Spatiotemporally-mediated effects of land use on the biodiversity of cavity-nesting Hymenoptera in coastal Ecuador

Dissertation
zur Erlangung des Doktorgrades
der Mathematisch-Naturwissenschaftlichen Fakultäten
der Georg-August-Universität zu Göttingen

vorgelegt von
Jason Tylianakis
aus Athen, Griechenland

Göttingen, Dezember 2005

D 7

Referent: Prof. Dr. Teja Tscharntke

Korreferent: Prof. Dr. Matthias Schaefer

Tag der mündlichen Prüfung:19.01.2006

Contents

Chapter
1

Introduction

Anthropogenic change and biodiversity loss – a problem at multiple scales

Anthropogenic modification of habitats, largely due to agricultural conversion, is a global threat to biodiversity (e.g., Tilman *et al.* 2002; Gaston *et al.* 2003). Much previous attention has focused on the use of set-aside areas for conservation; however, there is increasing recognition that protected areas are not sufficient to slow the biodiversity decline, and attention is now turning towards the potential utility of managed land for conservation (Novacek & Cleland 2001; Bengtsson *et al.* 2003; Tscharntke *et al.* 2005 – see also Chapter 2). Nowhere is this need more imperative than in the tropics, where the greatest diversity of species occurs (Myers *et al.* 2000), but conservation funding is low, increasing the reliance of these regions on managed land for biodiversity maintenance (Perfecto *et al.* 1996). Recent attention has therefore shifted to tropical agroforests, as their superficial resemblance to natural habitats and less intensive management practises, may make them an important candidate for conservation in the tropics (e.g., Perfecto *et al.* 1996, Moguel & Toledo 1999; Rice & Greenberg 2000; Perfecto *et al.* 2003). Nevertheless, the extent of their contribution to the biodiversity of many taxa is unclear, particularly in comparison to other more intensive (e.g. arable land) or less-intensive (forest) land use types. Previous studies have examined the effects of increased management intensity on a variety of taxa and found both negative (Steffan-Dewenter *et al.* 2002; Mas & Dietsch 2003; Schulze *et al.* 2004; Shahabuddin *et al.* 2005 – see also Chapter 5), and positive (e.g., DeVries *et al.* 1997; Lawton *et al.* 1998; DeVries & Walla 2001; Klein *et al.* 2002 - see also Chapter 4) effects on diversity. One reason for the lack of congruence in these studies may result from differences in the spatial and/or temporal scale of sampling, and recent studies have shown that the effects of habitat loss/modification can manifest themselves differently according to the scale examined (e.g., Roland & Taylor 1997; Hamer & Hill 2000; Willis & Whittaker 2000; Hill & Hamer 2004 – see also Chapters 2,4,5). Therefore, an understanding of the effects of land use on diversity requires an understanding of the manner in which these effects vary across spatial scales. Although effects at different temporal scales have received less attention, the same patterns appear to occur (DeVries *et al.* 1997 - see also Chapter 5); therefore, a clear understanding of the effects of land use on diversity requires analyses at multiple spatiotemporal scales (Ricklefs & Schluter 1993; May 1994), and across a broad range of habitats.

The overarching project

The work contained in this thesis took place within a project titled: Evaluation of **bio**logical diversity of land-use **sys**tems in mega-diverse regions of coastal Ecuador (BIO-SYS). A brief description of the project follows, so that the remaining chapters can be placed into their proper context within the project. Parts of this chapter were taken from Tylianakis *et al.* (2004).

Project rationale/components

Sustainable land use may produce a great variety of ecological goods and services (Altieri 1999). However, without payments for these services, environmentally-friendly land use may remain economically unattractive. Therefore, some kind of economic incentive may be necessary to encourage ecologically sustainable land use. Before incentives such as payment for ecosystem services can be initiated, however, information is needed regarding both the land management practices that are most beneficial for preservation of biodiversity, and the financial costs or benefits associated with these practices.

The BIO-SYS project lies at the interface of science and politics. We sought to evaluate species richness and ecosystem services in order to provide a scientific and operational basis for the implementation of payments for these services. Such payments, whether originating from the government or consumers, could potentially lift the economic burden of biodiversity preservation from landowners, allowing economically feasible conservation on private land.

The project was divided into four main components, one biological, one soil, one economic, and one land-use modelling. The aim of the diversity component was to determine the importance of differences in land-use types for the preservation of biodiversity and associated ecosystem functioning. Agroforests in particular may be important reservoirs for biodiversity (Perfecto *et al.* 1996; Moguel & Toledo 1999; Rice & Greenberg 2000; but see Rappole *et al.* 2003 for a caveat), and therefore received considerable attention.

The economic component made cost/revenue comparisons and risk analyses for the different land-use types. Finally, the overall diversity (soil, plants, arthropods, birds) and economic components will be integrated into a dynamic land-use model for the regions concerned. The major components of the project are as follows:

Soil analyses

These determined the effect of the interaction between soil type and land use management on the diversity of chemical, physical and biological soil characteristics at the plot and landscape level and its relation with other ecosystem functions such as plant diversity, nutrient cycling and carbon sequestration.

Plant community analyses

These used botanical surveys to map vegetation and determine the relationship between the diversity of plants and land-use type or combination of land use types. This was then related to bird diversity.

Bird diversity

Bird diversity in the different land use systems was determined by means of the point count method in different seasons. Bird diversity in natural forest and agroforestry systems was related to food availability.

Insect community analyses

The work contained in this thesis formed part of the insect component (see Research objectives p.13). A further study examined the effects of differences in Hymenoptera diversity on coffee pollination and revenues.

Economic

The economic component of the project focused on comparisons of different land-uses and land management practices, as well as quantification of opportunity costs for biodiversity conservation. Farmers' land allocation problems were studied in detail, considering that net revenues and risks are major determinants for land-use choice. Risk-analysis techniques included Montecarlo simulations and Stochastic Dominance. The biodiversity component of the overall research was integrated in this analysis by means of possible payments for environmental services, which may lead to relevant policy implications.

Dynamic modeling

The locally recorded ecological and economic information will be combined into a land-use model for the Manabi and Esmeraldas regions. This will allow regional-scale forecasts concerning land-use changes generated by financial incentives for providing ecosystem services. Through scenario studies we will identify potential trade-offs between biodiversity conservation, carbon sequestration and the production of agricultural and forestry products. Finally, it will be estimated how and where conservation measures can be implemented with the lowest opportunity costs. The model will be assigned from the local to the regional scale.

Study region

The research was carried out in the megadiverse “choco-manabi” region of coastal Ecuador. This region is characterised by high annual rainfall, and high diversity of many taxa. The primary study region was in the province of Manabi, close to the town of Jipijapa (Fig. 1.1, and Fig. 4.1 p.76). We conducted our research in this region for 17 months, using monthly evaluations of the trap-nests. The province of Manabi has been heavily modified by agricultural practices (Table 4.1, p.75, shows the

Figure 1.1. Map of Ecuador showing study regions in 1. Esmeraldas and 2. Manabi.

area occupied by the different land-use types in this study). This formerly humid region has become semi-arid (temperature and rainfall information is presented in Appendix 5.1, p.109) due to large-scale deforestation, and the little forest cover remaining suffers from fragmentation effects, removal of timber, and intensive activities such as burning of the adjacent arable land. The province of Manabi is therefore ideal for an assessment of the effects of agricultural modification on biodiversity, as it is too late to consider conservation of natural habitats in this region as a solution to biodiversity decline. The 48 study plots comprised private farms within the cantons: Jipijapa, Pajan and 24 de Mayo (see Appendix 5.2, p.110 for site location details).

In addition to this region, we also conducted research on trap-nesting Hymenoptera communities within the northern province of Esmeraldas (Fig. 1.1), close to the town of Cabo San Fransisco. This region is in direct contrast to Manabi, with very little agricultural conversion, and a large degree of forest cover. The data from Esmeraldas are not presented here, but will be used in future work.

The study system: Cavity-nesting Hymenoptera as bioindicators

The central problem surrounding direct measurement of biodiversity is the sheer number of species in most habitats, making indirect measurement techniques more heavily relied upon. Indirect measures generally incorporate presence/absence data from few taxa, such as lichens or aquatic invertebrates, as a basis for extrapolations to community-level diversity (e.g., Wolseley *et al.* 1994; Larsen *et al.* 1996). Several indicator taxa from different groups may even be used; however, these taxa may not show congruent patterns of diversity (Prendergast *et al.* 1993). This makes the selection itself of indicator taxa a partial determinant of the end diversity estimate. However, bioindicator groups can also be used in a broader sense to indicate changes in population parameters, ecological functions or community structure (e.g., Tscharntke *et al.*1998; Paoletti 1999; Davis *et al.* 2001). Insects make particularly useful bioindicators because they account for more than half of all species and their diversity allows for fine-scale resolution when differentiating between habitats.

Many surface-dwelling arthropods are used for bioindication because a) the taxa most often collected (such as carabid and staphylinid beetles and spiders) are polyphagous predators, and are therefore considered to be important for biological control, b) collections are made easily with pitfall traps, and c) catches are normally sufficiently large to allow statistical analyses (Duelli *et al.*1999). Pitfall sampling for ground-dwelling invertebrates may however lead to taxonomic difficulties and often unmanageable sample sizes. While these problems can be partially overcome with simpler survey techniques (e.g., Andersen *et al.* 2002), such surveys yield ultimately information only on individual and species number, without any ecological context regarding species interactions. These ecological interactions are integral to the concept of biodiversity, and their exclusion reduces ecosystem diversity to a simple number, which does not contribute fully to the understanding of ecosystem services in multitrophic communities (Montoya *et al.* 2003). For this reason community-based studies for evaluations of biodiversity are necessary. For example, marine crustacean, soil arthropod or cavity-nesting Hymenoptera (Hymenoptera: Apidae, Eumenidae, Sphecidae and Pompilidae) communities make useful bioindication tools, due to their discreet area, trophic complexity and species diversity (Sanchez-Moyano & Garcia-Gomez 1998; Tscharntke *et al.* 1998; van Straalen 1998). In terms of ecosystem services (sensu Costanza *et al.* 1997) or functional agricultural biodiversity (Gurr *et al.* 2003), communities of cavity-nesting bees and wasps (Fig. 1.2) are particularly salient, as their constituents are important pollinators of both crops and wild plants (Corbet *et al.* 1991; Klein *et al.* 2003). Anthropogenic declines in insect pollinators may have important consequences for plant biodiversity and stability of food crop yields (Allen-Wardell *et al.* 1998). Moreover, many cavity-nesting species are also predators or parasitoids, thereby acting as biological control agents (e.g., Harris 1994).

Trap-nests yield a suite of ecological information that can be used to compare habitats. As with other sampling techniques, they provide measures of overall abundance (Klein *et al.* 2002), and species richness (Chapters 3-7), as well as species richness of certain guilds, such as parasitoids (Chapters 3,6,7). These parameters can be used for habitat comparisons based on differences in successional stage (Gathmann *et al.* 1994), plant species richness (Tscharntke *et al.* 1998; Chapters 3,4), land-use intensity (Klein *et al.* 2002; Chapters 3-7) or habitat diversity (Steffan-Dewenter 2002). Moreover, trap-nests provide important and often-neglected information on ecological interactions such as the type of food provided to offspring (e.g., pollen, spiders, Lepidoptera larvae), rates of survival/parasitism (Chapters 6,7), or foraging time (Klein *et al.* 2004).

A description of the construction of trap-nests can be found in the Methods sections of Chapters 3-6, and a list of the species observed in the present study can be found in Appendix 6.1 (p.128).

Figure 1.2. Examples of (left) a trap-nest, (centre) a trap-nesting bee species (*Neofidelia* sp.; Hymenoptera: Megachilidae), and (right) a parasitoid of trap-nesting species (*Leucospis* sp.; Hymenoptera: Leucospidae).

Research objectives

The overall aim of this research was to examine the effects of anthropogenic habitat modification on the diversity and parasitism rates of cavity-nesting bees, wasps, and their natural enemies. This general aim could be broken down into separate themes relating to i) the effects of habitat modification on diversity, ii) effects across different spatial and temporal scales, and iii) the effects of diversity on rates of parasitism.

i) We began with a general discussion of the utility of managed land for conservation of insects, and an introduction of the manner in which this utility can vary at different spatial and temporal scales (Chapter 2). We then examined, for our particular study region, the effects of habitat heterogeneity on species diversity at three trophic levels (Chapter 3).

ii) We examined the effect of anthropogenic habitat modification on additively-partitioned Hymenoptera diversity, and the importance of source habitats and local floral resource availability. We also examined the manner in which these effects on α, β, and γ diversity vary across spatial (Chapter 4) and temporal (Chapter 5) scales. This approach allowed us to examine why previous short-term studies have had contradictory results in terms of the effects of habitat modification on species diversity. We also examined the impact of habitat modification on the proportion of habitat specialists, as examination of species richness alone gives no indication of the conservation value of the species considered (Chapter 5).

iii) Many studies have examined the effects of diversity on plant productivity, and recent studies have examined the effects of predator/parasitoid diversity on rates of predation/parasitism. However, these studies have almost entirely been conducted in mesocosms, so the applicability of the results to the real world remain unclear. We therefore examined the effect of bee, wasp and natural enemy diversity on rates of parasitism, and stability in parasitism through time (Chapter 6), and the effects of resource heterogeneity on the diversity/parasitism relationship (Chapter 7).

Chapter outline

Chapter 2 discusses the potential utility of managed land for conservation of insects, and briefly introduces the manner in which this can vary at different scales. It examines the biodiversity and ecosystem services that may be maintained in agroecosystems, and how these may be enhanced. It also questions the appropriateness of current agri-environment schemes for conservation on managed land, and suggests possible improvements to these schemes that incorporate the multiple scales at which land use affects biodiversity.

Chapter 3 examines how land use can affect soil heterogeneity and promote plant diversity, which in turn affects the diversity of bees, wasps and their natural enemies. This chapter demonstrates the importance of heterogeneity in resource distributions for the structure of ecological communities – a theme that recurs throughout this thesis.

Chapter 4 examines the effect of habitat modification on bee and wasp diversity. It also examines the effects of distance to source populations and floral resource availability on diversity, and how these effects vary across spatial scales. This chapter uses additive partitioning of diversity to examine the contribution of trap- (α) and plot- (β) scale diversity to the overall habitat type and regional (γ) diversity, noting the different partitioning of diversity in different habitat types.

Chapter 5 takes a step further, by including data over a longer time period, and examining the temporal species turnover in different habitat types. It explains why homogenous modified habitats may appear to have higher diversity than natural habitats when sampled over a short time period. This chapter also examines the relative specificity of the bees and wasps inhabiting different habitat types, showing that species richness is not the only useful measure of the contribution of a habitat to biodiversity.

Chapter 6 addresses the relationship between diversity and ecosystem functioning. Much research has been conducted on this subject; however, field studies are almost completely lacking, and in the instances where they have been conducted, possible methodological flaws have led to equivocal results. This chapter examines the effect of bee, wasp and natural enemy diversity on rates of parasitism, and stability in parasitism through time. It explains why previous studies may have yielded equivocal results, and draws on knowledge from the previous chapters to understand patterns in parasitism rates across different habitat types.

Chapter 7 examines the diversity/parasitism relationship itself, and how this varies according to heterogeneity in biotic and abiotic factors. It uses one focal host species and examines how heterogeneity, particularly patchiness in host abundance, leads to a stronger effect of natural enemy diversity on rates of parasitism. It also explains that mesocosm studies may not have contained the necessary heterogeneity to allow niche complementarity, and therefore have often found no effect of predator diversity on prey consumption.

References

Allen-Wardell, G., Bernhardt, P., Bitner, R., Burquez, A., Buchmann, S., Cane, J. & Cox, P.A. (1998). The potential consequences of pollinator declines on the conservation of biodiversity and stability of food crop yields. *Conservation Biology,* 12, 8-17.

Altieri, M.A. (1999). The ecological role of biodiversity in agroecosystems. *Agriculture, Ecosystems and Environment,* 74, 19-31.

Andersen, A.N., Hoffmann, B.D., Müller, W.J. & Griffiths, A.D. (2002). Using ants as bioindicators in land management: simplifying assessment of ant community responses. *Journal of Applied Ecology,* 39, 8-17.

Bengtsson, J., Angelstam, P., Elmquvist, T., Emanuelsson, U., Forbes, C., Ihse, M., Moberg, F. and Nyström, M. (2003) Reserves, resilience and dynamic landscapes. *Ambio,* 32, 389-396.

Corbet, S.A., Williams, L.A. & Osborne, J.L. (1991). Bees and the pollination of crops and wild flowers in the European community. *Bee World,* 72, 47-59.

Costanza, R., d'Arge, R., de Groot, R. Farber, S., Grasso, M., and Hannon, B. (1997). The value of the world's ecosystem services and natural capital. *Nature,* 387, 253-260.

Davis, A.J., Holloway, J.D., Huijbregts, H., Krikken, J., Kirk-Spriggs, A.H. & Sutton, S.L. (2001). Dung beetles as indicators of change in the forests of northern Borneo. *Journal of Applied Ecology,* 38, 593-616.

DeVries, P.J., Murray, D. & Lande, R. (1997). Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biol. J. Linn. Soc.*, 62, 343-364.

DeVries, P.J. & Walla, T.R. (2001). Species diversity and community structure in neotropical fruit-feeding butterflies. *Biol. J. Linn. Soc.*, 74, 1-15.

Duelli, P., Obrist, M.K., & Schmatz, D.R. (1999). Biodiversity evaluation in agricultural landscapes: above-ground insects. *Agriculture, Ecosystems and Environment,* 74, 33-64.

Gaston, K.J., Blackburn, T.M. & Goldewijk, K.K. (2003) Habitat conversion and global avian biodiversity loss. *Proceedings of the Royal Society of London, B.*, 270: 1293-1300.

Gathmann, A., Greiler, H.-J. & Tscharntke, T. (1994). Trap-nesting bees and wasps colonizing set-aside fields: succession and body size, management by cutting and sowing. *Oecologia,* 98, 8-14.

Gurr, G.M., Wratten, S.D. & Luna, J.M. (2003). Multi-function agricultural biodiversity: pest management and other benefits. *Basic and Applied Ecology,* 4, 107-116.

Hamer, K.C. & Hill, J.K. (2000). Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology*, 14, 1435-1440.

Harris, A.C. (1994). *Ancistrocerus gazelle* (Hymenoptera: Vespoidea: Eumenidae): a potentially useful biological control agent for leafrollers *Plantortix octo, P. exessana, Ctenopseustis oblique, C. herana*, and *Epiphyas postvittana* (Lepidoptera: Tortricidae) in New Zealand. *New Zealand Journal of Crop and Horticultural Science,* 22, 235-238.

Hill, J.K. & Hamer, K.C. (2004). Determining impacts of habitat modification on diversity of tropical forest fauna: the importance of spatial scale. *Journal of Applied Ecology*, 41, 744-754.

Klein, A.-M., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. (2002). Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology,* 16, 1003-1014.

Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. (2003). Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology,* 40, 837-845.

Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. (2004). Foraging trip duration and density of megachilid bees, eumenid wasps, and pompilid wasps in tropical agroforestry systems. *Journal of Animal Ecology,* 73, 517-525.

Larsen, J., Birks, H.J.B., Raddum, G.G. & Fjiellheim, A. (1996). Quantitative relationships of invertebrates to pH in Norwegian river systems. *Hydrobiologia,* 328, 57-74.

Lawton, J.H., Bignell D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature,* 391, 72-76.

Mas, A.H. & Dietsch, T.V. (2003). An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. *Ecological Applications*, 13, 1491-1501.

May, R.M. (1994). The effects of spatial scale on ecological questions and answers. In: P.J. Edwards, R.M. May & N.R. Webb (eds.) *Large-scale Ecology and Conservation Biology*. Blackwell Scientific, Oxford, UK.

Moguel, P. & Toledo, V.M. (1999). Biodiversity conservation in traditional coffee systems of Mexico. *Conservation Biology,* 13, 11-21.

Montoya, J.M., Rodriguez, M.A. & Hawkins, B.A. (2003). Food web complexity and higher-level ecosystem services. *Ecology Letters,* 6, 587-593.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature,* 403, 853-858.

Novacek, M.J. & Cleland, E.E. (2001) The current biodiversity extinction event: Scenarios for mitigation and recovery. *Proceedings of the National Academy of Sciences, USA* 98: 5466-5470.

Paoletti, M.G. (1999). Using bioindicators based on biodiversity to assess landscape sustainability. *Agriculture, Ecosystems and Environment,* 74, 1-18.

Perfecto, I., Rice, R.A., Greenberg, R., & Van der Voort, M.E. (1996). Shade coffee: a disappearing refuge for biodiversity. *BioScience,* 46, 598-608.

Perfecto, I., Mas, A., Dietsch, T. & Vandermeer, J. (2003) Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. *Biodiversity and Conservation*, 12, 1239-1252.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C. & Gibbons, D.W. (1993). Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature,* 365, 335-337.

Rappole, J.H., King, D.I., & Vega Rivera, J.H. (2003). Coffee and conservation. *Conservation Biology,* 17, 334-336.

Rice, R.A. & Greenberg, R. (2000). Cacao cultivation and the conservation of biological diversity. *Ambio,* 29, 167-173.

Ricklefs R.E. & Schluter, D. (eds.)(1993). *Species diversity in Ecological Communities: Historical and geographical perspectives*. University of Chicago Press. Chicago, USA.

Roland, J. & Taylor, P.D. (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature* 386, 710-713.

Sanchez-Moyano, J.E. & Garcia-Gomez, J.C. (1998). The arthropod community, especially Crustacea, as a bioindicator in Algeciras Bay (Southern Spain) based on spatial distribution. *Journal of Coastal Research,* 14, 1119-1133.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004). Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications*, 14, 1321-1333.

Shahabuddin, Schulze, C.H. & Tscharntke, T. (2005). Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia). *Biodiversity and Conservation,* 14, 863-877.

Steffan-Dewenter, I. (2002). Landscape context affects trap-nesting bees, wasps, and their natural enemies. *Ecological Entomology,* 27, 631-637.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421-1432.

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R. and Polasky, S. (2002) Agricultural sustainability and intensive production practices. *Nature* 418, 671-677.

Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998). Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology,* 35, 708-719.

Tscharntke, T., Klein, A.-M., Kruess, A., Steffan-Dewenter, I and Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters,* 8, 857-874.

Tylianakis, J., Veddeler, D., Lozada, T., López, R.M., Benítez, P., Klein, A.M., de Koning, G.H.J., Olschewski, R., Veldkamp, E., Navarrete, H., Onore, G. and Tscharntke, T. (2004). Biodiversity in coastal Ecuador and bioindication using trap-nesting bees, wasps, and their natural enemies. Proceedings de IV Congreso Ecuatoriano de Botánica and II Congreso de Conservación de la Biodiversidad en los Andes y en la Amazonía. *Lyonia* 6(2). Download at: http://www.lyonia.org/downloadPDF.php?PDFID=2.237.1

Van Straalen, N.M. (1998). Evaluation of bioindicator systems derived from soil arthropod communities. *Applied Soil Ecology,* 9, 429-437.

Willis, K.J. & Whittaker, R.J. (2002) Species diversity – scale matters. *Science,* 295, 1245-1248.

Wolseley, P.A., Moncrieff, C. & Aguirrehudson, B. (1994). Lichens as indicators of environmental stability and change in the tropical forests of Thailand. *Global Ecology and Biogeography Letters,* 4, 116-123.

Chapter

2

Integrating insect conservation in agricultural landscapes

T. Tscharntke, J.M. Tylianakis, M.R. Wade, S.D. Wratten, J. Bengtsson and D. Kleijn

In: Alan Stewart, Owen Lewis and Tim New (eds.) *Insect Conservation Biology*. CABI Publishing

Introduction

Agricultural land use and biodiversity conservation have been traditionally viewed as incompatible, but only recently, recognition has increased that a restriction of conservation efforts to natural, undisturbed ecosystems is of limited value (Pimentel *et al.* 1992, Bengtsson *et al.* 2003). "We are obviously past any point where strategies that focus on conservation of pristine habitat are sufficient for the job" (Novacek and Cleland 2001). Agriculture can make important contributions to high diversity of landscapes, while it also benefits from sustainable ecosystem services provided by agricultural conservation management (Daily 1997, Kremen 2005, Tscharntke *et al.* 2005). For example, enhanced biological pest control and improved crop pollination may directly increase the farmers' income (e.g. Östman *et al.* 2003, Ricketts *et al.* 2004, Olschewski *et al.* submitted).

In this chapter, we review negative and positive effects of agriculture for biodiversity conservation and the role of biodiversity in multifunctional agriculture, including ecosystem services such as biological pest control. Biodiversity patterns change with the spatial and temporal scales considered, so integrating conservation in agriculture requires a multiscale landscape perspective. Further, we discuss political options for sustainable landscape planning. We argue that there is a need for a diversity of "insurance" species, to support the landscape-wide capacity to reorganize after disturbance, and for tailoring agri-environment schemes at the landscape level.

Agriculture between habitat destruction and conservation

The greatest losses in biodiversity worldwide have been attributed to the expansion and intensification of agriculture (Robinson and Sutherland 2002; Tilman *et al.* 2002), and land use is often characterized by a transformation of complex ecosystems and landscapes into simple ones, resulting in reduced biodiversity (Fig. 2.1). Species loss does not affect all species similarly, which may result in the release of herbivores due to reduced control by natural enemies (see Fig. 2.1). Agricultural intensification happens at different spatial scales. Local intensification includes adverse effects such as shortened crop rotation cycles and increasing input of agrochemicals. On a landscape scale, fields have been amalgamated and enlarged, resulting in simplified landscapes without any noncrop habitats remaining (e.g., Swift and Anderson 1993, Tscharntke *et al.* 2005).

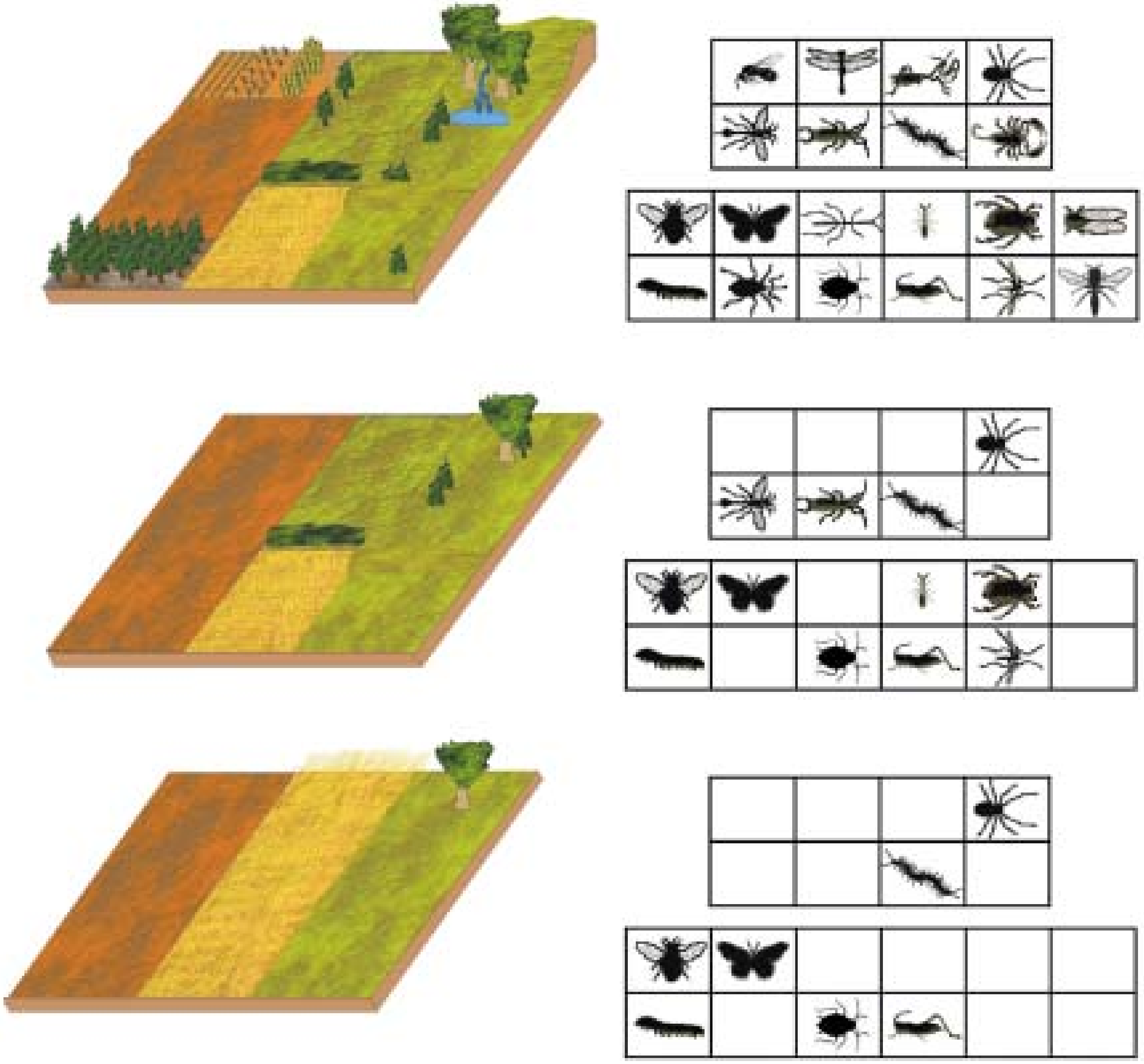


Figure 2.1. Decreasing insect biodiversity with decreasing landscape heterogeneity. From top to bottom, the agricultural landscape becomes simplified and the associated insect communities become less diverse. For each landscape type, insect symbols show herbivores (two rows on the bottom) and predators (two rows on the top). In the simplest landscape (bottom) only generalist species survive, pest outbreaks are common because higher trophic levels suffer more from simplification, and ecosystem services are limited.

However, agricultural land use does not just mean habitat destruction. Traditional and low-intensity land use practices may create species-rich habitats, which is well known from Europe (e.g., high diversity grasslands) but also known from the tropics (see Perfecto *et al.* 1996). For example, coffee and cacao agroforestry, shaded by diverse natural or planted trees, represent the last remaining forested habitats in many tropical landscapes (Rice and Greenberg 2000, Perfecto and Armbrecht 2003).

Insect and bird species in these managed ecosystems may be as high as in the adjacent forest remnants. Both in temperate and tropical regions, the neighbourhood of natural and managed ecosystems is often important for sustaining the agroecosystems' biodiversity and associated ecosystem services such as pollination and biological control. For example, field boundaries adjacent to temperate crop fields support colonisation by noncrop plants as well as insects, thereby facilitating biological control (e.g., Thies and Tscharntke 1999). Coffee agroforestry adjacent to rainforests profits from the invasion of pollinating bees, enhancing coffee yield and net revenues of the farmers (Olschewski *et al.* submitted).

Habitat manipulation of farmland offers great potential for conservation of non-arthropods too. Many songbird populations have declined markedly in western Europe, as have those of the grey partridge, *Perdix perdix* (L.) and some mammals such as the harvest mouse, *Micromys minutes* (Pallas). Recent work by scientists at the Game Conservancy Trust in the United Kingdom has led to dramatic improvements in the populations of these species by the use of simple but research-intensive protocols. Again, beetle banks are prominent in this regard; not only do they harbour up to 1000 predatory invertebrate individuals per square metre in the winter, but the greatest nesting densities of grey partridge and the harvest mouse now occur in these 'island habitats' (Thomas *et al.* 2001).

Methods for increasing the conservation value of agricultural land at the habitat scale are usually more familiar, and normally involve an attempt to decrease the intensity of management. Insect diversity and abundance can be enhanced by provision of woody borders or non-crop habitats adjacent to fields (e.g., Dyer and Landis 1997; Holland and Fahrig 2000), high shade-tree diversity in agroforests (Stamps and Linit 1997; Sperber *et al.* 2004, Veddeler *et al.* 2005) or through organic management (Hutton and Giller 2003;

Asteraki *et al.* 2004; Wickramasinghe *et al.* 2004; Bengtsson *et al.* 2005, Morandin and Winston 2005). Nevertheless, the primary goal of landowners is to maximise profit, and differences between those strategies that favour conservation and those that favour economic returns must be reconciled (Banks 2004). In this sense conservation efforts must be pragmatic, and search for strategies that are mutually beneficial for the landowners and biodiversity. Several options are available for this type of mutual benefit. First of all, financial incentives can be offered to landowners in exchange for providing conservation services, such as unsprayed headlands or the agri-environment schemes discussed below. Second, reduced intensity through organic farming can be beneficial to a variety of taxa, and any extra costs associated with organic farming can be offset by the consumer, so that the financial burden of conservation is shared (e.g., Collins *et al.* 1992).

Biodiversity in Agroecosystems and Habitat Manipulation for Enhanced Biocontrol

Agricultural ecosystems are traditionally considered to be biodiversity poor (see above). Consequently, the role of modified ecosystems such as agricultural and urban land in providing ecosystem services, such as biological control, climate regulation, food, fuel wood, gas regulation, pollination and soil formation has received little attention. The pivotal paper by Costanza *et al.* (1997), which calculated the economic value of 17 ecosystem services in 16 biomes to be in the range of US$16-54 trillion per year, with an annual average of US$33 trillion, actually attributed no dollar value to managed ecosystems. This is patently not true, especially when 'ecological engineering' techniques are available to enhance ecosystem services on farmland, such as habitat manipulation tactics for beneficial arthropods that are responsible for biological control (reviewed by Gurr *et al.* 2003, 2004).

