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Research Article

A Perspective on the Consequences for Insect Herbivores and Their Natural Enemies When They Share Plant Resources

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Thousands of insect species consume both animal and plant-derived food resources. However, little recognition is given to the fact that omnivory is a general feeding strategy common to all higher trophic levels. Species in multitrophic interactions can all directly rely on the same plant resources. Nonetheless, little is known about the effect of a change in the relative abundance of a shared plant resource on trophic dynamics. Here we describe how a relative change of resource availability can affect multitrophic interactions and we emphasise its importance. Changes in multitrophic interactions can be induced by unequal alterations of individual fitness across trophic levels, possibly leading to changes in population structure of interacting species. At least ten ecological mechanisms can be involved and these are explored here. It is concluded that shared plant resources that are differentially used over several trophic levels have the potential to modify community structure and energy flow within food webs and ecosystems in more complex ways than previously recognised. The synthesis presented here provides an understanding of this complexity and can lead to improved deployment of biodiversity when manipulating food webs to protect ecological communities or to enhance ecosystem services such as biological control of agricultural pests.

1. Introduction

Herbivores are trapped between "the devil and the deep blue sea", that is, between natural enemies and plant defences [1–4]. However, little recognition is given to the fact that many natural enemies also directly rely on plant-derived food resources, such as nectar, pollen, seeds, or leaves [5–8]. Thousands of species of terrestrial arthropods such as predatory carabids, coccinellids, mites, spiders, and syrphids, along with hymenopteran and dipteran parasitoids, consume both animal and plant food; that is, they are omnivores [9, 10]. Omnivores can feed on animal-and plant-derived resources throughout their life, as can coccinellids, or utilise animal and plant food in different life stages, exhibiting life-history omnivory [11]. Examples are syrphids and parasitoids [9, 12]. Supplementing prey diet with plant food increases the individual fitness of omnivorous natural enemies [12, 13] and also sustains natural enemy populations when prey or hosts are scarce [11]. Hence, omnivory can promote top-down control [14]. Altogether, omnivores are important and persistent regulators of herbivore populations [15].

Omnivory can be found in species that are usually considered to be primary consumers (e.g., grasshoppers), in intermediate secondary consumers (e.g., predatory arthropods) and in top predators, such as bears or humans. Species in multitrophic interactions can therefore all directly rely on the same plant resources [14]. For example, floral nectar is frequently shared between butterflies, their para-sitoids, and their hyperparasitoids (parasitoids whose hosts are other parasitoids) as a consequence of the spatial and temporal proximity of these organisms [16–18]. It is therefore common among arthropods that consumers in the herbivorous second (herbivores), the omnivorous third (natural enemies), and the omnivorous fourth trophic level (antagonists) all forage on shared plant resources (see Figure 1). However,

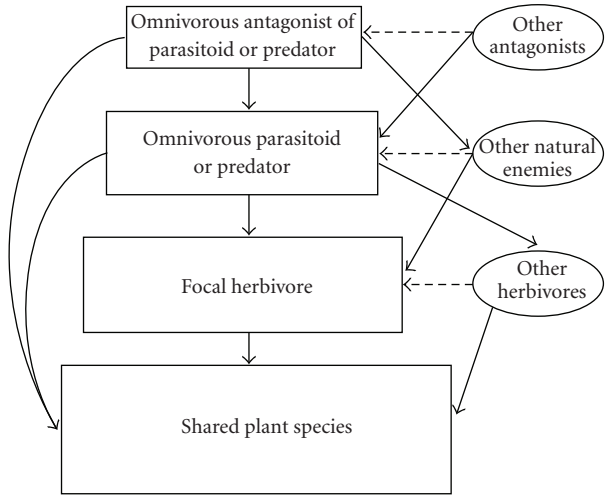

Figure 1: The main direct and indirect interactions among second trophic level herbivores, omnivores in the third trophic level, and omnivorous fourth trophic level consumers foraging on a shared plant resource. Solid arrows indicate consumer-resource interactions whereas dotted ones indicate indirect interactions, such as interspecific competition. For simplicity, other interactions such as intraguild predation, apparent competition, and prey defensive responses are not illustrated. See text for detailed explanations.

little is known about the effect of a change in the relative abundance of a shared plant resource such as nectar on food web structure and dynamics. This perspective is to our knowledge the first synthesis of the mechanisms in which differences in the abundance or quality of shared plant resources can lead to asymmetrical fitness changes between and even within trophic levels. We describe how such a change of resource availability can affect trophic cascades, and we emphasise the importance of this for community ecology and biological control.

