

REPORT

Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification

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Abstract

Concern over declining biodiversity and the implications for continued provision of ecosystem services has led, recently, to intense research effort to describe relationships between biodiversity and ecosystem functioning. Here we extend this effort to the relationship between natural enemy species diversity and natural pest control. From simple modelled food-webs and simulations of natural enemy species loss we derive specific predictions concerning the effect of herbivore life-history traits, such as life-cycle type and concealment, on the shape (reflecting diversity effects) and variance (reflecting species composition effects) of the relationship between natural enemy diversity and pest-control. We show that these predictions are consistent with the emergence of different pest types following intensification of rice production in Asia. We suggest that basic biological insights can help define the structure of ecological processes and allow more accurate predictions of the effect of species loss on the delivery of ecosystem services.

Keywords

Agroecology, arthropod natural enemies, biodiversity, ecosystem function, ecosystem services, insect pest control, rice pests.

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INTRODUCTION

Pest control has often been highlighted as an important ecosystem service provided by biodiversity (Mooney *et al.* 1995a; Mooney *et al.* 1995b; Schläpfer *et al.* 1999) and one that is threatened by modern agricultural practices (Naylor & Ehrlich 1997). Intensification of agriculture, defined as increased management intervention and increased external inputs with the intent of increasing agricultural yield, tends to simplify agricultural systems (Swift *et al.* 1996), reducing natural enemy diversity (Basedow 1990; Szentkirályi & Kozár 1991; Andersen & Eltun 2000; Miliczky *et al.* 2000; Brown & Schmitt 2001). Though this is known to destabilize arthropod populations, often resulting in pest outbreak (Swift *et al.* 1996), detailed understanding of how natural enemy species diversity or composition affect pest-control functioning is lacking. Here we use existing knowledge concerning the effect of life-history attributes of herbivorous insects on the diversity of their natural enemies to predict the relationship between species diversity and pest-control functioning in agroecosystems.

One of the mechanisms whereby species diversity has been hypothesized to influence ecosystem functioning is

species complementarity. This hypothesis states that if species occupy differentiated niches then as species diversity increases the proportion of total niche space occupied increases, and with it, ecosystem process rate (Tilman 2000). There is considerable evidence from empirical studies that there is a positive relationship between diversity and the rate of several ecosystem processes, though the relationship tends to be asymptotic saturating at relatively low levels of diversity (Schwartz *et al.* 2000). Studies have also highlighted that species may differ considerably in their influence on ecosystem processes and, as a result of these *species composition* effects, there may be a large amount of variance about the relationship between species diversity and ecosystem functioning (Hooper & Vitousek 1997; Hooper 1998; Petchey 2000). There is much controversy about the relative importance of species complementarity and species composition in ecosystem functioning, though recent empirical and theoretical results suggest that both attributes of communities explain a considerable proportion of variance in the rate of ecosystem processes (Tilman *et al.* 1997a; Tilman *et al.* 1997b; Hector *et al.* 1999).

Here, we investigate how species complementarity and composition effects may arise in natural enemy assemblages

with respect to their control of herbivorous insects. We use a simple simulation model to show that certain life-history traits of herbivorous insects can affect the shape and variance of the relationship between natural enemy species richness and pest-control functioning. These simulations suggest that the relative importance of composition and diversity effects will vary among herbivore types, which has important implications for control of different pest types under scenarios of declining biodiversity.

METHODS

The model

We simulate a group of natural enemy species attacking a single herbivorous insect species with four life-cycle stages. Survival s_i of each life-cycle stage i of the herbivore is determined by natural enemy induced mortality:

$$s_i = 1 - e_i m \quad (1)$$

where m is the maximum proportional mortality per life-cycle stage and e_i is the effectiveness of the predator assemblage attacking the life-cycle stage i . Determination of effectiveness is dependent on the particular assumptions of each simulation, as described later. Reproduction is assumed to occur only at the end of the adult stage, with a fecundity f , after which adults die. Thus, demography of the prey population is described by the population projection matrix:

$$\begin{pmatrix} 0 & 0 & 0 & s_4 f \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{pmatrix}$$

This particular matrix has four eigenvalues with the same modulus, so whatever the initial conditions, the herbivore population has a growth rate (λ) given by the modulus:

$$\lambda = f^{1/4} s_1^{1/4} s_2^{1/4} s_3^{1/4} s_4^{1/4} \quad (2)$$

In all simulations described here f was fixed at 200, an approximate centre point of the range of fecundities observed in insect pests of rice (Heinrichs 1994). The maximum mortality at each life stage, m was fixed at 0.734 since this gives $\lambda = 1$ with a set of natural enemies with maximum effectiveness (all $e_i = 1$). Thus, we assume that the fully functional natural enemy assemblage results in a stable herbivore population size. The parameters f and m scale the effect of natural enemy species loss. Varying either parameter within realistic limits ($10 < f < 500$; $0.1 < m < 0.95$) does not change the qualitative results obtained. This modelling framework also assumes that the temporal amplitudes of the life stages are equal. The results of our simulations are robust with respect to differences in temporal amplitude among life stages, which result in

unchanged mean trends, but increased variability about the mean.

