

ISSUES IN AGRICULTURAL AND FOREST ENTOMOLOGY

Are the ecological concepts of assembly and function of biodiversity useful frameworks for understanding natural pest control?

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Introduction

At a time when biodiversity is being lost at an unprecedented rate due to human activity, much research effort has been spent on assessment of the importance of biodiversity for the functioning and stability of ecosystems and for the delivery of ecosystem services. Pest control has been identified on numerous occasions as a valuable ecosystem service delivered by biodiversity (Mooney *et al.*, 1995a, b; Naeem *et al.*, 1999; Schläpfer *et al.*, 1999), and one that is at risk from human activity (Naylor & Ehrlich, 1997). There is considerable evidence that as agricultural production systems are intensified by increased use of external inputs to increase yield, they tend to lose biodiversity and become destabilized, with increased frequency and extent of pest outbreaks (Altieri, 1991; Swift *et al.*, 1996). However, we know relatively little about the ecological mechanisms that result in this destabilization, or how important natural enemy diversity is in maintaining pest-control functioning. Numerous studies exist which consider the ecological or theoretical basis of biological control (e.g. see Hawkins & Cornell, 1999) but relatively little attention has been given to understanding pest control as a natural ecosystem function and how changes in agricultural practice may affect function through impacts on biodiversity. This applies particularly to the non-equilibrium conditions that exist in short duration or seasonal cropping systems. As such, and whilst some notable exceptions exist, it can generally be argued that patterns of pest emergence remain poorly explained and attempts to improve natural pest control through modifications to management practices have limited ecological foundation. The aim of this paper is to explore how current ecological thinking can help to improve on this situation and to propose some ecological frameworks that may facilitate investigation of the importance of biodiversity and the impact of management practices on it.

Characterization of the relationship between biodiversity and ecosystem functioning has been a major research goal of ecology over the past decade. Numerous theoretical and empirical studies have been undertaken on many ecosystem

properties, including biomass production (producers, consumers and decomposers), nutrient uptake and retention, decomposition, soil pH, soil water and organic matter content and community respiration (Schläpfer & Schmid, 1999), although little has been published on the importance of diversity in natural enemy assemblages for pest control functioning (but see Rodríguez & Hawkins, 2000). The majority of these studies have observed a saturating positive relationship between diversity and ecosystem functioning (Schwartz *et al.*, 2000).

One mechanism whereby species diversity influences ecosystem functioning is resource-use complementarity. That is, different species occupy different niches allowing complementary functioning of species in heterogeneous or temporally variable environments. The slope of the relationship between species diversity and ecosystem functioning is partly dependent on the extent to which species overlap functionally, with respect to the particular ecosystem process of concern. If all species have an equal and non-overlapping effect on a particular process (perfect complementarity), then a linear reduction in the rate of the process would occur as species richness decreased (Fig. 1). At the other extreme, if there is no complementarity (species are 'redundant' with respect to the function concerned, see Walker, 1992; Lawton & Brown, 1993), then remaining species would be able to compensate for lost species and a sudden and complete loss of functioning would occur as the final functional species was lost.

Another mechanism resulting in a positive relationship between species diversity and ecosystem functioning has been termed the 'sampling effect' (Aarssen, 1997; Huston, 1997). This effect occurs if the probability of including a species with a strong influence on ecosystem functioning increases as species diversity increases. The sampling effect is viewed by some as a true diversity effect (Tilman *et al.*, 1997), but by others as an experimental artefact, because its expression is dependent on the probability of inclusion of species, which are under the control of the experimenter and usually do not reflect natural probabilities. The sampling effect is one expression of species composition effects, i.e. effects that arise from the fact that species differ in their functional capacity. More generally, compositional effects are expressed as variance in the relationship between diversity

