probability that a particularly well-adapted genotype would be introduced (Mack 1991, Kowarik 2003).

Evidence for an influence of introduction effort on naturalisation success has accumulated in a wide number of animal taxa, including birds introduced to New Zealand (Veltman et al. 1996, Duncan 1997, Green 1997), birds introduced to Australia (Newsome and Noble 1986, Duncan et al. 2001), ungulates introduced to New Zealand (Forsyth and Duncan 2001), mammals introduced to Australia (Forsyth et al. 2004), insects introduced for biological control (Williamson 1989, Hopper and Roush 1993), and birds and mammals translocated for conservation (Griffith et al. 1989). Evidence from plants is more limited, as reasonably complete historical records of plant introductions can be more difficult to obtain. One thorough study of ornamental woody plant introductions to south-eastern Australia documented a strong influence of introduction effort on the naturalisation of these species (Mulvaney 2001). There is also some evidence that a greater number of plantations increased the number of spontaneous occurrences of *Eucalyptus* species introduced to southern Africa (Rejmánek and Richardson, unpublished data cited in Rejmánek 2000).

The evidence for an effect of introduction effort on the spread of naturalised species is more limited. For New Zealand and Australian bird introductions, both of which showed a positive effect of introduction effort on naturalisation, an effect of effort on spread was found for the New Zealand group only (Duncan et al. 1999, Duncan et al. 2001). Similarly, a positive effect of introduction effort on spread was found for mammals introduced to Australia, but this effect was much weaker than that on naturalisation (Forsyth et al. 2004). Comparable analyses for plant species are very limited. In seminatural habitats in the Czech Republic, Pyšek et al. (1995) found that deliberately planted species were more abundant than unintentional introductions, although the same relationship was not apparent in man-made habitats.

Based on this literature, I anticipated that introduction effort (approximated by the estimated hectares planted for each *Trifolium* species) would have a strong positive effect at the naturalisation stage, and a weaker, though detectable, positive effect in the spread stage.

Nodulation with introduced *Rhizobium*. *Trifolium* species form mutualistic relationships with the nitrogen-fixing bacterial taxon *Rhizobium leguminosarum* biovar. *trifolii* (Burton 1985). Effective nodulation has high ecological importance for *Trifolium* species in many of their preferred habitats, where they often face strong competition (Greenwood and Pankhurst 1976, Turkington and Mehrhoff 1990). In New Zealand, effective nodulation depends on introduced *R. l.* biovar. *trifolii* organisms, as *Rhizobium* from New Zealand's native legumes do not effectively nodulate *Trifolium* (Greenwood and Pankhurst 1976, Jarvis et al. 1977). Furthermore, not all *R. l.* biovar. *trifolii* strains effectively nodulate all *Trifolium* species (Nutman 1965, Greenwood 1976, Greenwood and Pankhurst 1976, Burton 1985, Pryor and Lowther 2002). Experimental testing has established rough "effectiveness groups" within the genus, within which species form productive nodules with the same *R. l.* biovar. *trifolii* strains (Nutman 1965, Burton 1985).

Mathematical models suggest that successful invasion by legumes may be considerably less likely if their mutualist partners are scarce (Parker 2001), although little empirical work exists with which to evaluate this prediction (Richardson et al. 2000a). In New Zealand, there is suggestive evidence that a lack of suitable rhizobia may hinder invasion by some *Trifolium* species. For example, the absence of suitable rhizobia appears to be a limitation for *T. ambiguum* (Patrick et al. 1994, Patrick and Lowther 1995, Pryor et al. 1996, Elliot et al. 1998). In addition, in an experimental planting of 45 non-naturalised *Trifolium* species on a pasture soil in Palmerston North (southern North Island, elevation 45 m), only 4 species formed predominantly effective nodules with the resident *Rhizobium* population and 10 species formed no effective nodules at all (Greenwood 1976), illustrating the limits of New Zealand's current *Rhizobium* strains. In species trials conducted in a very different environment, the South Island high country (Mount John, Canterbury (elevation 770m), Earnsclough Station, Otago (elevation 650m), and Tara Hills, Otago (elevation 490m)), insufficient nodulation was also a suspected cause of *Trifolium* establishment failure (D. Scott, personal communication).

The first introductions of *R. l.* biovar. *trifolii* probably occurred unintentionally during the early days of European settlement (Greenwood 1976, Greenwood and Pankhurst 1976). These organisms may have been spread through the country by a variety of means, including animal

feed, seed, lime, agricultural implements, animal feet, dust, and flood water. As technology improved, the isolation of rhizobial strains highly effective with commercial *Trifolium* cultivars and the inoculation of sown seed with these strains rapidly increased. At the present time, the annual input of commercial strains to New Zealand soils can be quite large; for example, in 1973 and 1974, an estimated 300,000 hectares were sown with coated or inoculated seed (MacKinnon et al. 1977). What is known of current strain distribution in New Zealand soils largely bears the signature of this large-scale input. Where *T. repens* (white clover) is sown, most rhizobial strains form effective symbioses with it and with other species in its effectiveness group (e.g. *T. pratense*), but not with species in other effectiveness groups (e.g. *T. subterraneum*). The opposite relationship prevails where *T. subterraneum* (subterranean clover) dominates the agricultural system (Greenwood 1976).

These dynamics and experimental findings caused me to hypothesize that the presence in New Zealand soils of an *R. l. biovar. trifolii* strain that could effectively nodulate a particular *Trifolium* species would greatly increase that species' chances of naturalisation and spread. Furthermore, I expected that effective strains would have the greatest probability of being present for species important in commercial agriculture and members of their effectiveness groups, as these strains would most likely have experienced large-scale introductions by humans.

Opportunistic association with humans in New Zealand

Frequency as pasture seed contaminant. I assessed the importance of this variable for spread only, as the most complete data available were from New Zealand-based records.

In other locations, spread as a seed contaminant has been identified as the most important dispersal pathway for unintentionally introduced plant species (Mack 1991) and for plant species of agricultural ecosystems (Andersen 1995). In the northwestern United States, presence as a seed contaminant greatly increased alien plant species' rates of spread (Forcella 1985). In Australia, Gladstones and Collins (1983) used careful morphological analysis to argue that seed contamination had been an important determinant of the range of *Trifolium subterraneum*. For plant species without effective natural means of long-distance dispersal, Kowarik (2003) argues that secondary releases by humans (e.g. in contaminated seed) may act as a decisive factor in population expansion, transferring propagules to vast areas of suitable habitat that they could not reach on their own. In support of this argument, differential secondary release by humans may

explain differences in invasive behaviour among *Impatiens* congeners in Britain (Perrins et al. 1993) and among *Solidago* congeners in Europe (Weber 1998).

In New Zealand, the early agricultural literature indicates considerable contamination of pasture seed supplies (e.g. Kirk 1897, Cockayne 1916, Levy 1923b). Although seed purity improved greatly in the mid-twentieth century with the initiation of seed certification (Hadfield and Claridge 1931) and increased use of herbicides, inferior mixtures were still sown on less valuable land (Foy 1939). Botanists specialising in New Zealand's alien flora have identified seed contamination as an important pathway of weed introduction and spread (Healy 1952, Esler 1987).

This information led me to hypothesize that *Trifolium* species exhibiting greater frequencies as pasture seed contaminants would achieve greater rates of spread and larger current distributions in New Zealand.

Found in cultivated habitats in New Zealand? In addition to species purposely introduced for commercial or experimental agriculture, a number of other *Trifolium* species reached and persisted in New Zealand's cultivated areas "by their own scheming" (Guthrie-Smith 1930). They may have been sown onto these areas as seed contaminants or spread from other points of introduction. Once established on cultivated lands, such species would have had many of the same advantages as intentionally introduced agricultural species, including human cultivation and dispersal by stock. In addition, these species could have increased in frequency as pasture seed contaminants, potentially benefiting from that dispersal pathway as well. For these reasons, I expected that *Trifolium* species found in cultivated habitats would have achieved greater rates of spread and larger current distributions in New Zealand.

Native range attributes

Native range area and diversity of conditions tolerated. In reviews of the plant invasions literature, native range area has been highlighted as a robust and consistent predictor of both naturalisation and spread (Daehler and Strong 1993, Rejmánek 1995, 1996, 1999, but see Williamson 1999). It is likely related to introduction as well (Forcella and Wood 1984). Plant studies have found range area to be important in comparisons at a number of different taxonomic levels (e.g. within genera (Forcella and Wood 1984, Forcella et al. 1986, Rejmánek 1999); within

families (Rejmánek 1995, 1996); across a broad species sample (Starfinger 1998, Williams and Wiser 2004)). These relationships have received some support in other taxonomic groups as well, such as birds (Duncan et al. 2003b) and mammals (Forsyth et al. 2004). However, the mechanisms responsible are uncertain.

One explanation contends that species with larger native ranges have a higher probability of introduction to a new area (Forcella and Wood 1984). This could translate into greater cumulative introduction effort for species with larger ranges, promoting their naturalisation and spread. Higher introduction probability might be partly attributable to the higher local abundance often observed in widely-distributed species (Forcella and Wood 1984, Prinzing et al. 2002).

Alternatively, other authors argue that tolerance of a wide range of conditions, or “ecological versatility”, is an important aspect of native range size (Roy et al. 1991, Goodwin et al. 1999, Prinzing et al. 2002). They believe that species that can tolerate diverse conditions in their native ranges will be more likely to succeed in novel conditions. Some authors suggest that genetic attributes, including both phenotypic plasticity and genetic variation, could play a role in such tolerance (Forcella and Wood 1984, Roy et al. 1991, Rejmánek 1999, 2000). Indeed, for *Trifolium subterraneum* in Australia, it appears that introduction of a variety of genotypes has increased the range of occupied sites (Morley and Katznelson 1965, Gladstones 1966, Gladstones and Collins 1983). Expressing the “versatility” concept on a different scale, authors have also speculated that habitat generalism could underlie native range size and invasion success. However, others have noted that widely distributed species need not necessarily be habitat generalists; they may simply use widespread habitats (e.g. Venier and Fahrig 1996).

On the other hand, particular biological traits might be responsible for both large native ranges and invasion success. These traits include seed production (Rejmánek 1999, 2000), dispersal mechanism (Rejmánek 1999, 2000), and the timing (Roy et al. 1991) and length (Goodwin et al. 1999) of the flowering period. Additionally, one could imagine that a sampling effect might operate in the native range size relationship: species occurring at a larger number of sites in their native range would be more likely to occur at a site well-matched to novel conditions. I investigated this possibility using climate matching (see below).

Unfortunately, it is difficult to test these hypotheses using observational data sets; even in well-studied taxa it is not clear which mechanism predominates (Duncan et al. 2003b). Given previous findings, I expected to find a positive relationship between native range area and invasion success at all invasion stages. I also anticipated that it would be difficult to identify the

mechanisms responsible. However, I decided to directly test whether the broad-scale diversity of conditions tolerated (measured as the number of biomes in the native range) could predict invasion success at each stage. If this variable had significant explanatory power in a particular analysis, it would provide support for the ecological versatility hypothesis.

Match to New Zealand climate, New Zealand drought tolerance, New Zealand low temperature tolerance, and New Zealand frost tolerance. Climate can influence plant species' distributions in two important ways. First, beyond certain values of climatic parameters, a species will be unable to complete its life-cycle. Such parameter values place absolute limits on the distribution (Woodward 1987). I will refer to these influences as “tolerance” influences. Within the range of acceptable climate, however, many physiological processes (e.g. photosynthesis) reach an optimum rate at particular climate parameter values, and such optima differ among species (Grace 1987). These optima will be important in determining species' competitive abilities under different climatic conditions. Climatic effects on competitive ability can impact species interactions, ultimately exerting a second important influence on distribution (Davis et al. 1998a, Davis et al. 1998b, Rehfeldt et al. 2002). I will refer to this influence as the “match” influence.

In the absence of detailed knowledge of a species' climatic responses, invasion biologists have attempted to generate informed hypotheses using a process of “inferential modelling” (Sutherst 2003) based on the species' native distribution. Though such inference is laden with assumptions (Hulme 2003), its successful application in a number of cases suggests that it may be a useful, if imperfect, tool for the understanding and prediction of invasion processes.

Using their native ranges, I constructed indices to reflect both the “tolerance” and “match” components of *Trifolium* species' climatic responses, as I anticipated that both would be important in determining their invasive success (Sutherst 2003). The “match” index was based on each native range's climatic similarity to New Zealand, assessing similarity based on temperature, precipitation, and their seasonal distribution. The use of these criteria to assess climatic similarity is well-supported (Curnutt 2000, Kriticos and Randall 2001). I expected that this similarity value would reflect the proximity of New Zealand's climate to the climatic conditions in which the species could compete effectively. For the “tolerance” indices, I decided that cold and drought would be the most relevant parameters for two reasons. First, these parameters significantly influence *Trifolium* distribution in its native range (Cocks and Ehrman

1987, Ehrman and Cocks 1990, Beale et al. 1993). Second, agronomic publications on *Trifolium* in New Zealand (e.g. Boswell et al. 2003) often refer to the importance of these factors in limiting persistence. Within these parameters, I selected specific metrics hoping to capture the influences of both absolute limits on plant survival (minimum temperature) and curtailment of the time available for growth and reproduction (frost-free period and drought-free period) (Grace 1987). Calculation of the “tolerance” index for each metric then considered whether its values in New Zealand were more extreme than those in the native range, or not.

Although few studies have quantitatively assessed the power of climatic match or tolerance to explain invasion success, especially in comparison to other factors, limited empirical evidence suggests a role for climatic match in both naturalisation and spread (Blackburn and Duncan 2001a, Duncan et al. 2001, Forsyth et al. 2004), but see (Roy et al. 1991). I anticipated that my climate indices would also explain these transitions. Additionally, given the logic above it seemed reasonable that the tolerance indices would be more important for naturalisation, while the match indices would have greater explanatory power for spread.

Habitat characteristics

Elevation of native range. In their native ranges, *Trifolium* species inhabit landscapes from sea level to 4500m, with many species specialising in alpine areas (Zohary and Heller 1984). I expected that alpine *Trifolium* species would have been less likely to come into contact with humans than lowland *Trifolium* species, and consequently would have had lower probabilities of both intentional and unintentional introduction. Once again, this differential introduction effort could be expected to translate into an advantage for these species at the naturalisation and spread stages.

Independent of introduction effort, I hypothesized that *Trifolium* species adapted to lowland areas could have additional naturalisation advantages. First, the lowland vegetation of New Zealand has been the most extensively modified by humans (Norton 1989), increasing establishment opportunities for lowland-adapted species (Hobbs and Huenneke 1992, Hobbs 2000). Second, although *Trifolium* seed has been sown over nearly the entire range of elevation in New Zealand, lowland sowings have received a disproportionate share of cultivation (Aitken 1944c, b). Additionally, most plant breeding work in New Zealand has focused on lower-elevation environments (D. Scott, personal communication). However, I did not expect a similar

advantage for lowland *Trifolium* species in the process of spread. Since much of New Zealand's land area is hill or high country (Aitken 1944a), a species would have to be at least somewhat adapted to such environments to achieve a high rate of spread and a large current distribution at the national scale. Indeed, the agronomic literature has documented elevation restrictions for some *Trifolium* species (Boswell et al. 2003).

Canopy cover of native habitat. *Trifolium* species are native to a variety of habitats, from forests to more open scrub areas to completely open fields and meadows (Zohary and Heller 1984, Gillett and Taylor 2001). I expected that introduction probability would be highest for *Trifolium* species that are native to open habitats. For intentional introductions, people would have selected *Trifolium* species that showed promise as pasture plants, most likely species native to open environments. For unintentional introductions, I expected that most species would have come from either pasture environments or other disturbed habitats, again favouring species from open areas.

I also predicted that *Trifolium* species from open habitats would have higher naturalisation success. Human colonization reduced New Zealand's forest cover from 78% to 23% of the land area (Norton 1989, Atkinson and Cameron 1993, Craig et al. 2000), creating large areas of open land to which native plant species were unaccustomed. In addition, natural disturbances that initiate successional changes are widespread in New Zealand (Wardle 1991). Introduced species from open habitats would be pre-adapted to take advantage of all of these areas (Baker 1974, Crosby 1986, di Castri 1990, Roy 1990). Moreover, I expected that the areas to which most *Trifolium* species were introduced would have been open areas such as pastures or urban environments, where species adapted to such environments would be at an advantage. Supporting my prediction, plant species from high-light environments in Central Europe had a higher probability of introduction and naturalisation in Argentina than species from low-light environments (Prinzing et al. 2002). For spread, I did not anticipate such unequivocal dominance of *Trifolium* species from open habitats. Such species would have more habitat available to them than species from forested areas, but I expected that species from areas with intermediate cover, and especially from both open and closed areas, might ultimately achieve the largest distributions in New Zealand.

Native to human-influenced habitats? Because disturbance creates colonization opportunities, introduced plant species often receive important chances for establishment following both natural and anthropogenic disturbances (Hobbs and Huenneke 1992). Furthermore, introduced species may alter ecosystem disturbance regimes once established, often facilitating additional cycles of disturbance and naturalisation (Mack and D'Antonio 1998). The distribution of naturalised plants is strongly skewed toward disturbed habitats in many countries (Kornas 1990, Le Floch et al. 1990, Sykora 1990, Pyšek et al. 1998), including New Zealand (Norton 1989). Because habitats highly modified by humans, such as agricultural and urban areas, often experience significant disturbance levels (Hobbs 2000), species native to such habitats generally possess adaptations enabling success in disturbed environments. These species are then pre-adapted to take advantage of colonization opportunities and to persist in disturbed habitats when introduced to new areas. In addition, the advantage for *Trifolium* species from human-influenced habitats could be compounded by New Zealand's isolated history (Crosby 1986) and the fact that, as noted above, *Trifolium* species were likely to have been introduced into highly modified environments.

Worldwide, bird species that are human commensals had a higher probability of naturalisation (Sol et al. 2002), and in Australia, birds from suburban habitats also had higher naturalisation probabilities (Newsome and Noble 1986). For spread, North American plant species adapted to human habitats achieved greater distributions in Germany (Starfinger 1998). In addition, among American *Oenothera* species introduced to the Czech Republic, species from human-influenced habitats achieved the greatest spread rates (Mihulka 2001). Finally, for birds introduced to New Zealand, species that achieved the largest range sizes were those able to exploit human-modified habitats (Duncan et al. 1999). I predicted that *Trifolium* species native to human-influenced habitats would have a greater probability of introduction, for essentially the same reasons cited for native habitat canopy cover. Based on the literature, I also predicted that these species would have increased success in naturalisation and spread.

Biological traits: Genetic system

Lifespan. The ability to grow and flower rapidly, a pattern typified by annual species, has been hypothesized to promote plant invasion success (e.g. Baker 1974, di Castri 1990). However, studies that have quantitatively tested this hypothesis have met with mixed results (Roy 1990). In

the earlier invasion stages, introduction and naturalisation, an annual lifespan appears important for success of unintentionally introduced species (Esler 1988a, Pyšek 2003). However, in the later stages of naturalisation and spread, most studies that have considered a taxonomically diverse sample over a large area have found lifespan to be a poor predictor of invasion success (Perrins et al. 1992a, Lonsdale 1994, Goodwin et al. 1999, Maillet and Lopez-Garcia 2000, Lloret et al. 2004). This is most likely due to the differential success of different life-histories in particular habitats (Newsome and Noble 1986). Perennial species have been most successful at invading seminatural or natural closed communities, particularly in cool, damp climates, while annual species have generally dominated in disturbed open communities, especially in dry, warm climates (Kornas 1990, Le Floch et al. 1990, Pyšek et al. 1995, Thompson et al. 1995, Hodgkinson and Thompson 1997, Mihulka 2001). If one of these types of habitats predominates in the landscape considered, it may be possible to discern an overall advantage to a particular lifespan. For example, the predominance of disturbed habitats in many regions is thought to underlie the consistent finding that a short juvenile period promotes invasion of woody species (Richardson et al. 1990, Reichard 1994, Kowarik 1995, Rejmánek and Richardson 1996, Reichard and Hamilton 1997). Moreover, in the highly disturbed western Mediterranean, annual species of the genus *Medicago* were more successful than perennial species in completing the invasion process (Olivieri et al. 1991).

Because annual species have shorter generation times than perennials, annuals should have higher potential spread rates. Considering this potential along with the highly disturbed nature of the New Zealand landscape and the short time span of *Trifolium* introductions to New Zealand, I expected that annual *Trifolium* species would achieve the highest rates of spread and largest current distributions. Previous empirical findings also suggested that annuals should have greater success in unintentional introduction-naturalisation. However, I did not expect that lifespan would have a large effect on the naturalisation of intentionally introduced species.

Capable of self-pollination. The capability for uniparental reproduction is a trait that should promote invasion success (Baker 1974, Williamson and Brown 1986, di Castri 1990, Roy 1990, Lodge 1993, Pyšek 1998, Rejmánek 1999). Plants may achieve this through self-pollination.

Self-pollination provides a number of advantages to a species arriving in a new habitat. First among these is the ability to establish a sexually reproducing population from a single initial colonist (Baker 1955). This advantage can also be important for spread in a metapopulation

(Pannell and Barrett 1998). In addition, selfing plant species are more likely to have previously purged their deleterious alleles (Lande and Schemske 1985) and may experience less inbreeding depression than outcrossing species from bottlenecks associated with colonization (Gray 1986). Another important advantage of selfing is that reproduction is not dependent on the presence of suitable pollinators in the new area (Baker 1955, Reichard 1994). This advantage may be particularly relevant to this study, as New Zealand's isolated evolutionary history means that it initially lacked many of the insects capable of pollinating *Trifolium*.

There may also be some disadvantages associated with self-pollination. However, both obligate and facultative self-pollination occur in *Trifolium* (Zohary and Heller 1984), and the disadvantages for the former system may be less applicable to the latter. For example, obligately self-pollinating plant species do not have the ability to generate new, potentially adaptive genetic combinations through outcrossing. On the other hand, facultatively self-pollinating plant species would be able to generate some new genetic combinations, and the frequency of outcrossing events may increase in these species during colonizing situations (Gray 1986). Such an increase has been observed in *Trifolium subterraneum* (Cocks and Phillips 1979) and *Trifolium hirtum* (Jain and Martins 1979). However, some authors have argued that the "rapid multiplication of adapted genotypes" ensured by consistent self-pollination may be more important than new genetic combinations in invasion situations (Barrett and Richardson 1986). In addition, the population genetic structure engendered by self-pollination means that a single population in the native range of a selfing plant species will contain a smaller proportion of the species' genetic variation than a single population of an outcrossing species. This proportion would be smaller for obligate than for facultative self-pollinating species. Therefore, for a comparable introduction effort, the amount of genetic variation introduced would be lowest for obligately self-pollinating species, followed by facultatively self-pollinating species, and lastly by obligately outcrossing species (Barrett and Richardson 1986, Gray 1986, Warwick 1990). However, the large number of other factors associated with introduction events may dilute this effect (Gray 1986).

Several surveys have reported that self-pollination capability tends to be common among "weedy" or colonizing plant species (Mulligan and Findlay 1970, Price and Jain 1981). Also, it appears that high levels of genetic variation are not a prerequisite for plant invasion success (Barrett and Richardson 1986, Roderick and Howarth 1999). At the family level, obligate biotic pollination reduced invasion success in both natural and agricultural environments (Daehler 1998). However, selfing was not an independent predictor of invasion success in several

multivariate models (Perrins et al. 1992a, Reichard 1994, Reichard and Hamilton 1997, Maillet and Lopez-Garcia 2000), illustrating that other factors may often take precedence.

Given this background, I anticipated that *Trifolium* species that were capable of self-pollination would have an advantage over those that were not in both naturalisation and spread. Theoretically, I also expected facultatively self-pollinating species to have an advantage over obligately self-pollinating species, but sufficient data were not available to test this hypothesis.

Capable of vegetative reproduction. Vegetative reproduction may be associated with plant invasive ability (Baker 1974, Barrett and Richardson 1986, Williamson and Brown 1986, di Castri 1990, Lodge 1993, Rejmánek 1999). With vegetative reproduction, a plant population can establish from a single colonist without effective pollination relationships in the new habitat (Baker 1955, Roy 1990, Reichard 1994, Thompson et al. 1995, Heger and Trepl 2003). Furthermore, by mixing outcrossing with the capability for vegetative reproduction, a plant species can combine reproductive assurance benefits with the potential to generate new adaptive gene combinations (Roy 1990, Reichard 1994, Rejmánek 1999). Vegetative reproduction may also enable species to spread into sites that are too marginal to support an independent individual, or in which seedlings would have difficulty establishing (Healy 1961, Esler 1988a, Thompson et al. 1995, Rejmánek 2000, Heger and Trepl 2003, Pyšek et al. 2003). However, one potential disadvantage of vegetative reproduction is that it may reduce the resources available for seed production. Fewer seeds reduce a plant species' ability to take advantage of a number of long-distance transport pathways, especially those involving humans and stock, although vegetative fragments sometimes possess their own means of long-distance dispersal (Rejmánek 1999).

A number of authors have suggested that vegetative reproduction should be especially important in particular habitats (Newsome and Noble 1986). Natural and seminatural habitats are frequently mentioned (Pyšek et al. 1995, Thompson et al. 1995, Daehler 1998), possibly because opportunities for seedling establishment are reduced in such areas. Continuous disturbance, particularly in the form of mowing or grazing, may also favour plants that are able to reproduce vegetatively (Reichard 1994). This type of disturbance may prevent species from completing an entire seed production cycle and may fragment plants at their nodes, putting vegetatively reproducing plants at an advantage (Baker 1974). For *Trifolium* specifically, the vegetative reproduction strategies employed (stolons or rhizomes) also keep plant growing points close to

the soil surface. Such growth forms may provide a further advantage under continuous mowing or grazing by allowing plants to regenerate after the disturbance (Dodd and Sheath 2003).

Studies evaluating vegetative reproduction for woody taxa have found it to strongly promote invasion success (Mulvaney 1991, Reichard 1994, Reichard and Hamilton 1997, Daehler 1998). Results have been more mixed for herbaceous or broad species samples, with a number of studies finding a strong relationship (Esler 1988b, Thompson et al. 1995, Pyšek et al. 2003), some being somewhat equivocal (Pyšek et al. 1995, Heger and Trepl 2003), and one finding no relationship (Perrins et al. 1992a).

Based on these findings, I expected that vegetatively reproducing *Trifolium* species would have greater naturalisation success than those that could not reproduce vegetatively. However, I did not anticipate a strong relationship to spread, since the advantage of many seeds available for long-distance transport might counter the benefit of vegetative spread.

Polyploidy. Polyploidy is another aspect of the genetic system hypothesized to promote invasiveness in plants (Barrett and Richardson 1986, Gray 1986, di Castri 1990, Reichard 1994, Rejmánek 1996). Polyploid plant species often have wider distributions than related diploids (Stebbins 1971, Roy 1990, Thompson and Lumaret 1992) and frequently occupy a more diverse range of environments. Additionally, polyploids have been notably frequent on weed lists (e.g. Holm et al. 1977).

Wide polyploid distributions result from a number of possible genetic mechanisms (Gray 1986). These include gene duplication and subsequent diversification, fixed heterozygosity, and buffering against inbreeding depression in founder populations (Levin 1983, Barrett and Richardson 1986, Gray 1986, Roy 1990, Warwick 1990). In addition, polyploids may benefit from heterosis and the formation of new, adaptive gene combinations (Barrett and Richardson 1986, Thompson and Lumaret 1992). There is also some evidence that polyploids exhibit an increased capacity for self-pollination, giving them more flexible reproductive systems than related diploids (Levin 1983, Thompson and Lumaret 1992). It should be noted, however, that polyploids may also exhibit reduced seed production (e.g. Scott 1999), which could be disadvantageous for invasion.

Quantitative studies have not found a strong influence of polyploidy on plant invasion success. Several studies have shown no relationship (Roy 1990, Reichard 1994, Reichard and Hamilton 1997, Maillet and Lopez-Garcia 2000), although one found a positive correlation

between chromosome number and the probability of invasiveness (Mulvaney 1991). A study of *Medicago* species invading the western Mediterranean found a negative association between polyploidy and invasion success, although the authors suspected that lifespan was the true driver of this relationship (i.e. annuals were more successful than perennials, but were less likely to be polyploid) (Olivieri et al. 1991).

Given the potential advantages of polyploidy for invasion of novel environments, I expected to find that polyploid *Trifolium* species would have increased success in both naturalisation and spread. However, given the poor support for this relationship in the literature, it seemed likely that this relationship would not be particularly strong.

Reduced base chromosome number. The mass and volume of DNA in the plant cell nucleus has biophysical effects on the phenotype (Bennett 1971). Because cells with less nuclear DNA are able to complete the cell cycle in a shorter time, the amount of DNA in the nucleus may reflect a species' history of selection for shorter minimum generation time (Bennett 1987). Given the importance of rapid life-cycle completion for invasions of disturbed environments, some authors have proposed that plants with small genome sizes should be the most successful invaders of these habitats (Rejmánek 1996, Grotkopp et al. 1998, Rejmánek 2000).

Reviews of the plant invasions literature have concluded that there is as yet insufficient evidence for a firm relationship between genome size and invasion success (Gray 1986, Roy 1990), and a study of annual British weeds found quantity of DNA to be unrelated to weediness (Perrins et al. 1992a). However, global weed species were shown to have consistently smaller genomes than a sample of other angiosperm plants (Bennett et al. 1998). In a thorough study of genome size and its correlates in *Pinus*, genome size showed a relationship to invasiveness, but this was mediated through seed size (i.e. species with smaller genomes had smaller seeds, which then allowed them to be more invasive) (Grotkopp et al. 2004). However, in other groups of plants, genome size might more strongly reflect minimum generation time, especially if there are other important selection pressures on seed size.

As I expected that *Trifolium* would invade mainly disturbed environments, I anticipated that *Trifolium* species with a reduced number of base chromosomes (a proxy for genome size) would be more successful in spreading, especially when success was measured as rate of spread. I did not expect a similar effect for naturalisation.

Biological traits: Morphology

Height maximum and Habit. The height and habit of a plant species can have important consequences for its invasion success. First, taller species may achieve more effective seed dispersal (Edwards and Westoby 1996), especially if seeds are dispersed by wind or vertebrate animals (Reichard 1994), or by the inadvertent movements of humans (Falinski 1972). Second, in habitats where competition for light is intense, greater height may provide a vital competitive benefit (Newsome and Noble 1986). Conversely, in habitats subject to frequent grazing (Crawford et al. 1989, Russi et al. 1992, Scott 2001, Dodd and Sheath 2003), mowing (Esler 1988a), or treading (Baker 1974), low-growing species may be at an advantage. In these habitats, plants need to prevent the destruction of both their vegetative growing points and developing flowers and seeds (Dodd and Sheath 2003, Thomas 2003). In grazed habitats, the most advantageous reproductive strategy may be one of intermediate habit, so that some seeds are certain to survive near the mother plant, but others can take advantage of the long-distance dispersal opportunities provided by stock (Simao Neto et al. 1987, Thomson et al. 1990, Russi et al. 1992, Ghassali et al. 1998). Complicating the anticipated height effect, many *Trifolium* species have their primary opportunities for naturalisation and spread on roadsides or other wasteland areas adjacent to pastures (Healy 1973, Sykora 1990). While a short, prostrate habit may be advantageous inside the pasture fence, escaping species may face intense competition for light after leaving the pasture environment.

Several studies have identified height as a contributor to plant invasive success. The importance of this trait appears to be habitat-specific (Newsome and Noble 1986), with taller plants more successful in natural or seminatural mesic habitats with potentially strong competition (Pyšek et al. 1995, Hodkinson and Thompson 1997, Rejmánek 2000, Mihulka 2001). Height appears to be of lesser importance in habitats with greater human influence (Pyšek et al. 1995, Rejmánek and Richardson 1996, Hodkinson and Thompson 1997). Unsurprisingly, this habitat-specificity means that most studies evaluating a broad range of habitats have not found a significant effect of plant height (Perrins et al. 1992a, Lonsdale 1994, Reichard 1994, Thompson et al. 1995, Reichard and Hamilton 1997, Lloret et al. 2004). Species successfully invading New Brunswick, Canada from Europe were significantly taller than unsuccessful ones, but this relationship had little predictive power (Goodwin et al. 1999). Two studies did find a robust effect of plant height in a broad species and habitat sample; both of these reported that alien

plants in Britain tended to be markedly taller than native plants (Crawley et al. 1996, Williamson and Fitter 1996). Yet, even in this case, the effect may have been driven by species invading competition-intensive habitats (by aliens that were ‘more K-strategist’ than native K-strategists) (Crawley et al. 1996).

Given the trade-offs evident for plant height and habit, and their habitat-specific influences, I did not anticipate a strong effect of these variables. I expected that these measures would be more important for spread than for naturalisation, and that taller, more erect *Trifolium* species would have an advantage. These species should be able to colonize a wider range of habitats and to compete successfully in plant communities outside the pasture environment. In addition, the potential seed dispersal advantage enjoyed by tall, erect species may facilitate faster spread in vegetation communities sufficiently open to allow this advantage to be realised.

Biological traits: Seed size and dispersal

Seed size and Seed mass. Seed mass represents a major dimension of ecological variation among plant species, as it is correlated with a number of key ecological attributes (Westoby et al. 2002). Unsurprisingly, therefore, many researchers have suggested that seed size or mass should be related to plant invasion success. Advantages for both small- and large-seeded species have been proposed.

Small-seeded plant species are expected to have a dispersal advantage. First, lighter seeds are carried further by wind. Second, smaller seeds are better able to survive passage through the gut of grazing animals (Jones and Simao Neto 1987, Simao Neto et al. 1987), and there is significant size-based survival variation among *Trifolium* species (Thomson et al. 1990, Russi et al. 1992, Ghassali et al. 1998). The possession of seeds that can survive sheep digestion appears to be a crucial component of annual legume (*Medicago* and *Trifolium*) invasion success in Australia (Fortune et al. 1995). The capacity for gut dispersal may be important for plant naturalisation as well as for spread, as it allows species to be transported to favourable habitats at the most critical point in the naturalisation process (Malo and Suarez 1997). Third, small seeds have greater longevity in soil (Thompson et al. 1993), a characteristic that in and of itself may be important for invasive ability (Baker 1974). Additionally, small, long-lived seeds are better able to take advantage of the long-distance dispersal opportunity provided by human soil movement

(Hodkinson and Thompson 1997). Small seeds may also display greater dormancy, providing a mechanism for temporal dispersal in unpredictable habitats (Andersson 1996, Smith et al. 1996).

Small seed size is also correlated with other potentially advantageous characteristics. In a sample of British species, small seeds had more rapid rates of germination, which then led to higher abundance (Grime et al. 1981). Small-seeded plant species also often have higher relative growth rates (Grime et al. 1981), which may contribute to their invasive ability (Grotkopp et al. 2002, but see Bellingham et al. 2004). Additionally, small seeds may be less susceptible to predation than large seeds (Richardson et al. 1990). Finally and arguably most importantly, all else being equal, smaller seed size will translate into greater seed number (Westoby et al. 2002). Greater seed number has been frequently proposed as a trait that could promote invasion success (Baker 1974, Noble 1989, di Castri 1990, Roy 1990, but see Bergelson 1994). By allowing each planted individual to affect greater subsequent propagule pressure, greater seed number may allow a species to naturalise more quickly. In addition, greater seed number may increase the number of seeds that are able to exploit long-distance transport opportunities, which could be of paramount importance for spread.

On the other hand, large seeds also endow a plant species with characteristics that could enhance invasiveness. Foremost among these is greater seedling establishment success, especially under hazardous conditions such as competition, deep shade, defoliation, low nutrients, low water, and deep burial (Burke and Grime 1996, Westoby et al. 2002). Species able to successfully establish across a greater range of environments might have increased success in both naturalisation and spread. Larger seeds also tend to produce larger seedlings, which would have a competitive advantage over smaller seedlings (Turnbull et al. 2004). This initial size advantage could be compounded later in the life cycle if larger seedlings are able to pre-empt resources from their smaller competitors (Weiner 1990). Larger-seeded species may therefore have a strong advantage in environments where competition is intense.

Seed mass or size has been a good predictor of invasiveness in several plant studies. Conspicuous among these are studies within the genus *Pinus*, where it was found that smaller-seeded species were more invasive in both South African mountain fynbos (Richardson et al. 1990) and globally (Rejmánek and Richardson 1996). Weediness in agricultural environments also showed some association with small seeds, as exotic species had smaller seeds than their native congeners among American agricultural weeds in France (Maillet and Lopez-Garcia 2000).

Yet, there is also some indication that seed size, like such attributes as lifespan and height, might be best understood as promoting invasion success in particular habitats. Crawley et al. (1996) noted that British aliens tended to have larger seeds on average than British natives. They attributed this effect to the group of alien species invading competition-intensive habitats (aliens that were ‘more K-strategist’ than native K-strategists), but noted that there also appeared to be a group of aliens that specialized in more disturbed habitats (those ‘more r-strategist’ than native r-strategists), indicated by a tendency for aliens to have longer-lived seed banks. A number of studies that have found no evidence for an effect of seed size on invasiveness (Roy 1990, Lonsdale 1994, Reichard 1994, Thompson et al. 1995, Reichard and Hamilton 1997, Pyšek 2003). Again, this may be partially a function of the potential habitat-specific importance of this trait, although it is also possible that different trait values are advantageous at different stages of the invasion process, or that other associated factors are of greater importance (e.g. dispersal mode, Edwards and Westoby 1996).

I hypothesized that larger-seeded *Trifolium* would have greater naturalisation success because of the establishment advantages of larger-seeded plant species under challenging conditions. However, I expected smaller-seeded *Trifolium* to have greater spread success because of the dispersal, seed output, and persistence advantages of smaller-seeded plant species, as well as the predominance of disturbed habitats in New Zealand, to which smaller-seeded plant species are better suited.

Capable of long-distance dispersal. Dispersal ability varies considerably among *Trifolium* species. While the propagules of many species have no apparent morphological adaptation for dispersal, other species are adapted to wind dispersal, which may permit moderate increases in dispersal distance, or to external transport by animals, which may allow longer dispersal gains (Zohary and Heller 1984).

Unsurprisingly, it has frequently been noted that the possession of adaptations for long-distance dispersal should increase a plant species’ invasion success (Baker 1974, Williamson and Brown 1986, di Castri 1990, Lodge 1993, Pyšek 1998). This logic has largely been supported by mathematical modelling exercises (Auld and Coote 1980, Moody and Mack 1988, Higgins and Richardson 1999).

