REVIEWS AND SYNTHESES

Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management

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Abstract

Understanding the negative and positive effects of agricultural land use for the conservation of biodiversity, and its relation to ecosystem services, needs a landscape perspective. Agriculture can contribute to the conservation of high-diversity systems, which may provide important ecosystem services such as pollination and biological control via complementarity and sampling effects. Land-use management is often focused on few species and local processes, but in dynamic, agricultural landscapes, only a diversity of insurance species may guarantee resilience (the capacity to reorganize after disturbance). Interacting species experience their surrounding landscape at different spatial scales, which influences trophic interactions. Structurally complex landscapes enhance local diversity in agroecosystems, which may compensate for local high-intensity management. Organisms with high-dispersal abilities appear to drive these biodiversity patterns and ecosystem services, because of their recolonization ability and larger resources experienced. Agri-environment schemes (incentives for farmers to benefit the environment) need to broaden their perspective and to take the different responses to schemes in simple (high impact) and complex (low impact) agricultural landscapes into account. In simple landscapes, local allocation of habitat is more important than in complex landscapes, which are in total at risk. However, little knowledge of the relative importance of local and landscape management for biodiversity and its relation to ecosystem services make reliable recommendations difficult.

Keywords

Agri-environment schemes, biological control, dispersal, ecosystem functioning, land-use systems, pollination, resilience, spatial scale, sustainability, trophic interactions.

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INTRODUCTION

Agricultural land use affects large parts of terrestrial area, so its contribution to biodiversity is critical for successful conservation in the future. A landscape perspective is needed to understand why agricultural land use has the well-known negative and less known positive effects on biodiversity and related ecosystem services. Agricultural land use and biodiversity conservation have been traditionally viewed as incompatible. Ecologists and conservationists often focus on pristine or little intervened habitats to save the last remnants of wild nature. Only recently there has been an increasing recognition that such a conservation focus is of limited value (Collins & Qualset 1999; Bengtsson

et al. 2003; Schroth *et al.* 2004) and that the importance of population exchanges among areas of different disturbance regimes and among early and late successional habitats needs to be acknowledged. Intensified land use in agriculture and forestry is irrefutably the main cause of global change and biodiversity loss, but low-intensity land-use systems also may be important elements of large-scale conservation programmes. Here, we review negative and positive effects of agriculture on biodiversity conservation, the potential mechanisms of biodiversity–ecosystem service relationships, the role of biodiversity in multifunctional agriculture, and analyse the importance of biodiversity for ecosystem services, such as pollination and biological control, comparing local (the site) and landscape scales.

Current concepts of the biodiversity–ecosystem service relationships often ignore the influence of spatial scale, but species in a given area experience that area quite differently (Peterson *et al.* 1998). We analyse the often-neglected influence of landscape context on local (field) processes in agroecosystems and conclude with recommendations for agri-environment schemes, which financially compensate farmers [of the European Union (EU)] for any income loss because of changed management in favour of the environment or biodiversity (Kleijn & Sutherland 2003).

AGRICULTURAL INTENSIFICATION AFFECTS BIODIVERSITY ON A GLOBAL SCALE

During the last decades, worldwide losses of biodiversity have occurred at an unprecedented scale and agricultural intensification has been a major driver of this global change (Matson *et al.* 1997; Tilman *et al.* 2001). The dramatic land-use changes include the conversion of complex natural ecosystems to simplified managed ecosystems and the intensification of resource use, including application of more agrochemicals and a generally higher input and output, which is typical for agroecosystems as relatively open systems (Table 1). Not only the biodiversity of pristine habitats and traditional, low-intensity agroecosystems, but also the biodiversity of intensively used agroecosystems has been greatly reduced during the last decades. For example, the agronomically important, high-intensity pastures in Germany (*Lolio-Cynosuretum*) lost around half of the plant species in post-war Europe and are now extremely species poor (just 13–14

species per site; Isselstein 2003). Similarly, seed density in arable soils steeply decreased from 1900 onwards (Robinson & Sutherland 2002). Recent agricultural intensification also includes genetically modified crops, which offer new opportunities for increased yields in the coming decades, but also risk side-effects (Groot & Dicke 2002; Hails 2002).

Agricultural intensification happens at two spatial scales. The landscape scale of agricultural intensification adds to the local effects of intensified farming practices (Table 1). On a landscape scale, fields have been amalgamated and enlarged to enhance farming efficiency resulting in homogeneously farmed landscapes with little non-crop area. Fragmentation of remaining natural habitat because of expanded agriculture is a major cause of extinction of fragmented, small and isolated populations (Robinson & Sutherland 2002; Tilman *et al.* 2002; Benton *et al.* 2003), so species losses are because of both deterministic (by agricultural expansion) and stochastic processes (by habitat fragmentation). Examples of landscape-wide biodiversity losses include populations of many farmland birds, which declined severely across much of post-war Europe because of agricultural intensification (Donald *et al.* 2001). Cereal yield almost tripled from 1960 to 2000, and cereal yield alone, which is closely correlated with fertilizer use, can be used as predictor of over 30% of the variation in the decline of European bird populations (Donald *et al.* 2001). In another large-scale and long-term study, Benton *et al.* (2002) linked temporal changes in farmland birds with invertebrate numbers and agricultural practice in Scotland. Similar declines in farmland birds, insects, spiders and arable weeds

Table 1 Practices of agricultural intensification on local and landscape scales (see Tivy 1990; Swift & Anderson 1993; Matson *et al.* 1997; Vandermeer *et al.* 1998; Laurance 2001; Tilman *et al.* 2001, 2002; Hole *et al.* 2005)

Local intensification	Landscape intensification
Shortening crop rotation cycles	Farmers specializing on one or few (arable) crops instead of mixed farming
Decreasing crop diversity (minimizing undersowings, intercropping, polycultures, catch crops, etc.)	Converting perennial habitat (grassland) to arable fields
Increasing input of mineral fertilizers	Destroying edge habitats (hedges, field boundaries, buffer zones along creeks)
Increasing input of pesticides (herbicides, fungicides, insecticides, plant growth regulators, etc.)	Reallocating land to increase field size and make farms more compact
Winter, not spring sowing of cereals	Simplifying landscapes with a spatially and temporally limited number of land-use types increasing landscape homogeneity
Implementation of genetically modified (GM) crops	Giving up traditional, low-intensity land-use management
Deep ploughing, not minimum tillage	Avoiding set-aside fallows and cultivating formerly abandoned area (old fields, fallows)
Cultivating monocultures of high-yield varieties	Reducing resistance to invasion of introduced species
Increasing size of arable fields	Lowering landscape-wide water tables
Machine-driven farming	Fragmenting natural habitat
Lowering water table by drainage	

have been documented (Aebischer 1991; Sotherton 1998; Chamberlain *et al.* 2000).

