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# Birds and Habitat

## Relationships in Changing Landscapes

Edited by
**Robert J. Fuller**

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## Relationships in Changing Landscapes

Edited by

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## CHAPTER SEVEN

# The importance of habitat heterogeneity at multiple scales for birds in European agricultural landscapes

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Farmland throughout the world is frequently likened to a mosaic or patchwork and this heterogeneity is widely recognised as strongly influencing the abundance and diversity of species that these landscapes support. Globally, modern intensive agriculture has greatly reduced this 'patchiness' at a range of spatial and temporal scales. This change has been particularly well documented in temperate Europe (Benton *et al.*, 2003; Báldi *et al.*, 2005; Roschewitz *et al.*, 2005; Wretenberg *et al.*, 2006; Stoate *et al.*, 2009). The fine-grained, diverse habitat mosaic, typical of much 'traditional agriculture', has become increasingly uniform under modern agricultural management. This reduction in habitat complexity has been linked, at least in part, to declines in farmland biodiversity, including plants and invertebrates (Smart *et al.*, 2000; Sotherton and Self, 2000; Oliver *et al.*, 2010), mammals (Smith *et al.*, 2005) and birds (Donald *et al.*, 2001a; Benton *et al.*, 2003; Wilson *et al.*, 2005).

In general, the more habitat elements a farmed landscape contains, the wider the range of resources on offer and the higher the diversity and abundance of organisms supported. This may be due, in part, simply to the increased likelihood of a given farmed landscape containing a key habitat type (Heikkinen *et al.*, 2004). However, many species require a diversity of resources to complete their life cycle. At its most basic, birds require two essential resources: a suitable nest site and sufficient food throughout the year. These basic nesting and foraging requirements often vary within and between seasons. Bird-rich farmland should provide safe foraging habitats, offering abundant and accessible food in relatively close proximity to suitable cover for nesting and/or protection from predators or harsh weather. The extent to which farmland birds require a diverse landscape matrix, containing

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both semi-natural and cultivated habitat components, is illustrated by many examples in the following sections.

This chapter focuses on the importance of heterogeneity in the context of the requirements of individual species, rather than farmland bird communities as a whole. We demonstrate that avian life histories, even the simplest ones, require access to a broad range of resources over spatial and temporal gradients and we show how this is more likely to be delivered by a heterogeneous than a homogeneous landscape. Since this heterogeneity is scale-dependent, we examine bird requirements for, and responses to, heterogeneity at three scales: within fields (e.g. swards), between fields or at the farm scale (in cropped and non-cropped habitats), and at the landscape scale (between farms). We then briefly consider some approaches that could restore heterogeneity in areas where it has been reduced by intensive agriculture and the ways in which such restoration may benefit wider biodiversity and some key ecosystem services.

There are several caveats that should be made at the outset. First, we provide a broad overview of the importance of heterogeneity at different scales, rather than a comprehensive review. Second, the text has a temperate and lowland northwest European bias, since this is where the majority of the work has been undertaken and these are the systems with which we are most familiar. We acknowledge that patterns and processes may not be generic across all regions, particularly between the more intensively managed landscapes of northwest Europe and those of south and east Europe (Reif *et al.*, 2008; Erdös *et al.*, 2009; Stoate *et al.*, 2009; Batáry *et al.*, 2011a). Third, the distinctions between field, farm and landscape scale are not always clear cut, particularly at the farm and landscape scales. The issue of scale is further complicated by the fact that, while quantifying environmental heterogeneity depends on the scale of measurement, an organism's response to it actually depends on its perception of the environment, something that remains poorly understood and will vary between species (Wiens, 1989).

## Heterogeneity within fields

A common impact of agricultural intensification is a marked reduction in variation in grass and arable crop structure within and between fields (Tallowin *et al.*, 2005; Wilson *et al.*, 2005). Drainage, mechanised uniform sowing, intense agro-chemical use, efficient harvesting and increases in grazing and cutting intensity all tend to result in greater structural simplification and/or increasing sward density. There are two key sets of interactions in the way that crop structure affects birds. First, the interaction between the extent to which a sward provides concealment from predators and the extent to which it impacts on the detection of these predators; this applies to both foraging and nesting. Second, for foraging birds there is also an interaction between the extent to which the sward structure affects the abundance or diversity of prey and the accessibility of those prey (Wilson *et al.*, 2005; Schaub *et al.*, 2010). From a mechanistic perspective, there are also two parallel processes with respect to the effects of vegetation heterogeneity, namely whether they have functional or ecological significance. For example, dense swards may be needed to support invertebrate prey that only become accessible to birds when they move to more open areas (ecological significance). For some species, however, open sparse vegetation may be uniformly 'better' or preferred than tall dense vegetation, and heterogeneity is then only important insofar as the preferred habitat becomes scarce in the landscape (functional significance). We consider these interactions and mechanisms illustrated by a number of species-specific examples.

## Sward heterogeneity and foraging success

Heterogeneity in sward structure within fields, caused by factors such as differential seed set or plant growth, or variation in management regimes, can result in patchiness in abundance, visibility and/or accessibility of potential prey (Vickery *et al.*, 2001; Morris *et al.*, 2002). The structure of the vegetation affects foraging efficiency directly, through physical obstruction and its impact on the detectability and accessibility of prey, and indirectly through its impact on the trade-off between time allocated to feeding versus vigilance for predators. In general, food abundance is highest, accessibility lowest and predator detection poorest in structurally complex swards that are rich in plant species.