The modelled scenario is appropriate for seasonal cropping systems where the crop is the herbivore's resource and is abundant, hence we assume that the herbivore population is not resource limited and that the population growth rate of the herbivore is an index of the potential damage caused to the crop (Thomas & Waage 1996). Clearly, herbivores may become resource limited during pest outbreak, but this would usually occur after considerable crop damage since the crop itself, or some component of it, is the limiting resource in question. Thus, we assume the resource limitation of herbivore populations is not an important factor determining the extent of crop damage. In addition, we do not simulate natural enemy population dynamics, but assume that a fully functional natural enemy assemblage consumes a constant proportion of the herbivore population (Thomas 1999).

The effect of life-cycle type

Winged insects are taxonomically classified into two divisions, Endopterygota and Exopterygota, based on their development characteristics from egg to adult. Endopterygotes undergo dramatic morphological and behavioural changes between life-cycle stages, which often play very different ecological roles, consuming different food and occupying different sites. As a consequence, endopterygotes tend to have natural enemy assemblages that are segregated into groups attacking particular life-cycle stages (Waloff 1968; Barrion *et al.* 1991; Oatman 1995a, b; Luna & Sánchez 1999). By contrast, exopterygotes undergo gradual changes between life-cycle stages, and the stages often occupy similar sites and consume similar food. Therefore, exopterygote insects tend to have one group of natural enemies attacking a large proportion of the life cycle (Waloff 1968; Ooi & Shepard 1994; Tassan & Hagen 1995). To explore the implications of these food web structures for the resistance of pest control under scenarios of natural enemy species loss, we modelled simplified interaction webs of idealized exopterygote and endopterygote herbivores and their natural enemies. As indicated above, we assumed four life-cycle stages in each idealized herbivore type and a total of 20 natural enemy species (Fig. 1). In the endopterygote case, the natural enemies are separated into four groups of five natural enemy species and each group attacks an individual life-cycle stage. In the exopterygote case all natural enemy species form a single group of 20 species which attack all life-cycle stages. In addition, we assume that all natural enemies have equal effect on the prey. Within groups of natural enemies there is redundancy with respect to pest-control functioning, such that if one or more species is present the group is effective ($e_i = 1$) and if no species are

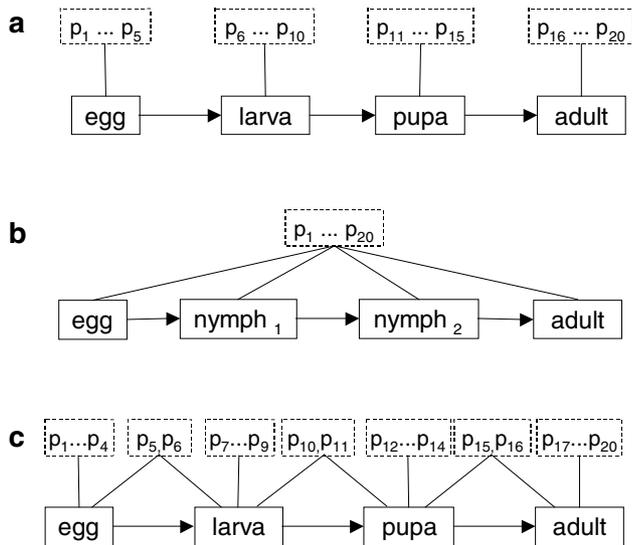


Figure 1 Food webs representing idealized (a) endopterygote and (b) exopterygote herbivores and their natural enemies used in simulations of natural enemy species loss together with (c) an intermediate structure of two species overlap also simulated.

present the group is ineffective ($e_i = 0$). Thus, we assume that within a natural enemy group attacking a particular life-cycle stage, there is compensatory activity among functional natural enemy species and no effect of species richness on the functional capacity of the group (Rodríguez & Hawkins 2000). Simulations involved a sequential random selection and deletion of one of the natural enemy species until none remained. λ was calculated after each species deletion.

