

**IDEA AND
PERSPECTIVE**

Functional landscape heterogeneity and animal biodiversity in agricultural landscapes

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Abstract

Biodiversity in agricultural landscapes can be increased with conversion of some production lands into 'more-natural' – unmanaged or extensively managed – lands. However, it remains unknown to what extent biodiversity can be enhanced by altering landscape pattern without reducing agricultural production. We propose a framework for this problem, considering separately compositional heterogeneity (the number and proportions of different cover types) and configurational heterogeneity (the spatial arrangement of cover types). Cover type classification and mapping is based on species requirements, such as feeding and nesting, resulting in measures of 'functional landscape heterogeneity'. We then identify three important questions: does biodiversity increase with (1) increasing heterogeneity of the more-natural areas, (2) increasing compositional heterogeneity of production cover types and (3) increasing configurational heterogeneity of production cover types? We discuss approaches for addressing these questions. Such studies should have high priority because biodiversity protection globally depends increasingly on maintaining biodiversity in human-dominated landscapes.

Keywords

Agri-environment scheme, crop diversity, field margins, field size, habitat fragmentation, intermediate heterogeneity hypothesis, landscape complementation, landscape composition, landscape configuration, spatial heterogeneity.

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INTRODUCTION

A fundamental concept in landscape ecology is that spatial heterogeneity affects ecological systems (Wiens 2002). Elements of landscape heterogeneity can influence a variety of ecological responses, including animal movement (reviewed in Fahrig 2007), population persistence (Fraterrigo *et al.* 2009), species interactions (Polis *et al.* 2004) and ecosystem function (Lovett *et al.* 2005).

For biodiversity conservation in human-dominated regions, it is particularly important to understand the relationship between spatial heterogeneity and biodiversity

in agricultural landscapes (Benton *et al.* 2003; Tscharntke *et al.* 2005; Le Roux *et al.* 2008). Together, croplands and pastures occupy *c.* 40% of the land surface (Foley *et al.* 2005) and these productive areas have particularly high biodiversity potential (Altieri 1999). At the same time, agricultural landscapes range widely in their degree of spatial heterogeneity as controlled, in part, by patterns of land tenure and the cumulative effects of cropping, grazing and other decisions made by individual farmers. More heterogeneous landscapes contain many different production cover types (e.g. different field crops, intensively grazed lands, orchards) which are distributed in a complex pattern and interspersed

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with other, more 'natural', cover types (e.g. extensively grazed or non-grazed woodlands, wetlands, field margins). Such patterns are characteristic of traditional farming systems, in contrast with intensive agricultural systems which typically contain only a few sown crop types distributed in large uniform fields (Baudry & Bunce 1991; Sirami *et al.* 2007).

We explicitly recognize two components of heterogeneity: a more heterogeneous landscape is a landscape with a larger variety of different cover types (compositional heterogeneity) and/or a more complex spatial patterning of them (configurational heterogeneity) (Fahrig & Nuttle 2005). Note that these two components are generalized versions of the first two elements of Duelli's 'mosaic concept', namely 'habitat variability (number of biotope types per unit area)' and 'habitat heterogeneity (number of habitat patches and ecotone length per unit area)', respectively (Duelli 1997). For both components, the land cover types can be defined either with or without explicit consideration of their relevance to a particular species or species group. We therefore make an important distinction between 'structural landscape heterogeneity', where different cover types are identified by their physical characteristics, without reference to a particular species or species group (e.g. using classified satellite imagery), and 'functional landscape heterogeneity', where different cover types are identified based on differences in resource dependencies of species or species groups. For example, if the species group is insects, cover types might be distinguished using criteria such as floristic and edaphic conditions.

We understand farmland biodiversity as the variety of species that coexist in agricultural landscapes and the complexity of the trophic interactions that link them. Because of the magnitude of the areas converted into agricultural landscapes, any change in their capacity to accommodate more wild plants and animals and more complex interaction networks could produce important changes in biodiversity relevant to local or global conservation priorities.

Given the importance of agricultural systems for the maintenance of biodiversity, policies and guidelines are needed to maintain and enhance biodiversity in changing agricultural environments. In this quest, the management of spatial heterogeneity of agricultural landscapes may be critical. The value of agricultural land for conservation has been recognized formally in Europe through some agri-environment schemes (e.g. Kleijn *et al.* 2006; Davey *et al.* 2010), but these are not organized to produce particular levels or types of heterogeneity at the landscape scale. In addition, the effectiveness of the numerous agri-environment schemes in Europe have been questioned (Kleijn *et al.* 2006); in many instances, they have yet to provide any detectable biodiversity benefits (e.g. Davey *et al.* 2010).

One reason may be that options within schemes are typically designed at the field scale and that farm-scale combinations of options do not consider the pattern, particularly the heterogeneity, of the surrounding landscape (Tschamtko *et al.* 2005; Concepción *et al.* 2008).

Many have speculated on the importance of landscape heterogeneity for biodiversity in agricultural landscapes. However, evidence to date is scant. First, most of this speculation is based on extrapolation to the landscape scale from results of local-scale studies on the effects of farmland features and patterns – e.g. intercropping, shade crops, grassy strips, hedgerow trees, agro-forestry – on biodiversity (e.g. Perfecto & Vandermeer 2002; Vickery *et al.* 2009). Second, the many studies that have been conducted at the landscape scale, i.e. comparing biodiversity across multiple agricultural landscapes (e.g. Jonsen & Fahrig 1997; Holland & Fahrig 2000; Thies *et al.* 2003; Holzschuh *et al.* 2010), generally do not address landscape heterogeneity directly. In the few that do, the more heterogeneous landscapes are typically the landscapes containing larger areas of 'more-natural' cover types, i.e. unmanaged (indigenous, regenerating or restored habitats, hedgerows and other vegetated field margins) or extensively managed (forest or grassland with low-intensity grazing) areas [see 'Questions for Landscape Heterogeneity–Biodiversity Research in Agricultural Systems' for a discussion of the term 'more-natural']. As an example of this type of study, in their article on the effects of 'landscape complexity' Thies *et al.* (2003) selected 15 landscapes on a gradient 'from extremely simple and structurally poor landscapes (< 3% of non-crop area, i.e. area that is not converted to annual crops) to complex and structurally rich landscapes (> 50% non-crop habitats)' (Thies *et al.* 2003). In other words, in their study, complex landscapes were complex because they contained a large area of intrinsically complex more-natural cover types.