In the plant invasions literature, the relative merits of abiotic compared to biotic dispersal mechanisms have been debated. Biotic mechanisms may provide habitat directionality (Reichard

1994, Heger and Trepl 2003), access to relatively undisturbed environments (Rejmánek 2000), and disturbance at the point of seed deposition (Schiffman 1997), while abiotic mechanisms provide relative certainty that the required dispersal agent will be present in the new area (Noble 1989, Richardson et al. 1990, Daehler 1998). However, there is evidence that biotically-dispersed species are frequently successful in locating appropriate agents in the new range (Simberloff and Von Holle 1999, Richardson et al. 2000a). As an additional complication, the dispersal pathways used by invaders may not be apparent from their morphology, which frequently confounds prediction efforts. In particular, associations with grazing animals (Lamont 1939, Esler 1988a) and humans (Andersen 1995, Hodkinson and Thompson 1997, Kowarik 2003) have been reported to promote long-distance movement of invaders with no apparent dispersal adaptation.

Several plant studies have confirmed the expected advantage of morphological adaptations to dispersal. These adaptations include external attachment to animals (Olivieri et al. 1991), wind dispersal (Richardson et al. 1990, Maillet and Lopez-Garcia 2000, Lloret et al. 2004), and, where this could be quantified, gut dispersal (Perrins et al. 1992b, Malo and Suarez 1997). However, the absence of a dispersal morphology effect in other studies (Mulvaney 1991, Perrins et al. 1992a, Reichard 1994, Reichard 1997, Reichard and Hamilton 1997, Pyšek 2003) illustrates that this may not be a universally important feature of invaders, especially if they are transported long distances by humans.

I expected that *Trifolium* species adapted to (external) animal or wind dispersal would achieve greater rates of spread and larger current distributions than species lacking such adaptations, but that dispersal morphology would not have a strong effect on naturalisation.

Biological traits: Other

Seed shape similar to white clover?. White clover (*Trifolium repens*) has played a prominent role in the New Zealand economy since the beginning of European colonization (Crosby 1986, Woodfield 1995). It has also tended to be among the least pure of New Zealand's pasture seeds (Cockayne 1914, Lancashire 1984), suggesting a potential introduction avenue for other *Trifolium* species. Seed shape, in addition to seed size, could be important in determining which *Trifolium* species were likely to be introduced by this means. In the early 1900s, agricultural reports suggest that seed adulteration, the purposeful dilution of seed lines with less valuable

species, was commonly practiced in white clover lines. Having a shape and size similar to white clover may have facilitated the selection of particular *Trifolium* species as adulterants. For example, Cockayne noted that “the very close resemblance of the seed of clustered clover [*T. glomeratum*] to that of white clover has already been taken advantage of by certain seed merchants, and adulterated lines are now quite common” (Cockayne 1914). In later years, as machine-cleaning of seeds became more rigorous, a similar shape and size may have enabled persistence in cleaned white clover lines (Hartley 1969).

For these reasons, I anticipated that *Trifolium* species with a seed shape similar to that of white clover would have a greater probability of unintentional introduction-naturalisation. I expected that seed shape might also be a reasonable predictor of spread in simple regression analysis. However, in multiple regression analysis, I expected that seed shape would be superseded by frequency as a pasture seed contaminant, as the contaminant frequency variable would provide a more direct test of the contaminant effect.

Corolla length. Invasion researchers have hypothesized that successful plant invaders should have unspecialised pollination requirements (Baker 1974, di Castri 1990). Pollinator limitation has been documented for at least one introduced legume species in the United States (Parker 1997), as well as for introduced *Ficus* species in New Zealand (Gardner and Early 1996) and elsewhere (Richardson et al. 2000a). Many *Trifolium* species are insect-pollinated (Zohary and Heller 1984), and *Trifolium* species with longer corollas require more specialised pollinators (Free 1993). The need for specialised pollinators is especially relevant in New Zealand, where most insect species capable of pollinating *Trifolium* were initially absent. Indeed, the failure of red clover (*Trifolium pratense*) to set seed in New Zealand before bumble bees were introduced (e.g. Anonymous 1877) is well-known (Richardson et al. 2000a). Limited evidence suggests that pollination may still present a problem to *Trifolium* with long corollas in New Zealand, as Hampton et al. (1990) note that “seed set in *Trifolium medium* is low because of poor pollination”. Interestingly, the requirement for specialised pollinators may even limit *Trifolium* seed set in its native range, as long-corollaed species have reduced seed set compared to short-corollaed species in similar habitats of the former USSR (Krylova 1979).

Given this evidence, I expected that some *Trifolium* species could experience pollinator limitation in New Zealand, with consequent reductions in their invasion success at both the naturalisation and spread stages. I used corolla length to estimate this potential effect, assuming

that species with longer corollas would experience greater pollinator limitation. Future study of this issue might examine more specific relationships involving pollinator abundance and distribution in New Zealand over time.

Biological traits: Phenology

Month flowering starts and **Month flowering ends (Native range and New Zealand)**. As the timing of germination and flowering tend to be somewhat correlated in *Trifolium*, I anticipated that my flowering time measurements might capture some of the variation in each of these processes. As such, a significant effect of flowering time might indicate that either process, or both, was important.

It is important for plant species to time the flowering period in a way that allows maximum successful reproduction, given the salient abiotic stresses in the environment (Grace 1987). For example, in environments with severe summer drought, species would need to complete most of their seed maturation before drought onset (Smetham 1980, Gladstones and Collins 1984, Lancashire 1984, Crawford et al. 1989, Dodd and Sheath 2003). However, completion of the life cycle substantially before the onset of abiotic stress may leave a species vulnerable to competition from others that make use of the entire available growth period (Perrins et al. 1992b, Dodd and Sheath 2003). Phenology may also be an important component of an invading plant species' interactions with competitors, as species with phenological patterns that differ from their competitors might gain access to underutilized resources (Roy 1990). In addition, the best phenology in a new environment would be one that coincides well with the availability of pollinators (Reichard 1994). In agricultural systems, reproductive phenology can also be essential to effective contamination of the harvested seed crop (Perrins et al. 1992b). Finally, for *Trifolium* specifically, the timing of flowering and fruiting can be vital to species' interactions with grazing animals. The optimal timing of these activities would be one that protects flowering heads from consumption by the animals, but that brings mature fruits into contact with these potential seed dispersers.

Limited study of the introduction stage in plants suggests that phenology may play a role, as earlier-flowering species were introduced sooner to the Czech Republic (Pyšek 2003). For the later invasion stages, plant species' phenology has been related to the spread of agricultural weeds (Maillet and Lopez-Garcia 2000), and to the perceived weediness of annual plants (Perrins

et al. 1992a, b). There is also evidence that some areas of New Zealand (e.g. dry South Island hill country) may present sufficient abiotic stress to render some phenological patterns more desirable than others (Smetham 1980, Lancashire 1984). Some support is also apparent for the importance of a phenology offset from that of competitors. Two studies found that an invasive species had a phenology that differed significantly from a related native (Matsuo 1999, Radford and Cousens 2000). In Britain, there was a slight tendency for alien species to flower either earlier or later than natives (Crawley et al. 1996), although flowering period did not differ among natives and aliens that had recently expanded their ranges in northwestern Europe (Thompson et al. 1995). The importance of phenology to plant invasion was not universal, however, as there was not strong support for this relationship in a broad sample of woody invaders of North America (Reichard 1994, Reichard and Hamilton 1997).

I expected that native range phenology would play a role in *Trifolium* unintentional introduction, in that species which flowered later in their native range would be more likely to have their fruiting periods overlap with those of co-occurring perennial pasture plants, increasing their chances for unintentional introduction as seed contaminants. For both unintentional and intentional *Trifolium* naturalisation, the role played by native range phenology would probably depend on its relationship to New Zealand phenology and/or how well it predicted species responses to abiotic conditions in New Zealand. Given the significant differences between these species' native environments and New Zealand, I did not expect these correlations to be particularly strong, and so did not anticipate a large effect of native range phenology on naturalisation. For *Trifolium* spread, I expected that New Zealand phenology would play the primary role. I anticipated that later flowering species might be able to contaminate the seed of perennial pasture plants in New Zealand in the same way as in their native range. However, there could also be an advantage to earlier flowering, which would allow species to reproduce at a time when competition from perennial plants was low and to avoid the effects of summer drought in drier regions. Therefore, given these conflicting influences, I did not expect an overall effect of New Zealand flowering time on spread.

Length of flowering period (Native range and New Zealand). A long flowering period, frequently correlated with a long fruiting period, has been hypothesized to promote invasion success in plants (Rejmánek 1999, 2000). Species that flower longer will have a greater probability of encountering appropriate pollinators (Reichard 1994, Reichard 1997). In situations

where the quantity of fruit available at any one time is not a factor in attracting dispersers, as is likely the case in *Trifolium*, longer-fruited species will have a greater chance of finding dispersal agents (Falinski 1972, Reichard 1994). For *Trifolium* species, longer flowering periods will also increase the chance that at least some immature reproductive heads escape consumption by grazing animals. For plant species generally, in environments where favourable habitat patch locations vary temporally, longer flowering and fruiting will increase the chance that at least some dispersed propagules will encounter a patch favourable for establishment (Gerlach and Rice 2003). Finally, longer flowering periods may indicate a plant species' ability to flower over a broader range of climatic conditions. If inappropriate flowering behaviour is a frequent cause of reproductive failure in novel climatic environments (Grace 1987), reproduction tolerant to a broader range of conditions may enable plant species to overcome this hurdle.

Long flowering and fruiting periods were a notable feature of woody invaders of North America (Reichard 1994, Reichard and Hamilton 1997). A study of *Centaurea* species in California also postulated that a longer flowering period contributed to the success of the most invasive species (Gerlach and Rice 2003). In a study of earlier invasion stages, European species that had been introduced and naturalised in New Brunswick, Canada had longer flowering periods than those that had not, although the relationship had low predictive power (Goodwin et al. 1999). Comparing invasive to native species, a *Senecio* species invading Australia had a longer flower period than its native congeners (Radford and Cousens 2000), although there was no difference in flowering period between natives and aliens that had recently expanded their ranges in northwestern Europe (Thompson et al. 1995). Conversely, a shorter flowering period might actually be advantageous for weeds of agriculture, possibly because it allows them to mature their seed before harvest (Maillet and Lopez-Garcia 2000).

For *Trifolium* flowering period length, I expected similar explanatory power of native range compared to New Zealand data as outlined for the timing of flowering. I expected that a longer flowering period would increase *Trifolium* invasion success at all stages.

2b Methods: Procedures

I followed Gillett and Taylor (2001) to construct the list of species in the genus *Trifolium*. This is the most recent publication that comprehensively lists *Trifolium* species, and it includes species discovered since the publication of Zohary and Heller (1984). In addition, Gillett and Taylor (2001) tended to lump rather than split contentious species, increasing the probability that reliable data could be located for all species on the list. To determine species synonymy, I consulted the ILDIS World Database of Legumes, version 6.00 (<http://www.ildis.org/>). If a synonym was not in this database, I consulted the United States Department of Agriculture Germplasm Resources Information Network taxonomy resource (http://www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl).

Response variables

Information regarding the type, coding, units, transformation, and sample size of response variables is listed in Table 2.3.

Intentional introduction. This is a binary variable with the world's 228 *Trifolium* species coded as either intentionally introduced to New Zealand (1) or not (0). Several data sources were used to define the list of intentionally introduced *Trifolium* species. First, the ALLWEEDS database held by Landcare Research New Zealand was consulted. This database lists all exotic species believed to be in New Zealand, including those in cultivation, and contains a total of approximately 24,700 records (Williams et al. 2002). These records were derived from a wide range of sources, including herbaria, horticultural societies, nursery catalogues, botanic gardens, arboreta, research institutions, and published literature (<http://www.landcareresearch.co.nz/research/biodiversity/plantsprog/herbarium.asp>). The primary information source for all *Trifolium* species listed in this database was obtained from P. Williams, and these sources were consulted to confirm species identities. Second, a database of *Trifolium* specimens held by New Zealand herbaria was created. Eight major herbaria were included in this survey, including institutions on both the North (AK, MPN, NZFRI, WELT) and South (CHR, CANU, LINC, OTA) Islands. The majority of *Trifolium* specimens were located at the CHR (Allan) Herbarium, and species identities for CHR specimens were confirmed by D.

Glenny, following Zohary and Heller (1984). The records in this herbarium specimen database were then separated into “cultivated” and “non-cultivated” groups. A specimen was judged to be “cultivated” if the label contained the words “cultivated”, “plot grown”, “experimental plot”, “sown pasture”, or “experimental garden”; all other specimens were assumed to be “non-cultivated”. All species in the “cultivated” group were then added to the list of intentional introductions. Third, introduction records from the historical database (see “Estimated hectares planted” below) were added. This database includes the results of a literature search to locate published reports of species introduction trials, including an intensive search of the New Zealand Science Database and follow-up of citations within the reports found. Finally, individuals known to have participated in *Trifolium* species evaluations were personally contacted, and additional species evaluated by these individuals were added to the list.

During the list construction, it became apparent that some species had been used in 20th century evaluation trials because they had previously naturalised in New Zealand, rather than naturalising as a result of these trials. Therefore, if a species was recorded as introduced before it had naturalised, I counted it as an intentional introduction; otherwise, it was considered to be an unintentional introduction whose naturalisation in New Zealand had prompted its subsequent use in trials. This categorization was modified as necessary using descriptions of the reason for species introductions (e.g. Kirk (1870) records *T. medium* as an intentional introduction for commercial agriculture). It was also modified for three species (*T. dubium*, *T. fragiferum*, and *T. subterraneum*) that were extensively used in commercial agricultural plantings, but whose first naturalisation may have pre-dated these plantings. For these species, I considered that my intentional introduction records (see “Estimated hectares planted” below) may not have recorded all introductions, especially in the pre-1900 period relevant to this distinction. Also, for a similar introduction situation suspected for *T. subterraneum* in Australia, the intentionally introduced genotypes have subsequently been found to dominate the species’ naturalised distribution (Gladstones and Collins 1983). Therefore, these three species were considered as intentional rather than unintentional introductions. Introductions considered to be unintentional were removed from the intentional list, and the final list version was sent out to a number of New Zealand *Trifolium* breeders and agronomists. No omissions were noted.

Naturalisation. Two response variables were used to characterise naturalisation for intentional and unintentional introductions. For intentional introductions, the 54 intentionally introduced

species were coded as naturalised in New Zealand (1) or not (0). For unintentional introductions, the 174 species of *Trifolium* for which there was no record of intentional introduction to New Zealand were coded as being unintentionally introduced-naturalised (1) or not (0).

To decide whether or not a species was naturalised, I used the herbarium specimen database described above, considering only specimens in the “non-cultivated” group. Each species represented by at least one reproductive “non-cultivated” specimen was considered to be naturalised. Naturalised species that were on the intentional introduction list were placed in the “naturalisation of intentionally introduced species” analysis. All other species were placed in the “unintentional introduction-naturalisation” analysis.

Coarse-scale current distribution. This continuous variable reflects the number of New Zealand regions (1-10) currently occupied by each of the 25 naturalised *Trifolium* species. Species presence/absence in each of 10 regions of New Zealand was extracted from Webb et al. (1988) by P. Williams. Figure 2.1 illustrates these regions, which correspond approximately to descriptions in Webb et al. (1988). Stewart Island is included as part of the Southland region, but no outlying island group is considered by this scheme. If a species had ever been recorded in a particular region, it was assumed to be present in that region.

Fine-scale current distribution. This continuous variable reflects the number of NZMS260 map sheets (termed grid cells) currently occupied by each of the 25 naturalised *Trifolium* species. It can vary between 1 and 333 grid cells. The “non-cultivated” herbarium specimen database records were used to derive the fine-scale current distribution and rate of spread measures. Although herbarium specimens are often the best record available for the reconstruction of plant invasions, and are used frequently in the invasions literature (e.g. Weber 1998, Mihaluk and Pyšek 2001), they contain a number of biases. First, rare species will be over-represented in the collections. I attempted to address this bias by adding all *Trifolium* occurrence records from the National Vegetation Survey (NVS) database (<http://nvs.landcareresearch.co.nz/>) to the data set. The NVS database is New Zealand’s national archive for vegetation data, containing records from approximately 45,000 survey plots. Because these plot surveys record systematic presence/absence data, I expected that they could contribute to a more accurate representation of *Trifolium* species frequencies in the landscape. However, the herbarium data had the advantage of historical completeness and coverage of all *Trifolium* species, suggesting that the combination

of the two data types would be the most informative. Second, for *Trifolium* species, a habitat bias was likely. Many of the *Trifolium* specimens were collected by individuals with a particular interest in the alien flora (e.g. A. J. Healy). These collectors often focused their searches in habitats rich in alien species, suggesting that species encroaching into more natural habitats may have been under-sampled. Because the NVS data were biased toward natural, especially forested, habitats, I anticipated that addition of this data source would also mitigate the potential habitat bias. Third, collection effort of both specimens and plot survey data was likely to have varied temporally over the time period I considered (1840-2000). This would not impact the distribution measures, but could substantially affect the rate of spread calculations (Delisle et al. 2003). Temporal bias was addressed using a re-sampling procedure, described under “Rate of spread” below. In addition, I counted the first naturalisation record for each species (see “Naturalisation date” below) as an additional occurrence record to reduce regional bias in the early collection of specimens.

Collectors of herbarium specimens and NVS plot survey data usually assigned their records to topographic map sheets of the current New Zealand Map Series. The series currently in use, the NZMS260 (Anonymous 2004), divides New Zealand into 329 map sheets, each 40km by 30km in size. These sheets form a grid over the country (Figure 2.1) that can be used to map species distributions. To this grid, I added the following outlying island groups, each considered as one unique “cell”: Auckland Islands, Campbell Island, Chatham Islands, and Kermadec Islands. Unfortunately, many of the records in my database had been assigned to prior versions of the map series, so the majority of records had to be re-assigned to the current series based on associated location information. Where the original collector had assigned the species to a NZMS260 sheet, this reference was accepted. Records with insufficient location information for map sheet assignment were excluded. At the end of the assignment process, the total number of grid cells occupied by each species was counted to produce the fine-scale distribution measure. If a species had ever been recorded in a particular grid cell, it was assumed to be present in that grid cell.

Rate of spread. This is a continuous variable reflecting the relative cumulative number of grid cells occupied per year by each of the 25 naturalised *Trifolium* species. Calculations were performed using the same list of “non-cultivated” herbarium specimens and NVS records used to assess fine-scale distribution. First, I removed duplicate records containing the same

species/year/grid cell combination from this list. This left a total of 1,817 records for the 25 species (1,181 herbarium records and 636 NVS records) collected between 1854 and 2000. Plotting this data indicated a significant temporal bias in collection effort; herbarium specimen collection had peaked in the 1950s and 1960s, while NVS records were concentrated in the 1980s. To calculate spread rates that accounted for this bias, I used a re-sampling procedure, written by R. Duncan and implemented with the R statistical package (<http://www.r-project.org/>).

This procedure divided the time period 1850-2000 into six 25 year intervals. The smallest total number of records in any one of these 25 year intervals was 12. We therefore carried out a re-sampling procedure whereby we selected 12 records at random from each of the six time intervals, and repeated this procedure 10,000 times. From these 10,000 samples, we calculated the mean number of records selected for each species in each time interval, and used these means to calculate the cumulative number of records per species through time, assuming a constant collection effort. Such cumulative record sums make the assumption that once a species had been recorded in a grid cell, it remained in that grid cell. Each species was assigned zero records for the time interval prior to its first record in the database. For each species, we fit a regression line through this zero point and its cumulative record sums for each time period. We fit linear regressions because visual examination of these plots did not reveal substantial non-linearity in the relationships. The slope of this regression line was used as a measure of the rate of species spread (Pyšek and Prach 1993, 1995, Weber 1998, Mihulka and Pyšek 2001, Delisle et al. 2003). Importantly, although this procedure corrected for the temporal bias in collection effort, it also had the effect of bounding the rate of spread by a maximum of 12 grid cells per 25 years. This means that the final spread rate measures generated are no longer the species' absolute rates of spread through New Zealand. Rather, they represent a relative measure that can be used to make objective comparisons among species with different naturalisation dates.

Explanatory variables

Information regarding the type, coding, units, transformation, sample size, and analyses of explanatory variables is listed in Table 2.3.

Global transport and use by humans

Centre of origin. For each of the 228 *Trifolium* species, this binary variable reflects whether it originated in the Mediterranean diversity centre (1) or in the African or American diversity centre (0) of the genus. Species were assigned to the Mediterranean, African, or American diversity centre using native range information from the United States Department of Agriculture Germplasm Resources Information Network taxonomy resource (http://www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl). In a small number of cases where the range overlapped two centres, a range map was created and the more centrally located diversity centre was assigned; all species were either restricted to one centre or were predominantly in one centre (>82% of native range).

Present in Britain? This is a binary variable reflecting whether each of the world's 228 *Trifolium* species was present in Britain during the European colonisation of New Zealand (1) or not (0). A number of *Trifolium* species became naturalised in Britain during the time period of this study (1840-2000). To create a dichotomous variable representing British presence or absence, I required a species to be native to Britain or to have naturalised before 1840. *Trifolium* species present in Britain c. 1840 were determined primarily from Lindley (1835), supplemented by historical information in Preston et al. (2002) and by other British floras from this period (Bentham 1865, Bentham and Hooker 1887). The following revisions were made to the list presented by Lindley (1835):

- 1) *T. strictum* and *T. bocconeii* were added. As these are native species with restricted distributions, it was assumed that they were present, but had not yet been catalogued. Bentham (1865) notes both species.
- 2) *T. occidentale* was added. This native species was not discovered until 1957 (Preston et al. 2002), and is thus absent from all of the early floras. Nonetheless, it seems that sufficient time has elapsed since this discovery for the species to have been recognized as introduced or naturalised in New Zealand.
- 3) *T. hybridum* and *T. incarnatum* were added. Preston et al (2002) document the first wild records of these species before 1840, and they were both widely cultivated during this period. They are also recognized as established by Bentham and Hooker (Bentham 1865, Bentham and Hooker 1887).

British distribution. This is a continuous variable reflecting the British distributions of all 228 *Trifolium* species. I recorded the British distribution of all species present by 1840, and set the value for the other species to 0. British distribution was measured as the number of 10 km² British grid cells occupied by the species, as recorded by a botanical survey conducted from 1987 to 1999 (Preston et al. 2002). Although data from a much earlier time period would have been preferred, high-quality data of this nature could not be located. Judging from the qualitative descriptions in the early floras, however, it seems unlikely that the rank order of species' British distributions has changed drastically over the time period of my study.

Economic uses (global). This continuous variable reflects the number of different ways (0-5) that each of the 228 *Trifolium* species is used economically throughout the world. The number of economic use categories listed for each species by the United States Department of Agriculture Germplasm Resources Information Network taxonomy resource (http://www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl) was recorded. The primary source for this database is Wiersema and León (1999). For the species that were used economically, the number of uses varied from one use (e.g., *T. uniflorum*, used as an ornamental plant) to five uses (*T. pratense*, used as animal fodder and forage, as a soil improver, as a bee plant, as a medicinal plant, and as a culinary herb).

Introduction effort

Introduction or naturalisation date. For the 54 intentionally introduced species, introduction date was recorded as a continuous variable (1840-2000). For the 25 naturalised species, naturalisation date was recorded as a continuous variable (1840-2000). For introduction dates, data sources included the historical database (see “Estimated hectares planted” below), the “cultivated” herbarium specimens, sources listed by the ALLWEEDS database, and Thomson (1922). For naturalisation dates, sources included Webb et al. (1988), primary sources listed in Webb (1980), and the distribution record list (non-cultivated herbarium specimens and NVS records). In each case, the earliest date found was used.

Estimated hectares planted and Introduced for commercial agriculture? Estimated hectares planted is a continuous variable estimating the total (cumulative) number of hectares planted in each *Trifolium* species between 1840 and 2000. Estimates were calculated for all intentionally

introduced species, as well as for all 25 naturalised species (i.e. including those that had been introduced unintentionally, but were later included in experimental trials). Introduced for commercial agriculture was also recorded for both the 54 intentionally introduced species and the 25 total naturalised species. It is a binary variable reflecting whether each intentionally introduced *Trifolium* species was introduced for agriculture on a commercial scale (1) or not (0). To measure these variables, I constructed a database of *Trifolium* introductions to New Zealand from 1840 to 2000.

Seed and plant catalogues were a primary source of information for the database records. I searched the entire catalogue collections of the Alexander Turnbull Library (Wellington), the Auckland War Museum, the Auckland Museum Herbarium, and the Lincoln University Archive (Christchurch). From the HortResearch Mt. Albert Library (Auckland), all agricultural and pre-1910 catalogues were searched, as well as a random sample of the remaining material. A random sample of catalogues from the Auckland Botanical Gardens library was also searched. In total, 1,343 catalogues were consulted, contributing 238 records to the database. As the bulk of these materials were from the 20th century, newspapers were also searched to better understand early activities. Auckland-based newspapers were the primary target of this search, as Auckland was an important centre of seed distribution during this period (J. Adam, personal communication). 1,130 newspapers were searched for the years 1843-1865 and 1883-84, contributing 322 records to the database. Government publications and research reports were another major data source. To access this information, I searched reports of the Department of Agriculture (1895-1915), the New Zealand Journal of Agriculture (1910-1945), and the New Zealand Science Database (predominantly post-1945 entries). The New Zealand Science Database search included searches for “*Trifolium*” and “clover” generally, but also incorporated a search targeted to locate introduction trial reports. In total, these 1,765 publications contributed 1,730 more records to the database. There were other minor sources of records as well. Agricultural and Pastoral Show catalogues provided 9 records from 156 catalogues searched, mostly in the form of advertisements. Acclimatisation Society Reports were consulted, but these rarely recorded particular plant species introduced. Consequently, they provided only 1 additional record for 30 reports searched. Finally, in the course of searching historical collections for the above material, advice documents of various sorts were located. These were documents instructing farmers on the seed and seed mixtures to plant for various conditions, and originated from a number of sources such as seed merchants, farmers’ groups, and independent authors. In total, 116 such

documents were searched, contributing 93 database records. The final database contained nearly 2,400 records.

When recording from these sources, I accepted common names under certain conditions, as this permitted a broader sample of source types and years. However, I only accepted a common name if it was equated with the same scientific name in every source where both names were listed, and if both of my synonymy sources (ILDIS and USDA-GRIN taxonomy) unambiguously assigned it the same scientific name. For example, the name “hop clover” was not accepted, as the ILDIS and USDA-GRIN databases equated this name with both *T. aureum* and *T. campestre*, as well as with *Medicago lupulina*. On the other hand, “suckling clover” was accepted as *T. dubium*, as all sources and databases assigned this name unambiguously. I recorded different types or cultivars of the same species as multiple introductions within the same record, and these raw introduction numbers were summed to generate the final introduction figures. However, the introduction pattern was qualitatively similar if each species was counted only once for each record.

From all the sources considered, three major types of database records emerged. First, many records reflected the availability of agricultural species in commercial seed catalogues. I designated database records from such catalogues as “commercial agriculture” (CA) records. Second, additional records reflected the frequency with which farmers were advised to plant particular agricultural species, through government publications, advice documents, and research activities. I designated database records from these sources as “advice/research” (AR) records. Third, some *Trifolium* species were occasionally mentioned as garden, lawn, herb, or medicinal plants in horticultural catalogues. I designated these database records as “horticulture/lawn” (HL) records.

After classifying the database records, the predominant reason for each species’ introduction could be determined. For the agricultural species, it was important to distinguish those that had been introduced on a commercial scale from those that had been planted in experimental trials only, since introduction effort and patterns differed drastically between these groups. I used a species’ presence in agricultural seed catalogues (CA records) as the criterion for assigning it to the “commercial” group. This was generally a fairly unambiguous assignment, as most such species had many CA records. The one exception was *T. medium*, which had few CA records but was nonetheless designated as a commercial introduction following Kirk (1870). After removing all species with CA records, the remaining species were divided into

“horticultural” and “experimental agricultural” introductions. Species with more HL than AR records were considered to have been introduced predominantly for horticulture, and the remaining species were designated as experimental agricultural introductions. I then assigned values for the introduced for commercial agriculture variable, assigning the commercial agricultural species a “1” for this variable and the horticultural and experimental agricultural species a “0”.

Calculation of the estimated hectares planted depended on the introduction reason assigned to each species. It also attempted to account for temporal variation in *Trifolium* planting effort over the time period of this study. For the commercial agricultural species, I estimated annual *Trifolium* planting effort as the total hectares planted in “grasses and clovers”. From 1840 to 2000, this quantity was recorded using official national statistics collected by the Registrar-General’s office (1851-1908), the Government Statistician's Office (1909-1920), the Census and Statistics Department (1921-1960), and the Department of Statistics (1961-2000). Values from 1840 to 1850 were extrapolated using the 1851 values and assuming land planted to be proportional to the European population. I assumed that all hectares planted in “grasses and clovers” would have included, on average, one species of *Trifolium*. This is a reasonable approximation, given the noted importance of *Trifolium* for pasture establishment throughout this period. For each decade, the proportion of hectares planted in each *Trifolium* species was estimated by constructing separate proportions for each species using the AR and CA record subsets, and then taking the mean of these to generate a proportion in which the “advice/research” and “commercial” components of planting were equally weighted. As each of these components has its unique strengths as a measure of planting effort, a combined proportion afforded the best measurement. Multiplying each proportion by the appropriate yearly hectare estimates and summing the resulting figures generated an estimate of the hectares planted over the study time period. For each species, the final estimate of hectares planted was generated by taking the sum of this estimate and the total hectares planted for seed production.

For the horticultural species, the hectares planted in “gardens” were recorded in the same way as those in “grasses and clovers”. However, as *Trifolium* were minor horticultural species, it was not reasonable to assume that they had been planted on all of this land. Therefore, for each decade, I divided the number of horticultural catalogues containing each species by the total number of horticultural catalogues that I had searched for that decade. The values were further divided by 100 as a conservative estimate of the number of other species per catalogue. The

resulting values provided rough estimates of the proportion of garden hectares on which each *Trifolium* species was planted in each decade. These values were multiplied by the appropriate yearly “garden” hectare estimates, and the resulting figures were summed to generate an estimate of the total hectares planted over the study time period.

For the experimental agricultural species, the total number of database records for each species was summed. Each species’ cultivated herbarium specimens were added to this total, excluding specimens that were clearly vouchers from trials in the database. This sum was multiplied by an average experimental plot size, estimated from the trial records to be 0.008 hectares.

Nodulation with introduced *Rhizobium*. This is a continuous variable reflecting my estimate of the degree to which an introduced species would have been able to nodulate with *Rhizobium* populations in New Zealand soils. This variable was only recorded for intentionally introduced species and for total naturalised species, as published data were insufficient to derive an estimate for all *Trifolium*. To generate this estimate, I first assumed that compatible strains of *Rhizobium* had been introduced for all of the commercial agricultural species. To estimate which other *Trifolium* species might form effective symbioses with these strains, I used the effectiveness groups suggested by three different data sources. These sources represent reviews of published experimental findings (Burton 1985) and recommendations of commercial inoculant providers (Smith et al. 1987, Anonymous 2003). Even with multiple data sources, many *Trifolium* species remained unassigned to a group. I therefore coded a species as 1 if it was placed in the same effectiveness group as a commercial agriculture species by any of the three sources, 0 if it had been studied by at least one of the sources but placed in a different group than all of the commercial agriculture species, and 0.5 if it had not been evaluated by any of the sources.

Opportunistic association with humans in New Zealand

Frequency as pasture seed contaminant. This is a continuous variable which estimates the frequency with which each of the 25 naturalised *Trifolium* species was found as a contaminant in the New Zealand pasture seed supply. To determine this estimate, I conducted a literature search. I found a number of contamination records during construction of the historical database (see “Estimated hectares planted” above). These were supplemented by searches of general scientific

databases (e.g. ISI Citation Index, CAB Abstracts) and the New Zealand Science Database. In total, I located 98 contamination records of New Zealand seed, falling between 1912 and 1998. This list was particularly strong in the period 1922-1931, during which detailed reports from the Official Seed Testing Station had been published in the New Zealand Journal of Agriculture. To these records, I added data from Flood (1986), which described contaminants found in pre-1900 British pasture seed samples. Although these records were not New Zealand-based, I considered their inclusion to be reasonable given that Britain supplied nearly 85% of New Zealand's grass and clover seed imports during this period (New Zealand Registrar-General's Office 1868-1900). This source added 6 additional records between 1869 and 1896. When I added up the raw number of records in which each species appeared as a contaminant, these frequencies formed four natural groupings: rare (1-5 records), occasional (15-23 records), frequent (54-69 records), and very frequent (93 records). Contaminant species were assigned an ordinal value (1-4) corresponding to the group to which they belonged. All species with no records were assigned a 0. After compiling this data set, I sent the final version out to a number of New Zealand *Trifolium* breeders and agronomists for examination. No omissions were noted.

Found in cultivated habitats in NZ? This is a binary variable reflecting whether each of the 25 naturalised *Trifolium* species occurs in cultivated habitats in New Zealand (1) or not (0). Species whose habitat descriptions in Webb et al. (1988) contained the phrase “cultivated land” were assigned a 1; all other species were assigned a 0.

Native range attributes

Native range area. This continuous variable records the estimated area of the native range (km²) for each of the 228 species of *Trifolium*. The native ranges for all *Trifolium* species were taken from the United States Department of Agriculture Germplasm Resources Information Network taxonomy resource (http://www.ars-grin.gov/cgi-bin/npgs/html/tax_search.pl). This resource records species' ranges at least at the national level. In many cases, regional and sub-administrative unit data are also provided (e.g. northwestern Turkey; California, USA). Sub-national data are always provided for very large countries (e.g. Russia, Canada, the United States, China, Brazil), reducing the possibility that a species' range area will be inflated simply because it occurs in a large country. Range data was digitized into a GIS (ArcView 3.2a, ESRI 2000).

Areas were determined using the World Behrmann projection, which provides accurate area calculations.

Diversity of conditions tolerated. This is a continuous variable reflecting the number of biomes (1-14) that occur in the native range of each of the 228 *Trifolium* species. Biome data were obtained as an ArcView shapefile from the World Wildlife Fund's Ecoregions of the World project (<http://www.worldwildlife.org/ecoregions/>). The definition of "biome" employed by this data set implies similarity in terms of climatic regime, vegetation structure, spatial pattern of biodiversity, floral and faunal guild structures and life histories, requirements and thresholds for maintaining biodiversity features, and sensitivity to human disturbance. Fourteen terrestrial biomes are defined; these are described in detail by Olson et al. (2001). In ArcView, I overlaid each species' native range on the biome data set and used the software to calculate the number of biomes within the range.

Match to New Zealand climate. This continuous variable estimates the area of New Zealand (in 10'x10' latitude-longitude grid cells) which is well-matched to the climate of the native range for each of the 228 *Trifolium* species. To calculate a climate match index for each species, I employed the climate-matching algorithm used by the CLIMATE software programme (Pheloung 1996). Computations were performed using a programme written by R. Duncan in the SAS statistical system, version 8.0 (SAS Institute 1999). As the meteorological data input to these analyses, I used the data set described by New et al. (2002). This data set contains climate data values for every terrestrial 10'x10' latitude-longitude grid cell (excluding Antarctica), and was constructed by interpolation of meteorological station data over the global land surface. For New Zealand, it contains data for North, South, and Stewart Islands, as well as the Auckland Islands and Campbell Island, but not for other outlying island groups.

For each *Trifolium* species, the 10'x10' latitude-longitude grid cells within the species' native range were selected in ArcView. Using the raw meteorological data associated with these cells, the 16 derived climate parameters used by the CLIMATE programme (Table 2.4) were calculated for each cell. A similar procedure was performed for all of New Zealand. Then, for each 10'x10' latitude-longitude grid cell in New Zealand, the 10'x10' latitude-longitude grid cell in the native range that best matched its climate was identified, and the New Zealand 10'x10' latitude-longitude grid cell was assigned the value of its match with that cell. The best match

from the native range was selected because this should represent the species' potential to succeed at that New Zealand location; the presence of less well-matched cells in its native range is irrelevant (Duncan et al. 2001). Matches between a pair of cells were calculated by taking the difference between the cells for the values of each of the 16 climate parameters, and dividing each difference by the global standard deviation for that parameter to generate standard scores. The standard scores were then squared and summed, and the square root of this sum was divided by 16 to generate a Euclidean distance. Finally, this distance was assigned a match value based on a normal distribution of reference scores. At the conclusion of this procedure for each species, every 10'x10' latitude-longitude grid cell in New Zealand had been assigned a match value. The number of cells with a 95% or better climate match to the species' native range was counted, and this count was taken as the final index for a species' match to the New Zealand climate.

New Zealand drought tolerance, New Zealand low temperature tolerance, and New Zealand frost tolerance. Each of these tolerance indices is a continuous variable estimating the area of New Zealand (in 10'x10' latitude-longitude grid cells) in which each of the 228 *Trifolium* species could tolerate the stated climatic stress, based on the level of climatic stress found in its native range. The meteorological data set (New et al. 2002) provides monthly values for all climate parameters. Although higher temporal resolution would have been desirable for the calculation of the tolerance indices, I chose to use this data set because of its superior spatial coverage. Climatic stresses were thus expressed on a monthly scale: the minimum temperature of the coldest month (low temperature), the number of months with significant frost, and the number of months with significant drought.

To calculate the tolerance indices, the first step was to determine the values of these three stresses for every 10'x10' latitude-longitude grid cell in the global data set. The calculations were implemented in the SAS system by R. Duncan. For low temperature stress, the minimum temperature for each month was first calculated from the raw meteorological data, using the equation (minimum temperature = mean temperature – 0.5*diurnal temperature range), as recommended by the data set authors. The lowest of these 12 monthly values was then selected for each 10'x10' latitude-longitude grid cell to represent the minimum temperature of the coldest month. For frost stress, a month with greater than 5 days of ground frost was arbitrarily designated as a month with “significant” frost. The number of months of the year meeting this

criterion was counted for each 10'x10' latitude-longitude grid cell to arrive at the final frost stress measure.