Within cereal crops, several species feeding on ground- or sward-dwelling invertebrates select short, sparse patches within the sward, often directing foraging towards tram lines (e.g. yellowhammers *Emberiza citrinella*: Morris *et al.*, 2002; Douglas *et al.*, 2009; and skylarks *Alauda arvensis*: Odderskær *et al.*, 1997; Schön, 1999). Douglas *et al.* (2009) showed that *c.* 87% of foraging sites for yellowhammers were along tram lines which, given that these account for a very small field area, suggests dense cereal swards offer poor foraging habitat. In the case of skylarks, several studies have shown positive effects of small patches of short swards or bare ground within fields, perhaps because these allow access to prey in the otherwise taller vegetation (Odderskær *et al.*, 1997; Schön, 1999; Buckingham, 2001). The creation of undrilled open patches within a cereal sward was developed as an agri-environment scheme option to enhance late-season foraging (and hence nesting) opportunities for skylarks in winter cereals in several countries (Morris *et al.*, 2004; Fischer *et al.*, 2009). In the absence of these undrilled patches, late-breeding pairs are forced to forage outside the nest field, increasing the energetic costs and decreasing reproductive success (Fig. 7.1). For birds foraging within cereal stubbles in winter, areas of bare ground facilitate access to seeds. Indeed, a preference shown by a number of granivorous birds for barley over wheat stubbles has been attributed to a combination of higher weed seed abundance and more bare ground, enhancing accessibility of

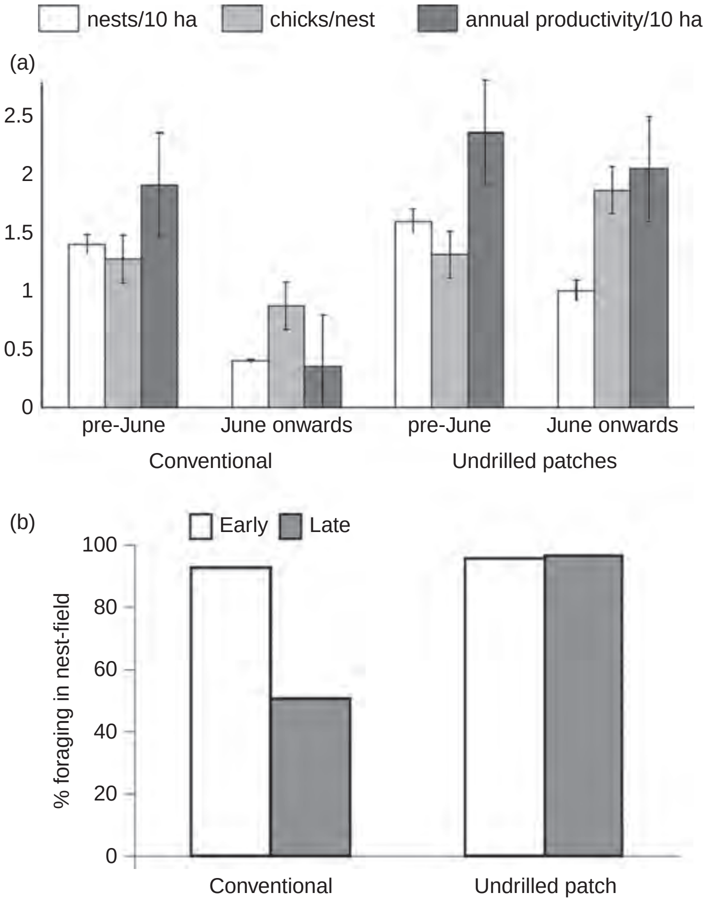

**Figure 7.1** (a) Effects of undrilled patches on skylark nest density, number of chicks per nest and annual productivity compared to conventional cereal fields in the UK, before June and after June. (b) Foraging activity of skylarks within the field where the nest is located with respect to season and management (undrilled patches vs conventional). In both graphs the positive effects of undrilled patches are particularly marked later in the season when the cereal sward is very dense, impeding access to key food sources. Based on unpublished data provided by Tony Morris; see further details in Morris *et al.* (2004).

seeds (Moorcroft *et al.*, 2002). Differences in anti-predation strategies also affect stubble use by different species. Starling *Sturnus vulgaris* and blackbird *Turdus merula* prefer shorter stubble, where the need for vigilance is less and so foraging more efficient. In contrast, skylarks, grey partridges *Perdix perdix* and meadow pipits *Anthus pratensis*, that tend to rely on camouflage rather than early detection of predators, prefer plots with taller stubble. It is possible, however, that stubbles varying locally in height and density provide better overall cover and camouflage for most species regardless of their anti-predation strategies (Whittingham *et al.*, 2006).

Within grasslands, heterogeneity is probably most important for species that obtain food from within the sward itself, such as larks, finches and buntings. Relatively tall heterogeneous swards support abundant invertebrates and seeds but these are mostly accessible only from patches of bare ground (Perkins *et al.*, 2000; Buckingham *et al.*, 2006; Menz *et al.*, 2009a; Martinez *et al.*, 2010; Schaub *et al.*, 2010). The importance of providing so-called 'kitchen dining room' swards for ground and foliar foraging passerines is well accepted in both grassland and arable contexts (Odderskær *et al.*, 1997; Whittingham and Markland, 2002; Bradbury and Bradter, 2004; Devereux *et al.*, 2004; Hoste-Danylow *et al.*, 2010; Schaub *et al.*, 2010; Arlettaz *et al.*, 2012). Two experimental studies demonstrate well the effect of food accessibility mediated by vegetation height. Douglas *et al.* (2009) found that the attractiveness of field margins to foraging yellowhammers could be increased by cutting patches within them, which rendered insect food more 'accessible' than was the case in uncut margins. The relative use of the cut margins by foraging birds was especially high in late summer when the uncut sward was tall and dense elsewhere. An experiment with captive redstarts *Phoenicurus phoenicurus* showed preferential hunting in short swards with bare ground, even if the adjacent high sward offered much more insect prey (Martinez *et al.*, 2010). The results of these experiments probably apply to a number of birds that feed on foliar or surface-dwelling invertebrates (e.g. Douglas *et al.*, 2009).

Radio-tracking studies in fruit-tree plantations, orchards and vineyards in continental Europe on insectivorous species such as hoopoes *Upupa epops* and wrynecks *Jynx torquilla* also suggest a preference for a mix of vegetation and bare ground (Tagmann-Ioset *et al.*, 2012, Fig. 7.2). The latter enhances prey accessibility for terrestrially foraging species such as the hoopoe (Arlettaz *et al.*, 2010b) and may also increase prey detectability for wrynecks and redstarts hunting visually from perches (Schaub *et al.*, 2010; Weisshaupt *et al.*, 2011). Similarly, woodlarks *Lullula arborea* foraging in vineyards prefer sites with around 55% vegetation cover at the foraging site scale (Arlettaz *et al.*, 2012). The common practice of removing grass, chemically or mechanically, along every second tree or vine row provides an ideal mix in which the grassy rows provide a good food supply, whilst bare rows ensure prey accessibility (Sierro and Arlettaz, 2003; Schaub *et al.*, 2010, Fig. 7.3).