One reason landscape heterogeneity has not often been directly studied in agricultural landscapes is the predominance of the habitat–matrix paradigm in landscape ecology (Fischer & Lindenmayer 2006) in which the landscape is divided into 'habitat', where all necessary resources are found, and hostile 'matrix' (Fig. 1). This paradigm arose from applying the island–sea context of island biogeography theory (MacArthur & Wilson 1967) to terrestrial landscapes (Burgess & Sharpe 1981; Haila 2002), and was reinforced by the development of metapopulation theory (Hanski & Gilpin 1991). The habitat–matrix view has been challenged by many authors who pointed out that the landscape matrix is not equivalent to the 'sea' of island biogeography (e.g. Ricketts 2001; Brotons *et al.* 2003; Burel & Baudry 2005; Dunford & Freemark 2005; Fischer & Lindenmayer 2006; Kupfer *et al.* 2006). It is now recognized that many species perceive landscapes in more complex ways and use resources from different cover types, which implies that,

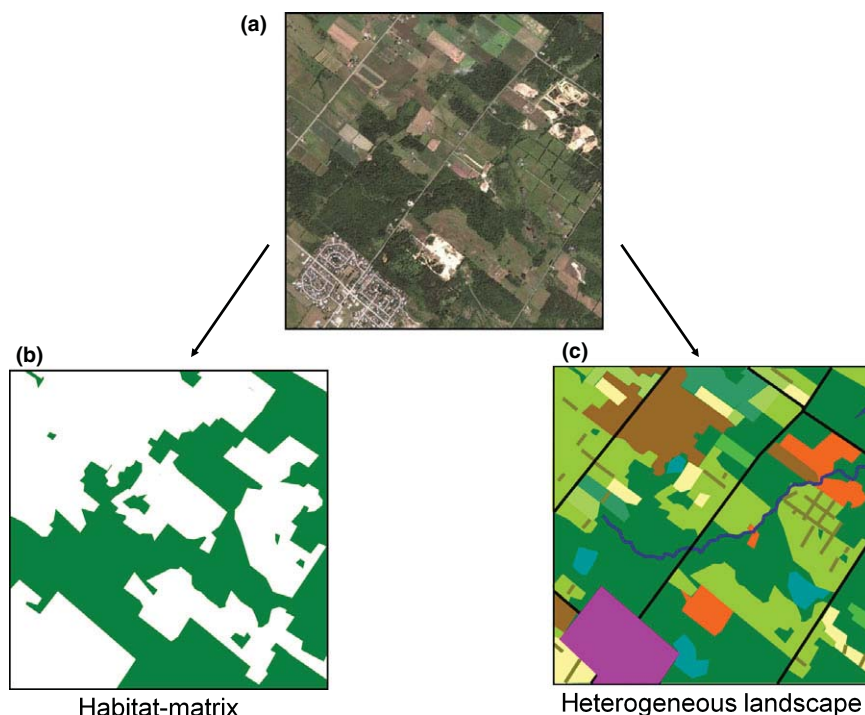


Figure 1 A landscape in eastern Ontario, Canada represented as: (a) a satellite image, (b) a habitat–matrix (forest vs. non-forest) representation of the same image and (c) a heterogeneous landscape representation of the same image showing different cover types.

to understand the effects of landscape structure on biodiversity, we need to replace the habitat–matrix view with a heterogeneous landscape view (Fig. 1).

Our objectives in this article are threefold. First, we develop a conceptual framework for the study of landscape heterogeneity in the context of agricultural landscapes, based on the concept of functional landscape heterogeneity. Second, we identify three important unanswered questions about the relationship between landscape heterogeneity and biodiversity in agricultural landscapes. Finally, we suggest a general methodological approach for studies to address these questions. While our examples are predominantly temperate ones, we suggest that the basic ideas could also be taken forward in many tropical contexts, though adjustments may need to be made for the fine-grain agro-forestry mosaics that are more commonly found in tropical than temperate agriculture (e.g. Gardner *et al.* 2009).

FUNCTIONAL LANDSCAPE HETEROGENEITY

The concept behind functional landscape heterogeneity is that the description and measurement of heterogeneity should be based on the expected functions (e.g. provision of food, nesting sites, dispersal routes) provided by that heterogeneity to the species or species group(s) of interest. To produce any measure of spatial heterogeneity (whether

structural or functional), we need to start with a map of cover types. However, a map of cover types perceived by the human observer (or remote-sensing device) does not necessarily represent relevant heterogeneity to a particular species group; cover types that we can distinguish are not necessarily functionally different for that species group and *vice versa* (Lima & Zollner 1996; Charrier *et al.* 1997; Schick *et al.* 2008). For example, for many ground-nesting farmland birds, access to bare ground combined with some vegetation cover is essential for nesting habitat, but the cover can be provided by any of several different crops (e.g. Gilroy *et al.* 2010). Therefore, for this response (ground-nesting farmland birds), these crops could be mapped as a single functional cover type (nesting habitat). Similarly, areas of open water and human habitation might be equally unsuitable for these species, hence differences between them might make no biologically significant (for these species) contribution to habitat heterogeneity and they could therefore be mapped as a single functional cover type (unsuitable). A map of functional landscape heterogeneity can also include subtle non-structural distinctions among cover types that are not apparent by eye or remote sensors but are relevant to a species response, i.e. the ‘invisible mosaic’ (Vasseur *et al.* 2008). Such distinctions are particularly important in the more intensively managed portions of agricultural landscapes where practices such as pesticide

application, soil management, fertilizer application and cropping history can have large effects on patch quality of both the managed and more-natural patch types, without apparent or at least large detectable effects on patch structure. For example, field management affects plant diversity in field margins, which defines habitat quality for flower-feeding insects (Le Cœur *et al.* 2002; Vickery *et al.* 2009). Weed density at the field scale is explained by crop rotation, weed management practices and the interactions between them (Doucet *et al.* 1999). Butterfly richness and abundance depend independently on local cultivation practices (e.g. 'conventional' vs. 'organic' agriculture) and the landscape context (e.g. proportion of organic fields) (Rundlof *et al.* 2008). In addition, signatures of ancient land use may persist with potential implications for present day plant and animal communities (Dupouey *et al.* 2002; Gustavsson *et al.* 2007). In creating a map of functional cover types for the species group of interest, important distinctions in farming practices therefore need to be incorporated.

