Landscape moderation of biodiversity patterns and processes - eight hypotheses

Teja Tscharntke[1,*], Jason M. Tylianakis[2], Tatyana A. Rand[3], Raphael K. Didham[2,4,5], Lenore Fahrig[6], Péter Batáry[1,7], Janne Bengtsson[8], Yann Clough[1], Thomas O. Crist[9], Carsten F. Dormann[10], Robert M. Ewers[11], Jochen Fründ[1], Robert D. Holt[12], Andrea Holzschuh[13], Alexandra M. Klein[14], David Kleijn[15], Claire Kremen[16], Doug A. Landis[17], William Laurance[18], David Lindenmayer[19], Christoph Scherber[1], Navjot Sodhi[20], Ingolf Steffan-Dewenter[13], Carsten Thies[1], Wim H. van der Putten[21] and Catrin Westphal[1]

[1] *Agroecology, Department of Crop Sciences, Georg-August University, Grisebachstrasse 6, 37077 Göttingen, Germany*

[2] *School of Biological Sciences, University of Canterbury, Private Bag 4800, Christchurch 8140, New Zealand*

[3] *USDA-ARS Northern Plains Agricultural Research Lab, Sidney, MT 59270, USA*

[4] *School of Animal Biology, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia*

[5] *CSIRO Entomology, Centre for Environment and Life Sciences, Underwood Ave, Floreat, WA 6014, Australia*

[6] *Geomatics and Landscape Ecology Laboratory, Department of Biology, Carleton University, 1125 Colonel By Drive, Ottawa, Ontario, Canada K1S 5B6*

[7] *MTA-ELTE-MTM Ecology Research Group Ludovika ter 2, 1083 Budapest, Hungary*

[8] *Department of Ecology, Swedish University of Agricultural Sciences, Box 7044, 750 07 Uppsala, Sweden*

[9] *Institute for the Environment and Sustainability, and Department of Zoology, Miami University, Oxford, OH 45056, USA*

[10] *Department of Computational Landscape Ecology, Helmholtz Centre for Environmental Research-UFZ, Permoserstr. 15, 04318 Leipzig , Germany*

[11] *Department of Life Sciences, Imperial College London, Silwood Park Campus, Ascot, Berkshire SL5 7PY, UK*

[12] *University of Florida, 111 Bartram, P.O. Box 118525, Gainesville, FL 32611-8525, USA*

[13] *Department of Animal Ecology and Tropical Biology, Biocenter, University of Würzburg, Am Hubland, 97074 Würzburg, Germany*

[14] *Ecosystem Functions, Institute of Ecology and Environmental Chemistry, Faculty III, Leuphana University of Lueneburg, Scharnhorststraße 1, 21335 Lueneburg, Germany*

[15] *Alterra, Centre for Ecosystem Studies, PO Box 47, 6700 AA, Wageningen, The Netherlands*

[16] *Environmental Sciences Policy and Management, 130 Mulford Hall, University of California, Berkeley, CA 94720-3114, USA*

[17] *Department of Entomology and Great Lakes Bioenergy Research Center, Michigan State University, East Lansing, MI 48824, USA*

[18] *Centre for Tropical Environmental and Sustainability Science (TESS) and School of Marine and Tropical Biology, James Cook University, Cairns, Queensland 4870, Australia*

[19] *Fenner School of Environment and Society, The Australian National University, Building 48 Linnaeus way, Canberra, ACT, 0200, Australia*

[20] *Department of Biological Sciences, National University of Singapore, 14 Science Drive 4, Singapore 117543, Republic of Singapore*

[21] *Netherlands Institute of Ecology, PO Box 50, 6700 AB Wageningen; and Laboratory of Nematology, Wageningen, University and Research Centre, PO Box 8123, 6700 ES Wageningen, The Netherlands*

ABSTRACT

Understanding how landscape characteristics affect biodiversity patterns and ecological processes at local and landscape scales is critical for mitigating effects of global environmental change. In this review, we use knowledge gained from human-modified landscapes to suggest eight hypotheses, which we hope will encourage more systematic research on

* Address for correspondence (E-mail: ttschar@gwdg.de).

the role of landscape composition and configuration in determining the structure of ecological communities, ecosystem functioning and services. We organize the eight hypotheses under four overarching themes. Section A: 'landscape moderation of biodiversity patterns' includes (1) the landscape species pool hypothesis—the size of the landscape-wide species pool moderates local (alpha) biodiversity, and (2) the dominance of beta diversity hypothesis—landscape-moderated dissimilarity of local communities determines landscape-wide biodiversity and overrides negative local effects of habitat fragmentation on biodiversity. Section B: 'landscape moderation of population dynamics' includes (3) the cross-habitat spillover hypothesis—landscape-moderated spillover of energy, resources and organisms across habitats, including between managed and natural ecosystems, influences landscape-wide community structure and associated processes and (4) the landscape-moderated concentration and dilution hypothesis—spatial and temporal changes in landscape composition can cause transient concentration or dilution of populations with functional consequences. Section C: 'landscape moderation of functional trait selection' includes (5) the landscape-moderated functional trait selection hypothesis—landscape moderation of species trait selection shapes the functional role and trajectory of community assembly, and (6) the landscape-moderated insurance hypothesis—landscape complexity provides spatial and temporal insurance, i.e. high resilience and stability of ecological processes in changing environments. Section D: 'landscape constraints on conservation management' includes (7) the intermediate landscape-complexity hypothesis—landscape-moderated effectiveness of local conservation management is highest in structurally simple, rather than in cleared (i.e. extremely simplified) or in complex landscapes, and (8) the landscape-moderated biodiversity *versus* ecosystem service management hypothesis—landscape-moderated biodiversity conservation to optimize functional diversity and related ecosystem services will not protect endangered species. Shifting our research focus from local to landscape-moderated effects on biodiversity will be critical to developing solutions for future biodiversity and ecosystem service management.

Key words: beta diversity, belowground-aboveground patterns, conservation management, ecosystem functioning and services, functional traits, insurance hypothesis, landscape composition and configuration, multitrophic interactions, resilience and stability, spatial heterogeneity.

CONTENTS

I. INTRODUCTION

Across the globe, many once-pristine natural ecosystems have been replaced by human-dominated mosaic landscapes, wherein a patchwork of human land-use patterns has been superimposed on pre-existing patterns of heterogeneity in environmental conditions. In such landscapes, species experience their environment across a range of spatial scales. Understanding scale dependence is vitally important to the wise management of natural resources and the conservation of biodiversity. Population dynamics, community composition and biotic interactions are all influenced by processes acting at multiple spatial scales, often much larger than the immediate local environment (Levin, 1992; Kareiva & Wennergren, 1995; With & Crist, 1995; Ricketts, 2001; Leibold *et al.*, 2004; Lindenmayer & Fischer, 2006; Chase & Bengtsson, 2010). Moreover, the matrix created by humans, which surrounds habitat fragments in these landscapes, is usually not completely hostile, unlike oceanic islands surrounded by the sea (Thies & Tscharntke, 1999; Haila, 2002; Lindenmayer & Fischer, 2006; Collinge, 2009). By contrast, resources may be gleaned from the matrix, with consequences for species persistence, dispersal, and colonization (e.g. Leibold *et al.*, 2004; Tscharntke & Brandl, 2004; Kremen *et al.*, 2007; Holt, 2010; Perfecto & Vandermeer, 2010). We use the term "habitat" for all locations that provide resources for an organism's survival, although we recognise that what constitutes habitat is largely species-specific (Lindenmayer & Fischer, 2006). Spatial separation of habitat elements in human-dominated mosaic landscapes forces many species to exploit several disconnected habitat patches across the landscape (for foraging, nesting etc.). Understanding how landscape structure (i.e. landscape composition and configuration) moderates the performance of species and communities is thus critical to comprehending their dynamics in increasingly human-dominated landscapes.

Traditionally, ecologists have focused on local mechanisms to explain population and community processes, while biogeographers have addressed spatial patterns at regional, continental and even global scales. Landscape-scale studies that merge these two approaches fall between these two paradigms and may be particularly important for understanding factors driving community structure and species interactions (Holt, 1996; Polis, Anderson & Holt, 1997; Landis & Marino, 1999; Levin, 2000; Leibold *et al.*, 2004; Laurance *et al.*, 2007). "Landscapes" are composed of a spatially explicit mix of ecosystems and land-use types. These elements, which often extend in size up to tens (or even hundreds) of kilometres, cover the short-term dispersal ranges of most (non-migratory) organisms. A "region", by contrast, is a broader geographical area tied together by a common macroclimate and sphere of human activity and interest, and is composed of many landscapes (Forman, 1995).

The earth is currently experiencing an unprecedented, accelerated loss of biodiversity (Sodhi & Ehrlich, 2010), altered interactions among species (Tylianakis *et al.*, 2008*a*) and a decline in associated ecosystem functioning and services (MEA, 2005). In human-managed landscapes, the loss of an ecosystem service can have cascading effects that further endanger biodiversity and related services. For example, landscape simplification in the Midwestern US is associated with loss of pest control services and increased pesticide use at regional scales (Meehan *et al.*, 2011) creating the potential to disrupt other arthropod-mediated services such as pollination (Isaacs *et al.*, 2009). Developing improved strategies for biodiversity conservation and sustainable land use requires improved knowledge of landscape-moderated biodiversity patterns and processes. Current ecological concepts increasingly acknowledge the influence of scale on patterns and processes, and reveal a variety of scale-moderated responses (Leibold *et al.*, 2004). Recognition of the importance of landscape-scale processes for local community structure has contributed to the emergence of several concepts in ecology, which merge landscape ecological and macroecological approaches better to understand patterns and species interactions at large spatial and temporal scales (Brown, 1995; Polis *et al.*, 1997; Gaston, 2000; Thies, Roschewitz & Tscharntke, 2005).

There is now well-established empirical and theoretical evidence for the emerging ecological principle that landscape and regional species pools strongly influence local species richness (e.g. Lawton, 1999; Gaston, 2000). Structurally complex landscapes support more species than simple landscapes, implying that habitat patches in complex landscapes receive a higher diversity of potential colonists from the overall species pool than do patches of the same size and quality in less complex landscapes. Movement across habitats is a common phenomenon in many species and the spillover of organisms from natural habitats to agroecosystems has been well documented in human-dominated landscapes (Thies & Tscharntke, 1999; Bianchi, Booij & Tscharntke, 2006; Öberg, Mayr & Dauber, 2008; Ricketts *et al.*, 2008), although few studies have examined movement in the opposite direction (Rand, Tylianakis & Tscharntke, 2006; Blitzer *et al.*, 2012). One reason for such cross-habitat movements is that organisms often exploit different resources that are spatially separated. Such "landscape complementation" (Dunning, Danielson & Pulliam, 1992) is commonly documented for vertebrates (e.g. Pope, Fahrig & Merriam, 2000; Tubelis, Lindenmayer & Cowling, 2004; Ethier & Fahrig, 2011), but is also important for invertebrates such as butterflies (host plants *versus* nectar supply by flowers, e.g. Steffan-Dewenter & Tscharntke, 1997), parasitoids (host *versus* food resources; Landis, Wratten

Table 1. Summary overview of the eight hypotheses on landscape moderation of biodiversity patterns and processes