Several studies have demonstrated a preference for set-aside or fallow-land equivalents, such as sown or naturally regenerated wildflower areas, over a range of other crop types in winter and summer. Species such as stonechat *Saxicola torquatus*, whitethroat *Sylvia communis* and corn bunting *Emberiza calandra* thrive in Swiss agricultural matrices revitalised with a network of wildflower areas (Birrer *et al.*, 2007; Revaz *et al.*, 2008). These essentially

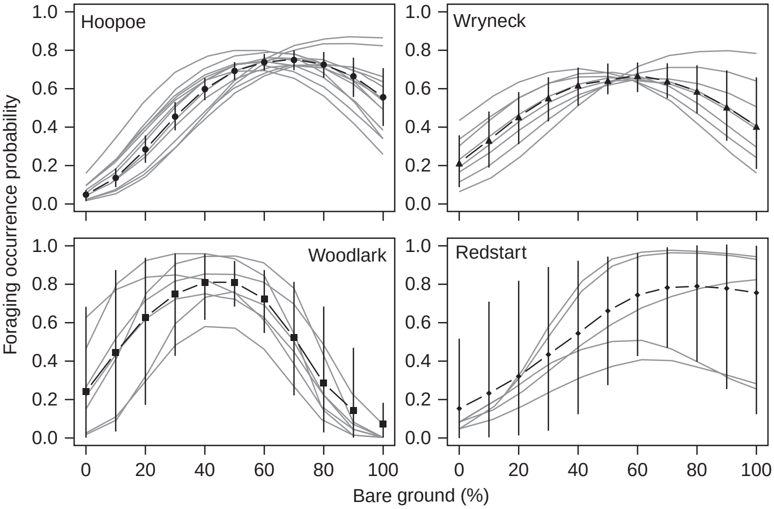

**Figure 7.2** Probability of occurrence of foraging hoopoe, wryneck (both in fruit-tree plantations), woodlark (vineyards) and redstart (orchards) with respect to the availability of bare ground at the site scale, i.e. foraging location (obtained from radio-tracking data). All data are from study sites in Switzerland. The bold curve shows the marginal (i.e. mean specific) value, the thin curves the individual responses. Adapted from Schaub *et al.* (2010).

uncultivated fallows support abundant plant and invertebrate resources (Revaz *et al.*, 2008). They may also enhance nesting opportunities, at least in part, because the patchiness of the sward (e.g. Wilson *et al.*, 2005) increases accessibility of prey and/or concealment from predators. This is supported by the fact that preferences are particularly marked for rotational rather than non-rotational set-aside, and younger rather than older non-rotational set-aside; both preferences being for the more heterogeneous sward (Henderson *et al.*, 2000a, 2000b). Similarly, within set-aside several species prefer a mixture of bare ground and vegetation. The abundance of granivores, for example, peaks at around 17% bare ground, whilst gamebird abundance peaks at around 40% at the foraging-site scale (Henderson and Evans, 2000; Henderson *et al.*, 2001). Interestingly, the abundance of skylarks in other non-cropped habitats, such as wildflower strips and fallow land, peaks at similar levels of percentage bare ground to those observed in set-aside (Wakeham-Dawson and Aebischer, 1998; Toepfer and Stubbe, 2001).

## Sward heterogeneity and nesting success of ground-breeding birds

The risk of failure for a nest within ground vegetation is determined by a trade-off between the extent to which the site protects it from adverse

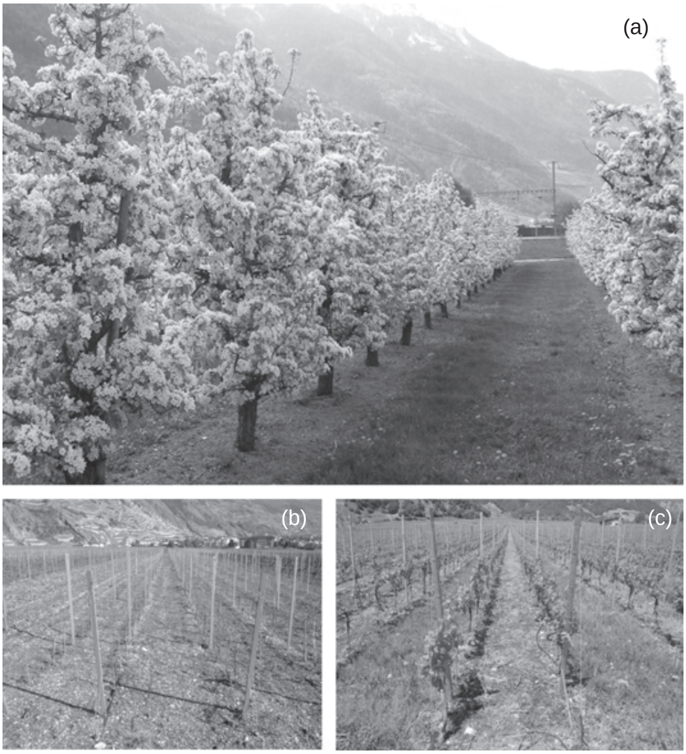

**Figure 7.3** 'Kitchen–dining room' configurations in different habitat types which favour terrestrially foraging farmland birds (Valais, southwestern Switzerland). (a) Fruit-tree plantations with herbicide application (or mechanical removal of grass, not illustrated as this is rare) at the foot of tree rows: typical habitat of wryneck and hoopoe; (b) conventional vineyards with a mineral appearance (systematic application of herbicides over the whole surface) and (c) novel management practices with chemical removal of grass every second row, which provides ideal foraging conditions for woodlark. Photos: Raphaël Arlettaz and Antoine Sierro.

weather or visually hunting predators, and the extent to which it obscures the view afforded to the parent birds on the nest (Wilson *et al.*, 2005). The outcome of this trade-off differs between species. Those, such as gamebirds, that rely on avoiding detection by predators often nest (and forage) in dense vegetation. However, species like lapwings *Vanellus vanellus* and stone-curlews *Burhinus oedicnemus* that rely on early detection of predators require open ground. In some cases the uniformity of vegetation cover might, in itself, make nests or birds more conspicuous to predators perhaps by reducing the effectiveness of camouflage (Baines, 1990). The preference shown by little bustard *Tetrax tetrax* females for set-aside as nesting habitat has, for example, been attributed to structural heterogeneity, which affords better concealment from predators (Salamolard and Moreau, 1999). Similarly, the preference of lapwings for nesting in short patchy vegetation or bare ground may be because this background increases the crypticity of nests (Galbraith, 1988; Wilson *et al.*, 2001; Sheldon *et al.*, 2005).