The main biodiversity losses are due to the post-war transformation of traditional to modern, high-intensity land-use systems in simplified landscapes. The decline of biodiversity may affect ecosystem functioning and yield (Russell 1989; Daily 1997), although the functional role of biodiversity is little known (see below). For example, landscape intensification may disrupt processes such as biological pest control (Andow 1983; Altieri & Letourneau 1984; Corbett & Rosenheim 1996; Thies & Tscharntke 1999; Östman *et al.* 2001; Symondson *et al.* 2002) and crop pollination (Kremen *et al.* 2002, 2004; Klein *et al.* 2003a,b; Ricketts *et al.* 2004). Similarly, local intensification may affect biological pest control (Russell 1989; Matson *et al.* 1997; Thies & Tscharntke 1999; Östman *et al.* 2001; Symondson *et al.* 2002; Barbosa 2003; Donald 2004; Perfecto *et al.* 2004; Tylianakis *et al.* 2004), grassland production (Bullock *et al.* 2001; Loreau & Hector 2001), pollination (Nabhan & Buchmann 1997; Kremen *et al.* 2002; Klein *et al.* 2003a,b) and resistance to plant invasion (Lyons & Schwartz 2001; Kennedy *et al.* 2002; Levine *et al.* 2004; Zavaleta & Hulvey 2004).

ENHANCEMENT OF BIODIVERSITY BY AGRICULTURE

Wilderness areas have priority for conservation (Mittermeier *et al.* 2003), but land use does not simply mean habitat destruction. Agricultural management has been shown to also enhance biodiversity and ecosystem functions, although this has not been acknowledged by most ecologists with their traditional emphasis on pristine ecosystems (Pimental *et al.* 1992; Jackson & Jackson 2002; Rosenzweig 2003). Although agricultural land holds much of the world's biodiversity (Pimental *et al.* 1992), the relative contribution of each management type to conservation is little known. Biodiversity conservation will not work without protecting the just 5% remaining pristine habitats, but also not without a recognition of the contribution of the 'rest'. In Germany, roughly 25% of endangered species can be found in the 2% area that is protected for conservation, whereas the remaining 75% depend on area managed by agriculture (50% of the country) and forestry (30%) (Kaule 1991).

Traditional, and low-intensity, land-use practices of agriculture and forestry greatly promoted habitat diversity in the European human-dominated landscapes during the last centuries, before the rapid agricultural intensification after the Second World War reduced this heterogeneity towards more homogeneous landscapes (Bignal & McCracken 1996; Isselstein 2003). Beneficial effects of non-intensive agricultural land use (mainly of grassland) are still important for conservation and its management (Bignal & McCracken 1996; Plachter 1999; Sutherland 2002a,b). In central Europe, natural ecosystems are almost absent and most nature reserves are anthropogenic and need management. These man-made reserves include much grassland, endangered by (i) agricultural intensification and (ii) succession to forests that must be inhibited using formerly widespread low-intensity land-use practices (Plachter 1999; Robinson & Sutherland 2002; Sutherland 2002b; Isselstein 2003). Non-intensively managed (once mown or little grazed) calcareous grasslands and heathlands are among the most species-rich reserves in central Europe (Plachter 1999; Krauss *et al.* 2003). European landscapes are characterized by high percentages of synanthropic species including many endangered flagship species such as the white stork, hares and many farmland birds and mammals. In Germany, the 350 species of arable weeds (mainly annuals) include 38% red list species.

Agricultural land-use intensification may not only mean higher extinction, but also more resources enhancing populations, even of uncommon or endangered species. The often higher productivity of land use, compared with natural systems, may provide more resources such as plant biomass and fruits for birds, mammals and butterflies. For example, Söderström *et al.* (2001) found highest avian species richness on recently cultivated land and a richness decrease with time since last management. Agroforestry often supports a diversity of fruits attracting birds (Wunderle 1998; R. Marché, A. M. Klein, L. Carrasco and T. Tscharntke, 2005, personal communication). Bumblebee populations increase in landscapes with high amounts of oilseed rape, because of the importance of this mass-flowering resource for colony founding (Westphal *et al.* 2003). Hence, the habitat value of agroecosystems is often determined by their large food resources, resulting from the high productivity (which also favours pest outbreaks), and not only by high disturbance levels.

Maintenance of biodiversity and ecosystem functioning requires closer collaboration with farmers and foresters (Jackson & Jackson 2002). In these human-dominated landscapes, conservation strategies are a matter of public debate over which type of ecosystem or landscape is wanted and should have priority for conservation. The diverse habitat mosaic created by low-intensity agriculture, as practiced in the middle of the 19th century, is the most appealing vision of a complex rural landscape for most conservation-minded people. Few conservationists argue in favour of just deciduous forests as natural, late-succession ecosystems. Hence, conservation programmes usually combine traditional man-made ecosystems (mainly grassland, heathland) with little used forests.

In contrast to the conservation effort in the small-scale land-use mosaic of European landscapes, much of the rest of the world puts priorities on the protection of large

wilderness areas (Sutherland 2002b). This is reflected by the mean size of protected area which is small in Europe (on average 17.4 km^2), and much larger in North America (340.6 km^2) and tropical regions (Southeast Asia: 286.1 km^2, western and central Africa: 432.2 km^2, South America and Brazil: 1505 km^2; data from Chape *et al.* 2003). In tropical regions, traditional conservation strategies focus mainly on pristine ecosystems, the mature rainforests, and any form of land use has been regarded as detrimental for biodiversity (Putz *et al.* 2001). Hence, the potential value of traditional land-use systems for tropical biodiversity has been greatly underestimated in the past (Pimental *et al.* 1992), but during the last decade, attitudes towards its value have changed. Only recently, Bawa *et al.* (2004) endorsed the calls of the Association for Tropical Biology and Conservation (ATBC) and of the Ecological Society of America (ESA) to shift their primary focus from the study of undisturbed ecosystems to interdisciplinary studies of human-influenced ecosystems for the betterment of human societies (see also Schroth *et al.* 2004; du Toit *et al.* 2004). Vandermeer & Perfecto (1995) raised some of the most challenging questions about conservation of tropical biodiversity in the context of socially and economically sustainable agriculture. For example, coffee agroforestry shaded by a diversity of natural or planted trees represents the last forested habitats in many tropical landscapes. Recent papers on the biodiversity in shade coffee systems provide ample evidence for their importance in biodiversity conservation (see Perfecto & Armbrecht 2003 for a recent review; and Rice & Greenberg 2000 for cacao agroforestry). Coffee shaded by a diversity of trees support a high diversity of birds, including species that depend on closed canopies and endangered migratory birds, which can be found in coffee in higher densities than in natural forest. Insecticide fogging of shade tree canopies in a traditional coffee plantation results in a similar diversity of canopy arthropods as found in pristine forest trees (Perfecto *et al.* 1996; Perfecto & Armbrecht 2003). The distance to nearest rainforest edge appears to be of major importance for the diversity of important functional groups such as bees and ants, so local and landscape management matter (Armbrecht & Perfecto 2003; Klein *et al.* 2003a,b; Ricketts *et al.* 2004).

LOCAL BIODIVERSITY–ECOSYSTEM SERVICE RELATIONSHIPS

Conservation biologists have been mainly concerned with biodiversity and agroecologists mainly with its function (Vandermeer & Perfecto 1997). However, simplification of agroecosystems caused by the intensification of agricultural practices may affect important ecosystem services via the loss of biodiversity. These include crop production, pest control, pollination and decomposition processes (Daily

1997; Altieri 1999; Schläpfer *et al.* 1999; Tilman *et al.* 2002; Wilby & Thomas 2002), although the design of biodiversity–functioning experiments and the relative role of potential mechanisms are still a matter of debate (see, for example, Lepš 2004; Swift *et al.* 2004; Schmid & Hector 2004). We discuss four principal relationships, species complementarity, sample effects, redundancy and idiosyncrasy (Gaston & Spicer 2004) and refer to papers providing evidence for each of these possibilities. The full meaning of biodiversity for ecosystem services cannot be realized with a discussion of these relationships on a local scale alone, so the next chapter broadens the perspective to larger spatial scales.