These initial simulations represent the extremes of food-web structures from complete overlap of natural enemies attacking all life-cycle stages to complete segregation of natural enemy groups between life-cycle stages. In addition, we conducted simulations to explore the consequences of relaxing segregation of natural-enemy groups, where two or four members of each group attacking each life-cycle stage attacked two consecutive stages (see Fig. 1c). These are perhaps more typical food web structures as, for example, larvae and pupae of endopterygotes often share natural enemies.

Species composition and the effect of predator avoidance

The model was also used to simulate species composition effects on the relationship between natural biological control and natural enemy species diversity. Strong species composition effects occur when there is large variation among species in their impact on ecosystem functioning, hence we modelled composition effects by prior labelling of natural enemy species as functional or non-functional,

within the food-web structure of an idealized endopterygote herbivore (Fig. 1a). The number of functional species per natural enemy group was varied from one to five to represent a gradient of extreme to negligible compositional effects, respectively. In the simulations, the presence of one or more functional species rendered the natural enemy group effective ($e_i = 1$), and the group was considered ineffective ($e_i = 0$) if only non-functional species or if no species remained. In effect, this simulates a reduction in the number of natural enemy species attacking the herbivore, which may result from biological characteristics such as reduced residence time in vulnerable life-cycle stages (Cornell & Hawkins 1993).

In the herbivore–natural enemy scenario, another mechanism whereby species composition effects arise is through morphological or behavioural concealment, which herbivores employ to protect vulnerable life-cycle stages from attack. Several studies have shown that concealment, most commonly in the form of endophagy (feeding within the tissues of the plant), reduces the number of natural enemy species attacking herbivores and increases the proportion of specialist species in the natural enemy complex (Askew & Shaw 1986; Hawkins & Lawton 1987; Memmott *et al.* 2000). This promotes extreme compositional effects, because relatively few specialist natural enemies induce mortality, with the remainder having little or no effect. Concealment of endopterygotes was modelled by labelling a single natural enemy as functional and the remainder non-functional from the group of natural enemies attacking the concealed life-cycle stage. For unconcealed life-cycle stages all natural enemy species were functional. As in previous simulations, the presence of one or more effective natural enemies rendered the group effective ($e_i = 1$), otherwise the group was ineffective ($e_i = 0$). We then varied the number of concealed life-cycle stages from zero (analogous to the previous simulations of an endopterygote herbivore) to four representing an increasing number of life-cycle stages protected from natural enemies.

RESULTS

Life-cycle type

For a given size (species number) of natural enemy complex, the population growth rate of an endopterygote herbivore is much more sensitive to loss of natural enemy species than that of exopterygote insects (Fig. 2). The difference arises because, unlike exopterygote insects, dissimilarity among life-history stages in endopterygote insects provides an axis for complementarity between natural enemy species. The simulation also indicated that once pest-control functioning is affected by loss of natural enemy species, the increase in population growth rate of the herbivore is much more

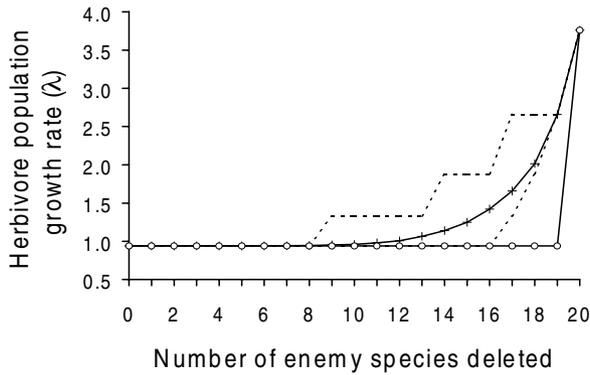


Figure 2 Simulation results of the effect of random, sequential natural enemy species loss on the population growth rate of idealized endopterygote (crosses) and exopterygote herbivores (circles). Solid lines denote the mean response of 500 simulations, dotted lines represent 2.5 and 97.5 percentiles of the endopterygote response (only one scenario is possible for the exopterygote model).