In Box 1 and Fig. 2, we show the steps for creating a map of functional cover types for a particular species group, from which spatial heterogeneity measures can then be calculated. When overall biodiversity is the response of interest, we suggest building the map of functional cover types by selecting a set of representative species for each species group, where each group is defined as a set of species that obtain resources (food, shelter, etc.) from the same land cover types. Note that this does not assume that all the species in a group use the same resources (e.g. eat the same species of plant) but that they use resources in the same land cover types. The set of functionally different cover types would then be identified for each representative species and these would be combined to produce an overall set of functional cover types to be mapped. This could be done qualitatively, or alternatively, classification and regression trees provide a way to objectively classify cover types that can be mapped onto the landscape (Urban 2002). This approach constructs binary classification trees based on categorical or continuous variables that maximize the deviance explained in each split of the tree. The method can be used to group species based on pre-defined criteria (e.g. Flynn *et al.* 2009) and it could also be used to map functional cover types in landscapes based on the resource requirements of species groups (Fig. 2).

Once the map of functional cover types has been created, functional landscape heterogeneity is then measured using metrics for compositional and configurational heterogeneity. The simplest measure of compositional heterogeneity is the number of different cover types (*cover type richness*; Fig. 3). Then, given two landscapes with the same cover type richness, if a small number of cover types dominate the first landscape, while the cover types are of similar

Box 1 Creating a map of functional cover types

A *landscape* consists of *patches* identifiable at a given spatial resolution.

To map a landscape of functional cover types, we consider the resource needs of each of a representative set of different animal species. Next, we identify the patches that contain these resources. A set of patches that offer the same resources (considering the needs of all exemplar species) is then a functional cover type.

For each species or species group, patches can be of one of three classes:

Dangerous – no resource benefit for the species and there is an active net cost in going into them, such as high predation risk, high thermoregulatory burden or high risk of drowning. Animals avoid them.

Neutral – no resource benefit for the species and there may be a passive cost in going into them, such as lost foraging time, lost breeding opportunities. Animals generally avoid them except they may move through them to go from one resource patch to another.

Beneficial – provide one or more resources for the species; there are usually multiple types for each species or species group. For a bird species, functional patches might provide one or more of: nest sites, summer food, winter roosting, winter foraging, brood-rearing habitat or song posts.

For example, skylarks *Alauda arvensis* (Linn.) on European farmland need seed-producing open fields in winter and insect-producing open fields in summer. These two *beneficial* cover types must be mapped separately because both are needed for this species. Cover types such as intensively grazed grassland and dense arable crops may be *neutral* for skylarks (and can be mapped as a single cover type), whereas woodland and urban areas are probably *dangerous* (and should be mapped as another cover type).

We then combine the cover types across the set of representative species to get an overall map of functional cover types, from which heterogeneity can be measured.

proportions in the second, the second landscape is more heterogeneous than the first (*cover type evenness*). Cover type richness and evenness can be combined into measures of compositional heterogeneity such as the *Shannon index* (e.g. Dorrough *et al.* 2007). Measures of configurational heterogeneity (Fig. 3) include metrics such as *mean patch size*, *edge density*, *large patch dominance*, *interspersal/juxtaposition* and *mean*

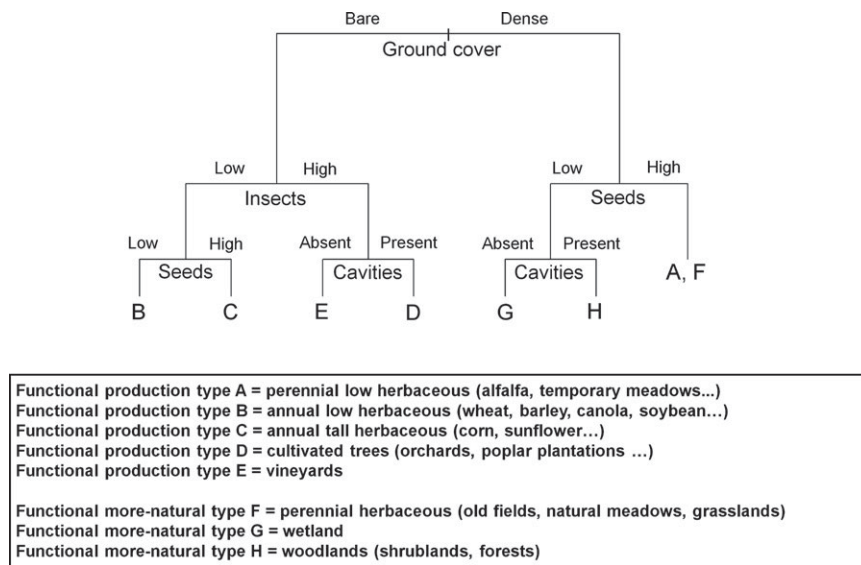


Figure 2 A classification tree of functional cover types according to the nesting (ground cover, nest cavities) or food (insects, seeds) resources provided for birds in agricultural landscapes. In this hypothetical example, each resource is treated as a binary classification variable, but continuous measurements of per-area resource availability could be used in the construction of functional cover types using regression trees.

patch shape variability (Cushman *et al.* 2008). For measures of configurational heterogeneity, the actual cover types are not taken into consideration, just their spatial pattern. For example, landscapes b and d in Fig. 3 have the same configurational heterogeneity but different cover types, and landscape a has larger mean patch size (lower configurational heterogeneity) than landscape b but the same cover types.

QUESTIONS FOR LANDSCAPE HETEROGENEITY–BIODIVERSITY RESEARCH IN AGRICULTURAL SYSTEMS

In this section, we suggest three high-priority research questions in landscape heterogeneity–biodiversity research in agricultural systems. Heterogeneity of both the more-natural and production cover types is central to our thinking, although we recognize that the distinction between these two categories of cover types is not clear-cut. In fact, there is a gradient of cover types in agricultural landscapes, from those where the primary production is almost entirely consumed by humans (e.g. intensively farmed crop fields, intensively grazed lands) to those where almost none of the primary production is consumed by humans (e.g. non-harvested forest patches, hedgerows, most wetlands). However, between these extremes there is a range of cover types with varying degrees of human consumption of the primary production. For example, semi-natural grasslands with low-intensity grazing, and naturally forested areas with livestock grazing or shade