Species complementarity

Biodiversity may enhance functioning when species add to the function via a unique (complementary) occupation of the total niche. Each species or species group may focus on different resource parts (resource partitioning) or promote positive intraguild interactions, thereby improving the ecological functioning. The enhancement of productivity in diverse grasslands can be caused by both complementarity and sampling effects (see below), but complementary effects through niche differentiation or facilitation appears to be of major importance (Loreau & Hector 2001; see Loreau *et al.* 2002). There is much experience with plant species complementarity in the agronomy literature on intercropping (Vandermeer *et al.* 2002). Such relations have been also shown for biological control. Using a modelling approach, Pedersen & Mills (2004) conclude that introduction of a number of species for biological control is a sound strategy because of niche separation (but others did not find evidence for a better suppression of the pest, Rosenheim 1998). Similarly, in a species-rich parasitoid complex, each of eight abundant parasitoid species contributed to high host mortality (Tscharntke 1992a,b). These were monophagous larval parasitoids and showed little overlap but significant segregation in host use, so each species focussed on spatiotemporally separated subpopulations of the one host. Further studies showed that the exclusion of predators and parasitoids almost triples cereal aphid densities and that there is a complementary effect of the vegetation- and ground-dwelling species (Schmidt *et al.* 2003; see also Symondson *et al.* 2002). Cardinale *et al.* (2003) found that pea aphid populations were most suppressed when all three species of enemies (a ladybird beetle, a damsel bug and a parasitoid) worked together (but intraguild predation can also be important, see below: Idiosyncrasy). Myers *et al.* (1989) reviewed 50 cases of successful biological control programmes and found that one-third were credited to a complex of introduced agents and two-thirds to only one of several introduced agents. We need to better understand when many or single species of biocontrol agents will result in better suppression of pests

(see Rosenheim 1998; Schellhorn & Andow 1999). Hence, there is evidence for complementarity in agriculturally important functional groups, but most examples do not explicitly or experimentally show how sequential addition of species enhance the ecosystem services.

Sampling effects (species identity)

Species differ in their potential contribution to ecosystem services, so increasing biodiversity enhance the probability that a species is present that strongly enhances ecosystem functioning. Hence, the identity of one or few species dominating ecosystem processes becomes important. Sampling (or selection) effects have been shown to be important in experiments with sown grasslands where the random inclusion of particularly productive species contributed to overall productivity (in addition to complementarity effects, Loreau & Hector 2001, see above). The chance of including a particularly effective species in a given environment appears to increase with the number of species in the available pool. This does not only hold for plant diversity (with respect to enhanced productivity), but also for other functional groups such as natural enemies in that enemy richness may be related to predation rates (Chang 1996).

Redundancy

Species redundancy means that a positive relation between diversity and functioning holds only for few species and additional species do not increase function, but plateau at higher diversity levels. Redundancy is important in the most commonly studied case of a biodiversity–ecosystem service, the importance of grassland plant diversity for productivity. Results indicate complementary and sampling effects (see above), but also redundancy when many species (> 5–15 species) are involved (Loreau *et al.* 2002), so complementarity and sampling effects occur up to only a limited number of species. Hence, increasing species diversity appears to enhance ecosystem functioning only up to a saturation point. However on a landscape scale, only high-diversity systems with 'redundancy' in functional groups can be expected to provide the capacity for reorganization after disturbance (see below: the insurance hypothesis).

Idiosyncrasy

Strong interactions among species may make the relationship between diversity and functioning extremely variable, as adding a further species may enhance or reduce the ecosystem service or may leave it unchanged (Peterson *et al.* 1998; Snyder *et al.* 2005). According to this model, the ecosystem service depends idiosyncratically on the involved species. This is well-known from biological control of aphid pests. There is evidence for facilitation among predators in that ladybird beetle foraging causes dropping of aphids to the ground thereby providing an additional resource for the ground-foraging carabid beetles (Losey & Denno 1998), but predators may also be more effective when foraging alone because of intraguild predation and cannibalism (Rosenheim *et al.* 1993; Rosenheim 1998; Symondson *et al.* 2002; Finke & Denno 2004). Similarly, a diversity of pollinators may mean pollen transfer from a larger number of conspecific individuals (i.e. several pollen donors), thereby increasing the chance of becoming fertilized by the best pollen (Paschke *et al.* 2002). In contrast, an enhanced number of pollinator species may reduce fitness because of little flower constancy, clogging the stigma with heterospecific pollen. Further, pollinators may either show complementary resource use of spatiotemporally separated flower populations or their joint effect may be reduced due to competition. Hence, species are idiosyncratic making the outcome of local diversity–functioning relationships hard to predict. In such situations, (agricultural) management may select for species combinations minimizing negative interactions within functional groups (e.g. Schellhorn & Andow 1999).

Conclusions

The four potential mechanisms of how biodiversity influences ecosystem services (species complementarity, sampling effects, redundancy and idiosyncrasy) are based on just a few published examples. There is little empirical evidence that local biodiversity is generally related to functioning, especially when taking the publication bias towards significant results into account. Such evidence is in favour of the null hypothesis of no relation between biodiversity and ecosystem functioning. For example, soil organisms are known to show high redundancy among functional species groups, so the loss of species or changes in composition may not affect decomposition rates, and there are few consistent trends for both aboveground and belowground systems (Wardle *et al.* 2000; Bardgett 2002; Wardle & van der Putten 2002; Hedlund *et al.* 2004). Similarly, Rodriguez & Hawkins (2000) did not find a relation between parasitoid species richness and parasitism rates, and parasitoids appeared to function better in simple (agricultural) than complex (natural) food webs (Hawkins *et al.* 1999; Halaj & Wise 2001; Montoya *et al.* 2003).

Despite this little understanding how biodiversity matters, there is also evidence that high-diversity ecosystems often clearly promote important ecosystem services. For example, hay yield has been shown to be higher (up to 60%) in species-rich (25–41 plant species) than species-poor sowings (6–17 species), although the mechanisms are not known (Bullock *et al.* 2001). Potential yield of these species-rich hay meadows

is only 30–60% of that of intensified grasslands (Isselstein 2003), and whether the loss of half the plant species in intensified grassland during the last decades (Isselstein 2003) has caused losses in productivity is unclear. Further examples include the yield increase because of cereal aphid predation by a rich community of ground-living natural enemies, estimated to be 23% (Östman *et al.* 2003). Insecticide applications in rice fields of south and Southeast Asia, which remove most generalist predators and thereby release pests from control, cause pest resurgence and high rice yield losses (Kenmore *et al.* 1984; Settle *et al.* 1996; Wilby & Thomas 2002). Availability of non-pest prey in the early season, when predators are not yet abundant, may cause effective switching between such alternative prey to pests (Settle *et al.* 1996; Scheu 2001). Further, reduced parasitoid richness in fragmented habitat is related to reduced host mortality (Kruess & Tscharntke 1994, 2000), and a diversity of insectivorous birds in agroforestry appears to prevent pest outbreaks (Perfecto *et al.* 2004).