	Name of the hypothesis	Explanation	References
A		**Landscape moderation of biodiversity patterns**	
1	The landscape species pool hypothesis	The size of the landscape-wide species pool moderates local (alpha) biodiversity.	Gaston (2000), Gering & Crist (2002), Harrison & Cornell (2008), and Pärtel *et al.* (2011)
2	The dominance of beta diversity hypothesis	The landscape-moderated dissimilarity of local communities determines landscape-wide biodiversity and overrides negative local effects of habitat fragmentation on biodiversity.	Quinn & Harrison (1988), Tscharntke *et al.* (2002*b*), Fahrig (2003), Tylianakis *et al.* (2005), Lindenmayer & Fischer (2006), and Collinge (2009)
B		**Landscape moderation of population dynamics**	
3	The cross-habitat spillover hypothesis	Landscape-moderated spillover of energy, resources and organisms across habitats, including between managed and natural ecosystems, influences landscape-wide community structure and associated processes.	Landis *et al.* (2000), Bianchi *et al.* (2006), Rand *et al.* (2006), Hendrickx *et al.* (2007), Ricketts *et al.* (2008), Collinge (2009), and Blitzer *et al.* (2012)
4	The landscape-moderated concentration and dilution hypothesis	Spatial and temporal changes in landscape composition can cause transient concentration or dilution of populations with functional consequences.	Bierregaard *et al.* (1992), Collinge & Forman (1998), Debinski & Holt (2000), Holt & Hochberg (2001), Grez *et al.* (2004), Sodhi *et al.* (2007), Tylianakis *et al.* (2007), and Thies *et al.* (2008)
C		**Landscape moderation of functional trait selection**	
5	The landscape-moderated functional trait selection hypothesis	Landscape moderation of species trait selection shapes the functional role and the trajectory of community assembly.	Vance *et al.* (2003), Henle *et al.* (2004), Larsen *et al.* (2005), Fahrig (2007), Tscharntke *et al.* (2008), Bengtsson (2010), Lee *et al.* (2009), Winfree *et al.* (2009), and Williams *et al.* (2010)
6	The landscape-moderated insurance hypothesis	Landscape complexity provides spatial and temporal insurance, i.e. higher resilience and stability of ecological processes in changing environments.	Yachi & Loreau (1999), Elmqvist *et al.* (2003), Hughes & Stachowicz (2004), Winfree *et al.* (2007), Griffin *et al.* (2009), and Laliberté & Tylianakis (2010)
D		**Landscape constraints on conservation management**	
7	The intermediate landscape-complexity hypothesis	Landscape-moderated effectiveness of local conservation management is highest in structurally simple, rather than in cleared (i.e. extremely simplified) or in complex landscapes.	Tscharntke *et al.* (2005*a*), Rundlöf & Smith (2006), Concepción *et al.* (2008), Batáry *et al.* (2010*b*), Batáry *et al.* (2011), Smith *et al.* (2010), and Geiger *et al.* (2010)
8	The landscape-moderated biodiversity *versus* ecosystem service management hypothesis	Landscape-moderated biodiversity conservation of endangered species will not optimize functional diversity and related ecosystem services in production systems.	Gurr *et al.* (2004), Gaston & Fuller (2008), Kleijn *et al.* (2011), and Tscharntke *et al.* (2012)

& Gurr, 2000), bees (nesting sites *versus* nectar and pollen; Klein, Steffan-Dewenter & Tscharntke, 2003*a*, *b*; Holzschuh *et al.*, 2007) and of course organisms that must change habitat during their ontogenies (e.g. frogs, dragonflies). Even plants can, in a sense, utilize resources from multiple habitats; for instance, a flowering plant in a remnant patch may draw its pollinators from the surrounding landscape (Parsche, Fründ & Tscharntke, 2011). Hence, movement among distinct habitats is an essential facet of the ecology of many species. The extent and ease of movement will be determined by landscape configuration and composition (With & Crist, 1995; Ricketts, 2001; Goodwin & Fahrig, 2002; Damschen *et al.*, 2006; Holzschuh *et al.*, 2010). The nature of the matrix determines whether it impedes or facilitates dispersal between patches (Tscharntke & Brandl, 2004; Cronin, 2007).

Just as different species (differing in body size, life history, resource requirements, etc.) experience their surroundings at different spatial and temporal scales (Wiens, 1989; Peterson, Allen & Holling, 1998; Steffan-Dewenter *et al.*, 2002; Schmidt *et al.*, 2008), food-web interactions also can be scale dependent (Kareiva, 1990; Brose *et al.*, 2005; Tscharntke *et al.*, 2005*a*; Bezemer *et al.*, 2010; Laliberté & Tylianakis,

2010). Different habitats within a landscape can vary widely in their food-web structure (Tylianakis, Tscharntke & Lewis, 2007), and adjacent habitats can influence each other's structure and dynamics, in particular *via* fluxes of resources (Reiners & Driese, 2004) and the movement of higher-level consumers (Knight *et al.*, 2005; McCann, Rasmussen & Umbanhowar, 2005; Gagic *et al.*, 2011; Rand, van Veen & Tscharntke, 2011). Understanding of these food-web effects is still very limited, and it will be a major challenge to derive generalities across systems. In particular, perception of the environment differs between species in below- and aboveground communities and the great range of body sizes from microorganisms to vertebrates complicates the interpretation of scale-dependence of interaction patterns.

Although the landscape-wide determinants of local species diversity and composition have received considerable attention recently (Wiens *et al.*, 2007; Collinge, 2009; Perfecto, Vandermeer & Wright, 2009), the literature is widely scattered, and many functional implications of these landscape-scale processes remain unexplored. Here, we review how landscape structure moderates local to landscape biodiversity patterns and how such structure influences population, community and ecosystem processes. We propose eight key hypotheses (Table 1; frequently related to conceptually similar hypotheses previously identified in the literature), review the evidence supporting them, and provide an overview of future research directions.

We organize the eight hypotheses into four sections. Section A on 'landscape moderation of biodiversity patterns' focuses on the dependence of local (alpha) biodiversity on the landscape-wide species pool and whether there is a dominant role of landscape-wide beta diversity for determining landscape biodiversity. Section B on 'landscape moderation of population dynamics' addresses landscape-moderated spillover across habitats and the transient dilution or concentration of populations in dynamic landscapes. Section C addresses the 'landscape moderation of functional-trait selection' driving the functional role of communities and their insurance effect in changing landscapes. The applied focus of Section D, 'landscape constraints on conservation management,' deals with landscape-dependent effectiveness of conservation management and the different measures needed for the enhancement of endangered species *versus* ecosystem services. We stress that these hypotheses address processes that are internally complex, act in concert, and are not mutually exclusive (see Fig. 1 for an overview). Both below- and aboveground communities respond to environmental changes on local and landscape scales, but belowground responses are different, including weaker and slower responses, as briefly discussed in Appendix 1. Our goal here is to encourage more systematic research efforts on the role of landscape composition and configuration in determining the structure of ecological communities and the impact of landscape modification on the provisioning of ecosystem services, and so we offer these hypotheses as potential organizing principles for guiding such research.
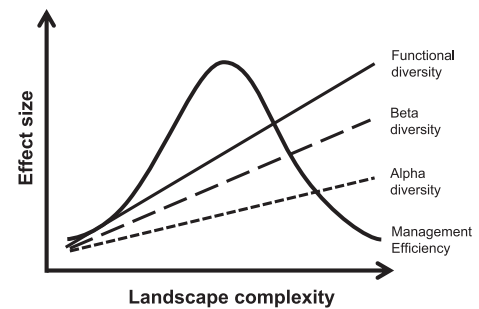

Fig. 1. Schematic overview of major landscape hypotheses, described in Table 1, showing effect sizes along a landscape complexity gradient (i.e. along increasing noncrop area and higher habitat type diversity). Increasing landscape complexity enhances alpha diversity less than beta diversity (Section A: the first two hypotheses). Both alpha and beta diversity contribute to overall functional biodiversity and associated insurance potential (Section C: fifth and sixth hypotheses). Population movements (Section B) are not necessarily related to changes in landscape complexity. Efficiency of conservation management (Section D) shows a hump-shaped relationship to landscape complexity.

II. SECTION A: LANDSCAPE MODERATION OF BIODIVERSITY PATTERNS

(1) Hypothesis 1: the landscape species pool hypothesis

The size of the landscape-wide species pool moderates local (alpha) biodiversity

Local ecological communities are governed by landscape-scale and regional-scale processes as well as local processes (e.g. abiotic filters in plant communities; Aarssen & Schamp, 2002; Harrison & Cornell, 2008); this has been called a macro-ecological law in ecology (Lawton, 1999). In hierarchical assessments of local-landscape-regional richness, landscapes exhibit great differences in geographic structure and associated biodiversity, differences that are critical to understanding heterogeneity in local-regional relationships (Gering & Crist, 2002; Gabriel *et al.*, 2006; Clough *et al.*, 2007). Local assemblages are often surprisingly open to colonisation and establishment of propagules, and local diversity does not appear to be tightly constrained by local biotic interactions such as local competition (Cornell & Lawton, 1992; Gaston, 2000). If species sort along environmental gradients, the main effect of connectivity may be to permit local sites to become accessible to an entire species pool, so that sorting can occur (Leibold *et al.*, 2004).

The shape of the relationship between local (alpha) and regional (gamma) diversity has been claimed to reflect whether local communities are saturated with species (illustrated by an asymptotic relationship between local *versus* regional species richness) or unsaturated (linear relationship) (Gaston, 2000). However, local-regional richness analyses have also been heavily criticised because of statistical and theoretical problems (e.g. the underestimation of local and overestimation of regional richness as well as

spatial autocorrelation when truly independent data sets were not available), and because the degree of linearity or non-linearity by itself cannot be used to assess the strength of local interactions (Loreau, 2000; Harrison & Cornell, 2008). In complex high-diversity (species-rich) landscapes containing communities of organisms with low dispersal abilities, the role of species sorting in response to variation in local environments is likely to be of major importance. Conversely, in simplified landscapes characterized by high-disturbance land use and by highly dispersive organisms, dynamics in habitat patches are likely to be determined primarily by the availability of landscape-wide remnant communities (Bengtsson, 2010). In such simplified landscapes, conservation management should be most effective in enhancing landscape-wide biodiversity (Tscharntke *et al.*, 2005a; Bengtsson, 2010; see Section V.1).

One key knowledge gap is determining the feedback between local processes and the composition of landscape species pools. The landscape pool is comprised by aggregating the composition of all its local communities. In strictly neutral community models, species composition is continually in flux because of immigration from external sources, *in situ* speciation, and local extinction (e.g. Hubbell, 2001). In heterogeneous landscapes, different species are clearly differentially adapted to different kinds of habitats, so strict neutrality cannot hold in that some species tend to be locally excluded by others, but stochasticity could still play a significant role in determining local community composition. Thousands of studies have shown that biotic interactions are important in determining individual species' performances, but it has been more challenging to demonstrate that local richness saturates due to factors such as resource competition or predation, constraining species coexistence (e.g. Ward, 2006; Lamb & Cahill, 2008; but see Crawley, 1997; Schmitz, 2008). The structure of local communities surely reflects the interplay of stochastic processes (of the sort built into neutral models), environmental filtering due to abiotic factors, positive as well as negative interactions, and indirect interactions, particularly across trophic levels (Lortie *et al.*, 2004). Understanding how local processes interact with spatial dynamics to influence regional coexistence of interacting species is a challenging theoretical and empirical problem (Chesson *et al.*, 2005; Melbourne *et al.*, 2005). If a landscape sustains a rich species pool, this may permit greater opportunity for recurrent spillover among habitats, locally sustaining species where they might not persist in completely isolated habitats, and also may permit a richer array of indirect interactions to arise. As noted above, some taxa may persist precisely because of the array of opportunities provided by landscape heterogeneity, such as mobile consumers' ability to exploit patchy and transient resources. These effects are more likely for some taxa (e.g. aboveground consumers) than others (e.g. belowground consumers, see Appendix 1).