The ultimate measure of drought stress I used was the amount of water in the soil each month relative to its water-holding capacity. To calculate this quantity, monthly values of both precipitation and evapotranspiration were required. Monthly precipitation was available from the meteorological data set. Expected evapotranspiration was calculated from the available meteorological data, using a method based on the Penman-Monteith equation developed by the FAO (Allen et al. 1998) (<http://www.fao.org/docrep/X0490E/x0490e00.htm#Contents>). This method incorporated raw monthly data on the latitude, elevation, mean temperature, maximum and minimum temperature (calculated using the diurnal temperature range), relative humidity, sunshine hours, and wind speed of each 10'x10' latitude-longitude grid cell. To complete the drought stress calculations, a data set of global soil water-holding capacity was acquired (the Global Data Set of Derived Soil Properties, 0.5-Degree Grid, created by the International Soil Reference and Information Centre-World Inventory of Soil Emission Potentials) (Batjes 2000). Monthly water balance in each 10'x10' latitude-longitude grid cell was then calculated as (water from previous month + precipitation – evapotranspiration), bounded at the lower end by 0 and at the upper end by the soil's water-holding capacity (Jamieson et al. 1984). I arbitrarily set the water from the previous month to 0 in January of the first year, and then ran the water balance model through for successive years until the monthly water values converged to stable estimates. These estimates were taken as the final quantities of soil water each month, and were compared to the soil water-holding capacity in each 10'x10' latitude-longitude grid cell. Based on discussions with agronomists and soil scientists, I defined a month with “significant” drought as one in which the soil water was less than 30% of the soil water-holding capacity. The number of such months in the year was counted for each 10'x10' latitude-longitude grid cell to arrive at the final drought stress measure.

The next step of the indices calculation was to determine the most severe stress levels experienced by each species in its native range. This was also implemented in the SAS system by R. Duncan. The programme selected the most severe value for each of the three stress types from the cells in each native range, using the native range 10'x10' latitude-longitude grid cells selected in ArcView for the climate matching procedure. Next, the ArcView-selected 10'x10' latitude-longitude grid cells comprising New Zealand were used to extract the three stress values for each New Zealand 10'x10' latitude-longitude grid cell from the global data set.

The final calculation of the tolerance indices was implemented in the R statistical package by R. Duncan. For each species, the procedure compared the most severe value of a particular stress in its native range to the value of that stress in each 10'x10' latitude-longitude grid cell in New Zealand. If the native range contained a stress value more severe or equal to the stress value in a New Zealand 10'x10' latitude-longitude grid cell, the New Zealand cell was assigned a 1; otherwise, it was assigned a 0. At the end of the procedure, the number of 1 values (= 10'x10' latitude-longitude grid cells in New Zealand where the species should not be excluded by the stress) were added up for each stress for each species. These sums were the tolerance indices.

Habitat characteristics

I determined key habitat characteristics for each of the 228 *Trifolium* species using both Gillett and Taylor (2001) and Zohary and Heller (1984). All habitat variables were categorical, scoring elevation of the native range as lowland (0), midland (1), or upland (2), canopy cover of the native habitat as closed (0), partially open (1), or open (2), and native to human-influenced habitats as yes (1) or no (0). For the **elevation of the native range**, the sources I used record elevational limits for species described as alpine or upland. Consequently, if no mention was made of a species' elevation limits, I assumed it was capable of inhabiting lowland areas and coded it as lowland. Species were also recorded as lowland if the mean elevation described for their range was less than 600m. I recorded a species as midland if the mean elevation described for its range was between 600m and 1500m, or if it was described as inhabiting areas "up to" 2000m or less. Highland species were those whose range descriptions specified a mean elevation greater than 1500m, or a range "up to" greater than 2000m. For **canopy cover of the native habitat**, I used key words to determine species assignments. Key words for placement in the closed category were "forest", "open forest", "forest and clearings", and "forest and scrub", while those for placement in the open category were "open", "grassland", and "grassy". I classified species as belonging to the partially open category if their habitat description featured the words "shrubs", "shrubland", "forest margin", or "forest clearing", or if the description contained terms from multiple canopy cover types, e.g. "open and forest" or "open and scrub". Species were classified as **native to human-influenced habitats** based on the following habitat descriptors: "roadside", "cultivated", "pasture", "waste place", "fallow field", "pathway", "lawn", "grazed",

“crops”, or “dikes”. If the description did not contain at least one of these terms, the species was assumed not to be native to such habitats.

Biological traits: Genetic system

Genetic system variables were recorded for all 228 *Trifolium* species. Each of these variables was binary, scoring lifespan as annual/biennial (0) or perennial (1), capability for self-pollination as present (0) or absent (1), polyploidy as present (1) or absent (0), capability for vegetative reproduction as present (1) or absent (0), and base chromosome number as reduced (0) or not (1). Gillett and Taylor (2001) and Zohary and Heller (1984) formed the primary data sources for the genetic system attributes. For **lifespan**, all possible lifespans listed in both of these sources were considered. If a species was capable of an annual or biennial lifespan, it was coded as an annual; otherwise, it was coded as a perennial. **Selfing** or out-crossing pollination was assigned as listed in Gillett and Taylor (2001). If either data source listed a species as possessing either stolons or rhizomes, it was coded as **capable of vegetative reproduction**. The descriptions “stems rooting at the nodes”, “stems sometimes rooting at the nodes”, and “stems may root at nodes” were considered to qualify as stolons, and “rhizomatous roots” and “tuberous roots” to qualify as rhizomes. For the chromosome counts, Gillett and Taylor (2001) was given precedence over Zohary and Heller (1984) where these sources differed, as it is the more recent publication. All species with ($2n$) chromosome counts greater than 16 were considered **polyploid**; otherwise, they were scored as diploid. **Chromosome base numbers** were interpreted as multiples of the $2n$ values. Where several base numbers were possible for polyploid species, primary sources of genetic data were consulted to make the determination (primary sources from Table 3.1, Cleveland 1985). If these did not provide sufficient information, the most frequent multiple was selected or, failing that, the highest multiple, as this would be a conservative estimate of chromosome reduction. Species with less than eight base chromosomes were considered to have a reduced base chromosome number.

Biological traits: Morphology

Height and habit were recorded for all 228 *Trifolium* species, recording height as a continuous variable (cm) and habit as a categorical variable representing prostrate (0), intermediate (1), and

erect (2) species. I entered the **maximum heights** recorded by Gillett and Taylor (2001) and Zohary and Heller (1984), giving precedence to Zohary and Heller (1984) as the more formal taxonomic treatment where these sources disagreed. All **habit** data given by both sources was accepted. I scored plants as predominantly upright if they were described as “erect” or “ascending”, and as predominantly prostrate if they were described as “reclining”, “decumbent”, “prostrate”, “procumbent”, “tufted”, “clumped”, “spreading”, or “mat-forming”. If a species was described by key words from both categories, it was coded as intermediate.

Biological traits: Seed size and dispersal

Seed size, mass, and dispersal were recorded for all 228 *Trifolium* species, recording seed size as a continuous variable (1-4), seed mass as a continuous variable (mg), and dispersal as a categorical variable reflecting whether species were capable of long-distance dispersal (0) or not (1). **Seed size** was entered as listed in Gillett and Taylor (2001). The seed size categories provided by these authors are small (< 1 mm), medium (1.1 - 1.5 mm), large (1.6 - 2.0 mm), and very large (> 2 mm). **Seed mass** was taken from version 5.0 of the Seed Information Database maintained by the Royal Botanical Gardens, Kew (<http://www.kew.org/data/sid/>). Where several values were provided for a species, the arithmetic mean was used. All values that appeared suspect were checked against the primary sources listed and corrected as necessary. **Capability for long-distance dispersal** was scored according to the outline provided by Zohary and Heller (1984) (pg. 14-15). All species in sections *Lotoidea* and *Trifolium* were assumed to be incapable of long-distance dispersal unless otherwise noted. Long-distance dispersal via anemochory was then assigned to the following taxa: section *Lotoidea* subsection *Calycospatha*, section *Mistyllus*, section *Vescaria*, section *Chronosemium*, and section *Involucrarium* subsection *Physosemium*. Anemochorous dispersal was also assigned if a species was described as having a “light and feathery calyx” or a “plumose calyx”, or if a species was in section *Lotoidea* and described as having a “persistent corolla”. Long-distance dispersal via exozoochory was assigned to species with “recurved calyx teeth” (functioning to disperse either single propagules or entire heads) or “spinescent” or “woolly” fruiting structures. All assignments were checked against the morphological descriptions and illustrations of the species.

Biological traits: Other

The additional biological traits of seed shape and corolla length were recorded for all 228 *Trifolium* species, recording corolla length as a continuous variable (mm) and seed shape as a binary variable reflecting whether seeds were the same shape as those of white clover (1) or not (0). **Seed shape** data were taken from Gillett and Taylor (2001). These authors classify white clover as having “mitten”-shaped seeds. I classified all other species with mitten-shaped seeds as similar to white clover; otherwise, they were classified as dissimilar. I used both Gillett and Taylor (2001) and Zohary and Heller (1984) to record **corolla length**, giving precedence to Zohary and Heller (1984) as the more formal taxonomic treatment where these sources disagreed. These sources provided a “corolla length” measurement for some species, a “flower length” measurement for others, and both measurements for a minority of species. From the species with both measurements recorded and the species illustrations, I determined that both “corolla length” and “flower length” represented essentially the same quantity, and accepted either as my corolla length measure. Where both measurements were provided, the mean of these was used. Final lengths were taken as the mean of the minimum and maximum values provided. If only a maximum was provided, this was accepted, as it represents a conservative measurement in this case.

Biological traits: Phenology (Native range)

Phenology variables were recorded for the 228 *Trifolium* species; all variables were continuous (1-12). The **month in which flowering starts and ends** in the native range was recorded from Gillett and Taylor (2001) and Zohary and Heller (1984), taking the widest period described by both sources. For species native to the southern hemisphere only (South American and southern African species), both phenology values were shifted by six months so that their seasonal patterns would be comparable to northern hemisphere species. For species native to both hemispheres, no adjustments were made. These were primarily tropical African species, for which a different seasonality would be expected. I calculated the **length of the flowering period** from the resulting values.

Biological traits: Phenology (New Zealand)

New Zealand phenology data were recorded for the 25 naturalised species only, using the same continuous measures (1-12) as the native range phenology variables. The **month in which flowering starts and ends in New Zealand** was taken from Webb et al. (1988). These values were adjusted by six months in the same way as described for the native phenology of southern hemisphere species. This ensured that the beginning of the flowering period would fall, numerically, before the end of the flowering period. I calculated the **length of the flowering period** from the resulting values.

Statistical analysis

General issues

Explanatory variables used in each analysis. A separate analysis was conducted for each invasion stage (Table 2.1). The analyses in which each explanatory variable was used are listed in Table 2.3. Explanatory variables were not evaluated at all stages for several reasons. In the later stages (naturalisation and spread), some variables no longer contained any variation among species. These included centre of origin (spread), New Zealand drought tolerance (intentional naturalisation, spread), and New Zealand low temperature and frost tolerance (spread). Economic use was not considered to be a plausible explanation for unintentional introduction-naturalisation and was not tested in that stage. It was also excluded for the spread stage because other data were available that provided a more direct test of the relevant hypothesis (e.g. estimated hectares planted). Nodulation with introduced *Rhizobium* was only examined for naturalisation and spread due to limited data availability. In addition, there were some variables that were only conceptually valid at particular stages. These included introduction/naturalisation date, introduced for commercial agriculture, and estimated hectares planted (for naturalisation and spread only), and frequency as pasture seed contaminant, found in cultivated habitats in NZ, month flowering starts (NZ), month flowering ends (NZ), and length of flowering period (NZ) (for spread only). Finally, for the intentional introduction of species, biological traits had limited plausibility as reasons for introduction. Consequently, I did not test these traits as explanatory variables in that stage. However, it is of interest to know which traits were indirectly selected as

a result of the intentional introduction process, as this could improve understanding of the interaction between biological traits and the invasion sequence. I performed a separate analysis to address this question (see below).

Multicollinearity of explanatory variables. Simple and multiple regression were the primary analysis techniques employed. However, because many of the explanatory variables were correlated, literal interpretation of the multiple regression results could lead to incorrect inferences (Graham 2003). I addressed this issue in two ways.

First, I examined the underlying structure of the biological and habitat data. I initiated this examination when I noted that multicollinearity was particularly strong among certain biological traits and among certain habitat characteristics. This pattern could be observed if the measured variables reflected a smaller number of underlying concepts. Such a situation may be present in *Trifolium*, as several genetic attributes were thought to reflect a single underlying “genetic system” in a previous study (Taylor et al. 1979c). Similar dynamics might plausibly occur for other *Trifolium* attributes (Zohary 1972, Zohary and Heller 1984); for example, the tight relationships observed between species’ height and habit might represent an underlying “morphology” dimension.

I explored the extent to which my observed variables might be reflections of such underlying concepts using a confirmatory factor analysis (CFA) technique, implemented with MPlus software version 3.0 (<http://www.statmodel.com/>). This technique is similar to principal components analysis (PCA) in that it uses the correlations among variables to determine the underlying structure of the data. However, it differs from PCA in two ways that may increase the interpretability of the dimensions identified. First, factor analysis allows rotation of the reference axes about the origin. Rotation moves the axes closer to the observed variable clustering pattern, so that the loading of each variable on each factor becomes more clearly significant or non-significant. Rotation also results in a more equal distribution of explained variance among factors (Hair et al. 1998). Rotation algorithms can be specified that either require the factors to be uncorrelated (orthogonal) or allow them to be correlated (oblique). As correlated factors often better reflect the real-world situation (Hair et al. 1998), I allowed factor correlation in my analysis. Second, in its confirmatory form, factor analysis allows the incorporation and evaluation of *a priori* hypotheses concerning the number of underlying dimensions (= factors) and their relationships to the observed variables. In CFA, one specifies the number of

hypothesized factors and their connections to the observed variables, and an assessment of the hypothesized model's fit to the data is then calculated. I present this analysis in more detail in Appendix 1 (Figure AP1.1 and Tables AP1.2-AP1.4).

Briefly, the CFA results provided support for the existence of five underlying factors in the biological trait and habitat data:

- 1) "Genetic system" (lifespan, capable of self pollination, capable of vegetative reproduction, polyploidy, reduced number of base chromosomes)
- 2) "Seed size and dispersal" (seed size, seed mass, capable of long-distance dispersal)
- 3) "Morphology" (maximum height, habit)
- 4) "Phenology" (month flowering starts, month flowering ends)
- 5) "Native habitat type" (canopy cover of native habitat, native to human-influenced habitats)

"Genetic system" was strongly correlated with "seed size and dispersal", and weakly correlated with "morphology" and "phenology". No other factors were significantly correlated. The elevation of the native habitat was confirmed to co-vary with each of these five factors. Of the remaining traits, the "length of the flowering period" was confirmed to represent a separate, sixth dimension of variation that was not strongly correlated with any of the other factors identified. Both seed shape and corolla length were moderately well-described by several of the factors, but could not be unambiguously assigned to a single factor.

Once the factors had been quantitatively specified, it was possible to estimate a score for each species on each factor. These scores approximate a combination of a species' values for all variables underlying each factor, although they cannot be determined exactly (Loehlin 1998). I generated factor scores, put them in place of the raw variables in the data set, and then ran the series of simple and multiple regressions that comprise my analysis (described below). However, as the results of these runs did not differ greatly from those found using the raw variables, I present the raw variable runs only. Nonetheless, when interpreting these results, it is essential to keep in mind the structure that exists in this data. In effect, the strong correlations among variables associated with the same factor mean that there is insufficient power to discriminate among them in identifying the determinants of invasion success. For example, if "reduced base chromosome number" were identified as a significant predictor of a particular invasion stage, it

would be most logical to conclude that the “genetic system” is important in influencing that stage, rather than the specific mechanisms involved with chromosome number. I used this logic to frame my discussion.

The second avenue I pursued to address the inter-correlated nature of the explanatory variables was structural equation modelling (SEM). This modelling was implemented for the intentional introduction, naturalisation of intentional species, and unintentional introduction-naturalisation stages only, as the small sample size at the spread stage unfortunately precluded the use of this technique (Hair et al. 1998, Loehlin 1998). SEM requires that the hypothesized relationships among all explanatory variables, as well as their relationships to the response variables, be specified *a priori*. It allows both causal and covariance relationships to be modelled. The parameter values for each specified relationship can then be simultaneously estimated, and the fit of the entire specified model to the data can be quantitatively assessed.

SEM also allows data structure identified by a factor analysis to be directly incorporated into the model. One specifies both the raw variables assumed to be related to each factor and the relationships of that factor to other variables in the model; all parameters are then estimated simultaneously. For the correlated explanatory variables that I had not included in the factor analysis (e.g. native range attributes), I had reasonable hypotheses for the way these variables should be causally related to each other. Therefore, I anticipated that structural equation models that combined these relationships with the factors identified in the CFA could allow greater understanding of the complex interrelationships present in this data.

However, a disadvantage of SEM is that many well-fitting models may be possible for a given set of data. Ideally, one can identify all possible alternative models, and use the SEM fit statistics to determine which model is best supported by the data (Shipley 2000). Yet, the identification of all alternative models can be quite difficult, especially if the number of variables is large. In such a case, the conclusion drawn from a single well-fitting SEM can only be that there is no evidence for the misfit of that particular model to the data. Still, even with this drawback, I expected that SEM might provide a valuable alternative perspective to that afforded by multiple regression, and that simultaneous consideration of the results of both analyses would offer the best insight into this data.

Phylogenetic relationships among species. The possibility that evolutionary relationships among species could confound the patterns identified was also considered. Specifically, it is possible that related species might have similar values for traits that were not measured in this study. If those traits were related to the response variables, the significance values attributed to traits that were measured could be distorted. This effect seemed unlikely for two reasons. First, by comparing congeners, I had already eliminated the potential for large differences in relatedness among species, and thus for large differences in unmeasured traits. Indeed, authors often compare pairs of congeneric species within larger invasion studies (e.g. Perrins et al. 1992a, Maillet and Lopez-Garcia 2000, Mulvaney 2001) with precisely this goal in mind. Second, the large number of traits that were measured reduced the likelihood that unmeasured traits could have large effects. Nonetheless, I explored the potential influence of species' phylogenetic relatedness on the response variables (Cassey et al. 2004a, Lloret et al. 2004) to be sure that it was not substantially distorting the results.

The phylogenetic tree used for this analysis was an unpublished molecular phylogeny of the entire genus *Trifolium*, kindly provided by Nick Ellison and Warren Williams. This tree is based on a combination of ITS and cpDNA sequence data and was constructed using the neighbour joining method. I used this phylogeny to divide the genus up into nine roughly monophyletic groups. Species' group membership was then tested as a factor variable for its ability to predict each of the response variables, using logistic regression (introduction and naturalisation) or analysis of variance (spread). The upshot of these analyses was that phylogenetic group membership was not a strong predictor of any of the response variables ($P > 0.10$ for naturalisation of intentional species and all spread measures). Group membership did have some relatedness to both intentional and unintentional introduction, but this was entirely attributable to the diversity centre (Mediterranean, African, or American) from which the species came. When diversity centre was added to the models first (as a factor variable), phylogenetic group failed to explain significant additional variation ($P > 0.10$). These results increased my confidence that phylogenetic relationships within the genus should not substantially distort the conclusions reached in the other analyses, and they were not considered further.

Specific procedures

Modelling of binary response variables: Intentional introduction, Naturalisation of intentionally introduced species, and Unintentional introduction-naturalisation

All regression analyses were performed using the R statistical package. For the binary response variables, logistic regressions were used. The `family = binomial` option was specified in R, indicating a regression analysis with a binomial error distribution and a logit link function. For the simple regressions, I compared each explanatory variable to the response separately. A sequential Bonferroni correction was applied to assess the significance of each test (Holm 1979).

In addition, although the biological traits were not considered plausible explanations for intentional introduction, it was relevant to know which biological traits may have been selected as a result of the intentional introduction process. I addressed this question using a separate series of simple regression analyses, with intentional introduction as the explanatory variable and each biological trait as a response. Regressions were logistic where the traits were binary and linear where the traits were continuous. A sequential Bonferroni correction was applied to assess each test's significance.

For the multiple regressions, I used a forward selection procedure to identify variables that independently explained invasion success. For each response, the variable explaining the greatest deviance in the simple regressions was placed into the model first. All other variables were then tested for their ability to explain additional deviance, using the change in deviance (likelihood ratio test) to assess explanatory ability. The variable explaining the greatest additional deviance was added to the model, provided that the additional deviance explained was significant at the 0.05 level. The remaining variables were then tested again in this fashion, and variables were added to the model until no variable could explain significant (at 0.05) additional deviance. Once all variables in the model had been identified, I tested the significance of all possible interactions between them. These tests were implemented using the `drop1` function in R, removing successive interactions if they did not explain significant additional deviance when added last to the model.

Notably, the interactions identified by this approach would most likely be those in which there was a difference in slope, but a similar direction, for the interactive effects of multiple variables on the response. Interactive effects exhibiting a change in direction would probably

have been prevented from entering the model in the first place, as they would be unlikely to explain significant deviance in a simple linear test. As the importance of such interactions in explaining invasion success has been noted (Gerlach 2001), this represents a drawback of my approach. To assess the degree to which interactions might have kept important variables out of the model, I also subjected this data to a classification tree analysis, implemented using the `rpart` function in R. Classification trees are constructed by searching iteratively for successive explanatory variables which best split the response into two groups. Thus, variable relationships important for only a subset of the data would be more easily identified by this method. However, I found that the results of this analysis were very similar to the multiple regression, increasing my confidence that the multiple regression had adequately captured the most important influences.

A structural equation model was constructed for each stage considered: intentional introduction, naturalisation of intentionally introduced species, and unintentional introduction-naturalisation. For intentional introduction, two additional models were constructed that considered the introduction of commercial agricultural and other (horticultural and experimental agricultural) species separately. I suspected that the processes responsible for intentional introduction would differ among these groups, based on the literature and the multiple regression results. To assemble the structural equation models, I took into account prior work and theoretical predictions, as well as the results of the simple and multiple regressions. Biological and habitat characteristics were included in factor form. Unfortunately, although I suspected diversity centre to be important in these models, it was not possible to include it because its statistical properties presented difficulties for the modelling software (i.e. zero species for particular combinations of attributes). In the initial model construction, I specified all relationships for which a reasonable hypothesis existed. I then estimated the fit of this model in MPlus using a mean- and variance-adjusted weighted least squares (WLSMV) estimator, the recommended estimator when response variables are binary (Muthén and Muthén 1998-2004). Fit indices were compared to the cut-off values recommended by Yu (2002) to assess model fit.

On the first runs, the models did not show an adequate fit for any of the stages, and many of the relationships I had specified were not statistically significant. Consequently, I employed a strategy of nested model comparison to determine more parsimonious models that might provide a better fit (Loehlin 1998, Shipley 2000). During this process, I removed paths that were theoretically less important and statistically non-significant, using a nested model framework to ensure that these deletions were not worsening the fit of the model. The same estimator and fit

criteria noted above were used for all model evaluations. When more parsimonious models had been identified, I also considered removing some of the less important variables from the model. In many cases, these variables were only weakly connected to the outcome of interest and in some cases they were not connected at all. Comparisons of models with and without particular variables were undertaken in a qualitative rather than a quantitative framework, selecting the model which appeared to best represent the most theoretically important processes. It should be noted that both of these modification processes may have reduced the models' general applicability by capitalising on chance variations in this particular data set (Loehlin 1998). Therefore, future testing of the models with independent data would be necessary to confirm the relationships they propose.

At the end of this process, I had constructed structural equation models which appeared to provide a reasonable explanation for the data, both theoretically and statistically. However, it was impossible for me to identify and assess the fit of all potential alternative models due to the large number of variables and lack of prior SEM study of these phenomena. Consequently, I concluded that there was no evidence for the misfit of these models to the data, but that other models with better fit might exist.

Modelling of continuous response variables: Current distribution (coarse-scale and fine-scale) and Rate of spread

For the continuous response variables, I used linear regression modelling with a Gaussian error distribution and an identity link function. As for the binary response variables, the simple regressions compared each explanatory variable to the response separately and employed a sequential Bonferroni correction for the assessment of significance (Holm 1979). The larger number of explanatory variables considered in these analyses resulted in a somewhat more strict significance criterion. I examined residual plots to make sure that the analysis assumptions were adequately met for each variable.

I performed the multiple regressions using a comparable forward selection procedure to that described for the binary variables. The significance threshold for model entry was similarly set at 0.05, but an F-test rather than change in deviance was employed to assess whether significant additional variation had been explained. In these analyses, the small number of observations meant that it was also important to avoid fitting a model that was overly complex relative to the available data (Crawley 2002). Therefore, for each additional variable that was

suggested for entry into the model, I visually assessed the relationship between that variable and the current model's residuals. Only relationships that appeared to be legitimate (e.g. not driven by one or two outlying points) were accepted. Once all model variables had been identified, I checked for interactions between them in a similar way to that described for the binary response variables. However, the small number of observations meant that only two-way interactions could be reliably assessed. To examine the possibility that interactions might be keeping important variables from entering the model, I also constructed regression trees, using the `rpart` function in R, for each of the spread response variables. Regression trees are similar in concept to classification trees, except that they select the explanatory variables at each split based on response variable means rather than counts of different outcomes. Again, however, these trees provided very similar results to the multiple regression, indicating that the important influences had most likely been captured. For each of the final multiple regression models, I examined residual plots to make sure that the assumptions of linear regression analysis had not been violated.

Table 2.1. Stages of invasion defined and analysed in this study.

Stage	Successful Species	Failed Species
Intentional introduction	Reported at least once as intentionally planted outdoors in a location suitable for the reproduction of at least one other vascular plant species	Never reported as intentionally planted outdoors in a location suitable for the reproduction of at least one other vascular plant species
Naturalisation of intentionally introduced species	Those intentionally introduced species collected or observed at least once in the reproductive state at a location not suggesting direct intervention by humans	Those intentionally introduced species never collected or observed in the reproductive state at a location not suggesting direct intervention by humans
Unintentional introduction-naturalisation	Collected or observed at least once in the reproductive state at a location not suggesting direct intervention by humans, with either no record of intentional introduction or prior to any record of intentional introduction	Never intentionally introduced and never collected or observed in the reproductive state
Spread	Continuous measurements of rate of spread and current distribution for all naturalised species	

Table 2.2. Predicted effects of explanatory variables. For continuous variables, strength of expected effects is indicated by the number of plus (+) or minus (–) signs. For categorical variables, strength is indicated by font colour, for **weak**, average, and **strong** effects. Grey-shaded cells indicate that a variable was not considered for analysis at that stage.

Explanatory Variable	Intent. Intro	Intent. Nat.	Unint. Int./Nat.	Spread (c-s dist.)	Spread (f-s dist.)	Spread (rate)
Global transport & use by humans						
Centre of origin	Med.	Med.	Med.			
Present in Britain?	yes	yes	yes	yes	yes	yes
British distribution	++	++	++	++	++	++
Economic uses (global)	++	++				
Introduction effort						
Introduction or naturalisation date				--	--	
Introduced for commercial agriculture?		yes		yes	yes	yes
Estimated hectares planted		+++		+	+	+
Nodulation with introduced <i>Rhizobium</i>		++		++	++	++
Opportunistic human assoc. in NZ						
Frequency as pasture seed contaminant				++	++	++
Found in cultivated habitats in NZ?				yes	yes	yes
Native range attributes						
Native range area	++	++	++	++	++	++
Diversity of conditions tolerated	+	++	++	++	++	++
Match to New Zealand climate	+	++	++	+++	+++	+++
New Zealand drought tolerance	+		+++			
New Zealand low temp. tolerance	+	+++	+++			
New Zealand frost tolerance	+	+++	+++			
Habitat characteristics						
Elevation of native range	lowInd	lowInd	lowInd	lowInd	lowInd	lowInd
Canopy cover of native habitat	open	open	open	p. open	p. open	p. open
Native to human-influenced habitats?	yes	yes	yes	yes	yes	yes
Biological traits						
Lifespan			annual	annual	annual	annual
Capable of self-pollination		yes	yes	yes	yes	yes
Capable of vegetative reproduction		yes	yes			
Polyploidy		yes	yes	yes	yes	yes
Reduced base chromosome number				yes	yes	yes
Height maximum				+	+	+
Habit				erect	erect	erect
Seed size		++	++	--	--	--
Seed mass		++	++	--	--	--
Capable of long-distance dispersal				yes	yes	yes
Seed shape similar to white clover?			yes			
Corolla length		--	--	--	--	--
Month flowering starts (Native range)			++			
Month flowering ends (Native range)			++			
Length flowering period (Native range)		+	++			
Month flowering starts (NZ)						
Month flowering ends (NZ)						
Length flowering period (NZ)				++	++	++

Figure 2.1. Division of New Zealand into 10 regions (A) and 329 grid cells (B) for the assessment of species spread. Regional divisions correspond approximately to descriptions in Webb et al. (1988), while grid cells correspond to the NZMS260 topographic map series (2004). For the fine-scale current distribution (grid cell) analysis, the following outlying island groups were each considered to represent one additional “cell”: Auckland Islands, Campbell Island, Chatham Islands, and Kermadec Islands. None of these groups were considered by the regional scheme, although Stewart Island was considered to be part of Southland.

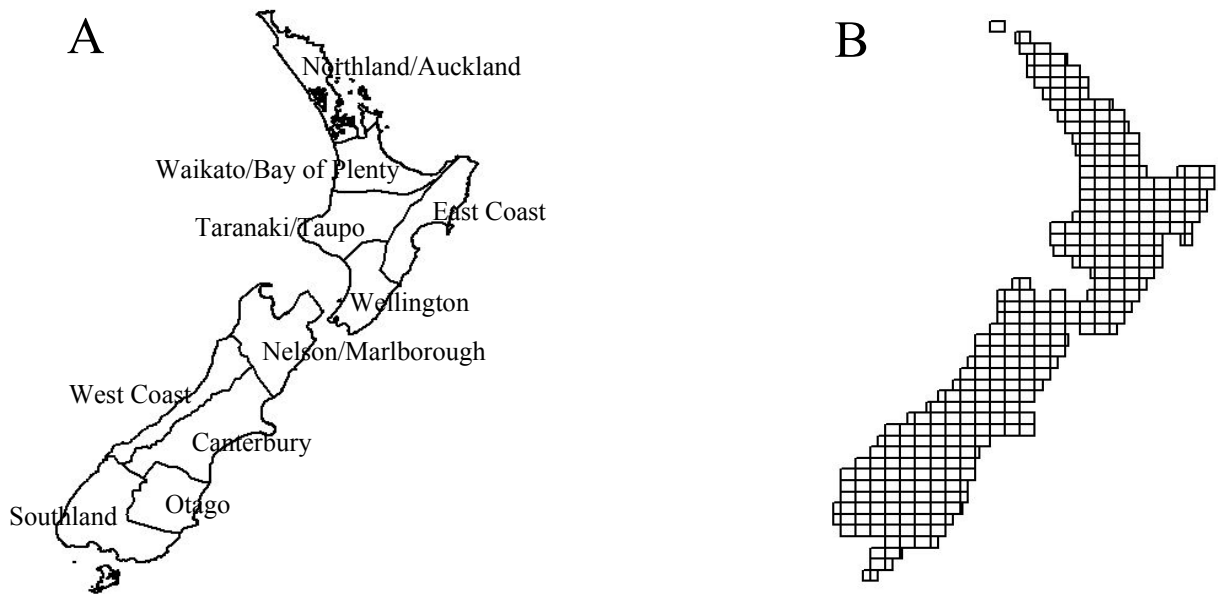


Table 2.3. Variables used in the statistical analyses. For the explanatory variables, the stage(s) at which the variable was evaluated are listed in the Stage column. Stage codes are as listed under Response variables, i.e. intentional introduction (I), naturalisation of intentional species (N), unintentional introduction-naturalisation (U), and spread (S). The number of species available for analysis is listed beside each variable (*n*). Variables are classified as either categorical (cat.) or continuous (cont.), and the extent to which they were transformed to better meet the assumptions of the statistical techniques is indicated (Trans.).

Category	Variables	Stage	<i>n</i>	Type	Coding or Units	Trans.
	Response					
	Intentional introduction	I	228	cat.	0 = no 1 = yes	
	Naturalisation of intentional species	N	54	cat.	0 = no 1 = yes	
	Unintentional introduction-naturalisation	U	174	cat.	0 = no 1 = yes	
	Current distribution (coarse-scale)	S	25	cont.	# of regions	
	Current distribution (fine-scale)	S	25	cont.	# of 1200km ² grid cells	LN
	Rate of spread	S	25	cont.	relative # of cumulative 1200km ² grid cells per year	
	Explanatory					
<i>Global transport and use by humans</i>	Centre of origin	I,N,U	228	cat.	0 = America or Africa 1 = Mediterranean	
	Present in Britain?	I,N,U,S	228	cat.	0 = no 1 = yes	
	British distribution	I,N,U,S	228	cont.	# of 10km ² British grid cells	LN (x+1)
	Economic uses (global)	I,N	228	cont. [†]	# of economic uses	
<i>Introduction effort</i>	Introduction or naturalisation date	N,S	54	cont.	year	
	Introduced for commercial agriculture?	N,S	54	cat.	0 = no 1 = yes	
	Estimated hectares planted	N,S	54	cont.	ha	LN (x+1)
	Nodulation with introduced <i>Rhizobium</i>	N,S	54	cont. [‡]	0 = no 0.5 = unknown 1 = yes	
<i>Opportunistic association with humans in NZ</i>	Frequency as pasture seed contaminant	S	25	cont.	0 = never listed as a pasture seed contaminant 1 = rarely listed 2 = occasionally listed 3 = frequently listed 4 = very frequently listed	

	Found in cultivated habitats in NZ?	S	24	cat.	0 = no 1 = yes	
<i>Native range attributes</i>	Native range area	I,N,U,S	228	cont.	km ²	LN
	Diversity of conditions tolerated	I,N,U,S	228	cont.	# of biomes	
	Match to New Zealand climate	I,N,U,S	228	cont.	# of 10' lat-long grid cells (NZ)	
	New Zealand drought tolerance	I,U	228	cont.	# of 10' lat-long grid cells (NZ)	
	New Zealand low temp. tolerance	I,N,U	228	cont.	# of 10' lat-long grid cells (NZ)	
	New Zealand frost tolerance	I,N,U	228	cont.	# of 10' lat-long grid cells (NZ)	
<i>Native habitat characteristics</i>	Elevation of native range	I,N,U,S	226	cat.	0 = lowland 1 = midland 2 = highland	
	Canopy cover of native habitat	I,N,U,S	203	cat.	0 = closed 1 = partially open 2 = open	
	Native to human-influenced habitats?	I,N,U,S	226	cat.	0 = no 1 = yes	
<i>Bio. traits: Genetic system</i>	Lifespan	N,U,S	228	cat.	0 = annual or biennial 1 = perennial	
	Capable of self-pollination	N,U,S	152	cat.	0 = yes 1 = no	
	Capable of vegetative reproduction	N,U,S	228	cat.	0 = no 1 = yes	
	Polyploidy	N,U,S	185	cat.	0 = no 1 = yes	
	Reduced base chromosome number	N,U,S	185	cat.	0 = yes 1 = no	
<i>Bio. traits: Morphology</i>	Height maximum	N,U,S	218	cont.	cm	
	Habit	N,U,S	220	cat.	0 = prostrate 1 = intermediate 2 = erect	
<i>Bio. traits: Seed size and dispersal</i>	Seed size	N,U,S	213	cont.	1 = <1.0mm 2 = 1.1-1.5mm 3 = 1.6-2.0mm 4 = >2.0mm	
	Seed mass	N,U,S	63	cont.	mg	LN
	Capable of long-distance dispersal	N,U,S	204	cat.	0 = yes 1 = no	
<i>Bio. traits: Other</i>	Seed shape similar to white clover?	N,U,S	206	cat.	0 = no 1 = yes	

	Corolla length	N,U,S	214	cont.	mm	
<i>Bio. traits:</i> <i>Phenology</i> <i>(Native range)</i>	Month flowering starts (Native range)	N,U,S	222	cont.	month (Northern Hem.)	
	Month flowering ends (Native range)	N,U,S	222	cont.	month (Northern Hem.)	
	Length flowering period (Native range)	N,U,S	222	cont.	months	
<i>Bio. traits:</i> <i>Phenology (NZ)</i>	Month flowering starts (NZ)	S	23	cont.	month (Northern Hem.)	
	Month flowering ends (NZ)	S	23	cont.	month (Northern Hem.)	
	Length flowering period (NZ)	S	23	cont.	months	

[†] This variable was treated as continuous in the regression analyses, but as ordered categorical in the SEM analyses, where its approximation as a continuous variable had a potentially greater influence on the analysis estimates.

[‡] For the spread analyses, the coding of this variable was changed to categorical, with the ‘no’ (0) and ‘unknown’ (0.5) observations forming the first category, and the ‘yes’ (1) observations forming the second. This was because there was only one species with a 0 value, making it an outlier with high leverage on the regression lines in the continuous coding system.

Table 2.4. Climate parameters used in the matching analysis, from Pheloung (1996).

Temperature parameters (°C)	Precipitation parameters (mm)
Mean annual temperature	Average annual rainfall
Minimum temperature of coolest month	Rainfall of wettest month
Maximum temperature of warmest month	Rainfall of driest month
Average temperature range	CV monthly rainfall
Mean temperature of coolest quarter	Rainfall of wettest quarter
Mean temperature of warmest quarter	Rainfall of driest quarter
Mean temperature of wettest quarter	Rainfall of coolest quarter
Mean temperature driest quarter	Rainfall of warmest quarter

3 Results

Response variables

Fifty-four of the 228 species in the genus *Trifolium* were intentionally introduced to New Zealand (Appendix 3, Table AP3.1). Of these, 42 species were introduced for experimental forage trials, 10 species were introduced for agriculture on a commercial scale and two species were introduced as ornamentals for horticulture. Nine of the 54 intentionally introduced species have currently naturalised in New Zealand. A further 16 species (from the pool of 174 species that were never intentionally introduced) have currently arrived and naturalised in New Zealand without the intentional aid of humans (Appendix 3, Table AP3.2). Hence, a total of 25 *Trifolium* species have currently naturalised in New Zealand for which I could analyse patterns of spread.

What determined the probability of intentional introduction?

Ten variables were significantly associated with the probability that a species was intentionally chosen for introduction to New Zealand from the pool of 228 *Trifolium* species worldwide (Table 3.1). The two variables having the strongest relationship were the number of global economic uses and native range area: species with a larger number of economic uses and species with a larger native range were more likely to have been introduced. In addition, species able to tolerate a wide diversity of environmental conditions, those with a good climate match and ability to tolerate drought in New Zealand, those originating from the Mediterranean region and, less strongly, species native to human-influenced habitats or habitats with partially open canopies and species with good ability to tolerate frost or low temperature in New Zealand were all significantly more likely to have been chosen for introduction.

In the separate analysis that assessed which biological traits were indirectly selected by the intentional introduction process, I found that intentionally introduced species had significantly longer native range flowering periods than those that were not intentionally introduced (likelihood ratio test (χ^2) on 1 df = 14.2, $P < 0.01$). No other traits differed significantly between the two groups of species.