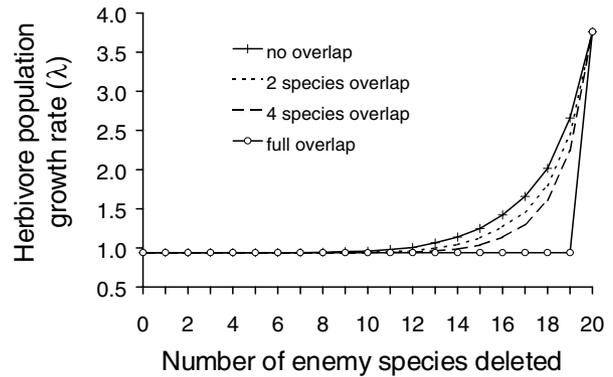


Figure 3 Simulation results showing of the effect of random, sequential natural enemy species loss on the population growth rate of intermediaries between the idealized endopterygote (no overlap) and exopterygote (full overlap) webs, in which two or four species of natural enemy were permitted to feed on two consecutive life-cycle stages. Curves denote means of 500 simulations.

gradual for endopterygotes than for exopterygotes. This is because whole life-cycle stages are periodically released from control during the species-loss sequence for endopterygotes, whereas exopterygotes remain under effectively constant natural enemy pressure until all natural enemy species are deleted, whereupon herbivore population growth rate increases dramatically. In addition, the way that species deletions are distributed among the complexes attacking different life-cycle stages adds stochasticity to the response in endopterygotes that is not observed in the fully redundant exopterygote system (as indicated by the endopterygote response envelope in Fig. 2). Although these simulations depict extreme structures of herbivore–natural enemy food webs, the intermediate simulations (in which some of the natural enemy species are permitted to feed on two adjacent life-cycle stages) show that there is a gradual transition of response between the two extremes (Fig. 3). Thus, the general conclusions are robust so long as the exopterygote–natural enemy web has more overlap between natural enemy species than the exopterygote web.

Composition and the effect of predator avoidance

With increasing strength of species composition effects (declining number of effective species per life-cycle stage), pest control became less resistant, on average, to reduction of natural enemy species richness (Fig. 4a). However, the simulation also highlighted changes in the variability of response with increasing strength of species composition effects (Fig. 4b). Although the mean trend showed declining resistance to species loss, variability increased over much of the species deletion sequence. Thus, prediction of response

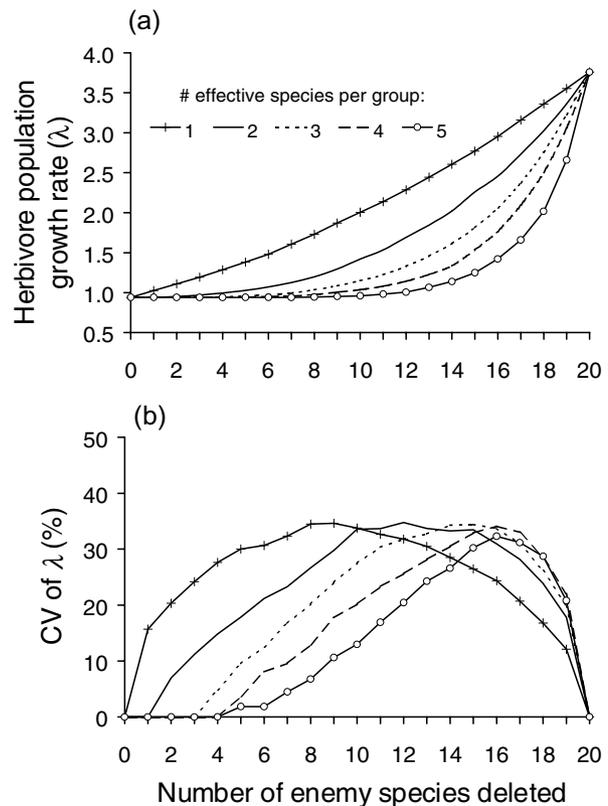


Figure 4 Simulation results showing the effect of size (species richness) of the natural enemy complex on the response of population growth rate of an idealized endopterygote herbivore to random, sequential natural enemy species loss. (a) Mean responses of 500 simulations are presented together with (b) coefficient of variation of the response. Curves shown reflect the range of 1–5 effective species per natural-enemy group.