It was only a few decades ago that awareness of functional biodiversity in farmland was raised. A key paper by Potts and Vickerman (1974) linked the role of functional invertebrate biodiversity in cereal crops to pest population dynamics. In this work, cereal aphid populations were reduced when total arthropod diversity increased (see Fig. 11 in Potts and Vickerman 1974). Parallel studies in cotton have shown that the predaceous fauna present is large. There are estimated to be over 250 species of predatory arthropods present in cotton in Australia, including 41 species that are commonly recorded (Room

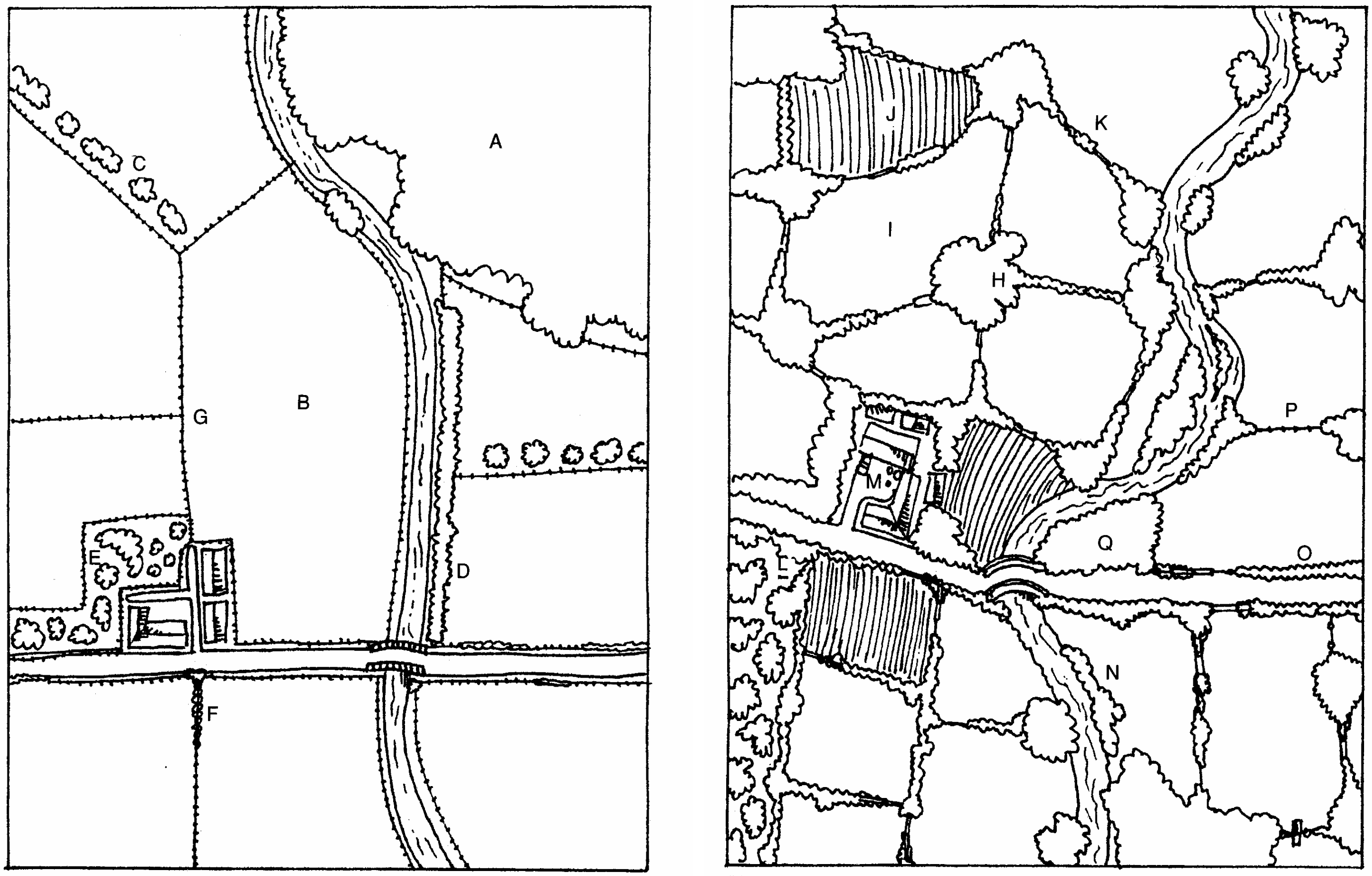
1979). This number is even greater in the USA, where approximately 600 predatory species are present in that crop (Whitcomb and Bell 1964). The value of field boundaries as refugia for beneficial arthropods such as Araneida and Coleoptera (Carabidae and Staphylinidae) has led to the development of 'beetle banks' across field centres, which are now a common part of the British landscape (Thomas *et al.* 1991). These permanently vegetated strips provide an alternative habitat for arthropods (as well as birds and small mammals), which is vital in annual cropping systems or when pesticides are used, as it ensures the colonisation, persistence and continuity of natural enemies to deliver the ecosystem service of pest control. A possible shortcoming of beetle banks and other types of refugia is the difficulty of ensuring that the individual arthropods that they harbour actually colonise the adjacent fields in the spring as the crops begin to grow (see Cameron *et al.* 1984).

Other recent work on functional biodiversity on farmland has explored the dynamics of arthropod dispersal, predation and parasitism rates, and population growth rates in more detail, and has included a strong emphasis on the spatial scale at which these processes operate. Some of this work has demonstrated the importance of uncultivated landscape elements in "driving" these landscape effects (reviewed by Tscharntke *et al.* 2005). These effects are clearly important, but there need to be policy changes before this information can be used most effectively, as the spatial scales involved transcend the scales at which individual landowners operate. In highly modified 'colonial' landscapes, such as lowland New Zealand, Australia and perhaps in other relatively new farming landscapes, most native vegetation has been removed from the agroecosystem. These landscapes are much simpler than their equivalent in Europe, particularly in relation to the 'nodes' where field corners join. In Europe these nodes can be rich 'hotspots' of invertebrate, vertebrate and plant diversity (Fry 1995; Fig. 2.2).

Adding functional biodiversity to agroecosystems can be a rapid process when particular predator-pest associations are targeted. For example, flowering plants such as alyssum (*Lobularia maritima* (L.) Desv, Brassicaceae), buckwheat (*Fagopyrum esculentum* Moench, Polygonaceae) and phacelia (*Phacelia tanacetifolia* Benth, Hydrophyllaceae) can be grown alongside horticultural crops which would otherwise be pure monocultures. These floral patches or strips provide nectar, pollen and shelter for beneficial arthropods, which can markedly improve the abundance, diversity and fitness of these arthropods, leading to marked reductions in crop pests (reviewed by Landis *et al.* 2000; see also Berndt *et al.* 2002; Tylianakis *et al.* 2004; Berndt and Wratten 2005; Lee and Heimpel 2005). However, in this type of work the plant biodiversity (both crop and flowers) added is usually non-native, as are the pest and beneficial species involved. Habitat manipulation methods remain valid for enhancing the biodiversity of native species, as demonstrated by beetle banks (see above). However, the results are typically generated more slowly because many of these native taxa have specialist food requirements, reproduce slowly and/or have low mobility (including colonisation abilities). For example, the invertebrate fauna associated with mature trees on farmland, in particular with the coarse woody debris which occurs in association with mature forests, is usually depauparate. Recent work in New Zealand is using untreated discs of pine wood to accelerate ecological succession; these discs provide many of the ecological functions of natural fallen logs and can harbour late-succession invertebrate communities which usually would not be present in highly-modified farming landscapes (Bowie and Frampton 2004).

A similar example from New Zealand which again involves designing end-of-succession habitats is the use of ‘Weta Hotels’. Wetas (Orthoptera: Anostostomatidae, Rhaphidophoridae) are large, iconic native insects that are usually associated with undisturbed forest landscapes. Weta hotels, which mimic coarse woody debris with cavities, harbour this specialist fauna on farmland on which this insect disappeared in association with forest clearance (Bowie *et al.* submitted). Populations of pollinating bees and predatory wasps in agroecosystems can be enhanced with the introduction of suitable nesting sites (Gathmann *et al.* 1994, Tscharntke *et al.* 1998).

Much of the above work on restoring functional biodiversity has concentrated on increasing the contribution of natural enemies to pest control in order to minimise the negative effects associated with agricultural intensification, such as pesticide use. In summary, agroecosystems can support a rich diversity of beneficial arthropods. Provided the land use areas are managed correctly, these arthropods should contribute to the ecosystem service of pest control. Habitat manipulation approaches, such as beetle banks



(a) New Zealand

(b) British

Figure 2.2. Contrast between a homogeneous (or simple) and a heterogeneous (or complex) farm landscape, exemplified by some (a) New Zealand and (b) British landscapes. Note the heterogeneity of habitats and the connectance features in the British landscape compared with the uniformity of the New Zealand farm landscape. **A** = indigenous plant reserve: these tend to be large tracts of land not integrated with farmland; **B** = pasture, exotic grasses; **C** = typical shelter belt (e.g. popular, *Cupressus macrocarpa*, *Pinus radiata*); **D** = riparian vegetation (e.g. willow, grasses, some indigenous species); **E** = farmhouse garden; **F** = small areas of patchy gorse; **G** = wire fences: common field boundaries; **H** = small wood-lot: a highly used but sustained feature; **I** = pasture; **J** = ploughed field; **K** = hedge fence; **L** = orchard; **M** = farmhouse garden; **N** = riparian vegetation; **O** = roadside vegetation, hedges, trees etc; **P** = wire fences or stone walls; and **Q** = woodland. Illustration by Cor Vink, used with permission from V. Keesing and S.D. Wratten, 1997, Integrating plant and insect conservation, In: Plant Genetic Conservation, eds. N. Maxted, B.V. Ford-Lloyd and J.G. Hawkins, Chapman Hall: London, p. 220-235.

and species-rich floral patches, provide the opportunity to enhance biological control, but also to conserve important species of invertebrates, vertebrates and plants.

Biodiversity patterns in agricultural landscapes

Despite this evidence that agricultural land can contribute greatly to biodiversity and ecosystem services, the extent of this contribution across different systems and scales is somewhat ambiguous (Tscharntke *et al.* 2005). Previous studies have compared insect diversity at different management intensities within a particular land use type (e.g., DeVries *et al.* 1997; DeVries and Walla 2001; Klein *et al.* 2002), or across a variety of land uses, comprising a gradient of intensity (e.g., Shahabuddin *et al.* 2005; Tylianakis *et al.* in press). The results of these studies have not always been consistent, for example, insect diversity has been shown to increase (DeVries *et al.* 1997; Lawton *et al.* 1998; DeVries and Walla 2001; Klein *et al.* 2002; Tylianakis *et al.* submitted), decrease (Di Guilo *et al.* 2001; Sinclair *et al.* 2002; Steffan-Dewenter *et al.* 2002; Maeto *et al.* 2002; Mas and Dietsch 2003; Schulze *et al.* 2004; Shahabuddin *et al.* 2005; Tylianakis *et al.* in press) or not significantly differ (Steffan-Dewenter and Leschke 2003) with increasing management intensity.

Recent evidence suggests that the varied responses of different taxa to habitat modification may be scale- or landscape context-dependent (Tscharntke and Brandl 2004). This is not surprising, as different forces will be structuring communities and populations at different scales, ranging from within the habitat, to the entire region or landscape in which the habitat is embedded. Interacting species may experience these scales differently according to their dispersal, feeding and life history strategies (Jonsen and Fahrig 1997; Krauss *et al.* 2003; Borges and Brown 2004; Chust *et al.* 2004; Stoner and Joern 2004; Ribas *et al.* 2005), and the influence of landscape-scale processes on habitat-scale interactions is frequently overlooked (Tscharntke *et al.* 2005). It is therefore necessary to examine the effects of agricultural management on diversity at different scales and to consider approaches to integrating multiscale effects in order to gain a full understanding of the contribution of agricultural landscapes to overall biodiversity.

Factors affecting biodiversity at different spatial and temporal scales

While the effects of management intensity are frequently considered at the farm scale, agricultural intensification has also modified entire landscapes, through the amalgamation of fields to improve efficiency, and the loss of natural habitats and mosaic quality of the landscape (Tscharntke *et al.* 2005). Such homogenisation of landscapes leads to fragmentation and isolation of natural habitats, ultimately causing species decline. For example, fragment size, shape and spatial configuration can all significantly affect insect diversity (Cane 2001; Tscharntke *et al.* 2002; Krauss *et al.* 2003; Steffan-Dewenter 2003; Stoner and Joern 2004; Summerville and Crist 2004; Tscharntke and Brandl 2004; Ribas *et al.* 2005). Isolation, the distance of a habitat from a natural insect source population (e.g., forest), can also be an important determinant of insect diversity, especially of functionally important groups such as bees and ants (Ambrecht and Perfecto 2003; Klein *et al.* 2003a,b; Ricketts *et al.* 2004; but see Cunningham *et al.* 2005). Proximity to natural habitats, a landscape scale factor, may therefore partly mitigate harmful management practices at the habitat scale.

The negative effects of agriculture at the habitat scale generally result from reduced plant diversity (e.g., Marshall *et al.* 2003) or usage of insecticides (e.g., Paoletti and Pimentel 2000). However, the biodiversity of a habitat is ultimately limited by the total species pool within the landscape, and these two spatial scales are inherently linked. The diversity of a habitat is usually unsaturated with respect to the regional species pool (Holt and Gaston 2002; Gaston and Spicer 2004), and the degree of saturation can be assumed to be lower in agroecosystems due to their high disturbance frequency (Tscharntke *et al.* 2005).

Although analyses at different spatial scales have received some attention, variation in diversity across different temporal scales is often neglected. Temporal heterogeneity in the biodiversity of different habitat types may result from temporal variation in resource availability (Wolda 1978, 1988), for example, during periods of mast flowering or anthropogenic sowing/harvesting. This can allow species to move between habitats, exploiting the availability of predictable, ephemeral resources (Wissinger 1997; Bambaradeniya *et al.* 2004). Studies that have explicitly examined temporal variation in insect diversity have concluded that small temporal sampling scales can lead to a serious underestimation of diversity (e.g., DeVries *et al.* 1997; Summerville and Crist 2005), or even a completely erroneous comparison of diversity between habitat types (Tylianakis *et al.* in press).

Therefore, rather than considering diversity in only one point in time and space, we need to also consider the turnover in species (beta diversity) between habitats within the landscape and across time. The challenge of assessing diversity at multiple scales can be met by partitioning diversity between different levels of a nested spatial and/or temporal hierarchy, thereby determining the scale across which the highest beta diversity occurs. This multi-scale approach was used by Summerville *et al.* (2003) to evaluate lepidopteran diversity in temperate forests in Ohio, USA, and Tylianakis *et al.* (2005) to compare the contribution of different land use types to Hymenoptera diversity in coastal Ecuador. Although beta diversity is often lower in agricultural systems than within or across natural habitats (Clausnitzer 2003; Tylianakis *et al.* in press), species turnover between different patches of managed habitats can still make a significant contribution to regional biodiversity (Tscharntke *et al.* 2002; Tylianakis *et al.* in press). Nevertheless, beta diversity at all scales is lost as homogeneity due to management intensity increases, such that homogenous habitats have low turnover within fields, between fields across the landscape, and through time (Tylianakis *et al.* in press).

On the basis of the varied responses of taxa to the environment at different scales, conservation tactics aimed at only one scale, or based on information from studies conducted at only one scale may be misguided. Conservation policies should simultaneously target both the individual farm and landscape scales to maximise overall success (Östman *et al.* 2001; Stoner and Joern 2004; Tscharntke *et al.* 2005).

At the landscape scale, insect biodiversity can be supported by moderating the effects of fragmentation and habitat loss, for example, by increasing connectivity between habitat types, to facilitate dispersal between metapopulations (e.g., Steffan-Dewenter 2003) Additionally, although single large conservation areas are often advocated over several small areas, the spreading of several small fragments across a large geographic area may maximise beta diversity, as has been shown for butterflies and grasshoppers in calcareous grasslands (Tscharntke *et al.* 2002; Peintinger *et al.* 2003). Fragmentation effects may also be reduced by the availability of non-cultivated land within the landscape. For example, parasitoids of rape pollen beetles usually show higher densities near overwintering sites such as edge grassy strips, but these edge effects are overwhelmed by high overall densities of the parasitoids when a high percentage of non-crop area (> 20%) remains in the landscape (Tscharntke *et al.* 2002).

Despite the utility of maintaining non-crop habitat, landscape-scale conservation does not necessarily require large set-aside areas. The above example shows that insects may benefit from natural habitats; however, the resources provided by cultivated habitats may also be beneficial. For example, Westphal *et al.* (2003) found that bumblebee densities did not respond to the proportion of natural habitat, but rather to the availability of rich floral resources (oilseed rape) within the landscape.

The detrimental effects of homogenisation through landscape scale intensification can be offset by maximising the heterogeneity of the landscape by planting different crops, rather than monocropping over large areas. For example, landscape heterogeneity has been shown to be a good predictor of Collembola diversity (Chust *et al.* 2003) and to enhance the diversity of a variety of other insect taxa (Steffan-Dewenter *et al.* 2002; Dauber *et al.* 2003; Krauss *et al.* 2003; Kruess 2003).

The insurance hypothesis and sustainable landscape planning

In the recent debates on the relationship between biodiversity and ecosystem functioning (summarized in Hooper *et al.* 2005) biodiversity can affect ecosystem services in two ways. Firstly, the magnitude of ecosystem services, such as pollination or biological control, can be affected locally by diversity, mainly because species are complementary in their effects on ecosystem functioning. This idea has its roots in parts of classical niche theory and is based on the fact the species differ in their impacts on the environment (Chase and Leibold 2003) and on ecosystem properties. This effect has been examined in numerous studies of experimental grasslands (e.g. Hector *et al.* 1999).

Secondly, and from the agricultural landscape perspective more importantly, diversity can affect the temporal variability and magnitude of ecosystem services because species differ in their responses to environmental conditions, for example by having different reaction norms to resource levels or abiotic factors or differing in tolerance to such factors. Consequently, diverse ecosystems are expected to vary less, be more robust to external disturbances, and have a higher rate of ecosystem functioning when studied over time. The concept of the Hutchinsonian niche is more appropriate in this case (Chase and

Leibold 2003). The idea was termed the insurance hypothesis by Yachi and Loreau (1999). To separate the diversity in responses to the environment from diversity effects on ecosystem properties, Elmqvist *et al.* (2003) coined the term response diversity.

The effect of biodiversity on the magnitude of ecosystem services acts through mechanisms of local interactions, such as species sorting or positive interactions with mycorrhiza. However, most ecosystems, in particular agro-ecosystems, are subject to disturbances and environmental variation acting at varying spatial and temporal scales, from local management of fields to climate change (Holling *et al.* 1996; Bengtsson *et al.* 2003). Recovery and reorganisation of biodiversity and ecosystem functioning (termed resilience by e.g. Gunderson 2000) after such disturbances require a species pool at the landscape level from which species can recolonize, emphasising the role of species dispersal and landscape structure for the stability, and ultimately also magnitude, of ecosystem services. The insurance hypothesis can have both a temporal aspect, as environmental conditions vary locally, and a spatial aspect when local patches are subjected to disturbances. It explicitly takes the interplay between local and regional landscape-level processes into account (Nyström and Folke 2001; Loreau *et al.* 2003). In a heterogenous mosaic landscape, species with different traits, tolerances and optimum requirements thrive in patches with different environmental conditions, ensuring that there will be at least some species available in source areas for recolonization after disturbances, and that species with optimum performance can more easily colonize patches of different quality (Bengtsson *et al.* 2003).

The theoretical background for the insurance hypothesis is, on one hand, island biogeography, metapopulation and metacommunity theory (see e.g. Leibold *et al.* 2004), and on the other hand theories for dynamic ecosystems (e.g. Holling *et al.* 1996; Norberg *et al.* 2001; Bengtsson *et al.* 2003). There is considerable theoretical support for it (Yachi and Loreau 1999; Norberg *et al.* 2001; Loreau *et al.* 2003), but it is intrinsically difficult to test explicitly, especially on the large spatial scale where it is likely to be most important for ecosystem services and society. The finding that mosaic agricultural landscapes, with a larger proportion of semi-natural areas, sustain higher levels of diversity in several organism groups (see e.g. Tscharntke *et al.* 2005) provides empirical support for one of its basic components. Experimental studies of the effects of spatial structure and landscape connectivity for diversity and biomass (Gonzales and Chaneton 2002) are also suggestive. On larger scales, Nyström and Folke (2001) highlighted the importance of source areas in the landscape for ecosystem or community recovery. Recent studies showing that seminatural habitats enhance the ecosystem service of coffee pollination (Klein *et al.* 2003b; Ricketts *et al.* 2004) imply that diversity on the landscape scale provides better ecosystem services to society. However, stringent tests of the insurance hypothesis need to vary local and regional diversity in landscapes of different structure in terms of, for example, connectivity and availability of natural habitats, and measure both diversity and the magnitude of ecosystem services over time, as environmental conditions vary and disturbances are allowed to occur. A daunting task, but cleverly designed studies of agro-ecosystems can be good candidates for observational tests of the insurance hypothesis.

Irrespective of whether we can provide hard experimental evidence for the insurance hypothesis, the fact that diversity in agricultural habitats often depends on landscape structure (see above; Tscharntke *et al.* 2005) as well as on local conditions, has implications for the maintenance of diversity and ecosystem services in agro-ecosystems. There are, as stated above, good reasons to believe that maintaining landscape mosaics with different disturbance regimes and successional stages, will contribute to biodiversity and a less variable delivery of ecosystem services, such as biological control or pollination. This is especially important in the face of climate change where the dispersal rates of species will determine how quickly ecosystems can respond. A low landscape diversity entails a small species pool and less genetic variation for adapting to new environmental conditions.

Agri-environment schemes at a landscape scale and political options

Agri-environment schemes are one of the most important political and nature conservation instruments to safeguard or promote wildlife in agricultural landscapes (EEA 2004). They stimulate farmers to adopt more environmentally friendly farming practices and compensate them for any loss of income associated with scheme implementation. Conservation measures usually consist of a reduction or cessation of the use of agro-chemicals and/or a reduction in stocking rates (Kleijn and Sutherland 2003) but may also include the establishment and maintenance of landscape features such as ponds and hedges.

The conservation of insects or specific insect groups is rarely mentioned specifically as an objective of agri-environment schemes. Many schemes aim to conserve biodiversity in general, however, and the class of insects is one of the most diverse taxa contributing to biodiversity in general. A considerable number of studies have examined the response of insects to agri-environment schemes (Kleijn and Sutherland 2003). Uncropped wildlife strips in the United Kingdom had positive effects on the species richness of carabid beetles and Heteroptera in cereal fields (Hassall *et al.* 1992). Schemes reducing stocking rates resulted in higher species richness of Auchenorrhyncha, Heteroptera, Coleoptera and Hymenoptera Parasitica in grasslands in northern Germany (Kruess and Tscharntke 2002). Dutch management agreements reducing agrochemical applications and delaying the first seasonal agricultural activities in wet grasslands were found to have positive effects on species richness of bees and hover flies (Kleijn *et al.* 2001). Implementation of the English Environmentally Sensitive Area Scheme and the Countryside Stewardship Scheme led to positive population trends in habitat specialist butterflies (Brereton *et al.* 2002). The positive effects of a wide variety of schemes on wide range of insect species groups suggest that insects in agricultural landscapes may be conserved easily and rapidly by means of agri-environment schemes.

Organic farming, being one of the more important agri-environment schemes in Europe, has mixed but mainly positive effects on diversity and density of insects (Bengtsson *et al.* 2005). In a literature review, predatory arthropods generally increased in diversity and density in organic farming systems, while the responses of non-predatory insects were more heterogeneous and on average not different from neutral (Bengtsson *et al.* 2005). The effects for arthropods were significantly positive on the smaller “field” and “plot” scales, but non-significant and highly heterogeneous on the farm scale (meta-analysis calculated from the arthropod subset of the data in Bengtsson *et al.* 2005, Appendices). Several recent studies show positive effects of organic farming on arthropod diversity or density (e.g. Kremen *et al.* 2002, Hutton and Giller 2003, Schmidt *et al.* 2005), but there are also exceptions for one or both variables (e.g. Purtauf *et al.* 2005). A common conclusion is that organic farming is less important for diversity than landscape factors.

This highlights the problem of how to design agri-environmental schemes when the effects are likely to vary according to the heterogeneity of the landscape (Bengtsson *et al.* 2005, Tscharntke *et al.* 2005).

Most studies examining the response of insects to changes in farm management were conducted at small spatial scales, usually comparing fields with different types of management. Furthermore, virtually all studies examined responses of adult individuals. Since adults of many groups of insects are mobile, it is often impossible to determine with certainty whether the observed response is caused by an increase in population size or due to a foraging response resulting in a concentration of individuals in resource-rich patches in the landscape. An enhanced reproduction rate of insects on scheme fields relative to conventionally managed fields would be a clear indication that schemes have positive effects on population size. Only Gardener *et al.* (2001) examined effects of agri-environment schemes on juvenile insects. They found no significant differences in the densities of carabid beetle larvae on fields with and without agri-environment schemes.

Considering the importance of landscape context for insect species richness (Duelli and Obrist 2003, Steffan-Dewenter *et al.* 2002, Kleijn and van Langevelde 2006), surprisingly little is known on whether the effects of agri-environment schemes depend on the structure of the surrounding landscape. Peter and Walter (2001) observed a positive effect of Swiss agri-environment schemes on the species richness of grasshoppers that was partially explained by distance from nature reserves. In the Netherlands, landscape structure did affect species richness of both bees and hoverflies but the effects of schemes did not depend on landscape context (Kleijn *et al.* 2004). Summarizing the scant literature on the topic, Tscharntke *et al.* (2005) hypothesized that conservation measures on farmland are most effective in landscapes with intermediate complexity (Fig. 2.3). Very simple landscapes may be devoid of potential colonizers of scheme fields whereas very complex landscapes support overall high levels of species richness resulting in a continuous colonization from the surrounding landscape of even the most intensively farmed fields.

Despite the generally positive effects of agri-environment schemes on insects in general, they rarely promote endangered insect species. This is largely because contemporary farmland, with or without schemes, rarely hosts Red Data Book species (Kleijn *et al.*

submitted). Originally, a wide range of endangered insect species occurred in various types of agricultural habitats such as low productive grasslands and arable fields or extensively managed vineyards and orchards. Due to agricultural intensification, this type of habitat has disappeared from north-western European farmland long before the introduction of the first agri-environment schemes and these habitats are now almost exclusively restricted to nature reserves. Consequently, most endangered insect species have already disappeared from agricultural areas and are now restricted to nature reserves. Red Data Book species may therefore only be able to benefit from agri-environment schemes if schemes are implemented within colonizing distance of the refuges of these species (e.g. see Peter and Walter 2001). In any case, agri-environment schemes may prevent more common species from becoming endangered in the near future.

In conclusion, most contemporary agri-environment schemes and particularly those implemented in landscapes with intermediate complexity, promote richness of common insect species thereby enhancing general biodiversity. This is a promising result since a more abundant and species-rich insect community may provide better ecosystem services such as pollination or pest control (Steffan-Dewenter and Tscharntke 1999, but see Wilby and Thomas 2002). On the other hand, the majority of agri-environment schemes fail to conserve the species that are most threatened by modern farming practices, usually because they are implemented in the wrong locations. It may therefore be prudent to differentiate the objectives of agri-environment schemes aimed at biodiversity conservation into schemes aimed to increase functional biodiversity and schemes aimed at the conservation of rare species. Schemes aimed to increase functional biodiversity may then be implemented throughout the countryside and with little regard for the initial quality of surrounding area. Schemes aimed to conserve endangered species should only be implemented in or near areas still hosting the target species.

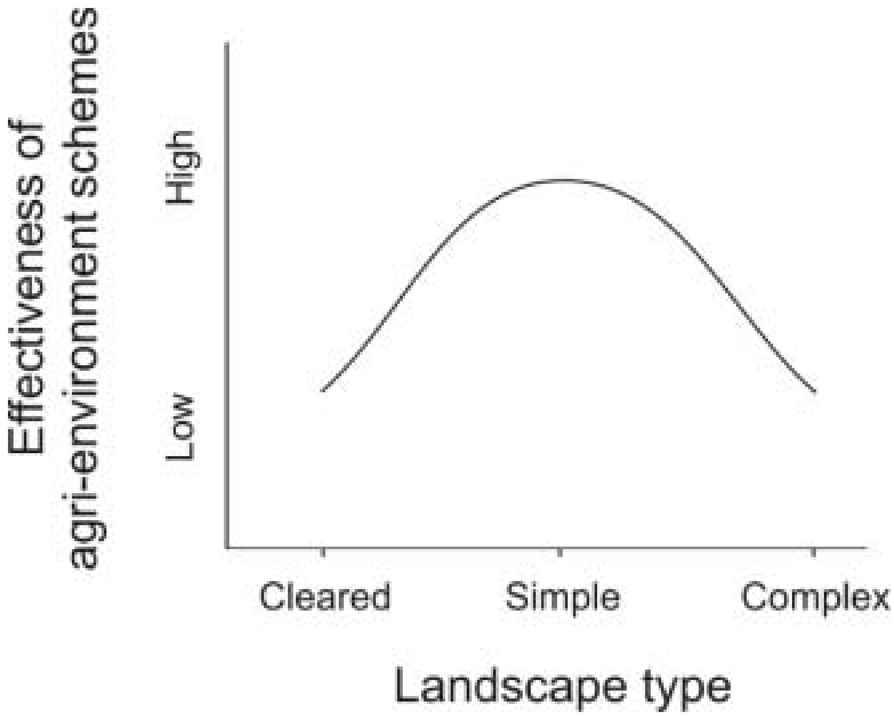


Figure 2.3. Effectiveness of agri-environment schemes in relation to landscape type. Effectiveness is measured as biodiversity enhancement due to management, such as the conversion from conventional to organic farming (Roschewitz *et al.* 2005) or the creation of crop field-boundaries (Thies and Tscharntke 1999, Tscharntke *et al.* 2002), compared to unmanaged control sites. Landscape type is classified as cleared (minimum diversity, < 1% non-crop habitat), simple (low diversity, 1-20% noncrop habitat) and complex (high diversity, > 20% noncrop habitat; see Andrén 1994, Tscharntke *et al.* 2002). The resulting hump-shaped relationship results from the different source pools in the surrounding landscape for recolonisation of managed habitat. In cleared landscapes, the very few species are not a sufficient basis to result in a recognizable response to management changes. Similarly, in complex landscapes, management does not result in a significant effect, because biodiversity is high everywhere. In contrast, simple landscapes support intermediate species pools that allow a significant response to management. (Illustration with permission from Tscharntke *et al.* 2005).

Conclusions and implications for conservation in agricultural landscapes

Planning for future sustainable landscapes requires that several aspects of today's approach to conservation are modified, to incorporate the recent advances in spatial ecology and ecosystem dynamics. Although individual farmers always play a key role in conservation, incentive structures need to be targeted to ensure that diversity is maintained or improved at the larger landscape (regional) level. Some basic propositions for the new landscape approach to rural planning are:

1. Fields and small management units should not be used as a basic unit for conservation, but at least whole farms and preferably whole landscapes. A problem is that different organisms will respond to landscape structure at different spatial scales (Tscharntke *et al.* 2005), but whole landscapes can be ”managed” taking this into account by imposing a variety of disturbances and management regimes, rather than single ones. Encouraging farmers to diversify and vary their land use is one way through which this may be accomplished.
2. Natural, seminatural and semipermanent managed areas allow many species to persist in the agricultural landscape, and should thus be the focus of most conservation efforts (Swift *et al.* 2004). The conservation of semi-natural and natural areas will most likely enhance ecosystem services in intensely managed fields (Thies and Tscharntke 1999; Östman *et al.* 2001; Klein *et al.* 2003; Ricketts *et al.* 2004).
3. Many current farming methods, especially organic or integrated farming, rely on species in less intensively managed ecosystems for biological control of pests, pollination of many crops, decomposition, etc. Recent discussions on the limits of oil reserves and increased oil prices imply that costs for agricultural inputs will increase. This means that in a future scenario where energy costs have increased dramatically, food production and security will rely more on natural ecosystem services. Hence, as an insurance against such a scenario, agricultural policies should strive to maintain and restore biodiversity in agricultural landscapes.

Agricultural systems may therefore harbour a significant diversity of insect species that can offer many services to landowners. In order for such ecosystem services to be maximised, and sustained in the future, action must be taken by landowners and policy makers. This action needs to consider the effects of management at different spatial and temporal scales, and the identity (and potential utility) of the species concerned.

Acknowledgements

Financial support for TT and JMT came from the German Research Foundation (Deutsche Forschungsgemeinschaft, DFG), the German Ministry for Research and Education (Bundesministerium für Bildung und Forschung, BMBF; BIOTEAM and BIOLOG program), and the EU project EASY.

References

Andrén, H. (1994) Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355-366.

Armbrecht, I. and Perfecto, I. (2003) Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighbouring coffee plantations of contrasting habitat quality in Mexico. *Agriculture, Ecosystems and Environment* 97, 107-115.

Asteraki, E.J., Hart, B.J., Ings, T.C. and Manley, W.J. (2004) Factors influencing the plant and invertebrate diversity of arable field margins. *Agriculture, Ecosystems and Environment* 102, 219-231.

Bambaradeniya, C.N.B., Edirisinghe, J.P., De Silva, D.N., Gunatilleke, C.V.S., Ranawana, K.B. and Wijekoon, S. (2004) Biodiversity associated with an irrigated rice agro-ecosystem in Sri Lanka. *Biodiversity and Conservation* 13, 1715-1753.

Banks, J.E. (2004) Divided culture: integrating conservation biology and agriculture. *Frontiers in Ecology and the Environment* 2, 537-545.

Bengtsson, J., Ahnström., J. and Weibull, A. C. (2005) The effects of organic agriculture on biodiversity and abundance: a meta-analysis. *Journal of Applied Ecology* 42, 261-269.

Bengtsson, J., Angelstam, P., Elmqvist, T., Emanuelsson, U., Forbes, C., Ihse, M., Moberg, F. and Nyström, M. (2003) Reserves, resilience and dynamic landscapes. *Ambio* 32, 389-396.

Berndt, L.A., Wratten, S.D. and Hassan, P.G. (2002) Effects of buckwheat flowers on leafroller (Lepidoptera: Tortricidae) parasitoids in a New Zealand vineyard. *Agricultural and Forest Entomology* 4, 39-45.

Berndt, L.A. and Wratten, S.D. (2005) Effects of alyssum flowers on the longevity, fecundity and sex ratio of the leafroller parasitoid *Dolichogenidea tasmanica*. *Biological Control* 32, 65-69.

Borges, P.A.V. and Brown, V.K. (2004) Arthropod community structure in pastures of an island archipelago (Azores): looking for local-regional species richness patterns at fine-scales. *Bulletin of Entomological Research* 94, 111-121.

Bowie, M.H. and Frampton, C.M., (2004) A practical technique for non-destructive monitoring of soil surface invertebrates for ecological restoration programmes. *Ecological Management and Restoration* 5, 34-42.

Brereton,T., Stewart, K.S. and Warren, M.S. (2002) *Developing a system for assessing the effect of agri-environment schemes on butterfly populations*. Report to Department of Farming and Rural Affairs.

Cameron, P.J., Powell, W. and Loxdale, H.D. (1984) Reservoirs for *Aphidius ervi* Haliday (Hymenoptera: Aphidiidae) a polyphagous parasitoid of cereal aphids (Hemiptera: Aphididae). Bulletin of Entomological Research, 74, 647-656.

Cane, J.H. (2001) Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology* 5, 3 [WWW document] URL:http://www.consecol.org/vol5/iss1/art3

Chase, J. and Leibold, M. (2003) Ecological niches. Linking classical and contemporary approaches. University of Chicago Press, Chicago, IL.

Chust, G., Pretus, J.L., Ducrot, D. and Ventura, D. (2004) Scale dependency of insect assemblages in response to landscape pattern. *Landscape Ecology* 19, 41-57.

Clausnitzer, V. (2003) Dragonfly communities in coastal habitats of Kenya: indication of biotype quality and the need of conservation measures. *Biodiversity and Conservation* 12, 333-356.

Collins, J.K., Cuperus, G.W., Cartwright, B., Stark, J.A. and Ebro, L.L. (1992) Consumer attitudes on pesticide treatment histories of fresh produce. *Journal of Sustainable Agriculture* 3, 81-98.

Costanza, R., d'Arge, R., de Groot, R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. and van den Belt, M.,

(1997) The value of the world's ecosystem services and natural capital. *Nature* 387, 253-260.

Cunningham, S.A., Floyd, R.B. and Weir, T.A. (2005) Do Eucalyptus plantations host an insect community similar to remnant Eucalyptus forest? *Austral Ecology* 30, 103-117.

Daily, G.C. (1997) *Nature's Services: Social dependence on natural ecosystems*. Island Press, Washington, DC. USA.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt. R,, Otte. A, and Wolters. V. (2003) Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture Ecosystems and Environment* 98, 321-329.

DeVries, P.J., Murray, D. and Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnaean Society* 62, 343-364.

DeVries, P.J. and Walla, T.R. (2001) Species diversity and community structure in neotropical fruit-feeding butterflies. *Biological Journal of the Linnaean Society* 74, 1-15.

Di Giulio, M., Edwards, P.J. and Meister, E. (2001) Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. *Journal of Applied Ecology* 38, 310-319.

Duelli, P. and Obrist, M.K. (2003) Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. *Basic and Applied Ecology* 4, 129-138.

Dyer, L.E. and Landis, D.A. (1997) Influence of noncrop habitats on the distribution of *Eriborus tenebrans* (Hymenoptera: Ichneumonidae) in cornfields. *Environmental Entomology* 26, 924-932.