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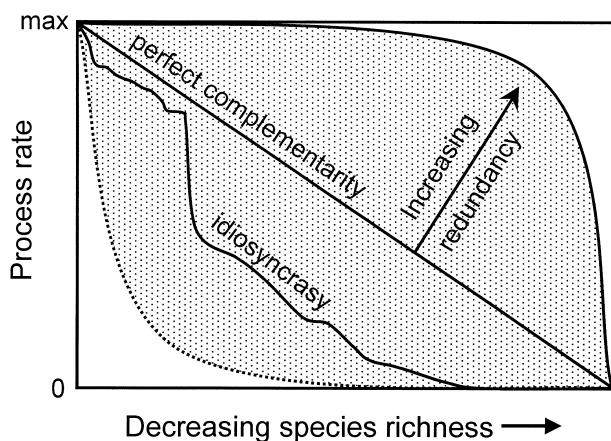


Figure 1 Hypothesized response of ecosystem function to decrease in species richness. If species are redundant then the response exhibits threshold behaviour in which significant reductions in functioning occur suddenly as the threshold is reached. By contrast, if species are complementary, each having non-overlapping roles, the response is a gradual loss of function with species loss. If species identity is important then the response can follow a broad range of trajectories (represented by the shaded region) depending on the order of species loss.

and ecosystem functioning (Hooper & Vitousek, 1997; Hooper, 1998; Petchey, 2000). In the extreme, a single species may have a much greater impact on process rate than other species (e.g. a keystone species). In such a scenario, the observed relationship between diversity and function would be idiosyncratic (Lawton, 1994), i.e. it could take any trajectory within a broad envelope of response (Fig. 1), depending on the order of species loss (Sala *et al.*, 1996). Thus, strong species composition effects mean that function cannot be predicted from species diversity alone.

Key attributes of a system determining important characteristics of the relationship between species diversity and ecosystem functioning are therefore the extent to which the functioning of species complement each other, and the extent to which species are unequal in their impact on a particular process. In order to predict the response of a particular ecosystem process to reductions in species diversity, we must understand the ecological mechanisms behind complementarity and species composition effects. To answer the broader question of what are the impacts

of human activity on the ecosystem process of interest (in our case natural pest control), we must additionally understand how and at what rate human activities have an impact on diversity. In ecological terms, this means the linked study of both the assembly and function of diversity in human-impacted ecosystems.

Linking assembly and function

A conceptual framework for linking diversity assembly and function can be made by identifying the traits of species that govern their membership to functional response groups and functional effect groups (Catovsky, 1998) (Fig. 2). In other words, by bringing together the traits we know govern response to management with those that are important for function we can formulate hypotheses concerning the effect of management on functioning. The way in which this linkage is made is somewhat dependent on the relative importance of diversity and composition effects in driving function. For example, if species composition effects do not strongly influence functioning, then we have extensive overlap between effect and response groups. That is, as species identity is not important, all species remaining after management are likely to have functional significance. If species are complementary in function, then any reduction in species diversity will reduce the functional capacity of the community, as each species functions uniquely to some extent. Alternatively, in a system with extensive redundancy among species, reduction in the size of the overlap between response and effect groups will have little impact on function. Where there are strong species composition effects, the amount of overlap between response and effect groups is reduced considerably and we must focus on the traits determining joint membership of response and effect groups.

Clearly then, as a starting point for implementing these ideas in the context of impacts on pest control of changes in biodiversity, a key issue to understand is the extent to which species composition or diversity effects predominate in determining function. To examine this issue further, we draw on a recent study concerning the effect of pest life-history characteristics and their influence on natural enemy complementarity and species composition effects via the influence on food web structure (Wilby & Thomas, 2002).

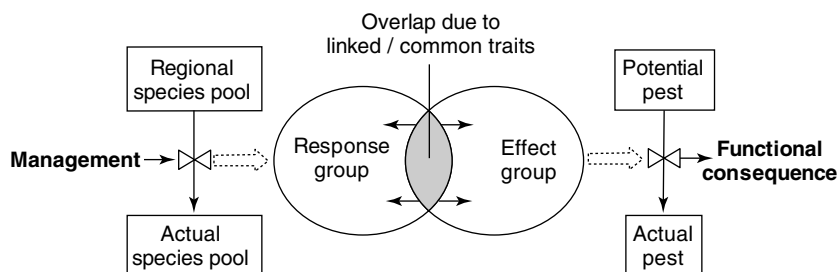


Figure 2 Conceptual scheme linking management effects to their functional consequences. Identification of the traits governing species membership to functional response groups and those governing membership to functional effect groups, allows logical connection between the impact of human activities and their functional significance.

