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**Conservation of forest biodiversity and ecosystem services in a
pastoral landscape of the Ecuadorian Andes**

A thesis
submitted in partial fulfilment
of the requirements for the Degree of
Master of International Nature Conservation

at
Lincoln University
by
Chloe A. MacLaren

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by

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High Andean cloudforests are home to a variety of unique wildlife, and are important providers of ecosystem services to people in the Andean regions. The extent of these forests has been severely reduced by agricultural expansion, threatening the future of Andean biodiversity, and the future of the Andean people who rely on forest-provided ecosystem services. However, agriculture is also important for food and for livelihoods, so a balance needs to be found between agricultural production and the conservation of forest biodiversity and ecosystem services.

Retaining forest vegetation can mitigate the impacts of forest conversion to pasture on biodiversity and ecosystem services. Remnant and regenerating forest vegetation in pastures contributes to the conservation of many forest plant species, as well as to the maintenance of several ecosystem services. Both biodiversity and ecosystem services increase in pastoral landscapes as tree cover increases. However, pasture productivity diminishes as tree cover increases, so that incorporating forest vegetation into pasture potentially compromises agricultural yields. The aim of this thesis is to identify how Andean farmers can maintain biodiversity and ecosystem services on their land whilst minimising any trade-offs with farm productivity.

Keywords: Biodiversity, ecosystem services, high Andean cloudforest, Papallacta, land-sharing, deforestation, agriculture, remnant vegetation.

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Chapter 1

Introduction

1.1 Adapting to climate change in the Andes

Climate change is a major threat to agriculture worldwide (Intergovernmental Panel on Climate Change (IPCC), 2007; Lobell and Gourджи, 2012). Changing temperatures and weather patterns are changing the environments in which we farm, and conventional farming practices may lack the capacity to adapt to these new conditions (Howden *et al.*, 2007; de Schutter, 2010). In the Andes, the effects of climate change can already be felt (Vuille *et al.*, 2008; Carey, 2010). Temperatures have been rising in the Andes since the 1940s, and while many nations are still absorbed in the debate of whether to acknowledge the existence anthropogenic climate change, the Andean nations are already struggling with its realities (Vuille *et al.*, 2008; Perez *et al.*, 2010). Near-surface temperatures have risen at around 0.1°C a decade, leading to a 0.7°C increase in average temperature in the last 70 years (Vuille *et al.*, 2008). Andean glaciers have retreated by 30% since the 1970s, and the freezing level height has risen by almost 75m (Vuille *et al.*, 2008). Loss of these ice reserves severely threatens water security in the region, as meltwater from glaciers and snowfall provides much of the water supply to both rural and urban populations in Andean nations (Carey, 2010). In addition, the frequency and intensity of extreme weather events, especially those associated with the El Niño cycle, are rising (Yeh *et al.*, 2009; Ministry for the Environment, 2011).

Andean countries are faced with the challenge of adapting to climate change, or suffering a reduced quality of life as their water supplies and agricultural production are impacted (Vergara, 2009; Perez *et al.*, 2010). Some of the most vulnerable people in these nations are the rural communities, whose incomes and livelihoods are influenced directly by climate impacts on agriculture (Perez *et al.*, 2010; Ministry of the Environment of Ecuador, 2011). One form of adaptation being widely promoted to these people in the Andean region is ecosystem-based adaptation, which 'integrates the use of biodiversity and ecosystem services into an overall strategy to help people adapt to the adverse impacts of climate change' (Colls *et al.*, 2009). This approach to adaptation is a response to worldwide experiences which indicate that many technological adaptations to climate change impacts (e.g. water supply infrastructure, flood defence walls) either fail to solve all of the problems caused by climate change, or cause further problems themselves by undermining local ecosystem functioning (Andrade Pérez *et al.*, 2010).

Ecosystem-based adaptation focuses on creating resilient ecosystems that provide a sustainable natural resource base to support human livelihoods and quality of life (Colls *et al.*, 2009; Andrade Pérez *et al.*, 2010). The ways in which ecosystems contribute to human welfare and survival are termed 'ecosystem services'. These include a wide variety of life-supporting processes such as nutrient cycling and water regulation (Millenium Ecosystem Assessment (MA), 2005). It has been shown that biodiversity is the source from which these ecosystem services are generated (Cardinale *et al.*, 2012; Naeem *et al.*, 2012), and therefore one approach to ecosystem-based adaptation is the restoration of biodiversity and natural habitats (Andrade Pérez *et al.*, 2010). For example, people living around the Chingaza Massif mountains of Colombia are restoring native plants to upper watersheds, riversides and landslide areas to improve water regulation and carbon sequestration, and reduce soil erosion (Colls *et al.*, 2009). In Madagascar, reforestation is being used to restore biodiversity and ecosystem services (such as water provision, flood regulation and erosion control) to increase their resilience in the face of climate change (Andrade Pérez *et al.*, 2010).

1.2 Care International and the upper Papallacta valley

This thesis is part of a project by the humanitarian organisation Care International to investigate a range of measures that could contribute to improving resilience to climate change in highland agriculture of the Ecuadorian Andes (Care, 2009). The project falls under the umbrella of the Project for Adaptation to the Impact of Rapid Glacier Retreat in the Tropical Andes (PRAA; Spanish acronym), a joint initiative between the governments of Ecuador, Peru and Bolivia. It is funded by the World Bank and implemented by Care International.

One of the adaptation measures selected for investigation in Ecuador by Care International is the retention of forest vegetation within pastoral landscapes. Remnant forest vegetation scattered throughout pastures is a fairly common sight in highland Ecuador, and Care International want to understand whether this practice should be promoted, and whether efforts should be made to persuade farmers to plant more woody vegetation in and around their pastures. Currently, vegetation is either left standing by farmers as they clear forests to create new pastures, or it re-establishes in cleared pastures through dispersal by birds or cattle (Murgueitio, 2004). Farmers leave standing trees and forest remnants primarily as shelter for cattle, as well as for additional forage and a timber supply (Harvey *et al.*, 2011; Harvey and Haber, 1999). Some farmers also believe it improves the quality of their pastures, and some leave it simply for 'Pachamama', the South American equivalent of Mother Nature (pers.comm., local farmers; Harvey and Haber 1999).

The research presented here took place in the upper Papallacta valley, which lies in the highest areas of the Napo Province, on the eastern slopes of the Andes (Figure 1.1). The upper Papallacta valley is a pastoral landscape that lies between two large protected areas, the Antisana Ecological Reserve and the Cayambe-Coca Ecological Reserve (Figure 1.2). The areas of the upper Papallacta valley that have not been cleared for agricultural are covered by high montane cloudforest (Figure 1.3). This vegetation type is found throughout the Andes, and is also referred to as 'elfin forest' (Lauer and Rafiqpoor, 2000), 'montane ceja' (Paniagua-Zambrano *et al.*, 2003), 'high montane evergreen forest' (Salgado, 2008) and 'humid high montane forest' (Pillajo and Pillajo, 2010). A comparison of published species lists suggests that this forest type is quite variable in its composition throughout the Andes, in terms of both species and genera (Young, 1993; Lauer and Rafiqpoor, 2000; Young and Keating, 2001; Sarmiento and Frolich, 2002; Paniagua-Zambrano *et al.*, 2003; Salgado, 2008). These changes in composition may be due to spatial climate variation in relation to the topography and rainshadow effects of the Andes (Salgado, 2008).

Within Ecuador, this type of forest has been almost entirely cleared from the highlands (Jokisch and Lair, 2002; Sarmiento 2002a). Some extensive areas remain on the western and eastern slopes of the Andes, and the upper Papallacta valley lies between two such forest areas. High montane cloudforest in the Papallacta area is important for several key ecosystem services that support both local rural populations, and downstream urban populations. The first of these is water regulation. Climate change is causing glacial retreat and leading to warmer and drier conditions in Andean environments, threatening the region with water shortages (Vuille *et al.*, 2008; Buytaert *et al.*, 2011). Forest cover is known to conserve water in the soil by maintaining low temperatures and so preventing evaporation, and creating a soil structure that allows high infiltration (Murcia, 1995; Gehlhausen *et al.*, 2000; Breshears, 2006). Therefore, maintaining or increasing forest cover is expected to contribute to higher moisture levels in the landscape, which are beneficial to local agriculture, as well as downstream populations that rely on mountain catchments for their water supply. The upper Papallacta valley is part of the catchment that supplies drinking water to Quito, Ecuador's capital city with 2.5 million inhabitants (Figure 1.1).

Given the difficulties posed by climate change, there is significant interest in maximising the abilities of ecosystems to sequester carbon (Colls *et al.*, 2009). High Andean ecosystems have naturally high stores of carbon in their soils, as the high humidity and low soil temperatures prevent organic matter from being decomposed (Buytaert *et al.*, 2011). Climate change is expected to reduce this capacity by creating conditions that lead to warmer, drier

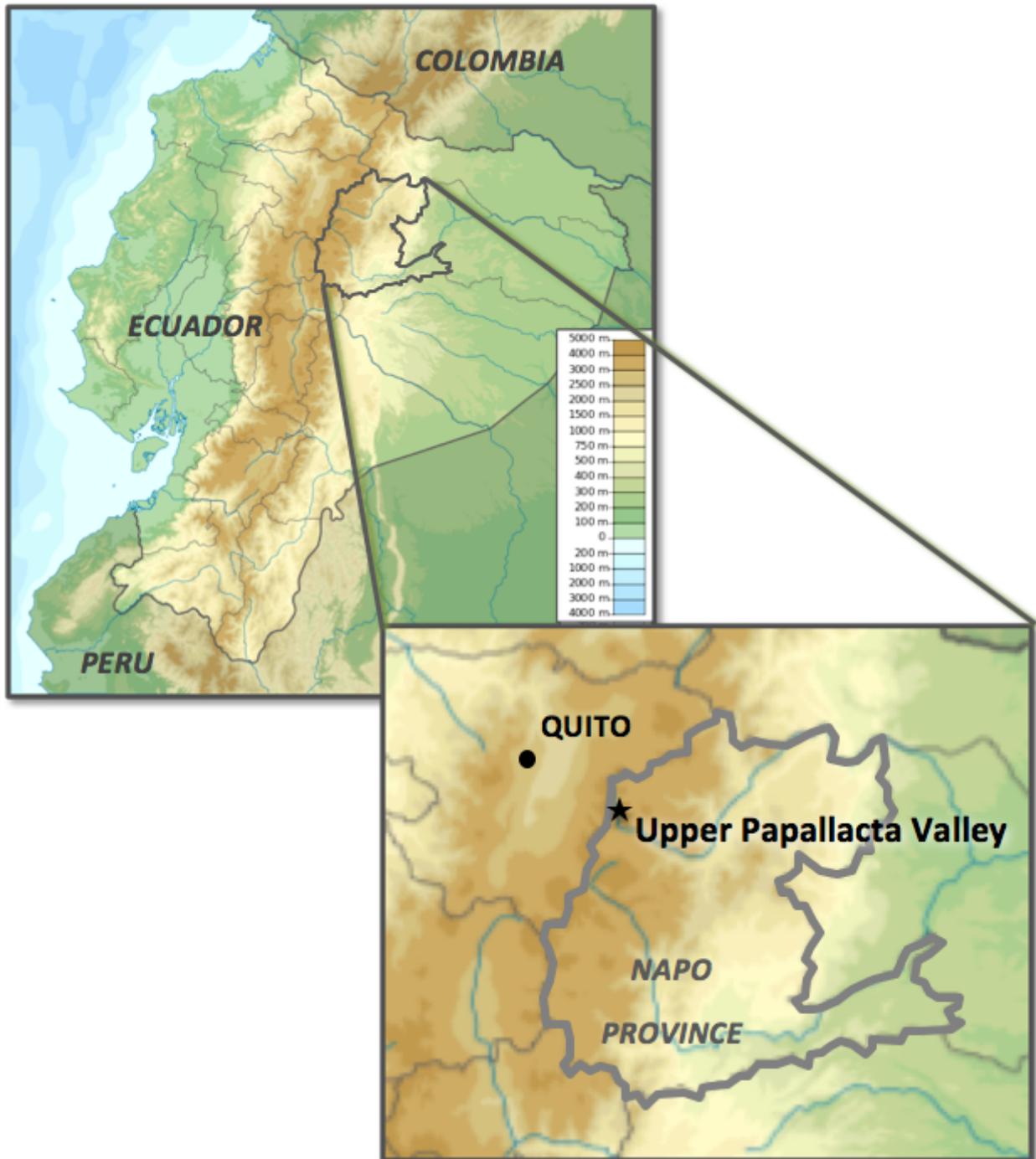


Figure 1.1: The location of the Napo Province within Ecuador, and the location of the upper Papallacta valley within the Napo Province. The upper Papallacta valley is approximately 50km eastward of the capital city Quito.

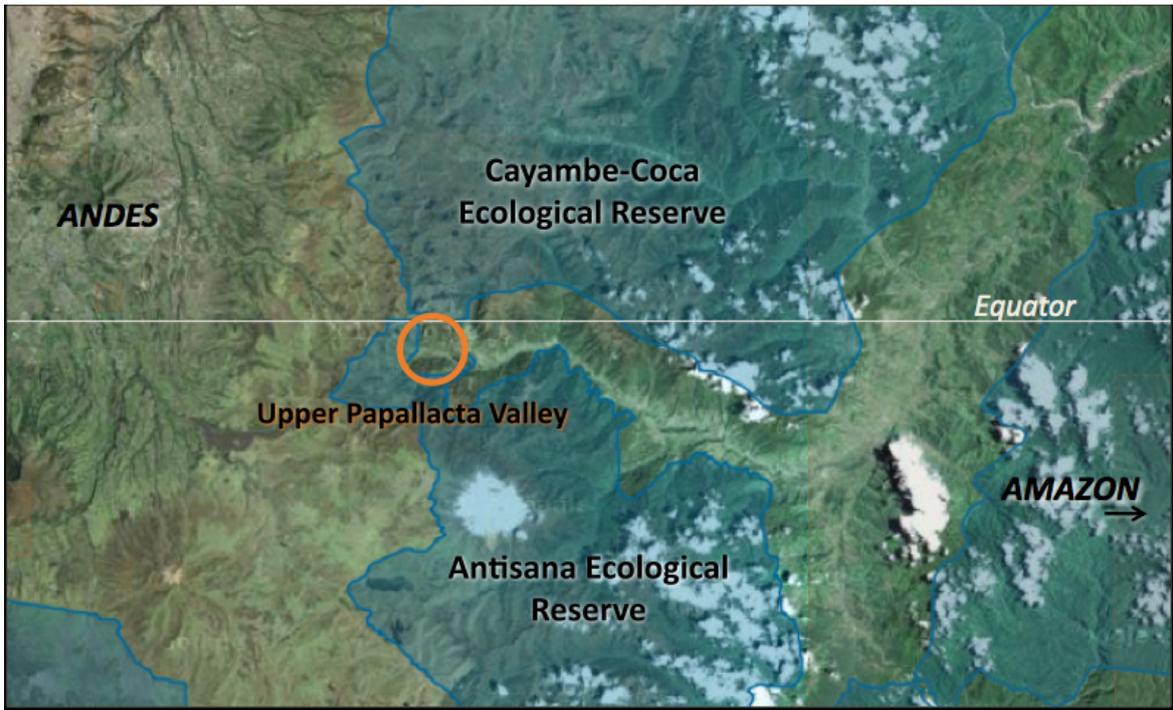


Figure 1.2: The location of the upper Papallacta valley between the Antisana and Cayambe-Coca Ecological Reserves.



Figure 1.3: Typical high montane cloudforest of the upper Papallacta valley.

soils, and allow more carbon to be released (Buytaert *et al.*, 2011). Maintaining forest cover may be able to slow this trend, by contributing to a cooler, more humid microclimate at ground level (Breshears, 2006).

The biodiversity of high montane cloudforest is important for a variety of other ecosystem services, including resources of timber, traditional foods, and medicines for local people (Pillajo and Pillajo, 2010). Several charismatic animals of the cloudforest, including the spectacled bear (*Tremarctos ornatus*), the mountain tapir (*Tapirus pinchaque*), and a variety of hummingbirds, make it an important tourist attraction, which brings additional income for the local communities. High montane cloudforest is also important simply because it is a unique natural habitat. Ecuador's national Constitution reminds us that nature has its own right to persist and that we have a duty to protect that right:

"Nature, or Pachamama, where life is reproduced and occurs, has the right to integral respect for its existence and for the maintenance and regeneration of its life cycles, structure, functions and evolutionary processes ... Ecuadorians have the duty and obligation to respect the rights of nature, preserve a healthy environment and use natural resources rationally, sustainably and durably."

Republic of Ecuador, 2008

1.3 Maintaining remnant forest trees for conservation within pastoral landscapes

The most widespread human activity in the upper Papallacta valley is pastoral livestock raising for milk and meat. This has led to substantial clearance of forest in the valley: cloudforest still remains on the steep slopes on either side of the valley, but in the lower areas the forest has become reduced and fragmented through clearance for pastures. The agricultural areas are now a mosaic of open pastures, pastures with scattered trees and woody shrubs, and forest fragments (Figure 1.4). Forest conversion to pasture is generally associated with the loss of biodiversity and ecosystem services (Pearce, 2001; Steffan-Dewenter, 2007; Foley *et al.*, 2007; Balmford *et al.*, 2012), but it is possible that this effect could be mitigated by increasing tree cover within this mosaic landscape (Luoma, 2004; Jose, 2009).

Trees and forest patches in agricultural areas can contribute to the conservation of biodiversity and ecosystem services by altering the environmental conditions found within pastures (Figure 1.5). The major above ground influences of trees are the interception of solar radiation and of precipitation, which create a microclimate beneath the tree's canopy that is distinct from the surrounding open areas (Scholes and Archer, 1997; Breshears, 2006;

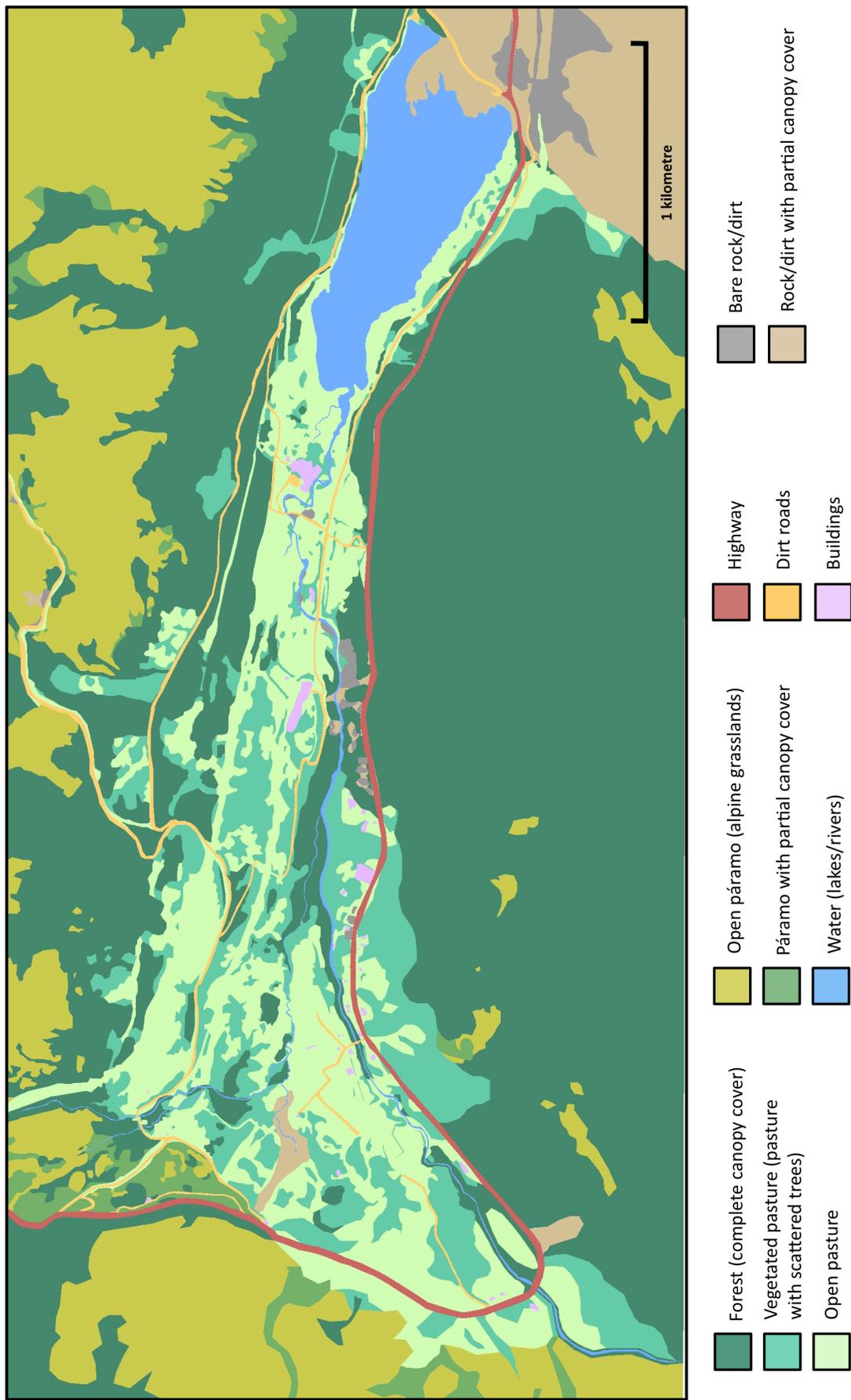


Figure 1.4: The upper Papallacta valley.

Manning *et al.*, 2006; Sánchez-Járdon *et al.*, 2010). Environments beneath tree cover are generally subject to less extreme temperatures, receive lower precipitation and so have less run-off, yet have higher soil moisture due to lower soil temperatures and consequently lower evaporation (Breshears, 2006). As described above, lower soil temperatures and lower soil evaporation lead to higher landscape moisture levels, and a higher capacity for carbon storage within soils.

Another major benefit of trees in pasture is their effects on soil nutrients. Trees can take up nutrients from soil levels lower than pasture grasses can, and these nutrients are then added to the topsoil via litterfall (Jóbbagy and Jackson, 2004; Manning *et al.*, 2006). This can contribute to the productivity of that land in terms of crop or pasture growth (Jose, 2009; Sánchez-Járdon *et al.*, 2010). In addition, trees contribute to preventing soil erosion by sheltering the soil surface from the impact of precipitation and stabilising it with their roots (Pimental and Kounang, 1998; Ataroff, 2002). Soil erosion is associated with the loss of nutrients from the landscape, and thus preventing erosion contributes to a more fertile farming environment (Lal, 2009).

Trees can provide habitats and resources to plants, animals and microbes that are otherwise usually absent in pasture (Nadkarni and Matelson, 1989; Guevara *et al.*, 1992; Harvey and Haber 1999; Cunningham *et al.*, 2008) (Figure 1.6). This associated biodiversity is responsible for the provision of many additional ecosystem services, such as pollination and supporting populations of predators that control agricultural pests (Sperber *et al.*, 2004; Steffan-Dewenter *et al.*, 2005; Bianchi *et al.*, 2006). In addition, the diversity and reliability of ecosystem services (particularly in the face of a changing climate) is known to increase as biodiversity increases (see Chapter 4; Naeem *et al.*, 2012).

Overall, increasing tree cover in pastoral landscapes creates an environment more similar to forest, and so is expected to be associated with increasing levels of forest biodiversity and ecosystem services. This has benefits for people living both inside and outside the upper Papallacta valley, specifically regarding resilience to climate change (Table 1.1). There are also intrinsic benefits for 'Pachamama' by creating an agroecological system in which nature can at least partially continue "*its existence and ... maintenance and regeneration of its life cycles, structure, functions and evolutionary processes*" (Republic of Ecuador, 2008). The mosaic of open pastures, vegetated pasture and forest fragments found within the upper Papallacta valley is representative of many pastoral landscapes in the high Andes of Ecuador, and so it is hoped the results of this research can also be used to inform land management decisions in other areas.

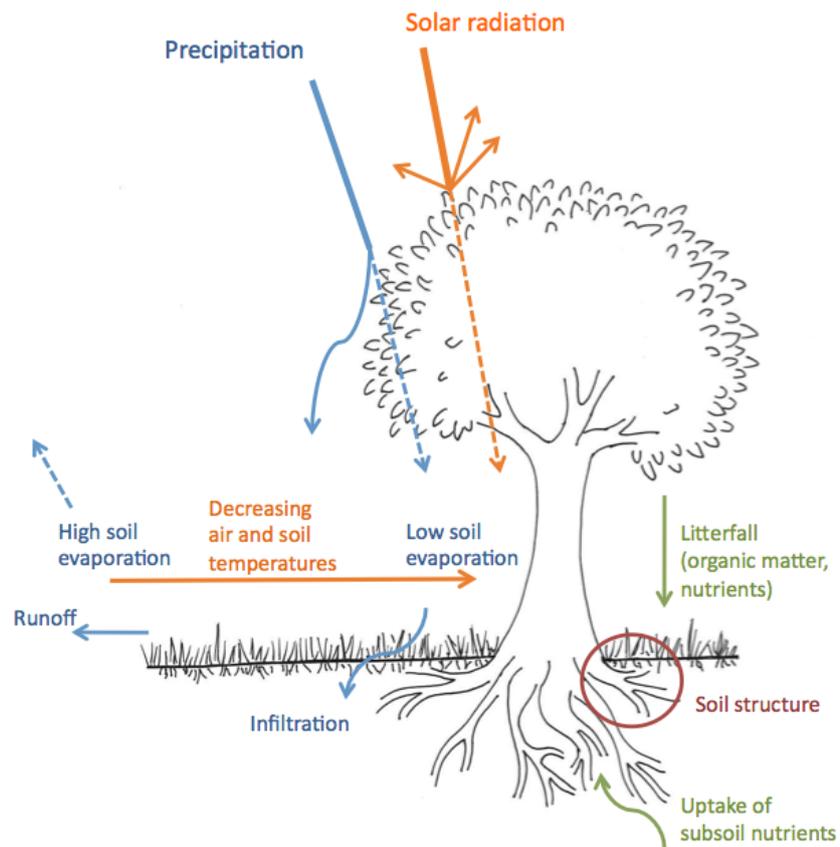


Figure 1.5: Interactions between a pastoral tree and its environment.

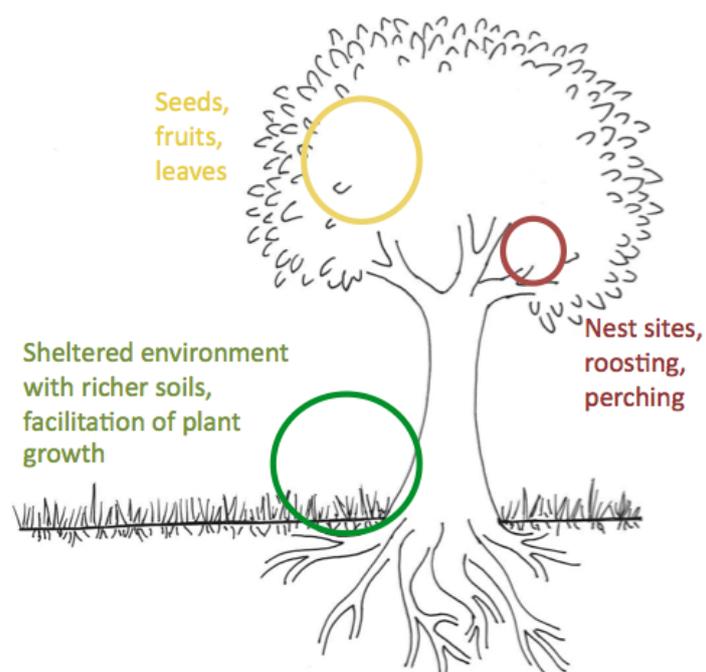


Figure 1.6: Some possible ways in which trees provide habitats and resources to other species which are not found in open pasture.

1.4 Investigating the role of remnant vegetation in the conservation of biodiversity and ecosystem service provision: thesis outline

To assess the benefits provided by remnant and regenerating vegetation in pastures, this thesis begins by defining the plant communities found within the upper Papallacta valley, and how these relate to both environmental variability and agricultural land use (Chapter 3). This provides a first step in understanding how human activities affect the natural vegetation, as well as how remnant and regenerating pasture contribute to conserving the natural community types of the area.

Chapter 4 focuses on quantifying the levels of biodiversity and ecosystem properties of different plant communities found within the upper Papallacta valley, and how these vary in relation to natural and agricultural factors. The ecosystem properties assessed have been chosen for their relevance to ecosystem services which will aid resilience to climate change: soil moisture to represent water retention capacity; soil organic matter to represent soil carbon and nutrient levels; and tree regeneration to represent a timber supply. Woody plant species richness was used as a measure of biodiversity (see Chapter 3 for more detail).