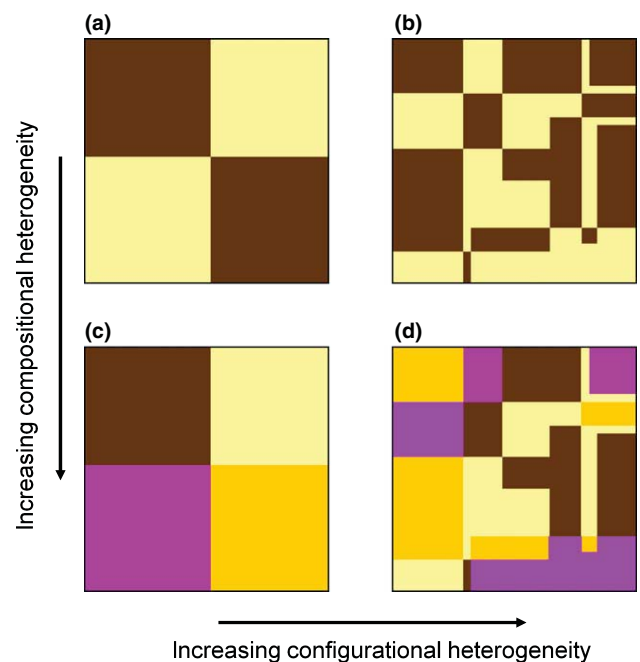


Figure 3 Illustration of the two major axes of spatial heterogeneity: compositional and configurational heterogeneity. Each large square is a landscape and different colours represent different cover types within landscapes. Compositional heterogeneity increases with increasing number and/or evenness of cover types. Configurational heterogeneity increases with increasing complexity of the spatial pattern.

crops in the understory lie somewhere in the middle of the gradient. Even an intensively farmed crop field will provide some food and resources to species other than humans (e.g. insects, some birds), whereas non-harvested woodlots and field margins may provide resources to wildlife species (e.g. deer) that are then hunted and consumed by humans.

Despite this complexity, we consider it important to distinguish between landscape heterogeneity arising from heterogeneity in more-natural cover types rather than in production cover types and *vice versa*. Policies aimed at increasing the heterogeneity of agricultural landscapes through conversion of highly productive lands into more-natural lands, thus reducing agricultural production, will frequently be considered unacceptable by farmers (Burton *et al.* 2008). While it is known that the introduction of such lands can benefit farmers through improved ecosystem services such as pollination and pest control (Kremen *et al.* 2004; Tschardt *et al.* 2007; Potts *et al.* 2010), converting an area of land from a high-output cover type (production land) to a zero- or low-output cover type has obvious economic impacts on the farmer. Therefore, in practical terms, it is important to understand the degree to which policies aimed at increasing heterogeneity of the production portion of agricultural landscapes will have benefits for biodiversity. The decision of whether to implement policies that take land out of production to increase the amount

of more-natural areas, or to implement policies aimed at increasing the spatial heterogeneity of the production areas, will depend on the benefits (to biodiversity) vs. the costs (to farmers) of the two options. For example, if it turns out that the biodiversity benefits of increasing the heterogeneity of the production areas are negligible in comparison to large biodiversity benefits of increasing the area of more-natural cover, policies for biodiversity should mainly be directed at increasing these more-natural areas, even though large economic incentives may be required. The questions we pose below therefore assume that the cover types in an agricultural landscape can be categorized into 'more-natural' and 'production' cover types; exactly how this is done will be context specific.

For the purposes of this discussion, more-natural cover types are defined as areas that meet all of the following three criteria: (1) most primary production is not consumed by humans (either directly or indirectly through livestock feed or grazing), (2) the main species found in the cover type have an evolutionary or long-term association with it and (3) the frequency and intensity of anthropogenic disturbances are low relative to those in annually cropped areas. As extreme examples, grassy field margins that are neither grazed nor mown for fodder would typically be considered more-natural areas, whereas fields or woodlands grazed by domestic animals would be considered production areas,

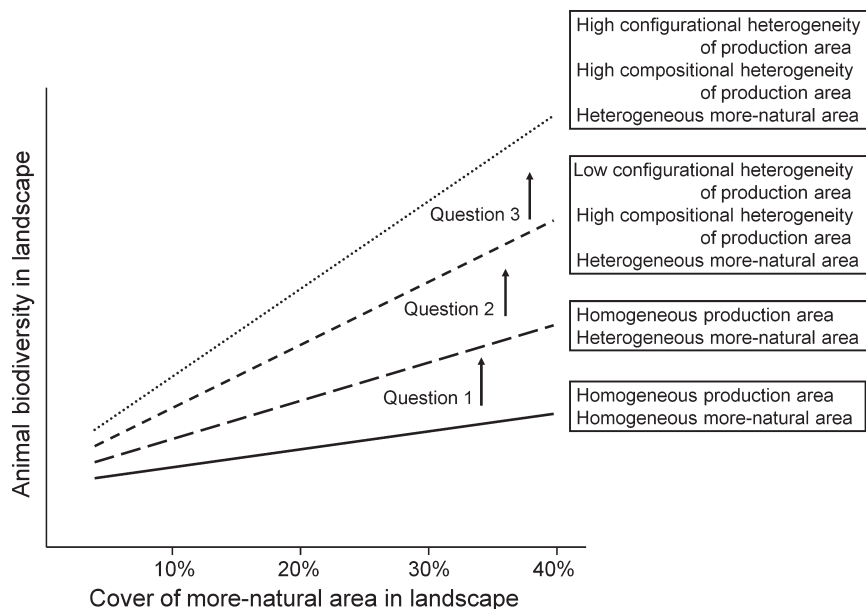


Figure 4 In an agricultural landscape ($\geq 60\%$ of area in production), animal biodiversity increases with increasing area of more-natural (unmanaged or extensively managed) cover in the landscape. We divide heterogeneity of agricultural landscapes into two components: heterogeneity of the more-natural areas within the landscape and heterogeneity of the production areas within the landscape. The three research questions ask, for a given area of more-natural cover, does animal biodiversity increase with (1) increasing heterogeneity of more-natural cover, (2) increasing compositional heterogeneity of the production area and (3) increasing configurational heterogeneity of the production area?

unless the grazing intensity is very low such that most primary production is not taken by the livestock and the main plant species are native. We predict that biodiversity should increase with increasing heterogeneity of both the more-natural cover types and the production cover types (Fig. 4). However, as mentioned above, it is important to consider these components of the landscape separately because the rate of increase in biodiversity with increasing landscape heterogeneity may differ in the two components. In addition, the management of heterogeneity in these two components implies different agri-environment policies and different agricultural and management practices with different economic incentives.

Question 1. Does biodiversity increase with increasing heterogeneity of the more-natural area in the landscape?

Although some research has been conducted on effects of more-natural cover types on biodiversity in agricultural landscapes, for the most-part this work has been limited to studies documenting the effects of the presence and/or amount of these cover types. For example, diversity of butterflies in western France is related to the presence of grassy linear elements (Quin & Burel 2002), and hedgerows and woodland in agricultural landscapes increase the densities of several breeding songbirds (Fuller *et al.* 1997). In landscapes dominated by agriculture, animal species richness increases with increasing proportion of more-

natural area (Aviron *et al.* 2005; Tschardtke *et al.* 2005; Billeter *et al.* 2008). This is probably at least partly due to the stability of these cover types (relative to production cover types; see above) (Millan de la Pena *et al.* 2003) and also to the inability of many species to find their critical resources in the high-production environment.