2. How Can Shared Plant Resources Alter Trophic Cascades?

Trophic cascades are defined as reciprocal consumer-resource relationships that alter the abundance, biomass, or productivity of species' populations across several trophic levels of a food chain [19]. A change in the relative availability of a shared plant species can therefore not only affect the trophic interactions between herbivores, omnivorous natural enemies, and omnivorous antagonists, but also alter the trophic cascade within a subset of the food web community ("species-level cascades" sensu 2). Changes in species-level cascades are induced either by unequal alterations of individual fitness across the different trophic levels or by modification of the population structures of herbivores, natural enemies, and antagonists. At the level of individuals, relatively stronger fitness alterations at one level compared with the other two may result from different effects of changes in resource availability on the reproductive success of species [20–24]. At the population level, such changes can alter the sex ratio of offspring across trophic levels [25]. This is particularly important for parasitoids and hyperparasitoids because only females attack the herbivorous host. A higher proportion of parasitoid females in a population lead to increased parasitism rates, and this can lead to greater herbivore population suppression (see [26]). However, a higher proportion of hyperparasitoid females can lead to increased suppression of herbivores' natural enemies and consequently reduced top-down control of herbivores.

3. How Are Species-Level Trophic Cascades Triggered?

A key question is how changes in relative availability of shared plant resources can have different effects on individual fitness or population structure across trophic levels. These effects can result from relative differences in the abundance, quality, or availability of shared plant resources, which can therefore favour one level of the trophic cascade over others by a range of mechanisms. These are summarised in Table 1 and are discussed in more detail here. (1) It is well known that the access of insects to floral nectar is determined by flower morphology [27]. (2) The attractiveness of plants, for example, shape, colour, and odour can differentially influence consumer guilds [27]. (3) Species in a trophic cascade are differentially affected by the chemical composition of plants, particularly the "secondary" compounds that determine the palatability of leaves, seeds, and pollen [28, 29]. Even easily accessible nectar differs in its sugar composition [30, 31], and Wäckers [32] showed that nectar consumers differ considerably in their demand for particular saccharides. Thus, even if a plant resource can be accessed by a number of consumer species, it may differentially affect them. (4) The temporal distribution of plant resource availability may favour one trophic level relative to the others because their phenology may only partially coincide [33]. (5) Mobility varies among species. Therefore, the spatial distribution of plant resources

Table 1: A summary of how differences in the abundance, availability or quality of a shared plant resource can lead to an asymmetrical enhancement of fitness across trophic levels. See text for references.

(1)	Plant morphology
(2)	The attractiveness of plant resources
(3)	The nutritional value and chemical composition of plants
(4)	The temporal availability of plant resources
(5)	The spatial distribution of plants
(6)	The extent of species-specific reliance on the shared resource
(7)	Species-specific numerical and functional responses to the shared resource
(8)	Interactions with other organisms, such as competitors, pollinators, alternative prey, and intra- and interguild predators
(9)	Behavioural changes in species, such as predator avoidance behaviour prey defensive responses
(10)	Changed benefits to natural enemies and antagonists from prey/host consumption

can differentially affect trophic levels [14, 34, 35]. (6) An asymmetrical enhancement of trophic levels within the food web may also result from the extent of species' reliance on shared resources [36]. The interaction strength between plants and their consumers is determined by consumers' feeding behaviour. For example, monophagous herbivores depend much more on a particular plant species than do omnivorous natural enemies. (7) Species-specific numerical and functional responses to the shared plant resource can favour members of one trophic level over the others [37, 38]. (8) Shared plant resources can modify a trophic cascade by altering species interactions with organisms outside the trophic cascade. For example, herbivores can suffer from increased interspecific competition [39, 40], and natural enemies can benefit from the presence of alternative prey [41] and can be exposed to altered intra- and interguild predation in the proximity of shared plant resources [42]. (9) Behavioural changes in species at different trophic levels can be induced by changes in relative availability of shared plant resources. For example, altered predation risk can induce behavioural changes in prey or hosts, such as predator avoidance behaviour and prey defensive responses [43]. These potentially costly behavioural changes may not only reduce prey/host reproduction but also feed back to higher-trophic-level consumers [44]. (10) Changes in relative availability of plant resources can directly affect the physiological condition of prey or hosts. This can occur as a consequence of altered intake of plant nutrients and toxins [45–47]. Altered prey or host quality can consequently affect higher-trophic-level consumers.