Natural enemy diversity and pest-control functioning

It is known that major life-history characteristics of an insect herbivore, such as whether development mode is hemi- or holometabolous, can have a major influence on the number and diversity of natural enemies in the herbivore's natural enemy assemblage (Fig. 3). Endopterygote insects (holometabolous development) undergo dramatic morphological and behavioural changes between egg, larva, pupa and adult, and these life stages often play very different ecological roles, utilizing different food and occupying different sites. By contrast, exopterygote insects (hemimetabolous development) undergo relatively gradual changes between life stages, which often occupy similar sites and utilize similar food. As a consequence of these differences, we expect differences in the structure of linkages between these insect types and their natural enemies. The natural enemy complex interacting with endopterygote insects should be largely segregated into groups attacking particular life stages of the herbivore; most of those enemies feeding on adults would not be expected to also feed on larvae or pupae (e.g. see Waloff, 1968; Barrion *et al.*, 1991; Mills, 1994; Oatman, 1995a, b; Luna & Sánchez, 1999). On the other hand, due to the similarity in site occupancy and behaviour, natural enemies feeding on exopterygote insects are expected to feed on both nymphs and adults. Hence, because of the life-cycle structure, the natural enemy complex feeding on endopterygote insects should exhibit more complementarity among species compared with that feeding on exopterygote insects. Simulation studies have shown that

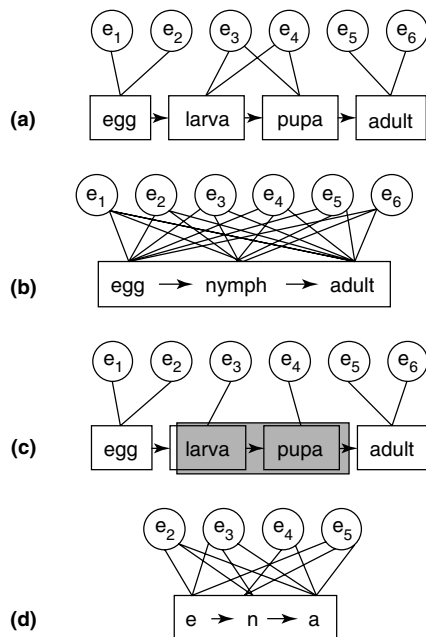


Figure 3 Life history characteristics of herbivorous insects and their hypothesized influence on the interacting natural enemy complex. (a) A simplified endopterygote insect, (b) a simplified exopterygote insect, (c) morphological or behavioural concealment, and (d) shortened life span.

the higher complementarity among natural enemies of endopterygote insects may result in gradual loss of pest control functioning with decreasing natural enemy species diversity, whereas control of exopterygotes should be relatively resistant, with a sudden loss of pest control functioning occurring only after extreme loss of natural enemy diversity. These predictions appear to be consistent with pest emergence patterns during intensification of Asian rice production systems (Wilby & Thomas, 2002).

Other aspects of herbivore life history are likely to influence the richness or characteristics of the natural enemy complex, with implications for pest control functioning. For example, morphological or behavioural concealment tends to promote tight linkage of population dynamics between the herbivore and natural enemy (Fig. 3c). Thus, with concealed herbivores, specialist parasitoids increase in importance compared with relatively generalist predators (Memmott *et al.*, 2000), although some concealed herbivores may be attacked by relatively more species of generalist parasitoid than specialist parasitoid (Hawkins, 1990; Hawkins *et al.*, 1992). In essence, tight linkages between specialist natural enemies and pests inflate the importance of species composition effects and increase the uncertainty about response to random species loss. This prediction is supported by simulation studies, which indicate that control of concealed pests should be relatively sensitive to natural enemy species loss, and that responses should be highly variable due to strong composition effects. These predictions are also borne out along intensification gradients in Asian rice (Wilby & Thomas, 2002).