In addition to the amount of more-natural area in the landscape, the heterogeneity of cover types within this area should increase biodiversity in agricultural landscapes (Devictor & Jiguet 2007). As different more-natural cover types are added to a landscape, biodiversity is expected to increase through an accumulation of species associated with the different cover types. A further increase in biodiversity occurs when there are species whose presence or abundance is enhanced by the occurrence of more than one cover type (Fig. 5). This increase in biodiversity is not necessarily linear, but depends on the responses of the different species to the combination of resources provided by these cover types. This 'added value' of heterogeneity is due to 'landscape complementation' (Dunning *et al.* 1992), in which different cover types are needed (or preferred) at different times in an organism's life cycle, or provide complementary resources, such as food and nest sites, at a particular time. For example, many amphibians need both aquatic and terrestrial habitats at different life stages, hence they are more likely to occur in landscapes containing a mosaic of the two (Pope *et al.* 2000). Increases in configurational heterogeneity of the more-natural cover types may also increase landscape

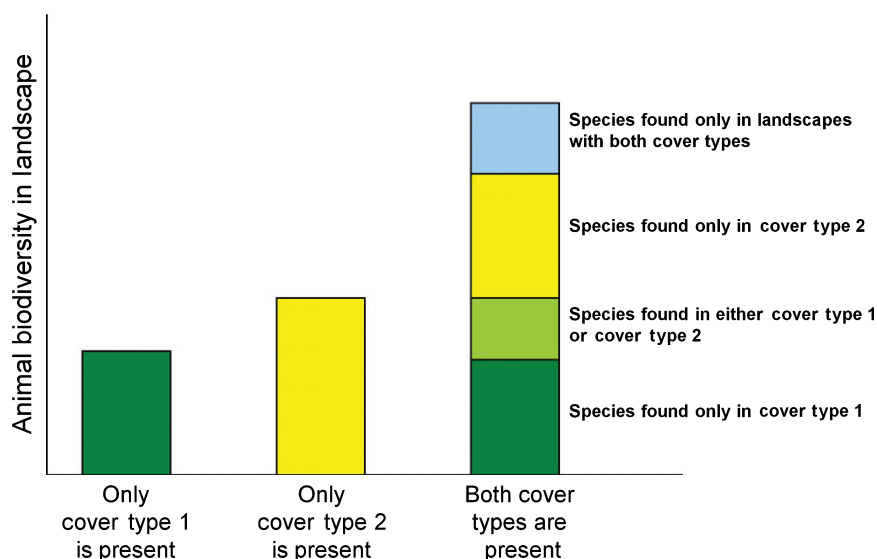


Figure 5 Illustration of the predicted effects of compositional heterogeneity on biodiversity. Animal biodiversity increases with the number of cover types in the landscape, because a subset of species found in each cover type are found only or preferentially in that cover type. Landscapes that contain multiple cover types could have higher overall observed biodiversity than one would predict from simply adding the species associated with each cover type individually. The increase in biodiversity would be due to the presence of species that require the presence of two or more cover types in a landscape (landscape complementation).

complementation (Brotons *et al.* 2004). For example, more complex shapes of patches of different cover types increases interspersed/juxtaposition and the length of boundaries between potentially complementary resources (Fig. 3).

Landscape heterogeneity might also increase biodiversity by influencing the outcome of interspecies interactions. Theory predicts that coexistence of competitors and of apparent competitors and persistence of consumer–resource systems are higher when dispersal rates between patches of the same cover type are reduced, because of reduced cross-patch synchrony in system dynamics (reviewed in Amarasekare 2008). In other words, reduced dispersal rates are predicted to increase metacommunity persistence. As an extension of these predictions, increasing landscape compositional heterogeneity should reduce dispersal rates between patches of the same cover type because with more cover types there will be less of each cover type in the landscape. This could indirectly increase biodiversity through reducing competition and de-coupling patch dynamics across the metacommunity.

It may seem obvious that the greater the diversity of cover types in a landscape, the more species that landscape should contain. However, as mentioned above and noted by Duelli (1997), for a given area of more-natural cover in the landscape, an increase in the number of different cover types leads to a decrease in the amount of each. This should produce a negative effect of compositional heterogeneity on habitat-specialists that have very large territories and/or that need large areas of contiguous or nearly contiguous habitat for population persistence, as they will disappear from landscapes in which the area of their required cover type is inadequate. Depending on the size of the landscape and the species pool under consideration, this could lead to a decrease in biodiversity at high levels of compositional heterogeneity, i.e. to a peak in biodiversity at intermediate levels of compositional heterogeneity.

While both compositional and configurational heterogeneity of the more-natural land covers should affect biodiversity, in practice they are much more difficult to control independently than are the compositional and configurational heterogeneity of the production land covers (see below). For example, wetlands can only occur in locations where the topography permits. In other words, while the farmer can control whether (s)he retains both forest and wetland or just one or the other, thus influencing compositional heterogeneity, (s)he has less flexibility in determining the spatial patterning of these natural elements than the spatial patterning of crop fields and pastures. For this reason, and in contrast to questions 2 and 3 on heterogeneity of the production areas, we do not consider separately the effects of compositional and configurational heterogeneity of the more-natural cover types.

Question 2. Does biodiversity increase with increasing compositional heterogeneity (richness and evenness) of production cover types?

Although there is some evidence that heterogeneity in cropping is correlated with diversity for some taxa and spatial scales (Siriwardena *et al.* 2000; Benton *et al.* 2003), it remains unknown whether increasing heterogeneity of production areas (e.g. by increasing the number of production cover types) in practice can result in significant benefits to biodiversity and how such benefits vary among taxa. Research in this area is complicated by a tendency for landscapes with a more heterogeneous production area to have a larger area of more-natural cover types. This will make interpretation of study results difficult as apparent effects of landscape heterogeneity on biodiversity could actually be due to effects of the amount of more-natural area in the landscape. However, it is important to distinguish these effects because, in agricultural landscapes, the flexibility for manipulating the amount and heterogeneity of more-natural cover types is constrained by the need to devote land to agricultural production. Agri-environment policies for altering the pattern of production cover types (e.g. smaller fields with a higher diversity of crop types; see Fig. 3) may in some situations be more feasible to implement than policies that require taking productive land out of production (or greatly reducing production on it) to increase the amount and heterogeneity of more-natural cover (Burton *et al.* 2008).