To summarise, sward heterogeneity can enhance foraging and nesting success for a range of species. In the case of foraging this tends to be because the structural complexity has an ecological function, namely the provision of so-called 'kitchen and dining room' swards. When nesting, species tend to prefer either tall/closed or short/open swards, depending on their predator avoidance strategy, but a heterogeneous sward may enhance crypticity or camouflage.

### Between-field or farm-scale heterogeneity

Between-field heterogeneity arises mainly as a result of differences in the cropped habitat types within fields and the presence of non-cropped boundary habitats such as margins, ditches and hedgerows between them. Here we focus on the availability of different boundary features and crops. Because these differences also account largely for heterogeneity at the landscape scale, in this section we consider the particular value of these components occurring in close proximity, often the within-territory scale and usually of no more than a few hectares.

## Heterogeneity at the farm scale: non-cropped boundary habitats

The overall value of features such as hedgerows, field margins, ditches and banks for farmland birds is well recognised. The composition of these uncropped, rather than cropped, habitats often has the largest effect on bird species composition and abundance in farmed landscapes (Fuller *et al.*, 1997). They are important nesting and foraging habitats (Macdonald and Johnson, 1995; Jobin *et al.*, 2001; Batáry *et al.*, 2007), providing cover and rich invertebrate prey (Maudsley, 2000) and plant food (seeds, fruits and berries) (Snow and Snow, 1988; Moorcroft *et al.*, 1997). They may also have a role in providing dispersal routes for birds (Hinsley and Bellamy, 2000) and insects (Joyce *et al.*, 1999).

Numerous declining farmland bird species benefit from sympathetic management of hedgerows and field margins (Rands and Sotherton, 1987; Bradbury and Stoate, 2000; Birrer *et al.*, 2007; Brambilla *et al.*, 2007; Vickery *et al.*, 2009). Heterogeneity within boundary features can also enhance resource provision for birds. For example, variation in hedge management and structure can enhance bird species richness and abundance (Parish *et al.*, 1994, 1995; Fuller *et al.*, 2001), and nest concealment and survival (Evans, 2004). Furthermore, where a boundary comprises a hedge and an uncultivated margin in combination, the abundance of plant and invertebrate food for birds is often higher in both, with positive effects on the abundance of passerines such as the yellowhammer (Bradbury and Stoate, 2000; Vickery *et al.*, 2009). Hedgerows and margins may also enhance weeds and/or invertebrate food resources within adjacent fields and/or enable birds favouring concealment to forage close to cover (Moorcroft *et al.*, 1997; Vickery *et al.*, 2002). Experiments have shown that local skylark density can be increased in homogeneous high-intensity farmland by introducing set-aside strips or margins, coupled with extensively managed meadows (Weibel *et al.*, 2001; Jenny *et al.*, 2002).

As well as their intrinsic value, boundary features often help birds to exploit food resources in adjacent crops. Many hedgerow nesting species are limited to foraging in crops within 500 m of the nest site (e.g. grey partridge – Green, 1984; tree sparrow *Passer montanus* – Field and Anderson, 2004; red-backed shrike *Lanius collurio* – Brambilla *et al.*, 2007; yellowhammer – Douglas *et al.*, 2009). Grey and red-legged partridge *Alectoris rufa* require hedgerows with good base vegetation in which to nest and nearby weedy cereal crops as foraging habitat (Rands, 1985). The length of permanent field boundary correlates closely with breeding densities and abundance of these species (Rands, 1986; Vargas *et al.*, 2006). Similarly, turtle doves *Streptopelia turtur* require large mature hedges for nesting close to weed-rich habitats for foraging (Browne *et al.*, 2004), and the abundance of yellowhammers also increases with increasing length of hedgerows with herbaceous basal vegetation (Stoate *et al.*, 1998). Red-backed shrikes in mixed grassland and arable land avoid both totally open areas (characteristic of modern agricultural management) and abandoned farmland where forest has encroached (a widespread situation in some European mountainous areas). The optimum appears to be around 15–35% of area covered by hedges and bushes within their breeding territories, a mix often found in low-intensity farmland (Brambilla *et al.*, 2007, 2010). Less commonly, the crop may be the nesting habitat and the margin the foraging habitat. For example yellow wagtails *Motacilla flava* and corn buntings in arable landscapes nest in crops, but may forage on emergent insects from water-filled boundary ditches (Anderson *et al.*, 2002; Bradbury and Bradter, 2004; Gilroy *et al.*, 2009) or in grass field margins, respectively (Brickle *et al.*, 2000), which may be a consequence of low food supply in crops with heavy chemical inputs.

Hedges and margins close to crops also facilitate hunting for some birds of prey. For example, in Switzerland, freshly mown grassland adjacent to wildflower strips provides preferred hunting habitat for kestrels *Falco tinnunculus* and long-eared owls *Asio otus*, possibly because voles from these strips invade the more open grassland where they become easy prey (Aschwanden *et al.*, 2005), though a similar effect is not evident for barn owls *Tyto alba* (Arlettaz *et al.*, 2010c). For woodchat shrikes *Lanius senator* a combination of scattered trees, which serve as nest sites and perches for hunting, and grassland with a heterogeneous sward structure appears to be beneficial (Schaub, 1996). Hedges or isolated boundary trees provide song posts and/or feeding perches for a variety of other species (ortolan bunting *Emberiza hortulana* – Goławski and Dombrowski, 2002; Vepsäläinen *et al.*, 2005; Menz *et al.*, 2009a, 2009b; wryneck – Mermod *et al.*, 2009; roller – *Coracias garrulus:* Avilés and Costillo, 1998; Avilés *et al.*, 2000; red-backed shrike – Brambilla *et al.*, 2007, 2009a).

Farm-scale heterogeneity does not benefit all species. Several avoid tall structures such as hedges and require large open fields, particularly skylark, lapwing and stone-curlew (Donald *et al.*, 2001b; Sheldon, 2002; Sheldon *et al.*, 2004; Batary *et al.*, 2007, 2011a). These species will suffer from encroachment of trees and shrubs, which effectively fragment their habitat (Atauri and de Lucio, 2001; Moreira *et al.*, 2005). This seems to be, at least in part, because such ground-nesters suffer higher predation in or close to field margins, as these act as a source of ground predators or provide perches from which crows, birds of prey or cuckoos *Cuculus canorus* can hunt or prospect (Roskaft *et al.*, 2002; Sheldon *et al.*, 2004; Morris and Gilroy, 2008). Landscapes with diverse crops, but lacking vertical boundary structures, can support exceptionally high skylark densities; landscapes with similar crop diversity, but many hedgerows and trees, carry lower densities (Batary *et al.*, 2011a).