EEA (2004) *High Nature Value Farmland - Characteristics, Trends and Policy Challenges*. European Environment Agency, Copenhagen

Elmqvist, T., Folke, C., Nyström, M., Peterson, G., Bengtsson, J., Walker, B. and Norberg, J. (2003) Response diversity, ecosystem change, and resilience. *Frontiers in Ecology and the Environment* 1, 488-494.

Fry, G. (1995) Landscape ecology of insect movement in arable ecosystems. In: Glen, D.M., Greaves, M.P. and Anderson, H.M. (eds) *Ecology and Integrated Farming Systems* Wiley: Chichester, England pp. 177-202.

Gardener, S.M., Allen, D.S., Gundrey, A.L., Luff, M.L. and Mole, A.C. (2001) *Ground Beetles*. Technical appendix to ecological evaluation of the arable stewardship pilot scheme 1998–2000. ADAS, Wolverhampton, UK.

Gaston, K.J. and Spicer, J.I. (2004) *Biodiversity. An Introduction*. Blackwell Publishing, Oxford, UK.

Gathmann, A., Greiler, H.-J., Tscharntke, T. (1994) Trap-nesting bees and wasps colonizing set-aside fields: Succession and body size, management by cutting and sowing. *Oecologia* 98, 8-14.

Gonzales, A. and Chaneton, E.J. (2002) Heterotroph species extinction, abundance and biomass dynamics in an experimentally fragmented ecosystem. *Journal of Animal Ecology* 71, 594-602.

Gunderson, L. (2000) Ecological resilience – in theory and application. *Annual Review of Ecology and Systematics* 31, 425-439.

Gurr, G.M., Wratten, S.D. and Altieri, M.A. (eds.) (2004) *Ecological Engineering for Pest Management: Advances in Habitat Manipulation for Arthropods*. CSIRO Publishing: Melbourne, Australia.

Gurr, G.M., Wratten, S.D. and Luna, J.M. (2003) Multi-function agricultural biodiversity: pest management and other benefits. *Basic and Applied Ecology* 4, 107-116.

Hassall, M., Hawthorne, A., Maudsley, M., White, P. and Cardwell, C. (1992) Effects of headland management on invertebrate communities in cereal fields. *Agriculture, Ecosystems and Environment* 40, 155-178.

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., Schulze, E.D., Siamantziouras, A.S.D., Spehn, E.M., Terry, A.C., Troumbis, A.Y., Woodward, F.I., Yachi, S. and Lawton, J.H. (1999) Plant diversity and productivity experiments in European grasslands. *Science* 286, 1123-1127.

Holland, J. and Fahrig, L. (2000) Effect of woody borders on insect density and diversity in crop fields: a landscape-scale analysis. *Agriculture, Ecosystems and Environment* 78, 115-122.

Holling, C.S., Schindler, D.W., Walker, B.W. and Roughgarden, J. (1995) Biodiversity in the functioning of ecosystems: an ecological synthesis. In: Perrings, C. A., Mäler, K. G., Folke, C., Holling, C. S. and Jansson, B. O. (eds) *Biodiversity loss. Economic and ecological issues*. Cambridge University Press, Cambridge, UK, pp. 44-83.

Holt, A.R. and Gaston, K.J. (2002) Occupancy-abundance relationships and spatial distribution: a review. *Basic and Applied Ecology* 3, 1-13.

Hooper, D.U. Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. and Wardle, D.A. (2005) Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75, 3-35.

Hutton, S.A. and Giller, P.S. (2003) The effects of the intensification of agriculture on northern temperate dung beetle communities. *Journal of Applied Ecology* 40, 994-1007.

Jonsen, I.D. and Fahrig, L. (1997) Response of generalist and specialist insect herbivores to landscape spatial structure. *Landscape Ecology* 12, 185-197.

Klein, A.-M., Steffan-Dewenter, I., Buchori, D. and Tscharntke, T. (2002) Effects of land use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conservation Biology* 16, 1003-1014.

Klein, A.-M., Steffan-Dewenter, I. and Tscharntke, T. (2003a) Fruit set of highland coffee depends on the diversity of pollinating bees. *Proceedings of the Royal Society of London, B* 270, 955-961.

Klein, A.-M., Steffan-Dewenter, I. and Tscharntke, T. (2003b) Flower visitation and fruit set of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology* 40, 837-845.

Kleijn, D., Berendse, F., Smit, R. and Gilissen. N. (2001) Agri-environment schemes do not effectively protect biodiversity in Dutch agricultural landscapes. *Nature* 413, 723-725.

Kleijn, D., Berendse, F., Smit, R., Gilissen, N., Smit, J., Brak, B. and Groeneveld, R. (2004) The ecological effectiveness of agri-environment schemes in different agricultural landscapes in The Netherlands. *Conservation Biology* 18, 775-786.

Kleijn, D. and Sutherland, W.J. (2003) How effective are European agri-environment schemes in conserving and promoting biodiversity? *Journal of Applied Ecology* 40, 947-969.

Kleijn, D. and van Langevelde, F. (2006) Interacting effects of landscape context and habitat quality on flower-visiting insects in agricultural landscapes. *Basic and Applied Ecology* (in press)

Krauss, J., Steffan-Dewenter, I. and Tscharntke, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography* 30, 889-900.

Kremen, C. (2005) Managing ecosystem services: what do we need to know about their ecology. *Ecology Letters* 8, 468-479.

Kremen, C., Williams, N.M. and Thorp, R.W. (2002) Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences, USA* 99, 16821-16816.

Kruess, A. (2003) Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. *Ecography* 26, 283-290.

Kruess, A. and Tscharntke, T. (2002) Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation* 106, 293-302.

Landis, D.A., Wratten, S.D. and Gurr, G.M. (2000) Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology* 45,175-202.

Lawton, J.H., Bignell D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D. (1998) Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature* 391, 72-76.

Lee, J.C., Heimpel, G.E.. (2005) Impact of flowering buckwheat on Lepidopteran cabbage pests and their parasitoids at two spatial scales. *Biological Control* 34, 290-301.

Leibold, M.S. Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M. and Gonzalez, A. (2004) The metacommunity concept : a framework for multi-scale community ecology. *Ecology Letters* 7, 601-613.

Loreau, M., Mouquet, N. and Gonzales, A. (2003) Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences, USA* 100, 12765-12770.

Maeto, K., Sato, S. and Miyata, H. (2002) Species diversity of longicorn beetles in humid warm-temperate forests: the impact of forest management practices on old-growth forest species in southwestern Japan. *Biodiversity and Conservation* 11, 1919-1937.

Marshall, E.J.P., Brown, V.K., Boatman, N.D., Lutman, P.J.W., Squire, G.R. and Ward, L.K. (2003) The role of weeds in supporting biological diversity within crop fields. *Weed Research* 43, 77-89.

Mas, A.H. and Dietsch, T.V. (2003) An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. *Ecological Applications* 13, 1491-1501.

Morandin, L.A. and Winston, M.L. (2005) Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecological Applications* 15, 871-881.

Norberg, J., Swaney, D.P., Dushoff, J., Lin, J., Casafgrandi, R. and Levin, S.A. (2001) Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. *Proceedings of the National Academy of Sciences, USA* 98, 11376-11381.

Novacek, M.J. and Cleland, E.E. (2001) The current biodiversity extinction event: Scenarios for mitigation and recovery. *Proceedings of the National Academy of Sciences, USA* 98: 5466-5470.

Nyström, M. and Folke, C. (2001) Disturbance and the spatial resilience of coral reefs. *Ecosystems* 4, 406-417.

Östman, O., Ekbom, B., Bengtsson, J. and Weibull, A.C. (2001) Landscape complexity and farming practice influence the condition of polyphagous carabid beetles. *Ecological Applications* 11, 480-488.

Östman, Ö., Ekbom, B. and Bengtsson, J. (2003) Yield increase attributable to aphid predation by ground-living polyphagous natural enemies in spring barley in Sweden. *Ecological Economics* 45, 149-158.

Paoletti, M.G. and Pimentel, D. (2000) Environmental risks of pesticides versus genetic engineering for agricultural pest control. *Journal of Agricultural and Environmental Ethics* 12, 279-303.

Peintinger, M., Bergamini, A. and Schmid, B. (2003) Species-area relationships and nestedness of four taxonomic groups in fragmented wetlands. *Basic and Applied Ecology* 4, 385-394.

Perfecto, I. & Armbrecht, I. (2003) The coffee agroecosystems in the Neotropics: combining ecological and economic goals. In: *Tropical Agroecosystems* (eds Vandermeer, J.H.). CRC Press, Boca Raton, USA, pp. 159-194.

Perfecto, I., Rice, R., Greenberg, R. and van der Volt, M. (1996) Shade coffee as refuge of biodiversity. *Bioscience* 46, 598-608.

Peter, B. and Walter, T. (2001) Heuschrecken brauchen ökologische Ausgleichsflächen. *Agrarforschung* 8, 452-457.

Pimentel, D., Stachow, U., Takacs, A., Brubaker, W., Dumas, A.R., Meaney, J.S., O'Neil, J.A.S., Onsi, D.E. and Corzilius, D.B. (1992) Conserving biological diversity in agricultural/forestry systems. *Bioscience* 432, 354-362.

Potts, R.W. and Vickerman, G.P. (1974) Studies on the cereal ecosystem. *Advances in Ecological Research* 8,107-197.

Purtauf, T., Roschewitz, I., Dauber, J., Thies, C., Tscharntke, T., Wolters, V. (2005): Landscape context of organic and conventional farms: Influences on carabid beetle diversity. *Agriculture, Ecosystems and Environment*, 108, 165-174.

Ribas, C.R., Sobrinho, T.G., Schroereder, J.H., Sperber, C.F., Lopes-Andrade, C. and Soares, S.M. (2005) How large is large enough for insects? Forest fragmentation effects at three spatial scales. *Acta Oecologica* 27, 31-41.

Rice, R.A. and Greenberg, R. (2000) Cacao cultivation and the conservation of biological diversity. *Ambio* 29, 167-173.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. and Michener, C.D. (2004) Economic value of tropical forest to coffee production. *Proceedings of the National Academy of Sciences USA* 101, 12579-12582.

Robinson, R.A. and Sutherland, W.J. (2002) Post-war changes in arable farming and biodiversity in Great Britain. *Journal of Applied Ecology* 39,157-176.

Room, P.M. (1979) Parasites and predators of *Heliothis* spp. (Lepidoptera: Noctuidae) in cotton in the Namoi Valley, New South Wales. *Journal of the Australian Entomological Society* 18, 223-228.

Roschewitz, I., Gabriel, D., Tscharntke, T. and Thies, C. (2005) Contrasting effects of landscape complexity on arable weed diversity in organic and conventional farming. *Journal of Applied Ecology* 42, 873-882.

Schmidt, M.H., Roschewitz, I., Thies, C. and Tscharntke, T. (2005) Differential effects of landscape and management on diversity and density of ground-dwelling farmland spiders, *Journal of Applied Ecology* 42, 281-287.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. and Tscharntke, T. (2004) Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications* 14, 1321-1333.

Shahabuddin, Schulze, C.H. and Tscharntke, T. (2005) Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia) *Biodiversity and Conservation* 14, 863-877.

Sinclair, A.R.E., Mduma, S.A.R. and Arcese, P. (2002) Protected areas as biodiversity benchmarks for human impact: agriculture and the Serengeti avifauna. *Proceedings of the Royal Society of London B*, 269, 2401-2405.

Sperber, C.F., Nakayama, K., Valverde, M.J. and Neves, F.D. (2004) Tree species richness and density affect parasitoid diversity in cacao agroforestry. *Basic and Applied Ecology* 5, 241-251.

Stamps, W.T. and Linit, M.J. (1997) Plant diversity and arthropod communities: Implications for temperate agroforestry. *Agroforestry Systems* 39, 73-89.

Steffan-Dewenter, I. (2003) Importance of habitat area and landscape context for species richness of bees and wasps in fragmented orchard meadows. *Conservation Biology* 17, 1036-1044.

Steffan-Dewenter, I. and Leschke, K. (2003) Effects of habitat management on vegetation and above-ground nesting bees and wasps of orchard meadows in Central Europe. *Biodiversity and Conservation* 12, 1953-1968.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. and Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* 83, 1421-1432.

Steffan-Dewenter, I. and Tscharntke, T. (1999) Effects of habitat isolation on pollinator communities and seed set. *Oecologia* 121, 432-440.

Stoner, K.J.L. and Joern, A. (2004) Landscape vs. local habitat scale influences to insect communities from tallgrass prairie remnants. *Ecological Applications* 14, 1306-1320.

Summerville, K.S., Boulware, M.J., Veech, J.A. and Crist, T.O. (2003) Spatial variation in species diversity and composition of forest Lepidoptera in eastern deciduous forests of North America. *Conservation Biology* 17, 1045-1057.

Summerville, K.S. and Crist, T.O. (2004) Constrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography* 27:, 3-12.

Summerville, K.S. and Crist, T.O. (2005) Temporal patterns of species accumulation in a survey of Lepidoptera in a beech-maple forest. *Biodiversity and Conservation* (in press).

Swift, M.J. and Anderson, J.M. (1993) Biodiversity and ecosystem function in agricultural systems. In: Schulze, E. D. and Mooney, H. A . (eds) *Biodiversity and ecosystem function* Springer Verlag, Berlin, Germany, pp. 15-41.

Swift, M.J., Izac, A.M.N. and van Noordwijk, M. (2004) Biodiversity and ecosystem services in agricultural landscapes – are we asking the right questions? *Agriculture, Ecosystems and Environment* 104, 113-134.

Thies, C. and Tscharntke, T. (1999) Landscape structure and biological control in agroecosystems. *Science* 285, 893-95.

Thomas, S.R., Goulson, D. and Holland, J.M. (2001) Resource provision for farmland gamebirds: the value of beetle banks. *Annals of Applied Biology* 139,111-118.

Thomas, M.B., Wratten, S.D. and Sotherton, N.W. (1991) Creation of island habitats in farmland to manipulate populations of beneficial arthropods - predator densities and emigration. *Journal of Applied Ecology* 28, 906-917.

Tilman, D., Cassman, K.G., Matson, P.A., Naylor, R. and Polasky, S. (2002) Agricultural sustainability and intensive production practices. *Nature* 418, 671-677.

Tscharntke, T. and Brandl, R. (2004) Plant-insect interactions in fragmented landscapes. *Annual Review of Entomology* 49, 405-430.

Tscharntke, T., Gathmann, A., Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology* 35, 708-719.

Tscharntke, T., Klein, A.-M., Kruess, A., Steffan-Dewenter, I and Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters* 8, 857-874.

Tscharntke, T., Steffan-Dewenter, I., Kruess, A. and Thies, C. (2002) Contribution of small habitat fragments to conservation of insect communities of grassland-cropland landscapes. *Ecological Applications*, 12, 354-363.

Tylianakis, J., Didham, R. and Wratten, S.D. (2004) Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology* 85, 658-666.

Tylianakis, J.M., Klein, A.-M. and Tscharntke, T. (in press) Spatiotemporal variation in the effects of a tropical habitat gradient on Hymenoptera diversity. *Ecology.*

Veddeler, D., Klein, A.M., Tscharntke, T. (2005) Contrasting responses of bee communities to coffee flowering at different spatial scales. *Oikos* (in press)

Westphal, C., Steffan-Dewenter, I. and Tscharntke, T. (2003) Mass flowering crops enhance pollinator densities at a landscape scale. *Ecology Letters* 6, 961-965.

Whitcomb, W.H. and Bell, K. (1964) *Predaceous insects, spiders, and mites of Arkansas cotton fields. Agricultural Experiment Station, University of Arkansas.* Division of Agriculture, Fayetteville, Bulletin 690, 84 pp.

Wickramasinghe, L.P., Harris, S., Jones, G. and Jennings, N.V. (2004) Abundance and species richness of nocturnal insects on organic and conventional farms: Effects of agricultural intensification on bat foraging. *Conservation Biology* 18, 1283-1292.

Wilby, A. and Thomas, M.B. (2002) Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecology Letters*, 5, 353-360.

Wissinger, S.A. (1997) Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biological Control* 10, 4-15.

Wolda, H. (1978) Seasonal fluctuations in rainfall, food and abundance in tropical insects. *Journal of Animal Ecology* 47, 369-81.

Wolda, H. (1988) Insect seasonality: why? *Annual Review of Ecology and Systematics,* 19, 1-18.

Yachi, S. and Loreau, M. (1999) Biodiversity and ecosystem productivity in a fluctuating environment: The insurance hypothesis. *Proceedings of the National Academy of Sciences, USA* 96, 1463-1468.

Chapter 3

Soil heterogeneity promotes a bottom-up tropical biodiversity cascade of plants, insects and their natural enemies

J. M. Tylianakis, M. López-Ulloa, T. Lozada, E. Veldkamp, G.H.J. de Koning,
R. Olschewski A.-M. Klein, and T. Tscharntke

Abstract

Heterogenous distributions of resources such as soil chemicals may reduce competition, thereby promoting species diversity of higher plants, and studies have shown that high plant or structural resource diversity can lead to high insect diversity. Therefore, it may be inferred that diversity of soil chemicals could promote plant diversity, which could in turn promote insect diversity; however such a pattern across several trophic levels has not yet been demonstrated in practice for a terrestrial system. Here we show for the first time that high soil heterogeneity (specifically variability in magnesium concentrations) leads to a domino effect of increased diversity across three trophic levels (herbaceous plants, cavity-nesting bees and wasps, and their natural enemies). The robustness of this bottom-up diversity cascade is strengthened by its consistency across three different habitat types, comprising a gradient of increasing anthropogenic disturbance in a tropical landscape in Southwest Ecuador. We show that beta diversity of herbs explains more variation in bee and wasp diversity than does herb species richness. However, natural enemy species richness was only correlated with bee and wasp richness, not beta diversity. Biodiversity of varied taxa may therefore be enhanced in managed systems by maintaining high habitat heterogeneity, and perturbations at one trophic level may have repercussions across the entire community.

Introduction

Anthropogenic modification of habitats alters entire landscapes and is largely responsible for the current global decline in biodiversity (Vitousek *et al.* 1997; Foley *et al.* 2005). An understanding of the direct and indirect effects of land use changes on diversity is necessary to mitigate this decline and guide conservation initiatives that incorporate managed land (Tscharntke *et al.* 2005). However, many studies examine the effects of habitat modification on different taxonomic groups in isolation, neglecting the effects of organisms on their adjacent trophic levels. For example, studies have often considered the effects of habitat modification on the diversity of plants (e.g., Tilman & Lehman 2001) or insects (e.g., Shahabuddin *et al.* 2005; Tylianakis *et al.* in press). Nevertheless, the effects of land use changes on the diversity of these species may have indirect consequences for the diversity of other species within the system, and the effects of habitat modification are seldom examined across multiple taxa (for exceptions see Lawton *et al.* 1998; Schulze *et al.* 2004).

The basis for the assumption that diversity at one level may propagate diversity at higher levels rests on the concept of resource-based niches (McKane *et al.* 2002). Diversity or heterogeneity of a limiting resource should provide a larger array of different niches, thereby promoting diversity in heterogenous habitats (e.g., Kassen *et al.* 2000; Benton *et al.* 2003). Indeed, the diversity of insect groups has previously been shown to be affected by plant or structural resource diversity (Murdoch *et al.* 1972; Siemann *et al.* 1998; Steffan-Dewenter & Tscharntke 2001; Potts *et al.* 2003; Ambrecht *et al.* 2004). However, the effect of resource heterogeneity on plant diversity is less clear. Stevens & Carson (2002) found that high light intensity, rather than heterogeneity maintains high plant diversity. At a large scale, based on satellite images, soil heterogeneity has been correlated with floristic similarity, but not diversity (Tuomisto *et al.* 2003), and another study (McMaster 2005) found that diversity of soil types explained vascular plant diversity on offshore islands, although this was partly confounded by island area. The effects of soil heterogeneity on plant diversity at smaller-scales, over which interspecific interactions and competitive exclusion can occur, have also produced mixed results. Previous studies have shown that small-scale heterogeneity in soils can be positively

(Fitter 1982; Lundholm & Larson 2003; Baer *et al.* 2005), negatively (Kleb & Wilson 1997) or not correlated (Wijesinghe *et al.* 2005) with plant diversity.

A pattern of heterogeneity affecting diversity has not to our knowledge been shown across a large number of levels in a terrestrial system. Furthermore, diversity patterns may vary across different habitats (Schulze *et al.* 2004; Tylianakis *et al.* in press), thereby obscuring any multi-trophic level effects.

Here we examine whether the diversity (species richness) and heterogeneity (CV of soil nutrients and beta diversity of plants and insects) of resources correlate with diversity of the taxa that utilise those resources, such that soil heterogeneity may promote increased diversity that cascades up different trophic levels. We examine this pattern in three different land use types that comprise a gradient of increasing anthropogenic modification (coffee agroforests, pasture and rice) in Southwest Ecuador. This region has suffered heavy anthropogenic modification, and is therefore appropriate for a comparison of managed land use types.

We focus here on the effect of soil heterogeneity on herbaceous plants, as their rapid growth in tropical regions means that they respond quickly to variation in abiotic conditions. We then examine the effects of diversity (species richness) and spatial heterogeneity (beta diversity) of herbs on cavity-nesting bees and wasps (Hymenoptera: Aculeata). Plant diversity is important for these species as it can affect the diversity and abundance of herbivore prey, for bee and wasp larvae (Siemann *et al.* 1998), and floral resources for adults (Steffan-Dewenter & Tscharntke 2001). Moreover, the importance of bees and wasps for pollination and biological control of pests (Klein *et al.* 2002, 2004), makes an understanding of the factors that determine their diversity essential for the maintenance of valuable ecosystem services. Finally, we examine the effects of species richness and beta diversity of cavity-nesting bees and wasps on the diversity of their natural enemies (parasitoids and cleptoparasites). Consequently, we aim to determine whether diversity at one level propagates itself up the food-chain in a diverse tropical region, and whether this effect varies with intensity of cultivation (from rice to pasture and agroforests). We also examine whether species richness itself or heterogeneity in species distributions (beta diversity) is more important for determining diversity of bees and wasps and their natural enemies.

Methods

Study region

The 36 study plots were spread across three cantons within the province of Manabi, Southwest Ecuador (Latitude 01º 16`-01º37´South, Longitude 80º 22´-80º 28` East, alt. 259m; for individual plot location details and a full description of the region see Tylianakis *et al.* in press). The region falls within the semi-arid tropics and is largely dominated by agriculture. Here we examine a gradient of anthropogenic modification using the predominant agricultural systems in the region - an arable crop (rice), pasture, and agroforestry (coffee), with twelve replicates of each habitat type. The area can be divided in 2 morphological units: the lower alluvial river valleys situated south and southeast of Pajan and Noboa and upper sloping areas including very steep slopes, mainly northwest of Pajan and Noboa. Six replicate plots per land use type occurred on slope soils, and the other six occurred on alluvial fans.

Sampling methods

In each plot, we marked nine points (in a 3 x 3 grid, each point 25 m apart). Sampling minimized edge effects by locating traps and surveys away from habitat boundaries. Replicate plots were representative of the particular land use type within the region. For each group, sampling effort was identical across all plots and land use types. Authors primarily responsible for data from each group are represented in the following by initials.

Soil: (M.L.-U., E.V.) We took a soil sample from the 0-0.25 m layer at each of the 9 points in each plot. These samples were air-dried, passed through a 2-mm sieve, and stored in plastic bags for laboratory analysis. Soil pH was determined in a slurry of 10 g soil and 25 ml de-ionized water (Anderson & Ingram 1993). In the laboratory, soil samples were analyzed for total organic carbon and nitrogen using an automated C & N analyzer (Heraeus Vario EL). Total phosphorus was determined after digestion under pressure with HNO_3 following the method described by Heinrichs (1989). Exchangeable calcium (Ca), magnesium (Mg), manganese (Mn), iron (Fe), potassium (K) and aluminum (Al) were extracted by leaching soil samples with 100 ml of unbuffered 1 M ammonium chloride (NH_4Cl) for 4-5 hours. Cations in the extracts were quantified by atomic absorption spectroscopy (König and Fortmann, 1996).

Soil heterogeneity was defined as the coefficient of variation (CV = standard deviation as a proportion of the mean) in concentrations of each of these soil parameters (pH, total N, total C, C:N ratio, bulk density, as well as Ca, Fe, Mn, Al, Na, K and Mg exchangeable cations) between sampling points within a plot. As concentrations of these chemicals may be correlated with one another, we conducted a spearman rank correlation test, and only included soil parameters that were not significantly correlated in the final model. These were: pH, total nitrogen, C:N ratio, and Al, Na, K and Mg exchangeable cations. It was also possible to substitute Na and Al for total P, but the result did not differ qualitatively (P had no significant effect), so only results for the former combination are presented.

Herbs: (T.L.) At the nine sampling points per plot, herb diversity was sampled in 2.5 x 2.5 m quadrants during two sampling periods (May and September 2003). All herb individuals (including ferns) were gathered, and voucher specimens were identified to the lowest possible taxonomic level by experts at Quito (QCA, QCNE) and Guayaquil (GUAY) herbaria in Ecuador. Total herb diversity (species richness) per plot was calculated by combining the results from the two sampling dates; however, we kept sampling points separate for calculations of beta diversity (see Statistical analyses below).

Insects: (J.M.T.) We placed a trap nest (Tscharntke *et al.* 1998), consisting of a PVC tube filled with reed (*Arundo donax* L., Poaceae) internodes of varying diameter, at each sampling point to provide nesting sites for aboveground cavity-nesting bees and wasps (Hymenoptera: Aculeata) and their natural enemies. Exposure of standardised trap nests is similar to the exposure of other resources, e.g. phytometer plants, but because the guild of aboveground cavity-nesting species reproduces in these traps, the problem of species appearing as 'tourists' in samples is eliminated. Cavity-nesting species usually build nests very close to the nesting site from which they pupated, so trap nests give an accurate representation of the community normally occurring in a particular habitat (see Tscharntke *et al.* 1998 and references therein). Trap nests were hung from trees in coffee systems and suspended from wooden posts in rice and pasture. Sticky glue (tanglefoot) was applied to the post or attachment point to deter ants. All traps were positioned 1.5 m above the ground.

We removed and replaced occupied reeds every month from June 2003 to October 2004 and opened occupied reeds for identification of primary occupants and any natural enemy (parasitoid or cleptoparasitoid) species present. Species were identified to family level, then where possible to genus or species level by D.W. Roubik, an expert in neotropical Hymenoptera, and by the authors using keys and reference collections from the Pontificia Universidad Católica del Ecuador. Remaining species were identified as morphospecies. For analyses of overall bee, wasp and natural enemy diversity, we pooled species richness data from each of the monthly evaluations to have one measure in each of the nine traps per plot.

Statistical analyses

We carried out all statistical analyses using Statistica 6.1 (StatSoft 2003). We used general linear models with backwards stepwise elimination of non-significant variables (under the GRM module of Statistica). Land use type was included as a categorical predictor in all models, and we tested for interaction effects between land use types and continuous predictors. Soil type (slope or alluvial) was also included as a categorical predictor in analyses of soil and plant interactions. Herb diversity was included as a covariable in analyses of the effects of bee and wasp diversity on natural enemy diversity, to ensure that the enemies were not simply responding to herb diversity. Post-hoc differences between categorical variables were assessed with Tukey's pairwise comparisons. All model residuals conformed to a normal distribution, so transformations were not necessary.

Beta diversity was calculated using additive partitioning (Lande 1996), a technique that is insensitive to differences in sampling effort among replicates, and therefore does not require rarefaction of data prior to analyses (Veech *et al.* 2002; Crist *et al.* 2003). For herb data, to ensure accurate estimation of beta diversity, given the very high diversity, we included only those species identified to at least genus level (98% of morphospecies). Beta diversity was calculated as the total number of species recorded for a plot minus the mean number of species in each of the nine sampling quadrats.

Because of the short generation times of bees and wasps, relationships between hosts and natural enemies may vary through time across habitat types, making comparisons that are pooled across many months inappropriate (Tylianakis *et al.* in press; Tylianakis *et al.* unpublished manuscript). Therefore, when analysing the effect of bee and wasp on natural enemy diversity, we used the mean number of species per month, and included temporal beta diversity for each plot within a given land use type as a covariable. This was calculated according to Tylianakis *et al.* (in press) as the total number of species found within that plot (over the entire year) minus the mean number of species per month for that plot. Spatial beta diversity was calculated as the total number of species found within a habitat type over the entire year minus the mean number of species per plot of that habitat type (over the entire year). For both herb and insect data, beta diversity for a plot was divided by the overall (gamma) plot diversity for analyses, to prevent differences in beta diversity being driven by differences in gamma diversity.

Results

Soil effects on plants

Of the seven soil chemicals included in the model, only heterogeneity in the concentration of magnesium significantly affected herb diversity ($F_{1, 31} = 9.54$, $P = 0.004$, $R^2 = 0.147$) (Fig. 3.1). Land use type also significantly affected herb diversity ($F_{2, 31} = 9.44$, $P < 0.001$), with rice and pasture having higher species richness than coffee, and slope soils having significantly higher herb diversity than alluvial soils ($F_{2, 31} = 5.42$, $P = 0.026$). Heterogeneity in Mg did not significantly interact with land use type or soil type; however, the strongest effect of soil heterogeneity on herb diversity was in coffee, where the overall model (including land use type, soil type and CV of the seven soil variables*)* explained a phenomenal 94% of the variance (adjusted for ties) and was highly significant ($F_{5, 6} = 37.11$, $P = 0.0002$). Soil heterogeneity did not significantly correlate with herb beta diversity. It may be argued that if many different soil chemicals are included in the analysis, the probability of committing a Type II error (erroneously accepting a false hypothesis) increases due to chance; however, the probability of achieving a level of significance of $P = 0.004$ (that of CV of Mg on herb diversity) from

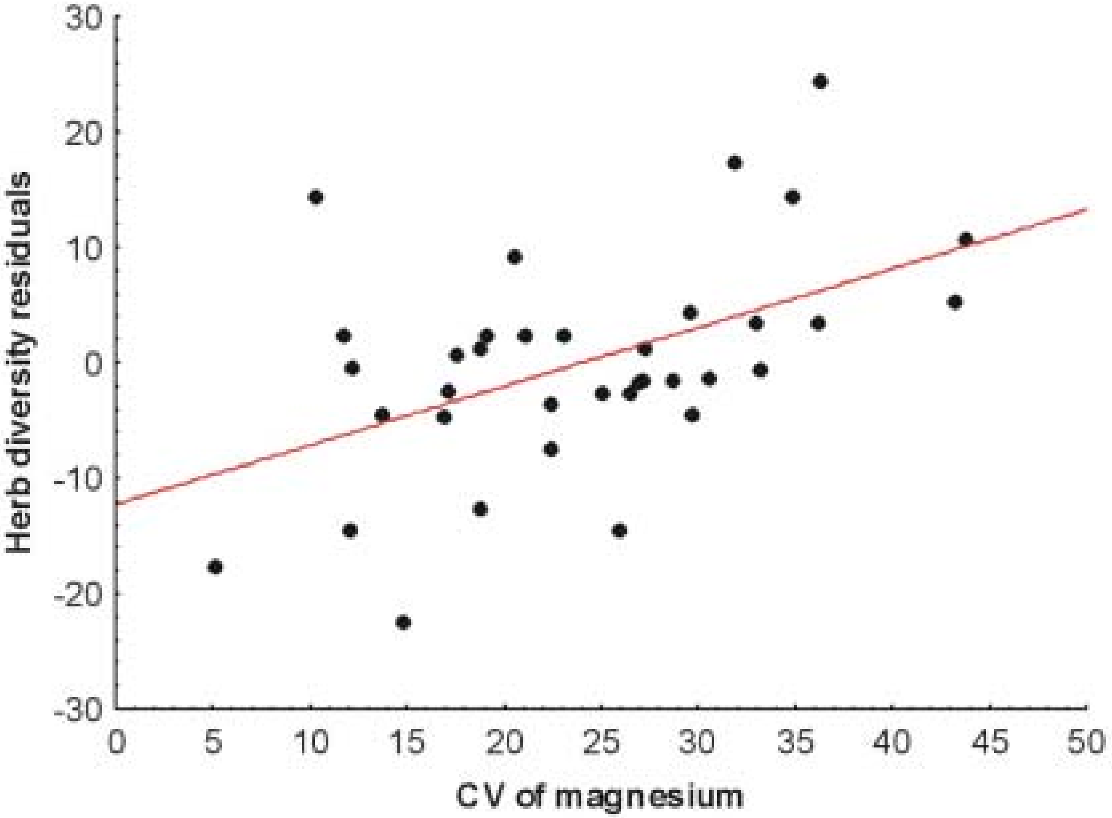


Figure 3.1. Correlation between variability (CV) in exchangeable cation concentration of soil magnesium and herb diversity (species richness) residuals after removal of variation due to soil type and land use type. The equation of the line is $y = 0.5102x - 12.2628$. Effect of Mg CV was significant at ($F_{1,\,31} = 9.54$, P = 0.004, $R^2 = 0.147$).

seven chemicals (the number included in the model) is only P = 0.028 (Moran 2003), and therefore still significant.

To determine whether variability in magnesium was directly associated with land use or soil type, we tested for an effect of land use and soil type (and interaction of the two) on CV of Mg (using a factorial ANOVA), and there were no significant effects (land use type: $F_{2,\,30} = 0.13$, P = 0.876; soil type: $F_{1,\,30} = 0.512$, P = 0.480).

Plant effects on bees and wasps

Herb diversity was significantly, positively correlated with cavity-nesting bee and wasp diversity. However, bee and wasp diversity was not as strongly correlated with herb species richness ($F_{1,\,33} = 4.46$, P = 0.026, $R^2 = 0.102$) as it was with herb beta diversity

($F_{1, 33}$ = 8.38, P = 0.007, R^2 = 0.193) (fig. 3.2). Land use type did not have a significant effect on overall bee and wasp diversity, nor did it interact with the effects of herb species richness or herb beta diversity.

Bee and wasp effects on natural enemies

Bee and wasp species richness (mean per month) was significantly positively correlated with natural enemy species richness per month ($F_{1, 33}$ = 21.29, P = 0.00006, R^2 = 0.253) (fig. 3.3). Land use type had no effect, nor did it interact with the effect of bee and wasp species richness. When all host variables were removed from the model, land use type significantly affected natural enemy diversity, indicating that the effect of land use is mediated via the diversity of bee and wasp hosts. Surprisingly, bee and wasp spatial beta diversity was weakly negatively correlated with natural enemy species richness ($F_{1, 33}$ = 5.98, P = 0.020, R^2 = 0.071); however, this effect disappeared when species richness was removed from the model. This was due to the bee and wasp richness being correlated with spatial beta, and the strong effect of the former explaining much of the variation also explained by the latter. Bee and wasp temporal beta diversity, herb species richness and herb beta diversity had no significant effect on natural enemy species richness.