Just as different more-natural cover types represent habitats for different species, different crops also provide resources for different species, e.g. nectar for pollinators, cover for dispersal and reproduction by small mammals, plant biomass for phytophagous insects and seeds for birds. This is particularly the case when the production areas have structural similarities to extant natural areas in the same landscape (e.g. cereal crops or improved grassland in landscapes containing remnant steppe or natural grasslands; Wolff *et al.* 2002). Increased compositional heterogeneity of such production cover types should result in higher landscape complementation and perhaps increased persistence of metacommunities (as discussed above), thereby increasing biodiversity. For example, some birds in intensive agricultural landscapes need particular adjacent contrasting land uses to provide different resources needed for breeding (e.g. lapwing *Vanellus vanellus* Linnaeus: Galbraith 1988; Little Bustard *Tetrax tetrax* Linnaeus: Wolff *et al.* 2002).

Question 3. Does biodiversity increase with increasing configurational heterogeneity of production cover types?

Questions 2 and 3 represent the separate effects of the two components of heterogeneity of the production cover types:

compositional and configurational heterogeneity (Fig. 3). Agricultural practices control both of these components. For example, compositional heterogeneity can be increased by increasing the number of different crop types grown, and configurational heterogeneity can be increased by reducing average sizes of fields or cropping areas within fields. Increasing the number of crop types would potentially have associated costs to farmers of changes in infrastructure (e.g. crop storage facilities) and marketing, whereas reducing field sizes or cropping areas may entail costs due to less convenient crop management (e.g. more visits to a given field using smaller equipment). Since the impacts on farming are different, and since it is possible to envision separate agri-environment policies aimed at each of these components of heterogeneity, it is important to know which, if either, component actually has a strong effect on biodiversity. For this reason, we suggest that these two questions should be addressed separately.

We expect configurational heterogeneity (or pattern complexity) of the production cover types to increase biodiversity by increasing landscape complementation, based on the same arguments as for configurational heterogeneity of the more-natural cover types. Smaller field sizes with higher shape complexity will increase the length of border among different kinds of production cover types and among production and more-natural cover types, thus increasing juxtaposition/interspersion and thereby resource accessibility. Note that the caveat regarding patch sizes (leading to a peaked heterogeneity–biodiversity relationship; see above) may not generally apply in the context of production cover types because many species responding positively to the presence and heterogeneity of production cover types may not have evolved in landscapes containing large patches of them. An exception would be species that evolved in steppe (or prairie) landscapes containing very large grassland areas; these species may respond in similar ways to the sizes of cereal fields.

Some preliminary support for the importance of configurational heterogeneity comes from studies of carabid beetles in agricultural landscapes in France. Beetle species richness accumulates more rapidly with total area sampled in fine-grain than in coarse-grain landscapes, even though the total richness and composition of the species pools are the same (Fig. 6). Fine-grain landscapes have smaller field sizes and shorter distances to hedgerows, resulting in greater configurational heterogeneity and higher species richness than in coarse-grain landscapes with similar crop types. Similarly, nesting solitary wasps responded positively to increasing configurational heterogeneity (measured as edge density) in agricultural landscapes in Germany (Holzschuh *et al.* 2010).

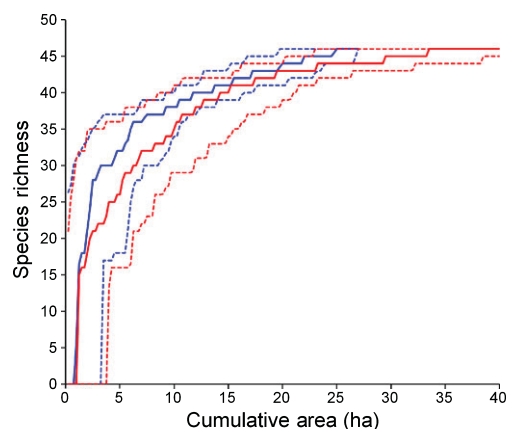


Figure 6 Cumulative species richness of carabid beetles with increasing sampling area in agricultural landscapes in Brittany, France. Fine-grain landscapes (blue lines) have smaller fields and shorter distances to hedgerows resulting in greater configurational heterogeneity than coarse-grain landscapes (red lines). The accumulation of species richness with area differs even though the total species pool is the same. Curves are the median cumulative richness and upper and lower 95% quantiles calculated from different starting positions within a sampling grid of 110–160 cells that were 0.25 ha in size.

METHODOLOGICAL APPROACH FOR STUDIES ON LANDSCAPE HETEROGENEITY–BIODIVERSITY RELATIONSHIPS IN AGRICULTURAL LANDSCAPES

In this section, we outline some criteria and considerations for study design, which will be important in any attempt to answer the questions outlined above. Our purpose in presenting these is to emphasize that the inferential strength obtainable from a study will depend strongly on its design. Given the resources needed for large-scale multi-landscape studies, it is important to maximize the value of the study by optimizing study design to the extent possible.

First, as the questions above deal with gradients in landscape heterogeneity (whether compositional or configurational), any study aimed at answering one or more of these questions will need data from a sample of different landscapes representing a gradient or gradients in heterogeneity (e.g. Devictor & Jiguet 2007; Holzschuh *et al.* 2010). Different data points in statistical analyses will then be data from different landscapes, hence the effective sample size will be the number of landscapes in the study. This means that if the number of sample sites is limited by funding or logistics, researchers should consider increasing the number of landscapes at the expense of the number of sample sites within each landscape. While increasing within-landscape replication contributes to the precision of each data point,

increasing the number of landscapes increases the number of data points and thereby contributes to the primary objective of uncovering the relationships among the variables. Each landscape would then be mapped in terms of its functional cover types (Box 1; Fig. 2), and from these maps measures of heterogeneity for the more-natural cover types and for the production cover types would be obtained.

An important consideration in study design will be to reduce or to avoid frequently occurring correlations among the major heterogeneity variables (Herzog *et al.* 2006). For example, agricultural landscapes with high compositional heterogeneity (e.g. many different crop types) typically have high configurational heterogeneity (e.g. small fields; Fig. 7). Effective agri-environment policies will be aimed at the variables that can be manipulated by farmers individually or collectively, and that actually affect biodiversity, not variables that are typically (though not necessarily) correlated with the causal agents. Therefore, we need to know which components of landscape heterogeneity actually