## Heterogeneity at the farm scale: cropped habitats

At the farm scale, a diversity of crops may benefit breeding birds by increasing the range of available foraging and nesting opportunities at any given time, especially as resource requirements may change and/or vegetation and crops develop through the season. The precise mechanisms by which mixed farming benefits species will depend on their ecology and are thus likely to be species-specific (Siriwardena *et al.*, 2000). A number of species require different crop types in close proximity in order to meet different foraging resource requirements throughout the year. Relatively few studies have documented a need for habitat heterogeneity at the farm scale in winter, probably because birds are, generally, more mobile in winter and requirements for different habitats may be met at the landscape scale. Perhaps the most important benefit of between-field heterogeneity in crop type is the provision, in close proximity, of resources required for both breeding and foraging. Lapwings, for example, will use spring cereal as nesting habitat and grassland as chick-foraging habitat. The occupancy of, and productivity in, spring tillage is heavily influenced by its proximity to grassland, with spring till adjacent to grassland significantly more likely to be occupied (Wilson *et al.*, 2001). Furthermore, the fledging success of lapwing broods hatched in spring till is much higher where chicks have direct access to pasture rather than having to cross an intervening field (Galbraith, 1988). The grain of the agricultural matrix may also be important, i.e. the size and number of parcels per unit area. In a wryneck population inhabiting mixed farmland dominated by fruit trees, the occupancy of a given territory over several years depended on the number of cropping units within the territory, demonstrating a positive effect of a fine-grained mosaic (Mermod *et al.*, 2009).

The importance of breeding and foraging resources in close proximity is even greater for species in which foraging or nesting requirements vary within the breeding season. This may result from changes in requirements at different stages of the breeding cycle or because habitats change in their suitability. Vegetation growth can result in some habitats becoming unsuitable late in the season. This is true for the lesser grey shrike *Lanius minor* that hunts large insects on open soil during the early breeding season, but selects mown meadows later in the season, when vegetation elsewhere is tall (Wirtitsch *et al.*, 2001).

Many pairs of skylarks fail to raise a second brood (or late replacement brood) in modern arable monocultures because of a lack of late-nesting habitat. For populations to be self-sustaining, pairs must make two or three nesting attempts per season, but this requires structurally diverse crop mosaics (Wilson *et al.*, 1997). Foraging efficiency, breeding density and productivity of skylarks are enhanced with increasing spatial and seasonal diversity of crops and crop structures (Schläpfer, 1988; Jenny, 1990; Chamberlain *et al.*, 1999, 2000). Yellow wagtails in eastern England may have a similar requirement, because as the breeding season progresses they switch their nesting habitat from winter-sown cereals to crops of potatoes and beans that have a more open structure (Gilroy *et al.*, 2010).

Farm-scale heterogeneity appears to be important to little bustards by providing suitable habitats for the entire courtship period, and habitat diversity is greater around centres of male activity (leks) than at randomly selected sites (Salamolard and Moreau, 1999). Interestingly, for this species seasonal vegetation development may result in a habitat that was originally suitable for displaying subsequently becoming suitable for nesting (Wolff *et al.*, 2002).

In summary, between-field complexity arising from differences between cropped and uncropped habitats, or from the fine-grained structure of the cultivated matrix, can enhance the foraging efficiency and breeding success of farmland birds. In many cases this is because such heterogeneity consistently provides nesting and foraging habitats in close proximity, which is essential where habitats change throughout the season. Where habitats have become homogeneous they frequently support much lower bird densities and, for some passerines, may also be characterised by lower overall reproductive success as a result of reduced numbers of nesting attempts. There are circumstances where heterogeneity is not beneficial, notably for some open-country species where the presence of tall boundary structures can reduce habitat suitability at both farm and landscape scales.

## Landscape-scale heterogeneity

At the landscape scale, habitat heterogeneity affects birds through two main mechanisms. First, the relative quantities of different habitat types, such as woodland and hedgerows, within landscapes has a large effect on the composition and diversity of bird communities (Fuller *et al.*, 1997; Berg, 2002; Winqvist *et al.*, 2011). Second, species with large home ranges or territories may benefit from being able to exploit widely spaced feeding and nesting opportunities. For relatively small farmland birds, factors at the local scale (field or farm) may be generally more important than factors at landscape scales.

Several authors have suggested that landscape-scale heterogeneity has less influence on species abundance than on species richness (Petersen, 1998; Siriwardena *et al.*, 2000; Moreira *et al.*, 2005). Increased species diversity frequently correlates positively with landscape-scale habitat heterogeneity (Preiss *et al.*, 1997; Delgado and Moreira, 2000; Verhulst *et al.*, 2004; Sierro *et al.*, 2009; Winqvist *et al.*, 2011). This pattern seems to be particularly pronounced in winter, perhaps reflecting a shift of some invertebrate feeding species towards mixed landscapes in winter as they become more reliant on grain and weed seed in the winter (Wilson *et al.*, 1996; Atkinson *et al.*, 2002).

Regarding abundance, a British study found that seven farmland bird species increased as the proportion of arable habitat rose in an otherwise largely grassland-dominated matrix (Robinson *et al.*, 2001). However, this relationship was much stronger where arable was scarce in the wider landscape than where arable was relatively common. Similar preferences for complex, heterogeneous habitat matrices have been found in corn and cirl buntings *Emberiza cirlus* in Italy (Brambilla *et al.*, 2008, 2009b). Most of these species showing abundance–heterogeneity relationships at the landscape scale are granivorous. Their distribution is likely to reflect a need for seeds and grain in winter – a sparse resource in grassland landscapes. In a multi-scale analysis of relationships between farmland habitat heterogeneity and abundance of 32 breeding bird species on British farmland, Pickett and Siriwardena (2011) found that, on average, the spatial mixing of land uses, rather than field size or density of boundaries, best explained variation in bird abundance.