LANDSCAPE CONTEXT OF BIODIVERSITY–ECOSYSTEM SERVICE RELATIONSHIPS: THE INSURANCE HYPOTHESIS

The long-term sustainability of ecosystems and the services they generate depend on the conservation of biodiversity on a landscape scale (Bengtsson *et al.* 2003; Loreau *et al.* 2003). High diversity of functional groups may allow reorganizations after disturbances (Bengtsson *et al.* 2003), due to a high number of insurance species (the insurance hypothesis of biodiversity, Loreau *et al.* 2003). The diversity of responses to environmental change, exhibited by species of the same functional group, is critical to resilience (the capacity to reorganize after disturbance) and has been called response diversity by Elmqvist *et al.* (2003). In dynamic landscapes, but also in nature reserves, disappearance of recolonization sources makes extinction the dominant population process (Pickett & Thompson 1978). Hence, agricultural landscapes must be a mosaic of well connected early and late successional habitats, to support a high biodiversity, and thereby, the capacity to recover from minor and major, small- and large-scale disturbances (Bengtsson *et al.* 2003).

Many agricultural landscapes are dominated by arable crops and early successional fields like fallows, and support only little non-crop area such as forest remnants and old grassland. In such human-dominated, dynamic landscapes, local extinction is a common process and immigration is of major importance. There are three principal possibilities of crop–non-crop exchanges of organisms: (i) exchange among (late-successional) non-crop habitats if the landscape matrix allows connectivity for dispersing habitat specialists, thereby sustaining the populations' persistence (Pickett & Thompson 1978; Hunter 2002), (ii) non-crop habitat as a source of (generalist) species invading crop area, enhancing the potential of pollination or biological control (Tscharntke & Kruess 1999; Kremen *et al.* 2002) and (iii) crop habitat as a source of (generalist) species invading the natural non-crop area, thereby affecting biotic interactions in natural habitats (Tscharntke *et al.* 2005; T. A. Rand and S. M. Louda, 2005, personal communication). Conservationists mainly focus on connectivity of late-successional habitats (and their specialized communities), which are often protected reserves, and aim to exclude disturbances. However, disturbances are intrinsic parts of all ecosystems, and ecological resilience, i.e. the capacity to absorb disturbance, reorganize and adapt to change, depends on landscapes providing this capacity through conservation of a diversity of dispersing species (Bengtsson *et al.* 2003; Elmqvist *et al.* 2003).

'Surplus' or redundant species (see above) may become important in an ever-changing environment, as formulated by the hypothesis of spatiotemporal insurance by biodiversity. The potential importance of the many rare species in communities is hard to establish, although they often make up 30–50% of all species. In a human-dominated landscape and an unpredictable future, diverse communities support species that may become important as soon as others disappear. Economically, this is an 'option value' for the future. For example, Perfecto *et al.* (2004) found that high tree richness in coffee agroforestry supports a diverse bird community that turned out to increase predation on lepidopterans. Hence, these diverse coffee landscapes appeared to provide an important function with the prevention of potential pest outbreaks. Similarly, only the combined effects of pathogens and predators may turn out to be important in the effective control of insect outbreaks (Dwyer *et al.* 2004).

Aphids are victims of a diversity of enemies (Snyder *et al.* 2005) making the aphid–enemy interaction a nice example for the role of enemy diversity for the functioning of biological control. The identity of naturally occurring enemies as cereal aphid antagonists greatly differs among regions and years (Thies *et al.* 2005). Around the city of Göttingen, Germany, there are years in which parasitoids are key mortality agents (e.g. Schmidt *et al.* 2003) and others where ladybird beetles (I. Roschewitz, T. Tscharntke and C. Thies, 2005, personal communication) or syrphid flies (Krause & Poehling 1996) cause most of the mortality. Around the city of Uppsala, Sweden, the impact of parasitoids is negligible, but ground-dwelling predators are most important (Östman *et al.* 2001). Hence, cereal aphids suffer from a large number of enemies, but the effectiveness of each enemy seems to vary with landscape, region and country (see Östman *et al.* 2001; Schmidt *et al.* 2003). This spatio-temporal variation in effectiveness of each enemy species emphasizes the need of biodiversity

preservation as insurance and to take large spatial scales into account. The long-term sustainability of ecosystems may depend on substitutable insurance species within each functional group (Bengtsson *et al.* 2003). Species in a functional group often operate at different scales, as in aphid enemies with, for example, ballooning spiders operating at a much larger-scale than parasitoids (Schmidt *et al.* 2005; Thies *et al.* 2005). This provides mutual reinforcement contributing to the resilience of a function, while at the same time minimizing competition (Peterson *et al.* 1998). As environmental constrains change with time and space, it is hardly predictable which life history traits of aphid enemies is best adapted. Hence, only a diverse species pool for one ecological function may provide the best chance to include at least one well adapted, efficient species in a given environmental situation.

In addition to biodiversity as insurance against changing environments and disturbances, there is increasing evidence that the collective role of many rare species may be important for ecosystem services. The contribution of each rare species is usually small, but all species together may be of quantitative importance. For example, the many solitary bee species on highland coffee are more effective pollinators than the few, but abundant, social species, thereby contributing to the positive relation of fruit set to bee diversity (Klein *et al.* 2003a). This mechanism is similar to that of the collective role of rare plant species providing resistance to a grassland invader (Lyons & Schwartz 2001). Removal of many rare plant species, but not removal of the same biomass of common species, enhanced invasion success of *Lolium multiflorum* (see also Levine *et al.* 2004). In such cases many rare species may turn out to be more important for ecosystem functioning than few abundant species.

LOCAL DIVERSITY AS A FUNCTION OF LANDSCAPE SPECIES POOLS

Local diversity is a function of regional diversity, but it constitutes only a proportion of regional richness, as local communities are mostly unsaturated (e.g. Holt & Gaston 2002; Gaston & Spicer 2004). This proportion can be expected to be lower in agroecosystems, because of their high disturbance levels, than in natural ecosystems. The assemblage of locally important organisms driving the main ecosystem processes depends on the recruitment of species to fill local niches (see above: Species complementarity). In structurally simple landscapes, local fields may not receive the set of species necessary to realize the potential ecosystem functions, thereby endangering the long-term stability of local processes (Bengtsson *et al.* 2002, 2003; Hunter 2002). The functional significance of biodiversity will appear only at larger spatial and temporal scales, because spatial exchanges among local systems provide spatial

insurance in heterogeneous landscapes when species may complement each other and better occupy spatial and temporal gradients (Bengtsson *et al.* 2002; Loreau *et al.* 2003).

Arable crop fields are like defaunated islands, relying on colonization from the regional species pool (Landis & Marino 1999; Tscharntke & Kruess 1999; Tscharntke 2000; Denys & Tscharntke 2002). Reorganization of such disturbed ecosystems depends on a diversity of source populations in the surrounding landscape, which assure the resilience of the systems for sustainable use (Folke *et al.* 1996). Swift *et al.* (2004) argue that biodiversity enhancement in an agricultural context is functionally justified more at the landscape than the plot scale, as plot diversity is managed in a strictly utilitarian direction.