Three variables independently explained introduction patterns in the multiple regression model: the number of economic uses, native range area and whether a species was present in

Britain or not (Table 3.2). The importance of the number of economic uses, however, was driven primarily by species introduced for commercial agriculture, most of which were present in Britain. A significant interaction between these two variables revealed that presence in Britain coupled with many economic uses led to a high probability of introduction (Fig 3.1). In fact, all 6 species from Britain with 3 or more economic uses were intentionally introduced, compared with 0 of the 12 British species with 0 or 1 economic use. In contrast, economic use was not nearly as important for species that were not present in Britain (Fig 3.1). A large native range increased intentional introduction probability for all species (Table 3.2), but played a larger role for horticultural and experimental agricultural species because of the importance of other factors in determining commercial agriculture introductions.

The structural equation modelling generally supported these inferences. The best models for the introduction of all species and for only commercial agriculture species were qualitatively similar, so I only show the model for all species (Fig 3.2; parameter values in Appendix 1, Table AP1.5). Here, the only direct effect on the probability of intentional introduction is the number of economic uses. Large native range has an indirect effect through its positive influence on economic uses, and a high diversity of conditions tolerated has an indirect effect through its positive influence on native range area. Species with a large number of economic uses also tended to be those with a good match to the New Zealand climate. In contrast, a model including only a direct positive effect of native range area, with diversity of conditions tolerated having an indirect effect through its positive influence on native range area, provided a reasonable explanation for horticultural and experimental agricultural introductions (Fig 3.3; parameter values in Appendix 1, Table AP1.6).

What determined the probability of naturalisation for intentionally introduced species?

Nine variables were significantly related to the probability that an intentionally introduced species was currently naturalised (Table 3.3). Presence and distribution in Britain were most strongly related to naturalisation probability, with present and widely-distributed species being more likely to naturalise. Species that were widely planted, introduced early, introduced for commercial agriculture, widely used economically, and well-matched to the New Zealand climate also had a higher naturalisation probability. Species with large native ranges and that were compatible with introduced strains of *Rhizobium* were somewhat more likely to naturalise as

well. In the multiple regression model, presence in Britain best explained the naturalisation of intentionally introduced species (Table 3.3), with no other variable accounting for significant deviance.

Nevertheless, presence in Britain (along with several other variables in Table 3.3) cannot be a direct cause of naturalisation success but must be correlated indirectly. Of the variables that could be causally linked to naturalisation probability, the strongest relationship is with estimated hectares planted. Similar measures of introduction effort relate strongly to naturalisation success in other invasion studies (Newsome and Noble 1986, Griffith et al. 1989, Williamson 1989, Hopper and Roush 1993, Veltman et al. 1996, Duncan 1997, Green 1997, Rejmánek 2000, Duncan et al. 2001, Mulvaney 2001, Forsyth et al. 2004, Marchetti et al. 2004), and number of hectares planted is strongly correlated with presence in Britain, which provided the majority of commercial agriculture species. A forward-selection multiple regression model that considered only potential causal variables included estimated hectares planted and match to New Zealand climate as independent explanatory variables (Table 3.4). This was confirmed by the SEM which included planting effort and match to New Zealand climate as positive direct effects, and introduction for commercial agriculture, economic uses, native range area, diversity of conditions tolerated, and match to New Zealand climate as positive indirect effects (Figure 3.4; parameter values in Appendix 1, Table AP1.7). Unfortunately, significance could not be assessed for the direct effect paths in this model because the SEM programme was unable to determine standard errors for the slope estimates, most likely because of the low sample size and the skewed distribution of naturalisation outcomes. However, note that these effects were highly significant in multiple regression (Table 3.4).

What determined the probability of unintentional introduction-naturalisation?

From the pool of 174 *Trifolium* species that were not intentionally introduced, fourteen variables were significantly related to the probability that a species was currently unintentionally introduced-naturalised (Table 3.5). The strongest of these relationships was with match to New Zealand climate, with well-matched species having much higher probabilities of unintentional introduction-naturalisation. Additionally, species that had larger native ranges, that were present and widely distributed in Britain, that were able to tolerate a wide diversity of environmental conditions and the frost conditions of New Zealand, that were native to human-influenced

habitats and to the Mediterranean diversity centre, and that were found at lower elevations were more likely to be unintentionally introduced-naturalised. Furthermore, some biological traits enhanced a species' unintentional introduction-naturalisation probability, including a short corolla, small seeds, a reduced number of chromosomes, an annual or biennial lifespan and seeds shaped differently than those of white clover.

Four variables independently explained unintentional introduction-naturalisation patterns in the multiple regression model (Table 3.6). In this model, species well-matched to New Zealand climate, native to human-influenced habitats, widely distributed in Britain, and capable of self-pollination had the highest probability of unintentional introduction-naturalisation.

The structural equation model supported several of these influences (Figure 3.5; parameter values in Appendix 1, Table AP1.8). It confirmed positive direct effects for match to New Zealand climate, native range area, and native habitat type (a factor variable incorporating human influence and canopy cover of the native habitat). Native range area may have been precluded from entering the multiple regression model because of its strong relationship to climate match. All of the direct effect variables also had indirect effects through their correlation with other variables in the model. In addition, there were indirect effects of a high diversity of conditions tolerated and a lowland native habitat.

What determined current coarse-scale distribution?

Only two variables were significantly related to current coarse-scale distribution in the simple regression analysis (Table 3.7). Species that were frequent pasture seed contaminants and that had longer flowering periods in New Zealand achieved the largest current coarse-scale distributions.

Four variables independently explained current coarse-scale distribution in the multiple regression model: frequency as a pasture seed contaminant, length of the New Zealand flowering period, polyploidy, and match to the New Zealand climate (Table 3.8). The model showed that species that were frequent pasture seed contaminants, that had longer New Zealand flowering periods, that were not polyploid, and that were better matched to the New Zealand climate had larger current coarse-scale distributions. Overall, the model explained approximately 81% of the variation in coarse-scale distribution.

What determined current fine-scale distribution?

Similarly, two variables were significantly related to current fine-scale distribution in the simple regression analysis (Table 3.9). As for coarse-scale distribution, species that were frequent pasture seed contaminants and that had longer flowering periods in New Zealand achieved the largest current fine-scale distributions. However, two additional variables showed marginal relationships: species that stopped flowering later in the year and those with wider British distributions had marginally larger current fine-scale distributions.

Three variables independently explained current fine-scale distribution in the multiple regression model: frequency as a pasture seed contaminant, habit, and length of the New Zealand flowering period (Table 3.10). The model indicated that species that were frequent pasture seed contaminants and that had longer New Zealand flowering period had larger current fine-scale distributions. In addition, species of intermediate habit had larger fine-scale distributions than those of erect habit, with prostrate species falling in the middle. Overall, the model explained approximately 77% of the variation in current fine-scale distribution.

What determined rate of spread?

Three variables were significantly related to the rate of spread (Table 3.11): frequency as a pasture seed contaminant, length of the New Zealand flowering period, and British distribution. In accordance with the trends for distribution, faster rates of spread were achieved by species that were more frequent pasture seed contaminants, that had longer flowering periods in New Zealand, and that were more widely-distributed in Britain. In addition, species that tolerated a wider range of environmental conditions in their native ranges achieved marginally faster rates of spread in New Zealand.

Three variables independently explained rate of spread in the multiple regression model: frequency as a pasture seed contaminant, native range area, and length of the New Zealand flowering period (Table 3.12). The model showed that species that were more frequent pasture seed contaminants, that had larger native ranges, and that had longer flowering periods in New Zealand achieved greater rates of spread. Overall, the model explained 86% of the variation in rate of spread.

How do the results differ among invasion stages?

In simple regression, a similar set of factors explained patterns of intentional introduction, naturalisation of intentionally introduced species, and naturalisation of unintentional introductions. Moreover, these factors tended to differ from those that explained patterns of spread (Table 3.13). The factors important in introduction and naturalisation were mostly associated with global transport and use by humans, native range attributes, and habitat characteristics. Nevertheless, there were important differences between intentional and unintentional naturalisation where introduction effort played a dominant role in intentional naturalisation, while habitat characteristics and biological traits played a stronger role for unintentional species. In contrast, patterns of spread were explained by variables associated with opportunistic human association in New Zealand (frequency as a pasture seed contaminant) and the biological trait length of flowering period. Similar relationships held in the multiple regression analyses but here the importance of native range attributes across all invasion stages became more apparent (Table 3.14). The importance of habitat characteristics for unintentional introduction-naturalisation, but not for the other stages, was also emphasized. In the spread stage, additional biological traits had explanatory power. Notably, biological traits of the genetic system appeared significant for both unintentional introduction-naturalisation and for spread.

Table 3.1. Simple regressions of intentional introduction on explanatory variables. Slope estimates and intercepts are parameters of logistic regression ($\log[p/(1-p)] = \alpha + \beta x$, where p represents the probability of intentional introduction, α represents the intercept, and β represents the slope estimate). LRT stands for likelihood ratio test, or the chance in deviance between the null deviance and the residual deviance present after the variable has been added to the model. This change in deviance is approximately χ^2 distributed with the listed degrees of freedom, and was tested against the appropriate χ^2 distribution. Significance values for the test are $^\dagger P < 0.10$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$, after application of a sequential Bonferroni correction.

Variable	Category	Est.	SE	Intercept	df	LRT
Global transport & use by humans						
Centre of origin	America or Africa	0		-1.90	1	11.8**
	Mediterranean	1.15	0.35			
Present in Britain?	no	0		-1.25	1	2.0
	yes	0.69	0.47			
British distribution		0.18	0.08	-1.29	1	4.9 †
Economic uses (global)		1.41	0.25	-1.78	1	45.3***
Native range attributes						
Native range area		0.76	0.14	-22.77	1	42.1***
Diversity of conditions tolerated		0.38	0.08	-3.43	1	29.1***
Match to New Zealand climate		<0.01	<0.01	-2.05	1	27.7***
New Zealand drought tolerance		1.36	1.57	-1276.10	1	12.6**
New Zealand low temp. tolerance		<0.01	<0.01	-4.31	1	7.0*
New Zealand frost tolerance		<0.01	<0.01	-3.32	1	8.3*
Habitat characteristics						
Elevation of native range	lowland	0		-1.14	2	<0.1
	midland	-0.02	0.55			
	highland	-0.05	0.34			
Canopy cover of native habitat	closed	0		-2.70	2	10.1*
	partially open	2.18	1.01			
	open	1.40	1.01			
Native to human-influenced habitats?	no	0		-1.55	1	9.6*
	yes	1.00	0.32			

Table 3.2. Multiple regression model explaining intentional introduction. The model was constructed using a forward selection procedure including all variables, with the threshold significance to enter the model set at $P=0.05$. Variables are listed in the order of their entry into the model. Slope estimates and intercepts are parameters of logistic regression ($\log[p/(1-p)] = \alpha + \beta x$, where p represents the probability of intentional introduction, α represents the intercept, and β represents the slope estimate). LRT stands for likelihood ratio test, or the change in deviance between the null deviance and the residual deviance present after the variable has been added to the model. This change in deviance is approximately χ^2 distributed with the listed degrees of freedom, and was tested against the appropriate χ^2 distribution. The null deviance for this model was 249.62 on 227 degrees of freedom; the residual deviance was 171.34 on 223 degrees of freedom.

Variable	Category	Estimate	SE	df	LRT	P-value
Intercept		-22.30	5.14			
Economic uses (global)		1.03	0.33	1	45.3	<0.001
Native range area		0.74	0.18	1	13.7	<0.001
Present in Britain?	no	0		1	13.4	<0.001
	yes	-16.17	22.11			
Economic uses (global) \times Present in Britain?	no	0		1	5.9	0.015
	yes	6.97	11.04			

Figure 3.1. Interaction between global economic uses and presence in Britain in the intentional introduction multiple regression model. Note that the relationships depicted are those controlling for native range area. For species present in Britain, having a large number of economic uses greatly increased the probability of intentional introduction to New Zealand. However, for species that were not present in Britain, the number of economic uses had negligible importance.

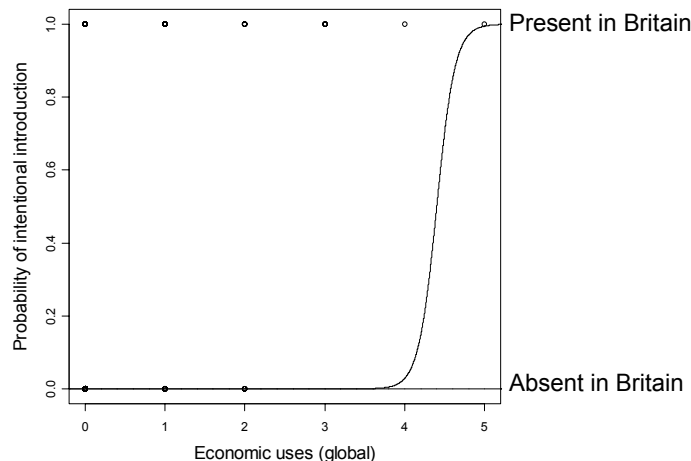


Figure 3.2. Intentional introduction structural equation model (SEM) including all intentionally introduced species. Single-headed arrows represent hypothesized causal relationships, while double-headed curved arrows represent covariances. Significance values for the slope estimates associated with each path are [†] $P < 0.10$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$, and thickness of path lines corresponds to slope significance levels. The direction of each relationship is shown beneath the path. There was no evidence for misfit of this model to the data, with all indices substantially on the recommended side of their threshold. Fit statistic values (and thresholds) were: χ^2 P -value = 0.767 (≥ 0.05), comparative fit index (CFI) = 1.000 (≥ 0.96), and weighted root-mean-square residual (WRMR) = 0.276 (≤ 1.0).

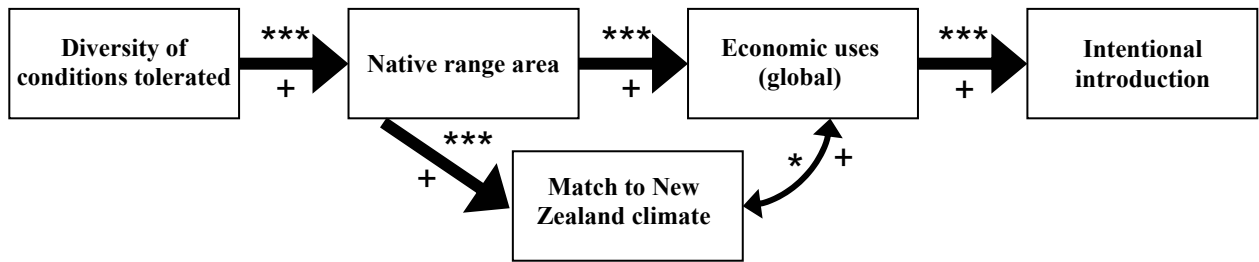


Figure 3.3. Intentional introduction structural equation model (SEM), including only species introduced for horticulture or experimental agriculture. Single-headed arrows represent hypothesized causal relationships. Significance values for the slope estimates associated with each path are [†] $P < 0.10$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$, and thickness of path lines corresponds to slope significance levels. The direction of each relationship is shown beneath the path. There was no evidence for misfit of this model to the data, with all indices substantially on the recommended side of their threshold. Fit statistic values (and thresholds) were: χ^2 P -value = 0.323 (≥ 0.05), comparative fit index (CFI) = 1.000 (≥ 0.96), and weighted root-mean-square residual (WRMR) = 0.380 (≤ 1.0).



Table 3.3. Simple regressions of naturalisation of intentional species on explanatory variables. Slope estimates and intercepts are parameters of logistic regression ($\log[p/(1-p)] = \alpha + \beta x$, where p represents the probability of naturalisation, α represents the intercept, and β represents the slope estimate). LRT stands for likelihood ratio test, or the change in deviance between the null deviance and the residual deviance present after the variable has been added to the model. This change in deviance is approximately χ^2 distributed with the listed degrees of freedom, and was tested against the appropriate χ^2 distribution. Significance values for the test are $^{\dagger}P<0.10$, $*P<0.05$, $**P<0.01$, and $***P<0.001$, after application of a sequential Bonferroni correction.

Variable	Category	Est.	SE	Intercept	df	LRT
Global transport & use by humans						
Centre of origin	America or Africa	0		-9.57	1	5.5
	Mediterranean	8.30	20.10			
Present in Britain?	no	0		-3.81	1	39.0***
	yes	14.37	42.25			
British distribution		3.17	10.36	-3.81	1	39.0***
Economic uses (global)		2.33	0.74	-5.71	1	28.9***
Introduction effort						
Introduction date		-0.06	0.02	112.15	1	30.0***
Introduced for commercial agriculture?	no	0		-3.76	1	29.1***
	yes	5.15	1.28			
Estimated hectares planted		0.32	0.08	-3.96	1	30.1***
Nodulation with introduced <i>Rhizobium</i>		19.88	58.25	-20.57	1	14.3**
Native range attributes						
Native range area		2.60	0.91	-78.34	1	17.8***
Diversity of conditions tolerated		0.45	0.18	-5.01	1	7.6
Match to New Zealand climate		0.04	0.01	-19.45	1	26.6***
New Zealand low temp. tolerance		0.03	0.07	-34.10	1	2.3
New Zealand frost tolerance		0.17	0.31	-191.40	1	7.6
Habitat characteristics						
Elevation of native range	lowland	0		-1.06	2	8.3
	midland	-0.33	1.19			
	highland	-9.51	28.16			
Canopy cover of native habitat	closed	0		-7.57	2	2.2
	partially open	5.45	26.67			
	open	6.47	26.67			
Native to human-influenced habitats?	no	0		-3.22	1	6.7
	yes	2.30	1.09			

Bio. traits: Genetic system						
Lifespan	annual or biennial	0		-1.87	1	0.5
	perennial	0.54	0.74			
Capable of self-pollination	yes	0		-1.32	1	<0.1
	no	-0.07	0.75			
Capable of vegetative reproduction	no	0		-1.74	1	0.3
	yes	0.44	0.79			
Polyploidy	no	0		-1.79	1	1.0
	yes	0.81	0.81			
Reduced base chromosome number	yes	0		-0.56	1	3.2
	no	-1.44	0.79			
Bio. traits: Morphology						
Height maximum		<0.01	0.02	-1.55	1	<0.1
Habit	prostrate	0		-1.25	2	0.6
	intermediate	-0.76	1.10			
	erect	-0.23	0.94			
Bio. traits: Seed size & dispersal						
Seed size		-0.38	0.40	-0.62	1	0.9
Seed mass		0.13	0.49	-0.69	1	0.1
Capable of long-distance dispersal	yes	0		-1.79	1	0.2
	no	0.33	0.77			
Bio. traits: Other						
Seed shape similar to white clover	no	0		-1.53	1	<0.1
	yes	-0.13	0.74			
Corolla length		-0.04	0.08	-1.12	1	0.3
Bio. traits: Phenology						
Month flowering starts		-0.03	0.20	-1.46	1	<0.1
Month flowering ends		0.32	0.21	-4.03	1	2.4
Length of flowering period		0.33	0.20	-2.67	1	2.8

Table 3.4. Multiple regression model explaining naturalisation of intentionally introduced species, using potentially causal variables only. The model was constructed using a forward selection procedure including all potentially causal explanatory variables, with the threshold significance to enter the model set at $P=0.05$. Variables are listed in the order of their entry into the model. Slope estimates and intercepts are parameters of logistic regression ($\log[p/(1-p)] = \alpha + \beta x$, where p represents the probability of naturalisation, α represents the intercept, and β represents the slope estimate). LRT stands for likelihood ratio test, or the change in deviance between the null deviance and the residual deviance present after the variable has been added to the model. This change in deviance is approximately χ^2 distributed with the listed degrees of freedom, and was tested against the appropriate χ^2 distribution. The null deviance for this model was 48.66 on 53 degrees of freedom; the residual deviance was 9.15 on 51 degrees of freedom.

Variable	Category	Estimate	SE	df	LRT	P-value
Intercept		-14.53	6.80			
Estimated hectares planted		0.36	0.17	1	30.1	<0.001
Match to New Zealand climate		0.03	0.02	1	9.4	0.002

Figure 3.4. Naturalisation of intentionally introduced species structural equation model (SEM). Single-headed arrows represent hypothesized causal relationships, while double-headed curved arrows represent covariances. The direction of each relationship is shown beneath the path. Significance values for the slope estimates associated with each path are $^{\dagger}P<0.10$, $*P<0.05$, $**P<0.01$, and $***P<0.001$, with the \S symbol indicating that significance could not be assessed. Thickness of path lines corresponds to slope significance levels, while dashed lines correspond to paths for which significance could not be assessed. Significance could not be assessed for some paths in this model because the SEM programme was unable to determine standard errors for the estimates of these slopes, most likely because of the low sample size and the skewed distribution of naturalisation outcomes. However, note that these effects were highly significant in multiple regression (Table 3.4). There was no evidence for misfit of this model to the data, with all indices on the recommended side of their threshold. Fit statistic values (and thresholds) were: χ^2 P -value = 0.245 (≥ 0.01 -0.05), comparative fit index (CFI) = 0.994 (≥ 0.95), root-mean-square error of approximation (RMSEA) = 0.077 (≤ 0.07 -0.08) and weighted root-mean-square residual (WRMR) = 0.450 (≤ 0.95).

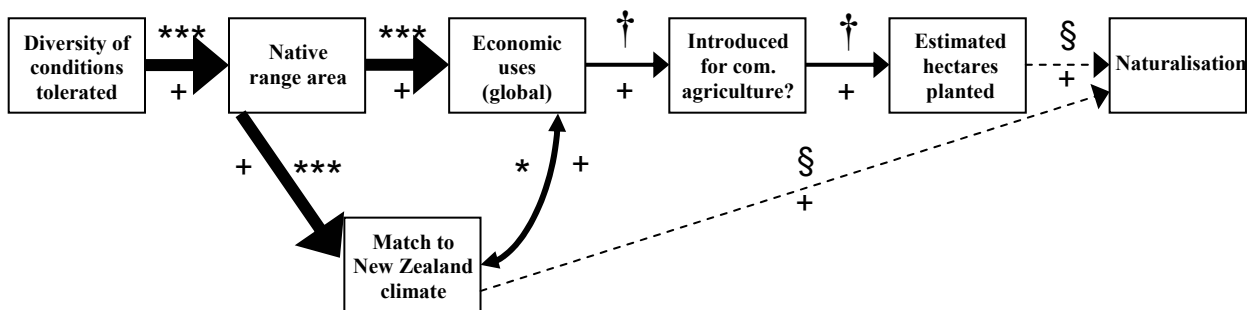


Table 3.5. Simple regressions of unintentional introduction-naturalisation on explanatory variables. Slope estimates and intercepts are parameters of logistic regression ($\log[p/(1-p)] = \alpha + \beta x$, where p represents the probability of unintentional introduction-naturalisation, α represents the intercept, and β represents the slope estimate). LRT stands for likelihood ratio test, or the change in deviance between the null deviance and the residual deviance present after the variable has been added to the model. This change in deviance is approximately χ^2 distributed with the listed degrees of freedom, and was tested against the appropriate χ^2 distribution. Significance values for the test are $^{\dagger}P<0.10$, $*P<0.05$, $**P<0.01$, and $***P<0.001$, after application of a sequential Bonferroni correction.

Variable	Category	Est.	SE	Intercept	df	LRT
Global transport & use by humans						
Centre of origin	America or Africa	0		-10.57	1	23.8***
	Mediterranean	9.08	12.81			
Present in Britain?	no	0		-3.43	1	47.8***
	yes	4.73	0.79			
British distribution		1.29	0.28	-3.49	1	56.5***
Native range attributes						
Native range area		2.49	0.58	-74.35	1	58.4***
Diversity of conditions tolerated		0.87	0.19	-7.80	1	37.3***
Match to New Zealand climate		0.03	0.01	-12.63	1	71.1***
New Zealand drought tolerance		1.11	1.68	-1048.36	1	4.5
New Zealand low temp. tolerance		0.10	0.17	-112.29	1	8.4 [†]
New Zealand frost tolerance		0.13	0.10	-148.28	1	23.3***
Habitat characteristics						
Elevation of native range	lowland	0		-1.78	2	14.3*
	midland	-0.17	0.81			
	highland	-8.79	15.56			
Canopy cover of native habitat	closed	0		-9.57	2	5.1
	partially open	6.88	18.72			
	open	7.72	18.71			
Native to human-influenced habitats?	no	0		-4.10	1	27.4***
	yes	3.19	0.77			
Bio. traits: Genetic system						
Lifespan	annual or biennial	0		-1.86	1	8.7*
	perennial	-2.27	1.03			
Capable of self-pollination	yes	0		-1.41	1	8.4 [†]
	no	-2.31	1.06			
Capable of vegetative reproduction	no	0		-2.03	1	7.8 [†]

	yes	-7.54	12.08			
Polyploidy	no	0		-1.94	1	0.3
	yes	-0.55	1.05			
Reduced base chromosome number	yes	0		-0.49	1	12.1*
	no	-2.07	0.58			
Bio. traits: Morphology						
Height maximum		-0.01	0.01	-2.00	1	0.2
Habit	prostrate	0		-2.40	2	3.0
	intermediate	0.72	0.83			
	erect	-0.27	0.85			
Bio. traits: Seed size & dispersal						
Seed size		-1.32	0.41	0.63	1	14.0**
Seed mass		-1.43	0.58	-1.09	1	7.9 [†]
Capable of long-distance dispersal	yes	0		-1.46	1	5.6
	no	-1.27	0.55			
Bio. traits: Other						
Seed shape similar to white clover	no	0		-1.70	1	8.9*
	yes	-2.31	1.04			
Corolla length		-0.33	0.10	0.54	1	15.8**
Bio. traits: Phenology						
Month flowering starts		-0.38	0.18	-0.56	1	4.9
Month flowering ends		-0.18	0.16	-1.12	1	1.4
Length of flowering period		0.09	0.15	-2.44	1	0.3

Table 3.6. Multiple regression model explaining unintentional introduction-naturalisation. The model was constructed using a forward selection procedure including all variables, with the threshold significance to enter the model set at $P=0.05$. Variables are listed in the order of their entry into the model. Slope estimates and intercepts are parameters of logistic regression ($\log[p/(1-p)] = \alpha + \beta x$, where p represents the probability of unintentional introduction-naturalisation, α represents the intercept, and β represents the slope estimate). LRT stands for likelihood ratio test, or the change in deviance between the null deviance and the residual deviance present after the variable has been added to the model. This change in deviance is approximately χ^2 distributed with the listed degrees of freedom, and was tested against the appropriate χ^2 distribution. British distribution was added as the third variable with an LRT value of 6.3 (on 1 df) and a P -value of 0.012; current significance results from missing values in the ‘capable of self-pollination’ variable. The null deviance for this model was 83.03 on 106 degrees of freedom; the residual deviance was 4.45 on 102 degrees of freedom.

Variable	Category	Estimate	SE	df	LRT	P -value
Intercept		-49.44	27.93			
Match to New Zealand climate		0.06	0.05	1	54.4	< 0.001
Native to human-influenced habitats?	no	0		1	14.7	< 0.001
	yes	26.47	20.06			
British distribution		9.34	7.35	1	0.7	0.392
Capable of self-pollination	yes	0		1	8.7	0.003
	no	-40.68	29.70			

Figure 3.5. Unintentional introduction-naturalisation structural equation model (SEM). Single-headed arrows represent hypothesized causal relationships, while double-headed curved arrows represent covariances. ‡ indicates that the loading for the indicator was fixed at a value close to 1, as the estimated model resulted in a negative residual variance (Heywood case). Significance values for the slope estimates associated with each path are † $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$, and thickness of path lines corresponds to slope significance levels. The direction of each relationship is shown beneath the path. There was no evidence for misfit of this model to the data, with all indices on the recommended side of their threshold. Fit statistic values (and thresholds) were: χ^2 P -value = 0.197 (≥ 0.05), comparative fit index (CFI) = 0.988 (≥ 0.96), root-mean-square error of approximation (RMSEA) = 0.050 (≤ 0.05) and weighted root-mean-square residual (WRMR) = 0.530 (≤ 1.0).

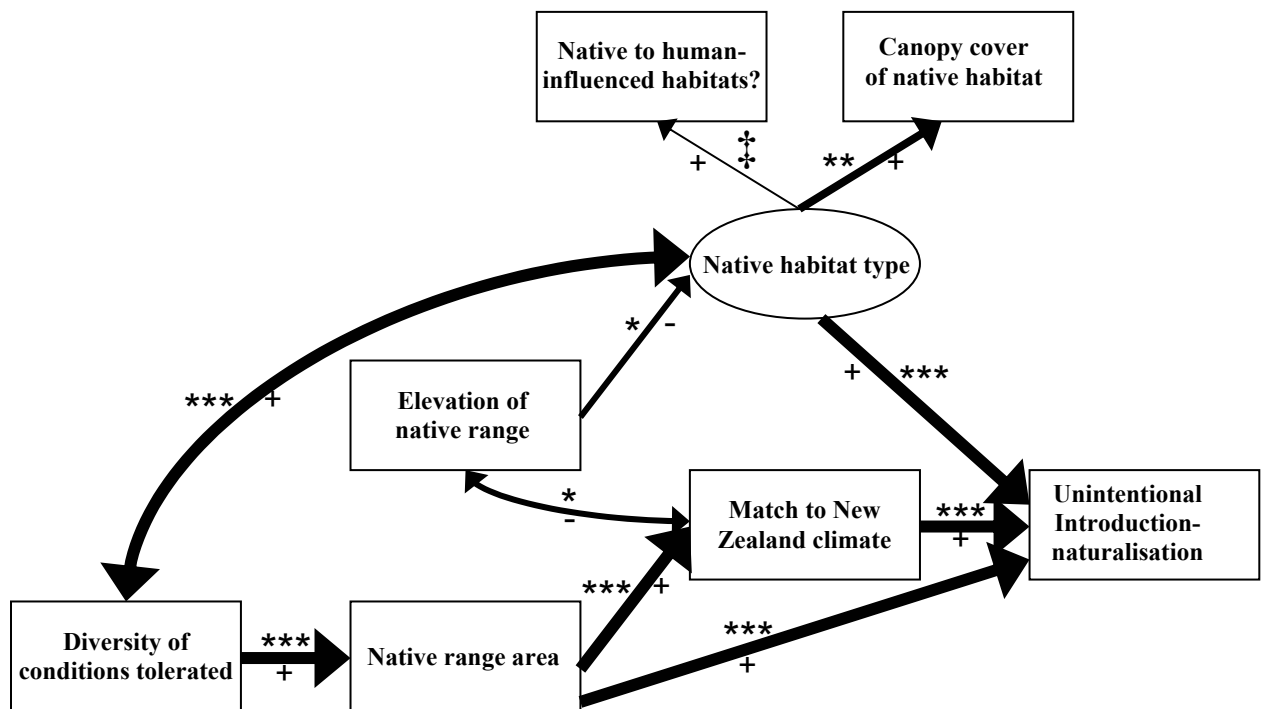


Table 3.7. Simple regressions of current coarse-scale distribution on explanatory variables. Parameters of least-squares linear regression are shown. Significance values are $^{\dagger}P<0.10$, $*P<0.05$, $**P<0.01$, and $***P<0.001$, after application of a sequential Bonferroni correction.

Variable	Category	Est.	SE	Intercept	df	Mean square	F
Global transport & use by humans							
Present in Britain?	no	0		4.00	1	30.33	3.3
	yes	2.58	1.42				
British distribution		0.60	0.19	3.22	1	76.02	10.5
Introduction effort							
Naturalisation date		-0.03	0.02	65.84	1	25.45	2.7
Introduced for commercial agriculture?	no	0		4.94	1	55.14	6.8
	yes	3.18	1.23				
Estimated hectares planted		0.20	0.07	4.85	1	65.73	8.5
Nodulation with introduced <i>Rhizobium</i>	no or unknown	0		4.11	1	48.07	5.7
	yes	2.89	1.21				
Opportunistic human association in New Zealand							
Frequency as pasture seed contaminant		2.06	0.34	3.82	1	148.45	36.1***
Found in cultivated habitats in New Zealand?	no	0		5.47	1	19.60	2.2
	yes	1.87	1.26				
Native range attributes							
Native range area		1.38	1.02	-35.46	1	18.18	1.9
Diversity of conditions tolerated		0.65	0.27	0.48	1	48.56	5.7
Match to New Zealand climate		0.03	0.02	-8.61	1	37.19	4.2
Habitat characteristics							
Elevation of native range	lowland	0		6.23	1	13.10	1.3
	midland	-2.23	1.95				
Canopy cover of native habitat	partially open	0		3.33	1	58.68	7.2
	open	3.61	1.35				
Native to human-influenced habitats?	no	0		6.00	1	0.01	<0.1
	yes	-0.05	2.00				

Bio. traits: Genetic system							
Lifespan	annual or biennial	0		5.68	1	6.02	0.6
	perennial	1.15	1.50				
Capable of self-pollination	yes	0		5.82	1	0.52	<0.1
	no	0.34	1.60				
Capable of veg. reproduction	no	0		5.82	1	3.69	0.4
	yes	1.18	1.99				
Polyploidy	no	0		5.86	1	1.39	0.1
	yes	0.64	1.77				
Reduced base chromosome number	yes	0		6.33	1	3.22	0.3
	no	-0.72	1.29				
Bio. traits: Morphology							
Height maximum		-0.03	0.04	7.02	1	5.65	0.5
Habit	prostrate	0		7.75	2	20.94	2.3
	intermediate	-0.95	1.79				
	erect	-3.20	1.77				
Bio. traits: Seed size & disp.							
Seed size		-0.64	0.68	7.23	1	8.91	0.9
Seed mass		-0.44	0.70	6.26	1	3.90	0.4
Capable of long-distance dispersal	yes	0		5.54	1	4.81	0.5
	no	0.88	1.29				
Bio. traits: Other							
Seed shape similar to white clover	no	0		5.80	1	2.56	0.2
	yes	0.80	1.62				
Corolla length		-0.19	0.15	7.52	1	16.05	1.6
Bio. traits: Phenology (Native range)							
Month flowering starts		-0.41	0.47	7.63	1	7.64	0.7
Month flowering ends		0.57	0.30	2.02	1	32.45	3.5
Length of flowering period		0.76	0.28	3.84	1	57.46	7.1
Bio. traits: Phenology (NZ)							
Month flowering starts		-1.02	0.50	10.60	1	31.75	4.2
Month flowering ends		0.80	0.25	-0.53	1	62.71	10.4
Length of flowering period		0.82	0.19	1.82	1	90.39	19.2**

Table 3.8. Multiple regression model explaining current coarse-scale distribution. The model was constructed using a forward selection procedure including all variables, with the threshold significance to enter the model set at $P=0.05$. Variables are listed in the order of their entry into the model. Parameters of least-squares linear regression are shown. The adjusted r^2 value for this model was 0.81, and the residual standard error was 1.29 on 18 degrees of freedom.

Variable	Category	Estimate	SE	df	Mean square	F	P-value
MODEL				4,18		24.2	< 0.001
Intercept		-5.06	3.47				
Frequency as pasture seed contaminant		1.45	0.28	1	113.46	68.8	< 0.001
Length of flowering period (New Zealand)		0.55	0.13	1	25.62	15.5	< 0.001
Polyploidy	no	0		1	13.33	8.1	0.011
	yes	-2.35	0.76				
Match to New Zealand climate		0.02	0.01	1	7.36	4.5	0.049
RESIDUALS				18	1.65		

Table 3.9. Simple regressions of current fine-scale distribution on explanatory variables. Parameters of least-squares linear regression are shown. Significance values are $^{\dagger}P<0.10$, $*P<0.05$, $**P<0.01$, and $***P<0.001$, after application of a sequential Bonferroni correction.

Variable	Category	Est.	SE	Intercept	df	Mean square	F
Global transport & use by humans							
Present in Britain?	no	0		2.03	1	6.61	4.1
	yes	1.20	0.60				
British distribution		0.26	0.08	1.75	1	14.51	11.4 [†]
Introduction effort							
Naturalisation date		-0.02	0.01	44.51	1	12.26	9.0
Introduced for commercial agriculture?	no	0		2.60	1	6.62	4.1
	yes	1.10	0.55				
Estimated hectares planted		0.07	0.03	2.56	1	8.12	5.2
Nodulation with introduced <i>Rhizobium</i>	no or unknown	0		2.18	1	8.38	5.5
	yes	1.21	0.52				
Opportunistic human association in New Zealand							
Frequency as pasture seed contaminant		0.85	0.15	2.06	1	25.32	31.6***
Found in cultivated habitats in New Zealand?	no	0		2.67	1	5.65	3.8
	yes	1.00	0.52				
Native range attributes							
Native range area		0.87	0.41	-23.05	1	7.16	4.5
Diversity of conditions tolerated		0.34	0.11	0.08	1	13.29	10.0
Match to New Zealand climate		0.02	0.01	-4.57	1	9.90	6.7
Habitat characteristics							
Elevation of native range	lowland	0		3.05	1	2.02	1.1
	midland	-0.88	0.83				
Canopy cover of native habitat	partially open	0		1.83	1	10.58	7.2
	open	1.53	0.57				
Native to human-influenced habitats?	no	0		2.98	1	<0.01	<0.1
	yes	-0.04	0.85				

Bio. traits: Genetic system							
Lifespan	annual or biennial	0		2.85	1	0.85	0.5
	perennial	0.43	0.64				
Capable of self-pollination	yes	0		2.89	1	0.07	<0.1
	no	0.13	0.68				
Capable of veg. reproduction	no	0		2.88	1	0.94	0.5
	yes	0.60	0.84				
Polyploidy	no	0		2.81	1	2.73	1.5
	yes	0.90	0.73				
Reduced base chromosome number	yes	0		3.24	1	1.90	1.0
	no	-0.55	0.54				
Bio. traits: Morphology							
Height maximum		-0.01	0.02	3.16	1	0.23	0.1
Habit	prostrate	0		3.68	2	4.94	3.2
	intermediate	-0.25	0.73				
	erect	-1.43	0.72				
Bio. traits: Seed size & disp.							
Seed size		-0.36	0.28	3.66	1	2.79	1.6
Seed mass		-0.38	0.29	3.06	1	2.86	1.7
Capable of long-distance dispersal	yes	0		2.83	1	0.37	0.2
	no	0.24	0.55				
Bio. traits: Other							
Seed shape similar to white clover	no	0		2.90	1	0.20	0.1
	yes	0.22	0.69				
Corolla length		-0.10	0.06	3.81	1	4.84	2.9
Bio. traits: Phenology (Native range)							
Month flowering starts		-0.18	0.20	3.67	1	1.45	0.8
Month flowering ends		0.20	0.13	1.57	1	3.97	2.3
Length of flowering period		0.28	0.13	2.16	1	7.91	5.1
Bio. traits: Phenology (NZ)							
Month flowering starts		-0.34	0.22	4.51	1	3.44	2.3
Month flowering ends		0.36	0.10	0.03	1	12.51	12.0 [†]
Length of flowering period		0.34	0.08	1.24	1	15.45	17.0*

Table 3.10. Multiple regression model explaining current fine-scale distribution. The model was constructed using a forward selection procedure including all variables, with the threshold significance to enter the model set at $P=0.05$. Variables are listed in the order of their entry into the model. Parameters of least-squares linear regression are shown. The adjusted r^2 value for this model was 0.77, and the residual standard error was 0.60 on 18 degrees of freedom.