Chapter 5 explores alternative approaches for integrating farming and nature conservation in the upper Papallacta valley. Although tree cover has the potential to greatly improve biodiversity and ecosystem services, this is not necessarily directly linked to improved farm productivity. Trees may also have some negative effects on pasture productivity as a result of competition with the pasture grasses for light, water and soil nutrients (Scholes and Archer, 1997; Ludwig *et al.*, 2004). If these negative interactions are stronger than the positive ones (e.g. trees increasing soil fertility through litterfall), then overall pasture productivity decreases (Sánchez-Járdon *et al.*, 2010), and the benefits of increased tree cover may be highly compromised from the farmers' point of view. Therefore the effect of tree cover on pasture productivity is investigated, and compared with the ecosystem service and biodiversity benefits provided by tree cover. Different methods of integrating tree cover and pasture are explored, and their relative performance assessed. This builds on the findings of the first two chapters regarding biodiversity and ecosystem services in an applied management context.

Chapter 6 discusses the overall contributions of forests and remnant forest vegetation to conserving biodiversity and ecosystems in pastoral landscapes of the high Andes. Management recommendations are developed to improve the conservation of ecosystem services and biodiversity within such landscapes, taking into account the necessity of farm production for local livelihoods.

Table 1.1: A summary of the potential benefits and drawbacks of increasing tree cover in the upper Papallacta valley. Effects marked with an asterisk * are those explored in this thesis.

Ecosystem services for agriculture inside the valley	Non-agricultural benefits provided inside the valley	Ecosystem services provided to people outside the valley
Water retained in the landscape * - improved pasture productivity in dry periods	Biodiversity conserved * - food and medicine supplies	Water retained in the landscape * - greater security of drinking water supply - reduced risks of flooding
Topsoil nutrients replenished * - Improved pasture productivity	Charismatic flora and fauna conserved - tourist attraction (income)	Carbon stored in the landscape * - contribution to mitigating climate change
Biodiversity conserved * - conservation of unidentified ecosystem services		Charismatic flora and fauna conserved - cultural importance
Shelter and additional forage provided for livestock - improved livestock health and productivity		

Chapter 2

Methods

2.1 Methods overview

This thesis first characterises the woody plant community of the upper Papallacta valley and its relationship with environmental variation (Chapter 3), then investigates how biodiversity and ecosystem services are related to environmental variation (Chapter 4). Finally, it explores how conservation can best be integrated with pastoral agriculture (Chapter 5). The analyses used in these investigations are listed in Table 2.1.

This chapter describes all of the methods that are used in more than one data chapter of this thesis. Common to all data chapters are the study area (Section 2.2), the sample sites and layout (2.3), the collection of geographical data and creation of the site map (2.4), and the collection of the vegetation data (2.5). Regression models with identical explanatory variables are used in both Chapters 3 and 4, so the modelling procedure and the explanatory variables are outlined here (Section 2.6). All other analyses and the collection of relevant data are described within in each chapter (Table 2.1).

Table 2.1: Overview of the analyses used in each data chapter of this thesis.

Chapter	Analysis	Purpose of analysis
Chapter 3 Classifying the composition of woody plant communities in the upper Papallacta valley	Cluster analysis and indicator species analysis	<i>To identify different plant community types and the species that characterise them.</i>
	Ordination: non-metric multidimensional scaling	<i>To identify trends in community composition variation between sites.</i>
	Regression modelling (of ordination results and environmental variables)	<i>To identify whether trends in community composition are associated with environmental variables.</i>
Chapter 4 Biodiversity and ecosystem services in relation to environmental variation	Regression modelling of ecosystem properties and environmental variables	<i>To identify whether the ecosystem properties (which represent biodiversity and ecosystem services) are associated with environmental variables.</i>
Chapter 5 Optimising land use to balance conservation and agricultural productivity	Calculation of average values of ecosystem properties and pasture productivity for different land cover types	<i>To identify how different land cover types contribute to pasture productivity and to the conservation of biodiversity and ecosystem services.</i>
	Comparison of different land use scenarios made up from different land cover types	<i>To identify the scenario that maximises pasture productivity as well as conservation of biodiversity and ecosystem services.</i>

2.2 Study area

Data were collected from the upper Papallacta valley in the area between latitudes 0°22'125" and 0°23'110", and longitudes 78°9'535" and 78°11'150". The area is located on the eastern slopes of the Andes, just below the treeline. The minimum altitude was 3355 m.s.l, and the maximum altitude was 3752 m.s.l. The Papallacta valley is a mosaic landscape of forest, remnant forest vegetation, and pasture (Figure 2.1).

2.3 Sample sites and layout

All data were collected from 10 × 10 metre quadrats (0.1 ha) located at sites across the landscape representative of the range of different vegetation types found in the study area (Figure 2.1). Sites were placed at least fifty metres away from the nearest site to avoid sampling sites which were very similar to one another merely due to their proximity. Terrain too steep to work safely on was avoided, as were areas with standing surface water. Data were collected between 1st December 2011 and 30th March 2012.

2.4 Geographical data collection and map creation

The geographical coordinates of each site were recorded using a Garmin eTrex 20 handheld GPS device. A map of the study area (Figure 2.1) was created using the software ArcMap 10 (ESRI, 2011) based on satellite imagery from Google Earth (2012). Different land cover types visible on the Google Earth satellite image were digitised by hand in ArcMap 10 and were ground-truthed at each site and at a variety of other points across the study area.

2.5 Vegetation data collection

The abundance of every woody plant species found within each 10 × 10m sample site was recorded. No plant shorter than 30cm in height was recorded, so that only established individuals were counted. Plant species were identified using the illustrated guidebook by Pillajo and Pillajo (2011), and plants not included in the guidebook were identified at the National Herbarium of Ecuador. An inventory of all woody plant species encountered during this study can be found in Appendix A.

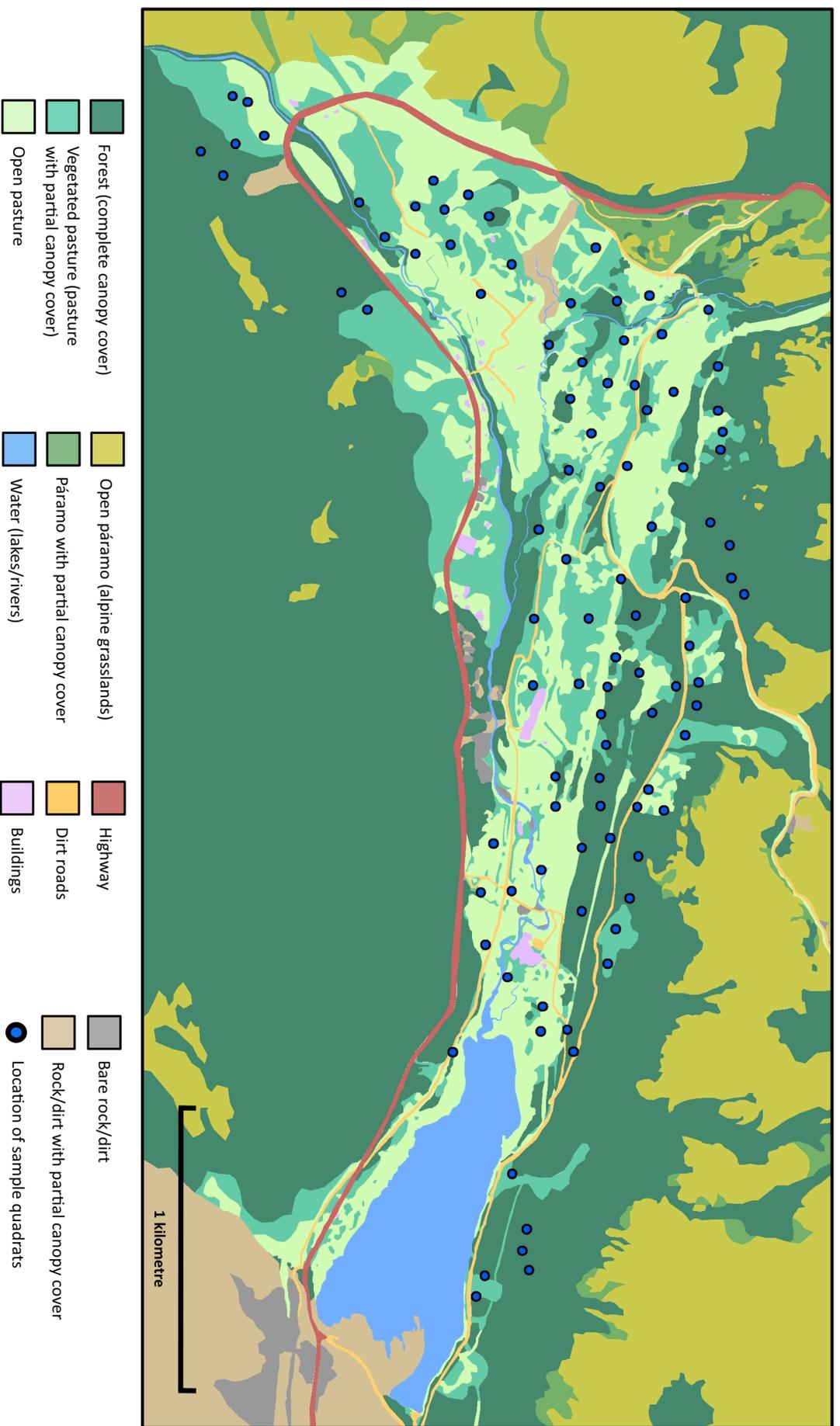


Figure 2.1: Map of the upper Papallacta valley showing the locations of sample quadrats.

2.6 Regression Modelling

Regression models are employed in Chapter 3 to explore which environmental variables are related to the changes in plant community composition identified in the nonmetric multidimensional scaling ordination. They are also used in Chapter 4 to investigate variation in biodiversity and specific ecosystem properties in relation to environmental variables.

The regression approach used is generalised least squares (GLS), a common regression method used when dealing with spatial data. Generalised least squares is robust to correlations in the response (Crawley, 2007), which are often present in spatial datasets if samples close to one another are more similar than sites more distant from one another.

2.6.1 Explanatory variable selection

The explanatory variables used in this study were selected to be representative of the range of environmental variables known to influence plant communities, whilst avoiding variables that were highly correlated with one another. The focus of the models is to explore the data, so the variables were chosen to give a broad overall picture of trends across the study area. The final variables and the rationale for using them in the models, are outlined below. All variables were standardised¹ before entering them into the model so that the regression coefficients were not affected by variables of different scales.

Altitude

The altitude of each site in metres above sea level was recorded using a Garmin eTrex 20 handheld GPS device. Altitude is considered to be a surrogate variable for climatic variables that were not able to be measured within the scope of this study, such as differences in temperature, precipitation, frost occurrence and wind exposure between the upper part and lower parts of the study area.

Percent canopy cover

Percent canopy cover, or the percent of sky obscured by branches and foliage over the site, was estimated visually from the centre point of the site. This variable was selected as a measure of the land use type, as it varies from zero in open pasture to eighty percent cover in undisturbed forest sites, with intermediate percent covers in vegetated pastures and forest edges. The variable correlates with other measures of the quantity or quality of forest in the vicinity of the site, and is therefore considered to be an overall representative measure of how similar the site is to natural undisturbed forest.

¹ Variables were standardised using the formula: $[x - \text{mean}(x)]/[\text{standard.deviation}(x)]$ (where x = the variable).

Hoofprint intensity

The level of livestock disturbance was recorded by visually estimating hoofprint intensity as either 'none' (no visible hoofprints), 'low' (some hoofprints visible in some parts of the quadrat) or 'high' (heavy prints obvious over at least 50% of the quadrat). Hoofprint intensity is a widely used measure of the intensity of livestock use of an area (e.g. Kohler *et al.* 2006, Dunne *et al.*, 2011). The dominant agricultural practice in the upper Papallacta valley is livestock farming, so stock movement and grazing is the most relevant aspect of agricultural disturbance on the vegetation. Creation of pasture by clearing forest is obviously also a significant part of the effects of agriculture on native ecosystems, but this is represented by the percent canopy cover variable above.

Nearest patch influence

To create this variable, the size of the nearest patch of each vegetation cover type (forest, vegetated pasture and open pasture) was divided by its distance from the sample site. The resulting value quantifies the influences of the nearby habitat patches (e.g. as sources of seeds, herbivores, pollinators etc) on the sample site, given that strength of any influence typically depends on the size of the patch, and its distance from the sample point (Collinge, 2009). Three versions of this variable are included in the model: one for forest patches, one for vegetated pasture patches, and one for open pasture patches. The size of the patch area and its distance from the sample site were calculated in ArcMap 10 (ESRI, 2011).

Distance to edge of own patch

The distance to the edge of each site's own habitat patch was calculated in ArcMap 10 (ESRI, 2011). This variable represents the influence of edge effects (see Chapter 3 for a definition and explanation of edge effects). This was entered into the model as an interaction term with whether the site was located in forest, vegetated pasture, or open pasture. Using the interaction term allows differences in vegetation types to be accounted for; e.g. edge effects within forest are likely to be the opposite of edge effects within pasture, as forest edges may receive more light than forest interiors, but pasture edges are tend to be more shaded than pasture interiors (see Chapter 3 for an explanation of edge effects).

2.6.2 Model diagnostics

Model diagnostics were performed on each model to check for violations in the regression model assumptions. Firstly, plots of the residual vs. fitted values were used to test the assumption of a linear relationship between the explanatory variables and response variable. Normal quantile-quantile (QQ) plots are used to test the assumption of Normality in the

distribution of the residuals. Semivariograms are used to check for the presence of spatial autocorrelation in the residuals, which would identify if any of the variation not explained by the model can be accounted for by the spatial layout of the sample sites (Crawley, 2007).

Plots for the model diagnostics for both Chapters 3 and 4 can all be found in Appendix B. Where the diagnostics are not referred to in the results of each chapter, there were no perceived violations of the model approach.

Multicollinearity between the explanatory variables was also investigated (Table 2.2 and Figure 2.2), as this can affect which variables are shown to be significant in the model. Levels of correlation between most variables in the models were below $R=0.4$ (Table 2.2) and so considered negligible. However, there was some indication of correlation between percent canopy cover and hoofprint intensity (Figure 2.2). The effects of this are explored in Chapter 3 (Section 3.3.2).

Table 2.2: Pearson's correlation co-efficients between numerical explanatory variables of the regression model.

	Altitude	% Canopy cover	Forest patch influence	Vegetated pasture patch influence	Open pasture patch influence
% Canopy cover	0.00				
Forest patch influence	0.12	-0.13			
Vegetated pasture patch influence	0.15	-0.12	-0.09		
Open pasture patch influence	0.18	-0.00	-0.08	-0.06	
Distance from own patch edge	0.26	0.34	-0.04	-0.21	-0.17

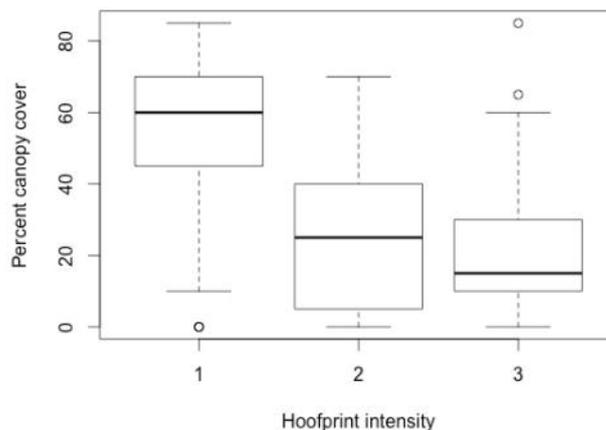


Figure 2.2: Evidence of a negative correlation between hoofprint intensity and percent canopy cover (correlation co-efficients cannot be calculated for categorical variables).

Chapter 3

Classifying the composition of woody plant communities within the upper Papallacta valley

3.1 Introduction

3.1.1 Forest communities and environmental variation

In order to understand how forests may best be conserved in the face of anthropogenic disturbance, we need to know how that disturbance affects the species that make up those forests. This can be investigated by examining how the composition of the forest community changes in relation to disturbance (Rao *et al.*, 1990; Sagar *et al.*, 2003; Chabrierie *et al.* 2012). Differences in community composition between undisturbed and disturbed areas can indicate which species of the community are the most sensitive to that disturbance (Pettit *et al.*, 1995).

The composition of plant communities varies within landscapes in relation to local environmental conditions (Ozinga *et al.*, 2005; Acebes *et al.*, 2010; Tsai *et al.*, 2012). These conditions determine which plants can establish and survive in which locations (Lortie *et al.*, 2004), and so spatial variation in environmental conditions leads to spatial variation in plant community composition (Ozinga *et al.*, 2005). Variation in environmental conditions is often natural, such as the change in temperatures from low to high altitudes. In the high Andes of Ecuador, it is typical for average temperatures to decrease by 0.5-0.75°C with every 100m increase in altitude (Lauer and Rafiqpoor, 2000). Other climatic variables, such as precipitation levels and fog cover, may also vary in relation to altitude (Beck and Richter, 2008). Such changes in physical conditions affect which species are capable of survival, and thus alter the observed community composition (Pellisier *et al.*, 2010).

Human activities are often major drivers of environmental variation within landscapes. For example, pastoral agriculture is a widespread, persistent source of disturbance to forests throughout the Andes (Jokisch and Lair, 2002; Sarmiento 2002a; Rodríguez-Morales *et al.*, 2009). Local environmental conditions are altered by the removal of the canopy cover and the loss of the biogeochemical interactions between trees and soil (Reiners *et al.*, 1994; Holl, 1999). This creates an environment with higher light levels, an exposed microclimate, and different soil conditions, which favours a different set of species than those adapted to sheltered forest conditions (Reiners *et al.*, 1994). Any regenerating vegetation in pasture areas

is also subject to grazing (Pettit *et al.*, 1995; Posada *et al.*, 2000), competition with introduced pasture grasses (Sarmiento, 1997), and regular clearance by farmers.

There are also indirect impacts on adjacent areas of remaining forest, caused by the influences of the pasture environment on the edges of the forests. These are termed 'edge effects', and include a variety of changes in the physical and biotic environments (Murcia, 1995; Lopez-Barrera *et al.*, 2007). These differences in conditions and resources favour the growth of different sets of plants, and plant community composition is often found to vary between the edges and interiors of habitat patches (Young, 1993; Oosterhorn and Kapelle, 2000; Gehlhausen *et al.*, 2000). Commonly reported edge effects caused by open areas adjacent to forests are an increase in light levels, an increase in wind, and an increase in the variation of temperature and humidity (Saunders *et al.*, 1991; Young, 1993; Murcia, 1995; Gehlhausen, 2000; Lopez-Barrera *et al.*, 2007). These effects tend to shift forest communities towards pioneer communities, so that edges become dominated by a less diverse group of relatively fast-growing and short-lived species (Saunders *et al.*, 1991; Laurance *et al.*, 2006; Tabarelli, 2008; Broadbent *et al.*, 2008). Forest fragments that are small relative to the extent to which light can penetrate into the edge can have their original community entirely displaced by 'edge' vegetation (Harrison and Bruna, 1999; Tabarelli *et al.*, 2008).

Disturbances such as agriculture can also affect forest plant communities by isolating small patches of forest. In addition to being vulnerable to edge effects, patches with a small size typically contain smaller populations and each species is therefore subject to a higher probability of extinction through stochastic processes (Collinge, 2009). Isolation can also reduce the number of seeds dispersing to a patch from other patches, because the distance reduces the probability of seeds arriving at the patch (Collinge, 2009). This probability may be reduced further for species that rely on animals to disperse their seeds, if the animals are unable to migrate between patches (Jesus *et al.*, 2012). The higher extinction risk in smaller patches combined with reduced dispersal to such patches means that small, isolated forest fragments typically have fewer species than extensive forest areas. In particular, they tend to lack species that rely on animals for dispersal (Tscharntke *et al.*, 2005; Collinge, 2009; McConkey *et al.*, 2012).

3.1.2 The forest community of the upper Papallacta valley

This chapter aims to describe and classify the composition of plant communities in the upper Papallacta valley. The naturally occurring vegetation of the area is high montane cloudforest (Figure 3.1.a). As described in Chapter 1, this forest plays a major role in the

hydrology of the catchment, is an important carbon sink, and is a vital habitat for montane wildlife.

Much of the natural cloud-forest of the upper Papallacta valley has been cleared for pasture (Figure 3.2). The valley is now a mosaic of open pasture, small forest patches, and vegetated pasture with scattered remnant trees and shrubs. Some extensive forest areas remain on the mountain slopes (Figure 3.1, Figure 3.2). Given that the mosaic of pasture and remnant forest is typical of pastoral landscapes in the Andes (Sarmiento 2002a; Young, 2009), the findings from this chapter will be useful to inform forest management strategies throughout the region.



Figure 3.1: Typical examples of a) natural cloudforest, b) a forest edge or fragment, c) vegetated pasture and d) open pasture.

3.1.3 Aims

The specific aims of this chapter are to:

1. Classify the woody vegetation of the upper Papallacta valley into defined community types, and determine the compositional differences between these community types based on indicator species and beta-diversity.
2. Determine which environmental variables are associated with variation in community composition across the landscape.
3. Identify how the clearance and fragmentation of forest, in combination with grazing pressure from livestock, alters plant community types within the upper Papallacta valley.

3.2 Methods

3.2.1 Data preparation

83 out of the total 98 sites sampled were analysed in this chapter. The excluded sites were herb-dominated sites, which had too few woody plant individuals to allow for meaningful analysis of the woody plant community.

3.2.2 Cluster analysis, indicator species analysis and beta-diversity

Cluster analysis investigates which sites form distinct groups based on their species composition, allowing the identification of different vegetation types (Kent, 2012). In this study, cluster analysis was undertaken in PC-ORD, Version 6 (McCune and Mefford, 2011). An agglomerative method of clustering was used, which starts by pairing each sample site with another site to which it is most similar. This pair of sites is then paired to the most similar other pair, and so on until the specified number of clusters has been reached (the number of clusters is selected using indicator species analysis; see the following section). The distance measure used to calculate similarity between points was the Bray-Curtis/Sørensen measure. This is the quantitative version of the Sørensen index, which takes into account the abundance data of each species rather than just presence/absence data (Magurran, 2004). This analysis includes abundance data (Chapter 2), so Bray-Curtis was considered to provide a more complete picture of community types than presence/absence measures. The Bray-Curtis/Sørensen index gives shared species a double weighting, thus making sites where the same species occurs more likely to be placed closer together in the cluster analysis (Magurran, 2004). This weighting is based on the ecological reasoning that the presence of a species means that a species can definitely grow in a site, whilst the absence of a species does

not mean the species definitely cannot grow there. Shared presences are therefore more informative than shared absences (Peck, 2010).

To explore whether the compositional differences between clusters could be explained by the environmental conditions, box plots were used to visualise whether any clusters were associated with certain levels of environmental variables. The clusters were also mapped onto the study site to investigate any spatial patterns. This exploratory analysis into the relationship between the composition of plant communities and their environment is developed further in subsequent analyses, using a non-metric multidimensional scaling ordination and regression models (see Sections 3.2.3 and 3.2.4).

Indicator species analysis

Species that were associated with particular clusters were identified using an indicator species analysis (Peck, 2010). The output of the indicator species analysis is an ‘indicator value’ that is calculated by combining the average abundance of a species within a group with its constancy of occurrence in that group. An indicator value of 100 would show that the species is always found when that community type is sampled, and never found in any other community types. A value of 0, would show that the species abundance and constancy of occurrence is not significantly higher for any one community type than any other. These indicator values are tested for significance by randomly assigning sample units to different groups to assess whether the indicator value of a species is higher for a group than would be expected by chance (Peck, 2010).

The indicator species analysis was also used to confirm that the number of clusters used in the cluster analysis was an appropriate choice. The optimum number of clusters is the number that gives the highest number of significant indicator species: with fewer clusters, sites with relatively different compositions are grouped together so fewer species are found consistently throughout each cluster. With more clusters, sites with similar compositions are split apart so each species is more likely to be found in more than one cluster.

Analysis of beta-diversity

To determine which clusters were most similar to one another and which were most different, a pairwise measure of beta-diversity was calculated. The inverse Morisita-Horn Index was calculated between each of the clusters using the formula (Magurran, 2004):

$$C_{MH} = \frac{2 \sum (a_i \cdot b_i)}{(d_a + d_b) * (N_a * N_b)}$$

where N_a is the total number of individuals at site A; N_b is the total number at site B; a_i is the number of individuals in the i th species at site A; b_i is the number of individuals in the i th species at site B; and d_a and d_b are calculated as follows:

$$d_a = \frac{\sum a_i^2}{N_a^2}$$

Values of this index close to 0 indicate high similarity and values close to 1 indicate low similarity. The Morisita-Horn Index was chosen for this analysis as it has been shown to perform well in situations where plant abundances are highly variable between sample sites (Magurran, 2004).

3.2.3 Nonmetric multidimensional scaling ordination

Ordination is a method of pattern-matching analysis that describes how similar or different the community composition of different sample sites is, based on the multi-dimensional ‘distance’ between them in the ordination plots (Kent 2012). The axes of ‘distance’ in ordination space represent turnover in species composition from one community type to another. Therefore, sites that share more of the same species lie closer together on the ordination plot. The axes often represent compositional differences arising from those environmental variables that are driving differences between communities in the real world (Kent, 2012).

A nonmetric multidimensional scaling (NMS) ordination was selected for this analysis over other types of ordinations, such as detrended correspondence analysis (DCA), because of its robustness. Unlike other ordination techniques, NMS does not assume specific distributions in the responses (Peck, 2010), and is less susceptible to the distortion problems of other ordination techniques such as the 'horseshoe' effect sometimes seen in Principal Coordinates Analysis (PCoA) (Kent, 2012).

The NMS ordination was run using the software PC-ORD (McCune and Mefford, 2011), based on the procedure outlined by Peck (2010). Firstly, the ‘autopilot’ function was used to work out the appropriate number of axes for the ordination. The ‘autopilot’ runs ordinations for configurations with one to six axes and compares the solutions. The general rule of thumb is that all significant axes are accepted; provided that adding an additional axis reduces the stress of the ordination fit by at least five points (Peck, 2010). The stress of an ordination is how closely the differences between sites can be represented in ordination space (Kent, 2012). In this case, all six axes were significant, but using four axes instead of three reduced the

stress by only four points (Figure 3.2), so three axes were chosen as the appropriate number of axes for the final ordination.

The final NMS ordination with three axes was run manually in PC-ORD, and set to analyse the data 250 times to ensure that the random starting point chosen did not lead to a ‘local minimum’ in stress; the NMS uses a stepwise approach in stress reduction when fitting axes (Peck, 2010; Kent, 2012). The whole NMS procedure was run three times to be certain the lowest stress solution was valid, and the results for each were checked to ensure the stress value was consistent and low, and that the P-values for axis significance were always below 0.05. All solutions produced were very similar, indicating that the results shown below are based on the optimal solution.

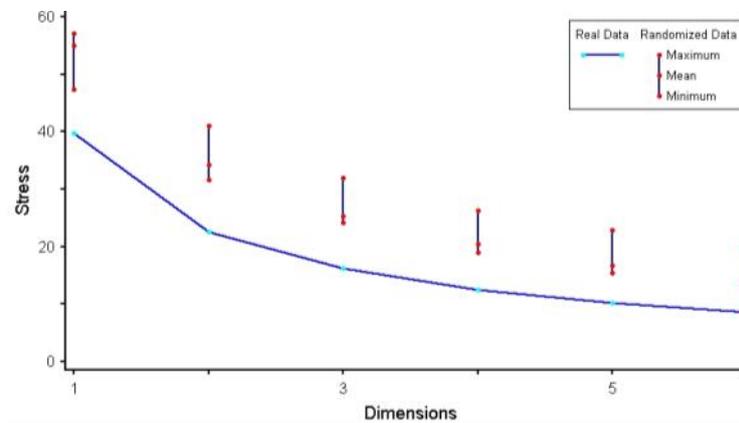


Figure 3.2: NMS scree plot showing the decrease in stress for each additional dimension.

3.2.4 Regression Modelling

Regression models were employed to determine which environmental variables were related to the changes in plant community composition represented by each axis of the NMS ordination. The procedure for these models is outlined in the methods chapter (Chapter 2, Section 2.4). There was one model for each axis, and the response variable of each model was the site scores of each axis from the NMS ordination. The explanatory variables included in the model were altitude, percent canopy cover, livestock hoofprint intensity, the influence (in terms of size and proximity) of the nearest habitat patches, and the distance of a site from the edge of its own habitat patch (these variables are described in Chapter 2, Section 2.4).