A corollary to this idea is the 'landscape-divergence hypothesis' (Laurance *et al.*, 2007), which postulates that locally unique disturbance dynamics and the varying composition of the matrix found in different fragmented landscapes causes fragments in those different landscapes to diverge in species composition, even if the fragments were initially quite similar. This hypothesis is supported by long-term studies of forest fragments in the Brazilian Amazon, in which tree communities in fragments within the same experimental landscapes progressively converged in species composition, whereas those in different landscapes progressively diverged (Laurance *et al.*, 2007). This example provides powerful evidence that the nature of the matrix can have a very strong impact on community dynamics within remnant habitat fragments.

Future research should examine how landscape composition and configuration affect fragment community dynamics and species pools, which components of the species pools are then locally represented in different habitat types, and how the composition and configuration of habitat types in turn can feed back to determine the regional species pool. The identity of the local habitat (i.e. habitat type) may more clearly shape a particular community structure in moderately simple than complex landscapes, because of the higher opportunity for spillover among distinct habitat types in complex landscapes. However, this hypothesis should be tested empirically. Habitats with high structural heterogeneity and larger area can be expected to contain a larger part of the landscape-wide species pool. Comparing different habitat types, nested in different landscape contexts, will be useful in determining how local communities are selected from landscape-level species pools. Although some aspects of the landscape species pool hypothesis have received significant attention, further important questions remain unanswered including the role of landscape context for mobile *versus* less mobile (or above- *versus* belowground) species. Theory and models of how local assemblages deviate from random representations of the species pool need to be confronted with data. The relative role of alpha and spatio-temporal beta diversity within each habitat type may change with shifts in landscape-wide species pools, and this needs to be investigated further. Continuous species losses in local communities within habitat fragments should eventually endanger the richness of landscape-level species pools (i.e. the landscape-level expression of local biodiversity) (Pärtel, Szava-Kovats & Zobel, 2011), which would be interesting to test.

(2) Hypothesis 2: the dominance of beta diversity hypothesis

The landscape-moderated dissimilarity of local communities determines landscape-wide biodiversity and overrides negative local effects of habitat fragmentation on biodiversity

The theory of island biogeography, which predicts decreasing species richness with decreasing area and increasing isolation of a habitat (MacArthur & Wilson, 1967), has been applied to predict diversity on oceanic islands, for which it was developed, as well as habitat islands on the terrestrial mainland. The species-area relationship, i.e. increasing

species richness with area, has been claimed to be of universal importance as one of the few laws in ecology (Rosenzweig, 1995; Lawton, 1999; Holt, 2010), and along with island biogeography theory shaped early thinking about fragmented landscapes. Habitat loss and habitat fragmentation *per se* (i.e. altered spatial arrangement of remaining habitat) are widely regarded as central drivers of biodiversity loss (Wiens, 1996; Collinge, 2009). However, the concept of habitat fragmentation has also been heavily criticised as having ambiguous value (Haila, 2002; Fahrig, 2003; Lindenmayer & Fischer, 2006, 2007; Yaacobi, Ziv & Rosenzweig, 2007; Laurance, 2008; Prugh *et al.*, 2008; Collinge, 2009; Bennett & Saunders, 2010, but see Ewers & Didham, 2007). There are at least three distinct arguments why fragmentation *per se* has been often overestimated as a driver of landscape-wide biodiversity losses and why beta diversity has been underestimated as a driver of landscape-wide biodiversity.

(1) Mechanisms driving biodiversity patterns in fragmented landscapes include not only the separate effects of habitat loss, fragmentation *per se* and landscape context (i.e. matrix effects), but also the interaction of these factors with the underlying spatial heterogeneity of the landscape prior to habitat modification and the landscape extent covered (Fig. 2). For a given total area of habitat, all other things being equal, the greater the degree of underlying spatial heterogeneity in the landscape, the greater the degree of community dissimilarity among habitat patches that are separated by increasing distances. This is because of the well-known fact that sites close to each other are usually more similar in environmental conditions than are distant sites (e.g. Fortin & Dale, 2005). Hence, when a given amount of habitat area is spread out in a landscape (*via* fragmentation) instead of remaining as a single large patch, beta diversity is increased (Fig. 2; although local population persistence decreases, see below, this section). The open question is whether this spatial pattern arises due to similar patches sampling different species from a regional pool which is related to the random sampling hypothesis of Coleman *et al.* (1982) or whether it reflects that there is almost always greater environmental variation among separate patches than found within a single patch. This observation relates to the question of whether conservation of "single large or several small" (SLOSS) habitats better maximizes biodiversity (Simberloff & Abele, 1976; Simberloff, 1986; Quinn & Harrison, 1988; Peintinger, Bergamini & Schmid, 2003). For instance, Cook *et al.* (2005) found in an experimentally fragmented landscape of patches undergoing succession that beta diversity was greater among small patches, than in similarly spaced arrays of samples within large quadrats. Tscharntke *et al.* (2002*b*) showed that 10 ha of protected area made up of 29 small grassland remnants harboured many more species than the same area made up by just 1-2 large habitats (Fig. 3A). This effect was not
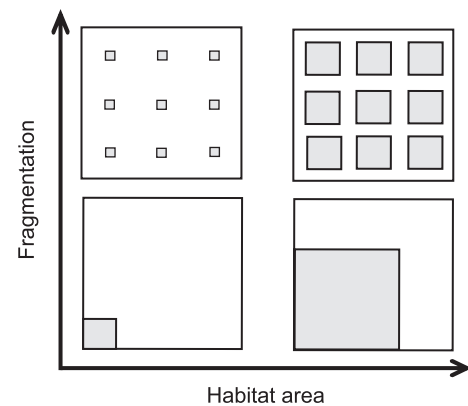

Fig. 2. A conceptual figure showing four scenarios of fragmented landscapes, separating habitat loss from habitat fragmentation *per se*. In addition to habitat loss and fragmentation as two distinct factors, the figure illustrates that splitting a single habitat patch into many habitat fragments leads often (but not necessarily) to a broader geographical area covered by habitat. Because landscape extent covered by fragments, overall habitat heterogeneity and dissimilarity of communities are positively correlated, beta diversity should increase in such a scenario of habitat fragmentation.

simply caused by common and generalist species, as endangered species showed the same pattern (Fig. 3B). Hence, assuming that small patches do not have any extinction debts (Kuussaari *et al.*, 2009) or that extinction debts have at least been overestimated (He & Hubbell, 2011), this case provides clear evidence of the benefit of many small island habitats, collectively spanning a large geographic distance and so covering greater environmental heterogeneity, thereby maximizing landscape-wide biodiversity. Such an increase in beta diversity is sometimes attributed entirely to fragmentation, when in fact it may stem at least partially from underlying spatial heterogeneity and variation in the geographical coverage of patch networks in differing landscapes. The importance of separating the purely spatial components of habitat fragmentation from underlying environmental causes of beta diversity in the landscape has not yet been grasped conceptually in the literature, let alone empirically tested, and thus merits more research attention.

(2) Whenever the matrix surrounding habitat fragments is not entirely hostile to species, but rather contains usable resources, island biogeographical and early metapopulation theory have limited applicability (Daily, Ehrlich & Sanchez-Azofeifa, 2001; Haila, 2002; Sekercioglu *et al.*, 2007; Lindenmayer *et al.*, 2008). Models of population dynamics in fragments need to be modified to consider colonisation and extinction dynamics due to organism spillover from the matrix (e.g. Janzen, 1983, 1986; Krauss, Steffan-Dewenter & Tscharntke, 2003*a*; Cook, Anderson & Schweiger, 2004; Pereira & Daily, 2006; Collinge, 2009; Holt, 2010). Matrix habitats can be surprisingly rich, even
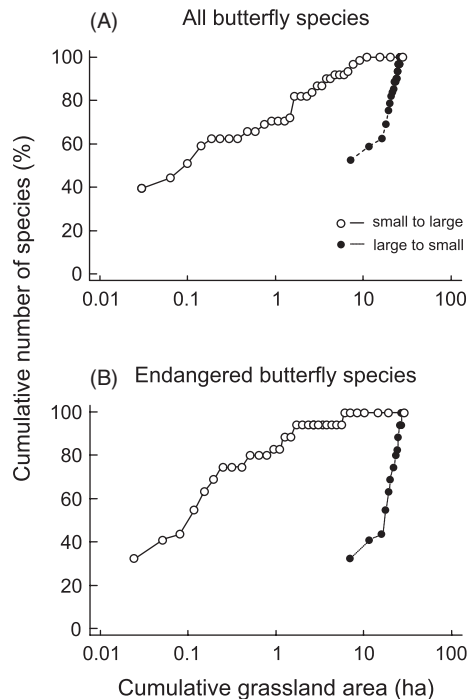
Fig. 3. Cumulative number of butterfly species in relation to cumulative grassland area (ha) of 33 calcareous grassland fragments (Tscharntke *et al.*, 2002*b*). These results suggest that on a landscape scale many small habitats capture more heterogeneity and thus higher species richness than single large habitats. For example, 10 ha from 29 small fragments support many more species than 10 ha from 1-2 fragments (3A). (A) % of all ($N = 61$) species; (B) % of $N = 38$ species listed in the Red Data Book of the German state Lower Saxony.

in species normally found in the fragments. In the Amazonian rainforest, for example, 40-80% of frogs, small mammals, birds and ants typical of primary forest were detected outside forest fragments, in a matrix composed of pastures and regenerating forest (Gascon *et al.*, 1999). However, edge effects can change with seasons (Lehtinen, Ramanamanjato & Raveloarison, 2003) and occurrence does not automatically imply long-term individual survival or population viability in modified habitats (e.g. Kuussaari *et al.*, 2009). The conditions under which these effects are most important might vary systematically between ecosystems or biogeographic regions. For instance, matrix effects appear to be more important in forested than open, and in tropical than temperate landscapes (Sodhi, Brook & Bradshaw, 2007), but this issue has received scant attention to date.

(3) Most studies do not effectively discriminate habitat fragmentation from habitat loss (see Fig. 2 and review by Fahrig, 2003), and the few published studies explicitly discriminating these two effects do not support the hypothesis that fragmentation *per se* (i.e. fragmentation in addition to habitat loss) reduces landscape-wide diversity (e.g. Yaacobi *et al.*,

2007). Historically, most research has focused on fragmentation at the patch, not landscape scale, and the landscape-wide amount of habitat was not simultaneously considered as a causal covariate (Fahrig, 2003; Lindenmayer & Fischer, 2006; Collinge, 2009; Mortelli *et al.*, 2010). According to Fahrig (2003), the famous Amazonian forest fragmentation study (Laurance *et al.*, 2007, 2011) is in this sense a study of forest loss, not fragmentation.