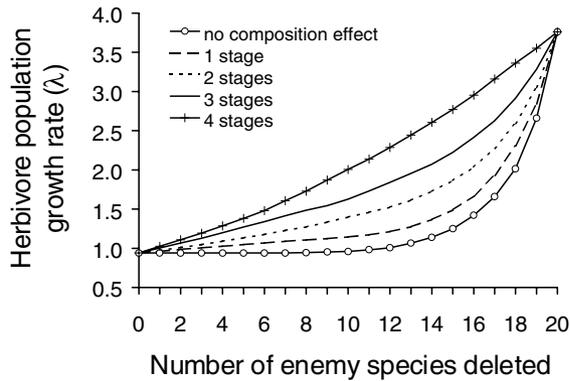


Figure 5 Simulation of the effect of random, sequential natural enemy species loss on the population growth rate of an endopterygote herbivore, where strong species composition effects (one effective species and four ineffective species) are applied to increasing number of life-cycle stages. Mean responses of 500 simulations are presented.

to natural enemy species loss may be less accurate in the presence of strong species composition effects. Similarly, our simulation of concealment, which extended strong species composition effects to increasing numbers of life-cycle stages, showed that resistance of control to natural enemy species loss decreased as the number of concealed life-cycle stages increased (Fig. 5).

DISCUSSION

Our simulations allow predictions to be made concerning the emergence of pests of different life-history types during agricultural intensification. These predictions are based on the evidence that intensification decreases natural enemy diversity (Basedow 1990; Szentkirályi & Kozár 1991; Andersen & Eltun 2000; Miliczky *et al.* 2000; Brown & Schmitt 2001). First, as control of exopterygotes was shown to be more resistant to natural enemy species loss, we predict that endopterygote herbivores will become relatively more important pests during the initial stages of intensification compared with exopterygote herbivores. Second, the large amount of redundancy in the natural enemy assemblages of exopterygote herbivores leads to the prediction that they are likely to emerge as pests only after extreme reductions in natural enemy species richness. Finally, our simulation of species composition effects suggests that concealed herbivores are likely, on average, to emerge as pests earlier in the intensification sequence than non-concealed pests.

Testing these predictions against existing records of pest impact is fraught with problems, because any effect of diversity is confounded by control measures employed against specific herbivores as they attain pest status.

Nevertheless, evidence from Asian rice production systems supports our predictions. Across Asia, national average rice yields range from 1300 kg/ha in Cambodia to 6100 kg/ha in Japan and the Republic of Korea. These differences in rice yield are associated with elements of intensification, such as the adoption of modern varieties, irrigation and the use of inorganic fertilizer (Hossain 1996). Using previously published estimates of rice yield loss due to pest damage across 10 countries or regions in southern Asia (Evenson 1996), we tested whether yield losses due to endopterygotes became relatively more important compared with losses due to exopterygotes as intensification increased. Consistent with our predictions, during the initial stages of intensification we found a significant positive relationship between the relative importance of endopterygote pests in causing yield loss and the average yield (reflecting the level of intensification) (Fig. 6). We may expect this relationship to change at high intensification when exopterygote pest outbreak becomes more frequent.

The rice literature also provides us with evidence supporting our second prediction, that control of exopterygote pests is resistant until extreme loss of natural enemy diversity occurs. The brown planthopper (*Nilaparvata lugens*), an exopterygote herbivore, became a major constraint to rice production throughout South and South-east Asia in the 1970s. However, it has now been demonstrated that the major factor determining pest status of *N. lugens* is early season insecticide application, which acts dramatically to remove most generalist predators, thus releasing *N. lugens* from predatory control (Heinrichs & Mochida 1984; Kenmore *et al.* 1984). Similarly, other exopterygote herbivores have also been shown to resurge as a result of

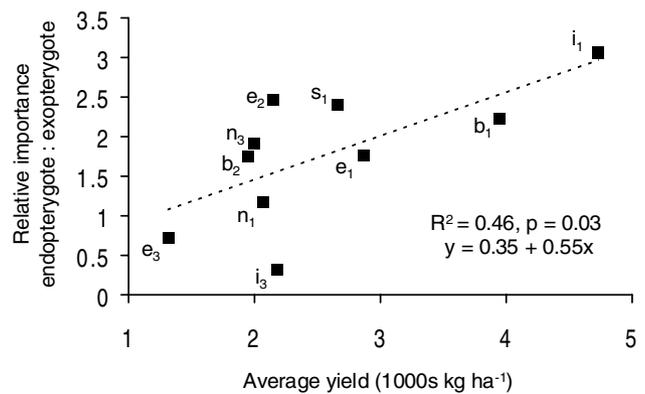


Figure 6 The relationship between the ratio of yield loss caused by endopterygote herbivores to that caused by exopterygote herbivores, and average rice yield (reflective of level of intensification) across regions and cropping systems in Asia. Data labels denote the region and cropping system represented: (e) East India, (s) South India, (n) Nepal, (b) Bangladesh, (i) Indonesia, and cropping systems: (1) irrigated rice, (2) rain-fed rice and (3) upland rice.

insecticide application (Cohen *et al.* 1994). In the absence of insecticides, such species rarely attain pest status even in intensively managed systems.