Agri-environment schemes provide incentives for biodiversity preservation through organic farming (Mäder *et al.* 2002; Pfiffner & Luka 2003; Bengtsson *et al.* 2005; Hole *et al.* 2005), but landscape context is also important (Söderström *et al.* 2001; Duelli & Obrist 2003; Weibull & Östman 2003; Bengtsson *et al.* 2005). The species pool of the landscape from which local communities are drawn may be even more important than the difference between organic and conventional agriculture, as shown for the diversity of spiders increasing with landscape complexity, but not farming system (Schmidt *et al.* 2005; Schmidt & Tscharntke 2005). Landscape complexity may also compensate for biodiversity loss because of local management intensity. For example, the diversity of arable weeds was higher in organic than in conventional fields, but only in simple landscapes (see Fig. 1 and below), as landscape complexity enhanced species diversity in conventional fields to a similar diversity level (Roschewitz *et al.* 2005). Figure 2 illustrates the point that the biodiversity differences between conventional (intensive) and organic (extensive) farming are mainly restricted to simple landscapes. The negative impact of intensive farming (e.g. herbicide applications) happens only in simple landscapes where colonization from the surrounding (in form of seed rain) is limited, whereas complex landscapes appears to mitigate local anthropogenic weed eliminations. Such compensation of intensive management by complex, high-diversity landscapes should be evident only for organisms of the aerial plankton and other highly mobile species.

DISPERSAL LIMITATION IN DYNAMIC LANDSCAPES

Allocation of habitat and contrasting effects of spatial scale

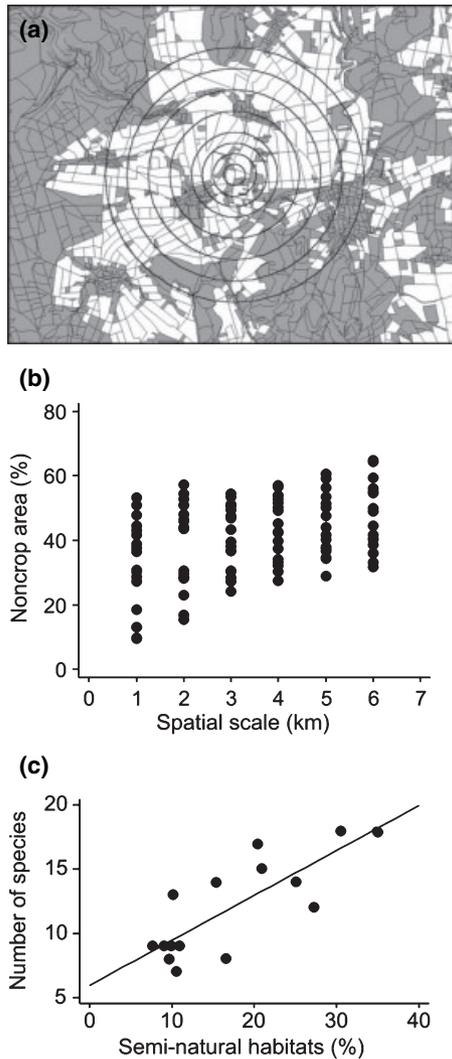Cleared, homogeneous landscapes characterized by arable fields cannot be expected to support a meaningful diversity

Figure 1 Landscape context of biodiversity in agroecosystems. (a) This landscape sector (around the city of Göttingen) shows nested circles ranging from 500 to 6000 m diameter, thereby defining different spatial scales that may influence populations. Landscape complexity within these diameters was used to explore whether species experience surrounding landscapes at different spatial scales (see Steffan-Dewenter *et al.* 2002; Thies *et al.* 2003). This is a structurally complex landscape (Ø 1500 m; 56.0% white area = annual crops). In samples of 15–20 such landscape sectors, percentage annual (arable) crops and habitat type diversity are negatively correlated, thereby covering a gradient from simple to complex landscapes. (b) Changes in the arcsine $\sqrt{p}$ non-crop area (area not converted to arable fields) with increasing diameter of the landscape sector and within each diameter, showing the large differences within and among spatial scales ($n = 18$ landscapes, each with six nested scales, data from Thies *et al.* 2003). (c) The number of flower-visiting bee species in relation to the percentage semi-natural habitat (non-crop habitat) in the landscape. Bee visitation was established on experimental patches of flowering plants in grassy field margin strips adjacent to cereal fields, which were exactly in the centre of the digitized landscapes [see (a)]. Diameter of the landscape sector was 1500 m. Regression line: $Y = 5.95 + 0.35 \ \mathrm{arcsin}\sqrt{x}$; $r^2 = 0.633$; $F = 22.43$; $n = 15$; $P = 0.0004$ (data from Steffan-Dewenter *et al.* 2002).

of populations as a source of immigration (Pickett & Thompson 1978; Bengtsson *et al.* 2003). In such simple landscapes local habitat creation or management changes may become important to reduce isolation from sources of colonizers and thereby, to improve ecosystem services. For example, creation of grassy field margin strips adjacent to oilseed rape fields allows parasitoids of the rape pollen beetle to hibernate in unploughed soil, and these parasitoid populations subsequently immigrate into adjacent rape fields and cause higher pest mortality. However, the threefold increase in mortality is observed only in simple landscapes, because in complex landscapes the percentage parasitism is high everywhere (with or without local field margin strips; Thies & Tscharntke 1999; Tscharntke *et al.* 2002a). Similarly, edge effects (lower survival of nesting passerines in edges) were stronger in fragmented than continuously forested landscapes (Driscoll & Donovan 2004). This is consistent
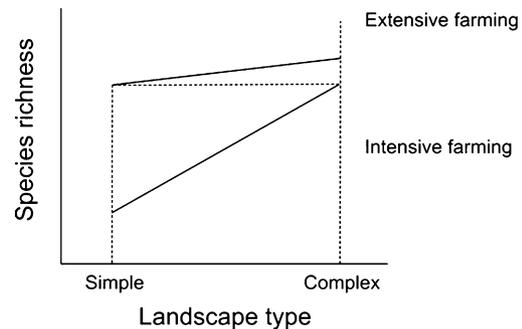
Figure 2 Diversity of arable weeds in relation to local management (extensive vs. intensive) and landscape composition (simple vs. complex; based on findings of Roschewitz *et al.* 2005). Intensive farming means conventional practices with applications of mineral fertilizers and pesticides, contrasting with extensive (organic) farming. The solid lines show the different responses, while the dotted lines are for orientation only and indicate that diversity is higher in organic fields, while landscape complexity can compensate for the intensive conventional agriculture. In addition to this weed biodiversity pattern, the higher weed cover means enhanced cereal aphid control (I. Roschewitz, T. Tscharntke and C. Thies, 2005, personal communication).

with simulation models showing that allocation of habitats in fragmented landscapes influences populations only in simple, not complex landscapes, thereby possibly compensating for local biodiversity loss (Andrén 1996). Simple

landscapes need well-allocated habitats to ensure reorganization after disturbance (see Bengtsson *et al.* 2003).

Dispersal limitation may also cause contrasting patterns in diversity or interactions, depending on the spatial scale considered. Such scale-specific patterns are now well acknowledged (Summerville *et al.* 2003). For example, coffee flower-visiting bees respond positively to flower density per shrub or branch, showing a clear numerical concentration effect, but on the field scale, concurrent flowering of most shrubs results in reduced flower visitation, showing dilution effects as a result of the limited size of bee populations in the surrounding landscape (D. Veddeler, A. M. Klein and T. Tscharntke, 2005, personal communication). Temporal scales may also matter. For example, diversity of trap-nesting Hymenoptera is significantly affected by land-use type. While intensive cropping systems such as rice and pasture exhibit higher diversity in certain months, greater species turnover through time in the abandoned coffee and forest plots account for the higher overall diversity in these habitats (J. Tylianakis, A. M. Klein and T. Tscharntke, 2005, personal communication).