Of the three arguments for the possible overestimation of fragmentation effects outlined above, the beta diversity effects have been the least considered. However, a growing body of evidence indicates the dominance of beta diversity in driving overall biodiversity across landscapes (at least in the majority of cases), mitigating negative fragmentation effects. For example, even though individual smaller habitat islands harbour impoverished communities, experience reduced frequency and strength of biotic interactions (Holt, 2010), show higher extinction probability (e.g. Krauss, Steffan-Dewenter & Tscharntke, 2003*b*; Kuussaari *et al.*, 2009), and are often lacking rare, fragment-area-sensitive species (see below, this section), these negative local patch effects on biodiversity are numerically overcompensated in terms of total species richness by the higher beta diversity among patches (Tscharntke *et al.*, 2002*b*). Habitat islands rarely have an identical suite of species and are therefore not completely nested subsets of mainland habitat (Tscharntke *et al.*, 2002*b*; Peintinger *et al.*, 2003; Fischer & Lindenmayer, 2005; Kier *et al.*, 2009). Thus, the mainland-island concept underestimates the importance of heterogeneity in driving community dissimilarity, which increases with distance in a poorly understood way (Gering & Crist, 2002; Gering, Crist & Veech, 2003; Cook *et al.*, 2005). A meta-analysis of over 150 data sets from habitat fragments and oceanic islands showed that 74% of the total landscape-level richness was due to species turnover among habitat fragments and 84% of the combined-island richness was due to turnover among islands. By contrast, species turnover among habitats or islands of different area explained only 27 and 41% of combined richness for habitat fragments and true islands, respectively. Beta diversity (turnover patterns or species gain/loss patterns) therefore has a dominant role in determining biodiversity patterns among fragments or islands, less than half of which can be attributed to variation in habitat or island area (T. O. Crist, in preparation).

Landscape-wide beta diversity has been shown to be poorly, and in some cases not at all, related to local alpha diversity, to contribute much more to overall diversity than does the latter, and generally, to be a better indicator of overall biodiversity patterns (Clough *et al.*, 2007; Hendrickx *et al.*, 2007; Kessler *et al.*, 2009; Flohre *et al.*, 2011). Beta diversity patterns may even provide a picture that contrasts with alpha diversity. For example, comparing bee and wasp communities along a land-use gradient, Tylianakis, Klein & Tscharntke (2005) found that while plot (= alpha) diversity was highest in intensively used agroecosystems,

beta diversity was significantly greater in less-intensively-used systems (due to higher habitat heterogeneity and associated higher community dissimilarity), resulting in overall higher biodiversity in the less-intensive systems, and contributing strongly to landscape-scale (gamma) diversity. We should caution that these patterns of beta-diversity dominance should hold for structurally simple and complex landscapes (as defined in section D, hypothesis 7), whereas cleared (extremely simplified) landscapes such as large-scale agricultural monocultures may sustain only a few surviving populations and nested, spatially homogenized communities.

One little-recognised component of the dominance of beta diversity hypothesis is that the same arguments made regarding the partitioning of species diversity across landscape scales can also be made in relation to intraspecific genetic variation. Parallel processes may govern spatial patterns in genetic diversity, as in community diversity. For instance, as with community dissimilarity, genetic dissimilarity increases with geographic distance between habitat fragments and with the landscape extent covered, providing evidence for a 'parallel' landscape-moderated intraspecific genetic diversity hypothesis, predicting that the underlying patterns of landscape-wide genetic dissimilarity of local populations determine intraspecific diversity following landscape modification and potentially override negative local effects of habitat fragmentation. The importance of intraspecific genetic differentiation across landscapes has been shown, for example, by studies in which pollen diversity increases the chance of selecting a particularly "good" donor for fertilization - a sampling effect of diversity (Paschke, Abs & Schmid, 2002). Such effects suggest that an increase in dispersal can have positive effects on adaptation. By contrast, reducing dispersal, and thereby maintaining population dissimilarity, can be important because intraspecific diversity differences between small and large habitats are small compared to the effect of intraspecific beta diversity reflecting local adaptation (Eckert, Samis & Lougheed, 2008). Gene flow can impede local adaptation in many plants and animals, which may be critical for effective habitat use (Kawecki, 2008; Leimu & Fischer, 2008). This has been shown for local adaptation of blue tits (*Parus caeruleus*) to peaks of food availability in deciduous forests, which can be prevented by genetic homogenization with populations that are adapted to use resources several weeks later in evergreen forests (Blondel *et al.*, 2006). Acting through high turnover in local genetic structure, landscape-scale genetic variability maintained by local adaptation may provide insurance against changing environmental conditions (Hughes & Stachowicz, 2004). In the same way, reducing gene flow is considered to be necessary in agriculture to keep a maximum diversity of different breeds (e.g. in farm animals, Simianer, 2005) with a low but non-zero level of cross-type breeding to prevent homogenization while at the same time maintaining a pool of genetic variation that may be needed to deal with environmental novelties (e.g. emerging infectious diseases).

At the same time, beta genetic diversity should become increasingly strongly controlled by the way humans manage landscapes, both in terms of landscape structure and land-use intensity (Harrison, Ross & Lawton, 1992; Dormann *et al.*, 2007). Increasing connectivity between spatially separated populations can be a double-edged sword and depends on whether a local (intraspecific "alpha" diversity) *versus* landscape (intraspecific "beta" diversity) perspective is adopted. From a local perspective, connectivity decreases random allele losses by genetic drift, inbreeding depression and extinction probability (the so-called rescue effect), for example in bumble bees (Herrmann *et al.*, 2007). This means that from a landscape perspective, landscapes containing originally connected populations with (mostly non-adaptive) genetic differentiation increasing with distance between populations, should be managed to maintain that connectivity according to common conservation advice (e.g. Pullin, 2002). By contrast, connectivity can also enhance homogenization, resulting in the erosion of potential local adaptations. Maintaining genetic variation across landscapes may also have intrinsic conservation value, which is in tension with the goal of enhancement of gene flow for local survival, which occurs at the expense of permitting a strong response to local selection. The relative value of these opposing effects under climate and land-use change is unknown: connectivity will certainly be essential to prevent extinctions, and to maintain a pool of variation to cope with environmental change, but can sub-populations at times be better off with a lack of genetic exchange that facilitates precise evolutionary adaptations to local conditions? Theoretical studies (e.g. Holt, Barfield & Gomulkiewicz, 2005; Kawecki, 2008) suggest that low to moderate levels of gene flow are often optimal for generating and maintaining local adaptation. However, the optimal level of connectivity is likely to differ among species, and may be difficult or even impossible to ascertain without sophisticated models that specify the nature of the environment, the suites of traits under selection, and the nature of the genetic architecture underlying those traits. There is no single level of connectively that is likely evolutionarily optimal for all species at once.

Despite the foregoing arguments, it is important to keep in mind that from a conservation point of view, community composition may change dramatically, even if the level of habitat fragmentation *per se* has little negative effect on overall biodiversity. There may be individual species that are strongly patch area and edge sensitive and in need of large contiguous areas of natural habitat, and these species may experience high extinction probabilities in small reserves. Conservation managers need to consider the fate of these often endemic and frequently charismatic flagship species, not just species richness, to craft effective conservation policies (Sodhi *et al.*, 2007; Collinge, 2009). The debate on habitat loss *versus* fragmentation has at times focused almost exclusively on species richness, rather than on community composition, which usually changes greatly and often at the cost of endangered and "valuable" species. For example, rainforest fragmentation reduces biomass and carbon sequestration, because the biggest trees die first (Laurance *et al.*, 2000). Additional ecosystem processes that

can suffer from habitat fragmentation include the resistance of fragments to species invasions (Janzen, 1983; Collinge, 2009) and to external disturbances such as hunting and fire (Cochrane & Laurance, 2002). Protection of a complex of both large and small reserves (Noss, 1983; Tscharntke *et al.*, 2002*b*) over as large an area as possible and maintaining flexible strategies (as to prioritizing few larger or many smaller reserves depending on the conservation focus) will be critical. In any case, expanding ecological research to incorporate a broader, landscape perspective will clearly be preferable to the traditional management focus on single reserves optimizing local biodiversity. Finding sustainable solutions that integrate different conservation goals such as enhancing local biodiversity across different functional or taxonomic groups, promoting landscape-wide biodiversity and associated ecosystem services, as well as maintaining viable populations of patch-area-sensitive (e.g. large or vagile) organisms, is difficult and underlying conservation priorities need to be more clearly articulated.

Future research should focus on separating effects of fragmentation *per se* from habitat loss in real landscapes, which has been described as "virtually logistically impossible" (Damschen *et al.*, 2006; Collinge, 2009) but is an innovative and, we think, still manageable enterprise (see Krauss, Steffan-Dewenter & Tscharntke, 2003*a*; Ewers & Didham, 2008; Smith *et al.*, 2009; Brückmann, Krauss & Steffan-Dewenter, 2010). In comparative studies, landscapes should be selected that have a similar total area of remaining habitat but differing levels of fragmentation (number of fragments), or similar levels of fragmentation but different total habitat area. There needs to be an explicit consideration of pre-existing gradients and other forms of environmental variation, which should be reflected in community composition both before and after fragmentation. Furthermore, we need a better mechanistic understanding of, and empirical evidence evaluating, the relative importance of small *versus* large or isolated *versus* non-isolated habitat fragments (and dissimilarity in their species composition) for landscape-wide biodiversity conservation. Landscape effects on biodiversity patterns may change along landscape-complexity gradients, latitudinal gradients and between different landscape types or biomes. For example, corridors in forested landscapes and in the tropics may be more effective than in open habitats and temperate regions (Sodhi *et al.*, 2007). Is this prediction based upon the traits of the species involved, or the magnitude of the contrast in the environment between corridors and surrounding matrix habitats? Edge effects may vary depending on fragment size and should be much better quantified (Ewers & Didham, 2006, 2008). The role of beta diversity in contributing to overall diversity patterns needs to be better explored, in particular assessing changes along landscape gradients or successional stages (e.g. Cook *et al.*, 2005). Patterns of beta diversity in relation to the increasing environmental variation with distance need to be explored, while the problem of limited sample sizes potentially causing overestimation of beta diversity needs to be taken into account. The conservation value of small as well as large

habitats for reducing extinction probability and maintaining food-web interactions needs to be analyzed in different landscape contexts and across different groups of organisms (from microbes to mammals). However, habitat loss results in a concomitant change in the spatial structure and patterning of habitat, so it is worthwhile looking for integrated assessments of impact that explicitly combine the effects of habitat loss and fragmentation (Ewers *et al.*, 2009). Future research should also address the question of the minimum cumulative habitat area necessary to provide the array of resources needed in a heterogeneous landscape to sustain landscape-scale diversity. Changes in species composition or evenness (Crowder *et al.*, 2010) can have larger effects on ecosystem function than do changes in species richness (Symstad *et al.*, 1998; Wilsey & Potvin, 2000), and this needs to be explored within a landscape framework. The genetic and population-level consequences of short-term rescue *versus* long-term homogenization effects also need to be empirically evaluated, to define trade-offs between maintaining genetic variation across landscapes *versus* viable local populations. Such studies should test whether translocation of individuals between long-established isolated populations can swamp local adaptations, while re-connecting populations that have been isolated only recently contributes to reduced extinction probability.

III. SECTION B: LANDSCAPE MODERATION OF POPULATION DYNAMICS

(1) Hypothesis 3: the cross-habitat spillover hypothesis

Landscape-moderated spillover of energy, resources and organisms across habitats, including between managed and natural ecosystems, influences landscape-wide community structure and associated processes

Cross-habitat spillover of organisms is the movement (including both dispersal and foraging) of organisms from one distinct habitat type to another. Environmental characteristics and associated community composition both change with proximity to edges, as has long been known in wildlife conservation studies (Fagan, Cantrell & Cosner, 1999; Ries *et al.*, 2004; Ewers & Didham, 2008). Spillover across habitat edges is determined by the neighbouring matrix and can play a key role in community composition and population dynamics (Polis *et al.*, 1997; Polis, Power & Huxel, 2004; Ries *et al.*, 2004; Lindenmayer *et al.*, 2008; Laurance *et al.*, 2011). The transferred organisms and materials may enhance predation pressure, prey availability or nutrient density and affect food-web structure. Changes in the trophic structure of one ecosystem can even cascade to an adjacent ecosystem (Knight *et al.*, 2005).