Our third prediction, that concealed species attain pest status earlier than non-concealed species, is also consistent with pest emergence patterns in rice. In most rice growing areas in tropical Asia, the dominant insect pests up to the 1960s were several species of stem borers and the rice gall midge, all endopterygote insects in which much of the life-cycle is concealed within plant tissues. By contrast, less concealed endopterygotes, such as the lepidopteran leaf folders, emerged as dominant pests only in the 1980s following further intensification (Khoo 1990; Napompeth 1990; Pathak & Kahn 1994). Similarly, in areas of less intensified rice production, such as West Africa, stem borers and gall midge remain the dominant insect pests (Adesina *et al.* 1994).

In addition to predicting earlier emergence of concealed pests under scenarios of declining natural enemy species richness, our simulation showed an increase in variability of response with increasing strength of species composition effects (Fig. 4b). Under extreme compositional effects, a broad range of responses is possible and the resistance of the pest-control process to species loss is dependent more on the order of species loss than on species diversity. This suggests that in cases of strong compositional effects, such as those occurring with concealed pests, accurate predictions of pest status or expected pest emergence will require an understanding of the order of species loss and not simply loss of diversity *per se*. We know that concealed pests are likely to be controlled by specialist natural enemies and evidence suggests that specialist natural enemies are more likely to become locally extinct following fragmentation of agroecosystems (Kruess & Tscharntke 1994; Thies & Tscharntke 1999; Kruess & Tscharntke 2000). Hence, due to the nonrandom nature of species loss, herbivores attacked largely by specialist natural enemies are likely to be released from control earlier rather than later, in the broad range of possible responses predicted under random species loss. This is likely to be another factor contributing to the trend of endophagous endopterygote pests dominating in the early stages of rice intensification.

Our predictions concerning the response of pest control to declining natural enemy diversity are derived from an appreciation of the structure of trophic links between natural enemies and life-cycle stages of their prey. We suggest that similar approaches adopting a more ecological, mechanistic framework relating structural linkage between species and particular ecosystem processes, will allow more accurate prediction of the shape and variability of the relationship between species diversity and ecosystem functioning. Our examples highlight that a variety of responses are possible from superficially similar systems, and that different

responses have different implications for the maintenance of functioning as species diversity declines. In situations exhibiting asymptotic relationships of low variance, functioning is likely to be relatively resistant to reductions in species diversity. However, where relationships, whether asymptotic or linear, exhibit high variance due to species composition effects, prediction of functional response to reductions in species diversity requires an understanding of the likely order, as well as the rate, of species loss.

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REFERENCES

- Adesina, A.A., Johnson, D.E. & Heinrichs, E.A. (1994). Rice pests in the Ivory-Coast, West-Africa: farmers perceptions and management strategies. *Int. J. Pest Manage.*, 40, 293–299.
- Andersen, A. & Eltun, R. (2000). Long-term developments in the carabid and staphylinid (Col., Carabidae and Staphylinidae) fauna during conversion from conventional to biological farming. *J. Appl. Entomol.-Z. fur angewandte Entomologie*, 124, 51–56.
- Askew, R. & Shaw, M. (1986). Parasitoid communities: their size, structure and development. In: *Insect Parasitoids* (eds Waage, J. & Greathead, D.). Academic Press, London, pp. 225–264.
- Barrion, A.T., Litsinger, J.A., Medina, E.B., Aguda, R.M., Bandong, J.P., Pantua, P.C., Jr., Viajante, V.D., de la Cruz, C.G., Vega, C.R., Soriano, J.S., Jr., Camañg, E.E., Saxena, R.C., Tyron, E.H. & Shepard, B.M. (1991). The rice *Cnaphalocricis* and *Marasmia* (Lepidoptera: Pyralidae) leafroller complexes in the Philippines: taxonomy, bionomics and control. *Philippines Entomologist*, 8, 987–1074.
- Basedow, T. (1990). Effects of insecticides on Carabidae and the significance of these effects for agriculture and species number. In: *The Role of Ground Beetles in Ecological and Environmental Studies* (ed. Stork, N.). Intercept, Andover, UK, pp. 115–125.
- Brown, M.W. & Schmitt, J.J. (2001). Seasonal and diurnal dynamics of beneficial insect populations in apple orchards under different management intensity. *Biol. Control*, 30, 415–424.
- Cohen, J.E., Schoenly, K., Heong, K.L., Justo, H., Arida, G., Barrion, A.T. & Litsinger, J.A. (1994). A food-web approach to evaluating the effect of insecticide spraying on insect pest population-dynamics in a Philippine irrigated rice ecosystem. *J. Appl. Ecol.*, 31, 747–763.