Community structure as a function of dispersal abilities

Different species operate at different spatial and temporal scales, as shown by the scaling relationship of body size and ecological function (Peters 1983). For example, mammalian seed dispersers and predacious birds show a broad range of body sizes with corresponding differences in landscape-wide resource use, spreading their impact on resources and their susceptibility to disturbance widely (Peterson *et al.* 1998). The spatial scale of how landscape influences population densities depends on the species-specific dispersal, so interacting communities are made up of species experiencing the surrounding landscape at different spatial scales (Steffan-Dewenter *et al.* 2001, 2002; Bestelmeyer *et al.* 2003; C. Westphal, I. Steffan-Dewenter and T. Tscharntke, 2005, personal communication). Current models assume implicitly that species involved in biotic interactions operate at the same scale, but populations and processes are not scale invariant, as shown by the following examples.

In a gradient from simple to complex landscapes using 15–20 true landscape replicates around the city of Göttingen, Germany, determinants of local population dynamics and community structure were analysed at different spatial scales (Fig. 1). Landscape composition changes from circles of 500 to 6000 m in diameter, particularly in the dynamic land-use mosaic typical for agricultural landscapes in central Europe. These large differences between and within landscapes (Fig. 1a,b) allow to determine the spatial scale (diameter of the surrounding landscape), exerting the greatest influence on local populations. In general, biodiversity increases with landscape complexity, exemplified with flower-visiting bees on standardized plant patches exposed on grassy field margin strips (Fig. 1c). The landscape context of population dynamics were found to differ, as some species are determined by small sectors of the surrounding landscape (within a circle of 500 m diameter) and others respond to large sectors (6000 m). Changes in biodiversity do not affect all species or guilds in a similar way, thereby changing food web interactions and ecological functions (Tscharntke 2000; Tscharntke *et al.* 2002b). For example, demographic risks and anthropogenic threats render large vertebrate consumers much more vulnerable to extinction than plants, leading to large impacts on ecosystem functioning (Duffy 2003). The diversity of carnivorous carabid beetles is more affected by landscape simplification than for phytophagous carabids (Purtauf *et al.* 2005).

Biotic interactions may change when the interacting organisms show specific functional scales and the surrounding landscape changes in composition (of different land-use systems) with diameter. For example, when a low- and a high-dispersal species compete, the low-dispersal species will suffer most from locally detrimental conditions. In contrast, locally favoured conditions, but detrimental landscape surroundings may cause competitive release of the low-dispersal species. This may be true for arable weeds, because their density is influenced by landscape structure (Gabriel *et al.* 2005a; Roschewitz *et al.* 2005). Further, solitary bees and honeybees show contrasting scales of resource use (500 m vs. 6000 m diameter; Steffan-Dewenter *et al.* 2002), affecting possible competition between solitary wild bees and the social honeybee (Steffan-Dewenter & Tscharntke 2000a). Coexistence within bumblebees includes a body size-dependent spatial strategy of resource use (C. Westphal, I. Steffan-Dewenter and T. Tscharntke, 2005, personal communication). Slight differences in the mean body length of bumblebee workers (11–15 mm) translated in great differences in foraging range, whereas large body size differences of solitary bees (5.5–24 mm) resulted in smaller differences in foraging range (Fig. 3a) (Gathmann & Tscharntke 2002). Similarly, body size of four parasitoid species could be related to the landscape scale experienced (Roland & Taylor 1995). Coexistence and competition of species need to consider the specific spatial scale experienced. Dispersal range can often be related to body size, but is also influenced by guild characteristics, resulting in guild-specific body size dispersal relations (Fig. 3a). The guild-specific differences between social and solitary bees (Fig. 3a) may be due to the fact that the social species are known to explore landscapes with better communication techniques than solitary species. Further, dispersal may be larger than expected from body size when (i) guilds regularly need to use spatially separated habitats with, for example, a large distance between nesting and food resources (multi-habitat users), or when (ii) guilds use temporally separated
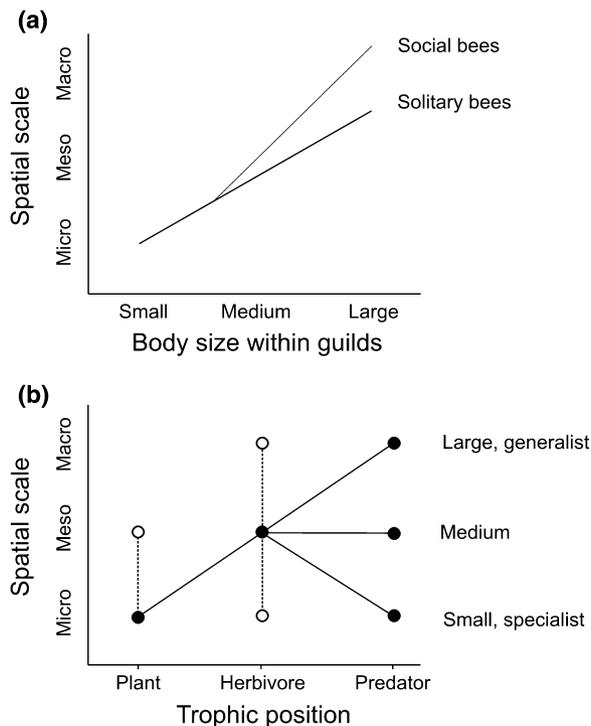
Figure 3 Interacting species may experience their surrounding landscape at different spatial scales. The micro (approximately 500 m diameter), meso (2000–3000 m) and macro (6000 m) scales are shown (see Fig. 1a). (a) The spatial scale is related to body size, but change with functional group involved, shown for the differences between social bumblebees and solitary bees (based on data from Gathmann & Tscharntke 2002; C. Westphal, I. Steffan-Dewenter and T. Tscharntke, 2005, personal communication). (b) The spatial scale of plants, herbivores and their predators or parasitoids. Three possible scenarios of scale-dependent trophic interactions are given for the third trophic level. In such tritrophic interactions, the spatial scale experienced is usually small in plants (influenced by microsite conditions) and intermediate in herbivores (which often use several plants). The spatial scale experienced by populations of the third trophic level appears to depend on the species' body size and specialization: (i) large and generalist (e.g. many mammals and birds), (ii) medium (many invertebrate predators and parasitoids with intermediate specialization and body size) and (iii) small and specialized (e.g. most parasitoids). The main relations are shown with filled points and solid lines, whereas variability within trophic position is illustrated using open points and dashed lines (for more details see text).

habitats as in host-alternating species or species migrating from summer to hibernation habitats.

Dispersal abilities and trophic interactions

Species-specific differences in the perception of landscape context may also affect trophic interactions (Fig. 3b). High-

trophic level species are often expected to be more likely to have large home ranges and population dynamics determined by landscape composition rather than local patch quality (Holt 1996; Ritchie & Olff 1999). However, this seems to fit only for trophic interactions where trophic level and body size (and thereby, dispersal) are positively related. This is the case in the widespread perception of food chains involving higher plants, insect herbivores, insectivorous vertebrates (e.g. birds or small mammals) and even larger vertebrate predators (e.g. raptors or cats). However, food chains are often composed of a different set of species, for example, when plants, phytophagous insects, parasitoids and predatory insects are involved (Thies *et al.* 2003). With respect to the first trophic level, diversity of annual plant communities is often affected by seed limitation, so seed rain originating from the surrounding landscape becomes important (Thurnbull *et al.* 2000; Roschewitz *et al.* 2005), whereas perennials are mostly microsite limited. In the second trophic level, herbivores also show a range of spatial strategies, from specialized insects closely associated with their host plant to insects switching among several host plants to grazing mammals with large-scale migrations. Such patterns (Fig. 3b) are in line with studies showing that plants are less affected by habitat fragmentation than the specialist (but not the generalist) members of the second trophic level (Steffan-Dewenter & Tscharntke 2000b). In the third trophic level, the landscape area experienced by small and specialized parasitoids contrasts with that of large, little specialized, insect-feeding vertebrates (Fig. 3b). For example, rape pollen beetles and their parasitoids are influenced at the same spatial scale (within 1500 m diameter), which is also the case for the thistle stem-borer *Melanagromyza aenoventris* and its parasitoids (1500 m; Kruess 2003). Primary parasitoids of cereal aphids were influenced by even smaller landscape sectors than their hosts (Thies *et al.* 2005).