In summary, changes in the relative availability of plant resources can indirectly amplify or mitigate top-down control [24, 45, 48]. This analysis of potential interactions within and between second, third, and fourth trophic levels mediated by a shared plant resource (Table 1) is certainly not complete. Even though most of these interactions are known to some extent, this is to our knowledge the first synthesis of the ways in which differences in the abundance, availability, or quality of shared plant resources can lead to asymmetrical enhancements of fitness within and between trophic levels. More research is needed to quantify the importance of each of these interactions for asymmetrical fitness enhancements within food webs. In the past, several studies modelled the influence of omnivory on multitrophic interactions and its persistence in predator-prey systems (e.g., [49–51]). In particular, Van Rijn et al. [14] developed a stage-structured predator-prey-resource model to explore the conditions under which individual plants gain protection from the plant-provided resources, such as extrafloral nectar and pollen, that are accessible to predators and herbivores. Their analysis revealed that the herbivore equilibria settle to lower values in the presence of supplementary food and that for the third trophic level the spatial distribution of shared resources is crucial. In conclusion, this synthesis of potential interactions within and between trophic levels (Table 1) provides a basis for understanding how trophic cascades can be triggered by shared food resources so that the implications of changes in the abundance of these resources can be predicted. This can in turn lead to more appropriate outcome-driven deployment of biodiversity in applied community ecology such as conservation and pest management. These aspects are discussed in more detail below.

4. Implications for Community Ecology

Omnivory is central to food web dynamics because it diffuses the effects of consumption across the trophic spectrum [52]. It increases web connectance and shortens food chains [53], as well as stabilising community interactions [54]. A strong change in the relative availability of a shared plant-derived resource, for example, as a result of plant invasion or extinction, may therefore alter the interactions among species (Figure 1) and as a result modify the entire food web [19]. A good example demonstrating the importance of plants in regulating the species composition of a community is the flower visitation web of a restored site in Mauritius [55]. Compared with a neighbouring, unrestored site that was heavily invaded by exotic plants, the restored site had a visitation web that was almost twice as species-rich and included visitors from several trophic levels. Also, the more complex pollinator community at the restored site allowed the native plant community to produce larger and heavier fruits with more seeds [55]. These results are supported by the broad literature on invasive and extinct plant species (e.g., [56–60]). Although invasive and endangered plant species are quite different in many aspects, both have the potential to play a disproportionately large role in shaping the community structure, especially if herbivores as well as omnivorous natural enemies and antagonists rely on these resources.

5. Implications for Biological Control

About 36% of the world's food and fibre production is lost to plant pathogens, weeds, and insect pests (14%, 12%, and 10%, resp.) despite all types of pest control measures [61]. While chemical pesticide use can increase yields of crops, these compounds can be broad-spectrum toxins, which have external costs such as effects on human health, lethal accidents, damage to the environment, and disruption of ecosystem function [62]. Top-down control of pests by natural enemies is therefore an extremely important alternative or complement to chemical pest control [8]. The ecosystem service of biological control that is provided by natural enemies has been valued at >US$400 billion per year globally [63]. Thus, the manipulation of top-down control within agriculture is of large economic as well as biological interest. However, modern agricultural practices suppress biological control and functional biodiversity, so "ecological engineering" techniques are needed to enhance natural enemies' contribution to sustainable agriculture [64]. However, an overall enhancement of natural enemy biodiversity does not necessarily result in greater top-down control of pest populations [65]. As this diversity increases, so does the potential for interference between natural enemy species [66], intraguild predation [67], changes in the antipredator behaviour of prey and hosts [68, 69], and redundancy among natural enemy species [70]. In fact, recent evidence indicates that increased insect pest suppression may be best achieved by suites of natural enemies that forage in complementary spatial and temporal ways [70, 71]. The targeted deployment of specific plant resources that favour the fitness of selected biocontrol agents relative to their prey or host and their own antagonists can therefore boost top-down control [14, 72]. An asymmetrical enhancement of the fitness of targeted omnivorous predators and parasitoids can be achieved by using awareness of the factors and conditions given in Table 1. Implementing an asymmetrical enhancement of the effect of omnivorous biocontrol agents by the provision of alternative plant-derived food sources involves sophisticated mixtures of complementary crops in polycultures and intercropping, sophisticated weed management that preserves selective food sources, and the targeted cultivation of favourable noncrop species [7, 8, 64, 73, 74]. For example, targeted flowering plant species such as sweet alyssum, buckwheat, and sunflowers were intercropped with great success in Californian vineyards and vegetable fields. These plants increased the abundance of natural enemies such as hoverflies and parasitoids and consequently improved the biological control of aphids, leafhoppers, and thrips [75, 76]. These measures for providing alternative plant resources are economically attractive and help to conserve biodiversity and its associated ecosystem services, such as pollination, nutrient cycling, erosion management, and recreation. [8, 77, 78]. Overall, the selective enhancement of top-down control is one of the most promising tools in pest management in largely monocultural agroecosystems to ensure the conservation of vital ecosystem services for improved food and fibre production, without compromising environmental integrity and public health [79].