One outlying data point was removed from the dataset. This data point had a value for forest patch influence of over 400,000 due to its close proximity to a very large forest patch. If this point was included, forest patch influence became significant in the model; if it was

omitted, forest patch influence was not significant. No single point should have such a large influence on the data set (Lee, 2008).

3.3 Results

3.3.1 Cluster analysis, indicator species analysis and beta-diversity

The 83 sites sampled were assigned to nine clusters based on the cluster analysis of their species assemblage (Figure 3.3). Nine was the number of clusters with the highest number of indicator species, confirming that using nine clusters neither groups dissimilar sites together nor splits similar sites apart (see Section 3.2). Of these nine clusters, three contained very few members: two groups contained only one member each and the third contained only two members. The limited number of members for these clusters results in an insufficient sample size to determine any characteristic features of those clusters and if their composition is driven by certain environmental conditions. For this reason, these three clusters have been excluded from all further analysis. One cluster with only three member sites was retained due to its striking difference from all other plant community types: this cluster was dominated by a thick cover of *Blechnum* ferns with a few, small trees (Figure 3.4). However, no strong conclusions regarding this cluster should be drawn based on a sample of only three sites. The other five clusters all have sufficient members to be considered relevant representations of distinct community types in the upper Papallacta valley.

The six clusters (five large clusters plus the one dominated by *Blechnum* ferns) were given descriptive names based on some of their defining features (see Figure 3.4 for typical photos of each cluster, and Figures 3.5 and 3.6 for boxplots of the levels of percent canopy cover and altitude associated with each cluster). The 'high-altitude edge' cluster is consistently found in the upper part of the valley (Figure 3.5), and the member sites are typically found in pasture with vegetation or near to the edge of forests (Figure 3.7). Two points from this cluster were further into the interior of the forest than the rest of the member sites. These two sites were both beneath canopy gaps with percent canopy covers of 50% and 60%. Such values are unusually low for forest sites (Figure 3.6) and may explain why these sites had a species composition closer to that of edge forest than mature forest and their subsequent cluster membership.

The 'low-altitude edge' cluster is also found in pasture with vegetation or near to the edges of forests, but at lower altitudes (Figure 3.5, Figure 3.7). This cluster contained several points that could be considered to be interior forest sites rather than edge sites based on their location on the map; however, all of these sites were accessible to cattle and other livestock. The

'mature forest' group contained sites that were allocated in interior forest locations (Figure 3.7) and were protected from cattle and livestock entry by small cliffs or impenetrable thickets of vines and shrubs.

The group labelled 'shrubby pasture' was made up of sites that were essentially pasture with a variety of shrubs present but little or no tree cover (Figures 3.4, 3.6). This community type had no significant indicator species (Table 3.1), suggesting that this cluster was more defined by a shared absence of species than the presence of any particular species. The 'regenerating pasture' cluster was named for its high abundance of *Baccharis latifolia* (Table 2.1), a species that can regenerate easily in open areas. As mentioned before, the final group contained only three member sites and was labelled '*Blechnum*-dominated' for its high abundance of *Blechnum* ferns (Table 2.1).

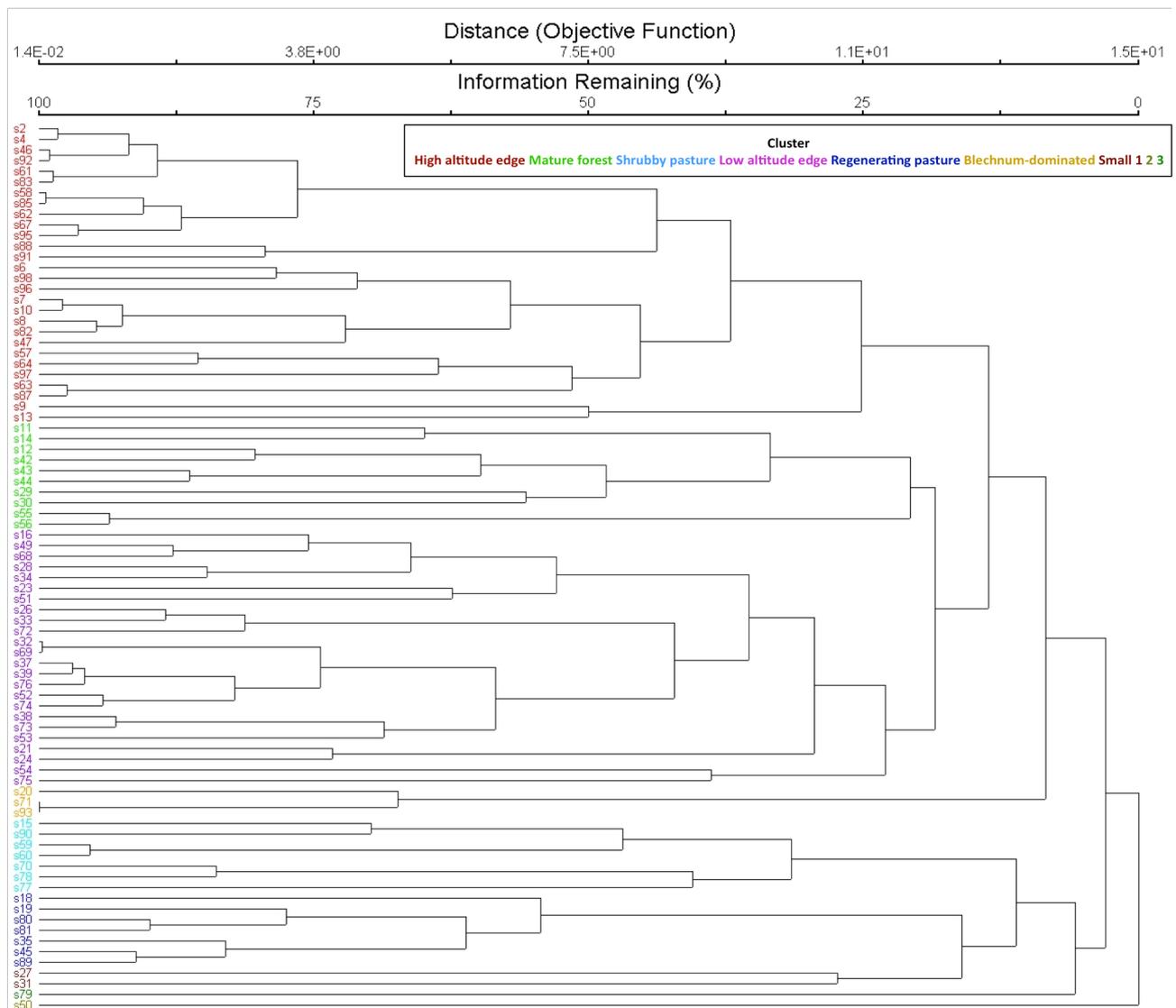


Figure 3.3: Cluster dendrogram.

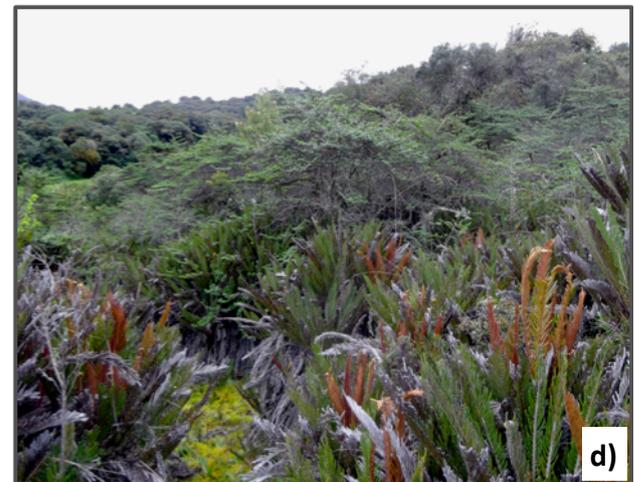
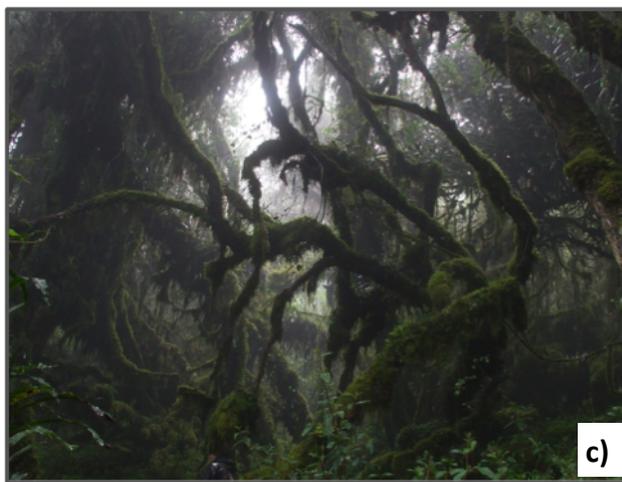


Figure 3.4: Examples of each vegetation cluster: a) high altitude edge, b) low altitude edge, c) mature forest, d) *Blechnum*-dominated, e) shrubby pasture, and f) regenerating pasture.

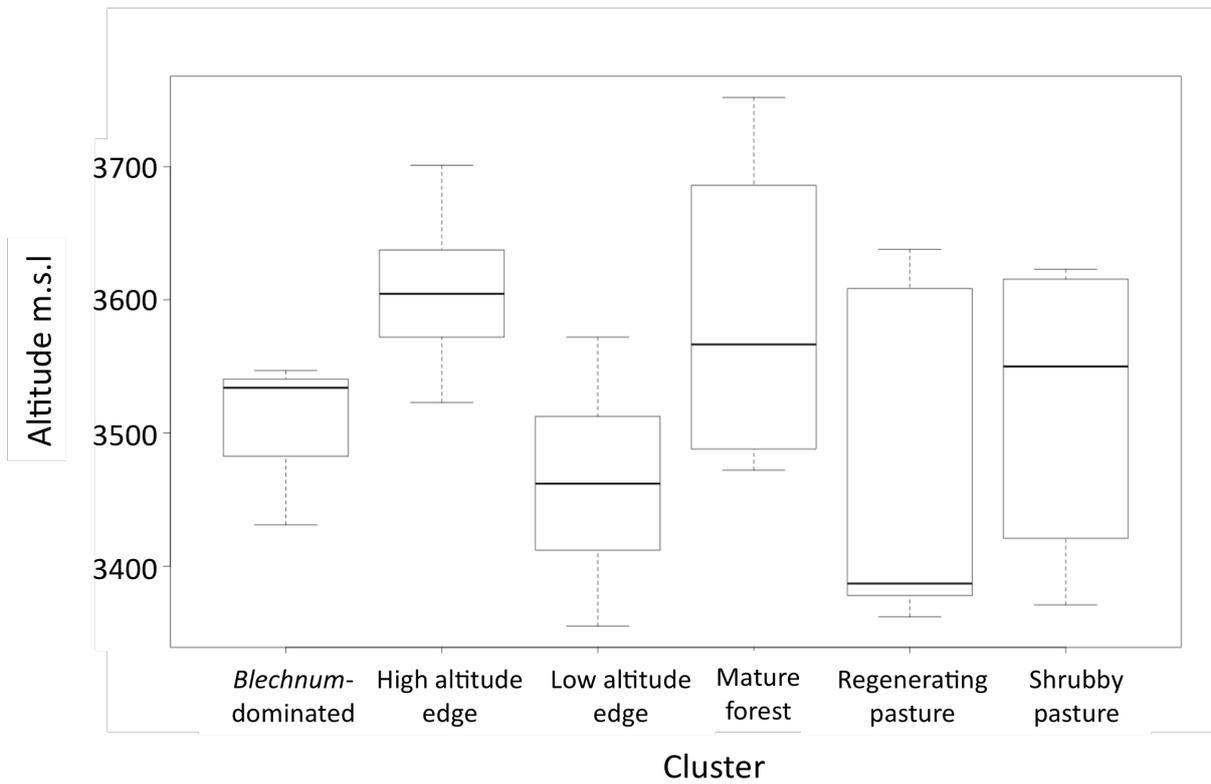


Figure 3.5: The distribution of altitude within each cluster.

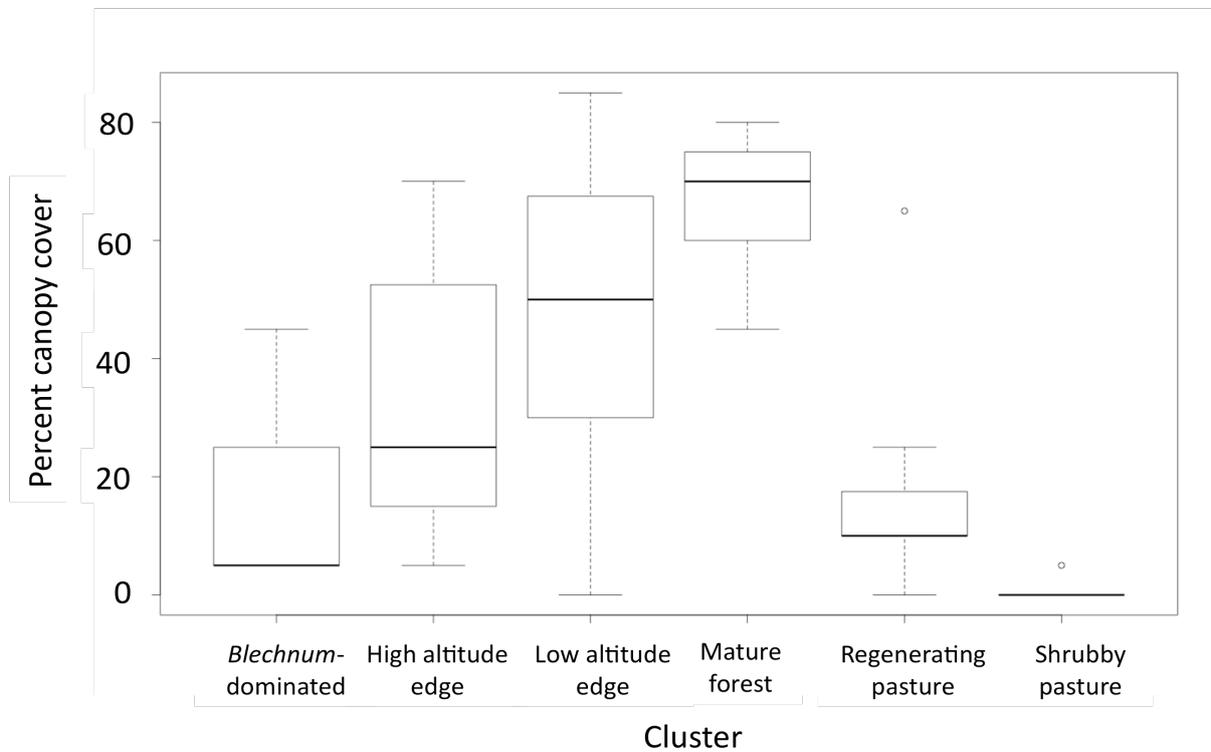


Figure 3.6: The distribution of percent canopy cover within each cluster.

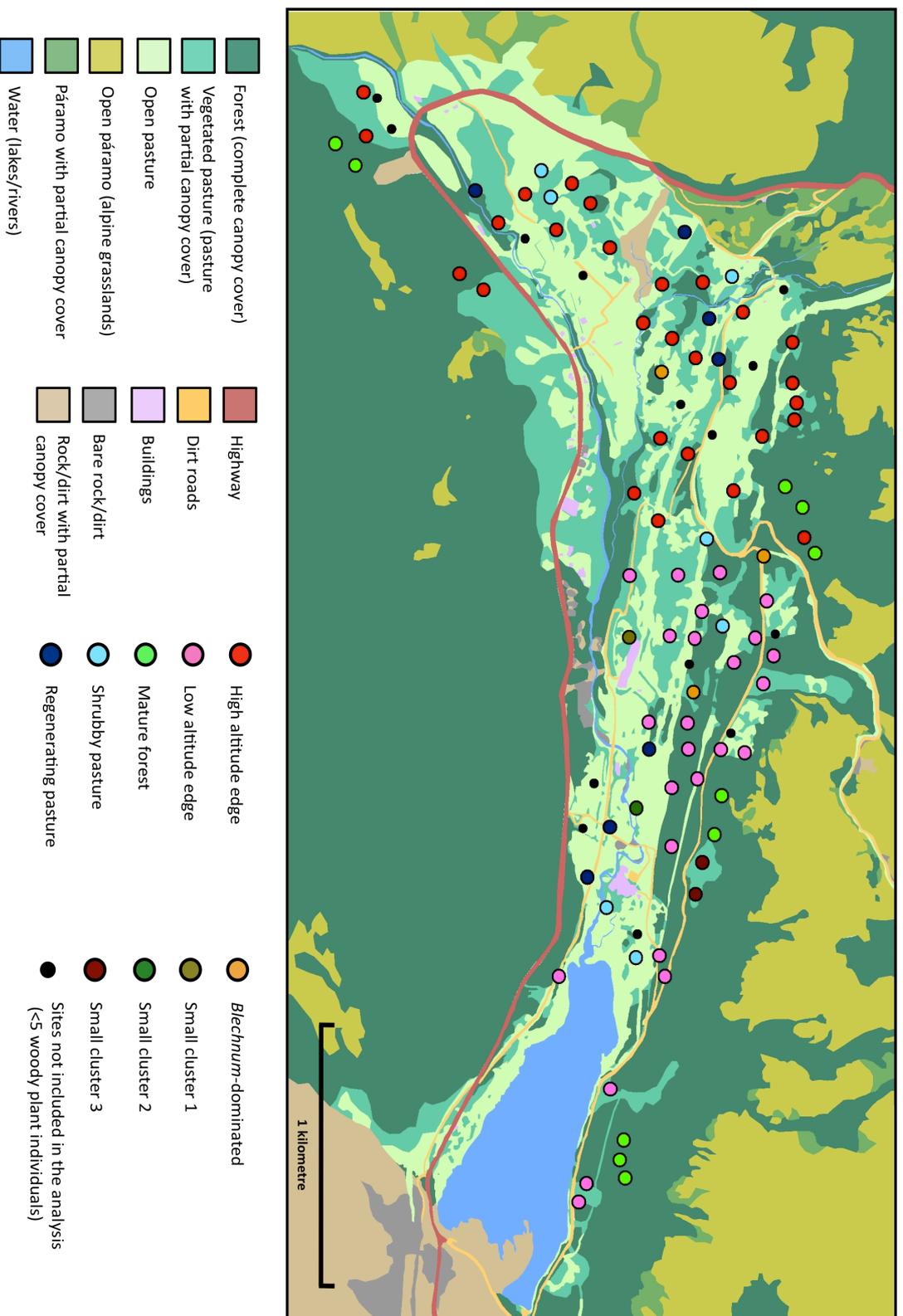


Figure 3.7: Location of clusters overlaid onto the site map. The colours for each cluster match those shown in the cluster dendrogram (Figure 2.6) and the ordination plots (Figure 2.7). The small black points are those excluded from the cluster analysis due to having too few woody plant individuals.

Indicator species analysis

A total of sixty-five woody plant species were found in the upper Papallacta valley (Appendix A). Of these, none were found exclusively in a single cluster, but several occur more frequently and with higher abundances in certain clusters (Table 3.1). These species can be used as indicators of community type. For example, a site with a high abundance of *Jungia rugosa* is likely to have a low altitude edge community, while a high abundance of *Oreopanax ecuadorensis* would indicate a site with a mature forest community.

Table 3.1: Indicator species associated with each cluster type.

Cluster	Species	Growth form	Indicator	
			Value	P-value
High altitude edge	<i>Gynoxys</i> (small-leaved morphotype ²)	Tree	44.8	0.04
	<i>Miconia salicifolia</i>	Tree	62.6	0.00
	<i>Muehlenbeckia tamnifolia</i>	Climber	74.4	0.00
	<i>Ribes ecuadorensis</i>	Climber	66.1	0.00
	<i>Rubus</i> species	Climber	45.7	0.00
	<i>Salpichroa tristis</i>	Climber	46.5	0.01
Mature forest	<i>Calceolaria lamiifolia</i>	Climber	52.9	0.03
	<i>Munnozia jussieui</i>	Climber	51.7	0.02
	<i>Oreopanax ecuadorensis</i>	Tree	58.7	0.01
	<i>Monnina</i> species	Tree	45.2	0.04
Shrubby pasture	None	-	-	-
Low altitude edge	<i>Jungia rugosa</i>	Climber/shrub	60.4	0.01
	<i>Solanum asperolatum</i>	Tree	75.2	0.00
Regenerating pasture	<i>Baccharis latifolia</i>	Tree	44.4	0.04
Blechnum-dominated	<i>Blechnum</i> species	Fern	96.0	0.00
	<i>Escallonia myrtilloides</i>	Tree	77.9	0.00
	<i>Pentacalia arbutifolia</i>	Shrub	83.9	0.00
	<i>Pernettya prostrata</i>	Shrub	56.8	0.02

² The species of *Gynoxys* present were unable to be identified in this study. There were two distinct morphotypes ('large-leaved' and 'small-leaved') but the author could not determine whether these represent multiple species, or an altitudinal gradient within a single species.

Analysis of beta-diversity

The calculations of beta-diversity show that the mature forest, high altitude edge and low altitude edge forests are all most similar to one another, and all share a high level of canopy cover (Figure 3.6). Shrubby pasture is most similar to high edge and regenerating pasture is most similar to low altitude edge, but the similarity is weak in both cases (both have an inverse Morisita-Horn index of 0.71; Table 3.2). The *Blechnum*-dominated group has high values of the inverse Morisita-Horn index with all other clusters, supporting the earlier statement that this cluster is very different from all other vegetation types encountered in the study area.

Table 3.2: Inverse Morisita-Horn Index (beta-diversity) measures for each pairwise comparison of clusters. Values close to 1 indicate dissimilar community composition and abundance between cluster pairs.

	High edge	Mature forest	Shrubby pasture	Low edge	Regenerating pasture
Mature forest	0.52				
Shrubby pasture	0.71	0.94			
Low edge	0.56	0.49	0.81		
Regenerating pasture	0.85	0.79	0.89	0.71	
<i>Blechnum</i> -dominated	0.91	0.95	0.89	0.94	0.76

3.3.2 Nonmetric multidimensional scaling (NMS) ordination

The NMS ordination identified three relevant axes that describe the variation between the species assemblages of each plot (Figure 2.8). The clusters identified above occur at different locations relative to the NMS axes. Notably, 'shrubby pasture' occurs at low values of axis 1 while 'mature forest' occurs at high values, and 'high altitude edge' occurs at low values of axis 2 while 'low altitude edge' occurs at high values of axis 2. This suggests that axis 1 represents a compositional gradient between pasture and forest environments, and that axis 2 is associated with altitude. These trends are investigated further in the following section using regression models.

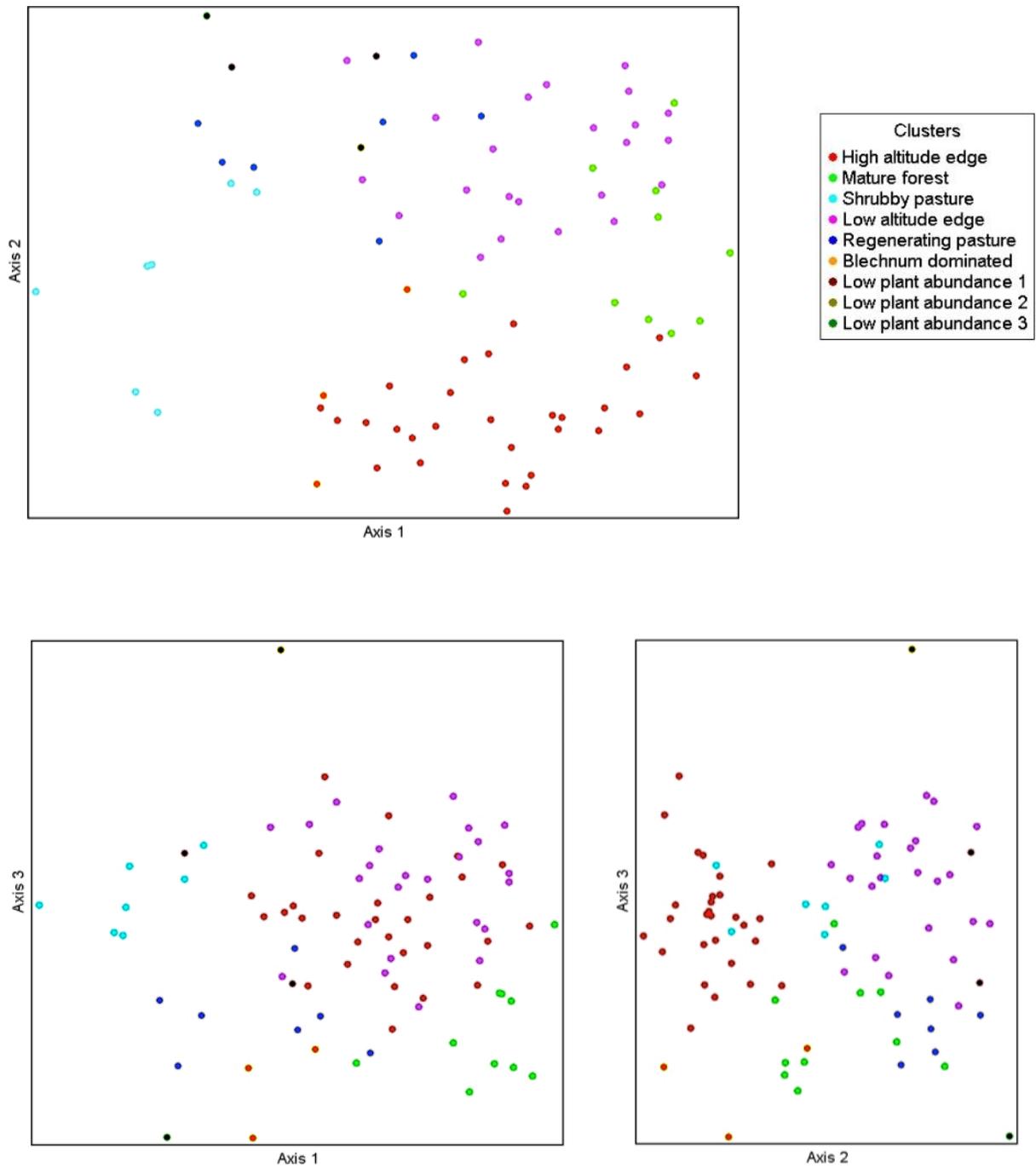


Figure 3.8: The NMS ordination plots with the sites from different clusters shown in different colours.

3.3.3 Regression modelling

Percent canopy cover was strongly related to the first axis ($P < 0.001$), and altitude to the second ($P < 0.001$). Also significantly associated with axis 1 was the distance to the edge of a site's own patch for sites located in pasture patches (Table 3.3). No significant variables were identified for the third axis (Table 3.3). This does not imply that the compositional change represented by the axis does not exist, rather it shows that none of the variables investigated in this study were significantly related to that compositional change.

Table 3.3: Co-efficients of variation and P-values of the explanatory variables included in the regression models of the three NMS axes. The three models are listed across the top of the table, and the explanatory variables are in the left-hand column. ‘Co-eff’ represents the coefficient of variation: positive values indicate a positive relationship, negative values an inverse relationship with the response variables. P-values of less 0.05 are marked with an asterisk; these indicate significant associations between the explanatory variables and each axis of the NMS ordination.

	Axis 1		Axis 2		Axis 3	
	Co-eff	P	Co-eff	P	Co-eff	P
Altitude	0.02	0.75	-0.34	0.00*	-0.09	0.19
Canopy cover	0.36	0.00*	0.09	0.15	-0.01	0.88
Hoofprint intensity: low	-0.11	0.41	0.00	0.97	-0.10	0.53
Hoofprint intensity: high	-0.18	0.25	0.29	0.06	0.10	0.58
Forest patch influence	0.07	0.16	-0.01	0.91	-0.01	0.89
Vegetated pasture patch influence	-0.01	0.19	-0.06	0.23	0.04	0.50
Open pasture patch influence	-0.07	0.89	-0.10	0.07	0.05	0.45
Distance to patch edge: forest	0.11	0.10	0.12	0.07	-0.13	0.09
Distance to patch edge: veg. pasture	0.01	0.95	0.01	0.94	0.08	0.55
Distance to patch edge: pasture	0.86	0.01*	0.12	0.21	-0.25	0.51

To explore the effect of the correlation between the explanatory variables percent canopy cover and hoofprint intensity (Chapter 2, Section 2.4.2), percent canopy cover was removed from the model, and the model re-analysed. Hoofprint density replaced percent canopy cover as being significantly related to axis 1 (Table 3.4), confirming the expected collinearity between these two explanatory variables. The distance to the edge of pasture sites remained significant. There was no change to the number of significant explanatory variables for axis 2 or axis 3 when percent canopy cover was removed (Table 3.4).