The effect of the distribution and size of seed-rich habitat patches on the winter-ranging behaviour and carrying capacity is an important issue for granivorous birds. Experimental provision of seed resources in winter has been shown to positively influence local breeding population trends in several farmland passerines (Siriwardena *et al.*, 2007). Within winter, local yellowhammer populations seem to share resources that are within a radius of 500–1000 m, suggesting this is the scale at which the birds perceive heterogeneity in the winter environment (Siriwardena *et al.*, 2006). However, the details of the effects of resource quantity or configuration within such areas on over-winter survival and, hence, breeding population responses, remain unknown (Siriwardena *et al.*, 2007).

Landscape diversity may also benefit a wide range of species that forage over large areas or have large territories. Swallows and martins use insect-rich features such as hedgerows and waterbodies, often at considerable distances from the nest (Evans *et al.*, 2003). In western France, hoopoes select diverse landscape mosaics, including woods and hedges that provide nest sites, and banks of sand tracks covered with short and sparse grass that offer accessible foraging grounds (Barbaro *et al.*, 2008). In Switzerland, wrynecks inhabit complex mixed farmland landscapes, with patches of bare ground providing high availability of ants adjacent to hedges, and forests offering hollow trees as nest sites (Coudrain *et al.*, 2010). In Poland, differences in the structure of the agricultural landscape explained 79% of the variation in density of grey partridges between study areas. Higher densities were correlated with larger areas of permanent cover without trees, probably because these represent safe and insect-rich foraging sites and hence enhance chick survival (Panek, 1997; Panek and Kamieniarz, 1998). In Spanish pseudosteppe, male little bustards prefer cereal–fallow mosaics within extensive agriculture rather than entirely fallow or entirely cereal landscapes (Morales *et al.*, 2005). Great bustards *Otis tarda* in cereal-steppe in southern Portugal use different habitats throughout the year, with differences in habitat preferences reflecting both changes in food availability and specific habitat requirements for displaying and nesting (Moreira *et al.*, 2004).

Even where habitat structures appear suitable, the nature of the surrounding matrix may be important. For example, the abundance of most farmland bird species breeding on fragments of semi-natural dry pastures in Sweden was generally higher on pastures that were surrounded by agricultural land rather than forest (Söderström and Pärt, 2000). This was attributed to the fact that many of these species forage over large areas and that they were supplementing their food by using the surrounding land. In the Crau area of southern France, the abundance of little bustard is higher where natural steppe habitats occur in close association with extensive agricultural land (Wolff *et al.*, 2001). Similarly, and also in the Crau, the presence of tawny pipit *Anthus campestris*, skylark and calandra lark *Melanocorypha calandra* in natural steppe fragments is affected by the nature of the agricultural landscape in which they are embedded. The majority of individuals occur where native steppe is surrounded by extensive pasture or fallows, rather than intensive agriculture (Brotons *et al.*, 2005).

Barn owls require some degree of landscape heterogeneity, and their habitat preferences vary according to season because agricultural activities impact on the densities and accessibility of small mammals (Tome and Valkama, 2001; Arlettaz *et al.*, 2010c). Lesser kestrels *Falco naumanni* also benefit from a landscape mosaic created by low intensity agriculture. This species feeds mainly on invertebrates (Orthoptera and Coleoptera) as well as small mammals and lizards, usually within 3 km of the colony. Early in the season they use grazed fallow and ploughed fields, but during chick rearing they exploit fields being harvested, as this activity results in a sudden increase in accessible insects (Franco *et al.*, 2004). A patchier landscape mosaic may also favour kestrels because, even in poor vole years, patches with the highest prey density are likely to be closer to the nest in mosaic landscapes than in uniform farmland (Valkama *et al.*, 1995).

A few species feed in different habitats and locations at day and night. Golden plovers *Pluvialis apricaria* and lapwings wintering on arable land in eastern England disperse more widely and visit more habitat types at night than during the day, probably because of variation in prey availability, and predator activity and detectability (Gillings *et al.*, 2005). Nocturnal feeding may be essential for these species to meet their daily energy requirements.

In summary, at the landscape scale, heterogeneity has an especially strong influence on bird community composition and species richness. However, there are many examples of how landscape heterogeneity can affect the abundance and distribution of wide-ranging species by enabling them to exploit local and sometimes temporary food patches.

### Restoring habitat heterogeneity in farmland

Habitat diversity and patchiness, typical under many forms of 'traditional agriculture', has become increasingly uniform and rare in more modern, intensive agricultural management (Donald *et al.*, 2001b; see overview table in Benton *et al.*, 2003). Previous sections highlighted the extent to which habitat heterogeneity, at all scales, is a key feature promoting diversity and abundance of farmland birds. The 'homogenisation' of farmland can consequently have deleterious consequences for farmland bird populations through a range of mechanisms. Large-scale restoration of traditional cultivated landscapes in order to reverse this trend is unrealistic. Agri-environment schemes offer the most widespread 'tools' for increasing habitat variation.

## Agri-environment schemes and field-scale heterogeneity

Few agri-environment options explicitly address the issue of 'sward homogeneity', although general reduction in the intensity of management within grass and arable crops is likely to result in structurally more diverse and plant-species-rich swards. Subsidies for extensification of grassland management, for example, may enhance habitat suitability for foraging and nesting birds by increasing vegetation patchiness. Several European countries have already adopted such schemes. The Swiss scheme specifies that 7% of the area of a farm is devoted to Ecological Compensation Areas (ECAs), a large proportion of which takes the form of extensive (49%) and low-intensity (21%) meadows, respectively (OFAG, 2010). Encouragingly such ECAs not only provide enhanced resources *in situ*, but also lead to higher invertebrate populations in adjacent conventionally cultivated fields (Albrecht *et al.*, 2010). In addition, many terrestrially foraging birds benefit from the presence of patches of bare ground within or close to invertebrate-rich grassy habitats (Fig. 7.2). Targeted removal of grass cover on small areas represents a novel option that is worth testing experimentally.