- Cornell, H.V. & Hawkins, B.A. (1993). Accumulation of native parasitoid species on introduced herbivores: a comparison of hosts as natives and hosts as invaders. *Am. Nat.*, 141, 847–865.
- Evenson, R. (1996). An application of priority-setting methods to the rice biotechnology program. In: *Rice Research in Asia: Progress and Priorities* (eds Evenson, R., Herdt, R. & Hossain, M.). CAB International, Wallingford, UK, pp. 327–346.
- Hawkins, B. & Lawton, J. (1987). Species richness for parasitoids of British phytophagous insects. *Nature*, 326, 788–790.
- Hector, A., Schmid, B., Beierkuhnlein, C., Caldeira, M.C., Diemer, M., Dimitrakopoulos, P.G., Finn, J.A., Freitas, H., Giller, P.S., Good, J., Harris, R., Hogberg, P., Huss Danell, K., Joshi, J., Jumpponen, A., Korner, C., Leadley, P.W., Loreau, M., Minns, A., Mulder, C.P.H., O'Donovan, G., Otway, S.J., Pereira, J.S., Prinz, A., Read, D.J. & Scherer Lorenzen, M. (1999). Plant diversity and productivity experiments in European grasslands. *Science*, 286, 1123–1127.
- Heinrichs, E. (1994). *Biology and Management of Rice Insects*. Wiley Eastern, New Delhi.
- Heinrichs, E.A. & Mochida, O. (1984). From secondary to major pest status: the case of insecticide-induced rice brown planthopper, *Nilaparvata lugens*, resurgence. *Protection Ecol.*, 1, 201–218.
- Hooper, D.U. (1998). The role of complementarity and competition in ecosystem responses to variation in plant density. *Ecology*, 79, 704–719.
- Hooper, D.U. & Vitousek, P.M. (1997). The effects of plant composition and diversity on ecosystem processes. *Science*, 277, 1302–1305.
- Hossain, M. (1996). Recent developments in the Asian rice economy: challenges for rice research. In: *Rice Research in Asia: Progress and Priorities* (eds Evenson, R., Herdt, R. & Hossain, M.), CAB International, Wallingford, UK, pp. 17–34.
- Kenmore, P.E., Cariño, F.O., Perez, C.A., Dyck, V.A. & Gutierrez, A.P. (1984). Population regulation of the rice brown planthopper (*Nilaparvata lugens* Stål) within rice fields in the Philippines. *J. Plant Protection Tropics*, 1, 19–37.
- Khoo, S. (1990). Use of natural enemies to control agricultural pests in Malaysia. In: *The Use of Natural Enemies to Control Agricultural Pests* (ed. Bay-Petersen, J.). Food and Fertilizer Technology Center, Taipei, Taiwan, pp. 30–39.
- Kruess, A. & Tschardtke, T. (1994). Habitat fragmentation, species loss, and biological-control. *Science*, 264, 1581–1584.
- Kruess, A. & Tschardtke, T. (2000). Species richness and parasitism in a fragmented landscape: experiments and field studies with insects on *Vicia sepium*. *Oecologia*, 122, 129–137.
- Luna, M. & Sánchez, N. (1999). Parasitoid assemblages of soybean defoliator Lepidoptera in north-western Buenos Aires province, Argentina. *Agric. For. Entomol.*, 1, 255–260.
- Memmott, J., Martinez, N.D. & Cohen, J.E. (2000). Predators, parasites and pathogens: species richness, trophic generality and body sizes in a natural food web. *J. Appl. Ecol.*, 69, 1–1.
- Miliczky, E.R., Calkins, C. & Horton, D. (2000). Spider abundance and diversity in apple orchards under three insect pest management programmes in Washington State, U.S.A. *Agric. For. Entomol.*, 2, 203–215.
- Mooney, H., Lubchenco, J., Dirzo, R. & Sala, O. (1995a). Biodiversity and ecosystem functioning: basic principles. In: *Global Biodiversity Assessment* (ed. Heywood, V.). Cambridge University Press, pp. 279–323.
- Mooney, H., Lubchenco, J., Dirzo, R. & Sala, O. (1995b). Biodiversity and ecosystem functioning: ecosystem analyses. In: *Global Biodiversity Assessment* (ed. Heywood, V.). Cambridge University Press, pp. 347–452.