Table 3.4: The co-efficients and P-values for the models of each NMS axis when canopy cover is omitted from the model. three models are listed across the top of the table, and the explanatory variables are in the left-hand column. ‘Co-eff’ represents the coefficient of variation: positive values indicate a positive relationship, negative values an inverse relationship with the response variables. P-values of less 0.05 are marked with an asterisk; these indicate significant associations between the explanatory variables and each axis of the NMS ordination.

	Axis 1		Axis 2		Axis 3	
	Co-eff	P	Co-eff	P	Co-eff	P
Altitude	-0.03	0.56	-0.40	0.00*	-0.08	0.18
Hoofprint intensity: low	-0.44	0.00*	-0.08	0.51	-0.09	0.53
Hoofprint intensity: high	-0.50	0.01*	0.21	0.14	0.11	0.52
Forest patch influence	0.06	0.31	-0.01	0.87	-0.01	0.89
Vegetated pasture patch influence	0.03	0.69	-0.06	0.29	0.04	0.51
Open pasture patch influence	-0.03	0.65	-0.09	0.10	0.05	0.46
Distance to patch edge: forest	0.15	0.00*	0.12	0.05	-0.13	0.09
Distance to patch edge: veg. pasture	0.12	0.46	0.03	0.77	0.08	0.56
Distance to patch edge: pasture	1.75	0.07	-0.17	0.54	-0.27	0.40

3.4 Discussion

3.4.1 Woody plant communities of the upper Papallacta valley

Six community types and two distinct trends of variation in composition were identified in the woody vegetation of the upper Papallacta valley. One of these compositional trends was associated with altitude, and the other with agricultural intensity (Tables 3.3 and 3.4). Four of the six community types can be classified by where they occur in relation to these two environmental gradients: the 'mature forest' cluster occurs only in the absence of agricultural pressure while the 'shrubby pasture' cluster occurs only in pastures where canopy cover has been completely cleared. There are two 'edge' clusters that occur at intermediate levels of agricultural intensity, which are found in vegetated pasture as well as in forest edges and forest fragment. These two edge clusters are separated from one another by altitude, with the 'high edge' community type generally occurring above 3550m, and the 'low edge' community usually below that.

The remaining two vegetation types were 'regenerating pasture' and '*Blechnum*-dominated'. Both were named for their dominant species in the absence of any clear environmental tendencies (beyond the fact that both are found in pastoral areas rather than undisturbed forest areas). 'Regenerating pasture' has a high abundance of *Baccharis latifolia*, a small tree species that establishes easily in pastures and is generally considered a weed by farmers (Pillajo and Pillajo, 2010). The '*Blechnum*-dominated' cluster is characterised by a heavy dominance of tall *Blechnum* ferns. It was only encountered in three locations, so the environmental conditions and agricultural pressures that determine its occurrence cannot be confirmed. However, it may be worth further research: this community has a high presence of the tree *Escallonia myrtilloides* (Table 3.1, Figure 3.4), which is thought to be locally threatened in the upper Papallacta valley due to exploitation for timber and charcoal (Pillajo and Pillajo, 2010). A community type that promotes its presence could be useful for the conservation of this species, both for its own sake and as a timber resource for local people.

3.4.2 Community composition and agriculture

Of the six woody plant community types identified in the upper Papallacta valley, only one community type occurred in undisturbed forest ('mature forest'), while five different communities were identified within areas influenced by agriculture (Figure 3.3, Table 3.3). Even the plant communities found within forest edges were different from the mature forest community (Table 3.2), indicating that high montane cloudforest is sensitive to edge effects caused by agriculture. However, beyond the initial compositional change that occurs between

mature forest and forest edges, the remaining forest species appear to be fairly resilient to increasing agricultural pressure. The same community found in forest edges was found throughout vegetated pasture, even where canopy cover was substantially reduced and grazing pressure was high. This finding is consistent with other studies of community responses to agriculture, which show natural forest communities tend to contain a group of highly forest-dependent species, which disappear from the system even at very low levels of agricultural intensity, while other species of the same communities may be resistant to relatively high agricultural intensity (Perfecto *et al.*, 2005; Phalan *et al.*, 2011; de Bonilla *et al.*, 2012).

All member sites of the mature forest cluster are known to be inaccessible to cattle, indicating that grazing has a significant impact on the forest community composition. Grazing affects some plant species more than others (depending on their resilience and palatability) and so community composition is altered as the vulnerable species disappear from the community (Pettit *et al.*, 1995; Burns *et al.*, 2011). Even low levels of grazing can be enough to significantly alter forest community compositions (Nugent *et al.*, 1997). Other sites located in forested areas which did not fall into the mature forest cluster could all be reached by cattle (pers. obs), apart from two sites which were located beneath canopy gaps (they had canopy covers of 50% and 60%, which are relatively low for mature forest communities; Figure 2.5). This suggests that the composition of the cloudforest community can also be affected by a change in light conditions. Most forest communities have a suite of light-demanding species which colonise treefall gaps and other open areas; these also tend to be the species that survive on forest edges and in forest fragments (Laurance *et al.*, 2006a). This would explain why these two sites were more similar to the edge vegetation types than to the mature forest community, even though they were inaccessible to cattle.

This distinction between the mature forest community and edge vegetation clusters indicates the presence of edge effects, and the significance of the canopy cover and livestock pressure variables in the models suggest that these are the major causes of edge effects. Distance to edge itself was not shown to be significant for forest in the model, as levels of canopy cover or hoofprint intensity already explain the differences between forest edges and forest interiors. However, distance to edge in pasture sites was significant, suggesting that forest edges play some role in the composition of pasture communities that was not measured in this study, perhaps as a source of seeds, soil nutrients, or pollinators (Murcia, 1995).

An interesting community type in terms of agricultural intensity is the regenerating pasture cluster. As mentioned above, this community was named because it is dominated by *B. latifolia* (Table 2.1). However, this community type seems to be promoting the regeneration

of more than just weedy species. A wide range of other species can be found regenerating beneath and between the 'weeds' of this community type, including forest species such as *Oreopanax ecuadorensis*. The establishment of *B. latifolia* has previously been found to promote the growth of seedlings of other species because its branched growth form means that it protects the area beneath its canopy from grazing and from climatic exposure (Posada *et al.*, 2000). In addition to *B. latifolia*, the regenerating pasture community is rich in *Berberis grandifolia* and *Barnadesia arborea*, both of which also grow readily in open pasture and have growth forms which could offer protection from grazing and exposure (pers.obs). This protection effect has been identified as important for the regeneration of trees within wooded pastures in Europe (Uytvanck *et al.*, 2007), and could be useful to promote the regeneration of forest trees within agricultural areas of the upper Papallacta valley.

Within the upper Papallacta valley, the major impacts of agriculture on vegetation composition result from the effects of tree removal and grazing pressure on the local environment. No evidence was found in this study to suggest that fragmenting forest alters plant communities by isolating forest fragments from one another, even though many forest species may be dispersed by animals (Downer, 2001). This may be due to the long thin shape of the upper Papallacta valley, which means that distances between forest patches are never more than 300m. It is possible that isolation does not have an effect at this scale. In addition, research suggests that the effects of isolation on community composition are small compared with the effects of habitat degradation caused by edge effects and grazing pressure in forest fragments (Harrison and Bruna, 1999; Bennett *et al.*, 2006; Tabarelli *et al.*, 2008). Any effects of isolation may therefore be difficult to distinguish from the effects of habitat degradation (Harrison and Bruna, 1999), given that all isolated fragments in this study were small enough to be heavily influenced by edge effects (Figure 2.1).

3.4.3 Community composition and altitude

Altitude is a well-known driver of compositional variation in Andean vegetation (Young, 1993; Lauer and Rafiqpoor, 2000; Salgado, 2008). In the upper Papallacta valley, variation in relation to altitude is most obvious outside of the mature forest community, suggesting that the creation of open environments for pasture generates more altitudinal variation than would otherwise be observed. The high edge cluster is rich in plant species generally associated with the treeline, or with the alpine shrublands and grasslands (páramo) above the treeline. These high altitude habitats are a more open environment than the forest, and so plants from these habitats could be adapted to colonise open pastures. The creation of pasture effectively reproduces the treeline and páramo environments at lower altitudes, allowing these species to

establish further down. Without agriculture the study area would be entirely forested (it lies below the treeline at 3800m) and the establishment of these open environment species would not occur. Agricultural disturbance effectively reduces the altitude of the transition from forest species to páramo species so that it occurs within altitudes spanned by this study.

The composition of the shrubby pasture cluster supports the idea that open areas favour high altitude plants, as this cluster is most similar to high altitude edge vegetation (Table 2.2), yet it is found at all altitudes within the study area (Figure 2.6). Such artificial extensions of páramo species to lower altitudes is thought to be widespread throughout the Andes as a result of clearing forest for pasture (Sarmiento, 2002). Some examples of woody plants found in the upper Papallacta valley in this study which are known to be associated with the treeline or with páramo are *Baccharis buxifolia*, *Baccharis odorata*, *Hesperomeles obtusifolia*, *Hypericum laricifolium*, *Lupinus pubescens*, *Pernettya prostrata* and *Valeriana microphylla* (Pillajo and Pillajo, 2010).

3.4.4 Conclusion

The findings of this chapter indicate that pastoral agriculture has a significant effect on the local plant community of the upper Papallacta valley, by altering the environment from closed forest to open pasture. Conservation of the mature cloudforest community can only occur in a closed forest environment in the absence of grazing. If conservation of cloudforest is a goal for the upper Papallacta valley, protecting large forest areas from further clearance should be a priority. It would also help to fence off forest to keep livestock out, as this would eliminate the edge effects caused by grazing (Burns *et al.*, 2011).

Retaining vegetation in pasture as either forest fragments or scattered vegetation can contribute to the conservation of some cloudforest species within the pastoral landscape. These community types tend to be dominated by pioneer species and by species from the treeline and páramo environments, but they also contain many forest species. It appears that the establishment of disturbance-sensitive species could be improved by promoting the growth of certain woody weeds (*B. latifolia*, *B. grandiflora*, *B. arborea*) which protect the ground beneath them from grazing and from exposure, allowing the seedlings of sensitive species to establish (Posada *et al.*, 2000; Uytvanck *et al.*, 2007).

Chapter 4

Ecosystem services and biodiversity in the upper Papallacta valley

4.1 Introduction

Ecosystem processes are responsible for creating the environment in which we can survive (Ehrlich *et al.*, 2012, Naeem *et al.*, 2012, Millenium Ecosystem Assessment (MA), 2005). Ecosystem processes are the biogeochemical interactions between organisms and their environments, and perform vital functions such as the cycling of oxygen and carbon dioxide, and the creation of soils (MA, 2005; Cardinale *et al.*, 2012; Naeem *et al.*, 2012). Many of these processes contribute to human survival and welfare, and these are termed 'ecosystem services'. Some ecosystem services underpin life as we know it, such as nutrient cycling and primary production. Some provide us with goods and resources, such as food and timber, while others stabilise ecosystem dynamics, and regulate processes such the spread of disease, or the flow of water through a landscape. Some simply add meaning to our lives, such as the relaxation and recreation opportunities found in wilderness landscapes (Costanza, 1997; MA, 2005; Ehrlich *et al.*, 2012).

Biodiversity underpins ecosystem processes, and therefore ecosystem services (Naeem *et al.*, 2012; Quijas *et al.*, 2012). The activities of each species within an ecosystem contribute to the overall processes of that ecosystem, with every activity from primary production to decomposition, and from nutrient uptake to habitat modification, altering the physical and chemical environment around the organisms (Naeem *et al.*, 2012; Cardinale *et al.* 2012). A higher diversity of species means a higher diversity of activities, all performed in different ways at different times under different environmental conditions. Therefore a higher diversity of species leads to a greater diversity, efficiency, and stability of ecosystem services (Hooper *et al.*, 2005; Tschardtke *et al.*, 2005; Isbell *et al.*, 2011; Naeem *et al.*, 2012; Cardinale *et al.* 2012).

As humans, we tend to modify large areas of the Earth's surface for specific purposes, such as the production of food and materials. In recent decades it has become obvious that although such modifications help us to serve many of our needs, we are simultaneously suffering huge losses of important ecosystem services associated with natural environments (Hooper *et al.*, 1995; Ehrlich *et al.*, 2012; Björklund *et al.*, 2012). For example, the conversion of natural

habitats to farmland might improve the immediate food production capacity of that land, but much of the natural biodiversity and its associated ecosystem services (such as the protection and renewal of soil, and the regulation of water quantity and quality) are lost (Vandermeer *et al.*, 1998; Foley *et al.*, 2005; Björklund *et al.*, 2012). A primary goal of the conservation of biodiversity and natural habitat is the maintenance of ecosystem services, to ensure quality of human life now and into the future (Cardinale, 2012; Naeem *et al.*, 2012).

One of the greatest concerns regarding the loss of ecosystem services is deforestation (Pearce, 2001; Foley *et al.*, 2007). Forests are key providers of ecosystem services, and play significant roles in nutrient cycling, climate regulation, hydrological regulation, and carbon storage (Costanza *et al.*, 1997; Pearce, 2001; Foley *et al.*, 2007). However, forests are disappearing at alarming rates worldwide (Pearce, 2001; Achard *et al.*, 2002; Foley *et al.*, 2005; da Fonseca *et al.*, 2007), threatening the sustainability of forest biodiversity and ecosystem services. A major cause of deforestation is the conversion of forest to agricultural land, which is estimated to have resulted in the loss of up to 11 million km² of forest worldwide (Foley *et al.*, 2005).

4.1.1 The effects of converting forest to pastoral land on biodiversity and ecosystem services

The conversion of forest to pastoral land is generally associated with a loss in biodiversity and in ecosystem services (Pearce, 2001; Steffan-Dewenter, 2007; Foley *et al.*, 2007; Karp *et al.*, 2012; Balmford *et al.*, 2012). The greatest losses occur where the complex forest ecosystem is completely replaced by crops or pastures dominated by one or two species (Foley *et al.*, 2005). However, fragmentation of forest areas interspersed with pasture can also lead to biodiversity loss in the remaining forest patches (Turner, 1996; Harrison and Bruna, 1999; Tabarelli *et al.*, 2008). Remnant forest patches in a fragmented landscape can lose species if the patches are not large enough to support viable populations, or if their small size and isolation leads to increased extinction risk for each species (Turner, 1996; Bennett *et al.*, 2006). Edge effects are the influences that neighbouring pasture areas have on adjacent forests, and tend to alter the forest environment by increasing light and disturbance levels (Murcia, 1995). The typical changes occurring from such edge effects favour less diverse pioneer communities at the expense of complex climax forest communities (Tabarelli *et al.*, 2008, Chabrierie *et al.*, 2012). Where remaining fragments are too small, so-called patches of 'forest' consist of nothing but 'edges', and the climax forest community is lost entirely (Turner, 1996, Harrison and Bruna, 1999, Tabarelli *et al.*, 2008).

Ecosystem services are lost as biodiversity is lost (Hooper *et al.*, 2012). Firstly, not all functions that can be provided by forests can be provided by pasture grasses. Compared to grasses, forest trees take up nutrients from deeper in the soil, deposit more organic matter to the topsoil, provide more structure and stability to the soil, and reduce evaporation from soil through shading (see Chapter 1; Breshears *et al.*, 2006; Scholes and Archer, 1997). These functions of trees generate the ecosystem services of higher soil fertility, regulation of runoff and soil moisture, and soil carbon storage (Jackson and Ash, 1998; Breshears *et al.*, 2006; Sánchez-Járdón *et al.*, 2012). Trees can also provide timber and foods such as fruits, and store carbon (Gordon *et al.*, 2004, Murgueitio, 2004; Harvey *et al.*; 2010).

There is now overwhelming evidence that it is not just the loss of a functional group (*e.g.* trees) that reduces ecosystem services, but that the total diversity within and between functional groups is also important to ecosystem service provision (Isbell *et al.*, 2011; Naeem *et al.*, 2012; Quijas *et al.*, 2012; Hooper *et al.*, 2012). Each species of tree may play a slightly different role in the services described above, and with the loss of each species, overall service provision diminishes (Hooper *et al.*, 2005; Tscharrntke *et al.*, 2005; Cardinale *et al.*, 2012). Therefore, the provision of ecosystem services in the face of environmental variation and disturbance relies on high levels of biodiversity. Some species are better than others at performing certain functions in certain environments (Hooper *et al.*, 2005; Isbell *et al.*, 2010; Cardinale *et al.*, 2012); and if you have two (or more) species which perform exactly the same function, then the function will continue to be performed even if one of those species goes extinct (Hooper *et al.*, 2005; Tscharrntke *et al.*, 2005).

Forest environments also support a wide range of other plants and animal species beyond trees, each of which may contribute to further ecosystem services such as pest control and disease regulation, or provide resources such as food and medicine (Foley *et al.*, 2007). When forests are converted to pasture or exposed to edge effects, the habitats of many of these species are degraded or lost (Harrison and Bruna, 1999; Tabarelli *et al.*, 2008), and the ecosystem services they provide disappear with them.

4.1.2 Conserving biodiversity and ecosystem services in pastoral landscapes

In order to address the problems caused by diminishing ecosystem services, research is now being undertaken into practical ways to improve the conservation of biodiversity and associated ecosystem services in pastoral landscapes (Altieri, 1999; Vandermeer *et al.*, 2008; Scherr and McNeely, 2008; de Schutter, 2010; Björklund *et al.*, 2012). These practical approaches often focus on the preservation or restoration of natural habitats within farming

landscapes, or on creating an environment similar to the natural ecosystem of the area within the farmland (Scherr and McNeely, 2008; Björklund *et al.*, 2012).

In naturally forested environments, incorporating forest trees into pastures can help to maintain some forest biodiversity and ecosystem services within pastures (Rhoades *et al.*, 1998; Harvey *et al.*, 2006; Jose, 2009). As described above, trees provide services such as increased soil fertility and a timber resource (Murgueitio, 2004) but they also provide habitat and resources to other forest species which are usually absent in pasture. For example, trees might facilitate the growth of forest shrubs through creating a shaded environment, and support forest insects, birds and mammals through the provision of nest sites and forage (Guevara *et al.*, 1992; Harvey *et al.*, 2006).

4.1.3 Biodiversity and ecosystem services in the upper Papallacta valley

The upper Papallacta valley is an example of a naturally forested landscape that has been partially cleared to create pasture. Areas of natural forest remain on either side of the valley, but the central parts are now a mosaic of open pasture, pasture with scattered trees, and forest fragments (Figure 1.4). This provides an opportunity to investigate the role of trees within agricultural landscapes in the conservation of forest biodiversity and ecosystem services.

As described in Chapter 1, the upper Papallacta valley is valued for several important ecosystem services by people living outside the valley. These include its role in the drinking water catchment for Quito (Ecuador's capital city), its role as habitat for internationally significant wildlife (such as the spectacled bear), and its potential to store high levels of carbon to contribute to climate change mitigation. People living inside the upper Papallacta valley value the landscape because the fertile soils are beneficial to agriculture, because the wildlife draws tourists, and because the local people still obtain timber as well as many traditional foods and medicines from the native plant life. All of these ecosystem services are associated with trees and forest biodiversity: water regulation is performed better by forested than agricultural areas (Costa *et al.*, 2003; DeFries and Eshleman, 2004), and the upper Papallacta valley's charismatic wildlife depends on its natural forest habitat (Downer, 2001; Katten *et al.*, 2004). Trees increase soil fertility through nutrient uptake and litterfall (Binkley and Giardina, 1998; Jobbágy and Jackson, 2004), and provide timber. Many local food/medicine species are primarily found in the forests (Bussman, 2006; Pillajo and Pillajo, 2010).

In this study, some key ecosystem properties have been chosen to represent these ecosystem services. An ecosystem property is a measurement of a certain aspect of the

ecosystem which can provide an indication of the levels of provision of certain ecosystem services. The ecosystem properties chosen for this study, and the ecosystem services they represent, are outlined below.

Soil organic matter content

Soil organic matter is related to a wide range of soil ecosystem services (Dominati *et al.*, 2010), and is considered to be a useful indicator of soil ecosystem service provision (Rutgers *et al.*, 2011). Of relevance to this study is that soil organic matter can be used to estimate soil fertility, as it is associated with higher levels of nutrients, soil biodiversity, and resilience to erosion (Lal, 2009).

It is also a measure of soil carbon storage (Lal, 2009). Carbon dioxide is naturally released to the atmosphere as organic matter decomposes in the soil, but when the rate of organic matter deposition exceeds the rate of decomposition, soils can become sinks for carbon dioxide (Berg *et al.*, 1995; Lal, 2004). In natural ecosystems of the high Andes, soil organic matter is naturally high: it breaks down very slowly due to the cold temperatures and high levels of soil moisture, which inhibit the organisms that perform decomposition (Hofstede, 1999; Schuur *et al.*, 2001; Buytaert *et al.*, 2011).

Soil moisture content

Soil moisture content was measured to estimate the ability of the landscape to retain water. Soils which can hold more moisture are expected to have a greater capacity to absorb heavy precipitation and avoid flooding, and also to retain more moisture in the landscape during dry spells. Both of these functions will become increasingly important as climate change brings both glacial retreat and increasingly intense rain events to the Andes (Vuille *et al.*, 2008).

Abundance of juvenile trees of timber species

The felling of trees for fenceposts has been identified as a major threat to forests neighbouring agricultural areas throughout South America (Murgueitio, 2004). The number of juveniles of timber tree species provides a forecast for the availability of timber and fuelwood in the future. Of interest in the upper Papallacta valley is whether timber species are regenerating within the agricultural areas, as this will avoid the need for farmers to seek timber from otherwise undisturbed forest areas in the future.

Species richness and Simpson's Diversity Index of woody plants

Woody plant diversity is a reflection of the diversity of traditional foods and medicines available to local people. There is also evidence that plant diversity is an indicator of biodiversity trends in other taxa, as it has been linked with diversity of some animal taxa

(Siemann *et al.*, 1998; Haddad *et al.*, 2009). Woody plant diversity may contribute to overall biodiversity by providing a greater range of habitats and forage resources to other plant and animal taxa (Siemann *et al.*, 1998; Harvey and Haber, 1999; Harvey *et al.*, 2006; Haddad *et al.*, 2009). Higher overall biodiversity is an indication of a greater overall diversity and resilience of ecosystem services (Isbell *et al.*, 2011; Naeem *et al.*, 2012).

Woody plant diversity is measured in this study using species richness and Simpson's diversity index. Species richness is the total number of species present at a site. Simpson's Diversity Index combines richness with evenness, and gives higher values of diversity for sites which have not only a greater number of species, but also a more even abundances of each species (Magurran, 2004). This means that sites with a high richness composed of a few dominant species and many rare species will be ranked more similarly to a less rich site where abundance is more evenly distributed between species.

4.1.4 Aims

The specific aims of this chapter are to:

- Determine whether levels of biodiversity and ecosystem properties vary in relation to environmental variables.
- Identify how the clearance and fragmentation of forest, in combination with grazing pressure from livestock, alters the capacity of landscape to support biodiversity and ecosystem services.

4.2 Methods

4.2.1 Ecosystem properties

Five ecosystem properties were selected to represent key ecosystem services. These properties were measured at the sites described in Chapter 2 and were obtained as follows:

Soil organic matter

Soil samples were taken from the centre point of forty of the 10x10m sample quadrats. The analysis was performed by the Agrocalidad soil laboratory in Tumbaco, Ecuador, and the results presented as % volumetric content of organic matter.

Soil moisture

Soil samples were taken from the centre of forty of the 10x10m sample quadrats, and delivered to the Agrocalidad laboratory. The measure of humidity used is gravimetric

humidity: the number of grams of water per 100g of soil. It is obtained by taking the wet weight of the soil sample, drying the soil out, and then taking the dry weight. The difference in these two weights is the weight of water lost from the soil during the drying process.

Tree regeneration

The number of juvenile trees of potential timber species were recorded at each site. A juvenile tree was defined as being greater than 30cm in height (so that only established individuals were recorded) but less than 2.5m in height or less than 10cm in breast-height diameter (at which point they would be considered adult trees). Species were designated as potential timber species if they regularly grow large enough and have sufficiently durable wood to be useful as a fencepost, or for larger constructions (Pillajo and Pillajo, 2010; pers. obs.).

Twelve species were identified as useful timber resources in the upper Papallacta valley. These were: *Buddleja* species, *Escallonia myrtilloides*, *Grosvenoria rimbachii*, *Gynoxys* (both the small and large-leaved morphotypes³), *Hesperomeles obtusifolia*, *Hesperomeles ferruginea*, *Miconia bracteolata*, *Oreopanax ecuadorensis*, *Saracha quitensis*, *Sessea crassifolia*, and *Vallea stipularis*.

Species richness

Species richness is the count of the total number of different woody species found in each quadrat.

Simpson's diversity index:

This measure takes into account both the species richness and evenness at a site (Magurran, 2004). This analysis used the complement of Simpson's diversity index ($1 - D$) so that the index falls between 0 and 1, with 0 representing low diversity and one representing high diversity. The formula used to calculate the diversity index (D) is:

$$D = \sum \left(\frac{n_i(n_i - 1)}{N(N - 1)} \right)$$

where n_i is the number of individuals in the i th species, and N is the total number of individuals.

³ The species of *Gynoxys* present were unable to be identified in this study. There were two distinct morphotypes ('large-leaved' and 'small-leaved') but the author could not determine whether these represent multiple species, or an altitudinal gradient within a single species.

4.2.2 Regression Modelling

The relationship between ecosystem properties and environmental variables within the upper Papallacta valley was explored using regression models. The procedure for these models is outlined in the methods chapter (Chapter 2, Section 2.4). There was one model for each ecosystem property. The explanatory variables included in the model were altitude, percent canopy cover, livestock hoofprint intensity, the influence (in terms of size and proximity) of the nearest habitat patches, and the distance of a site from the edge of its own habitat patch (these variables are described in Chapter 2, Section 2.4).

4.3 Results

Canopy cover explained a significant amount of the observed variation in four out of the five models: soil organic matter, number of juvenile timber trees, species richness, and Simpson's diversity index (Table 4.1). In all cases, the co-efficient was positive, indicating that these four ecosystem properties increase as canopy cover increases. Canopy cover is known to correlate with the gradient of forest to pasture communities (see Chapter 3; Section 2.3.2) so the significance of canopy cover in these models indicates that forest sites have higher soil organic matter, woody plant diversity and greater timber regeneration potential, than open pasture sites. Altitude was also significant in the model for the number of juvenile timber trees. The co-efficient was positive (Table 4.1), indicating that the number of juvenile timber trees is higher at higher altitudes.

Model diagnostics showed a relatively poor fit of the model for Simpson's diversity index (Appendix B, Figures B.4-B.6). Examination of the data revealed that the problems were caused by sites with a Simpson's diversity index of 0 (these sites had a species richness of zero or one). These can be seen as a consistently isolated group in the diagnostic plots (Appendix B, Figures B.4-B.6). To check how the results are affected by these sites, all ten sites with a Simpson's diversity index of 0 were removed and the model re-analysed (this resolved the issues shown in the diagnostic plots; Appendix B, Figure B.7). However, canopy cover was no longer significant in the model ($P=0.08$). All ten sites removed had a canopy cover of zero; therefore these results indicate that it is only possible to have a Simpson's diversity of zero when there is no canopy cover, but beyond that there is no significant relationship between canopy cover and Simpson's diversity index.

Table 4.1: Co-efficients and P-values of the explanatory variables included in the regression models of the five ecosystem property responses. The five models, defining the response variable, are listed across the top and the explanatory variables form the left-hand column. ‘Co-eff’ represents the regression co-efficient for each explanatory variable in the model. Positive values indicate a positive relationship, negative values an inverse relationship with the response variables. Significant P-values ($P < 0.05$) are marked with an asterisk.