Variable	Category	Estimate	SE	df	Mean square	F	P-value
MODEL				4,18		19.8	< 0.001
Intercept		1.17	0.57				
Frequency as pasture seed contaminant		0.56	0.12	1	19.34	54.6	< 0.001
Habit	prostrate	0		2	2.40	6.8	0.006
	intermediate	0.54	0.41				
	erect	-0.42	0.40				
Length of flowering period (New Zealand)		0.23	0.07	1	3.98	11.2	0.004
RESIDUALS				18	0.35		

Table 3.11. Simple regressions of rate of spread on explanatory variables. Parameters of least-squares linear regression are shown. Significance values are [†] $P < 0.10$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$, after application of a sequential Bonferroni correction.

Variable	Category	Est.	SE	Intercept	df	Mean square	F
Global transport & use by humans							
Present in Britain?	no	0		0.01	1	0.00132	4.2
	yes	0.0170	0.008				
British distribution		0.0040	0.001	<0.01	1	0.00330	14.6*
Introduction effort							
Naturalisation date		-0.0003	<0.001	0.51	1	0.00171	5.8
Introduced for commercial agriculture?	no	0		0.02	1	0.00167	5.6
	yes	0.0175	0.007				
Estimated hectares planted		0.0011	<0.001	0.01	1	0.00197	7.0
Nodulation with introduced <i>Rhizobium</i>	no or unknown	0		0.01	1	0.00184	6.4
	yes	0.0179	0.007				
Opportunistic human association in NZ							
Frequency as pasture seed contaminant		0.0133	0.002	0.01	1	0.00619	61.8***
Found in cultivated habitats in NZ?	no	0		0.01	1	0.00210	7.6
	yes	0.0193	0.007				
Native range attributes							
Native range area		0.0153	0.005	-0.44	1	0.00223	8.1
Diversity of conditions tolerated		0.0051	0.001	-0.02	1	0.00299	12.5 [†]
Match to New Zealand climate		0.0002	<0.001	-0.07	1	0.00138	4.5
Habitat characteristics							
Elevation of native range	lowland	0		0.02	1	0.00020	0.6
	midland	-0.0087	0.012				
Canopy cover of native habitat	partially open	0		0.01	1	0.00067	2.0
	open	0.0122	0.009				
Native to human-	no	0		0.01	1	0.00020	0.6

influenced habitats?							
	yes	0.0087	0.012				
Bio. traits: Genetic system							
Lifespan	annual or biennial	0		0.02	1	0.00028	0.8
	perennial	0.0079	0.009				
Capable of self-pollination	yes	0		0.02	1	0.00007	0.2
	no	0.0040	0.010				
Capable of veg. repro.	no	0		0.02	1	0.00033	0.9
	yes	0.0112	0.012				
Polyploidy	no	0		0.02	1	0.00167	5.6
	yes	0.0223	0.009				
Reduced base chrom. #	yes	0		0.03	1	0.00060	1.7
	no	-0.0098	0.007				
Bio. traits: Morphology							
Height maximum		<0.0001	<0.001	0.02	1	<0.00001	<0.1
Habit	prostrate	0		0.03	2	0.00033	0.9
	inter.	-0.0067	0.011				
	erect	-0.0141	0.011				
Bio. traits: Seed size & dispersal							
Seed size		-0.0049	0.004	0.03	1	0.00053	1.5
Seed mass		-0.0024	0.004	0.02	1	0.00011	0.3
Capable long-distance dispersal	yes	0		0.02	1	0.00003	0.1
	no	0.0020	0.008				
Bio. traits: Other							
Seed shape similar to white clover	no	0		0.02	1	0.00023	0.7
	yes	0.0076	0.010				
Corolla length		-0.0008	0.001	0.03	1	0.00028	0.8
Bio. traits: Phenology (Native range)							
Month flowering starts		-0.0012	0.003	0.03	1	0.00006	0.1
Month flowering ends		0.0041	0.002	-0.01	1	0.00171	5.8
Length of flowering period		0.0047	0.002	0.01	1	0.00218	7.9

Bio. traits: Phenology (NZ)							
Month flowering starts		-0.0073	0.003	0.05	1	0.00162	5.5
Month flowering ends		0.0043	0.002	-0.02	1	0.00185	6.5
Length of flowering period		0.0049	0.001	-0.01	1	0.00316	14.2*

Table 3.12. Multiple regression model explaining rate of spread. The model was constructed using a forward selection procedure including all variables, with the threshold significance to enter the model set at $P=0.05$. Variables are listed in the order of their entry into the model. Parameters of least-squares linear regression are shown. The adjusted r^2 value for this model was 0.86, and the residual standard error was 0.007 on 19 degrees of freedom.

Variable	Category	Estimate	SE	df	Mean square	F	P-value
MODEL				3,19		45.5	< 0.001
Intercept		-0.278	0.071				
Frequency as pasture seed contaminant		0.010	0.001	1	0.0056	110.4	< 0.001
Native range area		0.009	0.002	1	0.0010	18.8	< 0.001
Length of flowering period (New Zealand)		0.002	0.001	1	0.0004	7.3	0.014
RESIDUALS				19	0.0001		

Table 3.13. Comparison among stages of simple regression results. Significance values are $^{\dagger}P<0.10$, $*P<0.05$, $**P<0.01$, and $***P<0.001$, after sequential Bonferroni correction. Grey-shaded cells indicate that a variable was not considered for analysis at that stage.

Explanatory Variable	Intent. Intro	Intent. Nat.	Unint. Int./Nat.	Spread (c-s dist.)	Spread (f-s dist.)	Spread (rate)
Global transport & use by humans						
Centre of origin	**		***			
Present in Britain?		***	***			
British distribution	†	***	***		†	*
Economic uses (global)	***	***				
Introduction effort						
Introduction or naturalisation date		***				
Introduced for commercial agriculture?		***				
Estimated hectares planted		***				
Nodulation with introduced <i>Rhizobium</i>		**				
Opportunistic human assoc. in NZ						
Frequency as pasture seed contaminant				***	***	***
Found in cultivated habitats in NZ?						
Native range attributes						
Native range area	***	***	***			
Diversity of conditions tolerated	***		***			†
Match to New Zealand climate	***	***	***			
New Zealand drought tolerance	**					
New Zealand low temp. tolerance	*		†			
New Zealand frost tolerance	*		***			
Habitat characteristics						
Elevation of native range			*			
Canopy cover of native habitat	*					
Native to human-influenced habitats?	*		***			
Biological traits						
Lifespan			*			
Capable of self-pollination			†			
Capable of vegetative reproduction			†			
Polyploidy						
Reduced base chromosome number			*			
Height maximum						
Habit						
Seed size			**			
Seed mass			†			
Capable of long-distance dispersal						
Seed shape similar to white clover?			*			
Corolla length			**			
Month flowering starts (Native range)						
Month flowering ends (Native range)						
Length flowering period (Native range)						
Month flowering starts (NZ)						
Month flowering ends (NZ)					†	
Length flowering period (NZ)				**	*	*

Table 3.14. Comparison among stages of multivariate models. Highest significance in multiple regression or SEM (direct effect) is indicated; (uncorrected) significance values as in Table 3.13. Grey-shaded cells indicate that a variable was not considered for analysis at that stage.

Explanatory Variable	Intent. Intro	Intent. Nat.	Unint. Int./Nat.	Spread (c-s dist.)	Spread (f-s dist.)	Spread (rate)
Global transport & use by humans						
Centre of origin						
Present in Britain?	***	***				
British distribution			*			
Economic uses (global)	***					
Introduction effort						
Introduction or naturalisation date						
Introduced for commercial agriculture?						
Estimated hectares planted		***				
Nodulation with introduced <i>Rhizobium</i>						
Opportunistic human assoc. in NZ						
Frequency as pasture seed contaminant				***	***	***
Found in cultivated habitats in NZ?						
Native range attributes						
Native range area	***		***			***
Diversity of conditions tolerated						
Match to New Zealand climate		**	***	*		
New Zealand drought tolerance						
New Zealand low temp. tolerance						
New Zealand frost tolerance						
Habitat characteristics						
Elevation of native range						
Canopy cover of native habitat			*** †			
Native to human-influenced habitats?			***			
Biological traits						
Lifespan						
Capable of self-pollination			**			
Capable of vegetative reproduction						
Polyploidy				*		
Reduced base chromosome number						
Height maximum						
Habit					**	
Seed size						
Seed mass						
Capable of long-distance dispersal						
Seed shape similar to white clover?						
Corolla length						
Month flowering starts (Native range)						
Month flowering ends (Native range)						
Length flowering period (Native range)						
Month flowering starts (NZ)						
Month flowering ends (NZ)						
Length flowering period (NZ)				***	**	**

† significance in SEM of a factor for which variable was an indicator

4 Discussion

Intentional Introduction

New Zealand's geographical isolation meant that it was the last major land mass to be colonized by humans, and that it experienced its large-scale, persistent wave of immigration from Europe much later than other areas (Crosby 1986). Consequently, it is logical that the species brought by Europeans to establish a European-style agricultural system should have been those that had previously proven successful in their homelands, including other colonies. This is supported by *Trifolium* introductions to New Zealand. Disproportionately many introduced species are native to Britain, the homeland of the majority of New Zealand's European immigrants (King 2003). And of these British species, those with the most economic uses were disproportionately likely to have been introduced.

That species with a larger number of uses had a higher introduction probability than species with fewer uses could be explained by a number of interacting factors. Early settlers may have selected those species that seemed especially versatile, given the largely unknown conditions they would face in New Zealand. Later colonists may have selected species for more specific agricultural roles (e.g. permanent pasture, hay cuts, or green manure), and having a larger number of uses would increase the number of such roles that a species could fill. Perhaps most importantly, species with a large number of economic uses were likely to have been more abundant in the landscape of the settlers' home countries. Indeed, species with a larger number of global economic uses had greater local abundance in 19th century Britain (categorical abundance data extracted from Bentham and Hooker (1887); $r = 0.68$, $P < 0.05$). Higher abundance could easily have facilitated introduction, as colonists would likely have selected species that were readily available in significant quantities. In addition to their economic role, these abundant species may also have been selected for psychological reasons, as settlers sought to recreate familiar landscapes (Mack 2001, McNeely 2001).

My findings closely parallel those for the intentional introduction of birds to New Zealand (Duncan et al. 2003a). In these introductions, two bird families (Anatidae and Phasianidae) were significantly over-represented relative to their global species number. Game species are concentrated in these families (Lockwood 1999), suggesting that this economic use increased a species' probability of intentional introduction to New Zealand. In addition, New Zealand's

settlers tended to introduce bird species that were found in their home geographic region (the Palaearctic), just as I found for *Trifolium* species from Britain. Finally, for birds introduced to New Zealand from Britain, species that were abundant, resident, and widespread in their native range were more likely to be selected (Blackburn and Duncan 2001b). Although I did not examine abundance directly, it could quite plausibly play a role in the economic uses effect.

Experimental agricultural species were, on average, introduced much later than commercial agricultural species (commercial: 1881 ± 10.9 , experimental: 1967 ± 2.3 [mean \pm SE]), and with different goals in mind. By the mid-twentieth century, many agricultural scientists felt that continued breeding of traditional commercial agricultural species may not be able to meet all the needs of New Zealand's varied environment and diversifying agricultural economy (Charlton 1983). Difficulties were apparent, for example, in the high country (Scott 1985), in drought-prone areas (Williams et al. 1978), on Northland soils (Rumball and Lambert 1980), over the winter months (Williams et al. 1980), and in new cropping systems (Taylor et al. 1979b). Because *Trifolium* species had proven so successful in many parts of New Zealand, new species of this genus were sought to address these shortcomings.

Rapid growth in transportation and communication opportunities during this period in New Zealand's history (King 2003) allowed New Zealand scientists to conduct worldwide searches for the species they needed, rather than restricting their focus to familiar territory. Initially, new species came to New Zealand through correspondence with overseas plant breeding centres and scientists; later, targeted collecting trips were made to regions with similar climate and vegetation to that of the New Zealand region for which new species were needed (Burt and Forde 1987). Species with larger ranges would have an advantage for being selected for transport to New Zealand via both of these routes, as a larger range would make a species more likely to be stocked by research centres and encountered by collecting trips. Additionally, species with larger ranges often have higher local abundance (Gaston et al. 2000). A species abundant in its native range would be especially attractive to agricultural scientists, who often strive to establish high plant abundance in their systems. Range size might convey similar advantages for prospective horticultural species, making them more visible to collectors and providing more propagation material from each population found. Unfortunately, little historical information is available regarding the two horticultural *Trifolium* species, making it difficult to determine the exact mechanisms involved.

The intentionally introduced species also tended to have longer flowering periods than those that were not introduced. The most likely explanation for this finding is the correlation between flowering period and native range area in this data set ($r = 0.34$, $P < 0.001$). A very similar pattern was found for naturalised European species in New Brunswick, Canada (Goodwin et al. 1999). In this analysis, native range area was the best predictor of species (intentional or unintentional) introduction and naturalisation. However, flowering period length was correlated with native range area, and showed a significant relationship with introduction and naturalisation when native range area was not included in the model. Because data on failed introductions are difficult to obtain, invasion studies often assess combined probabilities of introduction and naturalisation. My result cautions against interpreting traits significant in such analyses as strictly biological effects on naturalisation. Clearly, the introduction process also has the potential to generate a species pool with a non-random sample of particular traits in the absence of biological mechanisms.

Naturalisation of intentionally introduced species

Introduction effort and climate match were most important for explaining the naturalisation of intentionally introduced species. There were very large differences in introduction effort among species, with the difference between the cumulative planted area for highly important commercial agricultural species and transiently considered experimental agricultural species spanning ten orders of magnitude. The importance of this effect is therefore not surprising. Larger cultivated populations would undoubtedly have increased propagule pressure to adjacent areas, increasing the likelihood that some of these “escaped” populations would persist in the face of demographic and environmental stochasticity (Shaffer 1981, Lande 1993). Furthermore, species with a larger cumulative introduction effort were likely introduced over a greater spatial and temporal extent, increasing the chance of encountering conditions favourable for the founding of naturalised populations (Crawley 1989). Greater introduction effort is also likely to have increased the probability that a particularly well-adapted genotype was introduced (Mack 1991, Kowarik 2003).

The influence of introduction effort on naturalisation success is supported by findings for a number of animal taxa (Newsome and Noble 1986, Griffith et al. 1989, Williamson 1989, Hopper and Roush 1993, Veltman et al. 1996, Duncan 1997, Green 1997, Duncan et al. 2001,

Forsyth et al. 2004, Marchetti et al. 2004). Several of these studies have also found introduction effort to be the most important factor of a range of attributes considered (Veltman et al. 1996, Green 1997, Duncan et al. 2001, Marchetti et al. 2004) (Table 1.1). Evidence from plants is more limited, and I could not find any published studies comparing the influence of introduction effort to that of other factors. Considering studies looking at effort only, a strong influence of introduction effort was found for the naturalisation of ornamental woody plant introductions to south-eastern Australia (Mulvaney 2001). A greater number of plantations also appears to increase the number of spontaneous occurrences for *Eucalyptus* species introduced to southern Africa (Rejmánek and Richardson, unpublished data cited in Rejmánek 2000).

The importance of climate match is also quite sensible. In other plant groups, where data on failed naturalisations are available, a climate inhospitable to survival, growth, or reproduction is among the most frequently cited reasons for failure (Grace 1987, Kornas 1990, Williamson and Fitter 1996, Pyšek 2003). Quantitative tests of this effect are somewhat rarer in the literature, but those that have been conducted usually report a significant relationship between climate match and naturalisation success (Blackburn and Duncan 2001a, Duncan et al. 2001, Forsyth et al. 2004), but see (Roy et al. 1991). Although I predicted that species' climate tolerances would have more influence on naturalisation than their climate match, the data did not support this hypothesis. I had originally constructed these indices in an attempt to capture the influence of climate on species' ability to survive and reproduce (tolerance) and compete effectively (match). While it is possible that my result reflects the greater importance of competitive interactions relative to survival and reproduction differences, it may equally have resulted from differences in the procedures used to construct the indices. Essentially, the criteria for assigning a species a "success" outcome in a particular New Zealand 10'x10' latitude-longitude grid cell were much stricter for climate match than for climate tolerance (mean number of suitable grid cells: low temperature tolerance 1111 ± 11.0 , frost tolerance 1066 ± 21.9 , climate match 287 ± 25.7 [mean \pm SE]). This generated more variation among species for the match index, which may have given it an advantage in the statistical analysis. The relative importance of these two climatic processes on invasion success would be fruitful ground for more detailed experimental investigation, as well as further development of climatic models.

Biological traits did not approach statistical significance in any of the analyses, despite numerous hypotheses for their relationships to naturalisation success. This result may have been observed for several reasons. First, particular traits may affect naturalisation, but the enormous

differences in introduction effort among this relatively small sample of species overwhelmed the impact of these traits. Second, regional climatic variation may influence the naturalisation process such that different traits are advantageous in different regions. For example, many researchers have noted that annual *Trifolium* tend to be more common in drier regions of New Zealand, while perennial species dominate wetter areas (e.g. Hyde and Suckling 1953, Levy 1970, Boswell et al. 2003). Finally, it is possible that these traits do not affect naturalisation in the hypothesized ways.

Taken together, the analyses of introduction and naturalisation for intentionally introduced species suggest a fairly straightforward path to success (Figure 3.4): the species that eventually naturalised were predominantly those planted on a large scale for commercial agriculture, which were the same species that were economically useful and present in the settlers' home countries (Figure 3.1). Within this species pool, variation in the extent to which species were suited to the New Zealand climate appears to have mediated their success to some degree. However, note that climate match and introduction effort are correlated: in addition to receiving the greatest introduction effort, species occurring in Britain were also among the most well-matched to the New Zealand climate. The relative roles of these two factors are thus difficult to resolve with this data set. For this reason, it might be interesting to compare my results with similar investigations in which the climates of the settlers' home countries and that of the colonized area differed more widely, such as the British colonization of tropical Australia or the northwest European colonization of South Africa. Yet, such historical investigations will always deviate significantly from randomized experiments, because people pre-select species that appear to match the recipient climate. Therefore, where feasible, randomized experiments could contribute important perspective for fully understanding the relative importance of introduction effort and climate match.

Although the influences of introduction effort and climate match are sensible and well-supported by previous studies, the results must be interpreted cautiously. The data do indicate conclusively that commercial agricultural species, which were introduced on a very large scale, were more likely to naturalise than horticultural and experimental agricultural species, which were introduced on a very small scale. Specifically, of the 10 introduced commercial agricultural species, 8 species naturalised, while only 1 of the 44 horticultural or experimental agricultural species did so. Beyond this, there is a very small sample size from which to draw more specific conclusions; the importance and model coefficients for specific introduction effort and climate

match variables were strongly influenced by attributes of the 2 non-naturalised commercial agricultural species and 1 naturalised experimental agricultural species. It is possible that other differences between these species groups may have influenced naturalisation outcomes. For example, horticultural and experimental agricultural species were introduced much later than the commercial agricultural species. If later introductions exhibit a lag phase (Kowarik 1995), this effect may be somewhat confounded with introduction effort differences. In addition, species introduced later would have encountered many more congeners that were already naturalised and adapted to the new environment (e.g. Callaway and Ridenour 2004). This could create greater potential for the later introductions to be competitively excluded from establishment sites, independent of introduction effort or climate match differences. Finally, many experimental species may not have had extended high-quality opportunities to naturalise, as trial land may have been cleared for other uses shortly after the conclusion of experiments.

Inference is also complicated by the fact that the three “outlier” species have unique attributes which could have contributed to their fates, independent of introduction effort or climate match. For *T. ambiguum*, a commercial agricultural species that has not naturalised, the absence of suitable rhizobia may be responsible (Patrick et al. 1994, Patrick and Lowther 1995, Pryor et al. 1996, Elliot et al. 1998), as this species has very specific rhizobial requirements (Burton 1985, but see Seguin et al. 2004). Introduced to New Zealand in 1955, it was also by far the latest introduction of the commercial agricultural species. This interval of introduction is especially short considering the species’ perennial, rhizomatous growth form. The briefness of the introduction interval may also have hindered the naturalisation of its compatible rhizobia, since these would have experienced a reduced cumulative introduction effort and a reduced diversity of introduction conditions compared to the rhizobia of commercial agricultural species with longer introduction intervals.

For *T. alexandrinum*, the other non-naturalised commercial agricultural species, rhizobia might also have played a role. I found commercial introductions of this species between 1912 and 1942, a period in which inferior technology for companion *Rhizobium* strain establishment may have resulted in nodulation failure for some of the introduced plants. However, two of my three sources place this species in the same “effectiveness group” as very widespread commercial agricultural species (*T. repens* and *T. pratense* (Anonymous 2003), *T. subterraneum* (Burton 1985)), for which compatible rhizobia were likely to have been widely naturalised by this time. A feature of *T. alexandrinum*’s biology more likely to have impacted its naturalisation is its long

history of cultivation by humans. The extent of domestication selection experienced by this species is evidenced by its listing in many sources as known “from cultivation only”; wild specimens can apparently no longer be found in what must once have been the species’ native range (Zohary and Heller 1984). *T. alexandrinum* would likely be less able to establish populations outside of cultivation because of this selection, possibly as a result of changes such as altered seed dormancy patterns (J. Emms, personal communication). However, it is also possible that poor frost tolerance is the key limiting factor for *T. alexandrinum* persistence in New Zealand (Taylor et al. 1979a), indicating that the climate match result may have real relevance for this species.

Finally, for *T. hirtum*, the naturalised experimental agricultural species, it is possible that additional unintentionally introduced propagules aided naturalisation. I defined a species as intentionally introduced if any of its historical introduction records pre-dated its naturalisation date. Thus *T. hirtum*, used in experimental trials in the 1960s and 1970s, was defined as intentionally introduced because it did not naturalise until 1981. However, the naturalisation record for this species is based on a single population located on a roadside in Bay View, outside the city of Napier (Webb et al. 1988). This location is approximately 100 km distant from the nearest trial record in my database (Wimbledon, Hawke's Bay: Williams et al. 1980), suggesting that the population may have originated from another source. Of course, it is possible that I overlooked other trial records in my search. Nonetheless, my multiple logistic regression model for unintentional introduction-naturalisation (Table 3.6) predicts a 93% probability for *T. hirtum* naturalisation by unintentional means, although note that the naturalisation date for *T. hirtum* is later than those of the species used to construct this model (Appendix 3).

The role of *Rhizobium* strains in facilitating or hindering naturalisation of *Trifolium* species in New Zealand is a topic that greatly merits further investigation. Newly introduced *Trifolium* species can have difficulty forming effective symbioses with existing New Zealand *Rhizobium* populations (Greenwood 1976), and insufficient nodulation is a suspected cause of establishment failure in species trials (D. Scott, personal communication). However, for overall naturalisation success, the importance of rhizobia relative to other ecological factors is unknown. Given available data, I was only able to quantify this effect in a very approximate way. I found a significant influence of my measure of nodulation potential in the simple regression analysis, but it was not included in the multivariate models. I suspect that the simple regression result reflects my assumption that all of the commercial agricultural species were introduced with a compatible

strain of *Rhizobium*; these species' higher naturalisation probabilities for other reasons could be responsible for the effect. Better data with which to more accurately quantify the influence of rhizobia will hopefully allow more definitive conclusions in future studies.

Unintentional introduction-naturalisation

In the unintentional introduction-naturalisation process, the probability of transport and introduction is likely to be the dominant influence. A greater probability of introduction would almost certainly lead to a larger number of introduction events, more individuals released in each event, or both. This differential propagule pressure may be entirely responsible for any naturalisation differences among introduced species. In the naturalisation stage, the paramount importance of propagule pressure relative to biological differences has been repeatedly demonstrated in other studies (Veltman et al. 1996, Green 1997, Duncan et al. 2001, Marchetti et al. 2004), as well as for intentionally introduced *Trifolium* species in this study. This scenario gains support when considering the enormous differences in introduction probability and, thus, propagule pressure that are likely to have been present among species, and the greater potential hazards posed by stochastic forces for unintentional as compared to intentional introductions.

Contamination of imported pasture seed was probably the most important route of accidental *Trifolium* species introduction to New Zealand early in New Zealand's European colonisation (Healy 1952, Esler 1987, Webb et al. 1988). This route may have allowed large numbers of propagules to be transported and introduced to New Zealand, and it resulted in a favourable environment for establishment relative to other unintentional introduction means (Esler 1987). For this introduction route, Mediterranean-centred species, especially those present in Britain, had an overwhelming advantage relative to species from other areas. As I have indicated, nearly all grass and clover seed imported prior to 1900 was directly or indirectly of European origin (New Zealand Registrar-General's Office 1868-1900). Over 90% of seed came from Europe or Australia, with the remainder arriving from the United States. While the presence of American species of *Trifolium* in the U.S. seed cannot be ruled out (although none naturalised), European contaminant species were also probably established there during this period (Mack and Erneberg 2002).

New Zealand greatly expanded its trading base in the twentieth century, but strong economic ties with Britain remained until the close of World War II (King 2003). Concurrently,

in the years leading up to and including World War II, two developments greatly reduced the importance of pasture seed importation as a means of species introduction. First, seed purity was rapidly improving, as a result of seed line certification, technological improvements, and increased use of herbicides (Saxby 1941, Johnson 1985). Second, New Zealand's domestic seed production industry was swiftly developing, and restrictions imposed by the War spurred this development to the point of self-sufficiency (Pool 1942). Indeed, trade records indicate that New Zealand's importation of pasture seed peaked early in the 1900s and then fell off (H. Gatehouse, unpublished data). Therefore, Europe, especially Britain, was the chief source of grass and clover seed in the years when importation of contaminants was most likely. In line with this argument, 15 of the 16 unintentionally naturalised *Trifolium* species did so before 1940. Although there may be other explanations for this pattern, it is consistent with the proposed importance of seed contaminants imported before 1940 as a source of unintentional species.

Species native to Europe could have further increased their propagule pressure advantage through several other potential introduction routes. European, and especially British, citizens formed the vast majority of immigrants to New Zealand after 1840 (King 2003). European species may have been inadvertently introduced by these individuals through such means as attachment to clothing or packing material (Healy 1952, Esler 1987). In addition, Gladstones (1966) notes that immigrants might have even introduced these "unintentional" species deliberately:

"Migrating farmers brought out their own seeds.... Moreover, by the early nineteenth century, the value of improved pastures, including clovers, was widely appreciated in England. Migrating farmers might have collected seed of any clovers they could find to take with them to the colonies, or they might have collected seeds in the vicinity of ports of call *en route*."

Finally, as noted above, European countries, especially Britain, were prominent among New Zealand's trading partners in the years before World War II. This could have conveyed an introduction advantage by several other routes, including soil imported with horticultural plants and ships' ballast (Healy 1952, Esler 1987, Simberloff 1989). For European species, these trade-related advantages diminished in subsequent years, but may still be evident in the unintentional naturalisation pattern if later introductions exhibit a lag phase (Kowarik 1995).

Not only were there potentially massive differences in propagule pressure among species from different locations, but the importance of propagule pressure may have been greater for naturalisation of unintentionally introduced species than for that of deliberate introductions.

Whereas deliberate introductions were often sheltered by cultivation, unintentional species may have been exposed to the full strength of stochastic forces, such as drought and disease, that can hinder population establishment (Mack 1995, 2000). Even species that indirectly received the benefits of cultivation when sown as seed contaminants may still have faced less than optimal conditions because management strategies, such as the grazing regime, would have been attuned to the tolerances of the sown species.

Taken together, these factors suggest great advantage for species from the Mediterranean diversity centre, and especially Britain, at the unintentional introduction-naturalisation stage. For example, all 16 of the unintentional species are of Mediterranean origin, and the ranges of 11 of these species include Britain (Appendix 3, Table AP3.2). Most of the biological traits significant in the simple regression analysis appear to be driven by Mediterranean origin (Taylor et al. 1979c, Zohary and Heller 1984), with the possible exception of seed size. The multiple regression model, however, is robust to the strong Mediterranean influence; if this analysis is repeated with the potential source pool restricted to Mediterranean species, the same model is selected.

In this study, climate match may be the most important explanatory variable because it best reflects a species' introduction probability, by effectively integrating a Mediterranean origin, a large range area, and presence in Britain. Equally, however, it is plausible that climate exerts a real influence on *Trifolium* species' ability to naturalise once they reach New Zealand. In other systems, both observational (Grace 1987, Kornas 1990, Williamson and Fitter 1996, Pyšek 2003) and statistical (Blackburn and Duncan 2001a, Duncan et al. 2001, Forsyth et al. 2004) evidence supports a key role for climate match in the naturalisation process. Here, it is certain that a number of non-British Mediterranean *Trifolium* species were unintentionally introduced to New Zealand and therefore very probable that other somewhat restricted Mediterranean species were as well. Such species may not have been adapted to the winter extremes of New Zealand's climate, especially with regard to frost. As many Mediterranean species have a winter annual life-history, frost susceptibility could completely prevent reproduction, leading to naturalisation failure.

The native range area effect also received some statistical support. As indicated in the structural equation model, the influence of native range area is most likely independent of climate match or ecological versatility (Figure 3.5), suggesting a role for introduction probability. In a study of plant species introductions to Australia, higher probability of introduction may have also

played significant role in the effect of native range size on invasion success (Forcella and Wood 1984). Indeed, in this study, I observed a direct effect of native range area on introduction probability for horticultural and experimental agricultural species. If some unintentional *Trifolium* species were deliberately selected by migrating farmers, as Gladstones (1966) suggests, similar range size-associated factors could have driven species selection. The inclusion of British distribution in my multiple regression model likely reflects similar introduction probability effects for the British *Trifolium* species. For *Trifolium* species occurring in Britain, British distribution and total native range area were significantly correlated ($P < 0.05$).

The association with human-influenced habitats was also strongly supported in all of the analyses. Presence in human-influenced habitats would make a *Trifolium* species' introduction more probable through all of the routes that I indicated above, including seed contamination. In addition, species would most likely be deposited into similar human-influenced habitats once they arrived in New Zealand (Simberloff 1989), which could have a strong influence on the probability of subsequent naturalisation. In fact, di Castri (1990) argues that habitat similarity may be even more important than climatic similarity in driving global invasion patterns. For birds, being native to human-influenced habitats appears to increase naturalisation probability (in Australia: Newsome and Noble 1986, globally: Sol et al. 2002), although there is little comparable work for plant species.

For the biological traits, genetic system traits had an independent influence on unintentional introduction-naturalisation probability, as indicated by the retention of the capable of self-pollination variable in the multiple regression analysis. Seed size may also have an effect, although it is moderately correlated with presence in human-influenced habitats. As indicated by the multivariate analyses, however, the importance of these traits is secondary to that of native range attributes and habitat characteristics.

The direction of effects for genetic system traits suggests that *Trifolium* species with high population growth rates (r) were more likely to be unintentionally introduced-naturalised. A high population growth rate allows an introduced population to increase quickly from a small size, minimizing the effects of demographic and environmental stochasticity (Shaffer 1981, Lande 1988). In addition, for unintentionally introduced *Trifolium* species specifically, gaps appearing in pastures may have created important establishment opportunities (Levy 1923a, Hyde and Suckling 1953). Species that can grow and mature quickly are best able to take advantage of these gaps, maturing seed before competition from sown species becomes too intense (Levy

1930, 1970, Esler 1988a). For self-pollination capability in particular, the ability to establish a population from a single initial colonist, and/or the ability to reproduce without effective pollinators in the new range, may have provided species with a naturalisation advantage (Baker 1955). However, as I have noted, the strong correlation of this trait with others of the genetic system makes it difficult to have confidence in this potential mechanism.

The advantage for small-seeded species has a number of potential explanations. Small seeds are most similar in size to those of white clover (*T. repens*) (Gillett and Taylor 2001), which would have made them difficult to spot in white clover seed lines and difficult to remove from these lines with seed-cleaning machinery. These advantages may have enabled small-seeded species to contaminate white clover lines with greater frequency. In addition, smaller seed size and mass often translate into greater seed number (Westoby et al. 2002), which could certainly increase introduction probability. Small seeds are also better adapted for transport in soil (Hodkinson and Thompson 1997), increasing their probability of introduction via such means as ships' ballast and soil about the roots of imported horticultural plants. Additionally, small seeds increase a species' ability to survive consumption by grazing animals (Jones and Simao Neto 1987, Simao Neto et al. 1987, Thomson et al. 1990, Russi et al. 1992, Ghassali et al. 1998). This ability could be vital to the naturalisation of newly introduced species, as it allows seeds to be transported to favourable habitats at the most critical point in the naturalisation process (Malo and Suarez 1997). Finally, smaller seeds may also display greater dormancy, allowing them to remain viable after introduction until habitat conditions are favourable for growth (Andersson 1996, Smith et al. 1996).

Other studies of unintentional introduction-naturalisation provide general support for my conclusions. In a qualitative analysis of fish unintentionally transported in ballast water, propagule pressure differences resulting from transport and introduction probability were a potential driver of naturalisation patterns (Wonham et al. 2000). Range size and abundance were also possible explanations for variation in transport probability. For ant species, the majority of which were unintentional introductions, "opportunistic" species were predominant among those that had been introduced and at least transiently established in new areas (McGlynn 1999). These species are frequently human commensals and have biological traits associated with disturbed habitats.

Three plant studies have examined combined probabilities of introduction and some form of establishment, including both transient and more permanently naturalised species (Prinzing et

al. 2002, Pyšek 2003) or only those considered fully naturalised (Goodwin et al. 1999) in their analysis. However, all three of these studies considered a mixture of intentionally and unintentionally introduced species. For European species naturalised in New Brunswick, Canada, native range size was the best predictor of success (Goodwin et al. 1999). For central European species naturalised in Argentina, species tolerating a greater diversity of environmental conditions and that had larger distributions in the source area were more likely to be successful (Prinzing et al. 2002). In that study, “occurrence in anthropogenic vegetation” in the native habitat was significantly related to success in simple regression analysis, but it was not retained in the multiple regression model, possibly because correlated traits were included. Finally, in an analysis of unintentionally introduced American species in the Czech Republic, annual lifespan and early flowering were related to earlier appearance (Pyšek 2003). Pyšek suggested that annuals should have a greater introduction probability due to their large seed set and ability to form seed banks and that early flowering species may be those best matched to the Czech climate.

Spread

In the spread stage, substantial variation among *Trifolium* species was found for both rate of spread and current distribution. It should be noted, however, that the actual rate of species’ spread most likely exceeded the rate at which they were recorded by botanists. The large-scale planting of *Trifolium* species before 1900, coupled with the comparatively slower development of the herbarium system, meant that many species were not recorded in particular locations until decades after they had likely arrived there. Even after 1900, documentation of naturalised species’ distributions was patchy in both time and space, being driven largely by the ambitions and opportunities of individual botanists (P. Bellingham, pers. comm.). For this reason, my spread rate measures cannot be interpreted as absolute measures of *Trifolium* species’ range expansion through time. Nonetheless, they should provide satisfactory measures of species’ *relative* spread dynamics, due to my efforts to correct for species frequency, habitat, and temporal collection biases.

At the spread stage of an invasion, species’ biological traits are usually thought to play a key role (e.g. Kolar and Lodge 2001). However, for *Trifolium* species in New Zealand, I found that human dispersal within the new range was the dominant factor, although biological traits

clearly played a part as well. Is this finding simply a consequence of the enormous scale of *Trifolium* planting in New Zealand, or might similar patterns exist in other systems as well? Although the scale of planting is undoubtedly a factor here, data presented by Kowarik (2003) also make a case for the importance of human dispersal. He found that the vast majority of problematic alien species in Germany had been dispersed within the country by humans, and that a significant proportion of problematic alien populations could be traced back to human-mediated secondary releases. Within New Zealand, the importance of seed contamination for spread is apparently not limited to *Trifolium*, as a number of botanists have noted a significant role for this pathway in the spread of naturalised species generally (Kirk 1897, Cockayne 1926, Healy 1952, Esler 1987). Seed contamination has been of key importance for spread in other locations as well (Forcella 1985, Mack 1991, Andersen 1995), although it has rarely been tested against biological traits as a competing explanation for spread success.

For pasture seed contaminants in New Zealand, a number of processes may have contributed to the spread success of these species. Foremost among these is the facilitation of long-distance dispersal. Although some *Trifolium* species have adaptations for wind dispersal or external dispersal by animals (Zohary and Heller 1984), these mechanisms are unlikely to be sufficient to move species between regions since their introduction less than 200 years ago. By contrast, contaminating seed would have rapidly moved species to locations throughout the country. In mathematical models of invasions, long-distance dispersal is the key driver of a rapid spread rate (Higgins and Richardson 1999). Furthermore, long-distance dispersal facilitates the formation of multiple foci of invasion, which serve to increase both the rate of spread and the distribution achieved (Auld and Coote 1980, Moody and Mack 1988). In addition, in contrast to other dispersal modes, species moved about in pasture seed would almost always have been deposited in habitats where conditions were suitable for their survival and reproduction. Kowarik (2003) and Pyšek et al. (1995) highlight the importance of human dispersal in enabling species to overcome the spatial isolation of appropriate habitats.

Some features of this data set may also play a role in accounting for the importance of pasture seed contaminant frequency. First, occurrence as a pasture seed contaminant is related to occurrence in pastures generally, which may provide a number of additional advantages. These include long-distance gut dispersal by stock (Lamont 1939, Healy 1952, Suckling 1952) and the benefits of human cultivation, including fertilisers and irrigation, which could have enabled species to build up robust populations and escape from the pasture environment (Mack 2000).

Second, this variable was correlated with introduction effort, as important commercial agricultural *Trifolium* species were also frequent pasture seed contaminants. Third, as New Zealand-based data were used to estimate pasture seed contaminant frequency, there is the possibility that species' spread influenced their contaminant frequency, as well as contaminant frequency influencing spread. The statistical effect thus estimates the importance of this entire positive feedback cycle in contributing to species' spread in New Zealand.