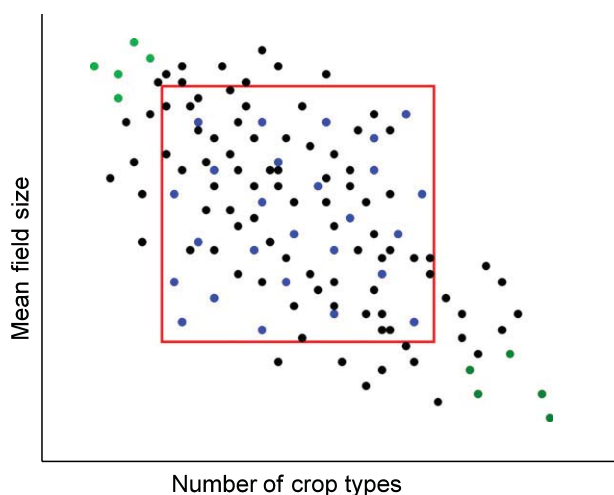


Figure 7 Illustration of the protocol for selecting landscapes for biodiversity sampling, to avoid cross-landscape correlations between compositional heterogeneity (here, increasing number of crop types) and configurational heterogeneity (here, decreasing mean field size). Each point represents a single landscape in an agricultural region. All possible landscapes are shown, from which a subset will be selected for the study (e.g. the blue dots). Across all landscapes there is a correlation between compositional and configurational heterogeneity. To avoid this correlation within the landscapes selected for the study, the selected subset should be selected within the red square, with even representation across the square. Data from these sample landscapes are then used to build statistical models relating biodiversity to compositional and configurational heterogeneity. Biodiversity sampling in a few landscapes at the extreme ends of each heterogeneity gradient (green dots) can then be used to test the robustness of the models to extreme heterogeneity levels.

influence biodiversity and how, which means we need study designs that can estimate independent effects of different heterogeneity variables on biodiversity. This requires a pseudo-experimental approach in which landscapes are not randomly sampled but are sampled specifically to avoid correlations among the predictor variables (e.g. Pope *et al.* 2000; Gabriel *et al.* 2010). For example, using a set of landscapes distributed along independent gradients of landscape structure and agricultural intensification Billeter *et al.* (2008) showed that bird species richness depends on both the proportion of more-natural elements and the total amount of fertilizers ($\text{KgN ha}^{-1} \text{ year}^{-1}$) in the landscape. They would not have been able to separate these effects if they had randomly selected landscapes because the proportion of more-natural elements in the landscape and fertilizer application would likely have been negatively correlated across a randomly selected set of landscapes.

Similarly, studies aimed at simultaneously answering questions 2 and 3 (above) will need to sample landscapes in all four categories of Fig. 3. An effective way to do this is to begin by plotting all possible landscapes on the two heterogeneity axes and then selecting from that distribution a set of sample landscapes such that there is no cross-landscapes correlation between compositional and configurational heterogeneity, while maintaining the maximum possible range of values for both. For example, in Fig. 7, the dots represent all possible landscapes in a region. The blue dots represent a set of possible sample landscapes that have been selected from within the red square, ensuring a nearly even spread over the red square. Within this set of landscapes (blue dots) there is no correlation between the two heterogeneity measures. The final set of selected landscapes should also be chosen to avoid, to the extent possible, any spatial trends or contagion of sites with similar heterogeneity values (Brennan *et al.* 2002; e.g. Carr & Fahrig 2001).

Once the statistical model relating biodiversity to heterogeneity has been built, based on the selected landscapes (e.g. blue dots in Fig. 7), it will be important to also collect information at the extremes of the gradients, i.e. very low and very high values of both compositional and configurational heterogeneity (green dots in Fig. 7). The model based on the blue dots would then be used to predict biodiversity in these extreme cases, to test the validity of extrapolating outside the red area. If it turns out that such extrapolation is not possible, we can conclude that the model has predictive power only for heterogeneity values within the red square; outside the red square we will have information, based on the data at the green dots, but only on effects of heterogeneity in general, not on the effects of the separate components of heterogeneity. This will necessarily result in less confidence when applying policies to alter heterogeneity in landscapes outside the red square. If, on the

other hand, extrapolation from the model is possible, effective policies can be aimed at specific components of heterogeneity.

Several studies have shown that apparent effects of landscape pattern on individual species responses and biodiversity depend strongly on the spatial extent over which the landscape variables are measured (e.g. Thies *et al.* 2003; Dunford & Freemark 2005). Therefore, data collected to answer the questions above will normally need to be analysed using heterogeneity measured at multiple spatial extents. The expected interaction between species biology and the particular heterogeneity variables can sometimes be used to bracket the scales. When the 'correct' scale is not known *a priori* and analyses are to be conducted at multiple scales, to identify the correct scale it is important to select the landscapes such that the heterogeneity variables show a large range of values across landscapes at all spatial extents of interest and that the heterogeneity variables remain uncorrelated across the sampled landscapes. This adds complexity to the site selection process: the site selection approach illustrated in Fig. 7 is applied at each extent and then a set of sample sites that satisfies the requirement for independence at all extents is selected. In practice this entails an iterative process beginning with the scale at which site selection is most constrained (i.e. where the red square in Fig. 7 is smallest).

There are two important considerations in designing a biodiversity sampling strategy across the sample landscapes. First, if the objective of the study is to understand the relationship between landscape heterogeneity and biodiversity in general, biodiversity should be measured for a range of taxa. This is important because different taxa perceive their environment differently, generally leading to weak cross-taxa correlations of biodiversity values, indicating that a single taxon (e.g. birds) is not likely to be representative of biodiversity in general (Wolters *et al.* 2006). Second, biodiversity sample points should be spatially distributed within each landscape to allow diversity estimation at a range of spatial scales, such that diversity can be partitioned into alpha and beta diversity components (Wagner *et al.* 2000; Crist & Veech 2006; Tschardt *et al.* 2007).

A useful starting point in conducting such a study might be to use existing large-scale biodiversity datasets such as those derived from large-scale monitoring programs like the North American Breeding Bird Survey, or the British Breeding Bird and Butterfly surveys. Such datasets provide point-scale data over very broad regions, hence a sub-sample of landscapes could be selected representing uncorrelated gradients in landscape heterogeneity (as in Fig. 7). Targeted supplementary data collection could be used to fill information gaps. Such an approach might be the most cost-effective way of obtaining the necessary large-scale biodiversity data sets. However, this approach will only

be useful if landscape data are available for the same areas as the biodiversity data, with sufficiently fine thematic resolution to measure functional landscape heterogeneity (see also below).

We emphasize that the study design considerations outlined above are presented within the context that, in the real world, trade-offs and compromises will inevitably produce a less-than-optimal study design. Potential sample sites may not exist such that: there are no correlations among the predictors at all spatial extents, heterogeneity levels are perfectly un-clumped in space and there is sufficient replication of landscapes across the heterogeneity axes. However, the 'more optimal' the study design can be made, the stronger the inferences that will come from it, hence we argue that it is important to consider the above issues carefully in advance of selecting sampling sites. Note that a different approach to site selection but with similar objectives – i.e. to avoid correlations among predictors, maximize the range of predictor values and avoid spatial contagion of predictor values – was used by Gabriel *et al.* (2010) in their study of the impacts of organic farming on biodiversity.