Spillover from natural to anthropogenic habitats, or *vice versa*, is an important process affecting wildlife populations in human-dominated, fragmented landscapes (Landis *et al.*, 2000; Krauss *et al.*, 2004; Ries *et al.*, 2004; Tubelis *et al.*, 2004; Clough *et al.*, 2005; Schmidt & Tscharntke, 2005*a*, *b*;

Bianchi *et al.*, 2006; Rand *et al.*, 2006; Hendrickx *et al.*, 2007; Ricketts *et al.*, 2008; Collinge, 2009; Gardiner *et al.*, 2009*a*, *b*; Blitzer *et al.*, 2012). Spatiotemporal stability of resource availability makes natural habitats a well-recognised source of populations whose individuals can move regularly or episodically into managed systems (e.g. Landis *et al.*, 2000; Bianchi *et al.*, 2006; Larrivée, Fahrig & Drapeau, 2008), an effect even observed in soil organisms such as fungal-feeding mites (Kardol *et al.*, 2009). Conversely, the often high productivity of crop fields, as well as temporal pulses in their resource availability from crop emergence until harvest, can at times make crop fields a source of organisms spilling over to adjacent wild habitats. While the latter phenomenon is likely to occur frequently in production landscapes, it has been surprisingly poorly studied to date (Kleijn, 1996; Rand *et al.*, 2006; Meyer, Jauker & Steffan-Dewenter, 2009; Jha & Dick, 2010; Blitzer *et al.*, 2012). Rand & Tscharntke (2007) found higher predation rates on nettle aphids by ladybird beetles in non-managed fallow strips along cereal fields, but only in cereal-crop-dominated landscapes, presumably due to the spillover of predators from cereals to nettles. Similarly, spillover of parasitoids (attacking pollen beetle on oilseed rape) from cropland to related wild plants outside cropland increased parasitism rates (Gladbach *et al.*, 2011). According to Westphal, Steffan-Dewenter & Tscharntke (2003, 2006), the nectar and pollen resources of oilseed rape greatly benefit bumble bee populations outside cropland.

Spillover across habitats often increases with increasing edge density (i.e. perimeter-area ratios), and this can enhance functional connectivity among habitats (e.g. Perović *et al.*, 2010), or, conversely, it can inhibit functional connectivity if edges function as barriers (e.g. Young *et al.*, 2010). Landscape complexity can benefit organisms by facilitating resource use in different habitats in two distinct ways (Dunning *et al.*, 1992): landscape complementation, which refers to landscapes providing organisms with a full complement of spatially separated resources that are all required to meet their needs (e.g. amphibians with aquatic larval and terrestrial adult habitats, Pope *et al.*, 2000; Knight *et al.*, 2005), or landscape supplementation, where landscapes provide organisms with supplemental habitats containing larger concentrations of their required resources (e.g. wild bees nesting in grassland but utilising more abundant foraging resources in arable crops; Westphal *et al.*, 2003, 2006; Holzschuh, Steffan-Dewenter & Tscharntke, 2008; Holzschuh *et al.*, 2011).

Despite these examples of cross-habitat movement, landscape-wide dispersal differs considerably among species, which have specific functional spatial scales at which they respond to landscape complexity (Fig. 4; Schmidt *et al.*, 2008; Tittler, Villard & Fahrig, 2009). Spillover generally occurs in species with high dispersal ranges, rather than for those species that depend on pristine habitat, avoid disturbed areas, have limited dispersal, or experience the matrix as hostile. The latter are unlikely to contribute much to spillover effects, and can only be protected with large reserves that minimize edge effects (Laurance, 1991; Didham *et al.*, 1996, 1998; Ewers & Didham, 2006, 2008; Sodhi *et al.*, 2007).
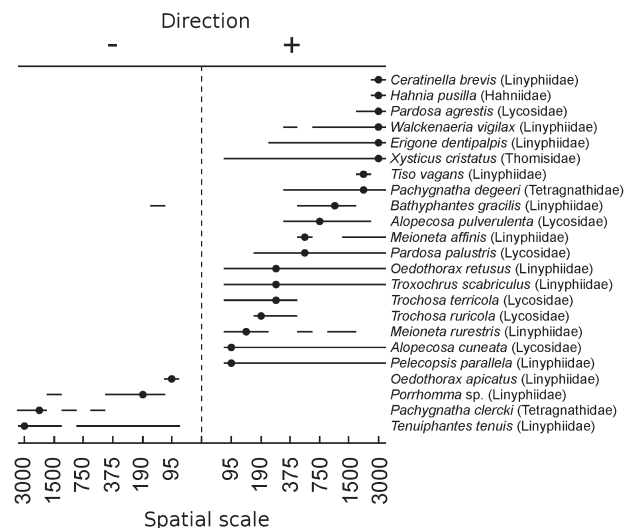

Fig. 4. Responses of arable spiders (captured in wheat fields) to landscape complexity on different spatial scales (Schmidt *et al.*, 2008). Spatial scale is the radius (m) of a circle around the studied wheat field; + means a positive and—a negative direction in density response to landscape complexity (which is measured as per cent noncrop habitat in these circles and which was positively related to habitat-type diversity). The most abundant spider species are shown here. Significant relations (of abundance to % arable crop in the surrounding landscape) are indicated by lines with the black dot showing where correlation coefficients are at their maximum.

Plant communities in stable environments can be comprised largely of perennials, with little evidence for substantial spillover effects, so in such circumstances spillover effects may be quantitatively unimportant. But for more mobile taxa that do not show such strong pre-emptive competition (e.g. plants of arable fields; Gabriel, Thies & Tscharntke, 2005; Gabriel *et al.*, 2006) and in landscapes with high functional connectivity, we conjecture that spillover species and species needing multiple cover types flourish, although this needs more documentation. Hence, landscape models considering all cover types in the landscape will resemble in reality more Levins' classical metapopulation model with its assumption of landscapes consisting of only habitat *versus* non-habitat (Levins, 1969; Lindenmayer *et al.*, 2003; Tscharntke & Brandl, 2004; Lonsdorf *et al.*, 2009; Perfecto & Vandermeer, 2010).

The importance of spillover is implicit in certain management practices. For example, natural or semi-natural habitat adjacent to crops is often seen as beneficial for services such as biological control or pollination (Thies & Tscharntke, 1999; Östman, Ekbom & Bengtsson, 2001; Kremen, Williams & Thorp, 2002; Bianchi *et al.*, 2006; Klein *et al.*, 2007; Meehan *et al.*, 2011), with 20% non-crop habitat per landscape being a rough threshold estimate for ensuring meaningful biodiversity and associated ecosystem processes (Tscharntke *et al.*, 2002*b*, 2011; Kremen *et al.*, 2004), in line with theoretical considerations (Andrén, 1994; Swift & Hannon, 2010; Hanski, 2011). However, spillover from

natural to managed systems can also provide dis-services and act as source of weed, pathogen or pest populations (Lavandero *et al.*, 2006; Zhang *et al.*, 2007; Eilers & Klein, 2009; Blitzer *et al.*, 2012). Similarly, the negative effects of managed systems on wild organisms [e.g. *via* pathogen infection (Lembo *et al.*, 2008) or spillover predation (Batáry & Báldi, 2004; Rand *et al.*, 2006)] are not necessarily ubiquitous, as agricultural systems may also benefit non-agricultural species (Blitzer *et al.*, 2012).

Future research should be directed at acquiring more empirical and modelling evidence to assess the widely held principle that "the matrix matters", a generality that has been questioned by Harrison & Bruna (1999; but see Ewers & Didham, 2006; Kupfer, Malanson & Franklin, 2006; Lindenmayer *et al.*, 2008). Further studies are needed to determine how species differ in their edge responses, which types of edges maximise spillover, how habitat size, configuration, quality and edge effects are related (e.g. Laurance & Yensen, 1991; Tscharntke, 1992; Ewers & Didham, 2006, 2008; Holzschuh *et al.*, 2010) and how effective are minor changes in landscape configuration such as narrow grass strips (Holzschuh, Steffan-Dewenter & Tscharntke, 2009), flowering patches (Tylianakis, Didham & Wratten, 2004; Haenke *et al.*, 2009), hedgerows (Burel, 1996) or different types of set-aside sowings (e.g. Pywell *et al.*, 2006; Tscharntke, Batáry & Dormann, 2011), in providing functionally important spillover into cropping systems. We also need to know how many species rely on multiple cover types, i.e. how important landscape complementation actually is. Finally, in the case of agroecosystems, it is important to conduct studies that examine the ecological and economic consequences of both negative and positive effects of spillover between habitats (i.e. services and disservices of spillover).

(2) Hypothesis 4: the landscape-moderated concentration and dilution hypothesis

Spatial and temporal changes in landscape composition can cause transient concentration or dilution of populations with functional consequences

Concentration or dilution effects on habitat specialist (but less so on habitat generalist) populations may be expected in situations of habitat destruction or restoration, which can lead to strong transient increases in abundance of that species in remnant habitat patches (Holt & Hochberg, 2001). For example, in newly isolated Amazonian forest fragments, bird numbers increased, but only for about 200 days after which population sizes fell below pre-isolation levels (Bierregaard *et al.*, 1992). Similar concentration or crowding effects have been observed for insects in short-term experimental fragmentation experiments (Collinge & Forman, 1998; Debinski & Holt, 2000; Grez *et al.*, 2004), and have been more generally postulated to alter species interactions within remaining natural habitat fragments (Saunders, Hobbs & Margules, 1991; Sodhi *et al.*, 2007). Concentration effects can also be caused by 'bottom-up' processes, when pulses of resources are provided to resident

consumers (Holt, 2008). Such dynamics, in concert with the small size of populations in fragments and their inherent vulnerability to edge and matrix effects, can also lead to a general increase in population and community dynamism in fragments - the so-called 'hyperdynamism hypothesis' (see Laurance, 2002).

Spatial and temporal landscape dynamics of consumers are particularly important in agricultural landscapes owing to rotations of annual crops (Wissinger, 1997) and changes in economic incentives determined by agricultural policy (Báldi & Batáry, 2011). Veddeler, Klein & Tscharntke (2006) found both concentration and dilution effects of resource density in coffee flower visitation, which were dependent upon spatial scale. Coffee-pollinating bees concentrated in response to high flower density at a branch and shrub level, while at a plot level, a dilution effect was found, because landscape-wide bee populations were not large enough to exploit fully the short-term increase in coffee flower resources. Similarly, landscape-wide increases in mass-flowering crops such as oilseed rape (canola) caused a dilution of bee pollinator density with negative effects on pollination of an endangered plant in adjacent natural grassland (Holzschuh *et al.*, 2011). Thies, Steffan-Dewenter & Tscharntke (2008) found that parasitism by specialized parasitoids decreased following landscape-wide expansion of the area planted in oilseed rape, and increased following subsequent reduction in the area cultivated, indicating inter-annual dilution and concentration effects. Stronger effects on per cent parasitism than herbivory (Thies *et al.*, 2008) support the idea that (i) concentration or dilution of interacting populations can be affected at different spatial scales and that (ii) higher trophic levels of specialists are more sensitive to disturbance and ecological change than those occupying lower trophic levels (Kruess & Tscharntke, 1994; Holt *et al.*, 1999; Tscharntke & Kruess, 1999; Tscharntke *et al.*, 2005a). Annual disturbances such as crop harvesting may result in the forced emigration of natural enemies or herbivores resulting in concentration in surrounding natural habitats (Rand *et al.*, 2006; Rand & Tscharntke, 2007; Rand, van Veen & Tscharntke, 2011).