Flowering period in New Zealand, a biological trait, also had high importance in explaining both rate of spread and current distribution. It is likely that the length of the flowering period is correlated with the length of the fruiting period (Reichard 1994, Rejmánek and Reichard 2001), which I did not measure. As I have noted, in pastures, where many species probably established invasion foci, temporary gaps create important establishment opportunities (Levy 1923a, Hyde and Suckling 1953, Esler 1988a). In these environments, longer flowering and fruiting would have increased the chance that dispersed seeds encountered such gaps (Gerlach and Rice 2003). In addition, species that flower longer would have a better chance of encountering pollinators (Reichard 1997). This increased opportunity may be of crucial importance because of the scarcity of *Trifolium* pollinators in New Zealand in early years (Guthrie-Smith 1921) and because of New Zealand's unpredictable weather conditions, which can cause large temporal fluctuations in pollinator activity and abundance. The flowering and fruiting period are also important components of species' interactions with grazing animals. During flowering, consumption of reproductive structures by grazing animals would be detrimental; however, during fruiting, consumption of mature seeds by these animals could provide an important dispersal mechanism (Lamont 1939, Healy 1952, Suckling 1952). Species with prolonged flowering and fruiting periods might be better adapted to cope with both of these processes, as a longer flowering period would ensure that at least some flower heads could survive or be re-grown, while a longer fruiting period would increase the chance that at least some of the fruiting heads would be consumed by the animals. Finally, a longer flowering and fruiting period might increase a species' chances of getting into the pasture or crop seed supply, which appears to provide a strong advantage for spread.

Surprisingly, flowering period length in the native range did not significantly explain flowering period length in New Zealand (simple linear regression, $P > 0.10$). On average, species flowered significantly longer in New Zealand than in their native ranges (Native range flowering period 2.91 ± 0.44 months; New Zealand flowering period 5.57 ± 0.51 months [mean \pm SE];

paired t-test $t = -4.51$, $df = 22$, $P < 0.001$). Of the 23 species for which data were available, 18 flowered longer in New Zealand than in their native range, 3 had an equivalent flowering period, and only 2 species flowered longer in their native range than in New Zealand. Interestingly, a similar pattern was observed for 11 passerine species introduced from the United Kingdom to New Zealand; although species' breeding seasons (calculated following MacArthur (1964)) tended to be longer in New Zealand, the relationship between breeding season length in the native and introduced range was weak (K. L. Evans, R. P. Duncan, T. M. Blackburn, and H. Q. P. Crick, unpublished data).

It seemed possible that the New Zealand flowering period effect I observed could have been an artefact of differences in species' distributions, rather than providing an explanation for these differences. In particular, if a species was present at only a few localities, it may not have been sufficiently observed for its full flowering capability to have been recorded. However, I did not find evidence that this was the case: species' current fine-scale distribution was unrelated to the difference between their New Zealand and native range flowering periods (simple linear regression, $P > 0.10$). There was also no evidence that insufficient observation of restricted species was obscuring an existing relationship between native range and New Zealand flowering period. When this relationship was analysed for the most widespread half of the species only, it still failed to reach significance (simple linear regression, $P > 0.10$).

Aspects of the spread process may explain why different attributes appeared important at different scales of spatial resolution. A genetic system conducive to fast population growth was important for current coarse-scale distribution, while habit appeared more important for current fine-scale distribution. This may reflect the relative importance of long-range (hundreds of kilometres) and mid-range (tens of kilometres) dispersal to these processes. For current coarse-scale distribution (long-range dispersal), the pasture seed contaminant pathway should have high importance, and a fast population growth rate may allow a species to maximize its contribution to the harvested seed crop. For current fine-scale distribution, pasture seed contamination is also paramount, but additional spread among adjacent grid cells (mid-range dispersal) may be accomplished by grazing animals. For this type of spread, a species with a morphology allowing it to persist in grazed areas should be most successful.

Native range area appeared highly important for rate of spread, while it was not as important for current distribution. I suspect that propagule pressure drives the native range effect; because propagule pressure played a large role in naturalisation probability, I expected

that it would also influence the number of individual naturalisation events. If this is the case, increased propagule pressure may have allowed species to colonize suitable areas sooner, whereas domestic seed transport and stock later brought species to most areas of suitable habitat. However, a role for ecological versatility, habitat generalism, or the use of widespread habitats cannot be ruled out. If these processes play a role, it is possible that more versatile or pre-adapted species were able to colonize new habitats more quickly, but that other species were ultimately able to catch up through adaptation, additional introductions of more appropriate genotypes, or both.

Overall, my spread results illustrate exactly the sort of phenomena that have long frustrated invasion biologists: the most important determinants of *Trifolium* species' fates in their new range were an opportunistic association (frequency as a pasture seed contaminant) and a novel biological trait (length of the New Zealand flowering period), rather than attributes that could be observed in the species' native ranges. Although seed contamination is of lesser importance to current invasions, modern seed contaminants may still have some advantage in spread. As such, knowledge of contamination mechanisms may prove useful. Within the data set, frequency as a pasture seed contaminant was significantly explained by British distribution and introduction effort. Widely distributed British species were likely more common contaminants of imported seed, an advantage that may have continued within New Zealand. Opportunistic seed harvesting and the planting of *Trifolium* in grass seed pastures may have allowed commercial agricultural *Trifolium* species to contaminate other seed lines. Additionally, contaminant species were probably well-adapted to the regional climates of seed production areas (A. Stewart, personal communication), although I could not test this.

Length of the New Zealand flowering period probably retains importance for contemporary invasions. However, no attribute in my data set significantly explained either the length of the New Zealand flowering period or the difference between the New Zealand and native range flowering periods. Physiological tolerance or phenotypic plasticity differences may underlie these effects (Vickery 1974, Sultan 2001). Alternatively, it is possible that the differences between flowering period in the native range and New Zealand are the result of complex shifts in the niches occupied by species in the two ranges (Wilson et al. 1988). Nevertheless, some indication of species' flowering behaviour in New Zealand might be gained by growing proposed introductions in quarantine field trials.

Notably, as indicated in the introduction, my measures of spread consider geographical extent only; they do not measure the impacts of these species or the types of habitats they invade. Factors affecting species presence in anthropogenic compared to naturally disturbed or relatively undisturbed habitats, as recorded in the published sources I consulted, might provide an interesting comparison with the geographic data in future analyses. However, because this information is confounded with specimen collection patterns, data from a random field sample would better address this issue. Furthermore, little published data on impacts of *Trifolium* in New Zealand exist, especially with regard to natural communities. Although species impact differences might be further elucidated by experimental study, invasion impacts might be more profitably investigated in another species group with greater apparent variation in this parameter.

As a final comment on spread, I note that seed dormancy differences, especially those occurring via hard seed content and softening patterns, may be an important component of *Trifolium* species' ecology in New Zealand that I did not investigate in this study. Although these traits are generally species-specific (Norman et al. 1998), they can also be affected by environmental conditions during seed maturation, harvesting, and storage (Quinlivan 1971). For this reason, it was difficult to locate a published data set that provided comparable information for the 25 naturalised species. Seed dormancy should be especially important for a species' persistence once it reaches an area (Esler 1988a, Boswell et al. 2003), and evidence suggests that seed banks are an important component of an invasive shrub species' persistence on New Zealand roadsides (P. Williams, unpublished data). I suspect that insufficient hard seed (Harrington 1916, Foy 1925) may be one explanation for the rarity of naturalised *T. incarnatum* populations despite wide commercial availability of this species until approximately 1950.

Stage comparison

Like other studies that have examined different stages of the invasion process for the same group of organisms (e.g. Duncan et al. 2001, Kolar and Lodge 2002, Forsyth et al. 2004, Marchetti et al. 2004), I found that different species attributes were important at different stages. This result is most useful when considered in relation to the processes or barriers expected to be important at each stage (Richardson et al. 2000b, Heger and Trepl 2003). Broadly, my analyses supported many of the ideas put forth by these authors, including the importance of human activities for introduction, of abiotic barriers, stochasticity, and mate location for naturalisation,

and of the need for effective dispersal mechanisms to suitable habitat for spread (Richardson et al. 2000b, Heger and Trepl 2003).

Looking across stages, it is clear that human actions were of primary importance throughout the invasion process. Species' biological traits, however, played their greatest role at the spread stage. Studies of animal taxa across stages have tended to find a strong role for human actions, particularly introduction effort, at the naturalisation stage, whereas there seems to be little role for these actions, but an important role for biological traits, at the spread stage (Veltman et al. 1996, Duncan 1997, Green 1997, Duncan et al. 1999, Duncan et al. 2001, Forsyth et al. 2004, Marchetti et al. 2004) (Table 1.1). My finding of a larger role for human actions in spread than that indicated by these studies may have several potential explanations.

First, plants are more dispersal-limited than the animal taxa that have been studied, such that long-distance dispersal by humans would more strongly enhance the spread of plant species. Second, the inconspicuousness of *Trifolium* propagules compared to those of the majority of studied animal species may have given *Trifolium* species an advantage in exploiting inadvertent human transport pathways. This advantage may apply more generally to plant species (e.g. Hodkinson and Thompson 1997) as compared to bird and mammal taxa. Third, *Trifolium* species were more intimately connected with human livelihoods in New Zealand than the studied animal species were in their respective locations. A majority of New Zealand stock farmers saw the establishment of *Trifolium* on their lands as a vital component of their economic well-being (Saxby 1940). In contrast, the introduced animal species that have been studied played more peripheral economic roles, such as game species (Duncan et al. 2003a). Because humans had more at stake in the widespread establishment of *Trifolium*, their involvement in promoting this spread was likely much higher, potentially accounting for the increased importance of this effect in my analysis. Finally, previous studies have tended to focus on only the initial introduction effort applied to establishing an animal species. Yet, within New Zealand, secondary releases by humans may have played a key role in the spread of some animal taxa, such as ungulates (Fraser et al. 2003) and possums (Montague 2000). This work clearly demonstrates the importance of quantifying the role of humans as dispersers within the new range.

Interesting similarities and differences were apparent in the comparison of results from individual stages. First, in the comparison of intentional introduction with naturalisation of intentionally introduced species, it was apparent that very similar factors were important. The overwhelming importance of introduction effort for intentional naturalisation meant that this

process was to a large extent determined by the cumulative probability of intentional introduction. However, the introduced species' match to the New Zealand climate may have had some additional influence on their naturalisation probability.

Comparing the introduction and naturalisation of intentional species with that of unintentional species revealed some interesting contrasts. Human actions appeared important for the naturalisation of both groups of species, whether intentionally or unintentionally. A large native range area seemed to increase propagule pressure at both stages. Climate match played a role in the naturalisation of both intentional and unintentional species, although it probably had greater importance for unintentional species. Intentional species were somewhat pre-selected for survival in New Zealand's climate, and human cultivation may have dampened climatic influences for these species (e.g. through irrigation) (Mack 2000). Similarity between native and introduced habitat likely played a role in the naturalisation of unintentional species, whereas habitat characteristics were not important for intentional species. Economic use may act as a surrogate for habitat similarity for the intentional species, since species would probably have been subject to similar uses in New Zealand, or human cultivation may have reduced the importance of compatible habitat (Mack 2000). Finally, biological traits, particularly the genetic system and seed size, had some importance for unintentional species, whereas they did not play a role for intentional species. Seed size was probably most important in facilitating transport for unintentional species, whereas human choices dictated this stage for intentional species. Genetic system traits may have played a greater role for unintentional species because they had smaller initial population sizes. In this situation, high population growth rate and uniparental reproduction would be an advantage.

In comparing naturalisation (intentional and unintentional) to spread, human actions again dominated both stages. For naturalisation, human propagule pressure was most important, while spread was most strongly facilitated by unintentional human dispersal. In both stages, however, introduction to a range of sites was probably an important component of the human influence. For naturalisation, introduction to a range of sites would increase the chance of encountering favourable conditions for persistence (Crawley 1989), while for spread its most important facet may be the establishment of new invasion foci (Auld and Coote 1980, Moody and Mack 1988). Climate match and habitat characteristics contributed significantly at the naturalisation stages, although not at the spread stage. This may reflect greater variation among species earlier in the process; most naturalised species were well-adapted to New Zealand's climate and to human

habitats. A key difference between these stages was that biological traits played a larger role for spread than they did for the naturalisation stages. The greater importance of flowering period length for spread may have been affected by the low correlation between native range and New Zealand flowering period. It is possible that species' flowering behaviour in New Zealand also influenced their naturalisation, but only native range data were available for these species.

Finally, it appeared that a genetic system conducive to rapid population growth had some importance for both unintentional introduction-naturalisation and spread. This finding provides a rare example of a biological trait that seemed to be important across stages. Interestingly, a different pattern emerged for bird species in a review of invasion stages: birds with a lower body mass (correlated with high population growth rate) had an advantage at the spread stage, whereas birds with a higher body mass (correlated with low population growth rate) were more likely to naturalise (Kolar and Lodge 2001, but see Sol 2001). Unfortunately for general predictive theories, the difference between my results and these highlights the possibility for situation-dependence in the similarity between naturalisation and spread traits.

Similarity between factors influential at the naturalisation and spread phases may depend on how much the process of spread resembles that of naturalisation, at the spatial scale spread is recorded. In other words, during the process of spread, how often are species in a situation where few propagules reach a new patch of habitat? At the local scale, this phenomenon may be most common for species adapted to frequent disturbance. At the landscape scale, it may be more common among species with effective long-distance dispersal, either human or biological. Also, each stage presents its own challenges, and it may be that the traits important at each stage overlap when they are coincidentally important in overcoming more than one of these challenges. Specifically, at the naturalisation stage, common challenges may include difficulty in finding mates and demographic and environmental stochasticity (Heger and Trepl 2003). A species may overcome these challenges with such attributes as uniparental reproduction, high population growth rate, and a long lifespan or dormant life-cycle stages. At the spread stage, a species will only succeed if it reaches a habitat where its particular trait combination enables it to successfully contend with the relevant abiotic and biotic challenges, and where it can find an effective means of dispersal (Richardson et al. 2000b, Heger and Trepl 2003). Some traits may coincidentally be advantageous for more than one of these processes. For example, vegetative reproduction may aid naturalisation by enabling a species to reproduce without mating partners, but it may also be an important component of habitat-specific ecological success, e.g. "survivor"-type invaders that

succeed due to their indefinite lifespans (Newsome and Noble 1986), or of dispersal under particular conditions, e.g. in aquatic systems (Rejmánek 2000).

In light of this reasoning, it appears that the across-stage importance of the genetic system in *Trifolium* may relate to similarities between the processes of naturalisation and spread for these species, as well as the roles played by different genetic system aspects at different stages. My findings for the spread stage reveal that, for *Trifolium* species, this process resembles one of repeated naturalisations. At the local scale, patchily-distributed gaps probably provide important spread opportunities, and stock frequently transport propagules to new areas. For landscape-level spread, the importance of seed contamination suggests that propagules were frequently deposited into new habitats, potentially with rather scattered distributions. One could imagine a situation, however, where continuous population expansion plays a more important role in species' spread (e.g. Andow et al. 1993), resulting in a spread process very unlike that of repeated naturalisations. My results also suggest that different aspects of the genetic system may have been important in overcoming the challenges of naturalisation and spread, generating a coincidental overlap between stages. While capability for self-pollination may have been vital to naturalisation, the possession of a general 'r' strategy may have been more important for successful spread in the disturbed environments for which *Trifolium* are best suited in New Zealand. Again, one could imagine a situation where attributes that aided a species in naturalisation were more independent of those on which it relied for its ecological success.

However, it is also possible that similarity of traits promoting naturalisation and spread is not unique to the New Zealand *Trifolium* situation. More study of this issue in other plant groups is clearly required to more fully evaluate successful strategies at each stage. Until a better understanding of this issue emerges, it may be most sensible to consider naturalisation and spread separately, evaluating the challenges for each in relation to species and habitats.

Implications

When considering implications, it is worth noting that this study shares a common limitation with other retrospective invasion studies, namely uncertainty in the extent to which processes important in the past are relevant to consideration of future invasions. In fact, since introduction effort of some *Trifolium* species in New Zealand is ongoing while that of others is not, different conclusions might be reached if this study were later repeated, even if no additional

species were introduced. However, the available data suggest some trends that are likely to be applicable to future *Trifolium* introductions.

First, for intentional species introductions, the key factors influencing the earlier, predominantly commercial introductions were different from those influencing the more recent, predominantly experimental introductions. Given New Zealand's diversified immigration base (King 2003) and the relatively static importance of major agricultural *Trifolium* species, the experimental species models would likely be more appropriate for predicting future intentional *Trifolium* introductions. For naturalisation of intentionally introduced species, it seems likely that high introduction effort, especially when the species is well-suited to the New Zealand climate, will continue to promote new naturalisations. Continuing to monitor the fate of experimental agricultural introductions may help to clarify the relative importance of introduction intensity (hectares per year) compared to the total length of the introduction period.

The specific models developed for unintentional introduction-naturalisation would likely have limited applicability to future *Trifolium* introductions, as the importance of both the seed contamination pathway and European trade as means of species introductions have both declined from their historic peaks. However, the general approach suggested by this model should remain relevant, in that the magnitude of unintentional propagule pressure, mediated by climatic and habitat suitability, is likely to remain important. Some recent risk assessment procedures attempt to anticipate the magnitude of unintentional propagule pressure, for example by developing estimates of the number of incoming sources and the number of propagules per source (Ruesink et al. 1995). Similarly, the spread models, while not applicable to future introductions in detail, should be applicable in concept. In particular, both human dispersal pathways and biological traits will likely remain important for the spread of future introductions. Estimates of the importance of various human dispersal pathways (e.g. those listed by (Kowarik 2003)) over time might offer understanding of the pathways likely to influence future spread. Knowledge of these pathways can then be combined with the biological traits identified by the spread models in order to estimate future spread of naturalised *Trifolium*. Clearly, retrospective invasion models need to be considered within their historical context to judge their applicability to future invasions.

For future research on biological invasions, this study demonstrates that a stage-based approach can improve understanding of the factors important throughout the invasion process. As I have discussed, different factors were important at different invasion stages, and the most significant factors were very sensible given current knowledge of the processes important at each

stage. A more detailed and refined understanding of the invasion process will undoubtedly lead to conceptual and practical improvements in our ability to predict invasion outcomes.

From this study alone, it is too soon to say whether and how New Zealand's Weed Risk Assessment (WRA) model should be refined to reflect the different processes at each invasion stage. Currently, this model assigns a single score to each species proposed for import which is intended to reflect its combined probability for naturalisation, spread, and impact. The model considers species attributes in eight main categories: domestication/cultivation history, climate and distribution, weed elsewhere, undesirable traits, plant type, reproduction, dispersal mechanisms, and persistence attributes (Pheloung et al. 1999). Each of 49 considered attributes is weighted more or less equally "in the absence of any evidence to the contrary" (Pheloung et al. 1999). However, as more stage-specific evidence accumulates, it may be possible to assess the predictive power of alternative formulations of the model, for example one in which stages (naturalisation, spread, and impact) are assessed separately and contribute multiplicatively to the final assessment score. Different categories of attributes could then be emphasized for the relevant stages. For example, this study suggests that the climate and distribution and domestication/cultivation categories might be emphasized at the naturalisation stage, while the dispersal category could be most important at the spread stage. However, final emphasis patterns should be decided using stage-specific study of plant groups with a variety of human uses (Ewel et al. 1999). A revised stage-specific WRA model could then be tested against the current system using a group of known introduced species, to estimate whether further developments in this direction are likely to provide practical increases in predictive power. Notably, a recently-convened group of experts in the United States recommended a stage-based framework for the development of risk assessment models in that country (Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States 2002).

My results can also be compared to a review of a sample of US and international risk assessment protocols (Ruesink et al. 1995). In this review, risk-assessment protocols for planned introductions were compared to those for unplanned introductions, a comparison similar to my evaluation of intentional versus unintentional introduction and naturalisation. For unintentional species, protocols tended to focus on climatic tolerance, anticipated propagule pressure, and the presence of dormant life-cycle stages (Ruesink et al. 1995). As these factors correspond very closely to my results for unintentional introduction-naturalisation, my study supports the

suitability of these currently available protocols for unintentional introductions. In contrast, protocols for intentionally introduced species tended to downplay the importance of propagule pressure and climate match, on the supposition that these species are intended to establish populations and are pre-selected for climatic suitability (Ruesink et al. 1995). Yet, my analysis suggested that propagule pressure and climate match are precisely the attributes that contribute most to the establishment of naturalised populations from intentional introductions. Fortunately, the New Zealand WRA model does include climate match and at least recognizes the importance of propagule pressure, although no explicit attempt is made to estimate and incorporate this parameter (Pheloung et al. 1999).

In terms of human influence on the invasion process, my results clearly illustrate the advantage of explicitly incorporating human actions into invasion analyses (Mack 2001, McNeely 2001). Considering human use as well as species attributes leads to models that allow a fuller understanding of the invasion process. Knowledge of relevant human actions also allows species traits to be evaluated in relation to them. For example, identifying the importance of pasture seed contamination for the spread of New Zealand *Trifolium* allowed me to evaluate flowering period length in light of its potential contribution to this pathway in addition to its other ecological effects. Furthermore, statistically controlling for the effects of human actions allows more accurate identification of species attributes which independently influence the invasion process (e.g. Veltman et al. 1996, Duncan 1997, Green 1997, Duncan et al. 1999, Duncan et al. 2001, Forsyth et al. 2004, Marchetti et al. 2004). Future invasion studies may especially benefit from including human actions at the spread stage, where this issue appears to have received the least attention thus far (Kowarik 2003).

The most useful application of my human-related findings may be in predicting which of New Zealand's cultivated species are most likely to naturalise (Mulvaney 2001). The ALLWEEDS database lists over 24,000 species believed to be cultivated in New Zealand, a pool from which recent naturalisations appear to be arising (Sullivan et al. 2004). Estimating propagule pressure for each of these species may provide important clues for identifying future naturalisations. Although this is undoubtedly a daunting task, my results suggest that even rough estimates will likely prove useful (compare the explanatory power of the rough "introduced for commercial agriculture?" with the more exact "estimated hectares planted" in Table 3.3). Over a broader species range, it may be possible to derive estimates by classifying species into economic "functional groups" (e.g. Halloy 1999 Figures 1 and 5). However, the habitat into which

propagules are deposited, as well as their raw number, can also be important for naturalisation (Pyšek et al. 1995, Kowarik 2003), limiting the benefits that can be realised from propagule pressure estimates alone.

Potentially, effort estimates for proposed introductions, based on their intended use(s) within New Zealand, could also be incorporated into the WRA model. The incorporation of intended use has been suggested for the Australian WRA model (Virtue 2003), on which New Zealand's model is based. This system may lead to the approval of species for particular uses, with the need to re-assess risk if a species is later proposed for a different use. However, the need for re-assessments may make regulation of introduced species more complex and enforcement of regulations more difficult. Also, it should be noted that the clear effect of use that I found for naturalisation of intentionally introduced New Zealand *Trifolium* may not apply as strongly for other plant groups or locations. For example, although I found only a 2% naturalisation rate for *Trifolium* species introduced in experimental trials, a $\geq 13\%$ rate was reported for a more diverse group of experimental species in northern Australia (Lonsdale 1994).

The New Zealand WRA currently includes a number of questions addressing the potential for human dispersal. In particular, a "yes" answer to each of the following questions earns a species one point: "propagules likely to be dispersed unintentionally", "propagules dispersed intentionally by people", and "propagules likely to disperse as a produce contaminant". My results suggest that these questions are warranted. It may be worth evaluating whether the inclusion of additional human dispersal pathways improves the model's ability to predict spread, given the central role that human dispersal played for *Trifolium*. If this is to be done, Kowarik (2003) provides a good list of human dispersal pathways to consider. Alternatively, the effect of simply assigning the "unintentional human dispersal" question more weight could be explored. In addition, if future studies identify other important human dispersal pathways (e.g. garden throw-outs, Hodkinson and Thompson 1997), these might provide targets for regulation (Kowarik 2003). For seed contamination, however, current incentives for pure seed production are probably sufficient so as to render formal regulation unnecessary.

Conclusion

This study has demonstrated the utility of the stage-based approach for explaining and understanding the invasion process. Important species attributes clearly varied across stages, a phenomenon that has been suggested to exist in plant invasions, but that has not been previously demonstrated in a single group of organisms. Considering each invasion stage as a separate analysis allowed solid statistical models to be constructed. In addition, results could be more clearly related to the challenges faced by a species at each stage. This work has also demonstrated the importance of including human actions at all stages of the invasion process. By collecting and explicitly incorporating such data, I found that humans played a key role at all stages of this invasion. Furthermore, biological traits appeared to have increasing importance relative to human factors as a species moved through the invasion sequence. Overall, these findings provide valuable insight into the process of invasion and suggest new directions for the further refinement of predictive models. Similar studies of other plant groups will now be necessary to confirm the general applicability of the results and thereby verify suggested model improvements. By further refining our models to reflect our increased understanding of this important process, we can improve our ability to predict and, ultimately, prevent invasions.

Acknowledgements

First and foremost, I would like to acknowledge the efforts of my supervisors, Richard Duncan, Jon Sullivan, and Peter Williams. The assistance, inspiration, and insight they provided at every turn played a significant role in making this project a positive experience. Peter Bellingham provided very helpful comments on an earlier draft. Funding from Fulbright New Zealand made my study and stay in New Zealand possible, and Fulbright personnel provided important logistical support throughout the implementation of this project. Funding from the Lincoln University Soil, Plant, and Ecological Sciences Division was instrumental in allowing the data collection to be completed. The Lincoln University Ecology and Entomology group also provided important logistical and moral support.

Brad Case played a vital role in the GIS analyses and helped me to realise the power of this tool for looking at biogeography questions. Alan Stewart, Dick Lucas, and Warren Williams taught me a great deal about the genus *Trifolium* and contributed a number of the ideas which were later incorporated as parts of the analysis. I also thank Nick Ellison and Warren Williams for providing a version of the *Trifolium* molecular phylogeny prior to its publication. Valuable discussion was provided by a number of Lincoln University post-graduate students, especially Hazel Gatehouse, Sean Bithell, and Alice Miller. The curators and personnel of the herbaria from which I recorded specimens (listed fully in Appendix 2) provided important assistance in accessing and interpreting the specimens. I would like to especially acknowledge the contributions of Aaron Wilton and Michelle Breach at the CHR herbarium, whose support was instrumental to the successful assembly of the herbarium specimen database.

Chris Berry classified many of the herbarium specimens to NZMS260 map sheets. I appreciated the helpful advice of Heather Pryor on *Rhizobium* biology and ecology, Peter Bellingham on invasive plant biology, and Linda Newstrom on pollination biology. Bruce McKenzie, Hamish Brown, and Christine Stark provided vital input on the climate modelling techniques. Sireerat (Agnes) Chetsumon assisted with constructing and interpreting the structural equation models. Rhonda Pearce, Sandy Hammond, and Hazel Gatehouse provided assistance with additional components of this study. I would also like to thank Brent Richards, Merv Spurway, and the Lincoln University glasshouse staff, as well as Ivan Baird and the staff of the AgResearch Lincoln farm, for assistance with additional study components.

References

- Aitken, M. 1944a. Farming in New Zealand: Climate and topography. *New Zealand Journal of Agriculture* **69**:121-127.
- Aitken, M. 1944b. Farming in New Zealand: Development of farming. *New Zealand Journal of Agriculture* **69**:323-330.
- Aitken, M. 1944c. Farming in New Zealand: Land under occupation. *New Zealand Journal of Agriculture* **69**:37-41.
- Allen, R. B., B. J. Anderson, and J. B. Wilson. *in review*. Predicting invasiveness of introduced fleshy-fruited woody plants and environmental vulnerability to invasion in New Zealand.
- Allen, R. G., L. S. Pereira, D. Raes, and M. Smith. 1998. Crop evapotranspiration: Guidelines for computing crop water requirements. FAO Irrigation and drainage paper 56, Food and Agriculture Organization of the United Nations (FAO), Rome, Italy.
- Andersen, U. V. 1995. Comparison of dispersal strategies of alien and native species in the Danish flora. Pages 61-70 *in* P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, editors. *Plant invasions - General aspects and special problems*. SPB Academic Publishing, Amsterdam, The Netherlands.
- Andersson, S. 1996. Seed size as a determinant of germination rate in *Crepis tectorum* (Asteraceae): evidence from a seed burial experiment. *Canadian Journal of Botany* **74**:568-572.
- Andow, D. A., P. M. Kareiva, S. A. Levin, and A. Okubo. 1993. Spread of invading organisms: patterns of spread. Pages 219-241 *in* K. C. Kim and B. A. McPherson, editors. *Evolution of insect pests*. John Wiley and Sons, New York, NY, USA.
- Anonymous. 1877. *The New Zealand Country Journal*, volume 1: A record of information connected with agricultural, pastoral, and horticultural pursuits, and rural sports in New Zealand. G. A. Makeig, Christchurch, New Zealand.
- Anonymous. 2003. Nodulaid 2003 Group Chart. Bio-Care Technology Pty. Limited.
- Anonymous. 2004. New Zealand Map Series 260. Land Information New Zealand, Wellington, New Zealand.
- Atkinson, I. A. E., and E. K. Cameron. 1993. Human influence on the terrestrial biota and biotic communities of New Zealand. *Trends in Ecology and Evolution* **8**:447-451.
- Auld, B. A., and B. G. Coote. 1980. A model of a spreading plant population. *Oikos* **34**:287-292.
- Baker, H. G. 1955. Self-compatibility and establishment after "long-distance" dispersal. *Evolution* **9**:347-349.
- Baker, H. G. 1974. The evolution of weeds. *Annual Review of Ecology and Systematics* **5**:1-24.
- Barrett, S. C. H., and B. J. Richardson. 1986. Genetic attributes of invading species. Pages 21-33 *in* R. H. Groves and J. J. Burdon, editors. *Ecology of biological invasions: An Australian perspective*. Cambridge University Press, Cambridge.
- Batjes, N. H. 2000. Global Data Set of Derived Soil Properties, 0.5-Degree Grid (International Soil Reference and Information Centre - World Inventory of Soil Emission Potentials). Data set available on-line [<http://www.daac.ornl.gov>] from Oak Ridge National Laboratory Distributed Active Archive Center, Oak Ridge, Tennessee, USA.
- Beale, P. E., M. Bounejmata, A. Lahlou, D. B. Marx, and S. Christiansen. 1993. Distributions of annual *Trifolium* species in Morocco. *Australian Journal of Experimental Agriculture* **44**:1303-1310.

- Bellingham, P. J., R. P. Duncan, W. G. Lee, and R. P. Buxton. 2004. Seedling growth rate and survival do not predict invasiveness in naturalized woody plants in New Zealand. *Oikos* **106**:308-316.
- Bennett, M. D. 1971. The duration of meiosis. *Proceedings of the Royal Society of London B* **181**:109-135.
- Bennett, M. D. 1987. Variation in genomic form in plants and its ecological implications. *New Phytologist* **106**:177-200.
- Bennett, M. D., I. J. Leitch, and L. Hanson. 1998. DNA amounts in two samples of angiosperm weeds. *Annals of Botany* **82**:121-134.
- Bentham, G. 1865. *Handbook of the British flora; a description of the flowering plants and ferns indigenous to, or naturalized in, the British Isles*. Lovell Reeve & Co., London, UK.
- Bentham, G., and J. D. Hooker. 1887. *Handbook of the British flora: a description of the flowering plants and ferns indigenous to, or naturalised in, the British Isles*, 5th edition. Reeve, London, UK.
- Bergelson, J. 1994. Changes in fecundity do not predict invasiveness: a model study of transgenic plants. *Ecology* **75**:249-252.
- Blackburn, T. M., and R. P. Duncan. 2001a. Determinants of establishment success in introduced birds. *Nature* **414**:195-197.
- Blackburn, T. M., and R. P. Duncan. 2001b. Establishment patterns of exotic birds are constrained by non-random patterns in introduction. *Journal of Biogeography* **28**:927-939.
- Boswell, C. C., R. J. Lucas, M. Lonati, A. Fletcher, and D. J. Moot. 2003. The ecology of four annual clovers adventive in New Zealand grasslands. Pages 175-184 *in* D. J. Moot, editor. *Legumes for Dryland Pastures*. New Zealand Grassland Association, Lincoln University, Lincoln, New Zealand.
- Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. *Ecology* **77**:776-790.
- Burt, R. L., and M. B. Forde. 1987. The provision of pasture legumes for difficult environments. *Proceedings of the New Zealand Grassland Association* **48**:83-88.
- Burton, J. C. 1985. *Rhizobium* relationships. Pages 161-184 *in* N. L. Taylor, editor. *Clover science and technology*. American Society of Agronomy, Inc., Madison, WI, USA.
- Caldwell, M. M., J. H. Richards, D. A. Johnson, R. S. Nowak, and R. S. Dzuree. 1981. Coping with herbivory: photosynthetic capacity and resource allocation in two semiarid *Agropyron* bunch grasses. *Oecologia* **50**:14-24.
- Callaway, R. M., and W. M. Ridenour. 2004. Novel weapons: invasive success and the evolution of increased competitive ability. *Frontiers in Ecology and the Environment* **2**:436-443.
- Caradus, J. R. 1995. Frost tolerance of *Trifolium* species. *New Zealand Journal of Agricultural Research* **38**:157-162.
- Cassey, P., T. M. Blackburn, K. E. Jones, and J. L. Lockwood. 2004a. Mistakes in the analysis of exotic species establishment: source pool designation and correlates of introduction success among parrots (Aves: Psittaciformes) of the world. *Journal of Biogeography* **31**:277-284.
- Cassey, P., T. M. Blackburn, G. J. Russell, K. E. Jones, and J. L. Lockwood. 2004b. Influences on the transport and establishment of exotic bird species: an analysis of the parrots (Psittaciformes) of the world. *Global Change Biology* **10**:417-426.
- Charlton, J. F. L. 1983. Lotus and other legumes. Pages 253-262 *in* G. S. Wratt and H. C. Smith, editors. *Plant breeding in New Zealand*. Butterworths, Department of Scientific and Industrial Research (DSIR), Wellington, New Zealand.

- Clapham, A. R., T. G. Tutin, and E. F. Warburg. 1962. Flora of the British Isles, 2nd edition. Cambridge University Press, Cambridge, UK.
- Cleveland, R. W. 1985. Reproductive cycle and cytogenetics. Pages 71-110 in N. L. Taylor, editor. Clover Science and Technology. American Society of Agronomy, Inc., Madison, WI, USA.
- Cockayne, A. H. 1914. White-clover seed: Its adulteration. New Zealand Journal of Agriculture **9**:315-328.
- Cockayne, A. H. 1916. Seed-impurities. New Zealand Journal of Agriculture **13**:208-212.
- Cockayne, A. H. 1926. The control of weeds. 3. Methods of distribution. New Zealand Journal of Agriculture **33**:23-28.
- Cocks, P. S., and T. A. M. Ehrman. 1987. The geographic origin of frost tolerance in Syrian pasture legumes. Journal of Applied Ecology **24**:673-683.
- Cocks, P. S., and J. R. Phillips. 1979. Evolution of subterranean clover in South Australia. I. The strains and their distribution. Australian Journal of Agricultural Research **30**:1035-1052.
- Committee on the Scientific Basis for Predicting the Invasive Potential of Nonindigenous Plants and Plant Pests in the United States. 2002. Predicting invasions of nonindigenous plants and plant pests. National Academy Press, Washington, D.C., USA.
- Craig, J., S. Anderson, M. Clout, B. Creese, N. Mitchell, J. Ogden, M. Roberts, and G. Ussher. 2000. Conservation issues in New Zealand. Annual Review of Ecology and Systematics **31**:61-78.
- Crawford, E. J., A. W. H. Lake, and K. G. Boyce. 1989. Breeding annual *Medicago* species for semiarid conditions in southern Australia. Advances in Agronomy **42**:399-437.
- Crawley, M. J. 1986. The population biology of invaders. Philosophical Transactions of the Royal Society of London B **314**:711-731.
- Crawley, M. J. 1989. Chance and timing in biological invasions. Pages 407-435 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. Biological invasions: a global perspective. John Wiley and Sons, New York, NY, USA.
- Crawley, M. J. 2002. Statistical computing: an introduction to data analysis using S-Plus. John Wiley and Sons, Chichester, West Sussex, England.
- Crawley, M. J., P. H. Harvey, and A. Purvis. 1996. Comparative ecology of the native and alien floras of the British Isles. Philosophical Transactions: Biological Sciences **351**:1251-1259.
- Crosby, A. W. 1986. Ecological imperialism: The biological expansion of Europe, 900-1900, 2nd edition. Cambridge University Press, Cambridge, UK.
- Cumming, B. G. 1959. Extreme sensitivity of germination and photoperiodic reaction in the genus *Chenopodium* (Tourn.) L. Nature **184**:1044-1045.
- Curnutt, J. L. 2000. Host-area specific climate-matching: similarity breeds exotics. Biological Conservation **94**:341-351.
- Daehler, C. C. 1998. The taxonomic distribution of invasive angiosperm plants: Ecological insights and comparison to agricultural weeds. Biological Conservation **84**:167-180.
- Daehler, C. C., J. S. Denslow, S. Ansari, and H.-C. Kuo. 2004. A risk-assessment system for screening out invasive pest plants from Hawaii and other pacific islands. Conservation Biology **18**:360-368.
- Daehler, C. C., and D. R. Strong, Jr. 1993. Prediction and biological invasions. Trends in Ecology and Evolution **8**:380-381.
- Davies, W., and E. B. Levy. 1931. Strain investigation of grasses and clovers. 4. White clover (*Trifolium repens*), part 2. New Zealand Journal of Agriculture **42**:75-89.