	Soil organic matter content		Soil moisture content		Number of juvenile timber trees		Species richness		Simpson's diversity index*	
	Co-eff	P-value	Co-eff	P-value	Co-eff	P-value	Co-eff	P-value	Co-eff	P-value
Altitude	0.01	0.94	0.02	0.92	0.32	0.00*	0.09	0.30	0.00	0.99
Canopy cover	0.41	0.03*	0.34	0.06	0.23	0.04*	0.68	0.00*	0.46	0.00* ¹
Hoofprint intensity: low	0.30	0.49	0.17	0.68	-0.45	0.07	0.01	0.94	0.10	0.69
Hoofprint intensity: high	-0.32	0.49	-0.66	0.15	-0.44	0.15	0.09	0.71	0.58	0.06
Forest patch influence	0.11	0.54	0.08	0.67	0.16	0.11	0.15	0.07	0.00	0.99
Vegetated pasture patch influence	0.19	0.31	0.28	0.12	-0.06	-0.57	0.01	0.92	0.10	0.33
Open pasture patch influence	0.18	0.42	0.23	0.29	0.03	0.77	-0.08	0.35	-0.02	0.82
Distance to edge of own patch: forest	0.01	0.95	0.10	0.59	-0.24	0.07	0.38	0.26	0.04	0.77
Distance to edge of own patch: veg. pasture	0.17	0.86	0.55	0.53	-0.02	0.95	-0.17	0.40	0.07	0.78
Distance to edge of own patch: pasture	0.68	0.14	0.72	0.11	0.19	0.65	-0.04	0.68	0.23	0.56

*¹ When sites with a Simpson's diversity index of zero were removed from the model, canopy cover was no longer significant ($P = 0.08$).

4.4 Discussion

Three out of the five ecosystem properties investigated in this chapter were found to increase as canopy cover increased: species richness of woody plants, the content of organic matter in the soil and the number of juveniles of timber tree species (Table 4.1). Given that forest sites have the highest levels of canopy cover (Chapter 3), these results indicate that forested areas are richest in woody plant species, hold the most organic matter in their soils, and contain the greatest number of juvenile trees of timber species. Open pasture sites have

the lowest values of these ecosystem properties as they have little or no canopy cover, and vegetated pasture sites have intermediate values, as vegetated pasture has intermediate levels of canopy cover (Chapter 3).

These findings suggest that ecosystem service provision is significantly improved by retaining tree cover in the upper Papallacta valley. As discussed in the introduction (Section 4.1.3), the ecosystem properties measured in this study were chosen as indicators of several ecosystem services. Specifically, soil organic matter levels are associated with the ecosystem services of soil fertility and carbon storage (Lal, 2009; Dominati, 2010; Rutgers *et al.*, 2011). The number of juvenile timber trees is a forecast of the future timber resource available to farmers, and the diversity of woody plants is a measure of the diversity of traditional foods and medicines available to the local people. It is likely that higher plant species richness also indicates higher biodiversity levels in other taxa (Haddad *et al.*, 2009), which in turn suggests that the overall diversity and resilience of ecosystem services may be higher where woody plant species richness is higher (Isbell *et al.*, 2011; Naeem *et al.*, 2012).

The number of juveniles of timber tree species was also found to be higher at higher altitudes (Table 4.1). Of the twelve timber species, *Gynoxys* (both morphotypes¹), *Hesperomeles obtusifolia*, *Hesperomeles ferruginea*, and *Miconia bracteolata* seem to be responsible for this trend, as their juveniles are both abundant and most frequently found at higher altitudes (Appendix C). This suggests that the establishment of these species is reduced at lower altitudes. However, it is beyond the scope of this study to distinguish whether establishment is low at lower altitudes because these species have naturally higher distributions, or because they are prevented from establishing by anthropogenic factors (too few individuals of each species were encountered in this study for robust analysis). The management of any of the twelve species as a timber resource in the upper Papallacta valley would benefit from further research into both its life history, and its response to human activities. At this stage, the only sound conclusion that can be drawn is that the overall future abundance of timber trees in the upper Papallacta valley is expected to be greater at higher altitudes.

4.4.1 Canopy cover and ecosystem properties

The results of this study indicate that maximising canopy cover in the upper Papallacta valley leads to benefits in soil organic matter content, regeneration of timber tree species, and woody plant species richness. As identified in Chapter 3, canopy cover in the upper Papallacta valley represents a gradient in environmental conditions between pasture and forest. This is a

gradient from low to high tree cover and therefore a gradient in the ecosystem functions performed by trees, such as the interception of solar radiation and precipitation, and the provision of materials and structure to the soil (Figure 1.5; see Chapter 1; Breshears *et al.*, 2006). The gradient from pasture to forest is also a gradient of grazing intensity, with low canopy cover found where grazing intensity is high (Chapter 3). It cannot be entirely distinguished whether the ecosystem properties measured here are responding to the tree cover or to agricultural intensity, but in pastoral-forest mosaics such as the upper Papallacta valley, these gradients are typically interrelated, as farmers tend to clear the most vegetation from the areas they graze the most. Forest therefore occurs in areas with minimal grazing pressure, and pasture occurs in areas with high grazing pressure. Below, the results of this study are discussed in terms of the relationship of each ecosystem property with both canopy cover and grazing intensity.

Canopy cover and soil properties

Trees enrich soil organic matter through litterfall (Breshears, 2006; Jose, 2009) and slow the loss of organic matter by regulating decomposition rates and preventing erosion (Pimental and Kounang, 1998; Lal, 2009). Canopy cover can lead to cooler soil temperatures and higher soil humidity (Breshears, 2006), which slows decomposition (Lal, 2004; Dominati *et al.*, 2010) so that nutrients and minerals are released more slowly and can be taken up effectively by plants. Where the rate of decomposition is higher than plant uptake, nutrients and minerals can be lost from the soils in run-off and leaching (Dominati *et al.*, 2010).

Trees also contribute to organic matter retention by preventing soil erosion. Tree canopies intercept precipitation, so that the soil surface receives lower precipitation levels, and rainwater reaching the ground does so at a lower velocity (Pimental and Kounang, 1998; Ataroff, 2002). The soil surface is less disturbed, and fewer soil particles are carried away by the flow. This prevents the loss of the top layers of soil, which are rich in organic matter (Dominati *et al.*, 2010).

Given that soil organic matter is also usually associated with soil humidity (Rutgers *et al.*, 2011), and that tree cover is expected to reduce soil evaporation (Breshears, 2006), it was unexpected that relationship between soil moisture content and percent canopy cover was not found to be significant in this study. It is likely that there are other explanatory variables in this relationship that were not accounted for in the models described here. For example, incident solar radiation may have differed depending on slope and aspect, and altered evaporation rates independently of canopy cover. Soil moisture is also known to vary with the physical properties of soil (Vereecken *et al.*, 1989; Dominati *et al.*, 2010), and the presence of

soil fungi (Augé *et al.*, 2001). Soil moisture may also not vary significantly within the scale of this study, where open areas between forest were rarely more than a few hundred metres wide. Studies assessing the impact of forest cover on water regulation tend to investigate effects at a catchment scale (Costa *et al.*, 2003; Ford *et al.*, 2011).

Canopy cover and woody plant diversity

Trees alter the environment beneath their canopy by sheltering them from precipitation and solar radiation, and by enriching the soils (see Chapter 1). These conditions facilitate the establishment and growth of forest-adapted species (Guevara *et al.*, 1992; Scholes and Archer, 1997; Breshears *et al.*, 2006). The native species of the upper Papallacta valley are mostly forest species and it is believed that the area would have been entirely covered in cloudforest prior to human settlement (Lauer and Rafiqpoor, 2000). The few species that are present in the upper Papallacta that are not associated with forests are post-disturbance pioneer species (e.g. *Baccharis latifolia*) or are associated with the alpine shrublands and grasslands above the treeline (e.g. *Hypericum lariifolium*) (Pillajo and Pillajo, 2010).

The observed decline in woody plant diversity associated with decreasing canopy cover is believed to be a result of a relatively low number of species able to grow well in the pasture environment, compared with a relatively high number of species which only thrive in a forest environment. Other studies have observed similar patterns of decline in the diversity of forest plant species in response to human-induced disturbance gradients (Rao *et al.*, 1990; Pettit *et al.*, 1995; Ramírez-Marcial *et al.*, 2001; Sagar *et al.*, 2003; Tabarelli *et al.*, 2008; Chabrerie *et al.*, 2012). This difference in species richness between undisturbed forest sites and pasture sites may be because the structural complexity of mature forest communities offers a greater variety of niches than pasture environments, and so supports a great number of species (Tabarelli *et al.*, 2008). It could also be that few species of the upper Papallacta valley are tolerant to the combination of reduced or absent canopy cover, grazing, and competition with introduced pasture grasses. This combination would not have occurred prior to the introduction of agriculture to the valley, so it is unlikely that many species would be adapted to withstand these pressures.

In several of the above studies, high disturbance levels were associated with the increasing dominance of a few species, and the disappearance of rare species. This would explain why Simpson's diversity index was not significantly related to canopy cover in this study, yet richness was. Simpson's diversity index equates a higher evenness with higher diversity, so that sites with relatively few rare species will have a higher rank compared with those which have many rare species. Given that a large proportion of tropical forest diversity is often

composed of rarely occurring species (e.g. Black *et al.*, 1950; Turner, 1996), Simpson's diversity index is perhaps not a particularly informative measure of biodiversity for these systems.

Canopy cover and timber tree regeneration

The increase in the number of juveniles of timber tree species with an increase in canopy cover suggests that overall, timber species are found more often in a forest habitat than a pasture habitat. However, twelve species were grouped together for this analysis and it is likely each has their own relationship with canopy cover (Appendix C). *Hesperomeles obtusifolia*, for example, is common in pastures at higher altitudes, while *Oreopanax ecuadorensis* is rarely encountered outside of forest areas. This study was too small to encounter sufficient individuals of each species for robust analysis on their distributions, so the timber species were grouped together to represent the timber resource.

If one was seeking to increase the numbers of regenerating timber trees within the agricultural areas of the upper Papallacta valley, research would have to be undertaken on the life history traits of each species, and their responses to grazing pressure. For example, the observed pattern in this study of higher timber abundance with higher canopy cover could be due to the fact that some species may not be able to disperse very far from their parents (Günter *et al.*, 2007; Vojta and Drhovská, 2012) and the parent trees of that species are also absent from pasture sites. Alternatively, some species may be good dispersers and successfully colonise a pasture site but never grow beyond the seedling stage due to grazing pressure (Posada *et al.*, 2000). Introduced pasture grasses may also be inhibiting seedling establishment (Sarmiento, 2002). Further research would allow techniques to be developed to promote the growth of these species, such as fencing off woodlots to prevent grazing, or manually planting seeds to overcome dispersal barriers.

4.4.2 Conclusion

The findings of this chapter suggest that woody plant richness and ecosystem services are best conserved within forest areas of the upper Papallacta valley. The highest richness and ecosystem services were associated with the highest levels of canopy cover, which are found in undisturbed areas of mature forest (see Chapter 3; Figure 3.6) This is consistent with general trends in tropical forests: biodiversity and ecosystem services are highest in climax forest communities, lower in disturbed forest vegetation, and substantially reduced in open pastures (Rao *et al.*, 1990; Sagar *et al.*, 2003; Harvey *et al.*, 2006; Foley *et al.*, 2007; Tabarelli

et al., 2008). Therefore, the protection of undisturbed forest areas should be a priority for the conservation of biodiversity and ecosystem services within the upper Papallacta valley.

This study suggests that tree cover is important to maintain soil fertility, timber resources, and woody plant biodiversity within pastoral areas. It is also hinted at here that retaining trees in pastoral areas, as either forest fragments, or vegetated pasture, can mitigate losses caused by forest clearance. Other studies have found that forest fragments provide refuges for specialist forest species to survive in pastoral landscapes (Devictor and Jiguet, 2007; de Bonilla *et al.*, 2012), and that remnant trees and shrubs in pastures can support a diversity of birds, bats, and insects (Fischer and Lindenmayer, 2002; Harvey *et al.*, 2006; Cunningham *et al.*, 2008). Keeping agricultural intensity at low levels and maintaining a variety of habitat types can lead to high levels of conservation of biodiversity and ecosystem services within agricultural landscapes (Tscharntke *et al.*, 2005; Devictor and Jiguet, 2007; Karp *et al.*, 2012). It is recommended that care is taken to both conserve existing forest vegetation within the upper Papallacta valley, and to increase the tree cover in open pastures by active planting and/or protection of juvenile woody species.

Chapter 5

Optimising land use to balance conservation and pastoral production

5.1 Introduction

Human welfare requires both agricultural production and the conservation of biodiversity and ecosystem services (Altieri, 1999; de Schutter, 2010). Even agricultural production itself depends largely on the continued provision of ecosystem services such as nutrient cycling and water regulation (Altieri, 1999; Costanza *et al.*, 1997; MA, 2005; de Schutter, 2010). Biodiversity underpins ecosystem service provision: it is the organisms within ecosystems that perform the ecosystem services, and a greater diversity of organisms leads to a greater diversity of ecosystem services, which are more resilient to disturbance (Cardinale *et al.*, 2012; Naeem *et al.*, 2012; see Chapter 4).

Ecosystems unmodified by humans are generally considered to be the greatest sources of biodiversity and ecosystem services, whilst extensively modified areas (e.g. by intensive agriculture) provide fewer services and contain fewer species (Costanza *et al.*, 1997; Foley *et al.*, 2005; Dobson *et al.*, 2006). To conserve ecosystem services and biodiversity we must then conserve large areas of natural ecosystems, or we must alter the way we modify environments in order to improve conservation within them. There is ongoing debate over which of these approaches is the most effective in the context of agriculture, a debate which is generally referred to as 'land-sharing vs. land-sparing' (e.g. Tscharntke *et al.*, 2012; Balmford *et al.*, 2012). These two terms capture the opposing views of whether we conserve large areas of natural ecosystems (land-sparing), or whether we attempt to conserve biodiversity and ecosystem services within agricultural areas (land-sharing).

Land-sparing is based on the idea that if we maximise agricultural productivity per unit area (i.e. by using high intensity practices such as monocultures, fertilisers, pesticides, irrigation) then we meet demand for food and other agricultural products using less area, and therefore more land can be spared as protected areas for the conservation of natural ecosystems (Ewers *et al.*, 2009; Hodgson *et al.*, 2010). Proponents of land-sparing point out that even areas of low intensity agriculture rarely support the same ecological communities as natural ecosystems, and therefore trying to integrate biodiversity and ecosystem services into

farmland impedes both agricultural production and nature conservation (Green *et al.*, 2005; Phalan *et al.*, 2011).

Conversely, advocates of land-sharing believe that protected areas (containing natural ecosystems) will never be extensive enough to effectively conserve global biodiversity and ecosystem services (Blann, 2006; Perfecto and Vandermeer, 2010). Currently, only approximately 5% of the world's land area has protected area status, and many of these protected areas suffer problems of illegal grazing, poaching, and harvesting (Newmark *et al.*, 1993; Green and Paine, 1997), whilst others are too small to conserve viable populations of important species (Bender *et al.*, 1998). Furthermore, segregation of biodiversity into protected areas means agricultural areas cannot benefit from it, leading to a situation where ecosystem services fail in agricultural lands and have to be replaced by fertilisers, pesticides, and other external inputs. The use of these inputs combined with intensive production practices leads to further environmental degradation and further loss of ecosystem services, culminating in diminished yields that cannot be rescued by external inputs (Altieri, 2002). Currently it is estimated that 40-50% of the world's arable lands suffer from such degradation (Oldeman, 1992; MA, 2005).

Land-sharing involves the integration of natural habitat with agriculture to support biodiversity and ecosystem services within farmed areas (Fischer *et al.*, 2008; Godfray 2011). This is put forth as a way to solve both problems presented above: biodiversity and ecosystem services can be conserved on wider scales, and biodiversity and ecosystem services can be used to improve farm yields in ways which strengthen the sustainability and resilience of agriculture, rather than undermine production through land degradation (Altieri, 1999; Fisher *et al.*, 2008, Fischer *et al.*, 2011, Tscharrntke *et al.*, 2012). Examples of land-sharing approaches include using tree cover to protect the soil from erosion and moisture evaporation, riparian plantings to prevent erosion and promote water quality, and designing production areas to attract beneficial wildlife through the use of certain plants and mulches, and the creation of habitat (Landis, 2000; Scherr and McNeely, 2008; Björklund *et al.*, 2012).

Land-sharing and land-sparing fall on opposite ends of a spectrum (Balmford *et al.*, 2012). Land-sparing calls for complete segregation of natural habitat and agriculture, while land-sharing calls for complete integration (Figure 5.1). Intermediates may appear as land-sparing (segregation) on a small spatial scale, yet land-sharing (integration) on a large spatial scale (Figure 5.1). The most appropriate point on this spectrum for effectively balancing agricultural yields and nature conservation changes from case to case (Fischer *et al.*, 2011; Godfray, 2011; Butsic *et al.*, 2012; Balmford *et al.*, 2012). In situations where land is resilient

to agricultural degradation, natural habitats are sensitive to disturbance, and protected areas are enforceable, land-sparing might be the best approach (Phalan *et al.*, 2011). On marginal lands with low yields and a high vulnerability to degradation, land-sharing is thought to be more beneficial to both farm production and the conservation of biodiversity and ecosystem services (Altieri, 2002; Fisher *et al.*, 2008).

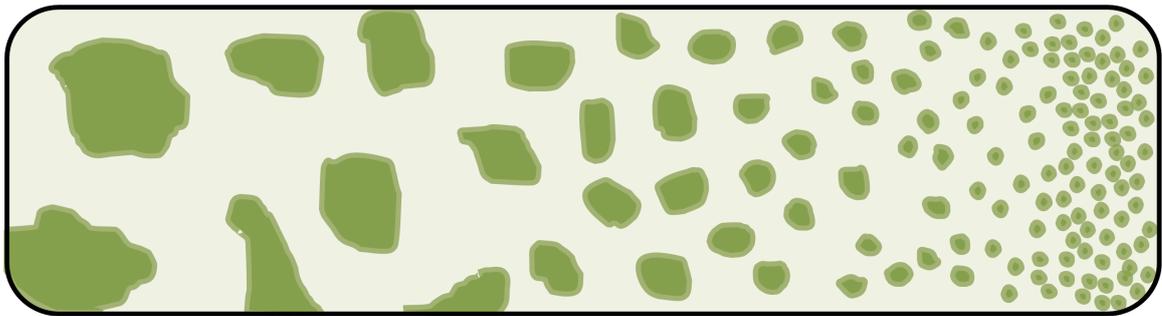


Figure 5.1: : An illustration of the land-sparing to land-sharing spectrum, with light green representing agricultural areas and dark green representing natural habitat. The left end of the image can be considered land-sparing, and the right end represents land-sharing. Intermediates can be considered as either land-sparing on a small scale, or land-sharing on a large scale.

5.2 Land-sharing or land-sparing in the upper Papallacta valley?

This chapter is an exercise in applying the concept of 'land-sharing vs. land-sparing' on a landscape scale. The landscape in question is the upper Papallacta valley, a pastoral landscape bordered by forest in the Ecuadorian Andes. The valley is important for the conservation of high Andean biodiversity, and important to downstream urban communities for its role in water regulation (Chapter 1). It is used for livestock raising by two local communities, Tambo and Jamanco. Some of the land is owned and managed by individual families, while some areas are farmed communally. In general, the farmers of the upper Papallacta valley are interested in conserving the nature around them (pers. comm.). They enjoy having the trees and associated birdlife on their lands, recognise that tree cover can be beneficial to their farms, and are aware of the importance of vegetation cover for downstream hydrological benefits (pers. comm., local farmers). However, these farmers are also reliant on the productivity of their farms for their income. Currently, forest clearance continues slowly throughout the Papallacta area (pers. obs), and in many similar areas throughout the Andes (Wunder, 1996, Sarmiento 2002a), as farmers seek to improve production by creating new

pasture. This conflict between agriculture and natural habitats makes the upper Papallacta valley an excellent case study for the 'land-sharing vs. land-sparing' concept.

The upper Papallacta valley is covered by a mixture of large forest areas, forest fragments, pasture with scattered remnant vegetation, and open pasture. To balance agriculture and conservation of biodiversity and ecosystem services within the upper Papallacta valley, the relative values of each land cover type in terms of pasture productivity, biodiversity, and ecosystem services must be taken into account. Previous findings indicate that biodiversity and ecosystem services are highest within large forest areas and lowest in open pastures, with intermediate levels found in forest edges and fragments, and pasture with remnant vegetation (Chapters 3 and 4). These findings are typical of many studies that indicate higher levels of native vegetation cover are associated with higher levels of biodiversity and ecosystem services (Costa *et al.*, 1993; Foley *et al.*, 1997; Riedel *et al.*, 2008; Tejeda-Cruz and Sutherland, 2004). The 'perfect' conservation scenario in terms of biodiversity levels and ecosystem function would be to return the upper Papallacta valley entirely to forest. However, it is an agricultural area, and the interests and livelihoods of the farmers who inhabit the valley must be taken into account and a balance between the two types of land use needs to be found.

This chapter explores different scenarios along the land-sharing/land-sparing spectrum (Figure 5.2), to identify the best approach to conservation of forest biodiversity and ecosystem services within the upper Papallacta valley. All scenarios include the conservation of existing areas of undisturbed natural forest. Given that the purpose of this research is to investigate how nature conservation in the upper Papallacta valley can be improved (see Chapter 1), it is assumed for this chapter that there is a desire to avoid clearing any of the remaining large forest areas. The aim is to determine whether a land-sparing or land-sharing approach leads to better conservation of the existing forest, and to what extent biodiversity and ecosystem services can be integrated into the pastoral landscape.

The first scenario explored is a true land-sparing approach (Scenario A, Figure 5.2), where all pasture outside of existing large areas of natural forest is cleared. The rationale behind this scenario is that by giving up habitats with lower biodiversity and ecosystem function (such as vegetated pasture and forest fragments), we increase productivity in the farmed areas. Following land-sparing logic, it would then be expected that the motivation to clear new areas of forest for pasture is reduced. The second two scenarios explore land-sharing, where tree cover is integrated into the pastoral landscape. In Scenario B, tree cover is retained as discrete forest fragments interspersed by open pasture. This scenario could be considered small-scale

land-sparing, but is still land-sharing at the landscape scale (Balmford *et al.*, 2012). Scenario C (Figure 5.2) is land-sharing at both a small scale and landscape scale, where scattered trees are maintained throughout pastures (as vegetated pasture).

In this study, the land-sparing scenario (A) is compared with the two land-sharing scenarios (B and C) to identify whether land-sparing or land-sharing conserves biodiversity and ecosystem services more effectively in the upper Papallacta valley. The two land-sharing scenarios (B and C) are also compared with one another, given that the capacity of scattered tree cover to conserve biodiversity and ecosystem services is different to that of forest fragments (Chapter 4). Whilst several studies have investigated the effects of large-scale land-sharing vs. land-sparing (Hodgson *et al.*, 2010; Phalan *et al.*, 2011; Egan and Mortenson, 2012), none have investigated whether different approaches to land-sharing alter its performance relative to land-sparing.

In a second evaluation of Scenario B vs. C, a minimum pasture productivity requirement is introduced to investigate how the performance of these two land-sharing approaches when there is a need for high pasture productivity. In order to gain pasture productivity in Scenario B, the area covered by forest fragments must be reduced to provide more space for open pasture. In Scenario C higher pasture productivity is achieved by reducing the density of trees, given that pasture productivity has a negative relationship with tree density (Figure 1.3).

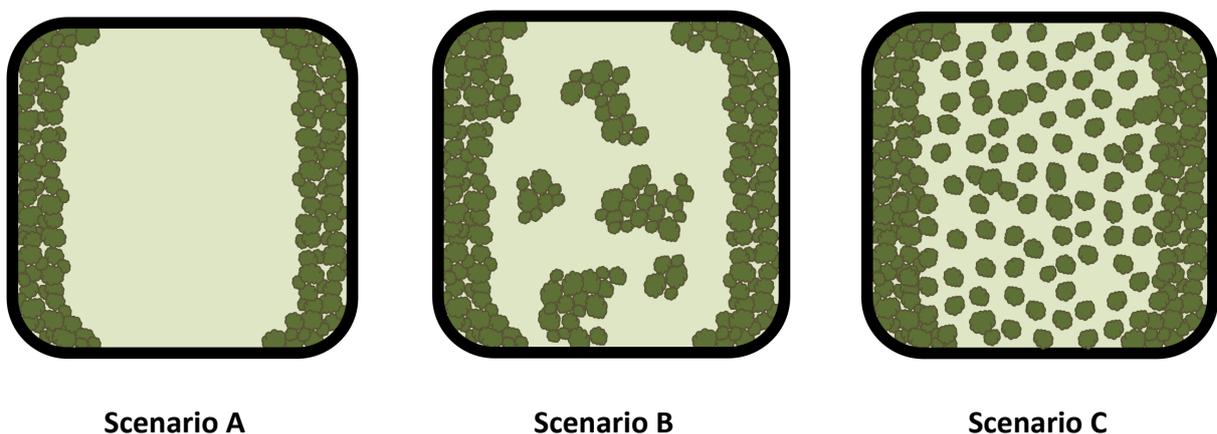


Figure 5.2: Possible scenarios to integrate conservation with pastoral livestock raising in the upper Papallacta valley. Each box represents the upper Papallacta valley, and the forest down each edge represents existing natural cloudforest. Scenario A depicts a scenario where all vegetation is cleared from pasture areas. Scenario B represents the integration of forest vegetation into pasture areas as forest fragments, and Scenario C represents the integration of forest vegetation as scattered tree cover throughout pastures (after Balmford *et al.*, 2012).

5.3 Aims

The optimal scenario for the upper Papallacta valley will provide maximum conservation of biodiversity and ecosystem services whilst minimising any reductions in pasture productivity. To identify the optimal scenario, this chapter evaluates:

- The performance of the land-sharing scenarios against the land-sparing scenario (Scenario A vs. Scenarios B and C).
- The performance of the land-sharing scenarios relative to one another (Scenario B vs. Scenario C).
- The performance of the land-sharing scenario when a minimum pasture productivity requirement is introduced (Scenario B vs. Scenario C).

5.4 Methods

5.4.1 Calculating the values of different land cover types

Each scenario assessed in this chapter is made up of one or more land cover types (Table 5.1). To calculate the values of biodiversity, ecosystem services, and pasture productivity for each scenario we must first know the values for each land cover type. For example, Scenario B is part forest fragments and part open pasture (Figure 5.2), so its total values of biodiversity, ecosystem services and pasture productivity will be a function of the ratio of edge forest to open pasture, and of the values held by each of those land cover types. The ratio of edge forest to open pasture can be altered for this scenario to favour either pasture productivity (by increasing open pasture) or biodiversity and ecosystem services (by increasing edge forest).

Table 5.1: The land cover types which make up each scenario (see Figure 5.2).

Scenario	Land cover types
A	Open pasture
B	Edge forest Open pasture
C	Vegetated pasture

Defining the land cover types

The land cover types used in this chapter are mature forest, forest edges/fragments, vegetated pasture, and open pasture. Each is defined below:

- **Mature forest:** This land cover type includes all sample sites belonging to the mature forest community type identified in Chapter 3. All sites in this community type are known to be undisturbed by agriculture.
- **Forest fragment:** The sites included in this land cover type can be from either the high or low altitude edge clusters identified in Chapter 3, as these clusters contained all sites located with forest fragments and forest edges. The sites must also be from an area with complete canopy cover, as identified by the map (Figure 2.1).
- **Vegetated pasture:** These sites are from either the high or low altitude edge clusters, (Chapter 3), provided they have only partial canopy cover (Figure 2.1).
- **Open pasture:** This land cover type consists of sites with 5% or less canopy cover, and includes members from the shrubby pasture cluster (Chapter 3), and all sites with five or fewer woody plant individuals.

Measures of biodiversity and ecosystem services

These measures are based on the analysis of Chapter 4. Three ecosystem properties are used to represent ecosystem service provision: soil organic matter content, soil moisture content, and the abundance of juveniles of timber tree species. The species richness of woody plants is used as a measure of biodiversity (see Chapter 4 for more detail).

Each land cover type was assigned a single value for each ecosystem property; this was the average of all sites making up each land cover type. These values were standardised so that the value for mature forest was set to one, and the values for each other land cover type were expressed as proportions of the levels found in mature forest. For example, if mature forest had an average species richness of 20 species per 100m² sample site and vegetated pasture had an average species richness of 10 species per sample site, then mature forest would be assigned the value of 1 and vegetated pasture would be assigned the value of 0.5. Values were standardised this way because mature forest is considered to be the ideal conservation land cover type for the upper Papallacta valley. It has the highest levels of canopy cover, and species richness, soil organic matter content and the number of timber tree juveniles are all positively related to canopy cover, so their highest values are found in mature forest (Chapter 4). Soil moisture content was not significantly related to canopy cover (Chapter 4), but it is still useful to identify whether there are any differences between land cover types.