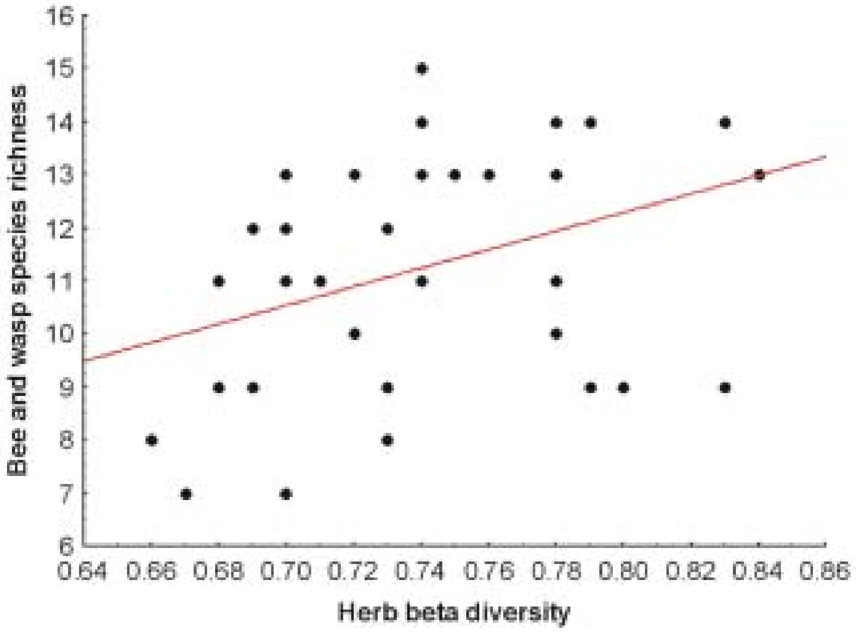


Figure 3.2. Correlation between plant beta diversity and species richness of bees and wasps. No differentiation is made between land use types as this had no significant effect. The equation of the line is $y = 17.5161x - 1.7314$. Effect was significant at ($F_{1, 33}$ = 8.38, P = 0.007, R^2 = 0.211).

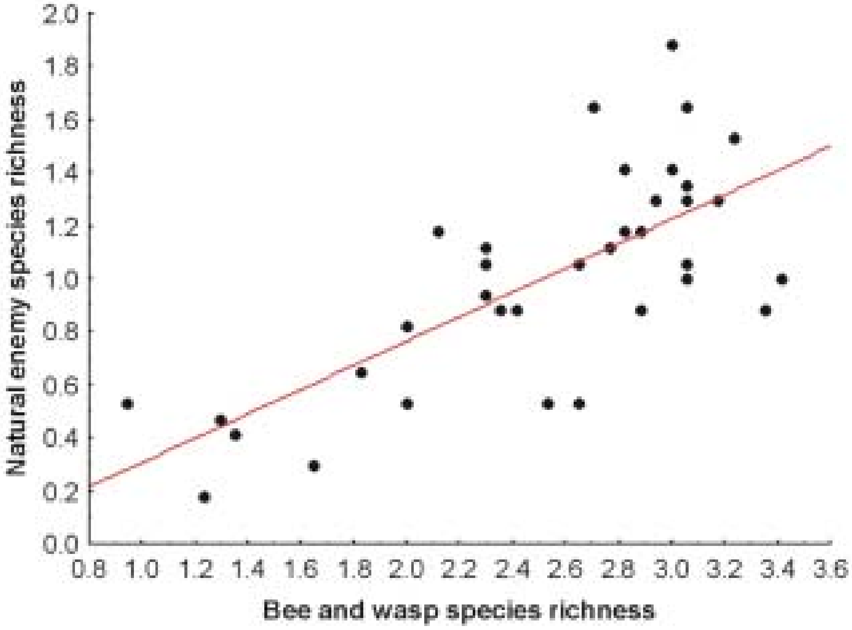


Figure 3.3. Correlation between bee and wasp and natural enemy species richness (both mean per month). No differentiation is made between land use types as this had no significant effect. The equation of the line is $y = 0.4587x - 0.1534$. Effect was significant at ($F_{1,33} = 21.29$, $P = 0.00006$, $R^2 = 0.253$).

Discussion

That soil heterogeneity led to increased herb diversity is not surprising, as the importance of habitat heterogeneity for structuring ecological communities has been frequently emphasised (Murdoch *et al.* 1972; Fitter 1982; Tuomisto *et al.* 1995; Ruokolainen & Tuomisto 2002; Benton *et al.* 2003; Lundholm & Larson 2003; Potts *et al.* 2003; Armbrecht *et al.* 2004; Baer *et al.* 2005; McMaster 2005). However, this direct effect of soil heterogeneity on plant diversity being strong enough to permeate up three trophic levels, amidst the noise of different land use types and numerous other influences, has not previously been shown in practice. Land use can strongly affect diversity of plants and insects (Lawton *et al.* 1998; Schulze *et al.* 2004; Tylianakis *et al.* in press), so the isolation of an effect of soil, over and above that attributable to land use alone, is testament to the importance of soil heterogeneity in the bottom-up structuring of herb and insect communities. Although magnesium is an important, sometimes limiting, nutrient for tropical plant species (Burslem *et al.* 1995; Hailes *et al.* 1997), and different species may respond to Mg availability in different ways (Gunatilleke *et al.* 1997), we emphasise that variability in the soil, rather than actual concentrations of Mg, drove the pattern of diversity (López *et al.* unpublished manuscript). Magnesium variability was correlated with the variability of other soil nutrients (e.g., exchangeable Ca and base cations) and Magnesium is associated with the overall clay content of the soil. Therefore, rather than suggesting an importance of Mg variability *per se*, Mg most likely indicated general variability in the soil structure and chemistry, and this variability allowed a greater variety of herb species to occupy separate niches.

Of course diversity of all taxa is driven by a great variety of mechanisms. Plant and insect diversity frequently respond to other factors such as light, landscape context and availability of other resources (Begon *et al.* 2005). Nevertheless, the integral link between plants and soil cannot be undermined, and bees and wasps are frequently dependent on floral resources at one or more life-history stages (Landis *et al.* 2000; Tylianakis *et al.* 2004). Similarly, parasitoids and cleptoparasites are intimately associated with their hosts, and the frequent host-specificity of these species may lead their diversity to map that of the available hosts. Therefore, it is possible that this type of diversity cascade may have general applicability across different habitats. Perhaps most surprising was the absence of an effect of habitat on this diversity cascade. Although diversity of plants differed across habitats, the soil variability/plant diversity correlation did not vary across habitats (no interaction effect of Mg variability with land use type was observed), suggesting some degree of generality in the cascade across habitats. However, all habitats examined were modified to some extent by agriculture, therefore further studies are needed in natural systems to ascertain the general applicability of this pattern.

In terms of habitat management, the results suggest that loss of biodiversity at one community level may have negative repercussions across the entire community. Previous studies have shown that different taxa respond differently to anthropogenic habitat modification (Lawton *et al.*1998, Schulze *et al.* 2004); however, the different taxa in these studies were selected for their value as bioindicators, rather than any expectation that they depend on, or interact with, one another. Here we show that within each habitat type, the diversity of taxa at different trophic levels may respond to the diversity or heterogeneity of their resources in the same manner. Therefore, management regimes that favour heterogeneity may generally enhance diversity – an effect that has been shown for independent taxa at habitat (Murdoch *et al.* 1972; Potts *et al.* 2003; Ambrecht *et al.* 2004; Tylianakis *et al.* in press) and landscape scales (Ewers *et al.* 2005; Gabriel *et al.* 2005). Increased diversity of these taxa may also provide increased ecosystem functioning in the form of higher plant productivity (van Ruijven & Berendse 2005) or rates of parasitism (biological control) (Tylianakis *et al.* unpublished manuscript).

Surprisingly, beta diversity of bees and wasps was not positively correlated with natural enemy diversity. It could be expected that heterogeneously distributed resources may allow spatial partitioning of niches, thereby reducing interspecific competition (e.g., Borer *et al.* 2004). Indeed, beta diversity of herbs was correlated strongly with bee and wasp diversity. However, many of the natural enemy species in our system are specialised on a limited number of hosts, and the number of host species, rather than spatial heterogeneity in host distribution, allows niche partitioning.

We emphasise that, even in anthropogenically modified habitats within a highly modified region, complex interspecific and cross trophic level associations can occur. Therefore loss of diversity at any level may have important repercussions over the entire system, and management of agricultural systems to maintain or maximise soil heterogeneity may contribute significantly to regional biodiversity.

References

Anderson, J.M. and Ingram, J.S.I. (1993). Tropical Soil Biology and Fertility. A Handbook of Methods, 2nd Edition, CAB International, Wallingford, UK.

Armbrecht I, Perfecto I & Vandermeer J (2004). Enigmatic biodiversity correlations: ant diversity responds to diverse resources. *Science*, 304: 284-286.

Baer, S.G., Collins, S.L., Blair, J.M., Knapp, A.K. & Fiedler, A.K. (2005). Soil heterogeneity effects on tallgrass prairie community heterogeneity: an application of ecological theory to restoration ecology. *Restoration Ecology*, 13, 413-424.

Begon, M., Townsend, C.R. & Harper, J.L. (2005). *Ecology: From individuals to ecosystems*. Fourth ed. Blackwell Publishers, UK.

Benton TG, Vickery JA & Wilson JD (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.*, 18: 182-188.

Borer, E.T., Murdoch, W.W. & Swarbrick, S.L. (2004). Parasitoid coexistence: linking spatial field patterns with mechanism. *Ecology,* 85, 667-678.

Burslem, D.F.R.P., Grubb, P.J. & Turner, I.M. (1995). Responses to nutrient addition among shade-tolerant tree seedlings of lowland tropical rainforest in Singapore. *Journal of Ecology,* 83, 113-122.

Crist, T.O., Veech, J.A., Gering, J.C. & Summerville, K.S. (2003). Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β and γ diversity. *American Naturalist*, 162, 734-743.

Ewers, R. Didham, R.K, Wratten, S.D. and Tylianakis, J. (2005). Remotely-sensed landscape heterogeneity as a rapid tool for assessing local biodiversity value in a highly modified New Zealand landscape. *Biodiversity and Conservation,* 14, 1469-1485.

Fitter, A.H. (1982). Influence of soil heterogeneity on the coexistence of grassland species. *Journal of Ecology*, 70, 139-148.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P. (2005). Global consequences of land use. *Science*, 309, 570-574.

Gabriel, D., Thies, C. & Tscharntke, T. (2005). Local diversity of arable weeds increases with landscape complexity. *Perspectives in Plant Ecology, Evolution and Systematics*, 7, 85-93.

Gunatilleke, C.V.S., Gunatilleke, I.A.U.N., Perera, G.A.D., Burslem, D.F.R.P., Ashton, P.M.S. & Ashton, P.S. (1997). Responses to nutrient addition among seedlings of eight closely related species of Shorea in Sri Lanka. *Journal of Ecology*, 85, 301-311.

Hailes, K.J., Aitken, R.L. & Menzies, N.W. (1997). Magnesium in tropical and subtropical soils from north-eastern Australia .1. Magnesium fractions and interrelationships with soil properties.

Kassen, R., Buckling, A., Bell, G. & Rainey, P.B. (2000). Diversity peaks at intermediate productivity in a laboratory microcosm. *Nature*, 406, 508-512.

Kleb, H. & Wilson, S. (1997). Vegetation effects on soil resource heterogeneity in prairie and forest. *American Naturalist*, 150, 283-298.

Klein, A.-M., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. (2002). Effects of land use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conserv. Biol.*, 16, 1003-1014.

Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. (2004). Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *J. Anim. Ecol.*, 73, 517-525.

König, N., and Fortmann, H. (1996). Probenvorbereitungs-, Untersuchungs- und Elementbestimmungs-Methoden des Umweltanalytik-Labors der Niedersächsischen Forstlichen Versuchsanstalt, 1-4, Berichte des Forschungszentrums Waldökosysteme, Reihe B, University of Göttingen, Germany, B46-B49, ISSN 0939-1339.

Lande, R. (1996). Statistics and partitioning of species diversity and similarity among multiple communities. *Oikos*, 76, 5-13.

Landis, D.A., Wratten, S.D. & Gurr, G.M. (2000). Habitat management to conserve natural enemies of arthropod pests in agriculture. *Annual Review of Entomology*, 45, 175-201.

Lawton, J.H., Bignell D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature,* 391, 72-76.

Lundholm, J.T. & Larson, D.W. (2003). Relationships between spatial environmental heterogeneity and plant species diversity on a limestone pavement. *Ecography*, 26, 715-722.

McKane RB, Johnson LC, Shaver GR, Nadelhoffer KJ, Rastetter EB, Fry B, Giblin AE, Kielland K, Kwiatkowski BL, Laundre JA & Murray G (2002) Resource-based niches provide a basis for plant species diversity and dominance in arctic tundra. *Nature*, 415: 68-71.

McMaster RT, (2005). Factors influencing vascular plant diversity on 22 islands off the coast of eastern North America. *Journal of Biogeography*, 32: 475-492.

Moran, M.D. (2003). Arguments for rejecting the sequential Bonferroni in ecological studies. *Oikos*, 100, 403-405.

Murdoch WW, Evans FC & Peterson CH (1972). Diversity and pattern in plants and insects. *Ecology,* 53: 819-829.

Potts SG, Vulliamy B, Dafni A, Ne'eman G & Willmer P (2003). Linking bees and flowers: how do floral communities structure pollinator communities. *Ecology*, 84: 2628-2642.

Ruokolainen K & Tuomisto H (2002). Beta-diversity in tropical forests. *Science*, 297: 1439a.

Schulze CH, Waltert M, Kessler PJA, Pitopang R, Shahabuddin, Veddeler D, Mühlenberg M, Gradstein SR, Leuschner C, Steffan-Dewenter I & Tscharntke T (2004). Biodiversity indicator groups of tropical land use systems: comparing plants, birds, and insects. *Ecological Applications*, 14: 1321-1333.

Shahabuddin, Schulze, C.H. & Tscharntke, T. (2005). Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia). *Biodiversity and Conservation,* 14, 863-877.

Siemann, E., Tilman, D., Haarstad, J. & Ritchie, M. (1998). Experimental tests of the dependence of arthropod diversity on plant diversity. *Am. Nat.* 152, 738-750.

StatSoft, Inc. (2003). STATISTICA (data analysis software system), version 6. www.statsoft.com.

Steffan-Dewenter, I. & Tscharntke, T. (2001). Succession of bee communities on fallows. *Ecography*, 24, 83-93.

Stevens, M.H.H. & Carson, W.P. (2002). Resource quantity, not resource heterogeneity, maintains plant diversity. *Ecology Letters*, 5, 420-426.

Tilman, D. & Lehman, C. (2001). Human-caused environmental change: Impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences, USA*, 98, 5433-5440.

Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998). Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*, 35, 708-719.

Tscharntke, T., Klein, A.-M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, 8, 857-874.

Tuomisto H, Poulsen AD, Ruokolainen K, Moran RC, Quintana C, Celi J & Cañas G (2003). Linking floristic patterns with soil heterogeneity and satellite imagery in Ecuadorian Amazonia. *Ecological Applications*, 13, 352-371.

Tuomisto H, Ruokolainen K, Kalliola R, Linna A, Danjoy, W. & Rodriguez, Z. (1995). Dissecting Amazonian biodiversity. *Science*, 269: 63.

Tylianakis, J., Didham, R. and Wratten, S.D. (2004). Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology* 85, 658-666.

Tylianakis, J.M., Klein, A.-M. & Tscharntke, T. (in press). Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology*..

van Ruijven, J. & Berendse, F. (2005). Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proc. Natl. Acad. Sci. USA*, 102, 695-700.

Veech, J.A., Summerville, K.S., Crist, T.O. & Gering, J.C. (2002). The additive partitioning of diversity: recent revival of an old idea. *Oikos*, 99, 3-9.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997). Human domination of the Earth's ecosystems. *Science*, 277, 494-499.

Wijesinghe, D.K., John, E.A. & Hutchings, M.J. (2005). Does pattern of soil resource heterogeneity determine plant community structure? An experimental investigation. *Journal of Ecology*, 93, 99-112.

Chapter
4

Spatial scale of observation affects α, β and γ diversity of Hymenoptera across a tropical land use gradient

J. M. Tylianakis, A.-M. Klein, T. Lozada and T. Tscharntke

(Submitted)

Abstract

AIM: Anthropogenic changes in land use may have major consequences for global biodiversity; however, species diversity is determined by a suite of factors that may affect species differently at different spatial scales. For the first time we tested the combined effects of land use and spatial scale on α, β and γ diversity in the tropics using experimental communities of cavity-nesting Hymenoptera (Aculeata). We aimed to determine whether 1) Land use intensity negatively affects diversity of cavity-nesting Hymenoptera, 2) beta diversity, both within and between plots, is higher in more natural systems, 3) diversity of flowering herbs positively affects species richness of Hymenoptera within and across habitats, 4) diversity of cavity-nesting Hymenoptera in highly modified habitats declines with increasing distance from natural or seminatural habitats, and 5) the effects of land use, herb diversity and forest distance on Hymenoptera α and β diversity vary at different spatial scales.

LOCATION: Manabi, southwest Ecuador.

METHODS: We examined diversity within 48 plots of five habitat types that comprised a gradient of decreasing agricultural intensity from rice and pasture to coffee agroforests, unmanaged abandoned agroforests and forest fragments using standardised nesting resources for reproducing communities of cavity-nesting bees and wasps.

RESULTS: 1) Land use significantly affected α diversity of trap-nesting Hymenoptera at the subplot scale, but not β diversity or plot-scale species richness (γ diversity). 2) Beta diversity was surprisingly higher between plots within a land use type than between land use types. 3) Diversity of Hymenoptera increased with diversity of flowering herbs at the subplot scale only. 4) Forest distance affected Hymenoptera diversity at the plot scale only. 5) Land use, herb diversity and forest distance each showed significant effects at only one spatial scale.

MAIN CONCLUSIONS: The effects of land use on species richness were highly dependent on spatial scale. Subplot-scale analyses showed that rice and pasture contained the highest species diversity, whereas plot-scale analyses showed no significant difference in the diversity of different land use types. We emphasize caution in the estimation of biodiversity at only one spatial scale and highlight the surprisingly large contribution of managed land to overall biodiversity.

Introduction

Tropical ecosystems are the greatest contributors to global biodiversity (Myers *et al.* 2000) and a lack of conservation funding increases the reliance of these regions on managed land for biodiversity conservation (Perfecto *et al.* 1996, Bawa *et al.* 2004). The contribution of different land use systems to tropical biodiversity requires thorough assessment; however, past studies on the effects of land use intensity on biodiversity have frequently measured diversity at only one spatial scale (e.g., Klein *et al.* 2002). This may mask subtle differences in species diversity, because the factors that determine diversity may not scale up or down across different spatial and temporal scales (Whittaker *et al.* 2001; Willis & Whittaker 2002). On a landscape scale, species richness can be affected by factors such as fragmentation (Didham *et al.* 1996; Cane 2001), matrix composition (Ricketts 2001; Dauber *et al.* 2003), landscape diversity (Steffan-Dewenter *et al.* 2002; Dauber *et al.* 2003; Krauss *et al.* 2003; Kruess 2003) or climate (James & Shine 2000; Opdam & Wascher 2004). At smaller spatial scales, factors such as habitat type (Kruess 2003; Weibull *et al.* 2003), habitat area (Richie & Olff 1999; James and Shine 2000; Krauss *et al.* 2003; Summerville & Crist 2004), management intensity (Klein *et al.* 2002; Perfecto *et al.* 2003) and inter- or intraspecific interactions (Veech *et al.* 2003) become more important in determining species distributions. Therefore, the spatial scale selected for the study may inadvertently determine the outcome, for instance, if species turnover is low within plots, but high between plots (e.g. Summerville *et al.* 2003).

The challenge of assessing diversity at multiple scales can be met by partitioning diversity between different levels of a nested spatial hierarchy (Willis & Whittaker 2002), thereby determining the spatial scale across which the highest beta diversity occurs. This multi-scale approach was used by Summerville *et al.* (2003) to evaluate lepidopteran diversity in temperate forests in Ohio, USA, and Wagner *et al.* (2000) used this technique to examine the plant species diversity of different land use systems, in an agricultural landscape on the Swiss Plateau.

Many studies on the effects of land use on biodiversity consider only a few related management systems, such as different intensities of coffee or cacao management (e.g., Perfecto *et al.* 2003; but see Ricketts *et al.* 2001). While this work can provide valuable guidelines for conservation and management of the systems concerned, it fails to assess the overall contribution of managed land to regional biodiversity.

Here we use a highly replicated field study to examine the effects of the five predominant land use types (rice, pasture, coffee, abandoned coffee and forest fragments) in southwest Ecuador, on the diversity of trap-nesting bees and wasps (Hymenoptera: Aculeata). Experimental communities of trap-nesting Hymenoptera make useful tools for investigations of biodiversity, due to their ease of physical manipulation, trophic complexity, and species diversity (Tscharntke *et al.* 1998). In terms of ecosystem services (sensu Costanza *et al.* 1997), communities of trap-nesting Hymenoptera are particularly salient, as many species are important pollinators of both crops and wild plants (Klein *et al.* 2003). Moreover, many predacious or parasitic trap-nesting species may act as biological control agents (Klein *et al.* 2004).

We use additive partitioning of beta diversity at multiple spatial scales to assess the land use types in which the greatest beta diversity occurs. Finally, we examine possible drivers of observed variation in species richness by assessing the effects of distance from forest remnants, and vegetational diversity on the diversity of trap-nesting Hymenoptera, and how these effects manifest themselves at different spatial scales. Such drivers are often absent from studies of human impacts on Hymenoptera diversity, and this can lead to broad, questionable generalisations (Cane 2001). The spatial scales we define are the subplot scale, which comprises variation between traps of a particular plot, the plot scale, which examines variation between different plots of a given land use type and the regional scale, which examines variation between land use types.

Specifically, we test the following hypotheses regarding the effects of land use on diversity of trap-nesting Hymenoptera at different spatial scales:

1) Land use intensity negatively affects diversity of trap-nesting Hymenoptera. In general, more natural habitats tend to exhibit higher biodiversity of a variety of insect taxa (e.g., Mas & Dietsch 2003; Shahabuddin *et al.* 2005). However, trap-nesting Hymenoptera may be able to exploit resources such as crop plants and their herbivore communities, and they have been previously shown to benefit from increased intensity of agroforest management (Klein *et al.* 2002). Nevertheless, agroforests comprise a relatively natural habitat compared with arable crops. We therefore aim to determine how

different land use types, rather than management intensity of a single type, affect diversity of this guild of bees and wasps.

2) Beta diversity, both within and between plots, is higher in more natural systems. Natural systems are more heterogenous than intensely managed land use types, and therefore provide a greater array of niches. We expect that this will lead to higher beta diversity in unmanaged systems than in the agricultural land use types (Clausnitzer 2003).

3) Diversity of flowering herbs positively affects species richness of Hymenoptera within and across habitats. Herb diversity has been shown to correlate positively with Hymenoptera diversity within coffee agroforests (Klein *et al.* 2003); however, the robustness of this effect across different land use types remains to be tested. Further, it is unclear whether high herb diversity attracts trap-nesting Hymenoptera into a habitat or land use type, or whether this effect only determines the distribution of species within a habitat, i.e. at the subplot scale.

4) Diversity of trap-nesting Hymenoptera in highly modified habitats declines with increasing distance from natural or seminatural habitats. Klein *et al.* (2003) found a negative effect of forest distance on the diversity of social bees, but not solitary species such as those that occupy trap nests. Natural habitats may act as source populations for trap-nesting species, thereby leading to higher diversity in traps or plots that are proximate to such habitats.

5) The effects of land use, herb diversity and forest distance on Hymenoptera α and β diversity vary at different spatial scales. Many factors affecting biodiversity are only examined at one spatial scale; however, these effects can not always be linearly ‘scaled up’ across space and time (Willis & Whittaker 2002).

Materials and Methods

Study sites

The study plots are located in the province of Manabi, southwest Ecuador. They comprise private farms spread across three cantons; Jipijapa (17N 546800m, E 9849274m alt. 259m), Pajan (17N 563969, E 9828342m alt. 142m) and 24 de Mayo (largest town: Noboa 17N 567374m, E 9844106 alt. 260m) (Fig. 4.1) (for individual plot location details and a full description of the region see Tylianakis *et al.* in press). The region falls within the semi-arid tropics and is largely dominated by agriculture, therefore the effects of agricultural intensification are directly relevant to this region. There are a variety of different crops cultivated in this area; however, in this study we consider the dominant ones - an arable crop (rice), pasture and agroforestry (coffee). Coffee agroforests can vary greatly with individual management; therefore, an effort was made to select plots that had been in cultivation for over 8 years, used no chemical fertilizers and had a similar degree of shade tree cover (60 – 80%). As there is no primary rainforest remaining in the zone (only few secondary and fragmented forest remnants), we used the most "natural" systems available, abandoned coffee agroforests and forest fragments, and these two types were treated separately in analyses. These land use types represent a gradient of decreasing management intensity. Their relative abundance and the total area within the study region are presented in Table 1. Twelve replicates of each managed land use type were sampled in the study, as were six abandoned coffee agroforests (abandoned for 10 - 15 years and now resembling secondary forest) and six forest fragments.

The study plots were generally clustered in groups of three or more different land use types so as to avoid spatial autocorrelation resulting from several plots of one land use type being clustered together (Fig 4.1). All plots had been occupied by the same land use type for at least five years.

Table 4.1. The area in hectares and percentage of the total canton area occupied by each of the land use types considered in this study (Segarra 2004).

Land use type	*Area*	*Percentage of study zone*
Agroforestry, predominantly coffee	59 347	54.8
Forests and partially intervened natural vegetation, including abandoned agroforests	18 660	17.2
Seasonal, permanent, and partly overgrown pastures	17 570	16.2
Rice and other annual crops	2 030	1.9
Total area of zone	108 241	100.0

Trap nests

Nine trap-nests were positioned (in a 3 x 3 grid, 25 m between adjacent traps) in the centre of each of the 48 plots to provide nesting sites for naturally occurring bee and wasp communities. Because the guild of aboveground cavity nesting species reproduces in these traps, the problem of species appearing as 'tourists' in samples is eliminated. Trap nests were constructed according to the methodology of Tscharntke *et al.* (1998). A PVC tube with a length of 22 cm and a diameter of 15 cm formed the outer case of the nest. Internodes of reeds *Arundo donax* L. (Poaceae) with varying diameter (2 – 20 mm)

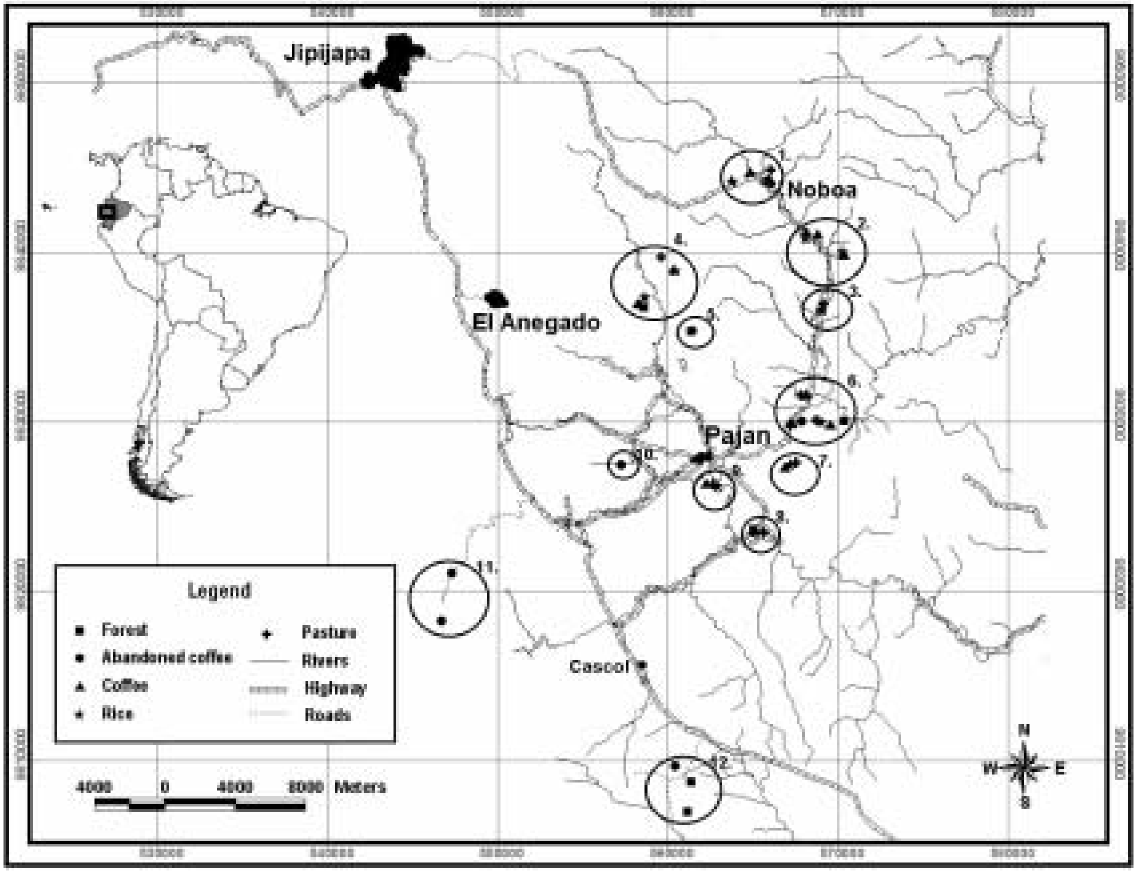


Figure 4.1. Map of study region showing distribution of plots in relation to the major towns: Jipijapa (17N 546800m, E 9849274m alt. 259m), Pajan (17N 563969, E 9828342m alt. 142m) and Noboa (17N 567374m, E 9844106 alt. 260m). Circles with number to top right indicate clusters of plots within a village or two adjacent villages.

and a length of 20 cm were inserted into this tube and provided the nesting sites for bees and wasps.

Trap nests were hung from trees in shaded (coffee, abandoned coffee and forest) systems and suspended from wooden posts in open (rice and pasture) systems. Sticky glue (tanglefoot) was applied to the post or attachment point to deter ants. All traps were positioned 1.5 m above the ground. A broad spectrum fungicide (Fitoraz® 76 PM, Bayer Crop Science S.A.: Propineb 21 g/L, Cymoxanil 1.8 g/L) that is not toxic to Hymenoptera was applied to each trap with a hand sprayer every month.

Each trap was evaluated every month during the dry season (June – December 2003), and all reed internodes that were occupied by Hymenoptera were removed and replaced with new internodes of the same diameter. Occupied reeds were opened and the larvae were reared to maturity for positive identification to Subfamily level. Genera and species were identified where possible by D.W. Roubik, an expert in neotropical Hymenoptera, and by the authors using keys and reference collections from the Pontificia Universidad Católica del Ecuador. Remaining species were identified as morphospecies. Species richness data from the six evaluations were pooled for each trap. Parasitoids and cleptoparasites were excluded from analyses, as their diversity is dependent partially on available host species.

Plant surveys

Plant surveys were conducted in 2.5 x 2.5 m quadrats below the traps in shaded systems or adjacent to the wooden posts, in open systems. The number of flowering angiosperm species potentially attracting Hymenoptera was counted in each quadrat. Ferns, grasses and other plants that did not require insect pollination were excluded, as these do not provide nectar resources that may influence populations of Hymenoptera. Two plant surveys were conducted (one in May/June 2003 and one in September/October 2003) in order to estimate herb diversity at the beginning and end of the dry season. The mean species richness from the two surveys was used in the analyses. Tree diversity (number of species) was also recorded in 10 x 10 m quadrats around each trap in the shaded land use types (coffee, abandoned coffee, and forest).

Forest distance

The distance to the nearest possible hymenopteran source population (hereafter: "forest distance") was measured for each trap in the open systems. This constituted the distance from each trap to the border of the nearest forested habitat type, i.e. forest fragment, agroforest or abandoned agroforest. This parameter could not be meaningfully assessed for the remaining land use systems, as the border between one agroforest and another was often arbitrarily based on ownership, rather than any biological significance, and all plots would essentially have zero values for this parameter. Distances up to one hundred metres were measured with a tape measure and greater distances were measured with GPS (Etrex Venture – Garmin: mean error for the measurements was 12.4 ± 4.36 m). For analyses, forest distance was partitioned into the distance from the forest to the plot (plot level) and the distance from the edge of the plot to each trap (subplot level).

Alpha, Beta, and Gamma diversity

Beta diversity is a measure of the proportion of total species diversity that is not present in each sample unit. We used additive partitioning (Lande 1996) to calculate this value such that regional species diversity γ is the sum of α diversity (the average within-sample diversity) and β diversity (species turnover). The benefit of this technique is that α, β and γ diversity can be defined according to a hierarchy of spatial scales, so that γ diversity at one level becomes α diversity for the next level. Thus, in our study, if α_{sub} is defined as the mean species richness at the subplot scale, i.e. the average number of species in each trap within a plot, β_{sub} is beta at the subplot scale and α_{plot} is the total species richness for a plot, then: $\alpha_{sub} = \alpha_{plot} - \beta_{sub}$.

At the next level of the hierarchy: mean α_{plot} for a land use type = $\alpha_{reg} - \beta_{plot}$ where α_{reg} is the total number of species within a land use type. Finally, mean $\alpha_{reg} = \gamma_{reg} - \beta_{reg}$ where γ_{reg} is the total number of species within the study region, i.e. across all land use types. In order to meaningfully compare alpha and beta diversity between different land use types, we compared them as a proportion of the total diversity for the land use type (arcsine square-root transformed). As α and β are correlated with eachother, we treated them as a multivariate response variable, and compared land use types as a fixed factor and plot cluster (Fig. 4.1) as a random factor (to eliminate variation due to spatial autocorrelation, see below) in a linear mixed effects model (Crawley 2002), under the Variance Components module of Statistica 6.1 (StatSoft 2003). This module calculates error degrees of freedom (DF) using Satterthwaite's method of denominator synthesis (Satterthwaite, 1946), and can yield non-whole-number DF values (these were rounded to whole numbers in the results).

Statistical analyses

A preliminary Mantel test, based on Pearson's product-moment correlation conducted in R (R Development Core Team 2004) found that our plots were spatially autocorrelated (Mantel statistic r: 0.2124, p = 0.005). Although the majority of this autocorrelation was between plots of different land use types, we nevertheless grouped our plots into 12 clusters (Fig. 4.1), and used this as a covariate in analyses. Grouping the sites in this manner actually increased the significance values of significant variables by removing unexplained variation due to spatial autocorrelation. Any plots within 2 km of each other were grouped into a cluster. This distance was conservative, as a study and review of solitary bee foraging ranges (Gathmann & Tscharntke 2002) found a maximum dispersal range of 1200m in large solitary bees.

To measure whether our samples were close to species saturation we calculated the abundance-based coverage estimator (ACE) and Chao1 estimates of species richness using the EstimateS software Version 5 (Colwell 1997). Sampled species richness was then divided by each estimator for each plot to calculate the percent species saturation. Remaining analyses were conducted in Statistica 6.0 (Statsoft 2003).

Model residuals were tested for adherence to a particular distribution before this was assumed in analyses. The effect of land use on subplot diversity was calculated using a mixed effects model with diversity of individual traps as the response variable, grouped with plot as a random factor. Plot level effects of land use on species richness were tested with ANOVA.

The effects of tree and herb diversity on species richness at the plot scale were tested with a linear mixed effects model, using land use as a fixed factor, plot cluster as a random factor, and tree or herb diversity as continuous predictors. At the subplot scale, traps were grouped into plots (random factor). The effect of tree diversity was analysed only in the shaded systems (rice and pasture were excluded).

In rice and pasture plots, the effect of forest distance on species richness was tested in a mixed effects model. Distance from forest to plot and distance from each trap to the plot edge closest to the forest were analysed as separate variables, with land use as a fixed factor and plot cluster as a random factor. Subplot samples were also blocked into plots. The division of forest distance into two components was necessary to determine whether traps within a plot that were closer to a forested habitat had higher diversity (e.g., through edge effects). The effects of plot age and area on plot-scale richness were also tested using a mixed effects model with land use type and plot cluster as covariables.