Future research could provide better experimental evidence for landscape dynamics causing dilution or concentration of populations. Experimental fragmentation of habitats (e.g. in the case of forest clearings or forest conversion to oil palm plantations) could provide a broader picture of biodiversity patterns and ecological functioning. In general, density dependence of species responses to resources may change dramatically with the spatial scale considered, and is a phenomenon which has rarely been studied (Veddeler *et al.*, 2006). The above examples of concentration in habitat fragments may not matter if immigrants are functionally inferior to residents and density-dependent interactions are strong, such that immigrants are likely to die rapidly or do not reproduce. Similarly, the population- and community-level consequences of temporal (annual) changes in habitat composition at a landscape scale (in particular in agricultural landscapes shaped by crop rotation and ever-changing agricultural policies) have only recently begun to be

investigated (Landis *et al.*, 2008; Thies *et al.*, 2008). Linking back to previous hypotheses, it will be important to determine whether small-scale management actions (i.e. fallow strips, hedgerows) in simplified landscapes simply concentrate biodiversity or actually support population growth or viability (Kleijn *et al.*, 2011). Further, the combination of landscape-driven concentration and spillover could have large effects on ecosystem functioning, in both the habitat that drives the concentration (e.g. through rapid increases in resource availability), as well as adjacent habitats. These functional outcomes following concentration or dilution of populations, including temporal shifts in concentration within seasons, have been rarely studied and require more attention.

IV. SECTION C: LANDSCAPE MODERATION OF FUNCTIONAL TRAIT SELECTION

(1) Hypothesis 5: the landscape-moderated functional trait selection hypothesis

Landscape moderation of species trait selection shapes the functional role and the trajectory of community assembly

Environmental changes including habitat destruction, habitat fragmentation, and landscape simplification do not affect all species equally. Instead, effects depend on species traits, landscape type and the spatio-temporal scale (Henle *et al.*, 2004; Ewers & Didham, 2006; Swift & Hannon, 2010). The landscape-scale selection of functionally important traits results in landscape-wide species sorting and is grounded in interactions between evolutionary and ecological dynamics, with dispersal being crucial to understanding community assembly and food-web interactions (Urban *et al.*, 2008). Adaptive evolution, with populations adapting genetically to changing landscape environments, is linked to species sorting, the environmental filtering of species with certain traits due to colonization-extinction dynamics. Fahrig (2007) contrasts natural landscapes containing a low-risk matrix, in which species have evolved moderate to high movement probabilities, with natural landscapes containing a high-risk matrix, in which species evolve relatively low movement probabilities. Landscape modification, including habitat destruction and reduced matrix quality, will affect the first set of species through a large increase in dispersal mortality. By contrast, the second set of species will be affected mainly through susceptibility to decreased immigration and colonization success, due to the increasing patch isolation that results from habitat loss.

In the following, we focus on landscape-wide species sorting due to differences in dispersal and habitat requirements in spatially and temporally heterogeneous and dynamic landscapes. The varying susceptibilities of species can change community structure, associated ecosystem functioning, and food-web interactions in a non-random way (e.g. Henle *et al.*, 2004; Larsen, Williams & Kremen, 2005; Lee *et al.*, 2009; Winfree *et al.*, 2009; Bengtsson, 2010; Laliberté & Tylianakis, 2010; Williams *et al.*, 2010).

The life-history traits that confer greatest risk in the face of environmental change are high habitat or resource specialisation and low reproductive rate (Vance, Fahrig & Flather, 2003; Holland, Fahrig & Cappuccino, 2005; Ryall & Fahrig, 2006; Rytwinski & Fahrig, 2011). Species surviving in human-dominated and dynamic landscapes require the ability to use a wide range of different resource types and reach scattered habitat patches (Tscharntke *et al.*, 2005*a*; Batáry *et al.*, 2007; Rand & Tscharntke, 2007). Tolerance of matrix habitats also turned out to be a key trait in Amazonian forest fragments (Laurance *et al.*, 2011). However, species with high dispersal tendency, in natural landscapes with a low-risk matrix will be most at risk from landscape change (Fahrig, 2007). Other potential traits typical of rare or endangered species include high population variability, which enhances susceptibility to environmental stochasticity, and concurrent population fluctuations counteracting the potential for compensatory immigration within metapopulations (Tscharntke, 1992; Bengtsson & Milbrink, 1995; Lawton, 1995). The effect of body size is unclear, as large species are often more affected by habitat loss, probably due to their lower reproductive rates (Vance *et al.*, 2003; Holland *et al.*, 2005), but may benefit from having higher mobility (Laurance, 1991; Lawton, 1995; Tscharntke *et al.*, 2002*a*; Hambäck *et al.*, 2007) allowing resource use on larger spatial scales (e.g. Concepción & Díaz, 2011). Mobile consumers reduce variability of food-web structure, while sessile resource users increase variability of food-web structure in modified habitats (Laliberté & Tylianakis, 2010). It is thought that changes in body-size distributions following landscape changes likely have functional consequences, both because large species such as top predators or trees may be lost, and because body size has large effects on feeding rates and other physiological traits associated with ecosystem functioning (Peters, 1983; Terborgh *et al.*, 2001; Lavorel & Garnier, 2002; Henle *et al.*, 2004; Larsen *et al.*, 2005; Chapron, Andrén & Liberg, 2008). Species at higher trophic positions are often more affected by environmental change, especially so when they are specialised in resource or habitat requirements (Holt *et al.*, 1999; Steffan-Dewenter & Tscharntke, 2000; van Nouhuys & Hanski, 2002; Thies, Steffan-Dewenter & Tscharntke, 2003; Ryall & Fahrig, 2006; Holt, 2010). This gives rise to what might be termed a specialist consumer hypothesis of landscape effects (Kruess & Tscharntke, 1994, 2000; Tscharntke & Kruess, 1999; Rand & Tscharntke, 2007) that specialised higher trophic-level species are more affected by landscape change than are their prey species.

In addition to species traits, landscape structure can filter whole functional groups (Petchey & Gaston, 2006). For example, birds of agricultural landscapes have greater habitat and diet breadth than species of forest landscapes (Tscharntke *et al.*, 2008). Further, diversity of insectivorous birds and predatory insects as well as pollinating bee species declines with agricultural transformation (Tscharntke *et al.*, 2008). As a result of landscape filtering, both functional redundancy and response diversity can decline following

habitat modification (Laliberté *et al.*, 2010), which, as discussed below, can reduce temporal stability and resilience of ecosystem functioning. While there is clear evidence for effects on functional traits, virtually nothing is known regarding what happens to traits that are of importance for future evolutionary processes. For example, are specific landscape characteristics needed for the maintenance of male and female populations of sexually dimorphic species?

Future research is needed to examine whether there are changes in function as a consequence of variation in landscape context filtering out certain traits and functional groups affecting food-web structure (Hedlund *et al.*, 2004). Again, different landscape types and taxa should be compared systematically and phylogenetic relatedness considered (Hambäck *et al.*, 2007; Purvis, 2008). Empirical analyses of possibly parallel *versus* discontinuous changes in below- and aboveground multitrophic interactions (Wardle, 2002; Bardgett, 2005; Scherber *et al.*, 2010) along land-use, landscape and biogeographic gradients (De Deyn & Van der Putten, 2005; Birkhofer *et al.*, 2008) would be of major importance in future research. Additionally, the identification of shifts in species traits that might be driving such patterns and their consequences for community organisation and ecosystem functioning in modified landscapes requires further exploration.

(2) Hypothesis 6: the landscape-moderated insurance hypothesis

Landscape complexity provides spatial and temporal insurance, i.e. high resilience and stability of ecological processes in changing environments

According to the insurance hypothesis, higher biodiversity in a functional group buffers ecosystem functioning against environmental changes (Lawton & Brown, 1994; Naeem & Li, 1997; Yachi & Loreau, 1999; Loreau, Mouquet & Gonzalez, 2003; Winfree *et al.*, 2007; Griffin *et al.*, 2009). This argument for the value of biodiversity is often used for promoting biodiversity conservation, and is analogous to the insurance effect of genetic diversity (Hughes & Stachowicz, 2004) or of food-web interaction diversity (Laliberté & Tylianakis, 2010, but see Gagic *et al.*, 2011). Redundancy within functional groups provides insurance, preventing declining ecosystem functioning when some species are lost. Even without extinctions, under changing environments or when species fluctuate spatially or temporally, the functional role of once abundant species can be substituted by other previously less-abundant species. Such functional redundancy is particularly important in dynamic landscapes and is often coupled with response diversity, whereby species respond differently to environmental change (Elmqvist *et al.*, 2003; Winfree & Kremen, 2009; Blüthgen & Klein, 2011). Only when whole functional groups are lost, will the function and the insurance effect disappear, although both effects may become less important when more species from the same functional groups disappear (Laliberté *et al.*, 2010), assuming multiple species of the same functional groups are not entirely functionally redundant. Therefore, it is not surprising that

higher species diversity has been shown to reduce variability of ecosystem functioning, e.g. the coefficient of variation in parasitism (Tylianakis, Tscharntke & Klein, 2006; Veddeler *et al.*, 2010), respiration (McGrady-Steed, Harris & Morin, 1997), primary production (Hooper *et al.*, 2005), flower visitation and pollination rates (Kremen *et al.*, 2004; Ebeling *et al.*, 2008; Klein *et al.*, 2008; Ebeling, Klein & Tscharntke, 2011).

By virtue of their high beta diversity, complex-structured landscapes can have a large regional diversity within functional groups, which can be important for maintaining spatial insurance in ecosystem functioning on multiple scales (Loreau *et al.*, 2003). Movements of species between landscape elements can allow them to carry out functions at different points in space and time (e.g. immigration following disturbance; Lundberg & Moberg, 2003), even though they may be less important in other places (Srivastava & Vellend, 2005). Movements may also guarantee resilience, the capacity to reorganize after disturbance in changing environments (Fig. 5). In addition to local insurance provided by alpha diversity, beta diversity and habitat-type diversity can provide a landscape-moderated insurance against large-scale synchronous environmental changes such as climate change or changing nutrient regimes (Parsche *et al.*, 2011), if movements across habitat boundaries are possible.

Insurance effects are context dependent and related to spatial and temporal scales. In heterogeneous environments,
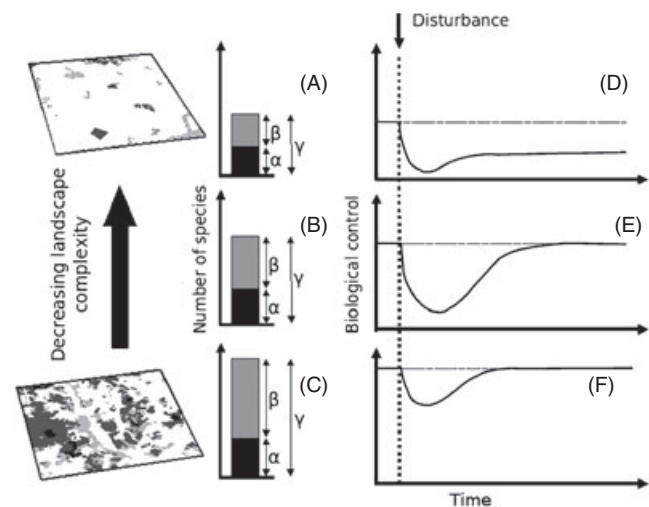

Fig. 5. Landscape complexity and resilience, the capacity to re-organize after disturbance, of an ecosystem service such as biological control. Landscape complexity decreases from bottom to top, influencing responses to disturbance in terms of species richness (A-C) and biological control by natural enemies (D-F). Increasing landscape complexity enhances the species pool (A-C) and the level of biological control, allowing quick recovery in biological control after a disturbance (D-F). Complex landscapes support more species, mainly due to the higher beta diversity, but often also higher alpha diversity (not shown here) and allow only a small dip and quick return in biological control after disturbance (Tscharntke *et al.*, 2007a, modified after Bengtsson *et al.*, 2003).

which contain a variety of niches, biodiversity effects on function are more important than in simplified model systems, as shown by Tylianakis *et al.* (2008*b*). Functional complementarity, based on niche differentiation allowing different contributions to a collective function, as well as functional redundancy, based on the same contributions but realized under different environmental conditions, are much more relevant under landscape-wide spatial and temporal heterogeneity. Functionally important organisms experience their environment at different scales given that environmental conditions change with area experienced. In addition, insurance (in terms of resilience) is argued to be enhanced if coexisting species both utilise different resources (niches) and have dynamics on different spatial and temporal scales (Peterson *et al.*, 1998). Larger species tend to use landscapes at larger scales, for example in the case of bumblebees, butterflies and birds (Steffan-Dewenter & Tscharntke, 1997; Westphal *et al.*, 2006; Concepción & Díaz, 2011), but other taxonomic groups show high variability in their extent of landscape use for unknown reasons (see Fig. 4). Body size of important parasitoid species attacking a major forest pest could be related to the landscape scale experienced (Roland & Taylor, 1995).