- Davis, A. J., L. S. Jenkinson, J. H. Lawton, B. Shorrocks, and S. Wood. 1998a. Making mistakes when predicting shifts in species range in response to global warming. *Nature* **391**:783-786.
- Davis, A. J., J. H. Lawton, B. Shorrocks, and L. S. Jenkinson. 1998b. Individualistic species responses invalidate simple physiological models of community dynamics under global environmental change. *Journal of Animal Ecology* **67**:600-612.
- Delisle, F., C. Lavoie, M. Jean, and D. Lachance. 2003. Reconstructing the spread of invasive plants: Taking into account biases associated with herbarium specimens. *Journal of Biogeography* **30**:1033-1042.
- di Castri, F. 1990. On invading species and invaded ecosystems: the interplay of historical chance and biological necessity. Pages 3-16 in F. di Castri, A. J. Hansen, and M. Debussche, editors. *Biological invasions in Europe and the Mediterranean basin*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Dillon, S. P., and F. Forcella. 1984. Germination, emergence, vegetative growth, and flowering of two silvergrasses, *Vulpia bromoides* (L.) S.F. Gray and *V. myuros* (L.) C.C. Gmel. *Australian Journal of Botany* **32**:165-175.
- Dingwall, A. R. 1969. The harmful effects of weeds. *Proceedings of the New Zealand Weed and Pest Control Conference* **22**:127-132.
- Dodd, M. B., and G. W. Sheath. 2003. Persistence: the key to legume performance in summer-dry hill country. Pages 73-79 in D. J. Moot, editor. *Legumes for Dryland Pastures*. New Zealand Grassland Association, Lincoln University, Lincoln, New Zealand.
- Duncan, R. P. 1997. The role of competition and introduction effort in the success of passeriform birds introduced to New Zealand. *American Naturalist* **149**:903-915.
- Duncan, R. P., T. M. Blackburn, and P. Cassey. 2003a. Factors affecting the release, establishment, and spread of introduced birds in New Zealand. in R. B. Allen and W. G. Lee, editors. *Biological invasions in New Zealand*. Springer-Verlag, Berlin. *In press*.
- Duncan, R. P., T. M. Blackburn, and D. Sol. 2003b. The ecology of bird introductions. *Annual Review of Ecology, Evolution, and Systematics* **34**:71-98.
- Duncan, R. P., T. M. Blackburn, and C. J. Veltman. 1999. Determinants of geographical range sizes: a test using introduced New Zealand birds. *Journal of Animal Ecology* **68**:963-975.
- Duncan, R. P., M. Bomford, D. M. Forsyth, and L. Conibear. 2001. High predictability in introduction outcomes and the geographical range size of introduced Australian birds: a role for climate. *Journal of Animal Ecology* **70**:621-632.
- Edwards, W., and M. Westoby. 1996. Reserve mass and dispersal investment in relation to geographic range of plant species: phylogenetically independent contrasts. *Journal of Biogeography* **23**:329-338.
- Ehrman, T., and P. S. Cocks. 1990. Ecogeography of annual legumes in Syria: Distribution patterns. *Journal of Applied Ecology* **27**:578-591.
- Elliot, R. M., H. L. McIntyre, B. C. Challis, H. N. Pryor, W. L. Lowther, and C. W. Ronson. 1998. *Rhizobium* issues affecting the contribution of caucasian clover to New Zealand pastoral agriculture. *Proceedings of the New Zealand Grassland Association* **60**:207-211.
- Esler, A. E. 1987. The naturalisation of plants in urban Auckland, New Zealand. 1. The introduction and spread of alien plants. *New Zealand Journal of Botany* **25**:511-522.
- Esler, A. E. 1988a. The naturalisation of plants in urban Auckland, New Zealand. 4. The nature of the naturalised species. *New Zealand Journal of Botany* **26**:345-385.
- Esler, A. E. 1988b. The naturalisation of plants in urban Auckland, New Zealand. 5. Success of the alien species. *New Zealand Journal of Botany* **26**:565-584.

- Esler, A. E. 1988c. The naturalisation of plants in urban Auckland, New Zealand. 6. Alien plants as weeds. *New Zealand Journal of Botany* **26**:585-618.
- ESRI. 2000. ArcView 3.2a. Redlands, CA, USA.
- Ewel, J. J., D. J. O'Dowd, J. Bergelson, C. C. Daehler, C. M. D'Antonio, L. D. Gómez, D. R. Gordon, R. J. Hobbs, A. Holt, K. R. Hopper, C. E. Hughes, M. LaHart, R. R. B. Leakey, W. G. Lee, L. L. Loope, D. H. Lorence, S. M. Louda, A. E. Lugo, P. B. McEvoy, D. M. Richardson, and P. M. Vitousek. 1999. Deliberate introductions of species: Research needs. *Bioscience* **49**:619-630.
- Falinski, J. B. 1972. Anthropochory in xerothermic grasslands in the light of experimental data. *Acta Societatis Botanicorum Poloniae* **41**:357-368.
- Flood, R. J. 1986. Investigation on old seed samples. *Journal of the National Institute of Agricultural Botany* **17**:257-266.
- Forcella, F. 1985. Final distribution is related to rate of spread in alien weeds. *Weed Research* **25**:181-191.
- Forcella, F., and J. T. Wood. 1984. Colonization potentials of alien weeds are related to their "native" distributions: Implications for plant quarantine. *Journal of the Australian Institute of Agricultural Science* **50**:35-40.
- Forcella, F., J. T. Wood, and S. P. Dillon. 1986. Characteristics distinguishing invasive weeds within *Echium* (Bugloss). *Weed Research* **26**:351-364.
- Forsyth, D. M., and R. P. Duncan. 2001. Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. *American Naturalist* **157**:583-595.
- Forsyth, D. M., R. P. Duncan, M. Bomford, and G. Moore. 2004. Climatic suitability, life-history traits, introduction effort, and the establishment and spread of introduced mammals in Australia. *Conservation Biology* **18**:557-569.
- Fortune, J. A., P. S. Cocks, C. K. Macfarlane, and F. P. Smith. 1995. Distribution and abundance of annual legume seeds in the wheatbelt of Western Australia. *Australian Journal of Experimental Agriculture* **35**:189-197.
- Foy, N. R. 1925. The Official Seed-Testing Station: Record of operations for 1924. *New Zealand Journal of Agriculture* **30**:321-326.
- Foy, N. R. 1939. Analysis of cheap seed: Farm lands detrimentally affected by deceptive trading. *New Zealand Journal of Agriculture* **59**:89-95.
- Fraser, K. W., J. P. Parkes, and C. Thomson. 2003. Management of new deer populations in Northland and Taranaki. Science for Conservation 212, Department of Conservation, Wellington, New Zealand.
- Free, J. B. 1993. Insect pollination of crops. Academic Press, London, UK.
- Gardner, R. O., and J. W. Early. 1996. The naturalisation of banyan figs (*Ficus* spp., Moraceae) and their pollinating wasps (Hymenoptera: Agaonidae) in New Zealand. *New Zealand Journal of Botany* **34**:103-109.
- Gaston, K. J., T. M. Blackburn, J. J. D. Greenwood, R. D. Gregory, R. M. Quinn, and J. H. Lawton. 2000. Abundance-occupancy relationships. *Journal of Applied Ecology* **47**:39-59.
- Gerlach, J. D. 2001. Predicting invaders. *Trends in Ecology and Evolution* **16**:545.
- Gerlach, J. D., and K. J. Rice. 2003. Testing life history correlates of invasiveness using congeneric plant species. *Ecological Applications* **13**:167-179.
- Ghassali, F., A. E. Osman, and P. S. Cocks. 1998. Rehabilitation of degraded grasslands in North Syria: The use of Awassi sheep to disperse the seeds of annual pasture legumes. *Experimental Agriculture* **34**:391-405.

- Gillett, J. M., and N. L. Taylor. 2001. *The World of Clovers*. Iowa State University Press, Ames, Iowa, USA.
- Gladstones, J. S. 1966. Naturalized subterranean clover (*Trifolium subterraneum* L.) in Western Australia: the strains, their distributions, characteristics, and possible origins. *Australian Journal of Botany* **14**:329-354.
- Gladstones, J. S., and W. J. Collins. 1983. Subterranean clover as a naturalized plant in Australia. *Journal of the Australian Institute of Agricultural Science* **49**:191-202.
- Gladstones, J. S., and W. J. Collins. 1984. Naturalized subterranean clover strains of Western Australia. Technical Bulletin No. 64, Department of Agriculture, South Perth, Western Australia.
- Goodwin, B. J., A. J. McAllister, and L. Fahrig. 1999. Predicting invasiveness of plant species based on biological information. *Conservation Biology* **13**:422-426.
- Grace, J. 1987. Climatic tolerance and the distribution of plants. *New Phytologist* **106**:113-130.
- Graham, M. H. 2003. Confronting multicollinearity in ecological multiple regression. *Ecology* **84**:2809-2815.
- Gray, A. J. 1986. Do invading species have definable genetic characteristics? *Philosophical Transactions of the Royal Society of London B* **314**:655-674.
- Green, R. E. 1997. The influence of numbers released on the outcome of attempts to introduce exotic bird species to New Zealand. *Journal of Animal Ecology* **66**:25-35.
- Greenwood, R. M. 1976. Populations of *Rhizobia* in New Zealand soils. *Proceedings of the New Zealand Grassland Association* **37**:95-101.
- Greenwood, R. M., and C. E. Pankhurst. 1976. The *Rhizobium* component of the nitrogen-fixing symbiosis. *Proceedings of the New Zealand Grassland Association* **38**:167-174.
- Griffith, B., J. M. Scott, J. W. Carpenter, and C. Reed. 1989. Translocation as a species conservation tool: status and strategy. *Science* **245**:477-480.
- Grime, J. P., G. Mason, A. V. Curtis, J. Rodman, S. R. Band, M. A. G. Mowforth, A. M. Neal, and S. Shaw. 1981. A comparative study of germination characteristics in a local flora. *Journal of Ecology* **69**:1017-1059.
- Grotkopp, E., M. Rejmánek, and T. L. Rost. 2002. Toward a causal explanation of plant invasiveness: Seedling growth and life-history strategies of 29 pine (*Pinus*) species. *American Naturalist* **159**:396-419.
- Grotkopp, E., M. Rejmánek, M. J. Sanderson, and T. L. Rost. 2004. Evolution of genome size in pines (*Pinus*) and its life-history correlates: Supertree analyses. *Evolution* **58**:1705-1729.
- Grotkopp, E., R. Stoltenberg, M. Rejmánek, and T. L. Rost. 1998. The effect of genome size on invasiveness. *American Journal of Botany* **85**:34.
- Guthrie-Smith, H. 1921. *Tutira: The story of a New Zealand sheep station*, 4th edition. University of Washington Press, Seattle, WA, USA.
- Guthrie-Smith, H. 1930. Grassland evolution at Tutira: Turfs of fifty years. *New Zealand Journal of Agriculture* **40**:84-92.
- Hadfield, J. W., and J. H. Claridge. 1931. Seed certification: Summary of operations during season 1930-31. *New Zealand Journal of Agriculture* **45**:343-347.
- Hair, J. F., R. E. Anderson, R. L. Tatham, and W. C. Black. 1998. *Multivariate Data Analysis*, 5th edition. Prentice Hall, Upper Saddle River, NJ, USA.
- Halloy, S. R. 1999. The dynamic contribution of new crops to the agricultural economy: Is it predictable? Pages 53-59 in J. Janick, editor. *Perspectives on new crops and new uses*. ASHS Press, Alexandria, VA, USA.

- Hampton, J. G., M. J. Hill, and M. P. Rolston. 1990. Potential for seed production of non-traditional herbage species in New Zealand. *Proceedings of the New Zealand Grassland Association* **52**:65-70.
- Harrington, G. T. 1916. Agricultural value of impermeable seeds. *Journal of Agricultural Research* **6**:761-796.
- Hartley, J. R. 1969. Cleaner seed by machine dressing. *Proceedings of the New Zealand Weed and Pest Control Conference* **22**:143-148.
- Healy, A. J. 1952. The introduction and spread of weeds. *Proceedings of the New Zealand Weed Control Conference* **5**:5-16.
- Healy, A. J. 1961. The interaction of native and adventive plant species in New Zealand. *Proceedings of the New Zealand Ecological Society* **8**:39-43.
- Healy, A. J. 1973. Weeds in New Zealand. Pages 105-114 *in* Fourth Asian-Pacific Weed Science Society Conference, Rotorua, New Zealand.
- Heenan, P. B., P. J. de Lange, E. K. Cameron, and P. D. Champion. 2002. Checklist of dicotyledons, gymnosperms, and pteridophytes naturalised or casual in New Zealand: additional records 1999-2000. *New Zealand Journal of Botany* **40**:155-174.
- Heger, T., and L. Trepl. 2003. Predicting biological invasions. *Biological Invasions* **5**:313-321.
- Higgins, S. I., and D. M. Richardson. 1999. Predicting plant migration rates in a changing world: The role of long-distance dispersal. *American Naturalist* **153**:464-475.
- Hobbs, R. J. 2000. Land-use changes and invasions. Pages 55-64 *in* H. A. Mooney and R. J. Hobbs, editors. *Invasive species in a changing world*. Island Press, Washington, D.C., USA.
- Hobbs, R. J., and L. F. Huenneke. 1992. Disturbance, diversity, and invasion: Implications for conservation. *Conservation Biology* **6**:324-337.
- Hodkinson, D. J., and K. Thompson. 1997. Plant dispersal: The role of man. *Journal of Applied Ecology* **34**:1484-1496.
- Holm, L. G., D. L. Plucknett, J. V. Pancho, and J. P. Herberger. 1977. *The world's worst weeds: Distribution and biology*. The University Press of Hawaii, Honolulu, HI, USA.
- Holm, S. 1979. A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* **6**:65-70.
- Hopper, K. R., and R. T. Roush. 1993. Mate finding, dispersal, number released, and the success of biological control introductions. *Ecological Entomology* **18**:321-331.
- Hulbert, L. C. 1955. Ecological studies of *Bromus tectorum* and other annual brome grasses. *Ecological Monographs* **25**:181-213.
- Hulme, P. E. 2003. Biological invasions: winning the science battles but losing the conservation war? *Oryx* **37**:178-193.
- Hyde, E. O. C., and F. E. T. Suckling. 1953. Dormant seeds of clovers and other legumes in agricultural soils. *New Zealand Journal of Science and Technology* **34 section A**:375-385.
- Jain, S., and P. S. Martins. 1979. Ecological genetics of the colonizing ability of rose clover (*Trifolium hirtum* All.). *American Journal of Botany* **66**:361-366.
- Jamieson, P. D., D. R. Wilson, R. Stoker, and P. Farrant. 1984. *Irrigation management: Water budgeting for surface irrigation*. AgLink Farm Production and Practice 89, Ministry of Agriculture and Fisheries (MAF), Wellington, New Zealand.
- Jarvis, B. D. W., T. S. MacLean, I. G. C. Robertson, and G. R. Fanning. 1977. Phenetic similarity and DNA base sequence homology of root nodule bacteria from New Zealand native legumes and *Rhizobium* strains from agricultural plants. *New Zealand Journal of Agricultural Research* **20**:233-248.

- Johnson, D. W. 1985. Seed testing in New Zealand, 1895-1985. Ministry of Agriculture and Fisheries, Advisory Services Division, Palmerston North, New Zealand.
- Johnston, T. H. 1924. The relation of climate to the spread of prickly pear. Transactions and Proceedings of the Royal Society of South Australia **48**:269-296.
- Jones, R. M., and M. Simao Neto. 1987. Recovery of pasture seed ingested by ruminants. 3. The effects of the amount of seed in the diet and of diet quality on seed recovery from sheep. Australian Journal of Experimental Agriculture **27**:253-256.
- Kareiva, P. M., I. M. Parker, and M. Pascual. 1996. Can we use experiments and models in predicting invasiveness of genetically engineered organisms? Ecology **77**:1670-1675.
- King, M. 2003. The Penguin history of New Zealand. Penguin Books, Auckland, New Zealand.
- Kirk, T. 1870. On the Naturalized Plants of New Zealand, especially with regard to those occurring the in Province of Auckland. Transactions and Proceedings of the New Zealand Institute **2**:131-137.
- Kirk, T. 1897. Fifth report of the Department of Agriculture. New Zealand Department of Agriculture, Wellington, New Zealand.
- Kolar, C. S., and D. M. Lodge. 2001. Progress in invasion biology: Predicting invaders. Trends in Ecology and Evolution **16**:199-204.
- Kolar, C. S., and D. M. Lodge. 2002. Ecological predictions and risk assessment for alien fishes in North America. Science **298**:1233-1236.
- Kornas, J. 1990. Plant invasions in central Europe: historical and ecological aspects. Pages 19-36 in F. di Castri, A. J. Hansen, and M. Debussche, editors. Biological invasions in Europe and the Mediterranean basin. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Kowarik, I. 1995. Time lags in biological invasions with regard to the success and failure of alien species. Pages 15-38 in P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, editors. Plant invasions - General aspects and special problems. SPB Academic Publishing, Amsterdam, The Netherlands.
- Kowarik, I. 2003. Human agency in biological invasions: secondary releases foster naturalisation and population expansion of alien plant species. Biological Invasions **5**:293-312.
- Kriticos, D. J., and R. P. Randall. 2001. A comparison of systems to analyze potential weed distributions. Pages 61-79 in R. H. Groves, F. D. Panetta, and J. G. Virtue, editors. Weed risk assessment. CSIRO Publishing, Collingwood, Victoria, Australia.
- Krylova, N. P. 1979. Seed propagation of legumes in natural meadows of the U.S.S.R. - Review. Agro-Ecosystems **5**:1-22.
- Lambrinos, J. G. 2002. The variable invasive success of *Cortaderia* species in a complex landscape. Ecology **83**:518-529.
- Lamont, N. 1939. How seed is spread by stock. New Zealand Journal of Agriculture **59**:153.
- Lancashire, J. A. 1984. The distribution and use of forage legumes in New Zealand. Pages 20-33 in R. F. Barnes, P. R. Ball, R. W. Brougham, G. C. Marten, and D. J. Minson, editors. Forage legumes for energy-efficient animal production. U.S. Department of Agriculture, Agricultural Research Service, Palmerston North, New Zealand.
- Lande, R. 1988. Genetics and demography in biological conservation. Science **241**:1455-1460.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist **142**:911-927.
- Lande, R., and D. W. Schemske. 1985. The evolution of self-fertilization and inbreeding depression in plants. 1. Genetic models. Evolution **39**:24-40.
- Le Floch, E., H. N. Le Houerou, and J. Mathez. 1990. History and patterns of plant invasion in Northern Africa. Pages 105-133 in F. di Castri, A. J. Hansen, and M. Debussche, editors.

- Biological invasions in Europe and the Mediterranean basin. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Levin, D. A. 1983. Polyploidy and novelty in flowering plants. *American Naturalist* **122**:1-25.
- Levy, E. B. 1923a. The grasslands of New Zealand. Series 1. Principles of pasture establishment. New Zealand Department of Agriculture, Wellington, New Zealand.
- Levy, E. B. 1923b. The grasslands of New Zealand: Principles of pasture establishment. Quality of seed and method of sowing. *New Zealand Journal of Agriculture* **26**:334-343.
- Levy, E. B. 1930. Relationship and control of annual grasses and clovers in pasture. The Hawke's Bay and Poverty Bay flats. *New Zealand Journal of Agriculture* **40**:147-158.
- Levy, E. B. 1970. Grasslands of New Zealand. A. R. Shearer, Government Printer, Wellington, New Zealand.
- Levy, E. B., and W. Davies. 1930. Strain investigation of grasses and clovers. 3. Red clover (*Trifolium pratense*). *New Zealand Journal of Agriculture* **41**:377-387.
- Lindley, J. 1835. A synopsis of the British flora; arranged according to the natural orders: containing vasculares, or flowering plants, 2nd edition. Printed for Longman, Rees, Orme, Brown, Green, and Longman, Paternoster-Row, London, UK.
- Lloret, F., F. Médail, G. Brundu, and P. E. Hulme. 2004. Local and regional abundance of exotic plant species on Mediterranean islands: are species traits important? *Global Ecology and Biogeography* **13**:37-45.
- Lockwood, J. L. 1999. Using taxonomy to predict success among introduced avifauna: Relative importance of transport and establishment. *Conservation Biology* **13**:560-567.
- Lodge, D. M. 1993. Biological invasions: Lessons for ecology. *Trends in Ecology and Evolution* **8**:133-137.
- Loehlin, J. C. 1998. Latent variable models: An introduction to factor, path, and structural analysis, 3rd edition. Lawrence Erlbaum Associates, Mahwah, NJ, USA.
- Lonsdale, W. M. 1994. Inviting trouble: Introduced pasture species in northern Australia. *Australian Journal of Ecology* **19**:345-354.
- Lumaret, R. 1990. Invasion of natural pastures by a cultivated grass (*Dactylis glomerata* L.) in Galicia, Spain: process and consequence on plant-cattle interactions. Pages 391-397 in F. di Castri, A. J. Hansen, and M. Debussche, editors. *Biological invasions in Europe and the Mediterranean basin*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- MacArthur, R. H. 1964. Environmental factors affecting bird species diversity. *American Naturalist* **98**:387-397.
- Mack, M. C., and C. M. D'Antonio. 1998. Impacts of biological invasions on disturbance regimes. *Trends in Ecology and Evolution* **13**:195-198.
- Mack, R. N. 1991. The commercial seed trade: An early disperser of weeds in the United States. *Economic Botany* **45**:257-273.
- Mack, R. N. 1995. Understanding the processes of weed invasions: The influence of environmental stochasticity. Pages 65-74 in C. H. Stinton, editor. *Weeds in a changing world*. British Crop Protection Council, Farnham, UK.
- Mack, R. N. 1996a. Biotic barriers to plant naturalization. Pages 39-46 in V. C. Moran and J. H. Hoffmann, editors. *Proceedings of the IX International Symposium on Biological Control of Weeds*, Stellenbosch, South Africa. University of Cape Town, South Africa.
- Mack, R. N. 1996b. Predicting the identity and fate of plant invaders: Emergent and emerging approaches. *Biological Conservation* **78**:107-121.
- Mack, R. N. 2000. Cultivation fosters plant naturalization by reducing environmental stochasticity. *Biological Invasions* **2**:111-122.

- Mack, R. N. 2001. Motivations and consequences of the human dispersal of plants. Pages 23-34 in J. A. McNeely, editor. The great reshuffling: Human dimensions of invasive alien species. International Union for the Conservation of Nature, Gland, Switzerland.
- Mack, R. N., and M. Erneberg. 2002. The United States naturalized flora: Largely the product of deliberate introductions. *Annals of the Missouri Botanical Garden* **89**:176-189.
- Mack, R. N., and W. M. Lonsdale. 2001. Humans as global plant dispersers: Getting more than we bargained for. *Bioscience* **51**:95-102.
- MacKinnon, P. A., J. G. Robertson, D. J. Scott, and C. N. Hale. 1977. Legume inoculant usage in New Zealand. *New Zealand Journal of Experimental Agriculture* **5**:35-39.
- Maillet, J., and C. Lopez-Garcia. 2000. What criteria are relevant for predicting the invasive capacity of new agricultural weeds? The case of invasive American species in France. *Weed Research* **40**:11-26.
- Malo, J. E., and F. Suarez. 1997. Dispersal mechanism and transcontinental naturalization proneness among Mediterranean herbaceous species. *Journal of Biogeography* **24**:391-394.
- Marchetti, M. P., P. B. Moyle, and R. Levine. 2004. Invasive species profiling? Exploring the characteristics of non-native fishes across invasion stages in California. *Freshwater Biology* **49**:646-661.
- Martin, R. J., and J. A. Carnahan. 1983. The effect of field storage and laboratory conditions on germination of five *Xanthium* species. *Australian Journal of Agricultural Research* **34**:249-260.
- Matsuo, K. 1999. Comparison of ecological distributions and life history characteristics between invasive and closely related native *Plantago* species in Japan. Pages 15-26 in E. Yano, K. Matsuo, M. Shiyomi, and D. A. Andow, editors. Biological invasions of ecosystems by pests and beneficial organisms: Proceedings of an international workshop. National Institute of Agro-Environmental Sciences, Tsukuba, Japan.
- McGlynn, T. P. 1999. The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography* **26**:535-548.
- McNeely, J. A. 2001. An introduction to human dimensions of invasive alien species. Pages 23-34 in J. A. McNeely, editor. The great reshuffling: Human dimensions of invasive alien species. International Union for the Conservation of Nature, Gland, Switzerland.
- Mihulka, S. 2001. Related alien species in their native and invaded ranges: A comparative study of the genus *Oenothera* in Arkansas (USA) and in the Czech Republic. Pages 133-144 in G. Brundu, J. Brock, I. Camarda, L. Child, and M. Wade, editors. Plant invasions: Species ecology and ecosystem management. Backhuys Publishers, Leiden, The Netherlands.
- Mihulka, S., and P. Pyšek. 2001. Invasion history of *Oenothera* congeners in Europe: a comparative study of spreading rates in the last 200 years. *Journal of Biogeography* **28**:597-609.
- Montague, T. L. (ed.) 2000. The brushtail possum: biology, impact and management of an introduced marsupial. Manaaki Whenua Press, Christchurch, New Zealand.
- Moody, M. E., and R. N. Mack. 1988. Controlling the spread of plant invasions: The importance of nascent foci. *Journal of Applied Ecology* **25**:1009-1021.
- Morley, F. H. W., and J. Katznelson. 1965. Colonization in Australia by *Trifolium subterraneum* L. Pages 269-285 in G. L. Stebbins and H. G. Baker, editors. The genetics of colonizing species. Academic Press, New York, NY, USA.
- Moulton, M. P., and S. L. Pimm. 1983. The introduced Hawaiian avifauna: biogeographic evidence for competition. *American Naturalist* **121**:669-690.

- Mulligan, G. A., and J. N. Findlay. 1970. Reproductive system and colonization in Canadian weeds. *Canadian Journal of Botany* **48**:859-860.
- Mulvaney, M. 2001. The effect of introduction pressure on the naturalization of ornamental woody plants in south-eastern Australia. Pages 186-193 *in* R. H. Groves, F. D. Panetta, and J. G. Virtue, editors. *Weed risk assessment*. CSIRO Publishing, Collingwood, Victoria, Australia.
- Mulvaney, M. J. 1991. Far from the garden path: An identikit picture of woody ornamental plants invading south-eastern Australian bushland. Ph.D. Australian National University, Canberra, ACT, Australia.
- Muthén, L. K., and B. O. Muthén. 1998-2004. MPlus user's guide, 3rd edition. Muthén & Muthén, Los Angeles, CA, USA.
- New, M., D. Lister, M. Hulme, and I. Makin. 2002. A high-resolution data set of surface climate over global land areas. *Climate Research* **21**:1-25.
- New Zealand Registrar-General's Office. 1868-1900. Statistics of the Colony of New Zealand, compiled in the Registrar-General's Office from official returns. Government Printer, Wellington, New Zealand.
- Newsome, A. E., and I. R. Noble. 1986. Ecological and physiological characters of invading species. Pages 1-20 *in* R. H. Groves and J. J. Burdon, editors. *Ecology of biological invasions: An Australian perspective*. Cambridge University Press, Cambridge, UK.
- Nilsen, E. T., and W. H. Muller. 1980. A comparison of the relative naturalization ability of two *Schinus* species in southern California. I. Seed germination. *Bulletin of the Torrey Botanical Club* **107**:51-56.
- Noble, I. R. 1989. Attributes of invaders and the invading process: Terrestrial and vascular plants. Pages 301-313 *in* J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley and Sons, New York, NY, USA.
- Norman, H. C., P. S. Cocks, F. P. Smith, and B. J. Nutt. 1998. Reproductive strategies in Mediterranean annual clovers: germination and hardseededness. *Australian Journal of Agricultural Research* **49**:973-982.
- Norton, D. A. 1989. Scientific basis for the conservation management of New Zealand plant communities. Pages 349-381 *in* I. F. Spellerberg, F. B. Goldsmith, and M. G. Morris, editors. *The scientific management of temperate communities for conservation*. The 31st symposium of the British Ecological Society. The British Ecological Society, Southampton, UK.
- Nutman, P. S. 1965. Symbiotic nitrogen fixation. Pages 363-383 *in* W. V. Bartholomew and F. E. Clark, editors. *Soil Nitrogen*. American Society of Agronomy, Inc., Madison, WI, USA.
- Olivieri, I., P. H. Gouyon, and J. M. Prosperi. 1991. Life cycles of some Mediterranean invasive plants. Pages 145-157 *in* R. H. Groves and F. di Castri, editors. *Biogeography of Mediterranean invasions*. Cambridge University Press, Cambridge, U.K.
- Olson, D. M., E. Dinerstein, E. D. Wikramanayake, N. D. Burgess, G. V. N. Powell, E. C. Underwood, J. A. D'Amico, I. Itoua, H. E. Strand, J. C. Morrison, C. Wettengel, P. Hedao, and K. R. Kassem. 2001. Terrestrial ecoregions of the world: A new map of life on earth. *Bioscience* **51**:933-938.
- Pannell, J. R., and S. C. H. Barrett. 1998. Baker's Law revisited: Reproductive assurance in a meta-population. *Evolution* **52**:657-668.
- Parker, I. M. 1997. Pollinator limitation of *Cytisus scoparius* (Scotch broom), an invasive exotic shrub. *Ecology* **78**:1457-1470.

- Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M. Kareiva, M. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L. Goldwasser. 1999. Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**:3-19.
- Parker, M. A. 2001. Mutualism as a constraint on invasion success for legumes and rhizobia. *Diversity and Distributions* **7**:125-136.
- Patrick, H. N., and W. L. Lowther. 1995. Influence of the number of rhizobia on the nodulation and establishment of *Trifolium ambiguum*. *Soil Biology and Biochemistry* **27**:717-720.
- Patrick, H. N., W. L. Lowther, and K. D. Trainor. 1994. Inoculation for successful establishment of Caucasian clover. *Proceedings of the New Zealand Grassland Association* **56**:101-105.
- Perrins, J., A. Fitter, and M. Williamson. 1993. Population biology and rates of invasion of three introduced *Impatiens* species in the British Isles. *Journal of Biogeography* **20**:33-44.
- Perrins, J., M. Williamson, and A. Fitter. 1992a. Do annual weeds have predictable characters? *Acta Oecologia* **13**:517-533.
- Perrins, J., M. Williamson, and A. Fitter. 1992b. A survey of differing views for weed classification: implications for regulation of introductions. *Biological Conservation* **60**:47-56.
- Pheloung, P. C. 1996. CLIMATE: A system to predict the distribution of an organism based on climate preferences. *Agriculture Western Australia*.
- Pheloung, P. C., P. A. Williams, and S. R. Halloy. 1999. A weed risk assessment model for use as a biosecurity tool evaluating plant introductions. *Journal of Environmental Management* **57**:239-251.
- Pool, A. L. 1942. New Zealand seed for British pastures. *New Zealand Journal of Agriculture* **64**:297-302.
- Preston, C. D., D. A. Pearman, T. D. Dines, H. R. Arnold, and J. M. Croft. 2002. New atlas of the British & Irish flora: an atlas of the vascular plants of Britain, Ireland, the Isle of Man and the Channel Islands. Oxford University Press, Oxford, England.
- Price, S. C., and S. K. Jain. 1981. Are inbreeders better colonizers? *Oecologia* **49**:283-286.
- Prinzing, A., W. Durka, S. Klotz, and R. Brandl. 2002. Which species become aliens? *Evolutionary Ecology Research* **4**:385-405.
- Pryor, H., and W. L. Lowther. 2002. Symbiotic relationship between *Rhizobium leguminosarum* biovar *trifolii* and *Trifolium nigrescens*. *New Zealand Journal of Agricultural Research* **45**:145-149.
- Pryor, H. N., W. L. Lowther, and K. D. Trainor. 1996. Natural reseeding of caucasian clover (*Trifolium ambiguum*) in tussock grasslands. *Proceedings of the New Zealand Grassland Association* **58**:171-175.
- Pyšek, P. 1998. Is there a taxonomic pattern to plant invasions? *Oikos* **82**:282-294.
- Pyšek, P. 2003. Czech alien flora and the historical pattern of its formation: what came first to central Europe? *Oecologia* **135**:122-130.
- Pyšek, P., J. H. Brock, K. Bímová, B. Mandák, V. Jarošík, I. Koukolíková, J. Pergl, and J. Štěpánek. 2003. Vegetative regeneration in invasive *Reynoutria* (Polygonaceae) taxa: The determinant of invasibility at the genotype level. *American Journal of Botany* **90**:1487-1495.
- Pyšek, P., and K. Prach. 1993. Plant invasions and the role of riparian habitats: A comparison of four species alien to Central Europe. *Journal of Biogeography* **20**:413-420.
- Pyšek, P., and K. Prach. 1995. Invasion dynamics of *Impatiens glandulifera* - A century of spreading reconstructed. *Biological Conservation* **74**:41-48.

- Pyšek, P., K. Prach, and B. Mandák. 1998. Invasions of alien plants into habitats of central European landscape: An historical pattern. Pages 23-32 in U. Starfinger, K. Edwards, I. Kowarik, and M. Williamson, editors. *Plant Invasions: Ecological mechanisms and human responses*. Backhuys Publishers, Leiden, The Netherlands.
- Pyšek, P., K. Prach, and P. Šmilauer. 1995. Relating invasion success to plant traits: An analysis of the Czech alien flora. Pages 39-60 in P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, editors. *Plant invasions - General aspects and special problems*. SPB Academic Publishing, Amsterdam, The Netherlands.
- Quinlivan, B. J. 1971. Seed coat impermeability in legumes. *Journal of the Australian Institute of Agricultural Science* **37**:283-295.
- Radford, I. J., and R. D. Cousens. 2000. Invasiveness and comparative life-history traits of exotic and indigenous *Senecio* species in Australia. *Oecologia* **125**:531-542.
- Rehfeldt, G. E., N. M. Tchebakova, Y. I. Parfenova, W. R. Wykoff, N. A. Kuzmina, and L. I. Milyutin. 2002. Intraspecific responses to climate in *Pinus sylvestris*. *Global Change Biology* **8**:912-929.
- Reichard, S. E. 1994. Assessing the potential of invasiveness in woody plants introduced in North America. Ph.D. University of Washington, Seattle, WA, USA.
- Reichard, S. H. 1997. Prevention of invasive plant introductions on national and local levels. Pages 215-227 in J. O. Luken and J. W. Thieret, editors. *Assessment and management of plant invasions*. Springer-Verlag, New York, NY, USA.
- Reichard, S. H., and C. W. Hamilton. 1997. Predicting invasions of woody plants introduced into North America. *Conservation Biology* **11**:193-203.
- Rejmánek, M. 1995. What makes a species invasive? Pages 3-13 in P. Pyšek, K. Prach, M. Rejmánek, and M. Wade, editors. *Plant invasions - General aspects and special problems*. SPB Academic Publishing, Amsterdam, Netherlands.
- Rejmánek, M. 1996. A theory of seed plant invasiveness: The first sketch. *Biological Conservation* **78**:171-181.
- Rejmánek, M. 1999. Invasive plant species and invulnerable ecosystems. Pages 79-102 in O. T. Sandlund, P. J. Schei, and A. Viken, editors. *Invasive species and biodiversity management*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Rejmánek, M. 2000. Invasive plants: Approaches and predictions. *Austral Ecology* **25**:497-506.
- Rejmánek, M., and S. Reichard. 2001. Predicting invaders. *Trends in Ecology and Evolution* **16**:545.
- Rejmánek, M., and D. M. Richardson. 1996. What attributes make some plant species more invasive? *Ecology* **77**:1655-1661.
- Richardson, D. M., N. Allsopp, C. M. D'Antonio, S. J. Milton, and M. Rejmánek. 2000a. Plant invasions - the role of mutualisms. *Biological Reviews* **75**:65-93.
- Richardson, D. M., R. M. Cowling, and D. C. Le Maitre. 1990. Assessing the risk of invasive success in *Pinus* and *Banksia* in South African mountain fynbos. *Journal of Vegetation Science* **1**:629-642.
- Richardson, D. M., P. Pyšek, M. Rejmánek, M. G. Barbour, F. D. Panetta, and C. J. West. 2000b. Naturalization and invasion of alien plants: concepts and definitions. *Diversity and Distributions* **6**:93-107.
- Roderick, G. K., and F. G. Howarth. 1999. Invasion genetics: Natural colonizations, non-indigenous species, and classical biological control. Pages 98-108 in E. Yano, K. Matsuo, M. Shiyomi, and D. A. Andow, editors. *Biological invasions of ecosystems by pests and beneficial organisms: Proceedings of an international workshop*. National Institute of Agro-Environmental Sciences, Tsukuba, Japan.

- Roy, J. 1990. In search of the characteristics of plant invaders. Pages 335-352 in F. di Castri, A. J. Hansen, and M. Debussche, editors. *Biological invasions in Europe and the Mediterranean basin*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Roy, J., M. L. Navas, and L. Sonié. 1991. Invasion by annual brome grasses: a case study challenging the homocline approach to invasions. Pages 207-224 in R. H. Groves and F. di Castri, editors. *Biogeography of Mediterranean Invasions*. Cambridge University Press, New York, NY, USA.
- Ruesink, J. L., I. M. Parker, M. J. Groom, and P. M. Kareiva. 1995. Reducing the risks of nonindigenous species introductions: Guilty until proven innocent. *Bioscience* **45**:465-477.
- Rumball, P. J., and J. P. Lambert. 1980. Plant introduction trials: Performance of some forage legumes in Northland. *New Zealand Journal of Experimental Agriculture* **8**:179-183.
- Rumball, W. 1983. Pasture plant breeding in New Zealand. Pages 215-220 in G. S. Wratt and H. C. Smith, editors. *Plant breeding in New Zealand*. Butterworths, Department of Scientific and Industrial Research (DSIR), Wellington, New Zealand.
- Russi, L., P. S. Cocks, and E. H. Roberts. 1992. The fate of legume seeds eaten by sheep from a Mediterranean grassland. *Journal of Applied Ecology* **29**:772-778.
- SAS Institute. 1999. SAS 8.0. Cary, NC, USA.
- Saxby, S. H. 1940. Grasses and clovers of New Zealand: Clovers are the key to high production. *New Zealand Journal of Agriculture* **60**:271-276.
- Saxby, S. H. 1941. Clean seed production in Otago: The link between the farmer and the merchant. *New Zealand Journal of Agriculture* **63**:199-207.
- Schierenbeck, K. A., R. N. Mack, and R. R. Sharitz. 1994. Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. *Ecology* **75**:1661-1672.
- Schiffman, P. M. 1997. Animal-mediated dispersal and disturbance: Driving forces behind alien plant naturalization. Pages 87-94 in J. O. Luken and J. W. Thieret, editors. *Assessment and management of plant invasions*. Springer-Verlag, New York, NY, USA.
- Scott, D. 1985. Plant introduction trials: genotype-environment analysis of plant introductions for the high country. *New Zealand Journal of Experimental Agriculture* **13**:117-127.
- Scott, D. 1999. Ecological considerations in plant invasion, with New Zealand examples. Pages 109-121 in E. Yano, K. Matsuo, M. Shiyomi, and D. A. Andow, editors. *Biological invasions of ecosystems by pests and beneficial organisms: Proceedings of an international workshop*. National Institute of Agro-Environmental Sciences, Tsukuba, Japan.
- Scott, D. 2001. Sustainability of New Zealand high-country pastures under contrasting developmental inputs. 7. Environmental gradients, plant species selection, and diversity. *New Zealand Journal of Agricultural Research* **44**:59-90.
- Scott, J. K., and F. D. Panetta. 1993. Predicting the Australian weed status of southern African plants. *Journal of Biogeography* **20**:87-93.
- Seguin, P., M.-S. Beaugard, and W. Zheng. 2004. Diversity of Kura clover-nodulating rhizobia from the Lower Caucasus. in Joint Meeting of the 39th North American Alfalfa Improvement Conference and the 18th *Trifolium* Conference, Quebec City, Canada. Available online at <http://www.naaic.org/Meetings/National/2004NAAIC&TC/generalschedule.htm>
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *Bioscience* **31**:131-134.
- Shipley, B. 2000. Cause and correlation in biology: A user's guide to path analysis, structural equations, and causal inference. Cambridge University Press, Cambridge, UK.