Measuring pasture productivity

Pasture productivity for each cluster was measured by the percent of ground covered by pasture species in a 2 x 2m quadrat located in the centre of each 10 x 10m sample site. Two measures were taken, one which included only species known to be definitely edible to cattle (grasses and the two herbs *Lachemilla orbiculata* and *Hydrocotyle bonplandii*), whilst the other included all herb species which may potentially be forage for cattle. To minimise underestimation of pasture productivity by excluding all unidentified herbs, as well as overestimation by including all herbs, the average of definitely edible pasture cover and potential forage cover was used for each cluster.

This measure of pasture productivity was standardised so that open pasture had the maximum value of 1 and the values for each other vegetation type were expressed as proportions of the level found in open pasture (Table 4.1). There is a negative relationship between pasture cover and tree density in the upper Papallacta valley (Figure 4.2), so it was assumed that the maximum possible cover values are those found in open pasture. Tree density was measured by counting the number of trees in each 10x10m sample quadrat. In this study, a 'tree' was defined as a woody plant either greater than 2.5m in height, or with a breast-height diameter of greater than 10cm.

5.4.2 Comparison of scenarios

Scenarios were compared based on their scores for ecosystem properties (relative to mature forest) and for pasture productivity (relative to open pasture). The scores for ecosystem properties and pasture productivity for each scenario were calculated based on the amount of each land cover type included in each scenario (Table 1.1). Scenario A consists entirely of open pasture, and Scenario C entirely of vegetated pasture. The scores for Scenario B depend on the proportions of area taken up by edge forest and by open pasture. These were calculated using the formula: $(x \times A) + (y \times B)$, where x is the value of an ecosystem property or of pasture productivity for edge forest, and y is the value for the same ecosystem property or pasture productivity for open pasture. A and B are the proportional covers of edge forest and open pasture respectively.

Two versions of Scenario B were created for comparison with Scenario C. In the first of these the ratio of edge forest to open pasture was chosen to match the values of ecosystem properties found in Scenario C. In the second, the ratio was chosen to match the pasture productivity found in Scenario C. These two scenarios illustrate how a) the pasture productivity differs between Scenarios B and C when they are designed to have the same

levels of ecosystem properties, and b) how the ecosystem properties differ between Scenarios B and C is they are designed to have the same level of pasture productivity.

5.4.3 Scenarios with a requirement for pasture productivity

To investigate the effects of increasing pasture production on biodiversity and ecosystem services within the land-sharing scenarios (Scenarios B and C), a target value for pasture productivity is set at of 0.9 of that found in open pasture. To increase pasture productivity in vegetated pasture (Scenario C) the density of trees can be reduced to permit greater pasture growth, given that there is a negative relationship between tree density and pasture productivity (see Results, Section 5.5.3). In Scenario B, overall pasture productivity can be increased to 0.9 by increasing the area of open pasture relative to edge forest.

The relationship between tree density and pasture productivity was investigated using scatterplots and 'lowess' (locally weighted scatterplot smoothing) lines. Pasture productivity was plotted against tree density, and lowess lines laid over the datasets to represent their relationships with tree density. 'Lowess', also known as 'loess' or local regression, is a form of regression which fits a trendline to a data set by splitting the data up into subsets and calculating a regression function for each subset. The resulting regression is non-linear and follows the trend of the data point by point. It was performed in this analysis using the function *lines(lowess)* of the software R (R Core Team, 2012). Lowess regressions were also used to identify the effects of reducing tree density on species richness, soil properties and juvenile timber regeneration.

5.5 Results

5.5.1 Values of ecosystem properties and pasture productivity for each land cover type

All ecosystem properties in this study declined as tree density declined from mature forest to open pasture. In general, edge forest performs very similarly to mature forest in terms of ecosystem properties (Table 5.2). Vegetated pasture has only slightly lower values for most ecosystem properties, although species richness is substantially lower than in mature and edge forest (Figure 5.3.a, *c.f.* 5.3.c and 5.3.d). Of all the ecosystem properties assessed, the most notable difference was the decline in average species richness between mature forest and open pasture (Figure 5.3.a).

Table 5.2: Mean values of species richness, soil properties, juvenile timber tree abundance and pasture productivity for each vegetation type. Species richness, soil properties and juvenile timber tree abundance are relative to the value found in mature forest; pasture productivity is relative to the value found in open pasture.

	Mature forest	Edge forest	Vegetated pasture	Open pasture
Species richness	1	0.96	0.76	0.13
Juvenile timber trees	1	0.97	1	0.11
Soil organic matter	1	1	0.91	0.77
Soil moisture	1	1	0.88	0.78
Pasture productivity	0.28	0.30	0.77	1

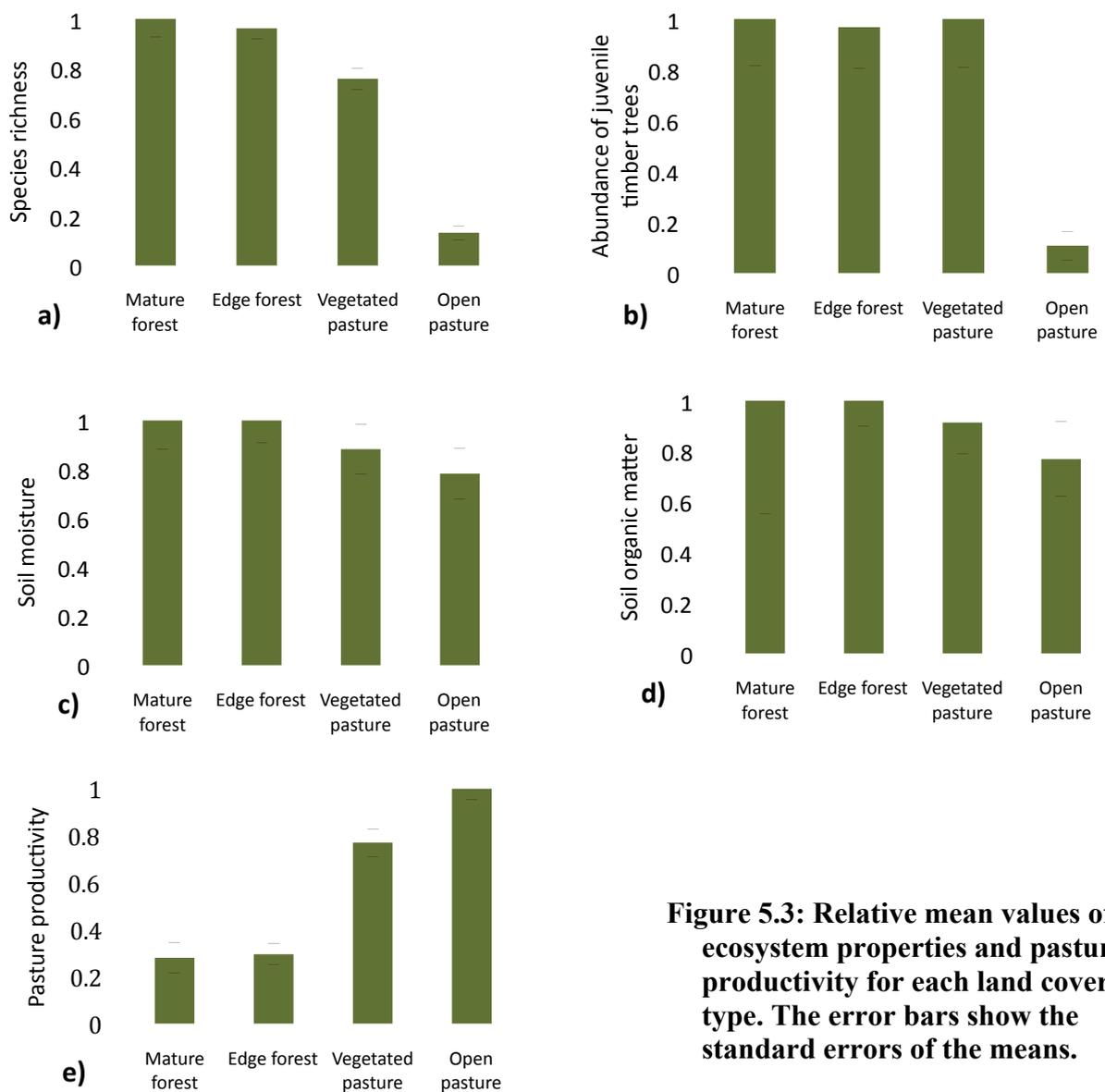


Figure 5.3: Relative mean values of ecosystem properties and pasture productivity for each land cover type. The error bars show the standard errors of the means.

As expected, pasture productivity showed generally opposite patterns from the ecosystem properties, and increased from forest to open pasture (Table 5.2). Note that vegetated pasture is more than twice as productive as either forest type, retaining 0.77 of the pasture productivity found in open pasture compared with approximately 0.3 in both mature forest and edge forest (Figure 5.3.e).

5.5.2 Comparing scenarios

Scenario A, which is entirely composed of open pasture (Figure 5.2) maintains the highest possible pasture productivity, but conserves a low average species richness and a low abundance of juvenile timber trees (Table 5.3). Soil organic matter and soil moisture are 0.77 and 0.78 respectively of levels found in mature forest. Scenario C, the land-sharing scenario composed entirely of vegetated pasture (Figure 5.2), performed better than Scenario A in terms of ecosystem properties, particularly with regard to species richness and the abundance of juvenile timber trees. This scenario retained .77 of the pasture productivity found in open pasture (Table 5.3).

Two versions of Scenario B were explored (Table 5.3). The first contained 70% edge forest and 30% open pasture (Scenario B.1), which approximates the values for ecosystem properties found in Scenario C. This version supported only 0.51 of the pasture productivity found in open pasture. The second version contained 30% edge forest and 70% open pasture (Scenario B.2), which provides a similar overall pasture productivity to Scenario C. However, the ecosystem properties were all lower in Scenario B.2 than in Scenario C (Table 5.3).

Table 5.3: The mean values of pasture productivity (relative to open pasture), and ecosystem properties (relative to mature forest) for each scenario evaluated.

	Scenario A	Scenario B.1	Scenario B.2	Scenario C
Species richness	0.13	0.71	0.38	0.76
Juvenile timber trees	0.11	0.71	0.37	1
Soil organic matter	0.77	0.93	0.84	0.91
Soil moisture	0.78	0.93	0.85	0.88
Pasture productivity	1	0.51	0.79	0.77

5.5.3 Scenarios with a requirement for pasture productivity

The pasture productivity requirement set was 0.9 of the productivity found in open pasture. The average pasture cover found in open pasture is 79%, of which 0.9 is 71%. In order to achieve this pasture cover in Scenario C, tree density needs to be 100 trees/ha (Figure 5.4). In the previous analyses, the average tree density of vegetated pasture was 600 trees/ha (based on the average tree density of the sample sites of vegetated pasture). Reducing the tree density from 600 to 100 trees/ha also reduces the levels of ecosystem properties found within vegetated pasture (Figure 5.5, Table 5.4).

For Scenario B, gaining a pasture productivity of 0.9 of that found in open pasture requires reducing the amount of edge forest relative to open pasture. The ratio required is 14% edge forest to 86% open pasture. Under this requirement for pasture productivity, the two scenarios now perform very similarly. Scenario B has slightly higher values for most ecosystem properties than Scenario C (Table 5.4).

Table 5.4: Relative mean values of ecosystem properties for Scenarios B and C when the requirement for pasture productivity is set to 0.9 of that found in open pasture. In this case, Scenario B consists of 14% edge forest and 76% open pasture, and Scenario C contains 100 trees/ha.

	Scenario B	Scenario C
Species richness	0.25	0.27
Juvenile timber trees	0.23	0.17
Soil organic matter	0.80	0.76
Soil moisture	0.81	0.79

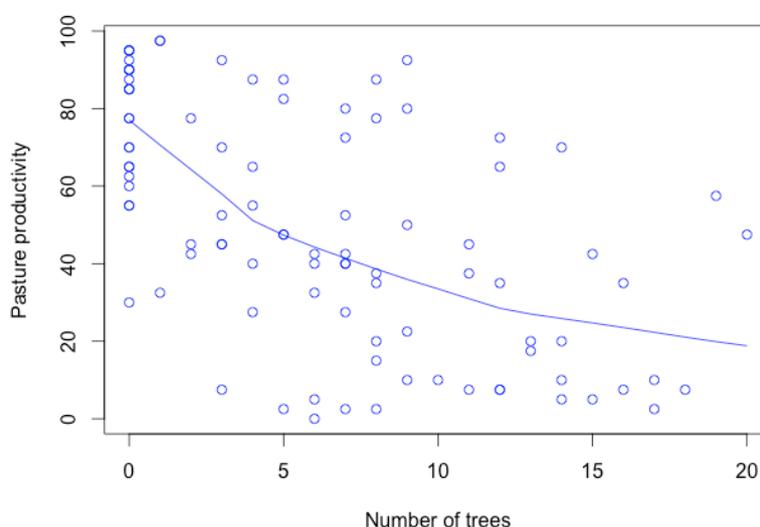


Figure 5.4: The relationship between tree density and pasture productivity illustrated with a lowess line.

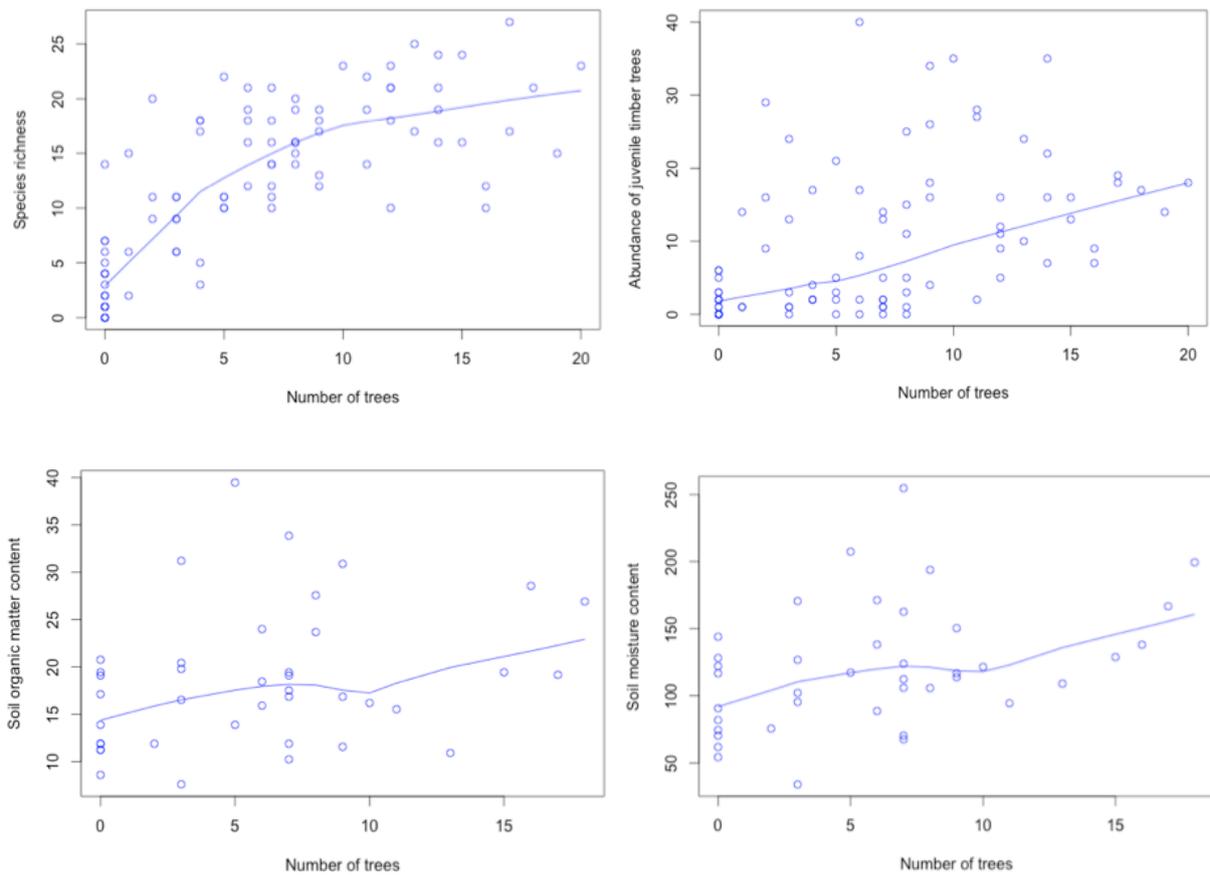


Figure 5.5: Scatterplots of ecosystem properties against tree density. Lowess regression lines show the relationship between tree density and the ecosystem properties.

5.6 Discussion

5.6.1 Land-sparing or land-sharing to protect the remaining forest areas?

Scenario A has the highest pasture productivity: the grasses and herbs of the upper Papallacta valley appear to grow better in the absence of tree cover (Figure 5.3). Trees can compete with grasses for light, water and nutrients, and so incorporating trees into pastures can suppress pasture productivity (Ong and Leakey, 1999; Sánchez-Járdon *et al.*, 2010; Scholes and Archer, 1997). From a land-sparing point of view, Scenario A could be considered the optimal scenario. It maximises pasture productivity, which could theoretically reduce the pressure on the surrounding natural forests: if farmers are producing an adequate yield from their pasture areas then perhaps they will not be motivated to clear further forest and expand their farms (Ewers *et al.*, 2009). It has been argued that this is the best way to succeed with nature conservation, especially in systems like the upper Papallacta valley where

the natural forest community is very sensitive to low levels of disturbance, and some species are lost from farmland regardless of how low intensity the agriculture is (Phalan *et al.*, 2011; Chapter 3).

However, the assumption that an increase in farm productivity reduces pressure on nearby natural ecosystems may be flawed. It is difficult to ensure that existing natural habitats are protected for conservation, whether or not agricultural yields are increased (Fischer *et al.*, 2011; Balmford *et al.*, 2012; Tschardtke *et al.*, 2012). For example, Perfecto and Vandermeer (2010) point out that higher yields may be actually be an incentive to increase agricultural expansion, because the perceived benefits of establishing new agricultural areas are higher. In addition, yield increases generated in land-sparing scenarios may not be sustainable: has been found that pasture yield increases associated with tree removal may not be continue in the long-term, as the lack of trees to replenish and stabilise soil can eventually lead to soil degradation (Kaur *et al.*, 2005). This could increase demand for new agricultural land in the future as the soils begin to degrade and yields begin to decline. In this study, lower levels of soil organic matter were found in open pasture (Chapter 4), implying that trees are important in maintaining soil fertility. Complete clearance of woody vegetation from agricultural areas is expected to lead to future pasture yield declines, and consequently to motivate further forest clearance to create new, more fertile pastures.

Another threat to neighbouring forest areas under Scenario A is the demand for timber. The felling of forest trees for fenceposts is known to be one of the greatest threats to forests neighbouring agricultural areas of South America (Murgueitio, 2004). Post and wire fencing is widely used in the upper Papallacta valley (Figure 5.6), and the necessity for timber needs to be incorporated into any land management plan. If trees are completely cleared from pastures to promote productivity, then farmers are likely to seek timber in neighbouring forests. Scenario A has a regeneration potential of only ~10% of what can be achieved in Scenarios B and C (Table 5.3), and this could be reduced further if farmers clear any regenerating vegetation to keep their pastures open. Scenarios B and C offer a way to maintain a timber resource within the pastoral landscape, reducing the threat of tree felling in neighbouring areas of undisturbed forest.

Overall, Scenario A is expected to put the surrounding natural forests at risk, due to the lack of on-farm timber supply and possible reductions in pasture yields over time. This is a common finding with land-sparing scenarios: intensifying agriculture to allow the expansion of undisturbed natural habitat may sound good in theory (Green *et al.*, 2005; Hodgson *et al.*, 2010; Phalan *et al.*, 2011), but in practice, land 'spared' by yield does not necessarily lead to

land being given over to undisturbed natural habitat (Balmford *et al.*, 2005; Fischer *et al.*, 2011; Tschardt *et al.*, 2012). Many authors propose that the only way to address the combined problems of agricultural land degradation, demand for natural resources such as timber, and the difficulties of creating and maintaining protected areas is to use a land-sharing approach (Altieri, 1999; Scherr and McNeely, 2008; Björklund *et al.*, 2012).



Figure 5.6: Fenceposts made from locally felled timber are widely used in the upper Papallacta valley.

5.6.2 The best approach to land-sharing: Scenario B or Scenario C?

Scenario C (vegetated pasture) was found to be the best scenario to maximise biodiversity, ecosystem services, and pasture productivity within the upper Papallacta valley (Table 5.4). Although the values of ecosystem properties were not as high per unit area in vegetated pasture as edge forest (Table 5.4), the fact that vegetated pasture maintains a relatively high pasture productivity beneath its canopy means that it can be maintained over larger areas than edge forest. Scenario C gives higher levels of ecosystem properties than Scenario B for the same overall level of pasture productivity (Table 5.4).

Scenario C outperforms Scenario B because the difference between the ecosystem properties of vegetated pasture and edge forest is small, and so having a greater area of vegetated pasture is preferable to a smaller area of edge forest. In other ecosystems and landscapes this difference could be large, and retaining forest fragments may in some cases be more effective than vegetated pasture for the conservation of ecosystem services and biodiversity within pastoral landscapes. No studies which explicitly investigated the relative

role of forest fragments compared with vegetated pasture could be found. However, studies of species richness between forest fragments and coffee plantations indicate that the relative performance of forest fragments can vary, depending on the types of organisms involved and their specific responses to the coffee plantations (Ambrecht and Perfecto, 2003; Daily *et al.*, 2003; Tejeda-Cruz and Sutherland, 2004).

Given that this study focused on only a few ecosystem properties, forest fragments should not be discounted as redundant in the upper Papallacta valley even if vegetated pasture was to be established throughout the valley. For example, the species richness of woody plants may not reflect the species richness of animals, and forest fragments may be more suitable than vegetated pasture for some types of animals (Ambrecht and Perfecto, 2003; Daily *et al.*, 2003; Schroth and Harvey, 2007; Riedel *et al.*, 2008). There are several areas of the upper Papallacta valley which are unsuitable for farming, and these could be left (or replanted) with complete forest cover to provide habitat and landscape connectivity for such species. Areas that could be maintained as forest fragments include the steep banks of the valley's rivers, and the steep hillsides around the highway on the southern side of the valley. No yield is lost from maintaining forest cover on these areas, and they would also be of benefit in reducing erosion and the risks of landslides (Andrade Pérez *et al.*, 2010; Björklund *et al.*, 2012).

Scenario B vs. C under a minimum requirement for pasture productivity

The relative roles of vegetated pasture and forest fragments were further investigated in this study under the condition of a minimum requirement for pasture productivity. This was set to 0.9 of the productivity found in open pasture. The tree density of vegetated pasture in Scenario C had to be reduced to gain the appropriate level of productivity (Figure 5.3). This reduces the values of the ecosystem properties of vegetated pasture (Figure 5.5), and so increases the difference in ecosystem properties between vegetated pasture and edge forest. Under the requirement of 0.9 of the productivity found in open pasture, Scenarios B and C become very similar in their performance, with Scenario B slightly outperforming Scenario C for most ecosystem properties. The reduction in ecosystem properties associated with the reduction in tree density in vegetated pasture means that Scenario C can now be matched by retaining only small areas of edge forest in Scenario B.

5.6.3 Conclusion

Vegetated pasture (Scenario C) is identified here as the optimal land-use for the agricultural areas of the upper Papallacta valley, as it has the highest capacity to support biodiversity and ecosystem services as well as pasture productivity. The roles of vegetated

pasture in providing a timber supply and maintaining soil organic matter within agricultural areas will help to reduce the motivation to clear new areas of forest, and so contribute to the protection of the remaining natural cloudforests of the upper Papallacta valley. However, if a high level of pasture productivity is required, it is more beneficial to retain small forest fragments than extensive areas of vegetated pasture with a low tree density. The dependence of the ecosystem properties measured in this study on canopy cover (Chapter 4) mean that vegetated pasture is not an effective conservation tool when tree density is low.

Vegetated pasture with a tree density of 600 trees/ha or higher is currently a common feature of the upper Papallacta valley (Figure 1.4), indicating that many farmers find tree cover desirable for either on-farm benefits or as a contribution to ecosystem services and to 'Pachamama' (see Chapter 1). The assessment of the value of vegetated pasture given here could help to further promote these ideas, and contribute to the goal of Care International to encourage more farmers to maintain and replant forest trees within their pastures.

Chapter 6

Discussion

6.1 Conserving forest biodiversity and ecosystem services for resilience to climate change in the Andes

The conservation of natural habitat can be an effective way to ensure resilience to climate change (Coles *et al.*, 2009; Andrade Pérez *et al.*, 2010). Natural habitat supports biodiversity, biodiversity generates ecosystem services (Cardinales *et al.* 2012; Naeem *et al.*, 2012), and ecosystem services can mitigate the impacts of climate change (Andrade Pérez *et al.*, 2010; Ford *et al.*, 2011). Climate change in the Andes is causing rising temperatures and glacial retreat, leading to a reduction in water supplies during the dry season (Vuille *et al.*, 2008). Extreme weather events are expected to increase in intensity and frequency, threatening Andean areas with heavy rainfalls interspersed by long dry spells (Ministry for the Environment of Ecuador, 2011). These impacts threaten water security for both rural and urban populations in the Andes, and increase the risk of disasters such as landslides and flooding (Care, 2009; Carey, 2010; Anderson *et al.*, 2011).

Andean forests are key providers of ecosystem services which can mitigate these impacts (Ataroff and Rada, 2000; Anderson *et al.*, 2011). Forests shelter soils from both solar radiation and precipitation, with the overall effect that less water is lost as runoff during rainfall events, and less water is lost through evaporation during day periods (Ataroff and Rada, 2000; Costa *et al.*, 2003; Breshears, 2006). This helps to reduce both flooding (caused by excessive runoff) and the drying out of soils during droughts (Ford *et al.*, 2011). Forests also improve soil nutrient levels by adding organic matter to the soil through litterfall (Jóbbagy and Jackson, 2004; Torn *et al.*, 2009). Organic matter is a source of nutrients and helps to store water in the soil, and can be a significant store of carbon (Lal, 2004; Lal, 2009; Dominati *et al.*, 2010). Carbon is released into the atmosphere as organic matter decomposes, but forests can help to ensure that much of this carbon stays trapped in the soil by creating cooler, more humid conditions (Berg *et al.*, 1995; Lal, 2004; Breshears, 2006).

Forests and their ecosystem services are threatened by human activities (Foley *et al.*, 2005; Anderson *et al.*, 2011). Most deforestation in the Andes is driven by the expansion of agriculture (Sarmiento, 2002; Jokisch and Lair, 2002), where complex forest ecosystems are transformed into pastures which contain fewer species and a lower provision of ecosystem services (Foley *et al.*, 2005; Foley *et al.*, 2007). This thesis explored the effects of pastoral

agriculture on forest using a case study of the upper Papallacta valley, a pastoral landscape bordered by forest in the Ecuadorian Andes. The environmental gradient between open pasture grazed by cattle to undisturbed mature forest was associated with a change in vegetation community composition (Chapter 3), and with a gradient in biodiversity levels and ecosystem service provision (Chapter 4). The lack of canopy cover in pastures combined with grazing pressure creates an environment in which only the most exposure- and disturbance-tolerant species of the upper Papallacta valley can survive (Chapter 3). Communities of such species were found to be significantly less effective in supporting biodiversity and providing ecosystem services than the undisturbed mature forest community (Chapter 4). This effect is commonly found where forest plant communities are shifted from mature forests to disturbed communities dominated by pioneer species (Foley *et al.*, 2007; Tabarelli *et al.*, 2008). The creation of pasture also affects the plant communities within remaining areas of forest, by allowing more light and disturbance into the edges of neighbouring forest areas (Chapter 3; Murcia, 1995; Bruna and Harrison, 1999). This causes further losses in biodiversity and ecosystem services within the landscape (Chapter 4; Tabarelli *et al.*, 2008).

The effects of deforestation on biodiversity and ecosystem services can be mitigated by retaining forest vegetation within pastoral areas, either as remnant trees scattered throughout pastures, or as forest fragments (Manning *et al.*, 2006; Harvey *et al.*, 2006; Karp *et al.*, 2012). In the upper Papallacta valley, plant communities in remnant forest vegetation were found to conserve many of the forest species, even though these communities tended to contain higher abundances of pioneer species and lower abundances of species associated with mature forest (Chapter 3). Biodiversity levels and ecosystem service provision within remnant vegetation communities were also significantly higher than in open pastures (Chapter 4).