In arable land, there are also specific options targeted at species like skylark and lapwing to create ‘vegetation gaps’ in crop monocultures to provide food and nest sites. Small, 4 $m^2$ undrilled patches within winter cereals have markedly increased the value of a field for late nesting attempts by skylark (Morris *et al.*, 2004; Fischer *et al.*, 2009; Fig. 7.1). In the case of lapwings, plots of at least 2 ha are similarly left undrilled in winter, but are cultivated in spring. This creates optimal nesting habitat in the form of sparse vegetation cover and, if managed and located appropriately, such fields can support both foraging and nesting birds (Chamberlain *et al.*, 2009). A similar approach has proved extremely successful for stone-curlews which have declined in southern England due both to mechanical destruction of nests in arable habitats and reductions in rabbit grazing that had previously maintained the sparse vegetation used for feeding and nesting. Protection of nests and creation of bare-ground nesting plots in fallow and semi-natural habitats under agri-environment schemes, underpinned the recovery of the species from 139 to 307 pairs between 1990 and 2005 (Green *at al.*, 2000; Wilson *et al.*, 2009).

## Agri-environment schemes and farm-scale heterogeneity

Some agri-environment measures are designed to diversify the number of crop types at the farm scale (e.g. the Swiss scheme requires at least four types of crops per farm, in non-dairy farms larger than 3 ha), others to restore nesting and foraging opportunities. A clear vision is still lacking for optimal spatial arrangement of compositional heterogeneity (crop and cover types) and configurational heterogeneity (complexity of the spatial pattern of fields), though Fahrig *et al.* (2010) provide a framework for progress.

Options for margins and boundaries can be popular with farmers and land owners when the financial incentives are attractive. Creation of small patches of semi-natural habitat such as farm woods, ponds and boundary ditches can greatly improve farm-scale habitat diversity. Changes in the cropped habitats are often more complicated to realise because market conditions remain the main driver of their management, but they are the most valuable approaches for conserving particular bird species (Butler *et al.*, 2007). Two examples follow. The habitat needs for breeding lapwings could be provided through the creation of fields with sparse vegetation, obtained perhaps through shallow cultivation, adjacent to managed meadows (Berg *et al.*, 2002). The combined reduction of rough grass and crop stubble caused the decline of cirl buntings in the UK; these habitats are required for summer and winter foraging, respectively (Evans, 1997). Specific agri-environment measures designed to provide suitably managed grassland for summer foraging and seed-rich winter stubbles in close proximity have been extremely successful in increasing local population density. Between 1992 and 1998 the population on land under these agri-environment measures increased by 83% compared with 2% increases on land outside these agreements (Peach *et al.*, 2001; Wotton *et al.*, 2004).

Within grassland, a mix of fields that differ in sward height and complexity may be achieved by adopting different grazing or cutting management intensities and time schedules in different fields (Atkinson *et al.*, 2005). As for within-field heterogeneity, overall extensification of grassland management will again provide spatial heterogeneity between fields (Buckingham *et al.*, 2004).

## Agri-environment schemes and landscape-scale heterogeneity

The 'local' addition of an arable crop or vineyard to grassland (or vice versa), for example, or a stubble followed by a fallow in cereal landscapes, will create additional and/or complementary foraging resources at a wider scale (Robinson *et al.*, 2001). However, enhancing habitat heterogeneity at a landscape scale through agri-environment measures targeted at individual farmers or land owners is difficult. In effect, birds with large territories that obtain some of their resources from farmland require measures beyond agriculture alone. For example, the density of raptors in open Mediterranean habitats in Spain varies with the nature of the forest–farmland mix. At the landscape scale, the breeding density of short-toed eagle *Circaetus gallicus*, booted eagle *Hieraaetus pennatus* and buzzard *Buteo buteo* tend to increase with forest cover, peaking in density at around 80% in the latter two species. Conservation of these raptors may thus require a regional approach towards habitat mosaics created by forestry and agriculture (Sánchez-Zapata and Calvo, 1999). This is an example of where agri-environment measures would greatly benefit from being integrated, coordinated and planned across sectors. A solution is currently implemented in Switzerland whereby a new policy provides financial incentives, on the top of other subsidies, to groups of farmers who implement local ecological networks under the supervision of agro-ecologists (OFAG, 2010).

For many species, agri-environment measures that encourage traditional low-intensity or extensive farming systems may be the most appropriate way to maintain habitat heterogeneity at a landscape scale. This sort of low intensity mixed farming is at risk of being lost either to agricultural intensification or abandonment (Britschgi *et al.*, 2006). In many marginal areas, it is frequently no longer economically viable, and will only survive with support through agri-environment, social and rural development measures (Woodhouse *et al.*, 2005; Brambilla *et al.*, 2010). The conservation of many steppe birds, such as great bustards, requires a mosaic of habitat types typical of low-profitability rotational crop systems (Moreira *et al.*, 2004). The recent increase in great bustards in Portugal can be attributed almost entirely to the increase at one key site where an agri-environment 'zonal plan' was established in 1995. This promoted a rotational cropping system with dry cereals, fallows and legumes, as well as reduced pesticide use and lower livestock densities (Pinto *et al.*, 2005). These measures have simultaneously benefited lesser kestrels (Franco *et al.*, 2004). For the little bustard in western France, successful schemes are being developed which improve nest survival through mowing constraints and enhance grasshopper abundance as chick food (Bretagnolle *et al.*, 2011).

A recent meta-analysis has established that agri-environment management provides contrasting outcomes for farmland biodiversity, depending on the dominant cultivation system and on landscape context (Batáry *et al.*, 2011b). In cropland, agri-environment measures increase species richness (but not abundance) in simple landscapes, typical of much modern farmland, but not in complex landscapes. In grassland, they enhance both species richness and abundance, irrespective of the landscape context. An example of how the relationships between birds and hedgerow length depend on landscape context is shown in Fig. 7.4 – richness and abundance are only positively affected by hedgerow length in simple landscapes. Concepcion *et al.* (2008) even demonstrated negative effects of agri-environment schemes in complex matrices. It seems, therefore, that agri-environmental measures are most successful when implemented in simple, homogenised farmland.

## Wider benefits of habitat heterogeneity

A fine-grained mosaic within agricultural habitats can deliver additional benefits beyond simply supporting rich farmland bird populations. First, increasing the heterogeneity of farmland will benefit species across a suite of taxonomic groups (Smith *et al.*, 2005; Winqvist *et al.*, 2011). Second, under some circumstances the biodiversity of adjacent habitats may be enriched, for example, through 'positive spillover' of invertebrates (cf. Rand *et al.*, 2006). Third, habitat heterogeneity may improve delivery of environmental services, including pollination, biological control, soil protection and protection of watercourses (Roschewitz *et al.*, 2005; Tscharntke *et al.*, 2005; Arlettaz *et al.*, 2010a; Winqvist *et al.*, 2011). Grass margins provide both nesting and feeding opportunities for birds, but can also act as buffer strips that reduce riparian pollution from diffuse sources by impeding water flow (Bradbury and Kirby, 2006). Similarly, small wetlands provide emergent insects as a source of food for birds and can simultaneously serve as flood regulators, slowing and holding surface water run-off and suspended solids (Bradbury and Kirby, 2006). Vegetating mineral vineyards in hilly landscapes with native herbs every second vine row not only benefits arthropods and birds such as the woodlark, but also helps reduce soil erosion (Arlettaz *et al.*, 2012).