Results

A total of 10,006 individuals from 22 morphospecies (Hymenoptera: Apidae, Eumenidae, Megachilidae, Pompilidae and Sphecidae) were collected from the 432 trap nests. Generally, there was little specialisation in land use selection by the bees and wasps, as there was a great overlap in the species that constituted the communities of each land use type. Pasture, rice and coffee each had one species specific to only that type, and a further bee species was specific to coffee and abandoned coffee. The mean species saturation per study plot (N = 48) was 96.3 ± 0.85% according to the ACE and 97.7 ± 0.86% according to the Chao1 estimators. Percent species saturation according to the estimators did not vary significantly between land use types (one-way ANOVA: $F<1$, $P>0.5$ in both cases), so we preferred to make direct comparisons with original species richness data, rather than estimated values.

Effects of land use on species richness

At the subplot level, land use strongly affected species richness ($F_{(4,43)} = 17.62$, $P < 0.0001$) (Fig. 4.2a) of trap-nesting Hymenoptera; however, at the plot level there was no significant effect of land use type on species richness ($F_{(4,43)} = 1.17$, $P > 0.33$) (Fig. 4.2b) or on ACE or Chao1 estimates of species richness ($F_{(4,43)} < 1.34$, $P > 0.272$).

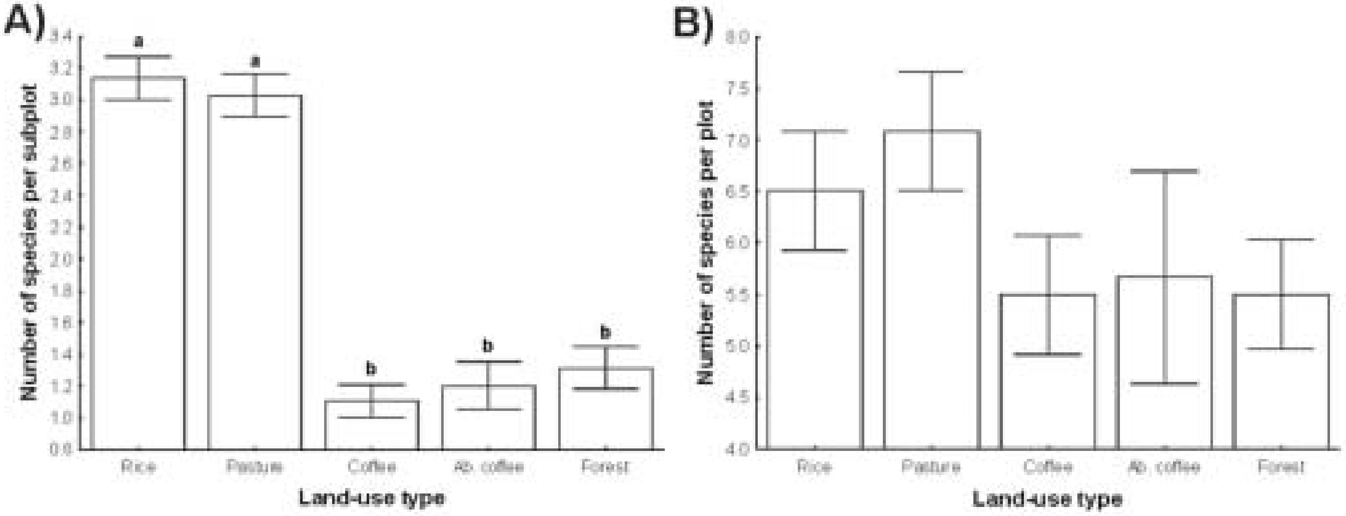


Figure 4.2. The effects of land use type on mean (± SE) species richness of trap-nesting Hymenoptera at the A) subplot and B) plot level.

Partitioning of species diversity across spatial scales

In general α diversity accounted for proportionately low levels of the total species richness (a mean of 15.3 ± 0.95% of α_{reg} and 10.8 ± 0.65% of γ_{reg}), and the highest proportions of α_{reg} and γ_{reg} were accounted for by species, β_{plot} (Fig. 4.3). Alpha diversity, as a proportion of total plot diversity (α_{sub} / α_{plot}) was affected significantly by land use type ($F_{(4,22)} = 14.65$, $P < 0.00001$), but relative beta diversity within plots (β/ α_{plot}) was unaffected ($F_{(4,22)}= 0.71$, $P > 0.05$) (Fig. 4.3).

Both alpha and beta as a proportion of plot diversity were significantly affected by plot cluster ($F_{(11,17)} > 2.59$, $P < 0.05$ in both cases), indicating that communities were partly affected by geographic location. Land use type and plot cluster did not interact significantly ($F_{(11,17)} < 1.63$, $P > 0.17$ in both cases).

Effects of plant diversity and abiotic variables on species richness

At the subplot scale, herb diversity significantly affected species richness of trap-nesting Hymenoptera ($F_{(1,39,7)} = 13.90$, $P < 0.001$) (Fig. 4.4); however, this effect was not apparent at the plot scale ($F_{(1,20.2)} = 0.32$, $P > 0.57$). Tree diversity in the shaded plots had no significant effect on Hymenoptera species richness at the subplot ($F_{(1,24.7)} = 0.02$, P >

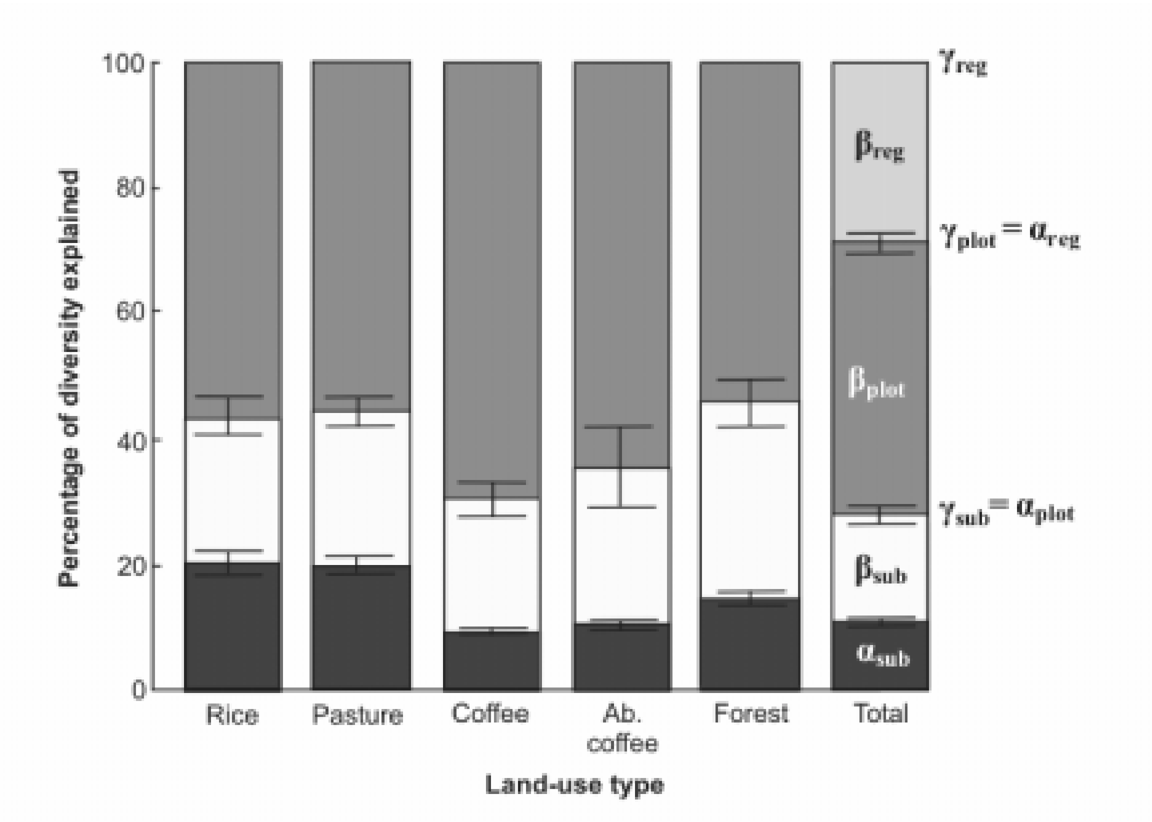


Figure 4.3. Additively partitioned diversity of different land use types presented as a percentage of total diversity for each type, and total diversity for the region.

0.89) or plot scale ($F_{(1,9.6)} = 0.01$, $P > 0.91$).

In the open land use types, forest distance had a significant positive effect on species richness at the plot scale ($F_{(1,10)} = 7.23$, $P = 0.02$) (Fig. 4.5), but not at the subplot scale ($F_{(1,101)} = 2.59$, $P > 0.11$). Therefore, proximity to forest patches did not cause significant variation between traps within a plot, even when the forest was adjacent to the plot. Plot-scale species richness was not affected by plot age ($F_{(117.3)} = 0.02$, $P > 0.89$) or area ($F_{(1,19.9)} = 0.\ 33$, $P > 0.\ 57$).

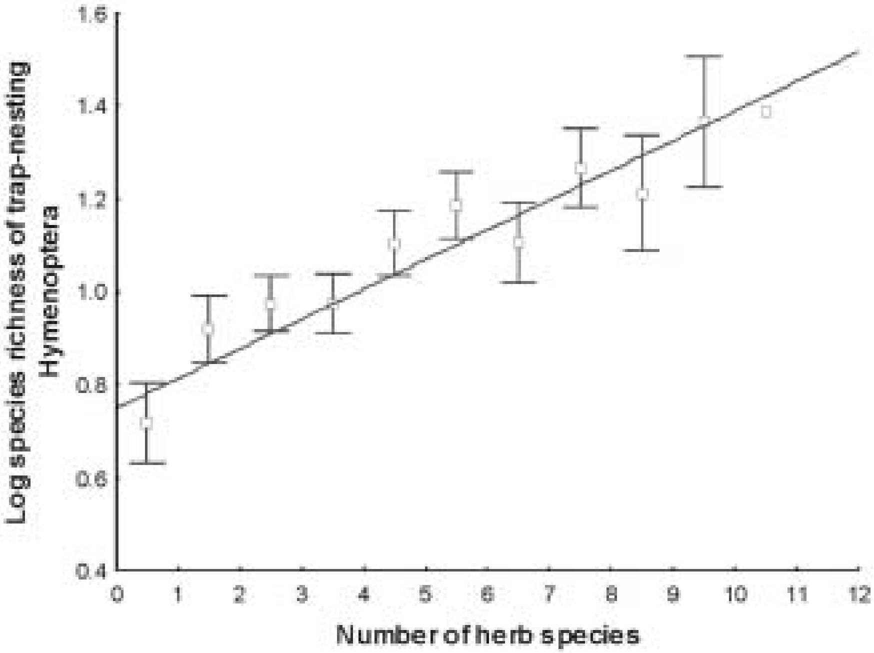


Figure 4.4. Mean number of species of trap-nesting Hymenoptera (Log +/- SE) related to the number of herb species at the subplot level.

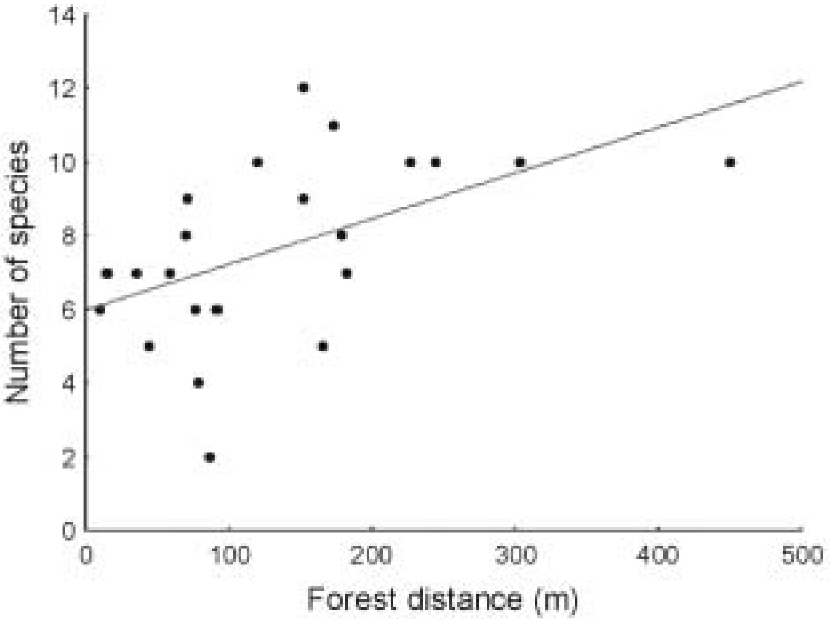


Figure 4.5. Number of trap-nesting species per plot in open (rice and pasture) systems related to forest distance. Rice and pasture are not separated as Hymenoptera in these land use types were not significantly different in their response to forest distance.

Discussion

Land use significantly affected species richness of trap-nesting Hymenoptera at the subplot (α_{sub}) scale, yet we found no effect on species richness at the plot (α_{plot}) scale. This seemingly contradictory result can be explained by differences in the proportionate α and β diversity of the different land use types. Alpha diversity explained a larger proportion of the total diversity in rice and pasture than in the other land use types, and this manifested itself as significantly higher per-trap (i.e. subplot) diversity. However, plot-scale diversity (α_{plot}) and beta (β_{sub}), as a proportion of total diversity, did not vary significantly between land use types (Fig. 4.3). This illustrates that land use does affect diversity (Hypothesis 1); however, alpha and beta diversity must be considered at multiple spatial scales in order to gain a full understanding of community structure (Hypothesis 5).

Alpha diversity in our traps accounted for, on average, 11% of the total diversity for the study region (Fig. 4.3). On average, a high percentage of the total species for a given land use type were not present in each plot (β_{plot} was 43%), a greater proportion in fact than beta between land use types (Fig 4.3). This contradicts the suggestion that within-taxa beta diversity should increase with environmental dissimilarity between plots (Harrison *et al.* 1992), such as between different land use types. Our results also lend support to the contention that human impacts reduce β relative to α diversity (Hypothesis 2; see also Thomas 1991).

The increased species richness we observed at the subplot scale in more intensively managed systems is in general accordance with Klein *et al.* (2002), who found higher diversity of trap-nesting Hymenoptera in more intensively managed agroforestry systems. This is also congruent with the results of DeVries and others (DeVries *et al.* 1997; DeVries & Walla 1999) who found higher diversity of butterflies in more disturbed forests in eastern Ecuador. However, we found this result across a variety of land use types, not simply across different management or disturbance intensities of a single type. These results contradict the common perception that managed land is depauperate in biodiversity, and show that it can be a very valuable contributor to regional conservation of cavity nesting Hymenoptera.

High herb diversity resulted in high diversity of Hymenoptera at the subplot scale, supporting Hypothesis 3 and consistent with the results of Klein *et al.* (2003), who found that diversity of solitary bees increased with increasing blossom cover in coffee agroforests in Indonesia. Floral resource subsidies have been shown to cause aggregation and increased reproduction in Hymenoptera (Tylianakis *et al.* 2004), and one of these mechanisms may have lead to the higher diversity that we observed. However, plot-scale herb diversity did not influence diversity of Hymenoptera. This suggests that floral resources are important for attraction of individual bees within plots, but (perhaps due to their ephemeral nature) are not primary determinants of community diversity at larger spatial scales (Hypothesis 5).

In open (rice and pasture) systems, diversity was higher in plots that were more distant from forest, the reverse pattern to that predicted by Hypothesis 4. However, within a plot, traps that were closer to forest did not differ significantly in species richness from traps that were further from forest. That forest distance only had an effect on larger spatial scales again lends support to Hypothesis 5. It is commonly assumed that natural habitats act as a kind of source population for many species within agriculturally intensified landscapes. For example, Klein *et al.* (2003) found a decrease in the number of social bee species in coffee agroforests with increasing forest distance, and Ricketts (2004) found that higher bee diversity at close proximity to forest led to improved pollination and fruit quality of coffee in Costa Rica. This would not be surprising if intensity of production does, in fact, go hand in hand with reduced biodiversity. However, the pattern found by Klein *et al.* (2003) did not hold for solitary species such as those in our study, and Krauss *et al.* (2003) found no effect of habitat isolation on butterfly diversity. Species richness of solitary wild bees has been shown to correlate positively with the percentage of seminatural habitats at scales of up to 750m (Steffan-Dewenter *et al.* 2002). If 'natural' habitats were to act as a source population for trap-nesting Hymenoptera, how then could we rationalise the contrary pattern of reduced diversity we observed in plots and patches that are proximate to forest-like habitats? It is possible that in regions that are heavily dominated by agriculture, where natural forest systems have been heavily fragmented and disturbed (such as in our study region), forest-specialising species cannot survive easily, and that open, disturbed habitat specialists proliferate. In this sense, many trap-nesting species, such as those of our study, may represent a special case of species that actually benefit from agricultural intensification, perhaps through a greater abundance of herbivore prey or flowering weeds. A similar phenomenon occurs in some tropical butterflies that benefit from feeding on flowering weeds in disturbed forest habitats (DeVries et al 1997). This would explain the positive effect of increasing forest distance we observed in open, more disturbed systems, and imply that determinants of diversity in landscapes depend on the taxa concerned, and possibly on the predominant land use of the region (in our study region, agriculture).

In summary, the significance of herb diversity at the subplot scale only and the surprising effect of forest distance at the plot scale highlight the importance of testing driving factors for differences in biodiversity at different spatial scales. Moreover, the effects of land use on species richness were highly dependent on spatial scale. If diversity estimates in our study region were based only on subplot-scale analyses, it would appear that rice and pasture contain the highest species diversity, and therefore merit the greatest attention. Conversely, a plot-scale analysis would give no indication of which land use system contains the most species. We emphasize caution in the estimation of biodiversity at only one spatial scale, as the selection of different scales for an investigation may result in completely disparate conclusions.

Acknowledgements

We thank J. Casquete and G. Sacoto, for laboratory assistance, C. Calderon, A. Choez and J. Lino for field assistance and K. Gaston, B. Hawkins and J. Krauss for helpful discussions. Y. Clough, D. Gabriel and K. Poveda assisted with analyses. The manuscript was greatly improved by the comments of T. Crist, R. Didham, T. Eggers, T. Rand, K. Summerville, and H. Wagner. D.W. Roubik kindly identified several of our bee species. M. Torres assisted with production of Figure 4.1. R. Olschewski, G. de Koning and B. Pico provided assistance in coordination of this research. This project is part of the BioTEAM research program sponsored by the Federal Ministry of Education and Research (<http://www.bmbf.de>BMBF), Germany.

References

Bawa, K.S., Kress, W.J., Nadkarni, N.M., Lele, S., Raven, P.H., Janzen, D.H., Lugo, A.E., Ashton, P.S. & Lovejoy, T.E. (2004) Tropical ecosystems into the 21st century. *Science* **306,** 227-228.

Bond, E.M. & Chase, J.M. (2002) Biodiversity and ecosystem functioning at local and regional spatial scales. *Ecol Letters* **5,** 467-470.

Cane, J.H. (2001) Habitat fragmentation and native bees: a premature verdict? *Conservation Ecology* **5,** 3 [WWW document] URL:http://www.consecol.org/vol5/iss1/art3

Clausnitzer, V. (2003) Dragonfly communities in coastal habitats of Kenya: indication of biotype quality and the need of conservation measures. *Biodiversity and Conservation* **12,** 333-356.

Costanza, R., d'Arge, R., de Groot. R., Farber, S., Grasso, M., Hannon, B., Limburg, K., Naeem, S., O'Neill, R.V., Paruelo, J., Raskin, R.G., Sutton, P. & van den Belt, M. (1997) The value of the world's ecosystem services and natural capital. *Nature* **387,** 253-260.

Colwell, R. (1997) EstimateS: Statistical estimation of species richness and shared species from samples, Version 501 available free at http://viceroyeebuconnedu/estimates

Crawley, M.J. (2002) *Statistical Computing: an introduction to data analysis using S-Plus.* John Wiley and Sons, England.

Crawley, M.J. & Harral, J.E. (2001) Scale dependence in plant biodiversity. *Science* **291,** 864-868.

Dauber, J., Hirsch, M., Simmering, D., Waldhardt. R., Otte, A. & Wolters, V. (2003) Landscape structure as an indicator of biodiversity: matrix effects on species richness. *Agriculture Ecosystems and Environment* **98,** 321-329.

DeVries, P.J., Murray, D. & Lande, R. (1997) Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biological Journal of the Linnean Society* **62,** 343-364.

DeVries, P.J. & Walla, T.R. (1999) Species diversity in spatial and temporal dimensions of fruit-feeding butterflies from two Ecuadorian rainforests. *Biological Journal of the Linnean Society* **68,** 333-353.

Didham, R.K., Ghazoul, J., Stork, N.E. & Davis, A. (1996) Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* **11,** 255-260.

Gathmann, A. & Tscharntke, T. (2002) Foraging ranges of solitary bees. *Journal of Animal Ecology* **71,** 757-764.

Hamer, K.C. & Hill, J.K. (2000) Scale-dependent effects of habitat disturbance on species richness in tropical forests. *Conservation Biology* **14,** 1435-1440.

Harrison, S., Ross, S.J. & Lawton, J.H. (1992) Beta diversity on geographic gradients in Britain. *Journal of Animal Ecology* **61,** 151-158.

Hughes, J.B., Daily, G.C. & Ehrlich, P.R. (2000) Conservation of insect diversity: a habitat approach. *Conservation Biology* **14,** 1788-1797.

Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschaniwskj, N.A., Pratchett, M.S., Tanner, J.E. & Willis, B.L. (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. *Nature* **397,** 59-63.

James, C.D. & Shine, R. (2000) Why are there so many coexisting species of lizards in Australian deserts? *Oecologia* **125,** 127-141.

Klein, A.-M., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. (2002) Effects of land use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps *Conservation Biology* **16,** 1003-1014.

Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. (2003) Pollination of *Coffea canephora* in relation to local and regional agroforestry management. *Journal of Applied Ecology* **40,** 837-845.

Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. (2004) Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *Journal of Animal Ecology* **73,** 517-525.

Koleff, P. & Gaston, K.J. (2002) The relationships between local and regional species richness and spatial turnover. *Global Ecology and Biogeography* **11,** 363-375.

Krauss, J., Steffan-Dewenter, I. & Tscharntke, T. (2003) How does landscape context contribute to effects of habitat fragmentation on diversity and population density of butterflies? *Journal of Biogeography* **30,** 889-900.

Kruess, A. (2003) Effects of landscape structure and habitat type on a plant-herbivore-parasitoid community. *Ecography* **26,** 283-290.

Lande, R. (1996) Statistics and partitioning of species diversity, and similarity among multiple communities. *Oikos* **76,** 5-13.

Loreau, M. (2000) Are communities saturated? On the relationship between α, β and γ diversity. *Ecology Letters* **3,** 73-76.

Luck, G.W., Daily, G.C. & Ehrlich, P.R. (2003) Population diversity and ecosystem services *Trends in Ecology and Evolution* **18,** 331-336.

Mas, A.H. & Dietsch, T.V. (2003) An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. *Ecological Applications* **13,** 1491-1501.

Myers, N., Mittermeier, R.A., Mittermeier, C.G., da Fonseca, G.A.B. & Kent, J. (2000) Biodiversity hotspots for conservation priorities. *Nature* **403,** 853-858.

Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation* **117,** 285-297.

Perfecto, I., Rice, R.A., Greenberg, R. & Van der Voort, M.E. (1996) Shade coffee: a disappearing refuge for biodiversity. *BioScience* **46,** 598-608.

Perfecto, I., Mas, A., Dietsch, T. & Vandermeer, J. (2003) Conservation of biodiversity in coffee agroecosystems: a tri-taxa comparison in southern Mexico. *Biodiversity and Conservation* **12,** 1239-1252.

R Development Core Team (2004) R: A language and environment for statistical computing. R Goundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org

Ricketts, T.H. (2001) The matrix matters: Effective isolation in fragmented landscapes. *American Naturalist* **158,** 87-99.

Ricketts, T.H. (2004) Tropical forest fragments enhance pollinator activity in nearby coffee crops. *Conservation Biology* **18,** 1-10.

Ricketts, T.H., Daily, G.C., Ehrlich, P.R. & Fay, J.P. (2001) Countryside biogeography of moths in a fragmented landscape: Biodiversity in native and agricultural habitats *Conservation Biology* **15,** 378-388.

Ritchie, M.E. & Olff, H. (1999) Spatial scaling laws yield a synthetic theory of biodiversity. *Nature* **400,** 557-560.

Roland, J. & Taylor, P.D. (1997) Insect parasitoid species respond to forest structure at different spatial scales. *Nature* **386,** 710-713.

Satterthwaite, F.E. (1946) An approximate distribution of estimates of variance components *Biometrics Bulletin* **2,** 110-114.

Segarra, P. (2004) *Informe técnico del mapa de Uso del Suelo y Cobertura Vegetal 1:50000 de la zona comprendida entre Jipijapa, Noboa y Paján Provincia de Manabí.* Proyecto Bio-Sys, Universidad de Goettingen, Alemania y Corporación Ecopar, Quito, Ecuador.

Shahabuddin, Schulze, C.H. & Tscharntke, T. (2005) Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia). *Biodiversity and Conservation* **14,** 863-877.

StatSoft Inc (2003) STATISTICA (data analysis software system), version 6 www.statsoft.com

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. (2002) Scale-dependent effects of landscape context on three pollinator guilds. *Ecology* **83,** 1421-1432.

Summerville, K.S., Boulware, M.J., Veech, J.A. & Crist, T.O. (2003) Spatial variation in species diversity and composition of forest Lepidoptera in eastern deciduous forests of North America. *Conservation Biology* **17,** 1045-1057.

Summerville, K.S. & Crist, T.O. (2004) Constrasting effects of habitat quantity and quality on moth communities in fragmented landscapes. *Ecography* **27,** 3-12.

Thomas, C.D. (1991) Habitat use and geographic ranges of butterflies from the wet lowlands of Costa Rica. *Biological Conservation* **55,** 269-281.

Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998) Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology* **35,** 708-719.

Tylianakis, J., Didham, R. & Wratten, S.D. (2004) Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology* **85,** 658-666.

Tylianakis, J.M., Klein, A.-M. & Tscharntke, T. (in press). Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology*.

Veech, J.A., Crist, T.O. & Summerville, K.S. (2003) Intraspecific aggregation decreases local species diversity of arthropods. *Ecology* **84,** 3376-3383.

Wagner, H.H., Wildi, O. & Ewald, K.C. (2000) Additive partitioning of plant species diversity in an agricultural mosaic landscape. *Landscape Ecology* **15,** 219-227.

Weibull, A.C., Ostman, O. & Granqvist, A. (2003) Species richness in agroecosystems: the effect of landscape, habitat and farm management. *Biodiversity Conservation* **12,** 1335-1355.

Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general hierarchical theory of species diversity. *Journal of Biogeography* **28,** 453-470.

Williams, S.E., Marsh, H. & Winter, J. (2002) Spatial scale, species diversity, and habitat structure: Small mammals in Australian tropical rain forest. *Ecology* **83,** 1317-1329.

Willis, K.J. & Whittaker, R.J. (2002) Species diversity – scale matters. *Science* **295,** 1245-1248.

Chapter

5

Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient

J. M. Tylianakis, A.-M. Klein and T. Tscharntke

In: *Ecology* (2005) 86:

Abstract

Understanding global biodiversity patterns requires analyses at multiple spatial and temporal scales, across a variety of different habitat types. We used a highly replicated study in coastal Ecuador to examine simultaneously for the first time spatial and temporal species turnover and the contribution of five different habitat types (rice, pasture, coffee agroforests, abandoned coffee agroforests and native forest fragments) to regional diversity in the tropics, using the experimental placement of standardised nesting structures for bees and wasps. There was notable overlap in the communities of different habitat types, indicating that even intensively managed land can provide a valuable contribution to the overall biodiversity of the landscape mosaic. Importantly, there was a significant effect of habitat type on temporal variation in diversity. While intensive cropping systems such as rice and pasture exhibited higher diversity in certain months, greater species turnover through time in the abandoned coffee and forest plots accounted for the higher overall diversity in these habitats. Overall, spatial and temporal turnover explained 38.6% and 23.1%, respectively, of partitioned regional species richness. A quantitative analysis revealed that the relative habitat specificity of Hymenoptera decreased with increasing habitat disturbance.

Introduction

Global biodiversity is declining at an alarming rate, and the impending loss of important ecosystem services (Luck *et al.* 2003) has made this one of the most pressing issues facing ecologists today. The realisation that set-aside conservation areas are no longer sufficient to slow this decline has led to an increased focus on managed land for conservation (Perfecto *et al.* 1996, Hughes *et al.* 2002; Bawa *et al.* 2004); however, the importance of such anthropogenic habitats remains somewhat ambiguous and a more complete understanding requires analyses at multiple spatial and temporal scales (Ricklefs & Schluter 1993; May 1994).

While the partitioning of spatial components of species turnover to determine local-regional diversity patterns has attracted considerable attention recently (Gering & Crist 2002; Gaston 2004), temporal variation in biodiversity patterns, such as the contribution of temporal regimes (abiotic, biotic or anthropogenic) in different habitat types to overall landscape diversity is a neglected issue. Some studies have shown that increased management intensity leads to decreased diversity of a variety of taxa (Steffan-Dewenter *et al.* 2002; Mas & Dietsch 2003; Schulze *et al.* 2004; Shahabuddin *et al.* 2005), whereas others have demonstrated higher species richness in disturbed habitats (e.g., DeVries *et al.* 1997; Lawton *et al.* 1998; DeVries & Walla 2001; Klein *et al.* 2002; Chapter 4). The temporally changing importance of habitat type for overall biodiversity may partly explain the contradicting results of these studies; however, this has not yet been examined over a range of different habitats. Temporal heterogeneity in the biodiversity of different habitat types may occur when important resources become available at different times (Wolda 1978, 1988), e.g., during periods of mast flowering or anthropogenic sowing/harvesting. Species may therefore move from one habitat to another, exploiting the availability of predictable, ephemeral resources (Wissinger 1997; Bambaradeniya *et al.* 2004). If there is strong temporal heterogeneity in habitat biodiversity, the time-scale of sampling could lead to a serious over- or underestimation of diversity within a given habitat type (Summerville & Crist 2005), or an unbalanced comparison of diversity between different habitats (Roubik 2001). This is especially pertinent to tropical regions, where relatively little seasonal variation in temperature means that biodiversity sampling is often carried out over short time scales and assumed to be representative of general patterns (e.g., Hughes *et al.* 2002; Shahabuddin *et al.* 2005; but see DeVries *et al.* 1997). Here we use a highly replicated study to examine simultaneously for the first time spatial and temporal species turnover and the contribution of different habitat types to regional diversity in the tropics. We assess the contribution of five different habitats to the biodiversity of a guild of bees and wasps. This variety of habitats is necessary, as many past studies examining the importance of different habitat types for biodiversity deal only with differing management intensities or disturbance levels of a single habitat type (or group of closely related habitats), and therefore cannot give accurate estimates of the overall contribution of managed land to regional biodiversity (but see Schulze *et al.* 2004; Shahabuddin *et al.* 2005). More importantly, we examine whether there is temporal variation in the spatial partitioning of biodiversity. Specifically, we ask 1) does partitioned biodiversity in the region show temporal variation, and is this variation consistent across habitats, 2) do the different habitat types show complementarity in partitioned biodiversity, 3) is there a seasonal shift of species between habitats, and 4) are there significant differences in the specific species composition of each habitat, such that species may be specific to just one type? Specificity is often given a cursory mention in biodiversity studies, as it is intuitively obvious that high diversity of cosmopolitan species is not preferable to slightly lower diversity of rare habitat specialists when global biodiversity decline is considered. Nevertheless, specificity is seldom quantified further than anecdotal observations that a species was only found in one habitat and must therefore be specific to that habitat (for exceptions see McGeoch & Chown 1998; Wagner & Edwards 2001; and references within).

For this study we use the guild of trap-nesting Hymenoptera, as they comprise an important group of pollinators and potential natural enemies of insect pests (Klein *et al.* 2002, 2004). The diversity of these communities is highly correlated with total bee and wasp diversity (Tscharntke *et al.* 1998). Therefore, our results have implications not only for the study and management of biodiversity, but also for the timing and availability of ecosystem services, such as crop pollination or pest population reduction, provided by these species. The habitat types we consider (rice, pasture, coffee agroforests, abandoned coffee agroforests and native forest fragments), represent a gradient of decreasing anthropogenic disturbance, and the predominant habitat types found in Southwest Ecuador.

Materials and Methods

Study region

The 48 study plots are spread across three cantons; Jipijapa (17N 546800m, E 9849274m alt. 259m), Pajan (17N 563969, E 9828342m alt. 142m) and 24 de Mayo (largest town: Noboa 17N 567374m, E 9844106 alt. 260m) within the province of Manabi, Southwest Ecuador (see online supplement for site details). The region falls within the semi-arid tropics and is largely dominated by agriculture. There are a variety of different crops cultivated in this area, however we consider only the dominant ones - an arable crop (rice), pasture and agroforestry (coffee). The structure of coffee agroforests can vary greatly with individual management. Therefore, an effort was made to select plots that had been in cultivation for over 8 years, used no chemical fertilizers and had a similar degree of shade tree cover (60 – 80%). Many coffee agroforests have been abandoned by owners due to low economic returns. As these abandoned agroforests occupy a large proportion of the landscape, we included abandoned coffee as a natural intermediate between cultivated coffee and forest. There is no primary rainforest remaining in the zone, so for this study we used the most “natural” systems available (which were partly disturbed forest fragments). Coffee is the most abundant land-use type within the landscape (54.8% of the study zone), followed by forest (including disturbed forest and abandoned agroforests) (17.2%), pasture (16.2%) and arable crops (1.9%) (Segarra 2004). Twelve replicates of each managed habitat type were sampled in the study, as well as six abandoned coffee agroforests (abandoned for 10 - 15 years and now resembling secondary forest) and six forest fragments.

The study plots were generally clustered in groups of three or more different habitat types so as to avoid spatial autocorrelation resulting from several plots of one habitat type being clustered together.

Trap nests

Nine trap-nests were positioned (in a 3 x 3 grid, 25 m between adjacent traps) in the centre of each of the 48 plots. Trap nests were constructed according to the methodology of Tscharntke *et al.* (1998). A PVC tube with a length of 22 cm and a diameter of 15 cm formed the outer case of the nest. Internodes of reeds *Arundo donax* L. (Poaceae) with varying diameter (2 – 20 mm) and a length of 20 cm were inserted into this tube and provided the nesting sites for bees and wasps. Trap nests were hung from trees in shaded (coffee, abandoned coffee and forest) systems and suspended from wooden posts in open (rice and pasture) systems. Sticky glue (tanglefoot) was applied to the post or attachment point to deter ants. All traps were positioned 1.5 m above the ground.

A broad spectrum fungicide (Fitoraz® 76 PM, Bayer: Propineb 21 g/L, Cymoxanil 1.8 g/L) that is not toxic to Hymenoptera was applied to each trap with a hand sprayer every month.

Sampling period

Each trap was evaluated every month from June 2003 to May 2004 (temperature and rainfall for this region is presented in Appendix A), and all reed internodes that were occupied by Hymenoptera were removed and replaced with new internodes of the same diameter. Occupied reeds were opened and the larvae were reared to maturity for positive identification to morphospecies (hereafter referred to simply as ‘species’). Data from each of the nine traps were pooled for each plot. Parasitoids and cleptoparasites were excluded from analyses, as their diversity is partially dependent on available host species.

Data analyses

We carried out all statistical analyses using Statistica 6.1 (StatSoft 2003). The effect of habitat type on overall diversity and abundance per plot was analysed with ANOVA and post hoc Tukey’s pairwise comparisons on data with normally distributed model residuals. Analyses of seasonal effects of habitat type on species richness, Shannon index, and abundance were conducted using repeated measures ANOVA.

The effects of habitat area and time in cultivation (plot age) on diversity were tested simultaneously using general linear models with habitat type as a fixed factor.