- Simao Neto, M., R. M. Jones, and D. Ratcliff. 1987. Recovery of pasture seed ingested by ruminants. 1. Seed of six tropical pasture species fed to cattle, sheep and goats. *Australian Journal of Experimental Agriculture* **27**:239-246.
- Simberloff, D. 1989. Which insect introductions succeed and which fail? Pages 61-75 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley and Sons, New York, NY, USA.
- Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species: invasional meltdown? *Biological Invasions* **1**:21-32.
- Smetham, M. L. 1980. The establishment and management of subterranean clover and other annual legumes on dry hill country of the South Island. Pages 326-346 in *Lincoln College Farmers' Conference*, Lincoln, New Zealand.
- Smith, C. S., W. M. Lonsdale, and J. Fortune. 1999. When to ignore advice: invasion predictions and decision theory. *Biological Invasions* **1**:89-96.
- Smith, F. P., P. S. Cocks, and M. A. Ewing. 1996. Short-term patterns of seed softening in *Trifolium subterraneum*, *T. glomeratum*, and *Medicago polymorpha*. *Australian Journal of Agricultural Research* **47**:775-785.
- Smith, R. S., S. Thome, and R. Randall. 1987. Rhizobia inoculants for various leguminous species. Technical Bulletin No. 102, The Nitragin Company.
- Sol, D. 2001. Predicting invaders. *Trends in Ecology and Evolution* **16**:544.
- Sol, D., S. Timmermans, and L. Lefebvre. 2002. Behavioural flexibility and invasion success in birds. *Animal Behaviour* **63**:495-502.
- Starfinger, U. 1998. On success in plant invasions. Pages 33-42 in U. Starfinger, K. Edwards, I. Kowarik, and M. Williamson, editors. *Plant Invasions: Ecological mechanisms and human responses*. Backhuys Publishers, Leiden, The Netherlands.
- Stebbins, G. L. 1971. *Chromosomal evolution in higher plants*. Addison-Wesley, Reading, MA, USA.
- Suckling, F. E. T. 1952. Dissemination of white clover (*Trifolium repens*) by sheep. *New Zealand Journal of Science and Technology* **5**:64-77.
- Sullivan, J. J., S. M. Timmins, and P. A. Williams. 2004. The role of urbanization in facilitating weed invasions in New Zealand. *Weed Technology* **18**: *in press*.
- Sultan, S. E. 2001. Phenotypic plasticity for fitness components in *Polygonum* species of contrasting ecological breadth. *Ecology* **82**:328-343.
- Sutherst, R. W. 2003. Prediction of species geographical ranges. *Journal of Biogeography* **30**:805-816.
- Sykora, K. V. 1990. History of the impact of man on the distribution of plant species. Pages 37-50 in F. di Castri, A. J. Hansen, and M. Debussche, editors. *Biological invasions in Europe and the Mediterranean basin*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- Taylor, A. O., K. A. Hughes, and B. J. Hunt. 1979a. Annual cool-season legumes for forage. I. A survey of lines for yield and disease resistance at Kaitaia and Palmerston North. *New Zealand Journal of Experimental Agriculture* **7**:141-147.
- Taylor, A. O., K. A. Hughes, and B. J. Hunt. 1979b. Annual cool-season legumes for forage. II. Seasonal growth patterns and effects of cutting frequency and cutting height on yield. *New Zealand Journal of Experimental Agriculture* **7**:149-152.
- Taylor, N. L., K. H. Quesenberry, and M. K. Anderson. 1979c. Genetic system relationships in *Trifolium*. *Economic Botany* **33**:431-441.

- Thébaud, C., A. C. Finzi, L. Affre, M. Debussche, and J. Escarre. 1996. Assessing why two introduced *Conyza* differ in their ability to invade Mediterranean old fields. *Ecology* **77**:791-804.
- Thomas, R. G. 2003. Comparative growth forms of dryland forage legumes. Pages 19-25 in D. J. Moot, editor. *Legumes for Dryland Pastures*. New Zealand Grassland Association, Lincoln University, Lincoln, New Zealand.
- Thompson, J. D., and R. Lumaret. 1992. The evolutionary dynamics of polyploid plants: origins, establishment, and persistence. *Trends in Ecology and Evolution* **7**:302-307.
- Thompson, K., S. R. Band, and J. G. Hodgson. 1993. Seed size and shape predict persistence in soil. *Functional Ecology* **7**:236-241.
- Thompson, K., J. G. Hodgson, and T. C. G. Rich. 1995. Native and alien invasive plants: more of the same? *Ecography* **18**:390-402.
- Thomson, E. F., S. Rihawi, P. S. Cocks, A. E. Osman, and L. Russi. 1990. Recovery and germination rates of seeds of Mediterranean medics and clovers offered to sheep at a single meal or continuously. *Journal of Agricultural Science* **114**:295-299.
- Thomson, G. M. 1922. *The naturalisation of animals and plants in New Zealand*. Cambridge University Press, London, UK.
- Tucker, K. C., and D. M. Richardson. 1995. An expert system for screening potentially invasive alien plants in South African fynbos. *Journal of Environmental Management* **44**:309-338.
- Turkington, R., and L. L. Mehrhoff. 1990. The role of competition in structuring pasture communities. Pages 307-340 in J. B. Grace and D. Tilman, editors. *Perspectives on plant competition*. Academic Press, San Diego, CA, USA.
- Turnbull, L. A., D. Coomes, A. Hector, and M. Rees. 2004. Seed mass and the competition/colonization trade-off: competitive interactions and spatial patterns in a guild of annual plants. *Journal of Ecology* **92**:97-109.
- Veltman, C. J., S. Nee, and M. J. Crawley. 1996. Correlates of introduction success in exotic New Zealand birds. *American Naturalist* **147**:542-557.
- Venier, L. A., and L. Fahrig. 1996. Habitat availability causes the species abundance-distribution relationship. *Oikos* **76**:564-570.
- Vermeij, G. J. 1996. An agenda for invasion biology. *Biological Conservation* **78**:3-9.
- Vickery, R. K. 1974. Growth in artificial climates: An indication of *Mimulus*' ability to invade new habitats. *Ecology* **55**:796-807.
- Virtue, J. G. 2003. Weed risk assessment - recent developments in Australia. Animal and Plant Control Commission, South Australia.
- Wardle, P. 1991. *Vegetation of New Zealand*. Cambridge University Press, Cambridge, UK.
- Warwick, S. I. 1990. Genetic variation in weeds - with particular reference to Canadian agricultural weeds. Pages 3-18 in S. Kawano, editor. *Biological approaches and evolutionary trends in plants*. Academic Press, London, UK.
- Webb, C. J. 1980. Checklist of dicotyledons naturalised in New Zealand 5. Leguminosae. *New Zealand Journal of Botany* **18**:463-472.
- Webb, C. J., W. R. Sykes, and P. J. Garnock-Jones. 1988. *Flora of New Zealand Volume IV: Naturalized pteridophytes, gymnosperms, and dicotyledons*. Botany Division, DSIR, Christchurch, New Zealand.
- Weber, E. 1998. The dynamics of plant invasions: a case study of three exotic goldenrod species (*Solidago* L.) in Europe. *Journal of Biogeography* **25**:147-154.
- Weber, E., and C. M. D'Antonio. 1999. Phenotypic plasticity in hybridizing *Carpobrotus* spp. (Aizoaceae) from coastal California and its role in plant invasion. *Canadian Journal of Botany* **77**:1411-1418.

- Weiner, J. 1990. Asymmetric competition in plant populations. *Trends in Ecology and Evolution* **5**:360-364.
- Westoby, M., D. Falster, A. Moles, P. Vesk, and I. Wright. 2002. Plant ecological strategies: Some leading dimensions of variation between species. *Annual Review of Ecology and Systematics* **33**:125-159.
- Widrechner, M. P., and J. K. Iles. 2002. A geographic assessment of the risk of naturalization of non-native woody plants in Iowa. *Journal of Environmental Horticulture* **20**:47-56.
- Wiersema, J. H., and B. León. 1999. *World economic plants: A standard reference*. CRC Press, Boca Raton, FL, USA.
- Williams, P. A., A. Wilton, and N. Spencer. 2002. A proposed conservation weed risk assessment system for the New Zealand border. Science for Conservation 208, Department of Conservation, Wellington, New Zealand.
- Williams, P. A., and S. Wiser. 2004. Determinants of regional and local patterns in the floras of braided river beds in New Zealand. *Journal of Biogeography* **31**:1355-1372.
- Williams, W. M., L. B. Anderson, and B. M. Cooper. 1978. Evaluation of clovers on sandy coastal soil. *Proceedings of the New Zealand Grassland Association* **39**:130-138.
- Williams, W. M., J. R. Caradus, and J. F. L. Charlton. 1980. Plant introduction trials: Comparative performance of annual legume species at three sites in the southern North Island. *New Zealand Journal of Experimental Agriculture* **8**:185-190.
- Williamson, M. 1989. Mathematical models of invasions. Pages 329-350 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmánek, and M. Williamson, editors. *Biological invasions: a global perspective*. John Wiley and Sons, New York, NY, USA.
- Williamson, M. 1999. Invasions. *Ecography* **22**:5-12.
- Williamson, M., and K. C. Brown. 1986. The analysis and modelling of British invasions. *Philosophical Transactions of the Royal Society of London B* **314**:505-522.
- Williamson, M., and A. Fitter. 1996. The characters of successful invaders. *Biological Conservation* **78**:163-170.
- Wilson, J. B., J. C. E. Hubbard, and G. L. Rapson. 1988. A comparison of realised niche relations of species in New Zealand and Britain. *Oecologia* **76**:106-110.
- Wonham, M. J., J. T. Carlton, G. M. Ruiz, and L. D. Smith. 2000. Fish and ships: relating dispersal frequency to success in biological invasions. *Marine Biology* **136**:1111-1121.
- Woodfield, D. R. (ed.) 1995. *White clover: New Zealand's competitive edge*. Agronomy Society of New Zealand and New Zealand Grassland Association, Lincoln University, New Zealand.
- Woodward, F. I. 1987. *Climate and plant distribution*. Cambridge University Press, Cambridge, UK.
- Yu, C.-Y. 2002. Evaluating cutoff criteria of model fit indices for latent variable models with binary and continuous outcomes. Ph.D. University of California Los Angeles, Los Angeles, CA, USA.
- Zimmerman, C. A. 1976. Growth characteristics of weediness in *Portulaca oleracea* L. *Ecology* **57**:964-974.
- Zohary, M. 1972. Origins and evolution in the genus *Trifolium*. *Botaniska Notiser* **125**:501-511.
- Zohary, M., and D. Heller. 1984. *The genus Trifolium*. The Israel Academy of Sciences and Humanities, Jerusalem.

Appendix 1:**Parameters of confirmatory factor analysis (CFA) and structural equation models (SEM)**

Table AP1.1. Transformations and convergence adjustments applied to variables prior to inclusion in the models. Slope estimates for all relationships should be interpreted with these adjustments in mind.

Variable	Transformation	Convergence adjustment
Centre of origin		
Present in Britain?		
British distribution	$\text{LN}(x+1)$	
Economic uses (global)		
Introduction or naturalisation date		
Introduced for commercial agriculture?		
Estimated hectares planted	$\text{LN}(x+1)$	/ 3
Nodulation with introduced <i>Rhizobium</i>		
Native range area	LN	/ 15
Diversity of conditions tolerated		/ 5
Match to New Zealand climate		/ 100
New Zealand drought tolerance		/ 100
New Zealand low temp. tolerance		/ 100
New Zealand frost tolerance		/ 100
Elevation of native range		
Canopy cover of native habitat		
Native to human-influenced habitats?		
Lifespan		
Capable of self-pollination		
Capable of vegetative reproduction		
Polyploidy		
Reduced base chromosome number		
Height maximum		/ 10
Habit		
Seed size		
Seed mass	LN	
Capable of long-distance dispersal		
Seed shape similar to white clover?		
Corolla length		
Month flowering starts (Native range)		
Month flowering ends (Native range)		
Length flowering period (Native range)		
Month flowering starts (NZ)		
Month flowering ends (NZ)		
Length flowering period (NZ)		

Trait and habitat confirmatory factor analysis (CFA). Potential factors underlying biological and habitat characteristics were deduced from several sources (Zohary 1972, Taylor et al. 1979c, Zohary and Heller 1984, Gray 1986, Gillett and Taylor 2001). Originally, a structure was proposed that included corolla length with “genetic system”, seed shape with “seed size and dispersal”, length of the flowering period with “phenology”, and elevation of the native habitat with “native habitat type”. However, there was evidence of substantial misfit of this model to the data.

Consequently, an exploratory factor analysis (EFA) was performed so that sensible modifications to these groupings might be indicated. This analysis showed length of the flowering period as a separate, independent factor. Therefore, it was removed from the factor analysis and could be considered on its own in subsequent work. Elevation of the native habitat seemed to load somewhat on all six of the suggested factors. Re-examination of the literature sources indicated that all of the proposed factors might logically be expected to vary with elevation. Elevation of the native habitat was thus removed as a factor indicator and specified instead as a covariate. The remaining two variables, corolla length and seed shape, seemed to load moderately on several factors. The CFA was re-run specifying each of these potential relationships in turn, but none seemed to have a satisfactory fit to the data. Therefore, because they could not be adequately accounted for by the proposed factors, corolla length and seed shape were removed from the analysis.

The remaining model had a reasonable fit to the data. At this stage, model modification indices were obtained. These indices suggested that adding covariance between several sets of indicator residuals would improve the fit of the model. Two of these suggested modifications made substantive sense and were therefore added: lifespan with capability for self pollination, and seed size with seed mass. The final CFA model is shown in Figure AP1.1 and described in Tables AP1.2-AP1.4.

Figure AP.1. Trait and habitat confirmatory factor analysis (CFA): Illustration of model.

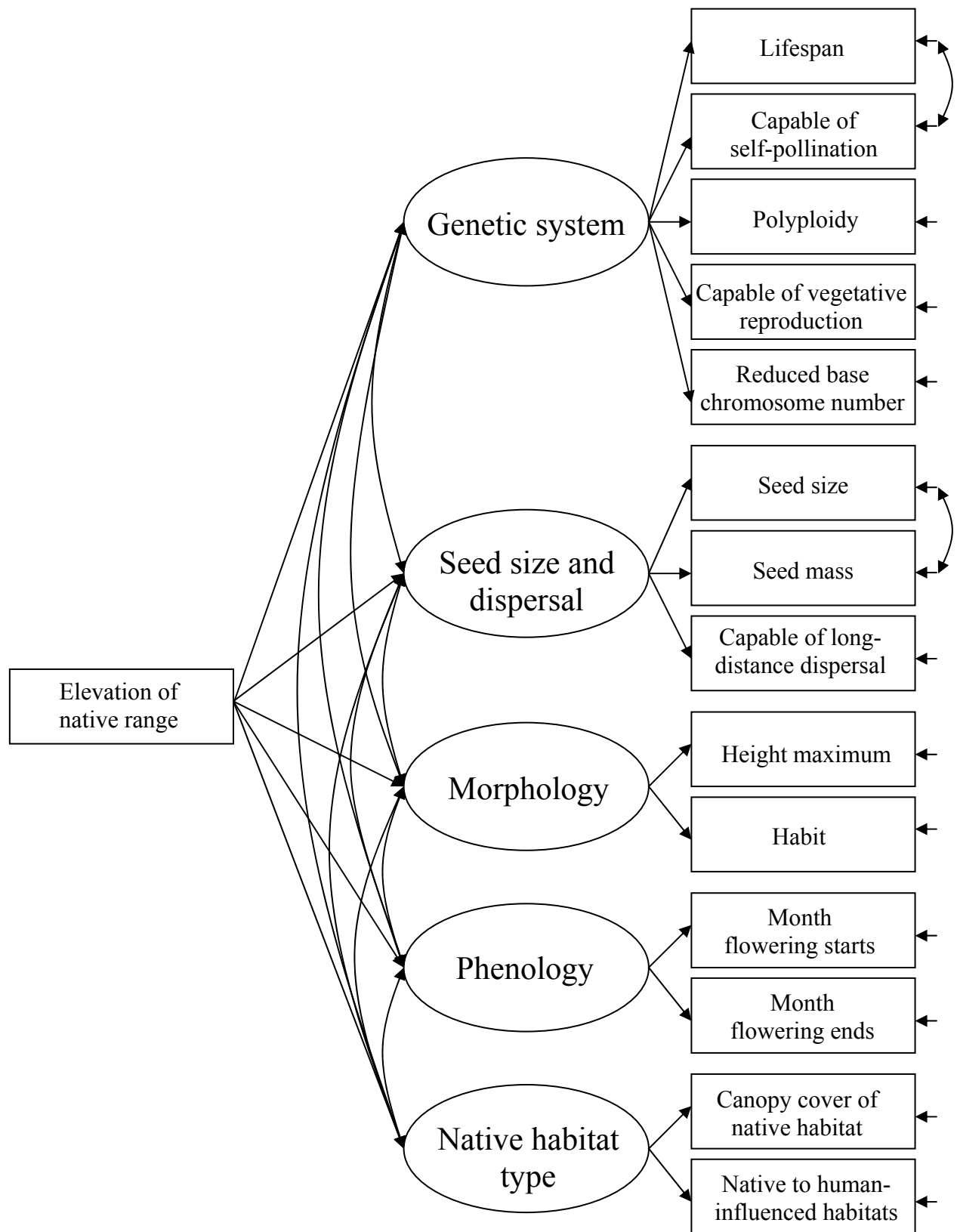


Table AP1.2. Trait and habitat confirmatory factor analysis (CFA): Factor loadings and residual covariances. Continuous indicators have parameters of standard linear regression listed ($y = \beta x + \alpha$, where β represents slope and α intercept). Standardized estimates are factor loadings. Binary and ordered categorical indicators have probit regression parameters listed. Probabilities for these indicators take the form $P(y = i | x) = F[-\tau_i + \pi x]$, where τ_i represents threshold i , π represents the regression slope, x is the value of the factor (= explanatory variable), and F is the standard normal distribution. Standardized estimates for these relationships cannot be directly interpreted as loadings. Rather, they represent the coefficient for the relationship between the factor and a hypothetical continuous latent variable (y^*) underlying the categorical indicator, and should be interpreted in conjunction with the threshold. Significance values for estimates are $^{\dagger}P < 0.10$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$. ‡ indicates that the loading for the indicator was fixed at a value close to 1, as the estimated model resulted in a negative residual variance (Heywood case). Four out of the five fit indices indicated no evidence for misfit of this model to the data, with the fifth index (χ^2 P -value) not far from its recommended threshold. Fit statistic values (and thresholds) were: χ^2 P -value = 0.0133 (≥ 0.05), Tucker-Lewis fit index (TLI) = 0.965 (≥ 0.96), comparative fit index (CFI) = 0.970 (≥ 0.96), root-mean-square error of approximation (RMSEA) = 0.050 (≤ 0.05) and weighted root-mean-square residual (WRMR) = 0.874 (≤ 0.95).

FACTOR LOADINGS						
Factor	Indicators	Estimate	SE	Stand. estimate	Intercept	Thresholds
Genetic system	Lifespan	0.950 [‡]	0.000	0.968		1 = 1.851
	Capable of self-pollination	0.848***	0.071	0.897		1 = 1.331
	Polyploidy	0.527***	0.109	0.618		1 = 1.920
	Capable of vegetative reproduction	0.769***	0.058	0.837		1 = 1.903
	Reduced base chromosome number	0.414***	0.108	0.500		1 = -0.110
Seed size and dispersal	Seed size	0.353***	0.088	0.404	2.284	
	Seed mass	0.310*	0.136	0.382	-0.017	
	Capable of long-distance seed dispersal	0.950 [‡]	0.000	0.954		1 = 0.156
Morphology	Height maximum	0.662***	0.137	0.350	4.323	
	Habit	0.950 [‡]	0.000	0.954		1 = -1.626
						2 = -0.668
Phenology	Month flowering starts	0.962***	0.094	0.676	3.276	
	Month flowering ends	1.074***	0.105	0.737	5.247	

Native habitat type	Canopy cover of native habitat	0.454***	0.120	0.477		1 = -1.660
						2 = -0.367
	Native to human-influenced habitats	0.883***	0.235	0.895		1 = -0.253
RESIDUAL COVARIANCES						
Variable 1	Variable 2	Estimate	SE	Stand. estimate		
Lifespan	Capable of self-pollination	0.133*	0.062	0.089		
Seed size	Seed mass	0.397***	0.093	0.512		

Table AP1.3. Trait and habitat confirmatory factor analysis (CFA): Relationships to covariate. Slope estimates for standard linear regression are listed. Significance values for estimates are [†] $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

Factor	Covariate	Estimate (slope)	SE	Stand. estimate
Genetic system	Elevation of native range	0.843***	0.107	0.616
Seed size and dispersal	Elevation of native range	0.333**	0.106	0.295
Morphology	Elevation of native range	-0.321***	0.090	-0.285
Phenology	Elevation of native range	0.854***	0.101	0.621
Native habitat type	Elevation of native range	-0.402**	0.133	-0.349

Table AP1.4. Trait and habitat confirmatory factor analysis (CFA): Factor correlation matrix. Standardized estimates (correlations) are presented. Significance values for estimates are [†] $P < 0.10$, * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

	Native habitat type	Phenology	Morphology	Seed size & dispersal
Phenology	-0.006			
Morphology	-0.070	0.082		
Seed size & dispersal	0.080	-0.097	-0.046	
Genetic system	-0.153	0.162**	-0.214**	0.413***

Table AP1.5. Intentional introduction SEM parameter estimates. Paths with continuous response variables have parameters of standard linear regression listed ($y = \beta x + \alpha$, where β represents slope and α intercept). Standardized estimates are path coefficients. Paths with binary or ordered categorical response variables have probit regression parameters listed. Probabilities for these variables take the form $P(y = i | x_1, x_2) = F[-\tau_i + \pi_1 x_1 + \pi_2 x_2]$, where τ_i represents threshold i , π values represent regression slopes for the explanatory variables, and F is the standard normal distribution. Standardized estimates for these relationships cannot be directly interpreted as path coefficients. Rather, they represent the path coefficient for the relationship between the explanatory variable and a hypothetical continuous latent variable (y^*) underlying the categorical response variable, and should be interpreted in conjunction with the threshold. These coefficients are best compared within, rather than between, response variables. Significance values for estimates are $^{\dagger}P < 0.10$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

PATHS						
Response variable	Explanatory variable	Estimate (slope)	SE	Stand. estimate	Intercept	Thresholds
Intentional introduction (all species)	Economic uses (global)	0.748***	0.156	0.734		1 = 12.727
Economic uses (global)	Native range area	8.329***	1.070	0.723		1 = 16.422
						2 = 17.243
						3 = 17.907
						4 = 18.671
						5 = 19.040
Native range area	Diversity of conditions tolerated	0.222***	0.008	0.816	1.606	
Match to New Zealand climate	Native range area	9.152***	0.911	0.611	-15.376	
COVARIANCES						
Variable 1	Variable 2	Estimate	SE	Stand. estimate		
Economic uses (global)	Match to New Zealand climate	0.338*	0.145	0.124		

Table AP1.6. Intentional introduction for horticulture or experimental agriculture SEM parameter estimates. Paths with continuous response variables have parameters of standard linear regression listed ($y = \beta x + \alpha$, where β represents slope and α intercept). Standardized estimates are path coefficients. Paths with binary or ordered categorical response variables have probit regression parameters listed. Probabilities for these variables take the form $P(y = i | x_1, x_2) = F[-\tau_i + \pi_1 x_1 + \pi_2 x_2]$, where τ_i represents threshold i , π values represent regression slopes for the explanatory variables, and F is the standard normal distribution. Standardized estimates for these relationships cannot be directly interpreted as path coefficients. Rather, they represent the path coefficient for the relationship between the explanatory variable and a hypothetical continuous latent variable (y^*) underlying the categorical response variable, and should be interpreted in conjunction with the threshold. These coefficients are best compared within, rather than between, response variables. Significance values for estimates are $^{\dagger}P < 0.10$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

PATHS						
Response variable	Explanatory variable	Estimate (slope)	SE	Stand. estimate	Intercept	Threshold
Intentional introduction (horticultural and experimental agricultural species)	Native range area	4.217***	0.923	0.468		1 = 8.602
Native range area	Diversity of conditions tolerated	0.221***	0.008	0.811	1.606	

Table AP1.7. Naturalisation of intentional species SEM parameter estimates. Paths with continuous response variables have parameters of standard linear regression listed ($y = \beta x + \alpha$, where β represents slope and α intercept). Standardized estimates are path coefficients. Paths with binary or ordered categorical response variables have probit regression parameters listed. Probabilities for these variables take the form $P(y = i | x_1, x_2) = F[-\tau_i + \pi_1 x_1 + \pi_2 x_2]$, where τ_i represents threshold i , π values represent regression slopes for the explanatory variables, and F is the standard normal distribution. Standardized estimates for these relationships cannot be directly interpreted as path coefficients. Rather, they represent the path coefficient for the relationship between the explanatory variable and a hypothetical continuous latent variable (y^*) underlying the categorical response variable, and should be interpreted in conjunction with the threshold. These coefficients are best compared within, rather than between, response variables. Standard errors marked (--) could not be determined by the analysis program, most likely because of the small sample size and skewed distribution of naturalisation outcomes (9 of 54 species successful). Significance values for estimates are $^{\dagger}P < 0.10$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

PATHS						
Response variable	Explanatory variable	Estimate (slope)	SE	Stand. estimate	Intercept	Thresholds
Naturalisation	Estimated hectares planted	44.807	--	0.698		1 = 244.945
	Match to New Zealand climate	23.695	--	0.408		
Estimated hectares planted	Introduced for com. agriculture?	0.505 [†]	0.277	0.992	-24.624	
Introduced for com. agriculture?	Economic uses (global)	2.812 [†]	1.508	0.958		1 = 54.375
Economic uses (global)	Native range area	9.344***	2.537	0.544		1 = 17.382
						2 = 18.145
						3 = 18.672
						4 = 19.520
						5 = 19.878
Native range area	Diversity of conditions tolerated	0.115***	0.012	0.757	1.768	
Match to New Zealand climate	Native range area	17.174***	4.310	0.606	-29.735	
COVARIANCES						
Variable 1	Variable 2	Estimate	SE	Stand. estimate		
Economic uses (global)	Match to New Zealand climate	0.731*	0.292	0.312		

Table AP1.8. Unintentional introduction-naturalisation SEM parameter estimates. Paths with continuous response variables have parameters of standard linear regression listed ($y = \beta x + \alpha$, where β represents slope and α intercept). Standardized estimates are path coefficients. Paths with binary or ordered categorical response variables have probit regression parameters listed. Probabilities for these variables take the form $P(y = i | x_1, x_2) = F[-\tau_i + \pi_1 x_1 + \pi_2 x_2]$, where τ_i represents threshold i , π values represent regression slopes for the explanatory variables, and F is the standard normal distribution. Standardized estimates for these relationships cannot be directly interpreted as path coefficients. Rather, they represent the path coefficient for the relationship between the explanatory variable and a hypothetical continuous latent variable (y^*) underlying the categorical response variable, and should be interpreted in conjunction with the threshold. These coefficients are best compared within, rather than between, response variables. [‡] indicates that the loading for the indicator was fixed at a value close to 1, as the estimated model resulted in a negative residual variance (Heywood case). Significance values for estimates are [†] $P < 0.10$, $*P < 0.05$, $**P < 0.01$, and $***P < 0.001$.

FACTORS						
Factor	Indicators	Estimate (slope)	SE	Std. est.	Intcpt	Thresholds
Native habitat type	Canopy cover of native habitat	0.382**	0.121	0.407		1 = -1.559
						2 = -0.496
	Native to human-influenced habitats?	0.925 [‡]	0.000	0.986		1 = -0.104
PATHS						
Response variable	Explanatory variable	Estimate (slope)	SE	Std. est.	Intcpt	Thresholds
Unintentional introduction-naturalisation	Native habitat type	0.519***	0.091	0.553		1 = 8.504
	Native range area	3.984***	0.528	0.518		
	Match to New Zealand climate	0.230***	0.062	0.397		
Native habitat type	Elevation of native range	-0.408*	0.165	-0.345		
Match to New Zealand climate	Native range area	7.670***	1.318	0.578	-12.691	
Native range area	Diversity of conditions tolerated	0.232***	0.017	0.762	1.589	
COVARIANCES						
Variable 1	Variable 2	Estimate	SE	Std. est.		
Elevation of native range	Match to New Zealand climate	-0.592*	0.283	-0.381		
Diversity of conditions tolerated	Native habitat type	0.143***	0.040	0.314		

Appendix 2: Acknowledgement of data sources

Herbarium specimens

Access to and identification of specimens in the following herbaria was helpfully facilitated by the listed individuals.

AK (Auckland Museum): Ewen Cameron and Mei Nee Lee

CANU (University of Canterbury): Reijel Gardiner

CHR (Allan Herbarium, Landcare Research, Lincoln): the entire staff, especially Aaron Wilton, Michelle Breach, and David Glenny

LINC (Lincoln University): Merv Spurway and Brent Richards

MPN (Massey University): Gillian Rapson and Lesley van Essen

NZFRI (Forest Research): Chris Ecroyd

OTA (University of Otago): Janice Lord and Kathryn Radford

WELT (Te Papa Museum, Wellington): Simon Whittaker and Barry Sneddon

National Vegetation Survey (NVS) database records

Permission to access and use data from the National Vegetation Survey database was graciously granted by the following organizations, facilitated by the individuals indicated.

New Zealand Department of Conservation

David Hunt (Bay of Plenty Conservancy)

Andy Grant (Canterbury Conservancy)

Colin Taylor, Kerry Hogan and Mike Thorsen (East Coast/Hawkes Bay Conservancy)

Malcolm Brennan, Simon Moore and Mike Hawes (Nelson/Marlborough Conservancy)

Bruce Kyle, Geoff Rogers and Tony Perrett (Otago Conservancy)

Carol West (Southland Conservancy)

Sean Goddard and Nicholas Singers (Tongariro/Taupo Conservancy)

Alison Perfect (Waikato Conservancy)

Astrid Dijkgraaf (Wanganui Conservancy)

Colin Miskelly (Wellington Conservancy)

Andy Grant (Project River Recovery)

Landcare Research

Rob Allen, Peter Bellingham, Fiona Carswell, Colin Meurk, Alan Rose and Susan Wiser

Forest Research

Rob Allen, Larry Burrows, David Hunt, Alan Rose, Eric Spurr, Glenn Stewart, and Caroline Thomson

District Councils

Marlborough District Council: Susan King and Robin Dunn

Timaru District Council: Colin Meurk

New Zealand Ministry for the Environment

James Barton (Carbon Monitoring System)

Appendix 3: Listing of *Trifolium* species introduced to New Zealand.

Table AP3.1. The 54 intentionally introduced *Trifolium* species, including reason for introduction, introduction and naturalisation dates, current distribution in New Zealand, and selected explanatory variables. For introduction reason, COM = commercial agriculture, EXP = experimental agriculture, and HOR = horticulture. For centre of origin, MED = Mediterranean, SSA = sub-Saharan Africa, and AMR = America. See Table 2.3 for other variable units and coding.

Species	Reason for intro.	Intro. date	Nat. date	Current dist. (coarse-scale)	Current dist. (fine-scale)	Centre of origin	Present in Britain?	Native range area ($\times 10^{12}$)	Estimated hectares planted	Freq. as pasture seed contam.
<i>alexandrinum</i>	COM	1904				MED	0	0.98	9.42×10^6	
<i>ambiguum</i>	COM	1955				MED	0	5.92	6.40×10^6	
<i>dubium</i>	COM	1868	1868	10	138	MED	1	10.47	1.43×10^7	4
<i>fragiferum</i>	COM	1898	1898	9	37	MED	1	17.62	2.13×10^7	1
<i>hybridum</i>	COM	1855	1882	9	35	MED	1	6.81	6.93×10^7	3
<i>incarnatum</i>	COM	1861	1878	5	8	MED	1	3.22	2.03×10^7	1
<i>medium</i>	COM	1869	1869	2	5	MED	1	13.72	1.76×10^6	0
<i>pratense</i>	COM	1850	1867	10	98	MED	1	21.09	2.40×10^8	3
<i>repens</i>	COM	1843	1864	10	181	MED	1	31.78	3.70×10^8	3
<i>subterraneum</i>	COM	1906	1906	10	56	MED	1	10.79	1.01×10^8	1
<i>hirtum</i>	EXP	1963	1980	1	1	MED	0	8.00	0.0886	0
<i>affine</i>	EXP	1972				MED	0	0.83	0.0081	
<i>alpestre</i>	EXP	1974				MED	0	10.17	0.0403	
<i>amabile</i>	EXP	1992				AMR	0	9.67	0.0081	
<i>argutum</i>	EXP	1963				MED	0	2.01	0.0081	
<i>badium</i>	EXP	1963				MED	0	4.80	0.0242	
<i>batmanicum</i>	EXP	1976				MED	0	0.18	0.0081	
<i>bejariense</i>	EXP	1963				AMR	0	1.18	0.0081	
<i>burchellianum</i>	EXP	1956				SSA	0	3.93	0.0322	
<i>canescens</i>	EXP	1953				MED	0	2.20	0.0483	
<i>caucasicum</i>	EXP	1990				MED	0	2.48	0.0081	
<i>cherleri</i>	EXP	1963				MED	0	10.47	0.0483	
<i>clypeatum</i>	EXP	1972				MED	0	1.01	0.0081	
<i>cryptopodium</i>	EXP	1962				SSA	0	2.94	0.0081	

<i>decorum</i>	EXP	1993				SSA	0	1.26	0.0081	
<i>echinatum</i>	EXP	1963				MED	0	5.58	0.0161	
<i>globosum</i>	EXP	1963				MED	0	1.02	0.0161	
<i>isthmocarpum</i>	EXP	1976				MED	0	4.13	0.0403	
<i>kingii</i>	EXP	1984				AMR	0	1.17	0	
<i>lappaceum</i>	EXP	1963				MED	0	10.90	0.0242	
<i>melchiorianum</i>	EXP	1977				MED	0	4.43	0.0322	
<i>montanum</i>	EXP	1990				MED	0	12.17	0.0242	
<i>nigrescens</i>	EXP	1972				MED	0	8.93	0.0161	
<i>obscurum</i>	EXP	1963				MED	0	3.97	0.0322	
<i>pallidum</i>	EXP	1953				MED	0	5.36	0.0403	
<i>pannonicum</i>	EXP	1906				MED	0	3.78	0.0725	
<i>parryi</i>	EXP	1969				AMR	0	1.01	0.0081	
<i>patens</i>	EXP	1963				MED	0	3.85	0.0081	
<i>polymorphum</i>	EXP	1992				AMR	0	6.42	0.0081	
<i>purpureum</i>	EXP	1963				MED	0	10.79	0.0161	
<i>rueppellianum</i>	EXP	1962				SSA	0	6.88	0.0081	
<i>semipilosum</i>	EXP	1972				SSA	0	3.35	0.0564	
<i>spumosum</i>	EXP	1963				MED	0	5.20	0.0242	
<i>squarrosus</i>	EXP	1963				MED	0	6.17	0.0322	
<i>stellatum</i>	EXP	1963				MED	0	10.58	0.0161	
<i>tembense</i>	EXP	1962				SSA	0	3.93	0.0322	
<i>thalii</i>	EXP	1975				MED	0	0.93	0.0161	
<i>trichocephalum</i>	EXP	1972				MED	0	2.03	0.0483	
<i>tumens</i>	EXP	1963				MED	0	2.80	0.0483	
<i>usambarense</i>	EXP	1962				SSA	0	5.69	0.0242	
<i>vesiculosum</i>	EXP	1962				MED	0	2.88	0.1047	
<i>willdenovii</i>	EXP	1963				AMR	0	1.23	0.0081	
<i>alpinum</i>	HOR	1933				MED	0	0.51	188.14	
<i>uniflorum</i>	HOR	1880				MED	0	1.54	164.11	

Table AP3.2. The 16 unintentionally introduced-naturalised *Trifolium* species, including naturalisation date, current distribution in New Zealand, and selected explanatory variables. For centre of origin, MED = Mediterranean, SSA = sub-Saharan Africa, and AMR = America. See Table 2.3 for other variable units and coding. ND = data not available.

Species	Nat. date	Current dist. (coarse-scale)	Current dist. (fine-scale)	Centre of origin	Present in Britain?	Native range area ($\times 10^{12}$)	Estimated hectares planted	Freq. as pasture seed contam.	Match to New Zealand climate	New Zealand flowering length
<i>angustifolium</i>	1938	5	14	MED	0	9.29	0.0161	0	507	6
<i>arvense</i>	1876	10	83	MED	1	26.55	0.1531	2	518	10
<i>aureum</i>	1891	4	20	MED	0	11.23	0	0	508	5
<i>campestre</i>	1867	9	46	MED	1	20.07	0.0645	1	518	7
<i>cernuum</i>	1929	7	17	MED	0	1.57	0.0081	1	379	8
<i>glomeratum</i>	1869	8	44	MED	1	7.68	0.2498	2	498	5
<i>micranthum</i>	1854	5	23	MED	1	9.96	0.0403	0	445	4
<i>ochroleucum</i>	1879	1	3	MED	1	8.93	0	0	445	ND
<i>ornithopodioides</i>	1930	8	26	MED	1	5.41	0.0322	1	430	8
<i>resupinatum</i>	1872	4	22	MED	1	12.54	0.0725	1	505	3
<i>retusum</i>	1966	2	2	MED	0	6.29	0.0081	0	452	1
<i>scabrum</i>	1879	4	9	MED	1	12.05	0.0081	0	518	1
<i>squamosum</i>	1879	1	2	MED	1	10.90	0.0242	0	444	ND
<i>striatum</i>	1876	6	44	MED	1	10.06	0.0806	2	517	4
<i>suffocatum</i>	1907	4	14	MED	1	8.93	0.0081	0	445	8
<i>tomentosum</i>	1891	5	21	MED	0	11.35	0	0	433	5