Many key ecosystem services provided by forests stem from the functions of trees in the landscape, such as nutrient cycling through root uptake and litterfall, and sheltering the soil from solar radiation and precipitation (Scholes and Archer, 1997; Breshears, 2006; Manning *et al.*, 2006; Sánchez-Járdón *et al.*, 2010). Trees also provide sheltered habitats and resources which are not otherwise found in pasture, and so facilitate the use of pastoral landscapes by a greater diversity of species (Guevara *et al.*, 1992; Harvey *et al.*, 2006). In this study, biodiversity and ecosystem services had a positive relationship with tree density (Chapters 4 and 5), indicating that conserving higher numbers of trees in pastoral landscapes leads to higher retention of biodiversity and ecosystem services.

6.2 Balancing the conservation of forest biodiversity and ecosystem services with the needs of pastoral agriculture

Both agriculture and forests are essential to human survival and welfare in the Andes: agriculture provides food and incomes, forests and their biodiversity provide ecosystem services. Land is limited, so it is necessary to identify the most effective land use strategy that maximises both agricultural production and the conservation of forest biodiversity and ecosystem services.

Large areas of unmodified forest are essential to effective conservation of biodiversity and ecosystem services (Pearce, 2001; Foley *et al.*, 2007; Dobson *et al.*, 2006). Such areas of forest are in increasingly short supply, threatening the future of Andean biodiversity, and the future of the Andean people who rely on forest-provided ecosystem services (Downer, 2001; Katten *et al.*, 2004; Anderson *et al.*, 2011). In this study it was assumed that further deforestation is highly undesirable, so the focus was on how to manage pastoral landscapes to a) contribute to the protection of surrounding forest areas and b) how forest biodiversity and ecosystem services could be integrated into pastoral landscapes to offset losses of biodiversity and ecosystem services from previous deforestation.

The 'land-sparing vs. land-sharing' concept was used to assess land use options in this thesis. 'Land-sparing' foregoes trying to incorporate biodiversity and ecosystem services into farmland, but assumes that increasing yields in pasture areas will lead to reduced need for new pasture, and thus reduced clearance of the surrounding forests (Balmford *et al.*, 2005; Ewers *et al.*, 2009; Phalan *et al.*, 2011). 'Land-sharing' integrates biodiversity and ecosystem services into the pastoral landscape, which in some cases comes at the expense of pasture yields, but in some cases contributes to farm productivity (Altieri, 2002; Fischer *et al.*, 2008; Tscharnkte *et al.*, 2012). In this study, 'land-sparing' equated to clearing all forest vegetation from pasture areas, while 'land-sharing' incorporated forest vegetation as either scattered trees and shrubs, or as forest fragments.

'Land-sharing' was found to reduce pasture productivity; however, it was not considered to reduce the threat of clearance to surround forest (Chapter 5). Firstly, demand for timber can be major cause of deforestation, and if no timber resource is maintained within the pastoral areas then farmers may seek timber supplies for adjacent forest (Murgueitio, 2004). Secondly, lower levels of organic matter were found within pasture than within forest, suggesting that pasture leads to a decline in soil fertility (Kaur *et al.*, 2005). This may lead to future reductions in pasture yields, and therefore contribute to future deforestation. 'Land-sharing' is recommended as the preferred option. Reasonably high pasture yields can still be maintained

when trees are incorporated into the pastoral landscape, and the timber supply and higher certainty of sustainable pasture yields are considered to offset the lower immediate yield in relation to land-sparing. Tree cover in pastures may also have a variety of benefits not assessed in this study, such as providing shelter and additional forage for livestock (Manning *et al.*, 2006; Harvey *et al.*, 2011), maintaining populations of predators which control agricultural pests (Sperber *et al.*, 2004; Bianchi *et al.*, 2006), preventing soil erosion (Jose, 2009), and providing habitat for charismatic wildlife species which draw tourists to these rural areas (Tinoco *et al.*, 2009).

Two versions of land-sharing were compared in this study to identify the best approach to maximising pasture productivity and the conservation of biodiversity and ecosystem services within the agricultural areas (Chapter 5). These were the maintenance of scattered remnant trees throughout pastures, or the maintenance of forest fragments interspersed with open pasture. Scattered remnant trees conserved higher levels of biodiversity and ecosystem services for a given level of pasture productivity than forest fragments, unless the requirement for pasture productivity was very high. In this case, a few small forest fragments conserve greater biodiversity and ecosystem services than a very low density of trees scattered through pasture.

6.3 Recommendations for the conservation of forest biodiversity and ecosystem services in pastoral landscapes of the high Andes

Several land management recommendations for the local people of the high Andes can be drawn from the findings of this thesis:

- Conserve large areas of forest where possible. Edge effects from pasture cause forest edges and small forest fragments to have a different species composition from undisturbed forest (Chapter 3). These edge communities tend to conserve lower levels of biodiversity and ecosystem services (Chapters 4 and 5).
- Fence forests to prevent cattle entering. This eliminates the edge effect of cattle entering the forests to graze, which alters the composition of the plant communities within these forest edges (Chapter 3).
- Retain trees in pastoral landscapes. Trees provide a timber resource, and a source of nutrients to pasture soils to maintain pasture productivity, which is expected to reduce the need to clear more forest in the future. In addition, these trees retain biodiversity and ecosystem services within the pastoral landscape, mitigating the effects of forest loss (Chapter 4).

- If the requirement for pasture productivity is moderate, trees scattered in pastures conserve a higher level of biodiversity and ecosystem services than trees retained as forest fragments (Chapter 5). However, if the requirement for pasture productivity is high enough that it requires pasture trees to be thinned to 100 trees/ha or less, it is more effective to conserve biodiversity and ecosystem services by maintaining 14% of the landscape as forest fragments and 76% as open pasture. This achieves the same level of pasture productivity as 100 trees/ha.
- Set aside areas unsuitable for farming (i.e. steep slopes) as forest fragments. Pasture productivity is not lost if the area is unsuitable to graze, while additional habitat and ecosystem service provision are gained. Tree cover on steep slopes can also help to reduce erosion and the risks of landslides.

6.4 Further research

The above management recommendations should be applied with caution until further research can be undertaken to confirm these findings. This thesis was based on an exploratory study into the broad trends of biodiversity and ecosystem services within high Andean pastoral landscapes, which aimed to provide an overall picture of the situation rather than to investigate any aspects in great detail. Therefore, there are several areas of further research that would greatly aid understanding of the conservation of biodiversity and ecosystem services in high Andean agroecosystems.

Firstly, a greater understanding of the relationship between farm production and tree cover is desirable. In this thesis, percent ground cover by pasture species was used as a very simple measure of pasture productivity. However, the amount of productivity could be better estimated by measuring biomass production (e.g. Sánchez-Járdón *et al.*, 2010), or an analysis of the nutrient content and digestibility of pasture species could be used to further understand the value of pasture to livestock (González-Hernández, 2004; Ku Vera, 2004). An alternative approach would be to investigate livestock growth or milk production in relation to tree cover, to directly identify any benefits or drawbacks of tree cover on farm production. Trees and shrubs in pastures are known to benefit livestock through the provision of shelter and additional forage (Topps, 1992; Murgueitio, 2004; Ku Vera, 2004), and these effects would not have been captured by measuring pasture productivity. A closer investigation into the relationship between trees and livestock may illuminate ways in which trees can be used to promote farm production, and thus land-sharing could be better optimised to improve both farm production and the conservation of biodiversity and ecosystem services.

The relationship between tree cover and high Andean wildlife also merits further investigation. This thesis identified that vegetated pasture contains higher levels of woody plant diversity than a mixture of forest fragments and open pasture, but was unable to answer whether the same is true for other taxa. Some taxa are expected to increase in association with woody plant biodiversity (Siemann *et al.*, 1998; Haddad *et al.*, 2009) and so will also be higher in vegetated pasture, but other taxa may require closed forest environments (Ambrecht and Perfecto, 2003). Of particular interest in the upper Papallacta valley is how large mammal species such as the spectacled bear and the mountain tapir can use either vegetated pasture or forest fragments as a corridor between the neighbouring Ecological Reserves (pers.comm., Care International staff). The conservation of charismatic species such as these is important for both tourism and for cultural values.

Finally, a major finding of this thesis has been that the conservation of mature forest is essential to conserve the full range of high Andean biodiversity and the full provision of ecosystem services. This raises the question of how mature forest can be conserved in the face of agricultural expansion. Chapter 5 briefly discussed the role of land-sharing to maintain pasture productivity and a timber supply so that neither soil degradation nor demand for timber incentivise further deforestation. However, other factors such as population growth continue to increase demand for agricultural land. Other projects around the world with the combined aims of protecting forest and of ensuring sustainable rural livelihoods promote practices such as agricultural intensification through product diversification (e.g. Perz, 2001; Coles *et al.*, 2009), or seek alternative incomes for rural communities that are not based on agriculture (Naughton-Treves *et al.*, 2005). Payments for environmental services could also be used, for example from Ecuador's capital Quito to the communities of the upper Papallacta valley, to arrange for the protection of Papallacta's forest areas to conserve the downstream benefits of water regulation on which Quito relies (Pagiola *et al.*, 2007; Wunder, 2006; Engel *et al.*, 2008).

6.5 Conclusion

The findings of this thesis suggest that the best approach to balance nature and agriculture in high Andean pastoral landscapes is for these areas to become dominated by vegetated pasture. Existing large areas of undisturbed forest would be conserved, while steep slopes (such as stream banks and roadsides) would be planted or left to regenerate to forest patches. This scenario would conserve habitat for Andean biodiversity within the pastoral landscapes, and conserve the ecosystem services which contribute to climate change resilience in the Andes.

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Appendix A

Woody plant species inventory of the upper Papallacta valley

Family	Genus	Species	Local name
Rosaceae	Acaena	elongata	?
Asteraceae	Baccharis	buxifolia	?
Asteraceae	Baccharis	latifolia	Chilco
Asteraceae	Baccharis	nitida	?
Asteraceae	Baccharis	prunifolia	Chilco del cerro
Asteraceae	Barnadesia	arborea	Alfilero
Scrophulariaceae	Berberis	grandiflora	Espino amarillo
Pterophyta	Blechnum	?	?
Melastomataceae	Brachyotum	ledifolium	Zarcilejo blanco
Scrophulariaceae	Buddleja	?	Quijuar
Calceolariaceae	Calceolaria	lamiifolia	Zapatitos
Campanulaceae	Centropogon	glabrifilis	Hierba de danta
Bambusoideae	Chusquea	scandens	Bambú
Nyctaginaceae	Colignonia	ovalifolia	?
Coriariaceae	Coriaria	ruscifolia	Shanshi
Asteraceae	Dendrophorbium	lloense	Isca
Asteraceae	Diplostephium	floribundum	?
Ericaceae	Disterigma	acuminatum	Yurak muyu
Escalloniaceae	Escallonia	myrtilloides	Chachaco
Onagraceae	Fuchsia	?	Arete de monte
Ecuador	Gnaphalium	elegans	?
Bromeliaceae	Greigia	mulfordii	Piñuelos
Asteraceae	Grosvenoria	rimbachii	Pussu pato
Asteraceae	Gynoxys	? (large leaves)	Piquil
Asteraceae	Gynoxys	? (small leaves)	Piquil
Rosaceae	Hesperomeles	ferruginea	Pujín
Rosaceae	Hesperomeles	obtusifolia	Wakra manzano
Asteraceae	Heterocondylus	vitalbae	?
Clusiaceae	Hypericum	laricifolium	Romerillo
Solanaceae	Jaltomata	viridiflora	Ushaki
Asteraceae	Jungia	rugosa	Cutzato
Asteraceae	Lasiocephalus	?	?
Asteraceae	Llerasia	?	?
Fabaceae	Lupinus	pubescens	Sacha chochos
Melastomataceae	Miconia	bracteolata	Alamoja
Melastomataceae	Miconia	crocea	Colca
Melastomataceae	Miconia	salicifolia	Sauce
Lamiaceae	Minthostachys	mollis	Tipo
Poligalaceae	Monnina	?	Azulina
Polygonaceae	Muehlenbeckia	tamnifolia	Anku yuyu
Polygonaceae	Muehlenbeckia	tiliifolia	?
Asteraceae	Munnozia	jussieui	?
Araliaceae	Oreopanax	ecuadorensis	Pumamaki
Fabaceae	Otholobium	mexicanum	?

Passifloraceae	Passiflora	mixta	Sacha taxo
Asteraceae	Pentacalia	arbutifolia	?
Ericaceae	Pernettya	prostrata	Taglli
Piperaceae	Piper	nubigenum	Luncug
Rosaceae	Polylepis	pauta	Árbol de papel
Dennstaedtiaceae	Pteridium	?	?
Saxifragaceae	Ribes	ecuadorensis	Sacha manzano
Rosaceae	Rubus	?	Mora
Solanaceae	Salpichroa	tristis	Chulalik
Solanaceae	Saracha	quitensis	?
Solanaceae	Sessea	crassivenosa	?
Campanulaceae	Siphocampylus	lucidus	Pukunero
Solanaceae	Solanum	asperolatum	Urku Wantuk
Solanaceae	Solanum	brevifolium	Mitsa muyu
Solanaceae	Solanum	nigrescens	Hierba mora
Ranunculaceae	Thalictrum	podocarpum	Moradilla
Urticaceae	Urtica	leptophylla	Ortiga
Valerianaeeae	Valeriana	microphylla	Valeriana
Elaeocarpaceae	Vallea	stipularis	Sacha capuli
Asteraceae	Verbesina	lloensis	Mimisca

Appendix B

Model diagnostic plots

B.1 Model diagnostic plots for Chapter 3

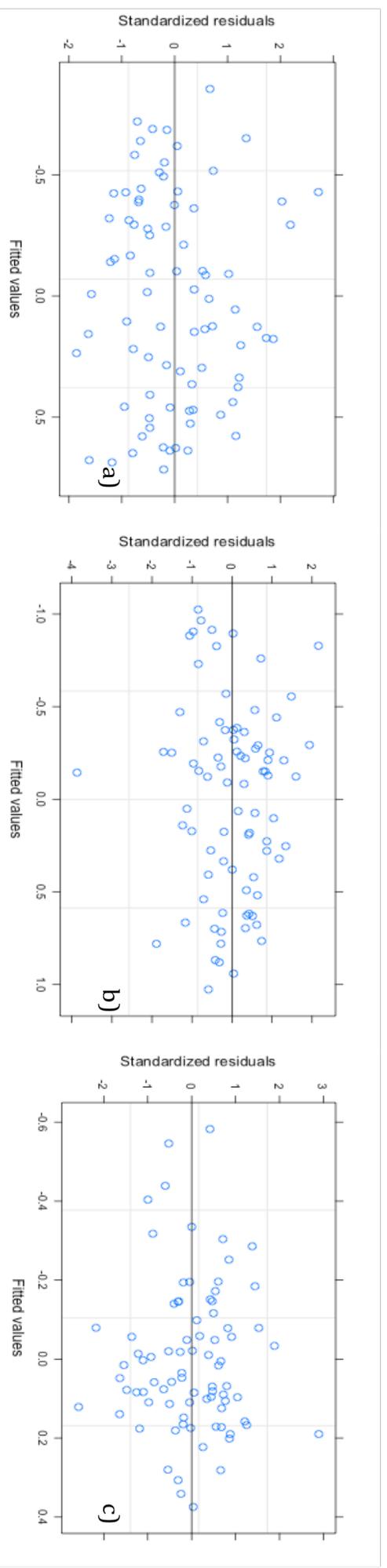


Figure B.1: Residual plots for each model used to investigate the environmental variables associated with each NMS axis (Chapter 2, Section 2.3.1): a) refers to axis 1, b) to axis 2, and c) to axis 3. No patterns are obvious in the residuals, indicating good model fit.

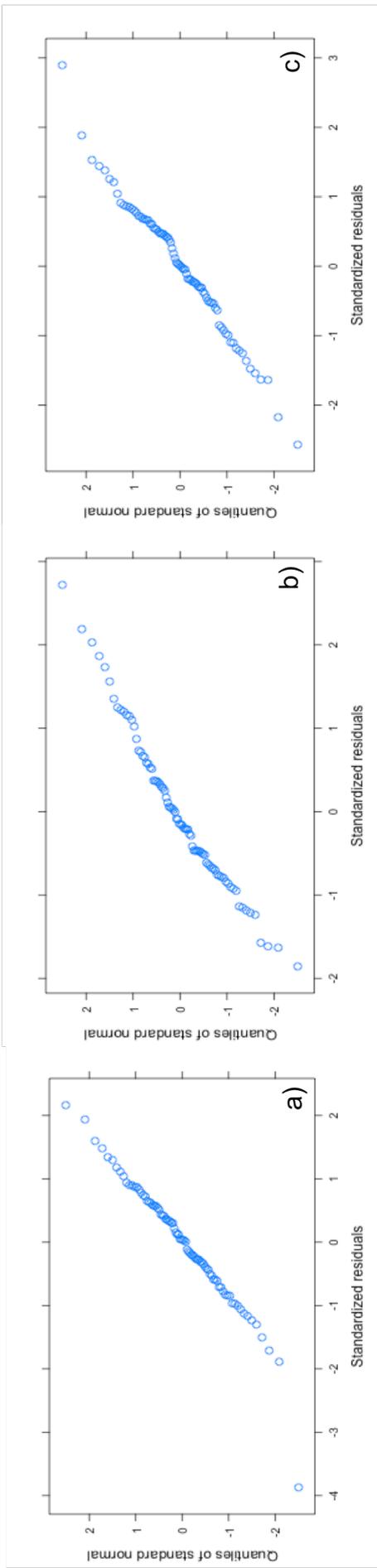


Figure B.2: Normal QQ plots for each model used to investigate the environmental variables associated with each NMS axis (Chapter 2, Section 2.3.1): a) refers to axis 1, b) to axis 2, and c) to axis 3. The linear distribution of points indicates good model fit.

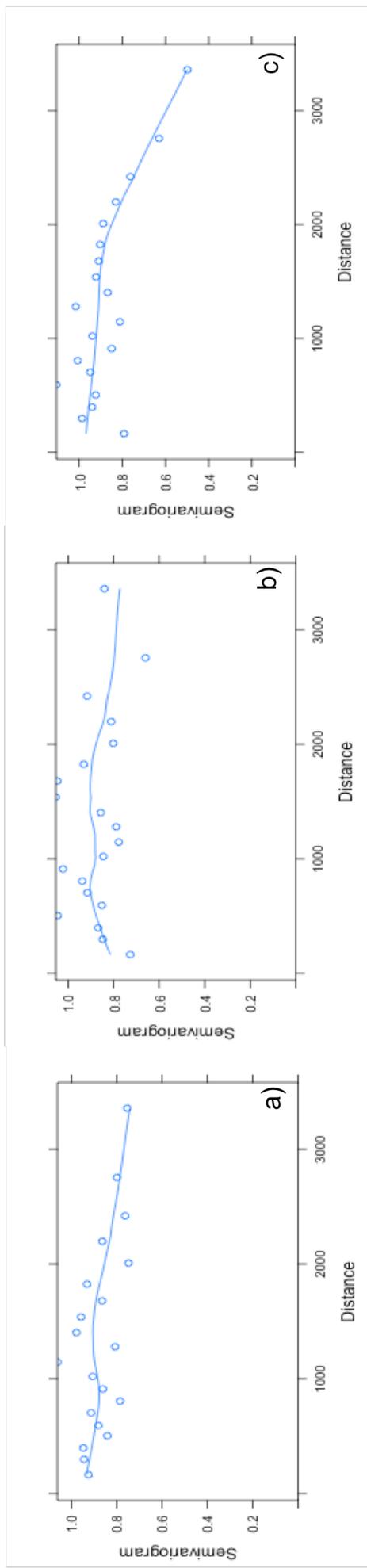


Figure B.3: Variograms for each model used to investigate the environmental variables associated with each NMS axis (Chapter 2, Section 2.3.1): a) refers to axis 1, b) to axis 2, and c) to axis 3. The lack of any upwards trends indicates the absence of spatial autocorrelation in the models.

B.2 Model diagnostic plots for Chapter 4

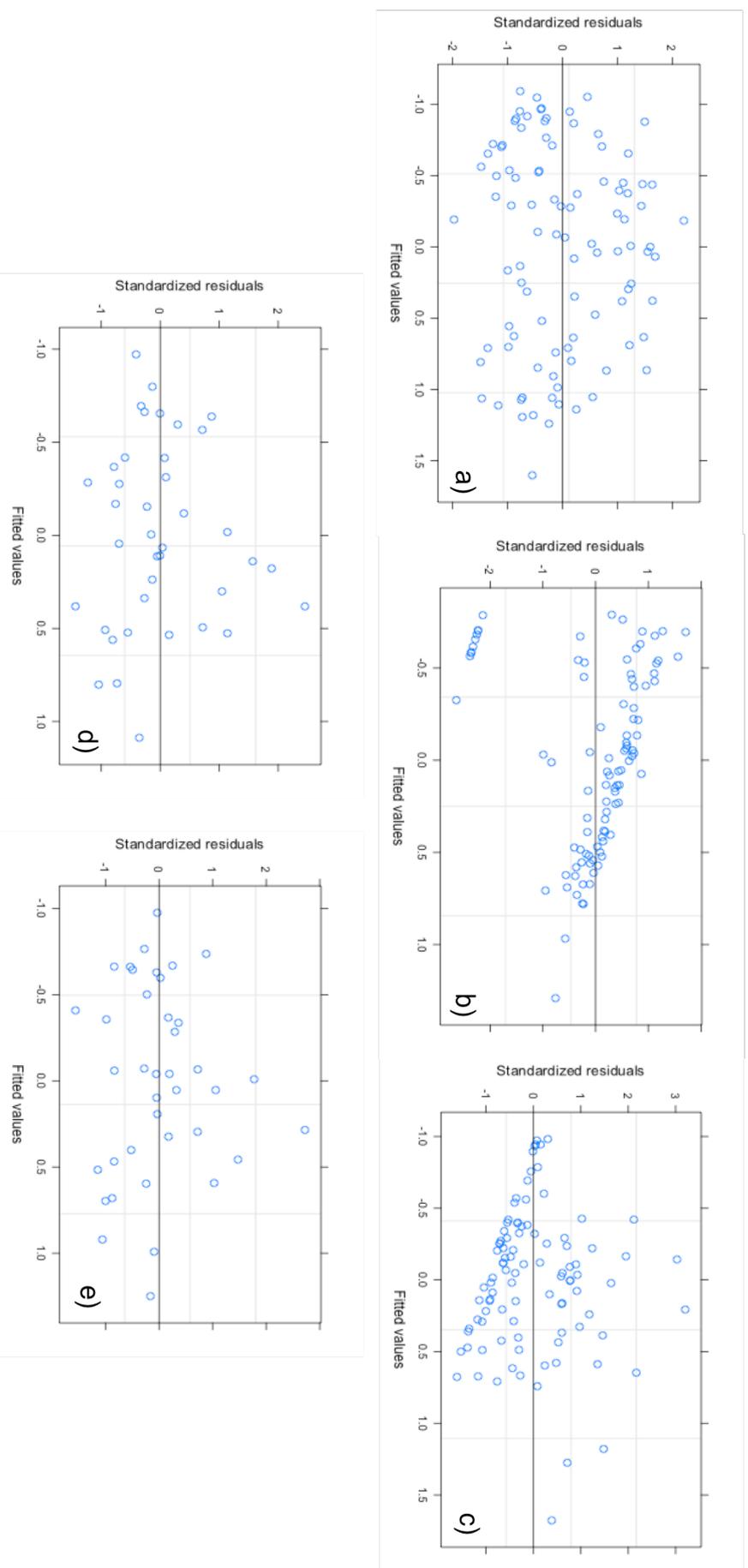


Figure B.4: Plots of residuals vs. fitted values for the models of a) species richness, b) Simpson's Diversity Index, c) abundance of juvenile timber trees, d) soil organic matter content and e) soil moisture content. The distribution of points in b) Simpson's Diversity Index suggests a poor model fit.

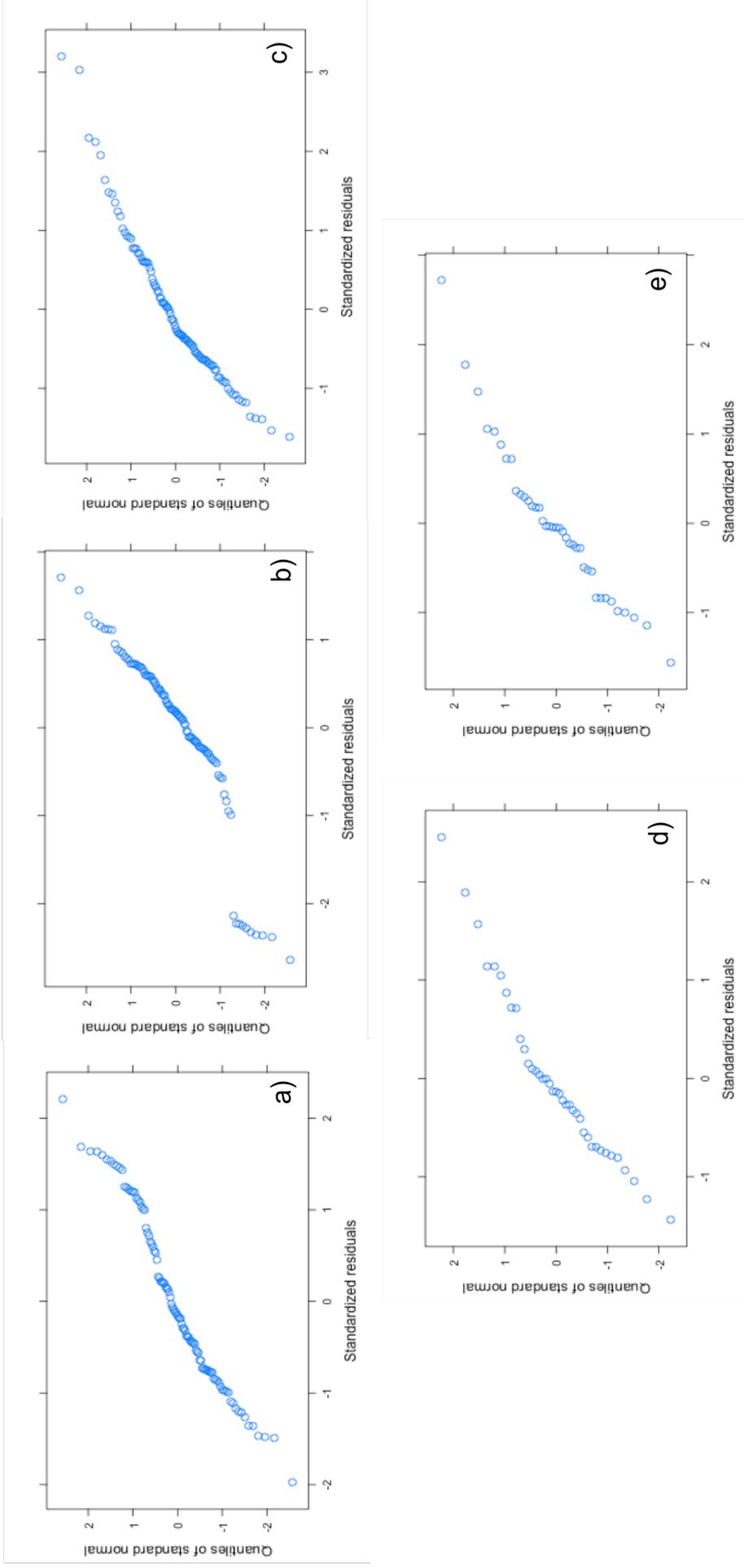


Figure B.5: Normal QQ plots for the models of a) species richness, b) Simpson's Diversity Index, c) abundance of juvenile timber trees, d) soil organic matter content and e) soil moisture content. The separation in the line of plot b) Simpson Diversity Index indicates a potential issue. In all other plots the points have a linear distribution, confirming that the assumption of Normality in the response is valid.