The previous discussion shows that attributes of the basic life-history characteristics of the organisms involved can lead to different predictions about the relative importance of diversity and species composition in determining pest control functioning. This allows us to move beyond arguments of whether species composition or diversity is the most important attribute of the natural enemy community, to a position where we can predict which types of pest are likely to require particular natural enemy types for control, and which are likely to be better controlled by a diverse assemblage of natural enemies. The characteristics discussed serve as examples of general widespread life-history characteristics that are hypothesized to influence the relationship between diversity and pest control. The list is by no means exhaustive, and other traits are immediately apparent. For example, herbivore life span is also likely to have important consequences for the richness and characteristics of the natural enemy complex. The shorter the life span of a herbivorous species, the smaller the number of natural enemy species that overlap phenologically with the herbivore (Cornell & Hawkins, 1993). Consequently, control of a pest with a shorter life span should depend on a group of natural enemies with less redundancy, either across the life cycle in the case of exopterygote insects, or within life-cycle stages in the case of endopterygote insects. In either case, and with all else being equal, control of short-lived insects should decrease earlier, on average, in response to natural enemy species loss.

The above examples show how herbivore characteristics may influence the relative importance of natural enemy

species diversity and composition and the types of natural enemies likely to be important, where composition effects are likely. The next step to facilitate prediction of the effects of agricultural management on pest control functioning is to link these arguments with management effects on diversity and composition.

Agroecosystem management and arthropod community assembly

One approach to understanding the effects of agricultural management on arthropod diversity is to consider management impacts in the context of arthropod community assembly. Assembly rules have a long history in community ecology, where the objective has been to predict which species will occur in a particular habitat (Keddy, 1992). Although many authors reserve the term 'assembly rule' for the processes of species interaction which limit inclusion of species in a community (e.g. Belyea & Lancaster, 1999), we prefer to take a broad definition that includes processes of dispersal and colonization in addition to interspecific interactions. We follow Roughgarden & Diamond (1986) in identifying three types of filtration that govern which species from the set of all species in the region can occupy a site (Fig. 4). We also make considerable use of the terminology of Kelt *et al.* (1995) and Belyea & Lancaster (1999), although we present the species filtration process in a sequential fashion, relating to the order, and scale at which species negotiate the filters.

In order for a species to be present at a particular site, it must first be capable of arriving at the site. Dispersal constraints govern which species from the regional species pool are included in the local species pool, i.e. those species that are able to disperse to the site in question. Of those species in the local species pool, only those species that are able to overcome environmental constraints imposed by abiotic filters at the site occupy the ecological species pool. Finally, internal community dynamics (or biotic filters), including intra- and interspecific processes govern composition of the actual species pool. In addition to governing presence of species in communities, these processes also influence species abundance. This allows the framework to be used to describe the important processes driving species diversity

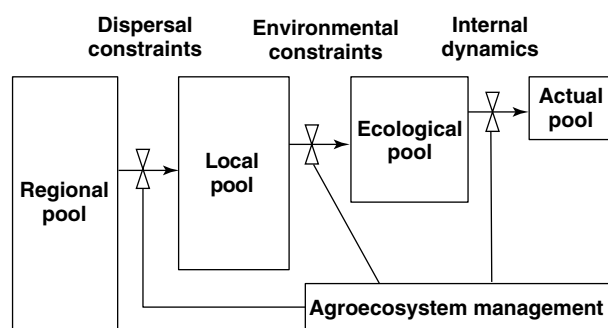


Figure 4 Community assembly encompassing dispersal, environmental filtering and internal community dynamics. Agroecosystem management can modify each of these processes.

and composition. The importance of this framework with respect to management effects on natural pest control derives from its description of the full range of ecological influences (at scales below continental and regional level processes) that can influence a species' abundance in a particular site. Although this may be somewhat heuristic, rather than explicitly mechanistic, its usefulness derives from the potential for generalizations to be made connecting the filters of the assembly process to particular biological traits likely to be most sensitive to changes in these filters. We can also relate particular management practices to the filters and to the biological traits that they are likely to affect.