To determine temporal species turnover, we used additive partitioning of species diversity (Lande 1996), a technique that is insensitive to differences in sampling effort among replicates, and therefore does not require rarefaction of data prior to analyses (Veech *et al.* 2002; Crist *et al.* 2003). Alpha diversity (α) was defined as the mean number of morphospecies per plot, per month. The temporal turnover in species richness between months was calculated for each plot (β_{TPlot}) within a given habitat type as: the total number of morphospecies found within that plot (over the entire year) minus the mean number of morphospecies per month for that plot (α). Overall β_T was calculated as the mean β_{TPlot} for a given habitat type. Spatial turnover (β_S) was calculated as: the total number of morphospecies found within a habitat type over the entire year minus the mean number of morphospecies per plot of that habitat type (over the entire year).

Therefore, the overall diversity of a habitat type, $\gamma = \alpha + \beta_T + \beta_S$.

As α and β_{TPlot} were replicated across plots, they were analysed as a proportion of γ (arcsine square root transformed), and treated as multivariate responses in a mixed effects model with habitat type as a fixed factor.

We estimated a habitat specificity index for each species by comparing observed and expected numbers of each species in each habitat type. Some published specificity measures (e.g., McGeoch & Chown 1998) are useful for within-habitat comparisons of species, but are biased by differences in sample size between habitats. We therefore calculated the expected number of individuals of species *i* for habitat *j* as:

$E_{ij} = N_i.P_j$

where N_i is the total number of individuals of species *i* across all habitats, and P_j is the proportion of the total individuals sampled (of all species across all habitats) that were found in habitat *j*. E_{ij} therefore represents the number of individuals of species *i* that we would expect in habitat *j* if this species showed no preference for any habitat type and distributed itself randomly across habitats proportionately to the relative abundance of all species in each habitat. We then used $\log_{10}\{(O_{ij}/E_{ij})+1\}$, where O_{ij} is the observed number of individuals of species *i* in habitat *j*, as a measure of specificity, i.e. the deviation of species *i* from the expected random distribution. The specificity measures for every species were compared across habitats using a non-parametric Friedman ANOVA by ranks, to determine whether the species had on average higher specificity in one or more habitats. Post-hoc pairwise comparisons were then made with Wilcoxon matched pairs tests.

Results

Seasonal analyses

In total, 15 047 individuals of 31 species (Hymenoptera: Apidae, Eumenidae, Megachilidae, Mutilidae, Pompilidae and Sphecidae) were collected from the 432 trap nests. Species richness was not significantly correlated with individual abundance (Spearman rank correlation, r = -0.15, N = 48, P > 0.1).

Season had a strong effect on species richness ($F_{(11,473)} = 7.30$, $P < 0.0001$) and Shannon index ($F_{(11,473)} = 6.83$, $P < 0.0001$) in the different habitat types, as did the habitat type itself ($F_{(4,43)} > 5.54$, $P \leq 0.001$ for richness and Shannon). Season and habitat interacted significantly on species richness, such that seasonal effects were different in the different habitat types ($F_{(44,473)} = 2.25$, $P < 0.0001$). On average per month, species richness and Shannon index were highest in the most intensive systems (Fig. 5.1). At the beginning of the dry season (June-August 2003), rice and pasture had significantly higher alpha diversity than other habitat types ($F_{(4,43)} > 9.97$, $P < 0.0001$ in each month). Rice and pasture were also highest in October 2003 and January-

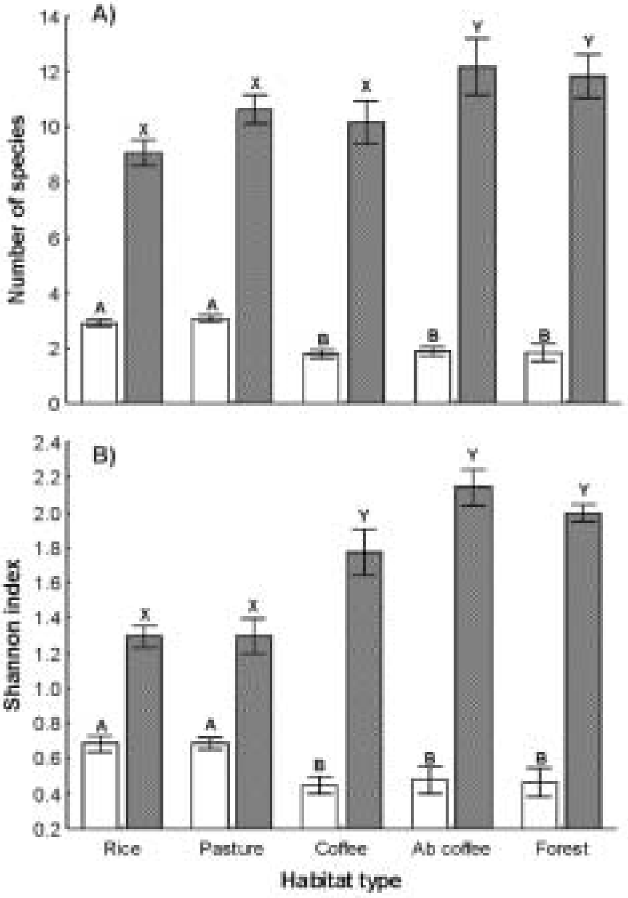


Figure 5.1. Mean (± SE) A) number of species and B) Shannon index per plot per month (white bars) and per plot over the entire year (shaded bars) in each of the five habitat types: rice, pasture, coffee agroforest, abandoned coffee agroforest and forest fragment. Letters represent significant differences between means in a post-hoc Fisher LSD test.

February 2004, although the effect was weaker in these months ($F_{(4,43)} > 2.72$, $P < 0.05$ in each month). Abundance of individuals was also affected by season ($F_{(11,473)} = 13.61$, $P < 0.0001$) and habitat type ($F_{(4,473)} = 18.93$, $P < 0.0001$), and these variables interacted significantly ($F_{(44,473)} = 6.97$, $P < 0.0001$).

In a comparison of the rainy vs dry season (see Appendix A), the mean number of species per plot was higher in the rainy season ($F_{(1,43)} = 9.90$, $P < 0.005$), and this effect did not differ significantly among habitat types (interaction effect: $F_{(4,43)} = 9.90$, $P > 0.05$). There were eight out of 31 species that were found in the rainy season and not in the dry season (and eight species that showed the reverse pattern), across all habitat types.

Effects of habitat on overall diversity and abundance

When data for the entire year were pooled for each plot, habitat type significantly affected the number of individuals ($F_{(4,43)} = 18.69$, $P < 0.0001$), which was highest in rice and pasture plots. Species richness ($F_{(4,43)} = 2.58$, $P = 0.050$) and Shannon index ($F_{(4,43)} = 11.09$, $P < 0.0001$) were also significantly affected by habitat type. However, despite having lower abundance of individuals, and lower diversity per month (see above) forest and abandoned coffee showed the highest richness and Shannon index per plot over the entire year, and coffee showed an equally high Shannon index (Fig. 5.1). In total, across all plots and months, rice contained 21 species, managed coffee contained 24, and the remaining habitat types contained 25 species each.

Habitat area and time in cultivation did not significantly affect species richness ($F_{(1,41)} < 0.71$, $P > 0.40$ for both age and area) or Shannon index ($F_{(1,41)} < 0.19$, $P > 0.66$ for both age and area) of trap nesting Hymenoptera.

Partitioning of species diversity across spatio-temporal scales

The different habitat types showed substantial differences in the relative partitioning of diversity across space and time (Fig. 5.2). The most intensive systems (rice and pasture) had proportionately higher diversity per plot (α/γ) ($F_{(4,43)} = 18.16$, $P < 0.0001$), and relatively high species turnover across plots (β_S); however, temporal species turnover (β_T) was low in these systems. Conversely, abandoned coffee and forest had a significantly larger proportion of γ explained by β_{TPlot} than did the other systems ($F_{(4,43)} = 3.27$ $P <$

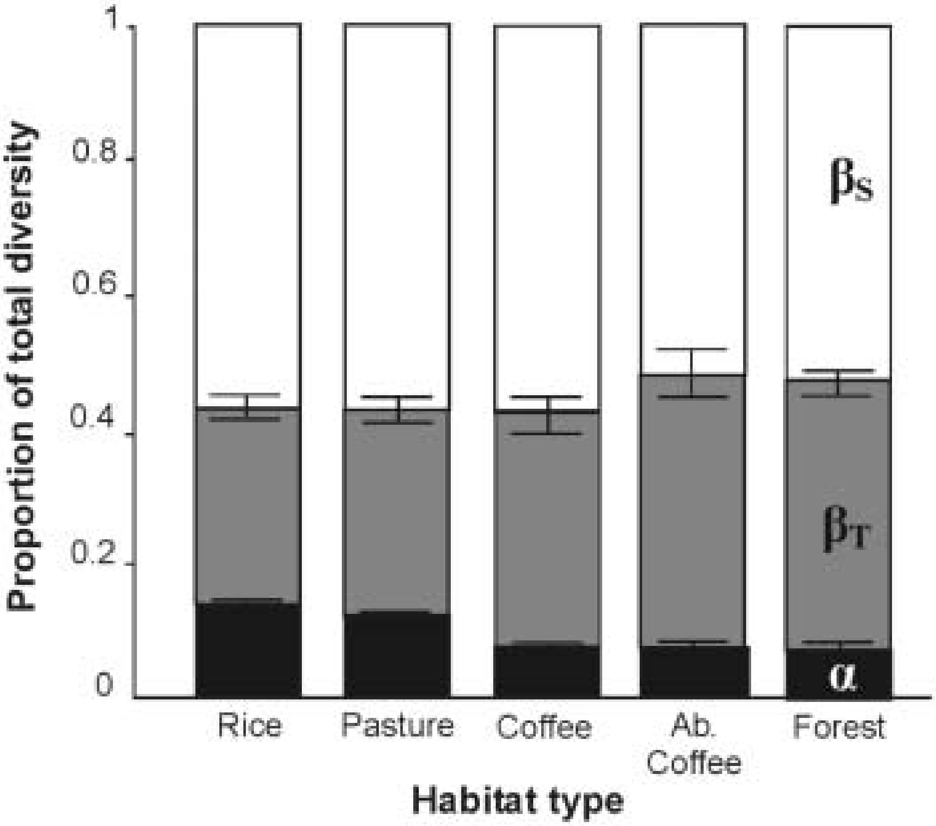


Figure 5.2. Proportion of total (γ) diversity partitioned into α diversity and temporal (β_T) and spatial (β_S) turnover. The mean number of species per plot, per month is represented by α diversity. Error bars show SE among plots.

0.02), and they also had relatively low α and β_S diversity (Fig. 5.2). Overall, at the level of sampling conducted, α diversity comprised 6.9% of the total diversity of our study region (31 species). Temporal and spatial turnover comprised 23.1% and 38.6%, respectively, of total diversity and the remaining 31.4% represented turnover in species between the different habitat types.

Specificity analyses

Although there was some variation in species composition across habitat types, overall specificity was relatively low. Abandoned coffee had no entirely specific species, forest had two (forest and abandoned coffee combined had an additional one) and each of the remaining habitats contained one species that was specific to that type. Specificity (as measured by the specificity index) varied significantly across habitats (Chi-sq = 11.63, N = 33, DF = 4, P = 0.020), with rice and pasture showing significantly lower specificity (below expected values), than coffee, abandoned coffee, or forest (Wilcoxon matched pairs tests: Valid N = 33, Z > 2.6, P < 0.0078 in significantly different pairs), which had median observed values that were higher than those expected by random distribution of individuals among habitats in proportion to sample size (Fig. 5.3).

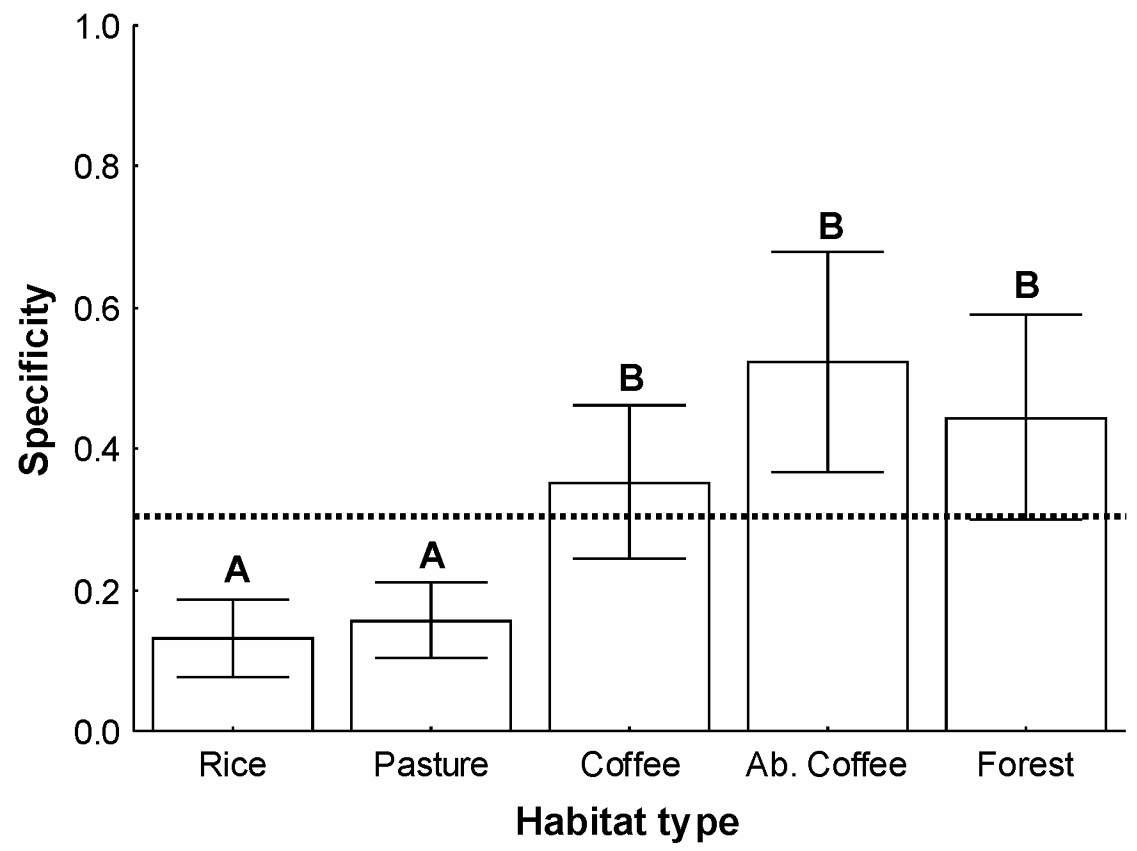


Figure 5.3. Specificity ($\log_{10}\{(\text{Observed}/\text{Expected})+1\}$ number of individuals per species) (median ± 95% CI) in the five different habitat types. Letters show significant differences based on pairwise comparisons using Wilcoxon matched pairs tests. The dotted line represents observed values equal to expected values, i.e. distribution among habitats in proportion to sample size.

Discussion

Diversity varied greatly among habitat types and seasons. If we had only carried out a ‘snapshot’ comparison of habitat types at the beginning of the dry season (June – August

2003), we would have falsely concluded that the most intensive cropping systems (rice and pasture) contained the highest diversity of trap-nesting bees and wasps in this study system (as found by Klein *et al.* 2002; Chapter 4). However, when we analysed data for the entire year, we found that the less disturbed habitats (forests and abandoned coffee agroforests) had higher temporal species turnover, which led to greater overall diversity. These highly contradictory outcomes demonstrate the necessity for adequate sampling regimes that incorporate the temporal component of variation in biodiversity, and may help to explain the varied responses of diversity to disturbance intensity that have been observed in previous, single season studies (e.g., Schulze *et al.* 2004; Shahabuddin *et al.* 2005; Chapter 4). This is particularly important for mobile species with short generation times such as insects.

Surprisingly, coffee agroforests did not maintain significantly higher overall species richness than did the more intensively managed crops, although Shannon index was significantly higher. This more marginal role of agroforestry is consistent with the results of Shahabuddin *et al.* (2005), and contrasts with the perception that shade coffee agroforests may be a potentially important refuge for biodiversity (e.g., Perfecto *et al.* 1996; Moguel & Toledo 1999). However, we found that agroforests that had been abandoned for 10-15 years were not significantly different from forest fragments in their associated diversity of Hymenoptera, and that both productive and abandoned coffee showed high habitat specificity scores (see below). This may imply that decreases in biodiversity are more ephemeral in agroforests compared with more destructive annual crops; however, studies are needed that compare several crop types that have been abandoned for the same period. Coffee also showed relatively high spatial and temporal turnover in diversity (Fig. 5.2), indicating that there may be great variation among different plots due to variation in management practices.

The increase in Hymenoptera diversity per plot that we observed in the rainy season was concomitant with higher herb diversity per plot at this time (T. Lozada, unpubl. data). This is in accordance with the broad pattern of high trap-nesting bee and wasp diversity in areas of high flowering herb diversity (Klein *et al.* 2002; Chapter 4).

Contrary to expectations, there was not a great degree of habitat specificity in communities of trap-nesting bees and wasps. All habitat types had one or two species specific to that type, but there was considerable overlap in community composition between habitats, rather than high complementarity. Coffee, abandoned coffee and forest fragments had the highest specificity scores, indicating that the proportion of habitat specialists (like overall diversity) declines with increasing habitat disturbance.

Total regional species richness did not show great variation between the dry and rainy seasons (23 species in each season); however, species composition changed dramatically (ca. 30% turnover in species identity between the two seasons – see online supplement), as did the distribution of species richness among the different habitat types. We found no direct evidence of seasonal movement between different habitat types, although there were a total of 16 species that we only observed in either the rainy or dry season. Whether these taxa migrate from outside the region, are present year-round at low densities, or spend part of the year in a larval or pupal stage is unclear. Metapopulation studies of individual species will be necessary to ascertain whether movement between different habitat types actually occurs. Furthermore, in order for the ecosystem services of different species to be utilised, the time at which they occur requires careful consideration. For example, Sperber *et al.* (2004) found that populations of beneficial parasitoids emigrated from Brazilian cacao agroforests to nearby forest remnants in winter, yet high tree diversity encouraged a greater diversity of parasitoid families in spring and summer.

In conclusion, although we found the highest overall biodiversity and specificity in the more natural systems (abandoned coffee and forest fragments), the diversity of Hymenoptera within each habitat type showed great temporal variability. This emphasises that temporal, as well as spatial, dynamics are integral to the distribution of biodiversity, and even studies conducted in the tropics must consider temporal variation when partitioning components of regional species diversity. Although our results indicate that temporal variation in biodiversity is very important, we realise that one year is, ecologically speaking, a relatively short time, and interannual temporal turnover may also explain a significant portion of overall species richness.

All habitat types contributed to between 60% and 70% of the total regional diversity observed in our study. Therefore, our results show that even intensively managed land can provide a valuable contribution to the overall biodiversity of the landscape mosaic.

Acknowledgements

Climate data were provided by the Instituto Nacional de Meteorología e Hidrología (www.inamhi.gov.ec). We thank J. Casquete, J. Pico, G. Sacoto, C. Valarezo, C. Calderon, A. Choez and J. Lino for laboratory and field assistance, T. Lozada for herb data, J. Krauss and K. Poveda for helpful discussions, and R. Olschewski, G. de Koning and B. Pico for assistance in coordination of this research. The manuscript profited from the insightful comments of R. Didham, T. Rand, M. Eubanks and two anonymous referees. This project is part of the BioTEAM research program sponsored by the Federal Ministry of Education and Research (<http://www.bmbf.de>BMBF), Germany.

References

Bambaradeniya, C.N.B., Edirisinghe, J.P., De Silva, D.N., Gunatilleke, C.V.S., Ranawana, K.B. & Wijekoon, S. (2004). Biodiversity associated with an irrigated rice agro-ecosystem in Sri Lanka. *Biodiversity and Conservation*, 13, 1715-1753.

Bawa, K.S., Kress, W.J., Nadkarni, N.M., Lele, S., Raven, P.H., Janzen, D.H., Lugo, A.E., Ashton, P.S., Lovejoy, T.E. (2004). Tropical ecosystems into the 21st century. *Science*, 306, 227-228.

Crist, T.O., Veech, J.A., Gering, J.C. & Summerville, K.S. (2003). Partitioning species diversity across landscapes and regions: a hierarchical analysis of α, β and γ diversity. *American Naturalist*, 162, 734-743.

DeVries, P.J., Murray, D. & Lande, R. (1997). Species diversity in vertical, horizontal, and temporal dimensions of a fruit-feeding butterfly community in an Ecuadorian rainforest. *Biol. J. Linn. Soc.*, 62, 343-364.

DeVries, P.J. & Walla, T.R. (2001). Species diversity and community structure in neotropical fruit-feeding butterflies. *Biol. J. Linn. Soc.*, 74, 1-15.

Gaston, K.J. (2004). Macroecology and people. *Basic and Applied Ecology*, 5, 303-307.

Gering, J.C. & Crist, T.O. (2002). The alpha-beta-regional relationship: providing new insights into local-regional patterns of species richness and scale dependence of diversity components. *Ecology Letters,* 5, 433-444.

Hughes, J.B., Daily, G.C. & Ehrlich, P.R. (2002). Conservation of tropical forest birds in countryside habitats. *Ecology Letters*, 5, 121-129.

Klein, A.-M., Steffan-Dewenter, I., Buchori, D. & Tscharntke, T. (2002). Effects of land-use intensity in tropical agroforestry systems on coffee flower-visiting and trap-nesting bees and wasps. *Conserv. Biol.*, 16, 1003-1014.

Klein, A.-M., Steffan-Dewenter, I. & Tscharntke, T. (2004). Foraging trip duration and density of megachilid bees, eumenid wasps and pompilid wasps in tropical agroforestry systems. *J. Anim. Ecol.*, 73, 517-525.

Lande, R. (1996). Statistics and partitioning of species diversity and similarity among multiple communities. *Oikos*, 76, 5-13.

Lawton, J.H., Bignell D.E., Bolton, B., Bloemers, G.F., Eggleton, P., Hammond, P.M., Hodda, M., Holt, R.D., Larsen, T.B., Mawdsley, N.A., Stork, N.E., Srivastava, D.S., Watt, A.D. (1998). Biodiversity inventories, indicator taxa and effects of habitat modification in tropical forest. *Nature,* 391, 72-76.

Luck, G.W., Daily, G.C. & Ehrlich, P.R. (2003). Population diversity and ecosystem services. *Trends Ecol. Evol.*, 18, 331-336.

Mas, A.H. & Dietsch, T.V. (2003). An index of management intensity for coffee agroecosystems to evaluate butterfly species richness. *Ecological Applications*, 13, 1491-1501.

McGeoch, M.A. & Chown, S.L. (1998). Scaling up the value of bioindicators. *Trends in Ecology and Evolution*, 13, 46-47.

May, R.M. (1994). The effects of spatial scale on ecological questions and answers. In: P.J. Edwards, R.M. May & N.R. Webb (eds.) *Large-scale Ecology and Conservation Biology*. Blackwell Scientific, Oxford, UK.

Moguel, P. & Toledo, V.M. (1999). Biodiversity conservation in traditional coffee systems of Mexico. *Conservation Biology*, 13, 11-21.

Perfecto, I., Rice, R.A., Greenberg, R. & Van der Voort, M.E. (1996). Shade coffee: a disappearing refuge for biodiversity. *BioScience*, 46, 598-608.

Ricklefs R.E. & Schluter, D. (eds.)(1993). *Species diversity in Ecological Communities: Historical and geographical perspectives*. University of Chicago Press. Chicago, USA.

Roubik, D.W. (2001). Ups and downs in pollinator populations: When is there a decline? *Conservation Ecology,* 5, 2. [online] URL: http://www.consecol.org/vol5/iss1/art2/

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Mühlenberg, M., Gradstein, S.R., Leuschner, C., Steffan-Dewenter, I. & Tscharntke, T. (2004). Biodiversity indicator groups of tropical land-use systems: comparing plants, birds, and insects. *Ecological Applications*, 14, 1321-1333.

Segarra, P. (2004). *Informe técnico del mapa de Uso del Suelo y Cobertura Vegetal 1:50000 de la zona comprendida entre Jipijapa, Noboa y Paján Provincia de Manabí.* Proyecto Bio-Sys, Universidad de Goettingen, Alemania y Corporación Ecopar, Quito, Ecuador.

Shahabuddin, Schulze, C.H. & Tscharntke, T. (2005). Changes of dung beetle communities from rainforests towards agroforestry systems and annual cultures in Sulawesi (Indonesia). *Biodiversity and Conservation,* 14, 863-877.

Sperber, C.F., Nakayama, K., Valverde, M.J. & Neves, F.D. (2004). Tree species richness and density affect parasitoid diversity in cacao agroforestry. *Basic and Applied Ecology*, 5, 241-251.

StatSoft, Inc. (2003). STATISTICA (data analysis software system), version 6. www.statsoft.com.

Steffan-Dewenter, I., Münzenberg, U., Bürger, C., Thies, C. & Tscharntke, T. (2002). Scale-dependent effects of landscape context on three pollinator guilds. *Ecology*, 83, 1421-1432.

Summerville, K.S. & Crist, T.O. (2005) Temporal patterns of species accumulation in a survey of Lepidoptera in a beech-maple forest. *Biodiversity and Conservation*, in press.

Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998). Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *J. Appl. Ecol.*, 35, 708-719.

Veech, J.A., Summerville, K.S., Crist, T.O. & Gering, J.C. (2002). The additive partitioning of diversity: recent revival of an old idea. *Oikos*, 99, 3-9.

Wagner, H.H. & Edwards, P.J. (2001). Quantifying habitat specificity to assess the contribution of a patch to species richness at a landscape scale. *Landscape Ecology*, 16, 121-131.

Wissinger, S.A. (1997). Cyclic colonization in predictably ephemeral habitats: a template for biological control in annual crop systems. *Biological Control*. 10, 4-15.

Wolda, H. (1978). Seasonal fluctuations in rainfall, food and abundance in tropical insects. *Journal of Animal Ecology*, 47, 369-81.

Wolda, H. (1988). Insect seasonality: why? *Annual Review of Ecology and Systematics,* 19, 1-18.

Appendix 5.1. Online Appendix

Jason Tylianakis, Alexandra-Maria Klein and Teja Tscharntke. 2005. Temporally-dependent effects of habitat on spatially partitioned Hymenoptera diversity within a tropical mosaic landscape. *Ecology* VOL: pp-pp.

Appendix A. Monthly temperature (^{o}C) and rainfall (mm) in Pajan (17N 563969, E 9828342m alt. 142m) within our study region in 2003.
The rainy season begins in December and ends in May.

	Dec	*Jan*	*Feb*	*Mar*	*Apr*	*May*	*Jun*	*Jul*	*Aug*	*Sep*	*Oct*	*Nov*
Temperature	25.8	25.7	25.8	26	25.9	25.9	25.6	25.3	25.4	25.6	25.6	25.4
Rainfall	73.3	197.1	276.1	307.1	293.6	143.2	35.8	18.4	7.3	6.7	4.5	28.8

Appendix 5.2. Online supplement: site_table.csv

Details of the location, age, area, and habitat type of each plot, with species richness, individual abundance and Shannon index over the entire year. Column (1) gives the habitat type (forest fragment, abandoned coffee, coffee, pasture or rice). The second and third columns give the GPS coordinates (UTM 17) of the plots in metres (2) East and (3) South respectively. Column (4) gives the elevation of the plot in metres. Column (5) gives the area of the plot in hectares and column (6) gives the age (years in cultivation with that particular habitat type) of the plot. Column (7) gives the species richness, (8) gives the number of individual larvae found in the traps and (9) the Shannon diversity Index over a 1 year sampling period.

Type	E	S	Elev.	Area	Age	Species	Indiv.	Shannon
Ab. Coffe	9835796	563314	354	2	15	7	56	1.687
Ab. Coffe	9828140	559366	230	1	10	13	151	2.146
Ab. Coffe	9822004	549768	401	2	10	13	75	2.367
Ab. Coffe	9819264	549200	358	1	12	14	175	2.289
Ab. Coffe	9830652	569611	128	1	16	14	157	2.370
Ab. Coffe	9811036	562421	346	1	15	12	120	2.006
Coffee	9844870	566670	180	5	15	10	215	1.597
Coffee	9841336	570482	228	6	25	10	105	1.917
Coffee	9832226	569803	132	10	30	12	202	2.107
Coffee	9837024	570716	126	3	30	6	72	1.588
Coffee	9830485	571246	148	1	15	15	193	2.285
Coffee	9827161	564191	136	2	24	10	65	2.167
Coffee	9824511	566837	125	1.5	8	9	73	1.878
Coffee	9840142	571993	198	2	20	10	99	1.845
Coffee	9839314	562322	467	2	30	5	297	0.660
Coffee	9837120	560633	471	6	20	9	190	1.075
Coffee	9828048	568651	194	0.8	8	14	129	2.241
Coffee	9830574	569064	190	1.5	40	12	139	1.907
Forest	9830698	572012	110	1	30	14	263	2.031
Forest	9824511	566837	140	2	40	14	195	2.055
Forest	9835774	563422	369	2	60	10	68	1.751
Forest	9837364	560303	471	10	2	12	130	2.106
Forest	9810148	563307	308	25	80	12	65	2.063
Forest	9805960	563128	347	25	80	9	67	1.971
Pasture	9844972	567846	205	0.75	25	13	189	1.700
Pasture	9841319	569843	180	2	20	13	699	1.601
Pasture	9832121	569533	130	1.5	50	11	833	1.402
Pasture	9837350	570866	136	1.5	9	9	538	1.039
Pasture	9830749	570410	121	1.5	40	11	539	1.110
Pasture	9827113	564587	125	1	30	11	398	1.383
Pasture	9824316	567452	160	1.5	20	10	380	1.588
Pasture	9840111	571780	186	5	30	13	371	1.591
Pasture	9840014	561598	477	2	20	9	268	1.372
Pasture	9837259	560441	471	2	30	7	612	0.821
Pasture	9828324	569287	193	8	14	9	751	0.470
Pasture	9830544	568947	187	1	40	12	438	1.487
Rice	9844318	565629	156	0.75	2	12	297	1.572
Rice	9841059	569801	179	1.5	8	11	605	1.592
Rice	9832126	569803	126	2	5	8	658	1.219
Rice	9837018	570716	126	1.5	10	6	337	1.040
Rice	9830614	570695	119	0.75	6	11	473	1.354
Rice	9826975	564833	120	2	7	8	466	1.497
Rice	9824383	566908	105	1.2	4	8	303	1.446
Rice	9840298	571901	189	0.75	8	10	236	1.389
Rice	9839223	562412	471	1	2	10	427	1.001
Rice	9837713	560684	470	0.6	5	8	330	1.438
Rice	9828204	568962	175	3	2	9	285	1.032
Rice	9830574	569064	190	1.5	6	8	552	0.930

Chapter

6

Diversity, ecosystem function, and stability of parasitoid-host interactions across a tropical gradient of habitat modification

J.M. Tylianakis, T. Tscharntke and A.-M. Klein

(Submitted)

Abstract

Global biodiversity decline has prompted great interest in the effects of habitat modification and diversity on the functioning and stability of ecosystem processes. However, the applicability of previous modelled or mesocosm community studies to real diverse communities in different habitats remains ambiguous.

We exposed standardised nesting resources for naturally-occurring communities of cavity-nesting bees and wasps and their natural enemies in coastal Ecuador, to test the effects of host and natural enemy diversity on ecosystem function (parasitism rates) and temporal variability in this function. Parasitism rates increased with increasing diversity of natural enemies and their hosts, exceeding the effects of increased enemy abundance alone. Temporal variability in parasitism was lower in plots with high mean natural enemy diversity and higher in plots with temporally variable host and natural enemy diversity. These effects of diversity on parasitism and temporal stability in parasitism rates were sufficiently strong to be visible across five different habitat types, representing a gradient of increasing anthropogenic modification.

Introduction

The modification of landscapes through human exploitation of the environment continues to reduce biodiversity on a global scale (Vitousek *et al.* 1997). This dramatic anthropogenically mediated decline in biodiversity has led to concern over the potential loss of important ecosystem processes (Foley *et al.* 2005), and the need for a clearer understanding of the ways in which diversity affects ecosystem functioning (Chapin *et al.* 2000; Daily *et al.* 2000; Hooper *et al.* 2005) and variability in this functioning over time (Rodriguez & Hawkins 2000; Halpern *et al.* 2005). The tenet that diversity increases ecosystem functioning has itself engendered some controversy (e.g., Huston 1997; Tilman *et al.* 1997; Naeem 2002), and several authors have argued for a clearer understanding of the interactions between abiotic factors and diversity/function (e.g., Loreau *et al.* 2001).

Much recent work has focused on the relationship between diversity and productivity in plant communities (e.g., Mouquet *et al.* 2002; Pfisterer & Schmid 2002; Cardinale *et al.* 2004; Lambers *et al.* 2004; van Ruijven & Berendse 2005); however, there is some evidence that the dominant impacts of biodiversity change on ecosystem functioning are trophically mediated by consumers (Duffy 2003). A recent link has therefore been made between the body of work relating to ecosystem function and that relating to predator-prey interactions (Ives *et al.* 2005).

Diversity effects on consumer-resource interactions have until now been examined using modelled (Fox 2004; Ives *et al.* 2005) or simplified communities in the laboratory (Gamfeldt *et al.* 2005) or in field cage (Cardinale *et al.* 2002; 2003; Finke & Denno 2004) environments. While this work has been critical to understanding the mechanisms through which diversity may affect ecosystem processes, the structure and diversity of experimental communities often differs markedly from the communities actually providing ecosystem services within real landscapes (Sih *et al.* 1998; Kremen 2005). Therefore, uncertainty remains as to how the results of such experiments scale up to landscapes and generalize across different spatiotemporal scales and habitat types (Loreau *et al.* 2001; Cardinale *et al.* 2004).

Related to the diversity/function debate is the effect of diversity on stability of ecosystems and their processes. This subject has received considerable attention (see

Pimm 1984; McCann 2000; Cottingham *et al.* 2001 for reviews), and carries important implications for conservation and sustainable agriculture, as consistency in ecosystem services is required over time. Moreover, diversity effects on ecosystem functioning and stability generally act in concert, so these factors are most meaningful when studied together (Pfisterer & Schmid 2002; Worm & Duffy 2003). As with diversity/function relationships, much of the diversity/stability literature has focused on stability of plant productivity (e.g., Tilman 1996; Tilman *et al.* 1998; Pfisterer & Schmid 2002; Caldeira *et al.* 2005). However, the importance of predator diversity for ecosystem stability remains poorly studied (Loreau *et al.* 2001), despite the importance of these species for biological pest control, and the fact that higher trophic levels frequently suffer more from landscape modification (Kruess & Tscharntke 1994). Although there is some evidence from the laboratory (Steiner *et al.* 2005), the effects of diversity on consumer-resource interactions and stability in real systems remain contentious (Rodriguez & Hawkins 2000; Montoya *et al.* 2003; Finke & Denno 2004). A recent meta-analysis found a destabilising effect of predator diversity on herbivore biomass (Halpern *et al.* 2005), whereas a field investigation of a parasitoid guild showed no effect of diversity on functioning and stability (Rodriguez & Hawkins 2000).

We address this dearth of field evidence by examining the effect of natural enemy diversity on ecosystem functioning (parasitism rates) and stability of parasitism rates through time. We also examine how these effects vary across different habitat types, forming a gradient of anthropogenic modification. We use a diverse guild of cavity-nesting bees and wasps, and their natural enemies in coastal Ecuador, and find that increased diversity of natural enemies (parasitoids and cleptoparasites) leads to increased parasitism rates, exceeding the effects of abundance of natural enemies or their hosts. We also show that high mean diversity per month leads to low between month variability in parasitism (i.e. high stability), even though high overall diversity across the entire sampling period had no significant effect on stability. Conversely, temporally variable natural enemy and host diversity led to variable rates of parasitism between months. These effects were found across five different habitat types, representing a gradient of increasing anthropogenic modification. Our results show that consistently high diversity can promote ecosystem functioning and temporal stability, whereas variability in diversity through time is inimical to the maintenance of high parasitism rates.