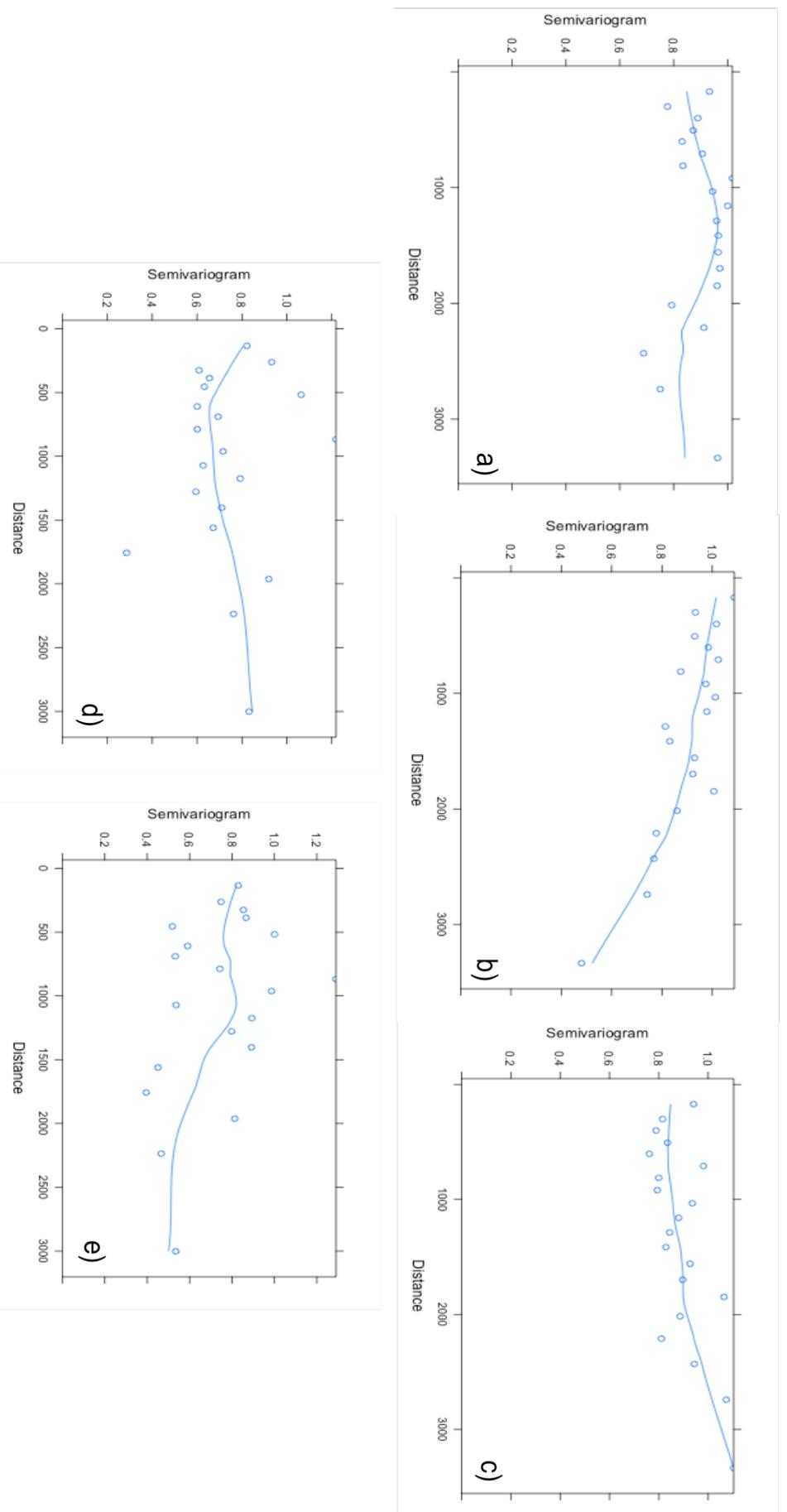


Figure B.6: Variograms for the models of a) species richness, b) Simpson's Diversity Index, c) abundance of juvenile timber trees, d) soil organic matter content and e) soil moisture content. The absence of upward trends indicates an the absence of spatial autocorrelation in the

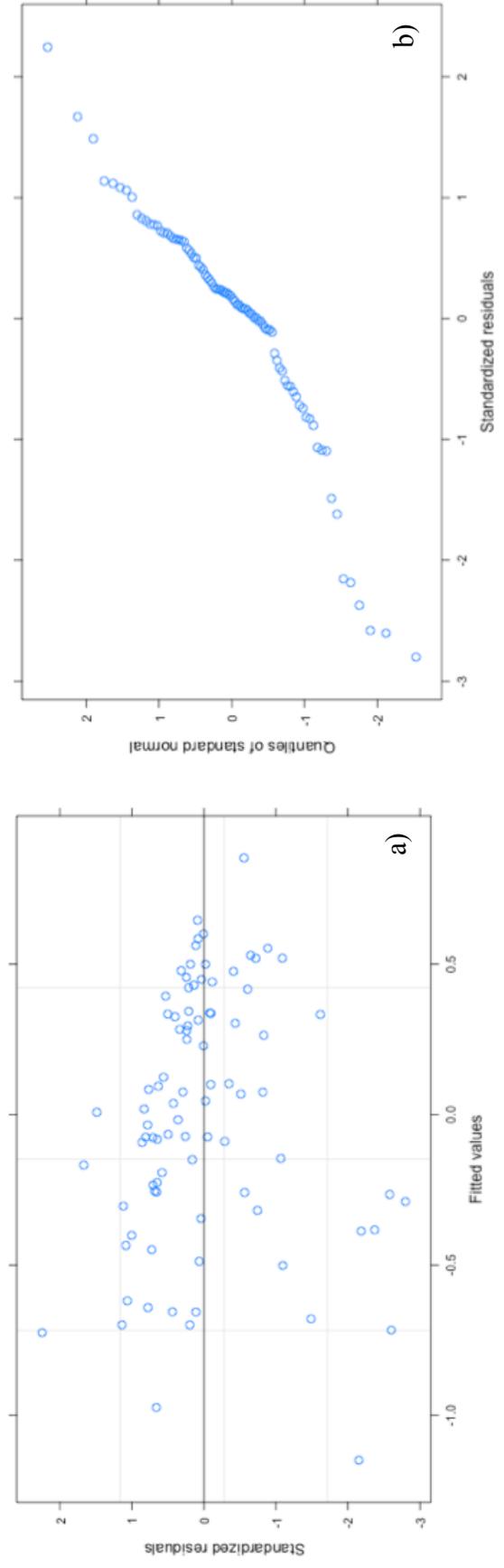


Figure B.7: After removing all sites with a Simpson's diversity index of 0, there are no issues with either the residuals vs. fitted value plot (a), or the Normal QQ plot (b) for the model of Simpson's diversity index.

Appendix C

Distributions of individual timber tree species by altitude and by canopy cover

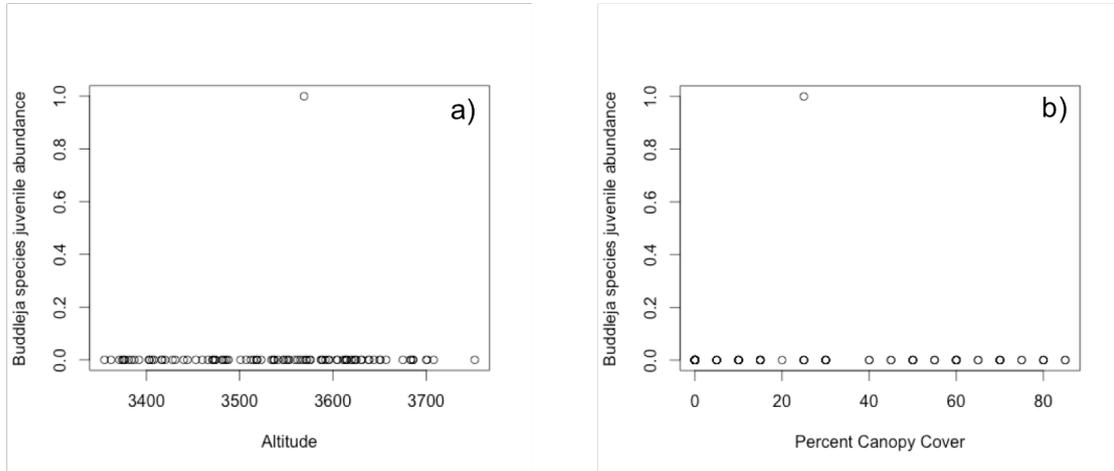


Figure C.1: The distribution of juveniles of *Buddleja* species in relation to a) altitude and b) percent canopy cover.

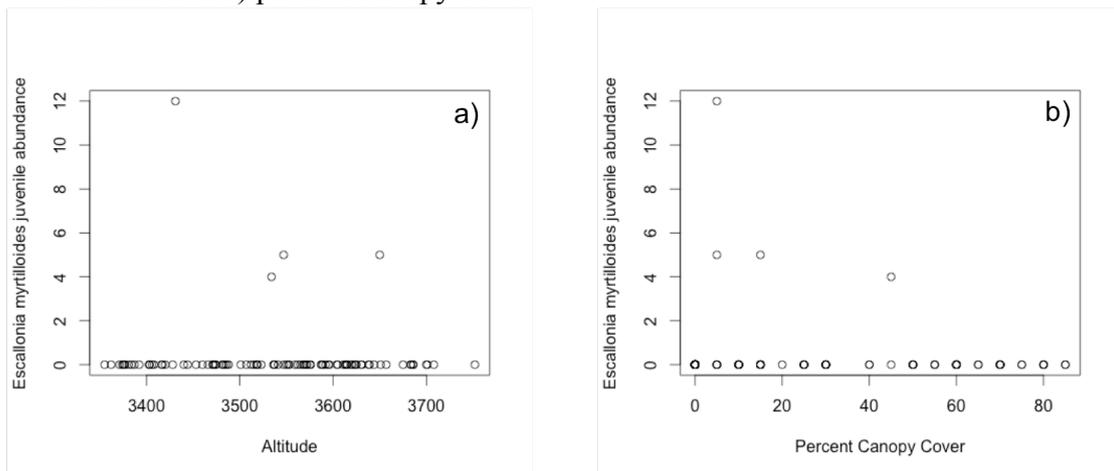


Figure C.2: The distribution of juveniles of *Escallonia myrtilloides* in relation to a) altitude and b) percent canopy cover.

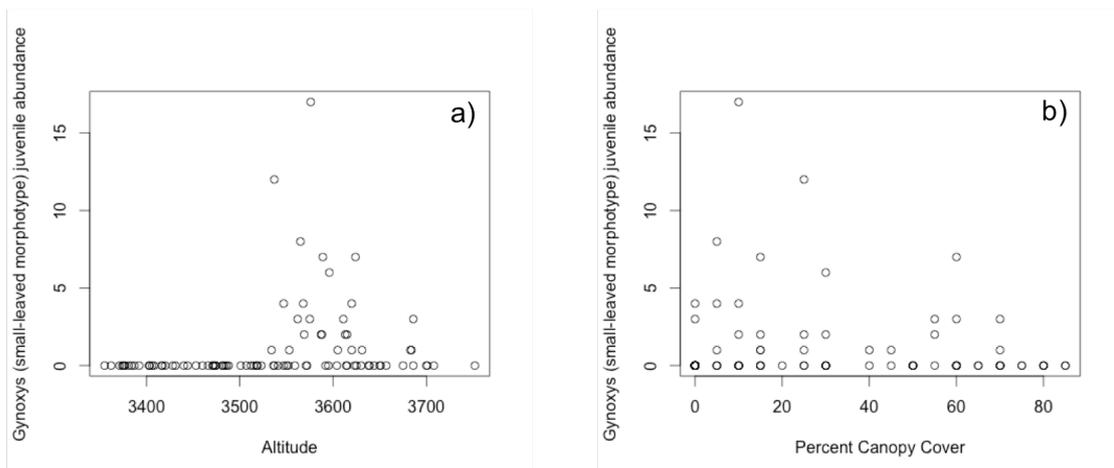


Figure C.3: The distribution of juveniles of the small-leaved morphotype of *Gynoxys* in relation to a) altitude and b) percent canopy cover.

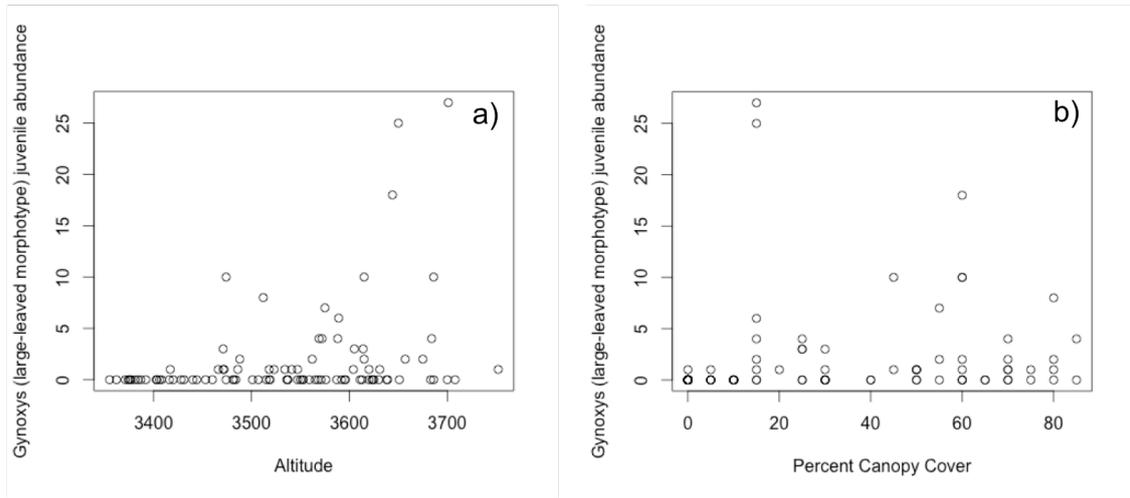


Figure C.4: The distribution of juveniles of the large-leaved morphotype of *Gynoxys* in relation to a) altitude and b) percent canopy cover.

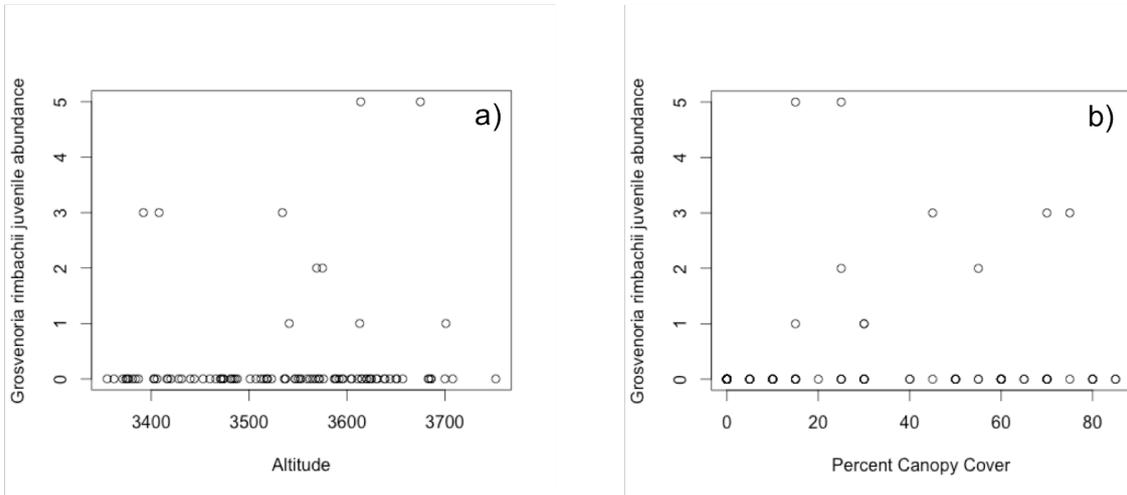


Figure C.5: The distribution of juveniles of *Grosvenoria rimbachii* in relation to a) altitude and b) percent canopy cover.

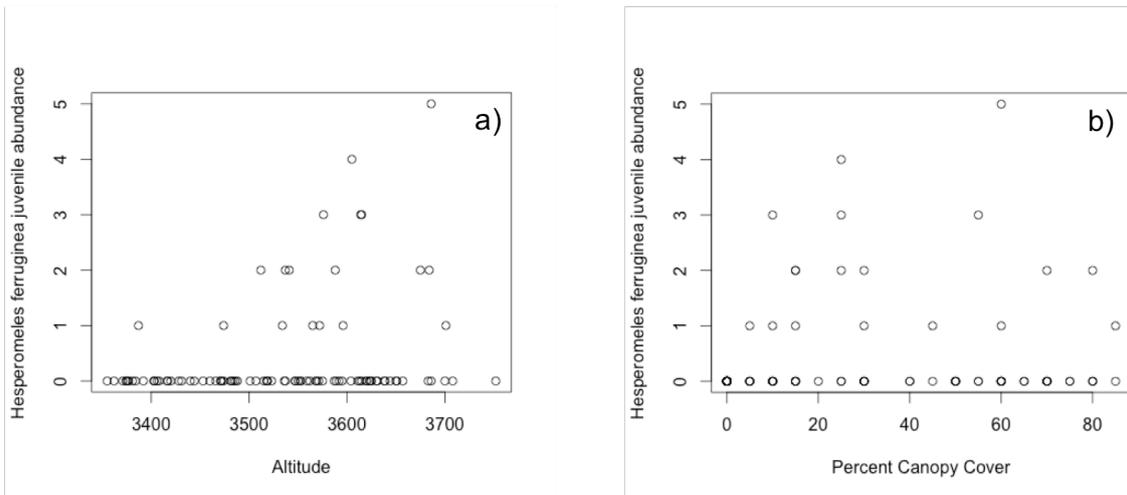


Figure C.6: The distribution of juveniles of *Hesperomeles ferruginea* in relation to a) altitude and b) percent canopy cover.

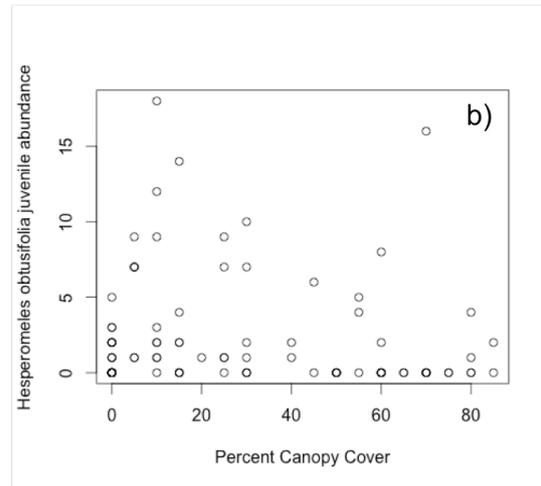
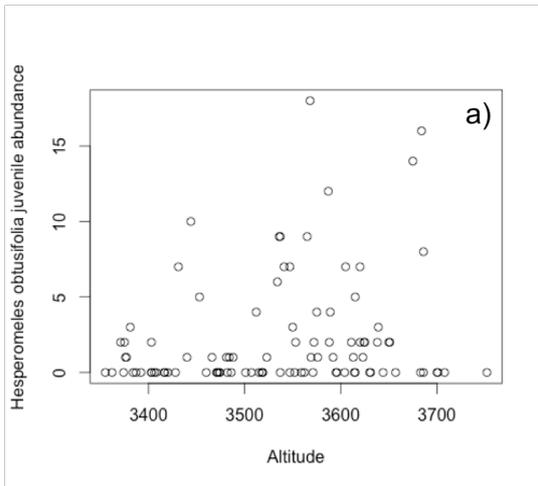


Figure C.7: The distribution of juveniles of *Hesperomeles obtusifolia* species in relation to a) altitude and b) percent canopy cover.

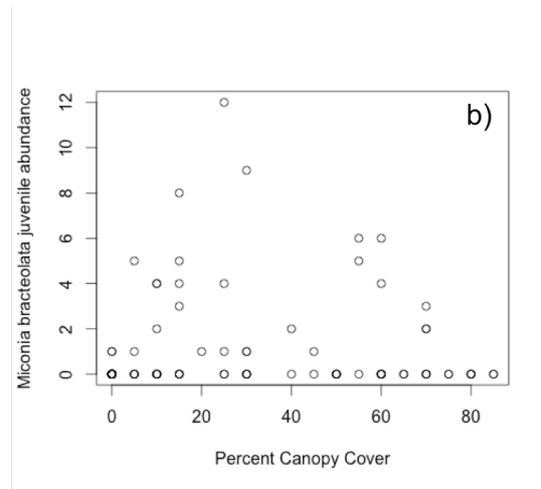
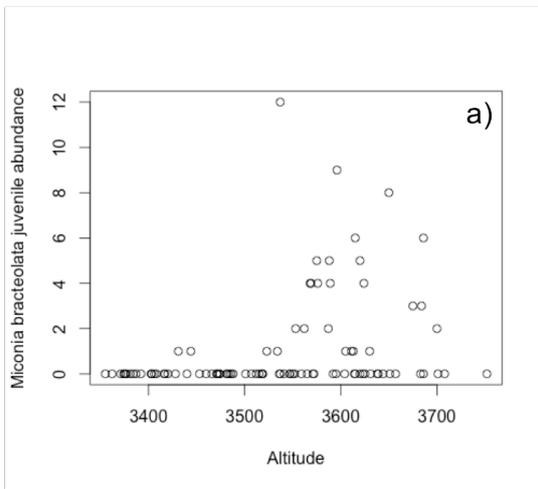


Figure C.8: The distribution of juveniles of *Miconia bracteolata* in relation to a) altitude and b) percent canopy cover.

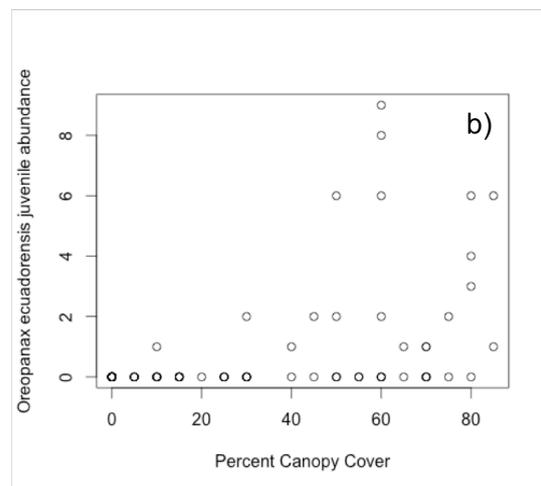
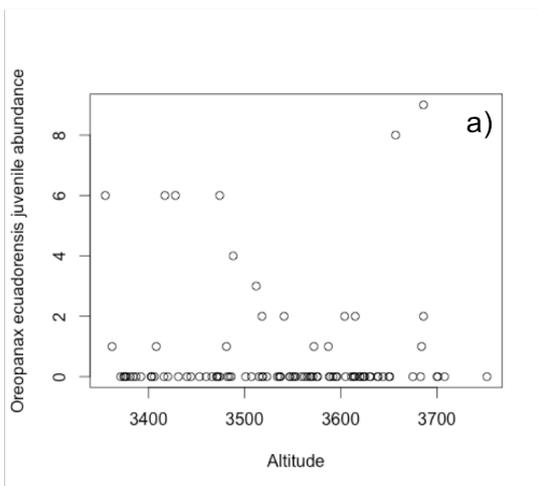


Figure C.9: The distribution of juveniles of *Oreopanax ecuadorensis* in relation to a) altitude and b) percent canopy cover.

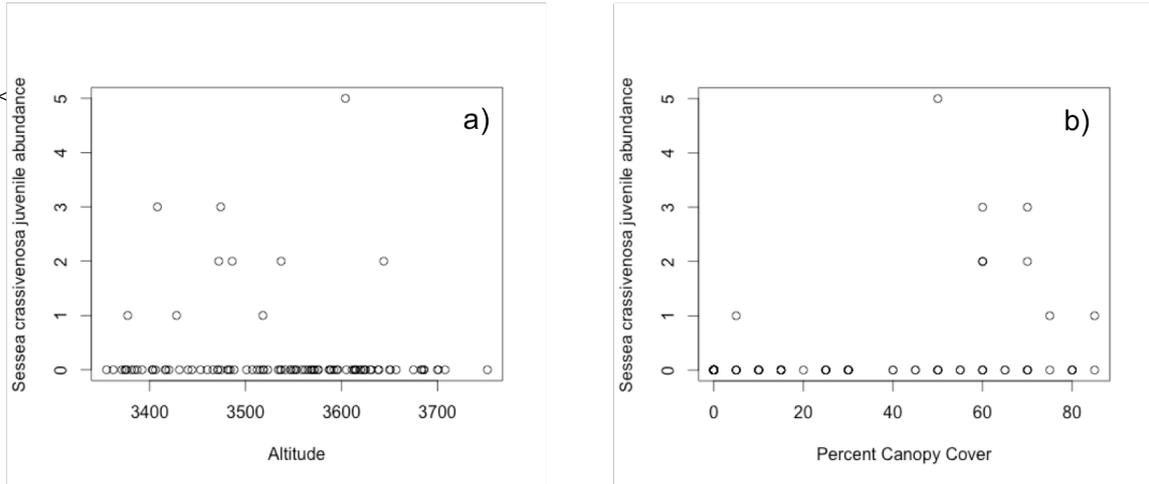


Figure C.10: The distribution of juveniles of *Sessea crassivenosa* in relation to a) altitude and b) percent canopy cover.

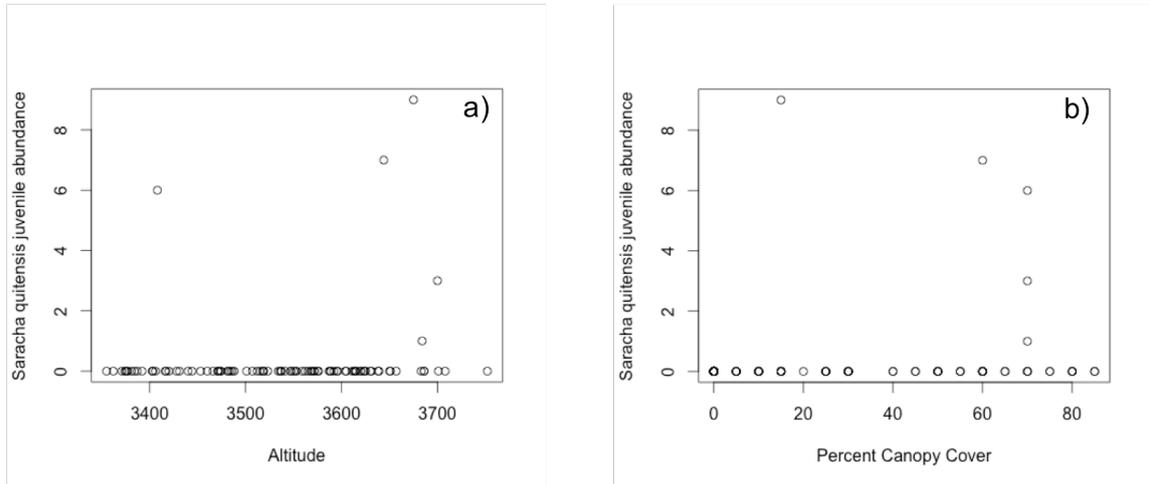


Figure C.11: The distribution of juveniles of *Saracha quitensis* in relation to a) altitude and b) percent canopy cover.

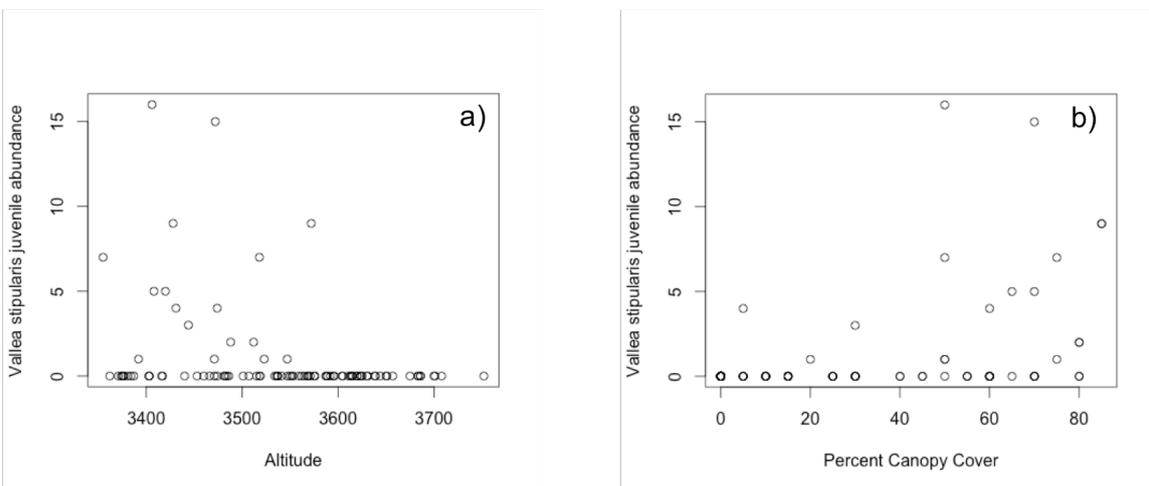


Figure C.12: The distribution of juveniles of *Vallea stipularis* in relation to a) altitude and b) percent canopy cover.