DISCUSSION

In the preceding sections, we have proposed a framework for analysing the role of landscape heterogeneity on biodiversity in agricultural landscapes. The study of landscape heterogeneity–biodiversity relationships in production areas is in its infancy, hence it is not yet known whether measures aimed at increasing landscape heterogeneity of these areas will produce large biodiversity benefits. We suggest that the time is ripe for development of a landscape-scale understanding of the relationship between landscape heterogeneity and biodiversity. This understanding should take into account the considerable existing knowledge of species–habitat relationships, as encapsulated in our proposed framework for mapping functional cover types (Box 1; Fig. 2), from which measures of functional landscape heterogeneity can be derived.

Developing these functional land cover maps will be an important challenge in conducting the proposed research. Most landscape mapping techniques rely on remote sensing which frequently will not provide sufficiently fine-grained distinctions among habitat elements that provide different resources to given species groups. However, this problem is diminishing due to the availability of newer, higher resolution landscape data, which can be combined with detailed information on crops and farming systems that are available from agricultural census data in many regions. Ground-based information, including information from farmers and other land-holders will also frequently be needed, particularly for information on agricultural practices

(e.g. pesticide application). Given the scale of analysis needed – probably *c.* 40–60 landscapes, each up to *c.* 4 km in diameter (e.g. Thies *et al.* 2003) – collecting data on land use at the level of detail needed will be an intensive but feasible undertaking. Deriving the functional cover types also depends on the availability of sufficient knowledge of the ecology of the species and species groups of interest. We suggest (see Box 1) a pragmatic approach of using species selected as indicators of groups of species with similar resource needs, but we acknowledge that the efficacy of this approach is far from certain (Cushman *et al.* 2010).

It is also important to note that the requirement for functionally defined cover types is based on the assumption that functional landscape heterogeneity will predict biodiversity better than structural landscape heterogeneity. The careful testing of this assumption would be, in itself, an important contribution of future studies. It is known that a more detailed landscape description does not necessarily produce more accurate predictions. For example, Bailey *et al.* (2007) found that a thematic resolution of 14 cover classes produced statistical models with stronger relationships to farmland biodiversity than statistical models based on a thematic resolution of 47 cover types. However, it should also be noted that a map of functional cover types could well be simpler than one of structural cover types, as physical variation that is irrelevant to the focal species or species group would be ignored in the former. In any case, an important research objective is to test the assumption that the additional resolution of defining heterogeneity in terms of functional cover types provides better predictability of biodiversity than simply using maps based on remotely sensed imagery without reference to species resource needs.

To determine whether there are general answers to the three research questions (above), it will be necessary to conduct replicate studies in very different agricultural regions, containing different species pools. This will identify the findings that can be generalized and those that require specific consideration of local conditions. For example, in some areas, policies can influence mainly more-natural habitats, whereas in other areas policies can only target production land. The landscape extent and grain that are amenable to modification by management and policy will also be constrained by local farming systems. Each such study would require commitments of funds and personnel, and conducting multiple studies in different regions would require a co-ordinated international effort to maximize the scientific and practical output. However, comparable large-scale datasets and agri-environment schemes exist in many different countries, potentially providing the seeds for such projects to be sown. Also, carefully chosen indicator taxa could reduce costs of field work to attainable levels.

In addition to policy implications, the knowledge gained through such studies will be an important contribution to

basic ecology. Of particular interest are the possible counteracting effects of landscape heterogeneity and habitat fragmentation. Increases in configurational heterogeneity tend to fragment habitat (see Fig. 3), such that large continuous expanses of habitat are broken into smaller patches (Fahrig & Nuttle 2005). A review of empirical studies of species responses to habitat fragmentation, while controlling for habitat amount (i.e. fragmentation *per se*), revealed nearly equal numbers of positive and negative responses to fragmentation (Fahrig 2003). One possible explanation for the positive responses to fragmentation is that they actually represent positive responses to configurational landscape heterogeneity through increased landscape complementation. Negative effects of fragmentation may be due to negative edge effects, minimum patch size requirements and loss of connectivity (Ouin *et al.* 2000; Baudry *et al.* 2003; Aviron *et al.* 2007). In addition, whether changes have positive or negative effects may depend on the nature of the initial habitat: increasing heterogeneity in a heavily modified habitat like intensive farmland is different from doing so in swathes of pristine habitat like primary forest. We therefore propose an ‘intermediate heterogeneity hypothesis’ in which increasing heterogeneity will positively affect biodiversity up to some point but when edge density becomes very high and patch sizes very small, the negative effects of fragmentation may outweigh the positive effects of heterogeneity, resulting in biodiversity declines (cf. Duelli 1997; Tscharntke *et al.* 2005).

We also note that biodiversity at a regional scale may not be maximized if the same target for heterogeneity is applied to all landscapes within the region. Such uniform targets could lead to ‘second order’ homogeneity caused by a lack of extremely large homogeneous patches (larger than a single landscape) which may be essential to some species. It may therefore be important to apply a heterogeneity of management targets to ensure a diversity of landscapes.

Our approach to functional landscape heterogeneity is focused on animal biodiversity, but many of the same principles could be applied to analysis of plant biodiversity. For plants, functional landscape heterogeneity might be based on how different cover types act as filters on plant species assemblages based on dispersal ability, response to disturbance or other plant traits that are favoured in different habitat types (Wagner *et al.* 2000; Flynn *et al.* 2009). We might also expect spill-over or mass effects to be especially common for plant species distributions along boundaries between crop or management types (Kunin 1998). In intensively managed crops with high levels of chemical inputs, within-field diversity is often very low and landscape-level plant diversity is largely due to species found in more-natural areas (Flynn *et al.* 2009).

What is the appropriate ‘target’ for biodiversity in farmland? Agriculture is meant for production of resources

for humans, and the market leads agriculture policies and actions. Therefore, agricultural systems are ever-changing because societal needs change. We suggest that it is not appropriate to compare biodiversity in such landscapes to what was there at some arbitrary point in the past or to landscapes without humans. Instead, agri-environment policy should aim to enhance biodiversity to the extent possible while still providing agricultural products for human consumption. Given the dynamic nature of cropped land and the uncertainties that inevitably surround its management, key policy elements should on one hand encourage agricultural practices that maximize biodiversity instead of minimizing it and on the other hand favour restoration and continuity of high quality more-natural habitats as part of the agricultural mosaic (Rey Benayas *et al.* 2008).

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