When high-dispersal predator populations are disadvantaged by dispersal-inhibiting landscape structure, the low-dispersal prey may particularly profit from locally beneficial situations. For example, thistle populations are influenced by landscape composition within a landscape circle of 1500 m diameter, whereas the antagonists (herbivore load by all stem-borers as well as the fungal pathogens) are influenced up to 6000 m (Kruess 2003; A. Kruess and T. Tscharntke, 2005, personal communication). In contrast, parasitoids of cereal aphids only profit from locally good conditions (nectar resources, alternative hosts within 1500 m diameter), while a landscape complexity at a large-scale (6000 m diameter) supports large enough cereal aphid populations (Thies *et al.* 2005).

Accordingly, specialized enemies like parasitoids have often smaller dispersal ranges than their hosts, so that parasitism success is affected by limited dispersal ability (Kruess & Tscharntke 1994, 2000; Holt *et al.* 1999; but see

Roland & Taylor 1995; Brodmann *et al.* 1997; van Nouhuys & Hanski 2002; J. A. Elzinga, S. van Nouhuys, D. J. van Leeuwen and A. Biere, 2005, personal communication), whereas important generalist biocontrol agents, such as spiders and predatory beetles, are influenced by the landscape matrix at large spatial scales (Symondson *et al.* 2002). High-dispersal ability and large home ranges are life history traits with three important consequences for a better survival in the dynamic and disturbed, agricultural landscapes.

(1) *Increased spatial flexibility and recolonization ability*. High-dispersal ability makes species less susceptible to extinction in mosaic landscapes dominated by human activities, where quick colonization of habitats and the escape from disturbance is an important characteristic of successful species. Locally enhanced species richness because of the surrounding complex, high-diversity landscape (Roschewitz *et al.* 2005; Schmidt *et al.* 2005), should be evident only for highly mobile organisms. Accordingly, management should take into account the landscape scale that determines most of the population dynamics.

(2) *Resources experienced at large spatial scales*. Populations experiencing large landscape sectors because of high-dispersal abilities may be less susceptible to (small-scale) changes in resource availability. In contrast, small-scale foragers need all requirements for survival within a small spatial sector (flowers and hosts for specialized and small parasitoids, flowers and nesting sites for solitary bees). Evidence for the superiority of large-scale resource exploitation comes from a study of bumblebees showing a positive relation of experienced spatial scale (500–6000 m diameter, Fig. 1a) and the species' colony size (see also Pywell *et al.* 2005; Williams 2005; C. Westphal, I. Steffan-Dewenter and T. Tscharntke, 2005, personal communication).

(3) *Low spatial turnover*. Generalists with high dispersal and colonization capacity contrast with specialized and small parasitoids, characterized by limited foraging ranges resulting in a high spatial turnover of species richness (β-diversity). When populations are little connected (via dispersal) at already small distances, the local, isolated communities should tend to change in composition with geographic distance. This idea is supported by analyses of the insect herbivore-parasitoid assemblages on clover and vetch. Parasitoid community structure changed from one patch to the other, whereas herbivore communities remained identical (Tscharntke *et al.* 2002a). α-Diversity of vetch and clover herbivores was on average 69% of γ-diversity (the diversity of all studied sites), contrasting with the 36% for parasitoids (Table 2).

Table 2 Comparison of α-diversity (mean number of species per site) and γ-diversity (all species from all experimental sites) within interacting communities of herbivores and parasitoids

	Herbivores	Parasitoids
Orchard meadows		
T. pratense	6.88 (8)	6.29 (13)
V. sepium	2.48 (5)	0.71 (4)
Experimental islands		
T. pratense	5.47 (8)	6.41 (16)
V. sepium	3.5 (5)	2.89 (8)
α-Diversity (%)	68.5 ± 7.4	35.5 ± 6.3

Herbivores (mainly beetles) and parasitoids attacking red clover (*Trifolium pratense*) and vetch (*Vicia sepium*) are compared using $n = 4$ experimental series (18 or 19 old meadow fragments of different area and 18 or 21 experimental habitat islands made out of potted plants and differing in isolation; data from Kruess & Tscharntke 1994, 2000). *Alpha*-Diversity (γ-diversity) is given. In the last line, the percentage of α-diversity (of γ-diversity) ± SE is shown and tested with a paired *t*-test.
Paired *t*-test: $t = 15.9$, $P < 0.0001$.

Hence, conservation of a high diversity of low-dispersal species such as these small, specialized parasitoids should take a large number of geographically distant habitat patches into account. This is in line with suggestions for a complementary approach in effective conservation planning (Pressey *et al.* 2004).

Summarizing these three points, trophic level position alone is not a good predictor of the spatial scale experienced. Specialist and small enemies, such as most parasitoids, are often dispersal limited, contrasting with highly dispersive, polyphagous predators. These differences in dispersal limitation are also the reason why the trophic level hypothesis of island biogeography holds only for food chains of specialists (Holt *et al.* 1999; Tscharntke & Kruess 1999; Steffan-Dewenter & Tscharntke 2000b). Predators experiencing the landscape at large spatial scales can cope with small-scale disturbances in dynamic landscapes, whereas small-scale foragers are more prone to extinction in situations characterized by disturbances, so that their survival depends on a geographic mosaic of little disturbed habitats with specific communities.

CONCLUSIONS ON THE LANDSCAPE-WIDE BIODIVERSITY CONSERVATION IN AGRICULTURE

In agriculture, management focuses on few species and their specific requirements, yet the potential services of many other species are ignored (Robertson & Swinton 2005). Such a one problem-one species approach may seem to be