Interacting communities are made up of species experiencing the surrounding landscape at different spatial scales, but current models assume implicitly that species involved in biotic interactions operate at the same scale (are scale invariant) (Tscharntke *et al.*, 2005*a*). Understanding this scale-dependence of functional importance, for example of biological control, is important for judging any insurance value. Potential competition between social (large-scale landscape experience) and solitary (small-scale experience) bees as well as between small and large bumblebees depends on whether the environment (e.g. resource availability) changes with the experienced area (Steffan-Dewenter *et al.*, 2002; Westphal *et al.*, 2006).

In a multidimensional niche space, long-term and large-scale complementarity may be hidden by apparent redundancy; where redundancy in one niche dimension and on one level does not exclude complementarity in another (Blüthgen & Klein, 2011). In diverse communities, ecological facilitation and increased niche specialisation can further enhance functional complementarity (Greenleaf & Kremen, 2006; Ebeling *et al.*, 2008; Ebeling, Klein & Tscharntke, 2011). Ignoring this real-world complexity in space and time easily leads to underestimating the stabilizing role of apparently redundant species.

Future research should be directed at elucidating the mechanisms underlying the insurance effects of biodiversity as amplified or modified by landscape structure at different temporal and spatial scales. Current biodiversity experiments mostly start from random loss scenarios, whereas in reality, specific functional groups and traits often drop out first (Leps, 2004; Zavaleta & Hulvey, 2004; Kremen, 2005; Larsen *et al.*, 2005). With landscape modification, some key groups may be more vulnerable than others. Furthermore, traits of species that determine their propensity to cross habitat boundaries (see Section III.1, hypothesis 3), will determine their ability to

provide functional insurance. Fragmentation of landscapes not only generates such boundaries and alters their structure, but entirely new habitats (e.g. crops) can be added to the landscape, while traits of certain species are filtered out (see Section IV.1, hypothesis 5). The interplay of these factors will determine the ability of mosaic landscapes to provide functional insurance, and research integrating these elements is needed. Another important question relates to spatial scale: how does landscape extent impact the effectiveness of the species' functional redundancy for maintaining ecosystem functions? If different species within the same functional group are separated in space (high beta diversity) over a large area, how does that separation affect their ability to replace each other and thereby maintain ecosystem function within the landscape in the face of environmental change? How can landscape management promote insurance effects? Do the effects of landscape heterogeneity on the relationship between biodiversity and ecosystem functioning match those of within-habitat heterogeneity (Tylianakis & Romo, 2010)? As with our earlier suggestions about genetic diversity, does a low to moderate amount of connectivity suffice for an insurance effect to operate?

V. SECTION D: LANDSCAPE CONSTRAINTS ON CONSERVATION MANAGEMENT

(1) Hypothesis 7: the intermediate landscape-complexity hypothesis

Landscape-moderated effectiveness of local conservation management is highest in structurally simple, rather than in cleared (i.e. extremely simplified) or in complex landscapes

The effectiveness of local biodiversity conservation management in human-dominated landscapes changes with landscape structure. Duelli & Obrist (2003, page 137) argued that "agri-environment schemes have a much better chance to be successful in regions where source populations survived in natural or semi-natural habitats". By contrast, a number of studies did not find the highest effectiveness of biodiversity conservation management (enhanced richness by management compared to the control) in the most species-rich landscapes, but in simple landscapes, i.e. in landscapes with intermediate structural complexity (Tscharntke *et al.*, 2005*a*; Rundlöf & Smith, 2006; Concepción, Díaz & Baquero, 2008; Fischer, Stott & Law, 2010; Smith *et al.*, 2010; Batáry, Matthiesen & Tscharntke, 2010*b*). In structurally complex landscapes with a high proportion of non-crop habitat (>20%), biodiversity and associated functioning (such as pest control or crop pollination) is high everywhere, so that local conservation management often does not result in a recognizable effect. Landscape complexity is related to the percentage of non-crop area, which in turn is closely and positively related to high habitat-type diversity in Central Europe, but these relationships may vary greatly depending on where you are in the world (Tscharntke *et al.*, 2005*a*). Low effectiveness may occur not only in
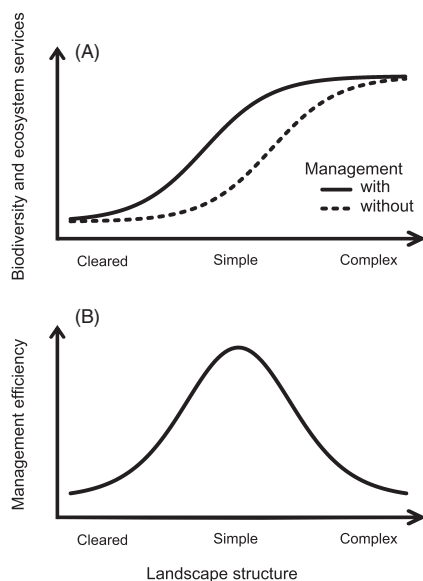
Fig. 6. The intermediate landscape complexity hypothesis. In "simple" (intermediate-complexity) landscapes, consisting of 1–20% noncrop area in Central Europe (Tscharntke *et al.*, 2005*a*), effectiveness of management such as agri-environmental measures is higher than in "cleared" (low-complexity) landscapes (<1% noncrop area) or "complex" (high-complexity) landscapes (>20% noncrop area). 1–20% noncrop area appears to be a threshold level (tipping point) (but this can be different in other regions of the world). (A) Biodiversity and ecosystem services in relation to landscape structure. The solid line shows management effects (e.g. organic farming) and the dotted line the control (e.g. conventional farming). The S-shaped curve makes clear that maximum biodiversity changes induced by management can be expected in simple landscapes. (B) Effectiveness (the difference between treatment and control) in relation to landscape structure.

complex landscapes, but also in largely cleared (extremely simple and structurally homogenous) landscapes, with few, or a single, habitat types and a very low proportion of non-crop habitat (<1%). In such cleared landscapes, too few source populations remain to allow success of any local management scheme. Hence, introducing organic farming, field margins, hedges or fallows provides greater enhancement of local diversity and ecosystem functioning (such as biological control, pollination or seed dispersal) in simple landscapes with intermediate proportions of non-crop habitat area (1-20%), compared to landscapes with greater or smaller non-crop area (Fig. 6; Thies & Tscharntke, 1999; Roschewitz *et al.*, 2005; Tscharntke *et al.*, 2005*a*; Holzschuh *et al.*, 2007; Williams & Kremen, 2007; Eilers & Klein, 2009; Isaacs *et al.*, 2009; Batáry *et al.*, 2010*b*).

Cleared landscapes without a substantial species pool do not have the capacity to respond to agri-environmental management. In the Netherlands, many landscapes have almost no semi-natural habitat left (<1%) and the diversity of bees and insect-pollinated plants is so low that conservation management does not have any effect (Batáry *et al.*, 2010*a*). In fact, in a comparison of five European countries, the only

country in which agri-environmental management had no effect on biodiversity was the Netherlands (Kleijn *et al.*, 2006; see also Kleijn *et al.*, 2001). Geiger *et al.* (2010) found higher farmland bird abundance and diversity in organic fields across Europe, but only in moderately simple, not cleared or complex landscapes. However, more empirical evidence confirming the low effectiveness of management in cleared landscapes is needed.

In a recent meta-analysis, Batáry *et al.* (2011) found, in concordance with the intermediate landscape complexity hypothesis, that local agri-environmental management practices in cropland have an effect on biodiversity in simple but not complex landscapes (however, there were not enough studies available to include cleared landscapes). Overall, results demonstrate that landscape context moderates the effectiveness of agri-environment management in terms of species richness, which is highest in arable crops of simple landscapes. In complex landscapes, biodiversity is high everywhere, which means that there is a risk of substantial biodiversity loss in complex landscapes when land-use is intensified. From a conservation point of view, the main priority in complex landscapes should be the preservation and, if necessary, restoration of natural and semi-natural habitats to maintain or achieve a greater total amount of habitat cover, as changes in local management are likely to have comparatively little effect. Conversely, in simple landscapes, agri-environment management at the local (field) scale will have a large effect on biodiversity and associated processes. In addition, when such local management is applied on many fields, conservation effects are synergistically enhanced (Holzschuh *et al.*, 2008; Rundlöf, Bengtsson & Smith, 2008; Dallimer *et al.*, 2010; Gabriel *et al.*, 2010). Hence, large-scale implementation of agri-environment schemes across several farms can collectively add to the landscape-wide effects of semi-natural habitats, as demonstrated by the positive effects of large-scale organic farming on bee diversity at a landscape scale (Holzschuh *et al.*, 2008).

In complex landscapes, agroecosystems are characterized by a high level of immigration of organisms from remnant natural or semi-natural habitat (Tscharntke, Rand & Bianchi, 2005*b*; Bianchi *et al.*, 2006; Ricketts *et al.*, 2008), which can outweigh effects of any local agri-environment practices (Kremen *et al.*, 2004; Tscharntke *et al.*, 2005*a*). Landscape complementation (Dunning *et al.*, 1992) is high, meeting the requirements of many species that must move between multiple habitat types to complete their life cycles (Kremen *et al.*, 2007, 2008). Accordingly, local (small-scale) management changes such as organic farming may not result in meaningful improvements, as intensive conventional farming is compensated by a high level of immigration from (semi-) natural habitat in the landscape matrix. This might be thought of as a form of 'landscape compensation' in which complex, but not simple or cleared, landscapes compensate for local disturbances, such as intensive agricultural practices, through enhanced colonization rates. For example, carabid beetles rapidly recolonize insecticide-treated fields from untreated semi-natural habitats (Lee, Menalled & Landis, 2001). This

has also been shown for non-crop plants and wild bees in arable fields (Roschewitz *et al.*, 2005; Holzschuh *et al.*, 2007), which had higher diversity on organic farms, but only when landscapes were structurally simple and not when landscapes were complex. The corollary is that in relatively simple landscapes, local management for biodiversity and associated ecological functioning can partly compensate for the lack of structural complexity at the landscape scale (Williams & Kremen, 2007; Holzschuh *et al.*, 2008), but presumably, complex landscapes still provide higher local biodiversity.