Materials and Methods

Study region

The 48 study plots were spread across three cantons in the region of Jipijapa (17N 546800m, E 9849274m alt. 259m), within the province of Manabi, Southwest Ecuador (for individual plot location details and a full description of the region see Tylianakis *et al.* in press). The region falls within the semi-arid tropics and is largely dominated by agriculture. Here we examine a gradient of anthropogenic modification using the predominant agricultural systems in the region - an arable crop (rice), pasture and agroforestry (coffee). We also examine forest fragments and use abandoned coffee agroforests as an intermediate between forest and agricultural systems. Twelve replicates of each managed habitat type were sampled in the study, as well as six abandoned coffee agroforests (abandoned for 10 - 15 years and now resembling secondary forest) and six forest fragments.

Trap nests

Nine trap nests were positioned (in a 3 x 3 grid, 25 m between adjacent traps) in the centre of each of the 48 plots, to provide nesting sites for naturally occurring bee, wasp and natural enemy communities. Exposure of standardised trap nests is similar to the exposure of other resources, e.g. phytometer plants, but because the guild of aboveground cavity nesting species reproduces in these traps, the problem of species appearing as ‘tourists’ in samples is eliminated. It may be argued that in open habitats, where fewer natural nesting sites are available, these trap nests will attract Hymenoptera more than in wooded habitats; however, this has been shown not to be the case. Rather, cavity-nesting species usually build nests very close to the nesting site from which they pupated, and trap nests give an accurate representation of the community normally occurring in a particular habitat (see Tscharntke *et al.* 1998 and references therein). Trap nests were constructed according to the methodology of Tscharntke *et al.* (1998). A PVC tube with a length of 22 cm and a diameter of 15 cm formed the outer case of the nest. Internodes of reeds *Arundo donax* L. (Poaceae) with varying diameter (2 – 20 mm) and a length of 20 cm were inserted into this tube and provided the nesting sites for bees and wasps. Trap nests were hung from trees in shaded (coffee, abandoned coffee and forest) systems and suspended from wooden posts in open (rice and pasture) systems. Sticky glue (tanglefoot) was applied to the post or attachment point to deter ants. All traps were positioned 1.5 m above the ground.

The natural enemies found in trap nests can be broadly classified as either ectoparasitoids (feed externally on the host) endoparasitoids (feed internally on the host) or cleptoparasites (feed on the host's food resources), and all kill the host larva/pupa (Appendix 1). Host identity was usually determined either from surviving hosts within a parasitised nest or by nest characteristics when all host larvae were parasitised.

A broad spectrum fungicide (Fitoraz® 76 PM, Bayer Crop Science S.A.: Propineb 21 g/L, Cymoxanil 1.8 g/L) that is not toxic to Hymenoptera was applied to each trap with a hand sprayer every month.

Each trap was evaluated every month from June 2003 to October 2004, and all reed internodes that were occupied by Hymenoptera were removed and replaced with new internodes of the same diameter. Occupied reeds were opened and the larvae were reared to maturity for positive identification to Subfamily level following Goulet & Huber (1993) for wasps, and Michener (2000) for bees. Genera and species were identified where possible by D.W. Roubik, an expert in neotropical Hymenoptera, and by the authors using keys and reference collections from the Pontificia Universidad Católica del Ecuador. Remaining species were identified as morphospecies. Data from each of the nine traps per plot were pooled for analyses.

Data analyses

Analyses were carried out in Statistica 6.1 (StatSoft 2003). Degrees of freedom were calculated using the Satterthwaite method of denominator synthesis (Satterthwaite 1946) which can yield non-whole number DF values. Post hoc tests for differences between habitat types were made using Tukey's pairwise comparisons.

Determinants of host and natural enemy diversity were examined using general linear models (GLM) with the number of individuals as a covariable, habitat type as a fixed factor and plot number as a random factor (to group different months within a plot). Host diversity was also included as a covariable in analyses of parasitoid diversity. Diversity data were square-root transformed, as model residuals were not normally distributed.

Parasitism rate was defined as the proportion of host individuals that were parasitised or cleptoparasitised per month per plot. Proportion parasitism data were arcsine square root (+ 0.5) transformed prior to analysis to meet the assumptions of normality and homogeneity of variances. They were analysed in a GLM with host and natural enemy species richness and abundance as continuous predictors, habitat type as a fixed factor and plot as a random factor.

To determine whether there was significant temporal variation in parasitism rates, we conducted a repeated measures ANOVA with habitat type as a predictor and time (month) as a within-factor.

We followed previous authors (e.g., Tilman *et al.* 1998; Rodriguez & Hawkins 2000; Kremen *et al.* 2004; Halpern *et al.* 2005) by measuring stability using the coefficient of variation (CV, i.e. the standard deviation expressed as a percentage of the mean) in parasitism rates, such that high stability is indicated by low CV (hereafter: “variability”) through time. To determine the effect of natural enemy diversity on variability, we examined the CV in parasitism rates (Ln transformed) in a GLM using the mean species richness of natural enemies per month, the variability (CV) in host and natural enemy species richness per month, and the total natural enemy species richness for the plot over the entire sampling period as continuous predictors and habitat type as a fixed factor.

A gregarious hymenopteran parasitoid species (*Melittobia acasta* Walk., Chalcidoidea: Eulophidae) occurred in our trap nests with up to 1,500 individuals in each nesting tube. Because this would overwhelm the 1-5 individuals of other natural enemy species, we defined the abundance of *M. acasta* as the number of host larvae parasitised by this species. This accords better with the other observed natural enemy species that on average produce one individual per parasitised host.

Results

Overall, 23,302 individuals of 33 species of bees and wasps (Hymenoptera: Apidae, Megachilidae, Mutilidae, Pompilidae, Sphecidae and Vespidae) occupied the trap nests. These primary occupants (hereafter: "hosts") were parasitised by an additional 1,924 individuals (plus 40,380 individuals of the gregarious *M. acasta*) of 9 natural enemy species (Hymenoptera: Eulophidae, Ichneumonidae, Leucospidae, Megachilidae and Chrysididae; Diptera: Bombyliidae) (Appendix 6.1).

Host and natural enemy species richness per month varied significantly across habitat types ($F_{(4,44.2)} = 3.51$, $P = 0.014$ for hosts; $F_{(4,44.6)} = 4.65$, $P = 0.003$ for natural enemies), and were higher in rice and pasture (the most highly modified habitats) than in the remaining habitat types (Tukey's pairwise comparisons). Species richness was positively correlated with number of individuals ($F_{(1,417.6)} = 197.9$, $P < 0.000001$ for hosts; $F_{(1,787.1)} = 186.2$, $P < 0.000001$ for natural enemies), which explained 19.1% and 8.3% of the variance in diversity of hosts and natural enemies respectively. Natural enemy species richness per month was also strongly positively correlated with host species richness ($F_{(1,570.9)} = 509.6$, $P < 0.000001$, $R^2 = 0.352$).

Rates of parasitism and cleptoparasitism (hereafter: "parasitism") in each month were significantly affected by habitat type, with abandoned coffee being significantly lower than rice and pasture, and forest and coffee intermediate ($F_{(4,46.9)} = 3.34$, $P = 0.010$). However, habitat type did not significantly interact with the effect of natural enemy diversity (interaction effect: $F_{(4,526)} = 1.66$, $P = 0.159$), so that the slope of the diversity/function graph did not vary across habitats. Parasitism rates were strongly positively correlated with natural enemy species richness ($F_{(1,570)} = 426.7$, $P < 0.000001$, $R^2 = 0.323$) (Fig. 6.1), and to a lesser extent by natural enemy abundance ($F_{(1,570)} = 243.4$, $P < 0.000001$, $R^2 = 0.185$), host abundance ($F_{(1,570)} = 25.1$, $P = 0.000001$, $R^2 = 0.019$), and host species richness ($F_{(1,570)} = 7.8$, $P = 0.005$, $R^2 = 0.006$). Altogether, the model explained 52.9% of the variance (adjusted for ties) in parasitism rates.

Parasitism rates showed significant temporal variation ($F_{(16,432)} = 6.9$, $P < 0.000001$), and this variation was not consistent across habitat types (time x habitat interaction effect: $F_{(64,432)} = 1.8$, $P < 0.001$). Temporal variability in parasitism rates (the inverse of stability) was significantly negatively correlated with the mean species richness of natural enemies

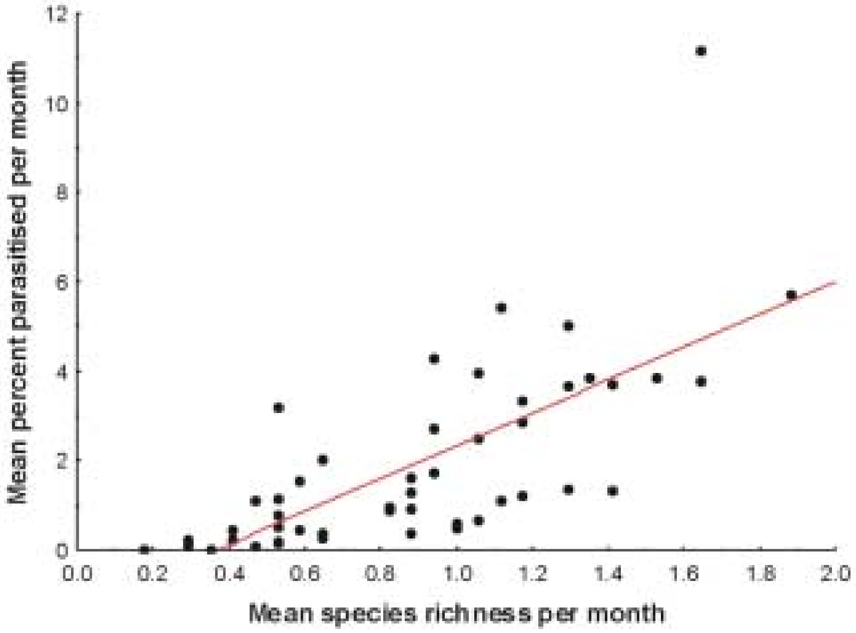


Figure 6.1. Mean proportion of host individuals parasitised vs. mean species richness of natural enemies per month for each plot. No distinction is made between habitat types as these did significantly affect the slope of the effect.

per month ($F_{(1,39)} = 243.0$, $P < 0.000001$, $R^2 = 0.722$) (Fig. 6.2A), such that plots with a high per month diversity had greater stability (lower CV) in parasitism rates. Conversely, temporal variability in parasitism rates was positively correlated with temporal variability (CV) in both natural enemy ($F_{(1,39)} = 48.6$, $P < 0.000001$, $R^2 = 0.145$) (Fig. 6.2B) and host

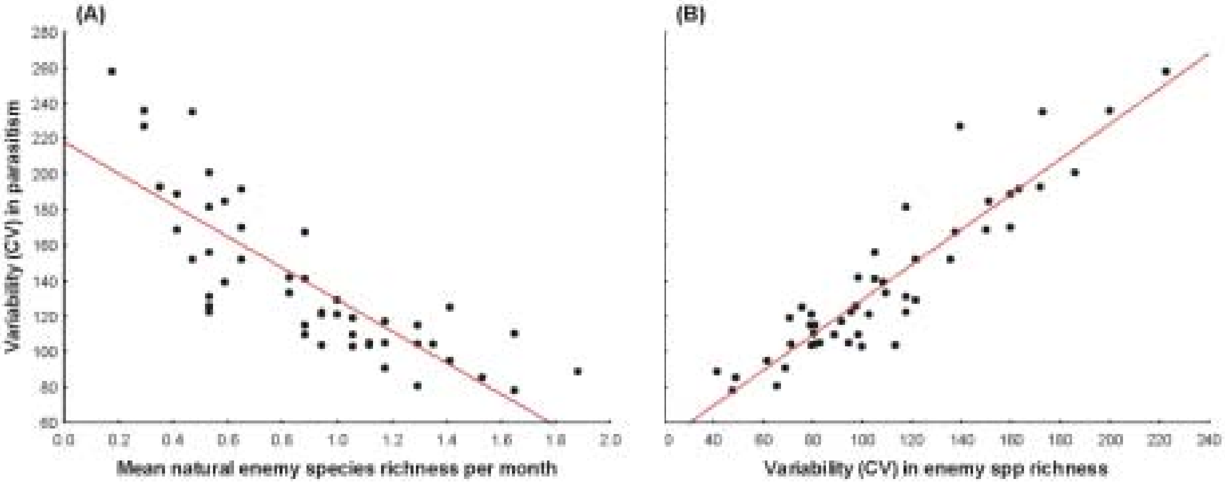


Figure 6.2. Variability (coefficient of variation, CV) in parasitism rates between months (A) decreases with mean natural enemy diversity per month, and (B) increases with monthly variation (CV) in natural enemy species richness.

($F_{(1,39)} = 5.4$, $P = 0.026$, $R^2 = 0.016$) species richness. Stability was not significantly correlated with overall species richness during the entire sampling period combined ($F_{(1,39)} = 0.4$, $P = 0.552$) or with habitat type ($F_{(4,39)} = 0.1$, $P = 0.991$). The entire model explained over 88.4% of the variance in temporal parasitism CV.

Discussion

Diversity-function

In our study system, an ecosystem function (parasitism) and stability of this function across time increased with increasing diversity of natural enemies. Effects of consumer diversity on prey consumption have been predicted by modelled and mesocosm studies of simplified communities (e.g., Cardinale *et al.* 2002, 2003; Fox 2004; Gamfeldt *et al.* 2005); however, previous field studies have found no effect (Rodriguez & Hawkins 2000) or even a negative effect (Finke & Denno 2004) of diversity on rates of predation/parasitism. The mixed results of these field studies may have been the result of specific characteristics of the systems examined. For example, Rodriguez & Hawkins (2000) found no effect of parasitoid diversity on rates of parasitism of grass-feeding *Tetramesa* spp,, or stability in parasitism. However, these hosts comprised one genus, with one life-history strategy, and all the natural enemies were hymenopteran larval parasitoids (Chalcidoidea). In contrast, our study system contained a diverse natural enemy and host community, and a high functional diversity of natural enemies (e.g., solitary parasitoids, aggregating parasitoids, cleptoparasites), an element of diversity that is very important for ecosystem functioning (Diaz & Cabido 2001) and emergent effects of multiple consumers (Sih *et al.* 1998). Furthermore, many of our natural enemy species were highly polyphagous (parasitising up to 15 host species). This sharing of natural enemies between host species in our study may explain why high host and natural enemy diversity did not lead to a reduction in parasitism such as that found by Montoya *et al.* (2003), who compared food webs where different herbivores did not share primary parasitoid species. Indeed that study found that omnivorous consumers (hyperparasitoids) did have an important effect on rates of parasitism. The natural enemy species in our study all required host resources for development, and although there were instances when more than one species of natural enemy parasitised a host nest, natural enemies could not survive only by consuming other natural enemies unless the latter had already consumed a host. Therefore, the type of intraguild predation that may lead to reduced ecosystem functioning in diverse consumer guilds (e.g., between spider species; Finke & Denno 2004) did not occur in our system.

We also emphasise the importance of examining diversity/function relationships at the spatiotemporal scales at which interactions take place (Cardinale *et al.* 2004). Pooling long term data on species richness neglects the importance of temporal turnover in species, such that all of the species recorded in a site over a year may not necessarily have the opportunity to interact with each other. For example, the effect of natural enemy diversity on parasitism rates and stability was much stronger when measured each month, than when diversity and parasitism rates were pooled over the entire sampling period, as in previous studies (Rodriguez & Hawkins 2000). Therefore caution is required when examining large-scale patterns based on small-scale processes, as diversity (Tylianakis *et al.* in press), functioning and stability may all vary with the spatiotemporal scale examined.

The surprising positive effect we found of host species richness on rates of parasitism, contrasts with a recent meta-analysis of consumer-resource experiments, which found that consumer effects tended to decrease as diversity of the prey assemblage increases (Hillebrand & Cardinale 2004). The potential mechanisms proposed for this effect (increased possibility of selecting unpalatable species, or positive prey interactions), may not have operated in our system, or these mechanisms may differ at higher trophic levels than the grazer-algal interaction examined by Hillebrand & Cardinale (2004). In our cavity-nesting communities host diversity appeared to provide a varied niche-base, supporting a higher diversity of natural enemies and allowing greater resource niche differentiation, with subsequent increased parasitism rates.

Diversity-stability

Species diversity has been shown to increase stability in plant biomass production (Worm & Duffy 2003; Caldeira *et al.* 2005) and crop pollination (Kremen et al 2002), two important ecosystem services. In simplified aquatic systems, diversity has been shown to enhance community-level food-web stability (Steiner et al 2005); however, a previous field study of a parasitoid/host system found no influence of parasitoid diversity on temporal stability in rates of parasitism (Rodriguez and Hawkins 2000). Here we used a diverse host and natural enemy community to examine parasitism as an ecosystem service, and found that parasitism rates varied significantly across time. We found that temporal variability in parasitism was lower when average natural enemy diversity was high, but increased with high temporal variability in host and natural enemy diversity. High overall pooled diversity (as measured by Rodriguez and Hawkins 2000) was not associated with reduced variability in rates of parasitism. Rather, overall stability increased with constantly high diversity in each month, and was in turn associated with high overall parasitism when the sampling period was combined. This led to our somewhat counterintuitive result of disturbed, homogenous systems (rice and pasture) with low beta diversity (Tylianakis *et al.* in press) but consistently high average diversity, having increased parasitism rates relative to temporally heterogenous systems. High spatiotemporal species turnover (beta diversity) has been shown previously to lead to higher overall diversity in unmanaged habitat types in our study system (Tylianakis *et al.* in press). However, high overall diversity that results from high temporal turnover in species did not increase stability in ecosystem functioning.

Effects of habitat

Surprisingly, the effects of diversity on ecosystem functioning and temporal stability were identifiable over the noise of environmental variation across habitats, which has been predicted to mask local effects of diversity on ecosystem function (Loreau 2000). Habitat type (level of anthropogenic disturbance) did not have a marked effect on parasitism, except that abandoned coffee had significantly lower rates of parasitism than the more disturbed habitats. Moreover, the slope of the diversity/function relationship did not vary across habitat types, despite predictions from theoretical modelling that this slope should decrease with increasing habitat disturbance (Cardinale *et al.* 2000). Additionally, habitat affected diversity of natural enemies and their hosts, which in turn strongly affected ecosystem functioning, and both of these variables were highest in rice and pasture.

Kremen *et al.* (2004) examined the effects of organic vs. conventional farming on stability in pollination services and found no effect of management practice. The proportion of natural habitat in the landscape surrounding the sites was found to significantly affect pollination, however, it is unclear whether this effect was mediated through bee diversity.

Conclusions

We showed that the positive effects of diversity on ecosystem functioning and stability were not simply the result of increased abundance of natural enemies being correlated with diversity, but rather an effect of diversity itself. Diversity itself, and the functions it provides may vary across time and space, and knowledge of the processes affecting diversity across ecosystems is essential for conservation and management (Loreau *et al.* 2003), and determination of the scales at which studies should be conducted. We recommend the further use of field-based studies to test predictions of models and experimental studies, and urge caution when extrapolating effects across habitats, community types and multiple spatiotemporal scales.

Acknowledgements

We thank Jubian Casquete, Jose Pico, Gricel Sacoto, Carlos Valarezo, Cesar Calderon, Angel Choez and Jesus Lino for laboratory and field assistance, and Roland Olschewski, Free de Koning and Betty Pico for assistance in coordination of this research. We also thank Sven Bacher, Brad Hawkins, Owen Lewis, Tatyana Rand, Stefan Vidal and Wolfgang Weisser for their time to provide helpful comments on the manuscript. We are grateful to D.W. Roubik and G. Onore for assistance with species identifications, and the Pontificia Universidad Católica del Ecuador, for allowing us to use their reference collection. Katja Poveda kindly assisted with parts of the statistical analysis. This project is part of the BioTEAM research program sponsored by the Federal Ministry of Education and Research (<http://www.bmbf.de>BMBF), Germany.

References

Caldeira, M.C., Hector, A., Loreau, M. & Pereira, J.S. (2005). Species richness, temporal variability and resistance of biomass production in a Mediterranean grassland. *Oikos,* 110, 115-123.

Cardinale, B.J., Nelson, K. & Palmer, M.A. (2000). Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, 91, 175-183.

Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, 415, 426-429.

Cardinale, B.J., Harvey, C.T., Gross, K. & Ives, A.R. (2003). Biodiversity and biocontrol: emergent impacts of a multi-enemy assemblage on pest suppression and crop yield in an agroecosystem. *Ecol. Lett.*, 6, 857-865.

Cardinale, B.J., Ives, A.R. & Inchausti, P. (2004). Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. *Oikos*, 104, 437-450.

Chapin, F.S., Zavaleta, E.S., Eviner, V.T., Naylor, R.L., Vitousek, P.M., Reynolds, H.L., Hooper, D.U., Lavorel, S., Sala, O.E., Hobbie, S.E., Mack, M.C. & Diaz, S. (2000). Consequences of changing biodiversity. *Nature*, 405, 234-242.

Cottingham, K.L., Brown, B.L. & Lennon, J.T. (2001). Biodiversity may regulate the temporal variability of ecological systems. *Ecol. Lett.*, 4, 72-85.

Daily, G.C., Söderqvist, T., Aniyar, S., Arrow, K., Dasgupta, P., Ehrlich, P.R., Folke, C., Jansson, A.M., Jansson, B.O., Kautsky, N., Levin, S., Lubchenco, J., Mäler, K.G., Simpson, D., Starrett, D., Tilman, D. & Walker, B. (2000). The value of nature and the nature of value. *Science*, 289, 395-396.

Diaz, S. & Cabido, M. (2001). Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.*, 16, 646-655.

Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.*, 6, 680-687.

Finke, D.L. & Denno, R.F. (2004). Predator diversity dampens trophic cascades. *Nature*, 429, 407-410.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P. (2005). Global consequences of land use. *Science*, 309, 570-574.

Fox, J.W. (2004). Modelling the joint effects of predator and prey diversity on total prey biomass. *J. Anim. Ecol.*, 73, 88-96.

Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. (2005). Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecol. Lett.*, 8, 696-703.

Goulet, H. & Huber, J.T. (1993). *Hymenoptera of the world: an identification guide to families.* Agriculture Canada: Research branch. IV Series. Canada.

Halpern, B.S., Borere, E.T., Seabloom, E.W. & Shurin, J.B. (2005). Predator effects on herbivore and plant stability. *Ecol. Lett.*, 8, 189-194.

Hillebrand, H. & Cardinale, B.J. (2004). Consumer effects decline with prey diversity. *Ecol. Lett.*, 7, 192-201.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3-35.

Huston, M.A. (1997). Hidden treatments in ecological experiments: re-evaluating the ecosystem function of biodiversity. *Oecologia*, 110, 449-460.

Ives, A.R., Cardinale, B.J. & Snyder, W.E. (2005). A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecol. Lett.*, 8, 102-116.

Kremen, C., Williams, N.M. & Thorp, R.W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proc. Natl. Acad. Sci., USA,* 99, 16812-16816.

Kremen, C., Williams, N.M., Bugg, R.L., Fay, J.P. & Thorp, R.W. (2004). The area requirements of an ecosystem service: crop pollination by native bee communities in California. *Ecol. Lett.*, 7, 1109-1119.

Kremen, C. (2005). Managing ecosystem services: what do we need to know about their ecology? *Ecol. Lett.*, 8, 468-479.

Kruess, A. & Tscharntke (1994). Habitat fragmentation, species loss, and biological-control. *Science*, 264, 1581-1584.

Lambers, J.H.R., Harpole, W.S., Tilman, D., Knops, J. & Reich, P.B. (2004). Mechanisms responsible for the positive diversity-productivity relationship in Minnesota grasslands. *Ecol. Lett.*, 7, 661-668.

Loreau, M. (2000). Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos*, 91, 3-17.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P, Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001). Ecology – Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804-808.

Loreau, M., Mouquet, N. & Gonzalez, A. (2003). Biodiversity as spatial insurance in heterogenous landscapes. *Proc. Natl. Acad. Sci. USA*, 100, 12765-12770.

McCann, K.S. (2000). The diversity-stability debate. *Nature*, 405, 228-223.

Michener, C.D. (2000). *The bees of the world*. The Johns Hopkins University Press. Baltimore, Maryland, USA.

Montoya, J.M., Rodriguez, M.A. & Hawkins, B.A. (2003). Food web complexity and higher level ecosystem services. *Ecol. Lett.*, 6, 587-593.

Mouquet, N., Moore, J.L. & Loreau, M. (2002). Plant species richness and community productivity: why the mechanism that promotes coexistence matters. *Ecol. Lett.*, 5, 56-65.

Naeem, S. (2002). Ecosystem consequences of biodiversity loss: The evolution of a paradigm. *Ecology*, 83, 1537-1552.

Pfisterer, A.B. & Schmid, B. (2002). Diversity-dependent production can decrease stability of ecosystem functioning. *Nature*, 416, 84-86.

Pimm, S.L. (1984). The complexity and stability of ecosystems. *Nature*, 307, 321-326.

Rodriguez, M.A. & Hawkins, B.A. (2000). Diversity, function and stability in parasitoid communities. *Ecol. Lett.*, 3, 35-40.

Satterthwaite, F.E. (1946). An approximate distribution of estimates of variance components *Biomet. Bull.*, 2, 110-114.

Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of multiple predators on prey. *Trends Ecol. Evol.,* 13, 350-355.

StatSoft, Inc. (2003). STATISTICA (data analysis software system), version 6. www.statsoft.com.

Steiner, C.F., Long, Z.T., Krumins, J.A. & Morin, P.J. (2005). Temporal stability of aquatic food webs: partitioning the effects of species diversity, species competition and enrichment. *Ecol. Lett.*, 8, 819-828.

Tilman, D. (1996). Biodiversity: population versus ecosystem stability. *Ecology*, 77, 350-363.

Tilman, D., Lehman, C. & Bristow, C.E. (1998). Diversity-stability relationships: statistical inevitability or ecological consequence. *Am. Nat.*, 151, 277-282.

Tilman, D., Lehman, C. & Thompson, K. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci. USA*, 94, 1857-1861.

Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998). Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *J. Appl. Ecol.*, 35, 708-719.

Tylianakis, J.M., Klein, A.-M. & Tscharntke, T. (in press). Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology*.

van Ruijven, J. & Berendse, F. (2005). Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proc. Natl. Acad. Sci. USA*, 102, 695-700.

Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997). Human domination of the Earth’s ecosystems. *Science*, 277, 494-499.

Worm, B. & Duffy, J.E. (2003). Biodiversity, productivity and stability in real food webs. *Trends Ecol. Evol.,* 18, 628-632.

Appendix 6.1. Natural enemy species/morphospecies, mode of attack, hosts parasitised in our study, and the habitat types (R = Rice, P = Pasture, C = Coffee, Ac = Abandoned coffee, F = Forest) in which they were found.

Family	Species/ morphospecies	Mode of attack	Observed hosts	Habitat types
Eulophidae	*Melittobia acasta*	Gregarious ectoparasite of several orders. Facultatively hyperparasitic	*Anthidium* sp. *Chrysis* sp. *Euglossa variabilis* *Megachile* sp.1 *Neofidelia* sp. *Pseudodynerus* sp. *Tetrapedia* sp. *Trypoxylon* sp.1 *Trypoxylon* sp.2 *Trypoxylon* sp.3 *Zeta* sp. Eumeninae Gen. sp.1 Eumeninae Gen. sp.3 Eumeninae Gen. sp.4 Sphecidae Gen. sp.2 Sphecidae Gen. sp.3 Pompilidae Gen. sp.1	All
Chrysididae	*Chrysis* sp.	Cleptoparasite (kills host to eat food resources) of Hymenoptera.	*Anthidium* sp. *Neofidelia* sp. *Pseudodynerus* sp. *Tetrapedia* sp. *Trypoxylon* sp.1 *Trypoxylon* sp.2 *Trypoxylon* sp.3 *Zeta* sp. Eumeninae Gen. sp.1 Sphecidae Gen. sp.2 Sphecidae Gen. sp.3 UnIDhost sp.1	All
Megachilidae	*Coelioxys* sp.	Cleptoparasite (kills host to eat food resources).	*Neofidelia* sp. *Tetrapedia* sp. *Pseudodynerus* sp. *Megachile* sp.1 *Megachile* sp.2 Megachilidae Gen. sp.5	All
Bombyliidae (Diptera)	Bombyliidae Gen. sp.1	Solitary ectoparasite	*Anthidium* sp. *Pseudodynerus* sp. Sphecidae Gen. sp. 2 *Zeta* sp.	R, P, C

Leucospidae	Leucospidae Gen. sp.1	Solitary ectoparasite of aculeate Hymenoptera. Facultatively hyperparasitic	*Anthidium* sp. *Trypoxylon* sp.3 Eumeninae Gen. sp.4 Megachilidae Gen. sp.5	R, P, C, Ac
Leucospidae	*Leucospis* sp.	Solitary ectoparasite of aculeate Hymenoptera. Facultatively hyperparasitic	*Neofidelia* sp. *Tetrapedia* sp. *Pseudodynerus* sp. Sphecidae Gen. sp. 2	P, C, Ac, F
Ichneumonidae	Phygadeuontinae Gen. sp.	Solitary endoparasitoid	*Neofidelia* sp. Sphecidae Gen. sp. 2	R, C, Ac, F
Chalcididae	Chalcididae Gen. sp.	Solitary endoparasitoid	*Pseudodynerus* sp.	R, P
Unidentified	UnIDenemy sp.	-	*Zeta* sp. Sphecidae Gen. sp.3	R, C

Chapter

7

Resource heterogeneity mediates the diversity/function relationship in the real world

J.M. Tylianakis, T.A. Rand, T. Tscharntke and A.-M. Klein

Summary

Global biodiversity decline has prompted great concern over the concomitant decline in ecosystem services and the manner in which ecosystems function (Naeem *et al.* 1994; Foley *et al.* 2005; Hooper *et al.* 2005). This has resulted in a recent explosion of biodiversity/ecosystem function (BDEF) studies, examining factors as diverse as plant productivity (Loreau & Hector 2001; Pfisterer & Schmid 2002), pollination (Fontaine *et al.* 2006) and rates of predation or consumption (Finke & Denno 2004; Ives *et al.* 2005). Despite the volume of studies examining the effect of consumer diversity on resource consumption, no consensus has yet been reached, and studies have shown positive (Cardinale *et al.* 2002; Gamfeldt *et al.* 2005), negative (Finke & Denno 2004) and no effects (Rodriguez & Hawkins 2000) of consumer diversity. Although many of these studies were conducted in mesocosms or field cages, complementary resource use by different species can only increase overall consumption when a diverse array of niches is available, and this mechanism may often not operate in homogeneous experimental systems (Wellnitz & Poff 2001; Ives *et al.* 2005). Here we examine the effects of natural enemy diversity, host resource heterogeneity and habitat heterogeneity on parasitism rates of a cavity-nesting eumenid wasp across five habitat types in coastal Ecuador. We found that parasitism of wasp larvae/pupae in standardised nests consistently increased with natural enemy diversity, and that the slope of this relationship became steeper in plots with greater heterogeneity in host abundance. The relationship also showed the tendency to decline in more highly modified habitats. This implies that the strength of the diversity/function relationship strongly depends on environmental context, and that a complete understanding of the effects of diversity on ecosystem functioning requires examination in more realistic environments with heterogeneous resources.

Introduction

The tenet that diversity increases ecosystem functioning has been the subject of considerable controversy (e.g., Tilman *et al.* 1997; Bardgett & Wardle 2003), due to variable results and contention over the effects of diversity *per se* versus sampling/species composition effects (Cardinale *et al.* 2000; Loreau & Hector 2001). Diversity effects require a degree of complementarity (niche partitioning) or facilitation, such that multiple species function synergistically, with an overall effect greater than any individual species in isolation. Conversely, sampling effects produce increased functioning of diverse systems simply due to a greater probability of including a highly efficient species, that produces more biomass or consumes more prey.

A critical turning point in BDEF literature was made when environmental context entered the debate, and theoretical analysis has shown that spatial heterogeneity may affect the slope of the diversity/productivity relationship and the relative importance of species diversity vs. composition effects in different habitats (Cardinale *et al.* 2000; Wellnitz & Poff 2001). Structural or resource heterogeneity can affect the diversity of insects (Steffan-Dewenter & Tscharntke 2001; Ambrecht *et al.* 2004) and other taxa (Benton *et al.* 2003), and spatial heterogeneity in general has long been known to be an important determinant of how resources are divided between species (Tscharntke 1992; Tilman & Kareiva 1997). However, the possibility that habitat or resource heterogeneity may mediate the BDEF relationship has not been tested empirically. Further, larger spatiotemporal scales of investigation incorporate greater habitat heterogeneity, thereby increasing the likelihood of complementarity effects over the sampling effects often found in short term, small scale experimental studies.

Much recent work has focused on the relationship between diversity and productivity in plant communities (e.g., Pfisterer & Schmid 2002; Cardinale *et al.* 2004; van Ruijven & Berendse 2005). However, the dominant impacts of biodiversity change on ecosystem functioning may be trophically mediated by consumers (Duffy 2003), and a critical new direction in diversity/function research involves a link to predator-prey interactions (Ives *et al.* 2005). This has also been examined from a slightly different perspective – biological pest control – where the effect of predator or parasitoid diversity on rates of prey consumption carries important practical implications for strategies regarding the problems or benefits associated with introducing multiple vs. single control agents (Wilby & Thomas 2002). As higher trophic levels are more active, have a greater variety of feeding modes, and suffer more strongly from habitat fragmentation (Kruess & Tscharntke 1994), they may offer important insights and new mechanisms through which diversity may affect ecosystem functioning. Despite this importance, there has been a distinct paucity of field studies examining the effects of diversity on predation or parasitism in real systems (but see Rodriguez & Hawkins 2000), hindering extrapolation of BDEF effects to the real systems within which diversity loss initially prompted the concern.

Here we examine the effects of within-habitat heterogeneity in structure and host resource distribution on the relationship between diversity and an ecosystem function: rates of parasitism by a functionally-diverse guild of natural enemies. We hypothesised that diverse natural enemy assemblages would exert higher rates of parasitism, and that the strength of this effect (the slope of the relationship) due to complementarity would increase with greater niche availability (i.e. heterogeneity) in the habitat (Fig. 7.1).