Dispersal constraints, for example, are largely influenced by structural alterations in the landscape that occur as a result of land-use change. It is known that the way in which insects respond to fragmentation is related to several traits. Body size, for instance, has been shown to affect the spatial scale of fragmentation to which populations of parasitoids are sensitive (Roland & Taylor, 1997). Larger parasitoids tend to be more mobile and have populations extending over large areas. Thus, as a habitat is fragmented, the larger parasitoids are affected first and as a result we may expect to find changes in the size distribution of natural enemies. If this extends to predators, then this is likely to be functionally significant, given the constraints of size on prey selection.

Continuing with this theme, there is a large body of literature concerning the effect of fragmentation on insect communities. Generally, fragmentation of habitats has a greater effect on the abundance and species richness of higher trophic levels, and parasitoids in general are known to be particularly susceptible (Kruess & Tschardtke, 1994; Zabel & Tschardtke, 1998; Tschardtke & Kruess, 1999). However, considerable complexity arises as dispersal constraints interact with abiotic and biotic constraints to determine how species respond to fragmentation. For example, agricultural development tends to result in an increase in crop area relative to non-crop area. We may expect therefore that species specializing on the crop habitat will respond in a different fashion to those specializing in non-crop habitats. For natural enemies, this may mean promotion of species specializing on crop pests and a decrease in the relative abundance of more generalist species. Referring to our earlier discussion, an emergent prediction from this is that control of endophagous pest species may be facilitated by increases in crop area, whereas control of external feeders, particularly endopterygotes, may be reduced. Of course, this prediction is based on the assumption that specialist natural enemies are able to persist in a crop habitat. It is known that many parasitoid species require alternative food sources such as nectar and pollen (Landis & Menalled, 1998) and may be sensitive to practices such as tillage during fallow periods (e.g. Nilsson, 1985). In this case, control of endophagous pests will only be sustained following increases in crop area if nectar sources are available and if tillage is asynchronously applied across the landscape so that natural enemies are able to re-colonize from adjacent undisturbed patches. In addition, the spatial scale at which management is synchronized will have a major influence on the ability of natural enemies to re-colonize, and this re-colonization is

likely to be related to their body size due to its relationship with mobility. Similarly, although we may expect generalist natural enemies to be reduced with increased scale and uniformity of crop environment, in practice, even limited non-crop areas adjacent to crops have been shown to help maintain natural enemy abundance and diversity within the crop by providing alternative food sources and refuges from disturbance (e.g. Risch *et al.*, 1983; Altieri & Schmidt, 1986; Andow, 1991a; Thomas *et al.*, 1991, 1992; Dennis *et al.*, 1994; Wratten & van Emden, 1995; Thies & Tscharnkte, 1999).