appropriate when the system is well-known and the necessary key resources defined for technical solutions. Examples include cases when one efficient pollinator, such as the honeybee, successfully pollinates fruit trees or when one efficient soil organism, such as an earthworm, leads to efficient mineralization, or when one efficient predator controls the target pest. However, three lines of evidence indicate the limitations of such an approach. First, only few cases are analysed sufficiently to reliably restrict management to only one type of interaction. For example, honeybees are now at risk from introduced pests (so wild bees are of increasing importance), decomposition processes depend on many more organism groups than earthworms and also sustainable pest control needs many enemy species in most cases (Scheu 2001; Steffan-Dewenter & Tscharntke 2000a; Kremen *et al.* 2002; Mäder *et al.* 2002; Symondson *et al.* 2002). Second, effects of species loss may not be immediately visible, but increases ecological susceptibility to disturbances (the insurance hypothesis). Risk avoidance in our human-dominated landscapes with unpredictable and ever-changing environments makes conservation of a maximum biodiversity the only reliable option for future sustainable land use. Third, the reality of agroecosystems is not captured by one interaction or function. Even simplified agroecosystems such as annually ploughed, arable fields exhibit a huge complexity of food web interactions (Altieri 1999), providing multiple services that are of unknown importance for future agriculture. Exploration of multi-function agricultural biodiversity is an important future research theme in sustainable agriculture (Gurr *et al.* 2003; Robertson & Swinton 2005; see Chapin *et al.* 2002). For example, even in intensified field crops, only 50% of crop nitrogen uptake comes from fertilizers, while the remainder is from mineralized soil organic matter (Robertson & Swinton 2005). Further, most (potential) pests are not controlled by pesticides but natural enemies, shown by experimental exclusion of cereal aphid enemies (Schmidt *et al.* 2003), fungal pathogens may be controlled by microbial antagonists (Clay 2004), and exclusion of naturally occurring pollinators in coffee reduces fruit production greatly (Klein *et al.* 2003a,b; Ricketts *et al.* 2004). Planting a diversity of crop plants, designed with multiple food and non-food functions in mind (e.g. polycultures instead of monocultures), often promotes biological control of insect pests, including control of viruses transmitted by insects, and contributes to risk avoidance in a changing environment (Matson *et al.* 1997; Vandermeer *et al.* 2002). In addition, understanding the relationship between biodiversity and ecosystem carbon dynamics will be central to reasonable global policy decisions combining carbon storage and biodiversity conservation (Catovsky *et al.* 2002; Huston & Marland 2003; Totten *et al.* 2003; for further ecosystem properties see Matson *et al.* 1997; Robertson & Swinton 2005). This complexity is still little
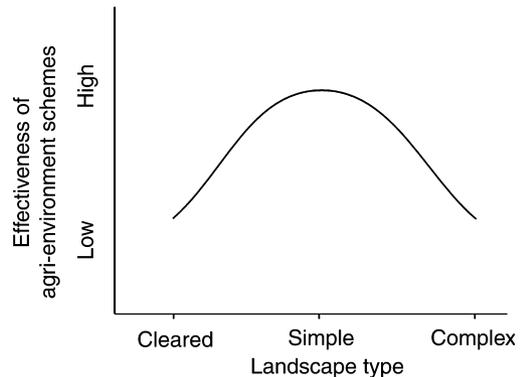

Figure 4 Effectiveness of agri-environment schemes in relation to landscape type. Effectiveness is measured as biodiversity enhancement because of management, such as the conversion from conventional to organic farming (Roschewitz *et al.* 2005) or the creation of crop field boundaries (Thies & Tscharntke 1999; Tscharntke *et al.* 2002a), compared with unmanaged control sites. Landscape type is classified as cleared (minimum diversity, < 1% non-crop habitat), simple (low diversity, 1–20% non-crop habitat) and complex (high diversity, > 20% non-crop habitat; see Andrén 1994; Tscharntke *et al.* 2002a). The resulting hump-shaped relationship is due to the different source pools in the surrounding landscape for recolonization 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.

understood, so only high-diversity agroecosystems connected with a diversity of habitats in complex landscapes may have the capacity to provide resilient ecosystems and a sustainable, multifunctional agriculture in temperate and tropical regions (Pimental *et al.* 1992; Jackson & Jackson 2002; Perfecto *et al.* 2004; Schulze *et al.* 2004).

Conservation of biodiversity and ecosystem services in agricultural systems requires a landscape perspective (Andow 1983; Hunter 2002; Bengtsson *et al.* 2003; Bestelmeyer *et al.* 2003; Tscharntke & Brandl 2004). The local–regional interplay means that landscape species pools influence local diversity and functioning of organisms (Fig. 2). In simple landscapes, large-scale (highly mobile) organisms, such as polyphagous predators, influence local food web interactions more than small-scale organisms, such as most parasitoids, characterized by dispersal limitation. Simple (high impact) and complex (low impact) agricultural landscapes appear to show contrasting responses to management (Fig. 4).

(1) In simple landscapes, local allocation of habitat (like field boundaries) can be expected to have greatest

effects on the biodiversity and ecological processes in adjacent crop fields, so management practices appear to be more effective in low-diversity than high-diversity landscapes (Fig. 4). Effectiveness is measured as changes due to management compared with unmanaged control sites. However, on a local scale, an equal shift in land-use intensity (e.g. reduction of the same amount of nitrogen fertilizer) may result in a less pronounced effect in high- than low-intensity fields (Kleijn & Sutherland 2003), because the (small) input reduction (starting from a high level) may not be enough to improve conditions for higher biodiversity.

(2) In complex landscapes with their large species pool, colonization of newly created habitat and population exchange is facilitated. Local management within these landscapes does not result in locally enhanced biodiversity, because biodiversity is high everywhere. Complex landscapes are in total at risk due to landscape-wide agricultural intensification. Preservation of high-diversity habitats and endangered species needs to have priority in complex landscapes. Hence, segregation of conservation (preservation of high diversity, not used habitats) and land use appears to be more appropriate in complex landscapes, whereas integration of conservation (creation of habitat, reducing agricultural intensity) and land use has merit in simple landscapes. In any case, the populations of high-diversity (as well as low-diversity) habitats are not sustainable without immigration, so that they need to be part of a dynamic landscape providing recolonization sources.

Such considerations are critical for agri-environment schemes because of the need to take both local and regional aspects into account (Sutherland 2002a). Key drivers of ecological processes inside systems are outside these systems, so ignoring landscape influence on local effect size may be misleading (Fig. 4). Agri-environment schemes of the EU acknowledge the farmers' potential to contribute to conservation and compensate farmers financially for any loss of income that may be associated with creating benefits for environment or biodiversity. In Germany, roughly half of the farmer's income comes from EU subsidies. However, subsidies and agri-environment incentives focus on only local changes of agricultural practices (e.g. reduced input of agrochemicals). On a landscape scale, enhancement of local (field) biodiversity addresses only a small part of the overall biodiversity, which is mainly driven by the high spatial turnover between fields in a given landscapes (as shown for arable weeds, Gabriel *et al.* 2005b). Financial support should consider the limited importance of local environmental changes, take a landscape perspective into account and better

adapt schemes to landscape type. The effectiveness of agri-environment schemes for the protection of biodiversity is a hot topic and the lack of robust studies makes evaluations difficult or impossible (Kleijn *et al.* 2001; Kleijn & Sutherland 2003). In contrast to what may be expected at first glance, introducing diverse habitats (and less intensive practices like organic farming) has a great effect only in simple landscapes and will positively influence resilience, i.e. the capacity to maintain (agro-)ecosystem services after disturbance (Fig. 4), whereas complex landscapes are already characterized by a high biodiversity sustaining ecosystem services. Agri-environment schemes may be particularly important in simple landscapes through the enhancement of common species, which are important for ecosystems services-like pollination and biological control. In contrast, complex landscapes harbour also many endangered species, so agri-environment schemes should become better targeted to the need of these species (see D. Kleijn, *et al.* 2005, personal communication).

Agriculture is a major driver of global change and can make important contributions to conservation, while it also profits from the sustainable management of biodiversity and ecosystem services. This practical importance contrasts with the little knowledge of biodiversity-driven agroecosystem functioning and the relative importance of local and landscape management for resilient agricultural landscapes. Only when more ecologists address such issues, we will be in a position to give reliable advice improving and upscaling the view of agri-environment schemes.

ACKNOWLEDGEMENTS

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