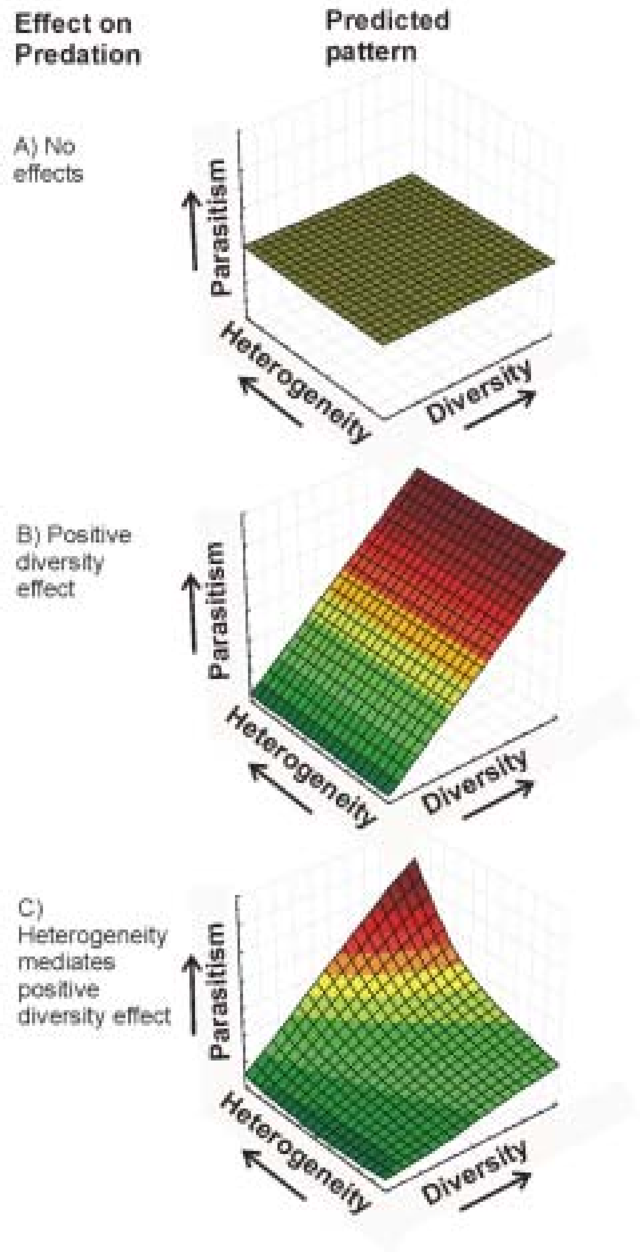


Figure 7.1. Hypothetical interactions of natural enemy diversity and resource or habitat heterogeneity on parasitism rates. A) Null hypothesis: Neither diversity nor heterogeneity affect parasitism rates. B) Basic diversity/function: Positive effect of diversity on rates of parasitism, with no effect of heterogeneity. C) Heterogeneity-mediated diversity/function: The strength (steepness) of the positive effect of diversity on rates of parasitism increases with increasing habitat/resource heterogeneity.

Methods

Study region

The 48 study plots were spread across three cantons in the region of Jipijapa (17N 546800m, E 9849274m alt. 259m), within the province of Manabi, Southwest Ecuador (for individual plot location details and a full description of the region see Tylianakis *et al.* in press). This area falls within the Choco-Manabi region (a biodiversity hotspot), but large-scale agricultural conversion threatens the local biodiversity and the ecosystem services it provides.

Trap nests

Nine trap nests were positioned in each of the 48 plots, to provide nesting sites for naturally occurring bee, wasp and natural enemy communities (Tylianakis *et al.* in press). Trap nests were constructed according to the methodology of Tscharntke *et al.* (1998), and evaluated every month from June 2003 to October 2004. Occupied reeds were opened and the larvae were reared to maturity for positive identification of any natural enemies. Data from each of the nine traps per plot were pooled across all months for analyses.

Of all the potential host species found in our traps (Appendix 6.1), the one with the greatest number of natural enemies (6 species) was a predatory wasp, *Pseudodynerus* sp. (Hymenoptera: Eumeninae). This species was also the second most abundant of all the host species (6884 individuals, 487 of which were parasitised), and had the most even distribution among habitat types – allowing statistical analyses in all habitats. We therefore used this species as our focal host for this study.

The natural enemies attacking *Pseudodynerus* were either gregarious ectoparasitoids, where many larvae feed externally on the host (*Melittobia acasta* Walk. Hymenoptera: Eulophidae); solitary ectoparasitoids, where one larva feeds on the host (*Leucospis* sp., Hymenoptera: Leucospidae; and Bombyliidae Gen. sp., Diptera); endoparasitoids, that feed internally on the host (Chalcididae Gen. sp., Hymenoptera); or cleptoparasites, that feed on the host's food resources rather than the host itself (*Chrysis* sp., Hymenoptera: Chrysididae; and *Coelioxys* sp., Hymenoptera: Megachilidae).

Heterogeneity parameters

To quantify the heterogeneity of each plot, we measured the following biotic and abiotic variables that may be of importance to the natural enemy species: 1) herb diversity, which may provide nectar resources to parasitoids, was measured in a 2.5 x 2.5m quadrat around each of the 9 traps per site, on two sampling dates (see Chapter 3). These measures for each trap and sampling date were pooled to give one measure of herb diversity for the entire plot.

2) Tree diversity, a measure of structural complexity, was also recorded in 10 x 10m quadrats around each trap and the total species richness was pooled for the site.

3) The total volume of dead wood (from fallen trees or branches) was estimated within 10 x 10m quadrats around each trap. Dead wood comprises potential nesting sites for the cavity-nesting species, and is an indicator of structural complexity. Heterogeneity of dead wood was calculated as the coefficient of variation (CV, the standard deviation expressed as a proportion of the mean) of dead wood between each of the 9 quadrats per site.

4) The heterogeneity in host distribution was calculated similarly for each plot as the between trap nest CV in host (*Pseudodynerus*) abundance. Abundance was measured as the number of *Pseudodynerus* larvae in all occupied reeds over the entire sampling period. This heterogeneity was not affected by habitat type (GLM: $F_{4,38} = 1.59$, $P = 0.198$), overall host abundance for the site ($F_{1,38} = 1.59$, $P = 0.214$), and these variables did not interact ($F_{4,38} = 0.78$, $P = 0.544$).

5) The mean of five light measures, taken with a luxmeter (Gossen Mavolux Digital) at each sampling point, was used to calculate the CV in light between the 9 sampling points for a plot. Light may affect search efficiency and thermal state of foraging parasitoids.

Statistical analyses

Analyses were conducted in Statistica 6.1 (Statsoft 2003). The proportion of *Pseudodynerus* larvae parasitised per plot was arcsine square root transformed prior to analyses. Overall effects of habitat and natural enemy diversity on rates of parasitism were tested in a general linear model (GLM), with Type I sums of squares. Habitat type entered the model first, then natural enemy abundance, followed by natural enemy species richness and a habitat type x species richness interaction effect. Not surprisingly, rates of parasitism were higher when natural enemy abundance was higher ($F_{1,37} = 25.90$, $P = 0.00001$, $R^2 = 0.160$), and abundance and diversity of natural enemies were correlated (after removal of variation due to habitat type $F_{1,42} = 14.06$, $P = 0.0005$, $R^2 = 0.144$). Therefore, to be conservative and ensure that effects of high natural enemy diversity were not merely the result of high abundance, we used the residual variation of natural enemy species richness (after removal of the variance explained by abundance) in all further analyses. The effects of heterogeneity parameters on parasitism and the diversity/parasitism relationship were tested separately for open (rice and pasture) and shaded (coffee, abandoned coffee and forest) systems, as open systems did not have significant quantities of dead wood or trees to include in analyses. The effects of heterogeneity variables were tested using GLMs with backwards stepwise elimination of non-significant variables. Habitat type was included as a fixed factor, and natural enemy species richness residuals were treated as a continuous predictor. The biotic and abiotic heterogeneity measures were included as continuous predictors, and interaction effects between natural enemy diversity residuals and each of the other continuous predictors and habitat type were included in the model. These interaction effects were most important, as they determined the ways in which heterogeneity affected the diversity/parasitism relationship.

Results

Overall, we found that rates of parasitism were significantly higher in plots with high natural enemy diversity ($F_{1,37} = 40.71$, $P < 0.00001$, $R^2 = 0.252$), congruent with the general predictions of the effects of diversity on ecosystem function, and with previous work in our system using a diverse host guild (Chapter 6). Parasitism rates varied significantly across habitat types ($F_{4,37} = 8.41$, $P = 0.0006$), and were highest in pasture (which was significantly higher than forest and abandoned coffee) and rice (significantly higher than abandoned coffee only), and coffee was intermediate. Additionally, the effect of natural enemy diversity on parasitism (the slope of the relationship) varied significantly across habitat types (interaction effect: $F_{4,37} = 6.06$, $P = 0.0007$), and this slope was significantly lower in rice and pasture than in the remaining habitats. In fact, the slope of the diversity/parasitism relationship showed a tendency to decrease along the gradient of increasing management intensity (as predicted by Cardinale *et al.* 2000), except that abandoned coffee, rather than forest, had the steepest slope. The equations of the diversity (x) vs. proportion parasitised (y) relationship were: Rice $y = 0.0321x + 0.1952$, Pasture $y = 0.0597x + 0.1665$, Coffee $y = 0.1263x + 0.0732$, Abandoned coffee $y = 0.2523x + 0.0041$, and Forest $y = 0.1427x + 0.0023$.

Heterogeneity (CV) in host abundance mediated the positive effect of diversity on parasitism rates in both shaded (Interaction effect: $F_{1,23} = 5.79$, $P = 0.025$, $R^2 = 0.208$) and open (Interaction effect: $F_{1,21} = 9.79$, $P = 0.005$, $R^2 = 0.248$) systems, such that increased diversity had a stronger effect on parasitism rates in sites with more heterogeneously distributed hosts (Fig 7.2).

In the open systems, the only other significant predictor remaining in the model was herb diversity, which was positively correlated with rates of parasitism ($F_{1,21} = 13.64$, $P = 0.001$, $R^2 = 0.345$), possibly due to enhancement of natural enemies by floral resource subsidies (Tylianakis *et al.* 2004), but herb diversity did not affect the slope of the relationship between diversity and parasitism.

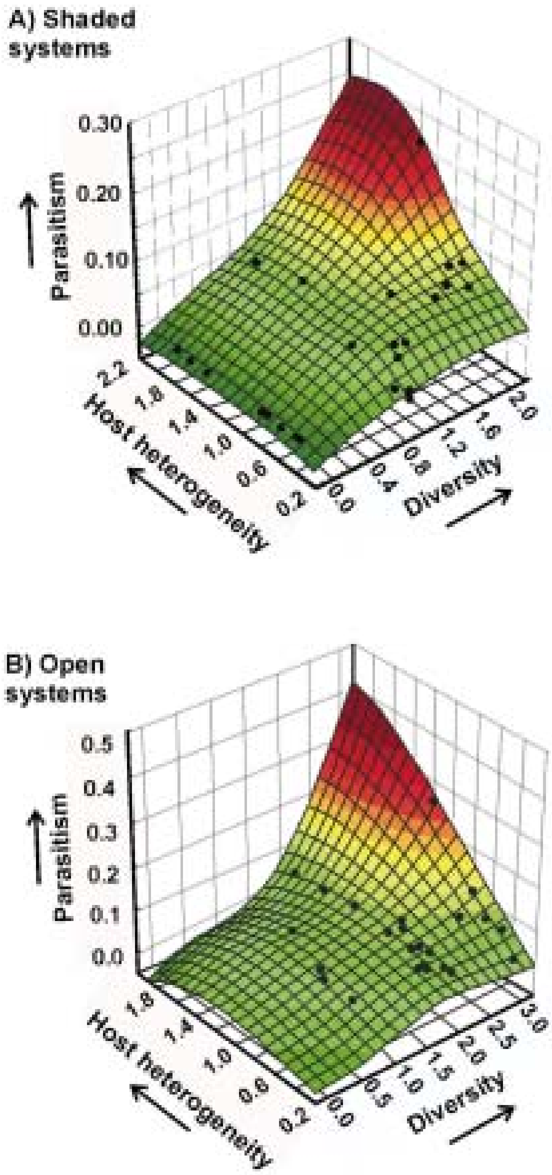


Figure 7.2. The effects of heterogeneity in host abundance on rates of parasitism of *Pseudodynerus* sp. in A) shaded (coffee, abandoned coffee and forest) and B) open (rice and pasture) systems. Heterogeneity in host abundance was calculated as the coefficient of variation (CV) between the 9 sampling points per plot.

Although no other variables had significant effects on parasitism, or the slope of the diversity/parasitism relationship (all were removed from the models during backwards stepwise elimination), host heterogeneity will also partly respond to other habitat variables.

Discussion

Our results provide evidence for the tenet that biodiversity can increase the level of an ecosystem function in real habitats, and more importantly, that the extent of this increase is context-dependent. Moreover, we argue that in order for mechanisms such as niche complementarity to occur, sufficient niche space or heterogeneity is required. In fact, when varied niche space is unavailable, the probability increases of negative interspecific interactions such as intraguild predation (Finke & Denno 2004). Conversely, complex habitats with heterogenous resource distributions, allow resource partitioning, such that parasitoids may use different search criteria and attack different host subpopulations (Tscharntke 1992; Costamanga *et al.* 2004). The effect of such complementarity is increased overall parasitism with increasing natural enemy diversity.

We have shown that host resource heterogeneity affects the slope of the diversity/function relationship for a guild of parasitoids. Resource heterogeneity may also have positive effects on plant productivity (Cardinale *et al.* 2000), and spatial heterogeneity may increase community stability (Brown 2003), thereby reducing the negative effects of temporally variable diversity on ecosystem function (Benedetti-Cecchi 2005). If our results are applicable across different systems and/or ecosystem functions, it would imply that in order to maximise the effect of diversity on ecosystem functioning, we must not only conserve species, but also the complex habitats in which they interact. While important for testing certain specific mechanisms, previous mesocosm studies using random species assemblages, that have not incorporated environmental heterogeneity, may not have contained the varied niche space required for effective expression of complementarity effects. Although recent years have seen enormous strides in understanding of the BDEF relationship, our results combine with calls from theoretical work to suggest that expanding research to include more realistic conditions, such as variable habitats or resources will be critical towards further understanding these relationships.

Acknowledgements

For field, laboratory and office assistance we thank M. Arboleda, C. Batioja, J. Casquete, A. Choez, X. Haro, J. Pico, B. Pico, G. Sacoto, E. Suarez, M. Torres, and C. Valarezo. Herb data was kindly provided by T. Lozada. We are grateful to D.W. Roubik and G. Onore for assistance with species identifications, and the Pontificia Universidad Católica del Ecuador, for allowing us to use their reference collection. This research was carried out within the Bio-Sys project, which is part of the BioTEAM research program sponsored by the Federal Ministry of Education and Research, Germany (<http://www.bmbf.de>BMBF). T.R. was funded by an Alexander von Humboldt Foundation Fellowship.

References

Armbrecht I, Perfecto I & Vandermeer J (2004). Enigmatic biodiversity correlations: ant diversity responds to diverse resources. *Science*, 304: 284-286.

Bardgett, R.D & Wardle, D.A. (2003). Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, 84, 2258-2268.

Benedetti-Cecchi, L. (2005). Unanticipated impacts of spatial variance of biodiversity on plant productivity. *Ecology Letters*, 8, 791-799.

Benton TG, Vickery JA & Wilson JD (2003). Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol. Evol.*, 18: 182-188.

Brown, B.L. (2003). Spatial heterogeneity reduces variability in stream insect communities. *Ecology Letters*, 6, 316-325.

Cardinale, B.J., Nelson, K. & Palmer, M.A. (2000). Linking species diversity to the functioning of ecosystems: on the importance of environmental context. *Oikos*, 91, 175-183.

Cardinale, B.J., Ives, A.R. & Inchausti, P. (2004). Effects of species diversity on the primary productivity of ecosystems: extending our spatial and temporal scales of inference. *Oikos*, 104, 437-450.

Cardinale, B.J., Palmer, M.A. & Collins, S.L. (2002). Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature*, 415, 426-429.

Costamanga, A.C., Menalled, F.D. & Landis, D.A. (2004). Host density influences parasitism of the armyworm *Pseudaletia unipuncta* in agricultural landscapes. *Basic and Applied Ecology*, 5, 347-355.

Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.*, 6, 680-687.

Finke, D.L. & Denno, R.F. (2004). Predator diversity dampens trophic cascades. *Nature*, 429, 407-410.

Foley, J.A., DeFries, R., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R., Chapin, F.S., Coe, M.T., Daily, G.C., Gibbs, H.K., Helkowski, J.H., Holloway, T., Howard, E.A., Kucharik, C.J., Monfreda, C., Patz, J.A., Prentice, I.C., Ramankutty, N. & Snyder, P. (2005). Global consequences of land use. *Science*, 309, 570-574.

Fontaine, C., Dajoz, I, Meriguet, J. & Loreau, M. (2006). Functional diversity of plant-pollinator interaction webs enhances the persistence of plant communities. *PLoS Biology*, 4, e1.

Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. (2005). Species richness changes across two trophic levels simultaneously affect prey and consumer biomass. *Ecol. Lett.*, 8, 696-703.

Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M., Loreau, M., Naeem, S., Schmid, B., Setala, H., Symstad, A.J., Vandermeer, J. & Wardle, D.A. (2005). Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecol. Monogr.*, 75, 3-35.

Ives, A.R., Cardinale, B.J. & Snyder, W.E. (2005). A synthesis of subdisciplines: predator-prey interactions, and biodiversity and ecosystem functioning. *Ecol. Lett.*, 8, 102-116.

Kruess, A. & Tscharntke (1994). Habitat fragmentation, species loss, and biological-control. *Science*, 264, 1581-1584.

Loreau, M. & Hector, A. (2001). Partitioning selection and complementarity in biodiversity experiments. *Nature*, 412, 72-76.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P, Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D. & Wardle, D.A. (2001). Ecology – Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, 294, 804-808.

Naeem, S., Thompson, L.J., Lawler, S.P., Lawton, J.H., and Woodfin, R.M. (1994). Declining biodiversity can alter the performance of ecosystems. *Nature*, 368, 734-737.

Pfisterer, A.B. & Schmid, B. (2002). Diversity-dependent production can decrease stability of ecosystem functioning. *Nature*, 416, 84-86.

Rodriguez, M.A. & Hawkins, B.A. (2000). Diversity, function and stability in parasitoid communities. *Ecol. Lett.*, 3, 35-40.

StatSoft Inc (2003) STATISTICA (data analysis software system), version 6 www.statsoft.com

Steffan-Dewenter, I. & Tscharntke, T. (2001). Succession of bee communities on fallows. *Ecography*, 24, 83-93.

Tilman, D. & Kareiva, P. (eds) (1997). Spatial Ecology: the role of space in population dynamics and interspecific interactions. Princeton University Press.

Tilman, D., Lehman, C. & Thompson, K. (1997). Plant diversity and ecosystem productivity: theoretical considerations. *Proc. Natl. Acad. Sci. USA*, 94, 1857-1861.

Tscharntke, T., Gathmann, A. & Steffan-Dewenter, I. (1998). Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *J. Appl. Ecol.*, 35, 708-719.

Tylianakis, J., Didham, R. and Wratten, S.D. (2004). Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology* 85, 658-666.

Tylianakis, J.M., Klein, A.-M. & Tscharntke, T. (in press). Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. *Ecology*.

van Ruijven, J. & Berendse, F. (2005). Diversity-productivity relationships: Initial effects, long-term patterns, and underlying mechanisms. *Proc. Natl. Acad. Sci. USA*, 102, 695-700.

Wellnitz, T. & Poff, N.L. (2001). Functional redundancy in heterogeneous environments: implications for conservation. *Ecology Letters*, 4, 177-179.

Wilby, A.& Thomas, M.B. (2002). Natural enemy diversity and pest control: patterns of pest emergence with agricultural intensification. *Ecology Letters*, 5, 353-360.

SUMMARY

Global biodiversity decline has prompted great interest in the effects of habitat modification on species diversity and the functioning and stability of ecosystem processes. Anthropogenic changes in land use may have major consequences for global biodiversity; however, species diversity is determined by a suite of factors that may affect species differently across habitats and at different spatial and temporal scales. Further, the effects of resource heterogeneity on the diversity of organisms has not been examined across multiple trophic levels. Diversity and resource heterogeneity may also affect ecosystem functions such as parasitism rates, but the applicability of previous modelled or mesocosm studies on this subject to real communities remains ambiguous.

Here we assess the contribution of managed land to conservation of insects, and the ecosystem services that they provide. For the first time we tested the combined effects of land use and spatial and temporal scales of analysis on α, β and γ diversity in the tropics. We aimed to determine whether: 1) resource heterogeneity leads to increased diversity of the organisms that use that resource, and whether this bears consequences for higher trophic levels; 2) land use intensity effects vary at different spatiotemporal scales; 3) beta diversity, both within and between plots, and through time, is higher in more natural systems; 4) diversity of natural enemies and/or hosts leads to higher rates of parasitism, and stability of parasitism rates through time; and 5) resource heterogeneity affects the diversity/function relationship itself.

We used standardised nesting resources for reproducing communities of cavity-nesting bees and wasps (Hymenoptera: Aculeata), within 48 plots of five habitat types in coastal Ecuador. These habitats comprised a gradient of decreasing agricultural intensity from rice and pasture to coffee agroforests, unmanaged abandoned agroforests and forest.

1) We show for the first time that high soil heterogeneity (specifically variability in magnesium concentrations) led to a domino effect of increased diversity across three trophic levels (herbaceous plants, cavity-nesting bees and wasps, and their natural enemies). The robustness of this bottom-up diversity cascade was strengthened by its consistency across three different habitat types. We show that beta diversity of herbs explained more variation in bee and wasp diversity than did herb species richness.

However, natural enemy species richness was only correlated with bee and wasp richness, not beta diversity. 2) We also show that land use affected diversity of cavity-nesting Hymenoptera differently at different spatiotemporal scales, with the strongest effects being at the lowest (alpha diversity) scale of subplot diversity per month. 3) Additionally, overall spatial and temporal turnover (beta diversity) explained 38.6% and 23.1%, respectively, of partitioned regional species richness. Beta diversity between plots and especially through time, was significantly higher in the more natural habitats – abandoned coffee and forest. This shows that studies conducted at small spatiotemporal scales will tend to over represent the diversity of intensively managed, homogeneous systems, and under represent the diversity of natural systems. Nevertheless there was notable overlap in the communities of different habitat types, indicating that even intensively managed land can provide a valuable contribution to the overall biodiversity of the landscape mosaic. 4) We also found that parasitism rates increased with increasing diversity of natural enemies and their hosts, exceeding the effects of increased enemy abundance alone. Temporal variability in parasitism was lower in plots with high mean natural enemy diversity and higher in plots with temporally variable host and natural enemy diversity. 5) Finally, the slope of the natural enemy diversity/parasitism rate function increased in systems with more heterogeneous host distributions. This indicates that niche complementarity is more likely to lead to a positive diversity/function effect in heterogeneous habitats. These effects were sufficiently strong to be visible across five different habitat types, over the noise of different management regimes.

In conclusion, biodiversity of a variety of taxa may be enhanced in managed systems by maintaining high habitat heterogeneity, and perturbations at one trophic level may have repercussions across the entire community. However, the effects of land use on species richness may be highly dependent on spatial and temporal scale, and we emphasise caution in the interpretation of studies conducted at only one scale. Conservation strategies need to take a landscape scale approach, in order to maximise beta diversity (species turnover) within and between fields, and between habitat types. Maintaining high diversity may also have great benefits for biological pest control, through higher rates of parasitism, and stability of parasitism rates through time.

Author Publications / Publikationen des Autor

Peer reviewed journals / Zeitschriften

Tylianakis, J., Klein, A.M. & Tscharntke, T. (in press) Spatiotemporal variation in the effects of a tropical habitat gradient on Hymenoptera diversity. *Ecology*.

Irvin, N. A., Wratten, S.D., Frampton, C.M., Chapman R.B. and **Tylianakis, J.M.** (in press). The effects of floral understoreys on parasitism of leafrollers (Tortricidae: Lepidoptera) on apples in New Zealand. *Agricultural and Forest Entomology*.

Didham, R.K, **Tylianakis, J.M.**, Hutchison, M.A, Ewers, R.M. and Gemmel, N.J. (2005) Are invasive species the drivers of ecological change? *Trends in Ecology and Evolution* **20,** 470-474.

Ewers, R. Didham, R.K, Wratten, S.D. and **Tylianakis, J.** (2005) Remotely-sensed landscape heterogeneity as a rapid tool for assessing local biodiversity value in a highly modified New Zealand landscape. *Biodiversity and Conservation* **14,** 1469-1485.

Tylianakis, J., Didham, R. and Wratten, S.D. (2004) Improved fitness of aphid parasitoids receiving resource subsidies. *Ecology* **85,** 658-666.

Kean, J., Wratten, S., **Tylianakis, J.** and Barlow, N. (2003) The population consequences of natural enemy enhancement, and implications for biological control. *Ecology Letters* **6**, 1-9.

Wratten, S.D., Bowie, M.H., Hickman, J.M., Evans, A.M., Sedcole, J.R. & **Tylianakis, J.M.** (2003) Field boundaries as barriers to movement of hover flies (Diptera: Syrphidae) in cultivated land. *Oecologia* **134**, 605-611.

Wratten, S.D., Lavandero, B.I., **Tylianakis, J.**, Vattala, D., Cilgi, T. & Sedcole, R. (2003) Effects of flowers on parasitoid longevity and fecundity. *New Zealand Plant Protection* **56,** 239-245.

Book chapters / Kapitel

Tscharntke, T., **Tylianakis, J.M.,** Wade, M.R., Wratten, S.D., Bengtsson, J. and Kleijn, D. (in press). Integrating insect conservation in agricultural landscapes. In: *Insect Conservation Biology*. A. Stewart, O. Lewis and T. New (eds). CABI Publishing.

Wratten, S.D., Gurr, G.M., van Emden, H.F. and **Tylianakis, J.** (in press). Cultural control of aphids. In: *Aphids as crop pests*. H.F. van Emden and R. Harrington (eds). CAB International, Wallingford.

Wratten, S. D., Hochuli, D. F., Gurr, G. M., **Tylianakis, J. M.** and Scarratt, S. (in press). Conservation biology, biodiversity and IPM. *Perspectives in Ecological Theory and Integrated Pest Management*. M. Kogan and P. Jepson, Cambridge University Press.

Gurr, G.M., Wratten, S.D. **Tylianakis, J.**, Kean, J. and Keller, M. (2005). Providing plant foods for insect natural enemies in farming systems: balancing practicalities and theory. In: *Plant-provided food for carnivorous insects: a protective mutualism and its applications*. F.L. Wackers, P.C.J. van Rijn and J. Bruin (eds). Cambridge University Press, Cambridge. pp. 326-347.

Tylianakis, J., Wratten, S.D. and Gurr, G.M. (2005). Interactions of insects with other pests (weeds, pathogens, nemotodes). In: *Encyclopedia of Plant and Crop Science*. R.M. Goodman (ed.). Marcel Dekker: New York. **DOI:** 10.1081/E-EPCS-120010495

Lavandero, B.I., Wratten, S.D., Hagler, J. and **Tylianakis, J.** (2004) Marking and tracking techniques for insect predators and parasitoids in ecological engineering. In: *Ecological Engineering for Pest Management*. G. Gurr, S.D. Wratten and M. Altieri (eds.). CSIRO Publishing. Pp. 117-131.

Conference proceedings and published abstracts / Tagungsbeiträge

Tylianakis, J., Klein, A.M. & Tscharntke, T. (2005) Temporally-dependent effects of region and habitat on spatially partitioned Hymenoptera diversity within a tropical mosaic landscape. Abstracts of the 90th ESA Annual Meeting/INTECOL IX International Congress of Ecology, Montreal, Canada.

Klein, A.M., **Tylianakis, J.**, Steffan-Dewenter, I. & Tscharntke, T. (2004) Landscape context affects bee diversity and pollination in European and tropical agroecosystems. In. Hartfelder, K. & De Jong, D. (eds.) Proceedings of the 8th International Conference on Tropical Bees and VI Encontro sobre Abelhas.

Tylianakis, J., Klein, A.M. & Tscharntke, T. (2004) Diversity of trap-nesting bees, wasps, and their enemies in different land-use systems of coastal Ecuador. In:

Biodiversity and dynamics in tropical ecosystems; Abstracts of the 17th Annual Conference of the Society for Tropical Ecology, University of Bayreuth (ISSN 0944-4122), p. 259.

Tylianakis, J., Veddeler, D., Lozada, T., López, R.M., Benítez, P., Klein, A.M., de Koning, G.H.J., Olschewski, R., Veldkamp, E., Navarrete, H., Onore, G. and Tscharntke, T. (2004) Biodiversity in coastal Ecuador and bioindication using trap-nesting bees, wasps, and their natural enemies. Proceedings de IV Congreso Ecuatoriano de Botánica and II Congreso de Conservación de la Biodiversidad en los Andes y en la Amazonía. *Lyonia* **6**(2). Download at: http://www.lyonia.org/downloadPDF.php?PDFID=2.237.1

Tylianakis, J., Klein, A.M., Sacoto, G. & Tscharntke, T. (2003) Bio-indicacion usando trampas-nidos Himenoptéras. IV Congreso Ecuatoriano de Botánica and II Congreso de Conservación de la Biodiversidad en los Andes y en la Amazonía.

Wratten, S.D., Berndt, L.A., Gurr, G.M., **Tylianakis, J.**, Fernando, P. & Didham, R.K. (2003) Adding floral diversity to enhance parasitoid fitness and efficacy. *Proceedings of the First International Symposium on the Biological Control of Arthropods: Honolulu, Hawaii, January 2002*, 211-214.

Articles in preparation / Eingereicht oder in Vorbereitung

Tylianakis, J.M., Tscharntke, T. & Klein, A.M. (in review) Diversity, ecosystem function and stability of insect natural enemies across a tropical gradient of habitat modification. *Ecology Letters.*

Tylianakis, J.M., Klein, A.M. & Tscharntke, T. (in review) Spatial scale of observation affects α, β and γ diversity of Hymenoptera across a tropical land use gradient. *Journal of Biogeography*.

Rand, T., **Tylianakis, J.M.**, & Tscharntke, T. (in review) Spillover edge effects: the dispersal of agriculturally-subsidized insect natural enemies into adjacent natural habitats. Invited review: *Ecology Letters*.

Tylianakis, J.M., López, R.M., Lozada, T., Veldkamp, E., Klein, A.M., Veddeler, D., de Koning, G.H.J., Olschewski, R., & Tscharntke, T. (in preparation) Soil heterogeneity promotes a bottom-up biodiversity cascade.

Tylianakis, J.M., Rand, T.A., Tscharntke, T. & Klein, A.-M. (in preparation) Resource heterogeneity mediates the diversity/function relationship in the real world.

Richter, A., Klein, A.-M., Tscharntke, T. & **Tylianakis, J.M.** (in preparation) Abandoned coffee fields as habitat for arthropod communities.

Lopez-Ulloa, M., de Koning, G.H.J., Veldkamp, E., Lozada, T. & **Tylianakis, J.M.** (in preparation) Soil heterogeneity and topography influence plant diversity in a tropical mosaic landscape.

Acknowledgements

I owe a great debt to my PhD supervisors: Prof. Dr. Teja Tscharntke and Dr. Alexandra-Maria Klein. Not only did they provide me with the opportunity to be involved in such an exciting project, but they also gave considerable assistance and provided positive encouragement throughout my field work and the writing process. This research would not have been possible without them, and their broad knowledge and kind manner made this work much more enjoyable.

I am extremely grateful to Gricel Sacoto, Carlos Oswaldo Valarezo, Jose “Pepe” Pico and Jubian Casquete for their assistance in the laboratory, and friendship during my stay in Ecuador. Their work was often boring, but their kind spirits and sense of humour made the days pass quickly.

The field work would not have been possible without the assistance of Cesar Calderon in Manabi and Edgar Suarez in Esmeraldas, both of whom regularly checked my traps for occupancy, and assisted with trap placement. Angel Choez, Jesus Lino and Cesar “Chino” Soledispa also provided field assistance at various times during this research. I really appreciate the very hard work these people carried out.

Yann Clough, Doreen Gabriel and Katja Poveda helped me, especially in the early stages, with statistical analyses. I really appreciate their support in this regard.

I thank Tannya Lozada for allowing me to use her herb data in Chapter 5.

Roland Olschewski, Free de Koning and Betty Pico provided assistance in coordination of this research. I thank them for their help and involvement with site selection, visas drivers licence, transport, information, funding, and many other tasks throughout my research. The entire project would not have been possible without them. I also thank Hella Grabe, who provided assistance with administration and coordination while I was at Goettingen.

I am grateful to D.W. Roubik and G. Onore for assistance with species identifications, and the Pontificia Universidad Católica del Ecuador, for allowing us to use their reference collection.

This thesis profited considerably from discussions with Raphael Didham, Kevin Gaston, Brad Hawkins, Jochen Krauss, and Katja Poveda and specific comments on the chapters from: Tom Crist, Raphael Didham, Till Eggers, Tatyana Rand, Keith Summerville, and

Helene Wagner (Chapter 4); Raphael Didham, Tatyana Rand, Micky Eubanks and two anonymous referees (Chapter 5); Sven Bacher, Brad Hawkins, Owen Lewis, Tatyana Rand, Stefan Vidal and Wolfgang Weisser (Chapter 6). Pre-revision of manuscripts takes a considerable amount of time, and I am very grateful to these people for their effort.

The entire project depended on the kindness of those landowners who allowed us to conduct our research on their farms. They were (in no particular order): Aquiles Toala, Volter Merchan, Aquilino Muñiz, Carlos Quintero, la familia Paucar, Gabriel Nieto, Gregorio Echeveria, Idilio Lopez, Jesus Nieto, Joselo Cevallos, Justo Pin, Lorenzo Bosada, Marco Loor, Pepe & Rosa Bosada, Pepe Yuccha, Ramon Guasmo, Ruben Andrade, Rufina Gutierrez, Rufino Cedeno, Santos Lopez, Sr. Acebo, Sr.Aranea, Tomas Rodriguez, Trinidad Solis, Filomena Ponce, Paolo del Valle, Alfonso Cedeño, Hugo Caña, Mercedes Cevallos, Sofia Pua, Sr. Billenton, Fernando Quiñonez, Bolivar Chica, Manuel Palacio, Lucio Chica, Narcilo Leon, Antonio Leon, Alberto Gracias, Sr. Cifuentes, Amelia Arce, Yunior Bautista, Eufemia Trejo, Silveria Castañeda, Oswaldo, Eliseo Chica, Teofilo Arias, Angel Cedeño, Wiliam Arias, Ramon Palacio, Alejandro Chila, Filemon Quiñonez, Eliseo Chica, Leodan, Narcilo Leon, Franklin Bautista, Gustavo Guerrero and Cristobal de la Cruz. I also wish to thank the remaining people of Jipijapa and Cabo San Fransisco for welcoming me into their communities, and offering me their friendship.

Last, and by no means least, I thank my friends and family for their continued support, both nearby and at a distance. Especially Mum, Anne, and all those who have helped me get through these three years.

This research was carried out within the Bio-Sys project, which is part of the BioTEAM research program sponsored by the Federal Ministry of Education and Research, Germany (<http://www.bmbf.de>BMBF).

Lebenslauf

Persönliche Angaben

Name:	Jason Mihalis Tylianakis
Geburtstag:	20.01.1978
Geburtsort:	Athen
Staatsangehörigkeit:	Griechisch /Neuseeländisch
Familienstand:	ledig

Ausbildung

seit 01.2003	Vorbereitung eines Promotionsvorhabens im Fachgebiet Agrarökologie
03.2000-12.2002	MSc Zoologie „Ecological Enhancement of an aphid parasitoid“ Betreuer: Dr. R.K. Didham. University of Canterbury, Christchurch, Neuseeland.
03.1996-05.1999	BSc Zoologie/Botanik. Massey University, Palmerston North, Neuseeland.
1991-1995	Burnside High School
1987-1990	Grundschule

Stipendien & Auszeichnungen

- Fahrtkostenerstattung der Royal Society of New Zealand - 2002.
- Stipendium der University of Canterbury Masters Stiftung - 2001/2002.
- Stipendium der Charles Cook/Warwick House Stiftung – 2001/2002.
- Auszeichnung für herausragende sportliche Leistung der University of Canterbury ‘blues’ - 2001.

Fremdsprachen

Englisch : Muttersprache

Spanisch: fließend

Griechisch: gut

Japanisch, Deutsch : Grundkenntnisse