Future research should be directed at comparing more systematically management practices across the full spectrum of cleared, simple and complex landscapes, as the intermediate landscape complexity hypothesis has so far been based on only a few case examples and rarely includes a functional component. Particularly little is known about management effects in cleared landscapes, which sustain only very few, and often small, natural populations. Can biodiversity loss and alteration of ecosystem services in such landscapes be mitigated, and what will it take? Furthermore, responses of populations and communities to management can be expected to differ greatly, contingent on landscape type, so comparing open *versus* forested landscapes and tropical *versus* temperate landscapes is likely to be a worthwhile endeavour. For example, the threshold values for simple and complex landscapes given above for Central Europe probably do not hold for many other regions in the world. Comparisons between temperate-zone landscapes, characterized by strong seasonality, and high-biodiversity biomes such as chaparral and fynbos, prairie and steppe or savanna, evolved in the context of dynamic fire regimes, would be interesting. Natural habitats in complex landscapes can indeed act as a source of biodiversity and compensate for local disturbances, but this may be restricted to certain taxa and functional groups. Which disturbed habitats act as sinks (or ecological traps, Gilroy & Sutherland, 2007) or sources of viable populations, and which provide complementary as opposed to supplementary resources for species mainly adapted to other habitat types, remains to be understood. This relates to the question of what size of source patches and/or the overall total habitat area within a landscape is necessary to sustain viable populations of different organisms, and whether habitat size and area requirements can be altered (reduced) by enhancing matrix quality. If landscapes are themselves dynamic (e.g. due to crop abandonment or rotation), this adds an additional dimension of complexity.

(2) Hypothesis 8: the landscape-moderated biodiversity *versus* ecosystem service management hypothesis

Landscape-moderated biodiversity conservation to optimize functional diversity and related ecosystem services will not protect endangered species

A mosaic of managed and natural habitat can maximize crop pollination and yield (Kremen *et al.*, 2002; Klein *et al.*, 2007; Priess *et al.*, 2007; Winfree *et al.*, 2007), biological pest control (Thies & Tscharntke, 1999; Östman *et al.*, 2001; Tscharntke *et al.*, 2007a; Meehan *et al.*, 2011) and cultural services providing traditional landscape beauty. A matrix of wildlife-friendly agroecosystems and natural habitat patches may enhance dispersal and therefore survival of populations (Tscharntke *et al.*, 2005a; Perfecto *et al.*, 2009). Further, habitat mosaics scattered across landscapes generally provide more protection to biodiversity than does a single large remnant of a similar area (see Section II.2). However, such multifunctional landscapes allow long-term survival of only those species that are adapted to human land use (or analogous natural landscapes with high heterogeneity and disturbance frequency; Bengtsson *et al.*, 2003; Barlow *et al.*, 2007). For example, bird diversity can be high in modified tropical landscapes, but endangered forest species are rare in such land-use systems (Daily *et al.*, 2001; Maas *et al.*, 2009). Similarly, reducing shade in cacao agroforestry from 80% to 40% supports both high crop yield and high biodiversity, but most forest species are lost (Steffan-Dewenter *et al.*, 2007; Clough *et al.*, 2011; Tscharntke *et al.*, 2011). Patch-area-sensitive populations experience high extinction rates in fragmented landscapes and many of the most endangered plants and animals need a very large pristine habitat area to survive. In fact, dependence on large pristine habitat is a key spatial feature of vulnerability of endangered rainforest species (Didham, 2011; Laurance *et al.*, 2011). Rare or endangered species generally play a minor functional role in ecosystems and therefore contribute little to ecosystem services provided by biodiversity (other than cultural services). With respect to cultural services, the public is often concerned about the loss of common species, such as the currently declining common farmland birds in Europe (Whittingham, 2011). These species (e.g. skylark *Alauda arvensis*, yellowhammer *Emberiza citrinella*, tree sparrow *Passer montanus*) are highly appreciated and part of the cultural services provided by complex mosaic landscapes.

The differential sensitivity of endangered species and more abundant species adapted to intensive human land use and associated landscape configurations suggests they require different conservation approaches (Kleijn *et al.*, 2011). Conservation initiatives with intrinsic biodiversity objectives should focus on remnants of natural habitat and, for farmland specialists, on extensively used systems and structurally complex regions. By contrast, conservation of functionally important biodiversity providing major services such as pollination and biological control should focus more on intensively farmed areas, because of higher potential benefits such as improved crop yields, reduced household vulnerability to environmental changes and less negative externalities than agrochemical use (Kleijn *et al.*, 2011; Foster *et al.*, 2011; Tscharntke *et al.*, 2012). Gurr *et al.* (2004) provide examples of how functionally important biodiversity could be enhanced in such areas by means of 'ecological engineering' that manipulates land-use systems to make them less vulnerable to pests and more hospitable to beneficial organisms. 'Conservation Biological Control' aims at habitat manipulation to improve natural-enemy fitness by enhancing resources such

as nectar, pollen, prey or hosts, nesting resources and refuges for hibernation (Gurr *et al.*, 2004). For example, fallow strips of perennial tussock-forming grasses may function as 'beetle banks' in arable fields, and 'flower power' strips as facilitators of nectar-consuming aphid enemies and rape pollen-beetle enemies (Haenke *et al.*, 2009; Scheid *et al.*, 2011).

Future research should focus on determining the relative value of natural habitat remnants in human-dominated landscapes for conservation of endangered species, compared to larger habitat areas. A better understanding of how traditional land-use systems, which may offer valuable resources, can help to sustain populations of endangered species, will be important for landscape planning. Finding trade-offs between goals of 'fundamental' conservationists (in favour of species with little tolerance to habitat disturbance) and 'applied' conservationists (in favour of promoting biodiversity within human-dominated landscape mosaics to enhance and protect ecosystem services) is a major challenge for our future, and can contribute to fulfilling the dual goals of the Convention on Biological Diversity, i.e. preservation and sustainable use of biodiversity. Given the highly dynamic nature of many land-use systems, how can functionally important populations be effectively and sustainably protected? Can land-use heterogeneity be increased in agricultural landscapes by optimizing crop composition and configuration, based on a given amount of natural habitat (Fahrig *et al.*, 2011)? Is the promotion of evenness of the major players providing ecosystem services more important than biodiversity *per se* (Crowder *et al.*, 2010)? Currently, conservation initiatives on farmland rarely have clearly defined biodiversity objectives (Kleijn *et al.*, 2011), and joint management of aboveground and belowground ecosystem services needs to be further explored. A universal answer cannot be expected and effective conservation management needs to be regionally adapted.

VI. CONCLUSIONS

(1) Landscape structure plays a dominant, yet relatively little synthesized, role in moderating biodiversity patterns and ecological processes. The main reason for this appears to be the high real-world complexity shaping these patterns, which is a huge challenge for empirical research.

(2) There is a need to address this complexity with highly replicated and multi-factorial field studies supplemented by experimental manipulation (to reveal underlying mechanisms) and linked to simulation and theoretical models (to extrapolate and predict future scenarios, and aid in interpretation).

(3) The study of multitrophic interactions across taxonomic levels (from microorganisms and arthropods to vertebrates), across below- and aboveground systems, across local subplot and plot types and across gradients in landscape heterogeneity is a major challenge. Yet it is the only way to develop reliable and robust recommendations for conservation and ecosystem management in a changing world.

Reductionism may be worthwhile for particular systems and patterns, but a broader view on landscape-moderated effects is needed to find sustainable solutions for our future.

(4) One particularly valuable, yet largely absent, research opportunity could be the functional importance of landscape-moderated changes in community composition and food-web structure. A focus on the functional consequences of landscape change is essential for developing management solutions to sustain key ecosystem processes and services such as biological control, pollination or decomposition. In addition, responses to environmental changes will vary from small to large scales contingent on the intensity of environmental change, resulting in not just linear, but also exponential or saturation effects, possibly revealing important nonlinear thresholds.

(5) Few studies have examined landscape effects on multitrophic interactions or entire aboveground-belowground food webs and consequences for ecosystem service provisioning across the large-scale real-world heterogeneity experienced by a diversity of interacting species. In this review, we have presented a number of testable hypotheses to focus and stimulate future research.

VII. ACKNOWLEDGEMENTS

VIII. APPENDIX 1: LANDSCAPE MODERATION OF BELOWGROUND COMMUNITY STRUCTURE

Both below- and aboveground communities respond to physical disturbances such as agricultural intensification

(Wardle & van der Putten, 2002; Bardgett, 2005; van der Putten *et al.*, 2009). Belowground responses to changing environments are often different and appear to be weaker and slower than aboveground responses (Scherber *et al.*, 2010). Conversion of natural habitats to agriculture causes biodiversity loss of certain soil biota such as earthworms and arbuscular mycorrhizal fungi, and causes a microbial community shift from fungal- to bacterial-dominated composition, because of both enhanced soil disturbance (Helgason *et al.*, 1998) and increased inputs of easily decomposable resources (Bardgett, 2005). Changes in the composition of soil communities are not greatly influenced by fragmentation of the landscape (Rantalainen *et al.*, 2008; but see Sousa *et al.*, 2006). This is mainly due to their different perception of landscape dimensions relative to the scale at which humans fragment landscapes. On the other hand, soil biota may be influenced by landscape processes, but our perception of the landscape needs to be scaled down to the level at which it actually influences soil biota (Hedlund *et al.*, 2004; Flohre *et al.*, 2011). In a long-term biodiversity experiment, arbuscular mycorrhizal communities, as well as entire soil food webs, were more similar between plants of the same species, especially when these plants occurred in the same type of plant communities. The soil communities were less similar when compared within a plant species collected from different plant communities (Bezemer *et al.*, 2010; van de Voorde *et al.*, 2010) and even less similar when compared between different plant species collected from the same plant communities. Thus, the landscape perception of entire soil food webs can change between plant individuals in the same plant community (Bezemer *et al.*, 2010). Soil communities recover much more slowly from changes in land use than do aboveground communities, because of poor dispersal, slow re-colonization, and poor habitat and resource conditions for later successional soil organisms in disturbed habitats (Lindberg & Bengtsson, 2006; Van der Wal *et al.*, 2006; Van der Putten *et al.*, 2009; Scherber *et al.*, 2010). Rapid and repetitive changes in the use of soil or stress effects imposed on soil communities (Griffiths *et al.*, 2001), as well as individual plant species and variations in plant community composition (Kardol *et al.*, 2010), have much stronger effects on belowground communities than habitat fragmentation *per se*.

Different functional groups seem to exhibit different responses to fragmentation. Decomposer organisms, including microbes and invertebrates occupying higher trophic levels, are more influenced by soil disturbance than by habitat fragmentation (see the reviews of Ettema & Wardle, 2002; Swift, Izac & van Noordwijk, 2004; Bardgett, 2005; Tylianakis *et al.*, 2008*a*). Microarthropod density and diversity can be independent of spatial isolation (Schneider, Scheu & Maraun, 2007), while reductions in diversity of the decomposer community (Rantalainen *et al.*, 2005) and abundance of microarthropods and fungal biomass (Rantalainen *et al.*, 2006) have been recorded in experimentally fragmented habitats at quite small spatial scales. Wardle *et al.* (2003) found that larger habitat islands

(spatially separated epiphytes or treetop "islands" in tree canopies) supported a greater diversity of macrofauna and microarthropods, whereas distance to islands had no effect.

In conclusion, landscape moderation of biodiversity results in different patterns for soil biota than for many aboveground biota. Climate, soil type, topography and identity of the plant's rhizosphere appear to be particularly important for soil communities. Applicability of major hypotheses, developed for the aboveground world, needs further research with approaches linking below- and aboveground patterns and processes and their interactions.

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