6. Conclusions

This novel perspective emphasises that relative differences in the abundance of plant resources not only affect invertebrate herbivores but also directly affect the fitness and abundance of omnivorous natural enemies that rely on such food sources. Plant resources that are differentially used over several trophic levels have the potential to modify community structure and energy flow within ecosystems in more complex ways than is currently recognised. It is important that ecologists and environmental managers are aware of this complexity when attempting to manage and manipulate food webs to protect ecological communities against invaders, maintain biodiversity, or enhance top-down control of agricultural pests. A better understanding on how trophic cascades are triggered by shared food resources will certainly enhance the success of nature conservation programs and pest management schemes.

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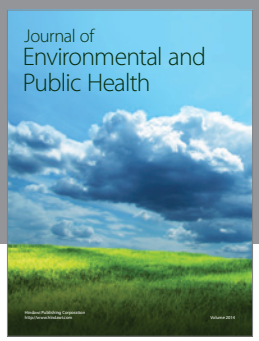

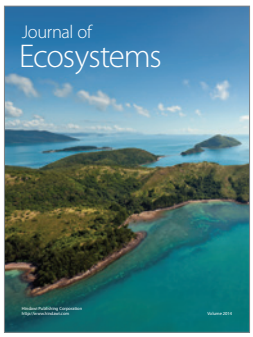

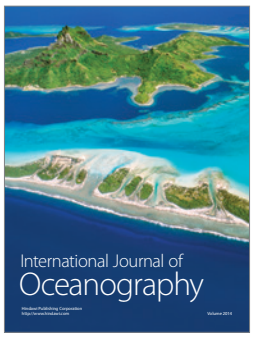

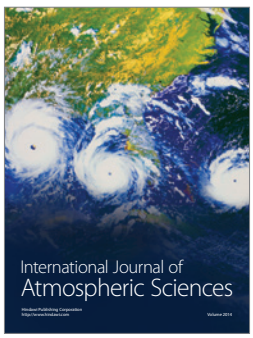

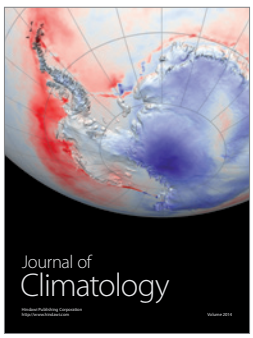

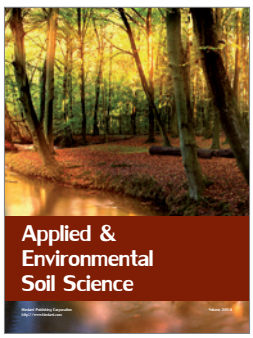

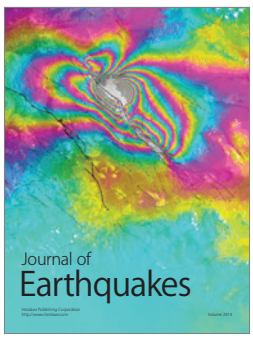

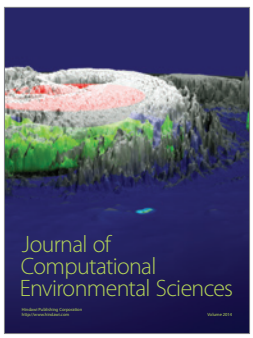

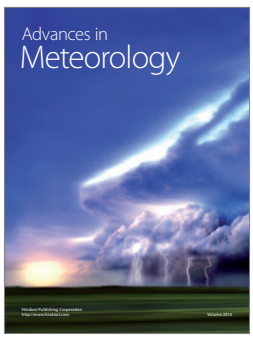

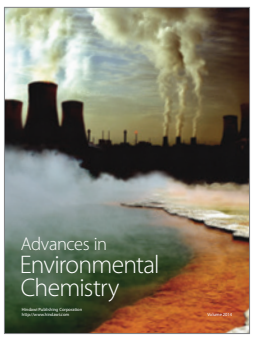

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