Moving down the assembly hierarchy, we can also identify agricultural management practices that act as abiotic filters. Insecticides, for example, generally have a broad impact across arthropod communities. The extent to which they act as a filter to alter diversity and abundance between the local and ecological species pools depends on the differential impact on individual taxa; some species may be physiologically or ecologically resistant, whereas others may be susceptible. The implications for pest-control functioning depend in particular on differential effects on herbivore and natural enemy types. Where herbivores show greater resistance and/or higher recovery rates than natural enemies, we might expect pesticide-induced resurgence. Indeed, pest resurgence following insecticide use has been recorded in many types of pests (Hardin *et al.*, 1995). However, set in the context of our framework for the role of natural enemy diversity in pest control functioning, the effects of insecticides on control of external feeding exopterygotes are expected to be particularly striking. For these pests, we predict that control can be maintained even where there is minimal natural enemy diversity. Nonetheless, control will be lost if diversity and abundance are reduced too far. Thus, insects such as the brown planthopper (*Nilaparvata lugens*) may be controlled adequately by natural enemies even under intensive rice production systems in South-east Asia, but when insecticides are applied, it can become a devastating pest (Reissig *et al.*, 1982; Heinrichs & Mochida, 1984; Kenmore *et al.*, 1984; Heong, 1991). The mechanism for this phenomenon has been well elucidated and it seems that the key is the near complete removal of a guild of generalist predators which impose considerable mortality on planthopper populations and are sustained by alternative prey, such as detritivorous insects, at times when *N. lugens* is scarce (Settle *et al.*, 1996). *Nilaparvata lugens* is able to escape control partly because its eggs can survive insecticide treatment, because it is highly dispersive and can recolonize rice fields quickly, and because it has a high population growth rate (Heinrichs & Mochida, 1984). In contrast, the key complex of generalist predators have no protected stages and show slow recovery because they are, on the whole, less dispersive. As important, the build-up and/or maintenance of generalist predators is greatly hampered by the insecticide-induced reductions in alternative prey populations. Again, this illustrates the interaction between mechanisms acting at different points in the assembly process. Here, pesticides act as an abiotic constraint but their significance is mediated by biotic interactions and the differential response of predators and herbivores (and crop-associated

detritivores), which is determined in part by colonization processes that link back to dispersal constraints and aspects of habitat heterogeneity (over space and/or time).

Finally, agricultural management also has an impact on internal community dynamics, the third filter of our assembly framework. The abundance of weeds within a crop, for example, influences the diversity and composition of natural enemy assemblages. Generally, the change from relatively diverse vegetation to virtual monoculture, which occurs with increased weed management, is associated with a decrease in diversity of natural enemy species (although not necessarily abundance) and a decrease in the relative abundance of generalist predators (Andow, 1991b; Tonhasca & Byrne, 1994). Thus, weed management may be expected to reduce levels of control of pests attacked by generalist predators and also, perhaps, those concealed species controlled by parasitoids that require alternative food sources. Similarly, returning to another example from rice production systems, management of crop residues and levels of organic matter in the soil have been demonstrated to influence the abundance of detritivores, which play an essential role in supporting early season build-up of generalist natural enemies (Settle *et al.*, 1996). It is these natural enemies that keep later successional species such as brown planthopper in check, unless disrupted through insecticide treatment (see above).

Conclusions

The aim of this paper was to explore whether ecological concepts developed during the study of biodiversity and ecosystem functioning, and community assembly, could provide insights into the impact of agricultural intensification on pest control. Although what we present here is very much a first step in addressing this issue, we believe that making an explicit link between community response to management with potential functional implications of this response represents a valuable advance towards the ability to predict and perhaps mitigate pest emergence with agricultural intensification. Our mechanistic approach to considering the relationship between natural enemy community composition and pest control functioning reveals a number of testable predictions which appear consistent with patterns reported in the literature. We are confident that further generalizations can be made concerning the relationship between natural enemy community composition and pest control functioning. Our assembly framework for examining community response also provides us with certain testable predictions. However, it is clear that interactions and feedback between processes at different points along the assembly chain make generalizations difficult. This highlights a need for further research to identify traits that govern species' response to the major elements of agricultural intensification. In this, the assembly framework provides a heuristic model for structuring the research questions, which has received little attention in the agricultural context. Already, for example, it is apparent that dispersal constraints may be extremely important to the effects of management because, as well as determining the response

to changes in landscape structure, they also govern the ability of species to recover from transient environmental pressures such as insecticide treatment or soil tillage. Moreover, one recent study showed that agri-environment schemes, which tend to focus on mitigating abiotic and biotic constraints at the local scale, were ineffective at protecting biodiversity because diversity was limited by dispersal constraints at a higher level (Kleijn *et al.*, 2001). Perhaps with more studies and a greater appreciation of the mechanisms that underpin the assembly process, useful generalizations concerning species' response to particular agricultural practices will emerge and more effective management strategies (either pest management or biodiversity management for conservation) can be developed.

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