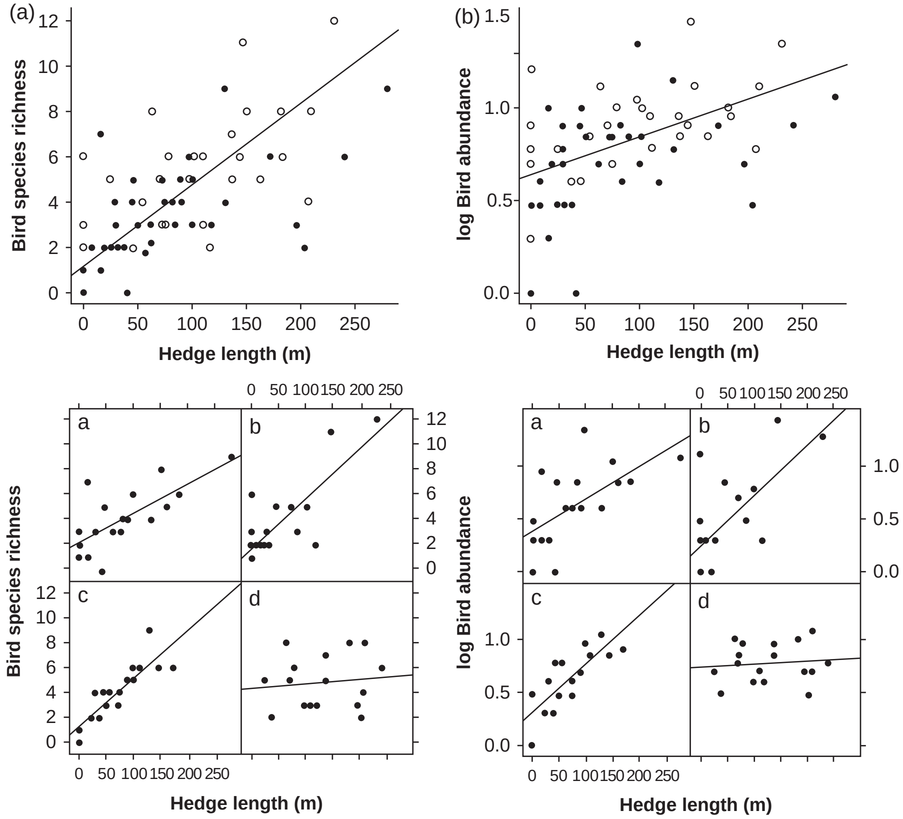

**Figure 7.4** Effects of hedgerow quantity and landscape complexity on bird species richness and abundance as shown by work in Germany. Upper panel: relationship of bird species richness (a) and abundance (b) (log scale) to hedge length in organic (open circles) and conventional (closed circles) meadowland and cereals (line: regression from general linear model); note the absence of a difference in effects between the two farming systems. Lower panel: interaction plot showing the relationships between bird species richness (left) and abundance (right) and hedge length within a 500 m radius of bird point-count locations. These are shown for four different levels of landscape complexity, as measured by the proportion of semi-natural habitats around the points: (a) 0–1.5%; (b) 1.5–4.5%; (c) 4.5–17%; (d) >17%. A positive effect of hedges is only evident when the proportion of semi-natural habitat is low, at less than 17%. From Batáry *et al.* (2010).

Finally, increased heterogeneity in agricultural landscapes may prove increasingly important in the face of climate change. A diversity of habitats throughout the agricultural matrix may allow species, especially those with low mobility, to adapt to climate change by facilitating their spatial movements when they redistribute to track their climate envelope (Donald and Evans, 2006).

## Concluding remarks

Cultivated landscapes have constantly changed due to evolving farming practices, but 'traditional agriculture' has contributed to the creation of a rich habitat mosaic, often associated with high levels of biodiversity. A drive for higher and higher yields has favoured specialisation in farming and the expansion of industrial agriculture. This resulted in a massive loss of habitat heterogeneity at the field, farm and landscape scales, causing a collapse of farmland wildlife. The socio-economic and ecological mechanisms behind these major changes are well documented (Vickery *et al.*, 2001).

Over the last three decades farmland ecologists have gathered an immense knowledge about the fate of wildlife in agro-ecosystems and the basic ecological requirements of plant and animal species occurring in cultivated landscapes. A wealth of scientific evidence, originating mostly from north-west and central Europe, strongly suggests that habitat heterogeneity at multiple scales is required to maintain and enhance the quality of farmland habitats for foraging and nesting birds. Although different habitat–species associations may apply in other regions (Chapter 3), habitat heterogeneity of various kinds appears to serve a crucial set of functions everywhere for most farmland bird species. This has been particularly well documented at the field and farm scales, possibly because this is the scale at which farmland birds operate. Less work has been done, however, in relation to the ideal configuration of agricultural landscapes to promote rich communities of plants and animals. Landscape-scale conservation action is often complicated by the conflicting requirements of different potential target communities. For example, open-field species can be hampered by dense hedge networks that favour several other species. Perhaps there is a need to develop regional goals for farmland biodiversity. Maximising heterogeneity at all scales is not desirable in all contexts (Batáry *et al.*, 2010, 2011a). We need different types of heterogeneity in different places to suit different farmland bird assemblages; a sort of diversity of diversities.

It remains to be seen which kind of financial incentives to farmers may enable agri-environment schemes to promote and sustain a sufficient spatio-temporal habitat heterogeneity for biodiversity. This requires readily-adopted approaches (political and practical) for subsidising farmers that can adapt and respond to constantly changing market conditions in a way that ensures a mix of options are adopted (Drechsler *et al.*, 2007; Cooke *et al.*, 2009). Biologists and agro-economists must work together to design multi-functional agricultural landscapes that are capable of maintaining optimal agricultural yield, basic environmental functions and ecosystem services, and a rich wildlife.

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