- Napompeth, B. (1990). Use of natural enemies to control agricultural pests in Thailand. In: *The Use of Natural Enemies to Control Agricultural Pests* (ed. Bay-Petersen, J.). Food and Fertilizer Technology Center, Taipei, Taiwan, pp. 8–29.
- Naylor, R.L. & Ehrlich, P.R. (1997). Natural pest control services and agriculture. In: *Nature's Services* (ed. Daily, G.C.). Island Press, Washington, pp. 151–174.
- Oatman, E. (1995a). Lepidopteran complex on tomatoes. In: *Biological Control in the Western United States* (eds Nichols, J., Andres, L., Beardsley, J., Goeden, R.D. & Jackson, C.). University of California Press, Oakland, pp. 190–191.
- Oatman, E. (1995b). Omnivorous looper and *Amorbia cuneana* Walsingham. In: *Biological Control in the Western United States* (eds Nichols, J., Andres, L., Beardsley, J., Goeden, R.D. & Jackson, C.). University of California, Oakland, pp. 185–187.
- Ooi, P.A.C. & Shepard, B.M. (1994). Predators and parasitoids of rice insect pests. In: *Biology and Management of Rice Insects* (ed. Heinrichs, E.A.). Wiley Eastern, New Delhi, pp. 586–612.
- Pathak, M. & Kahn, Z. (1994). *Insect Pests of Rice*. International Rice Research Institute, Manila.
- Petchey, O.L. (2000). Species diversity, species extinction and ecosystem function. *Am. Nat.*, 155, 696–702.
- Rodríguez, M.A. & Hawkins, B.A. (2000). Diversity, function and stability in parasitoid communities. *Ecol. Lett.*, 3, 35–40.
- Schläpfer, F., Schmid, B. & Seidl, I. (1999). Expert estimates about effects of biodiversity on ecosystem processes and services. *Oikos*, 84, 346–352.
- Schwartz, M.W., Bringham, C.A., Hoeksema, J.D., Lyons, K.G., Mills, M.H. & van Mantgem, P.J. (2000). Linking biodiversity to ecosystem function: implications for conservation ecology. *Oecologia*, 122, 297–305.
- Swift, M.J., Vandermeer, J., Ramakrishnan, P.S., Anderson, J.M., Ong, C.K. & Hawkins, B.A. (1996). Biodiversity and agroecosystem function. In: *Functional Roles of Biodiversity: A Global Perspective* (eds Mooney, H.A., Cushman, J.H., Medina, E., Sala, O.E. & Schulze, E.D.). Wiley, New York, pp. 261–297.
- Szentkirályi, F. & Kozár, F. (1991). How many species are there in apple insect communities?: testing the resource diversity and intermediate disturbance hypotheses. *Ecol. Entomol.*, 16, 491–503.
- Tassan, R. & Hagen, K. (1995). Iceplant scales. In: *Biological Control in the Western United States* (eds Nichols, J., Andres, L., Beardsley, J., Goeden, R.D. & Jackson, C.). University of California, Oakland, pp. 196–197.
- Thies, C. & Tschardtke, T. (1999). Landscape structure and biological control in agroecosystems. *Science*, 285, 893–895.
- Thomas, M.B. (1999). Ecological approaches and development of 'truly integrated' pest management. *Proc. Nat. Acad. Sci. U.S.A.*, 96, 5944–5951.
- Thomas, M. & Waage, J. (1996). *Integration of Biological Control and Host-Plant Resistance Breeding: A Scientific and Literature Review*. Tropical Centre for Agricultural and Rural Cooperation, Wageningen, The Netherlands.
- Tilman, D. (2000). Causes, consequences and ethics of biodiversity. *Nature*, 405, 208–211.

- Tilman, D., Knops, J., Wedin, D., Reich, P., Ritchie, M. & Siemann, E. (1997a). The influence of functional diversity and composition on ecosystem processes. *Science*, 277, 1300–1302.
- Tilman, D., Lehman, C.L. & Thomson, K.T. (1997b). Plant diversity and ecosystem productivity: Theoretical considerations. *Proc. Nat. Acad. Sci. U.S.A.*, 94, 1857–1861.
- Waloff, N. (1968). Studies on the insect fauns on Scotch Broom *Sarothamnus scoparius* (L.) Wimmer. *Adv. Ecol. Res.*, 5, 87–208.

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