Supplementary Electronic Material: Chapter 4

Mechanisms and processes underlying landscape structure effects on bird populations

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Appendix: E4.1 *Landscape structure: terminology, attributes and measurement as applied to two landscape paradigms (dichotomous and heterogeneous)*

DICHOTOMOUS (BINARY): *habitat versus non-habitat e.g. forest/non-forest*	**HETEROGENEOUS LANDSCAPE MOSAIC**: *e.g. mosaics of woods, crops and urban; or mosaics of different forest growth stages*
Composition: extent or amount	
Extent of focal habitat, commonly expressed as percentage of landscape area	**Area of each constituent habitat** – may be absolute or relative. Can quantify as landscape diversity (or equitability), or as ratios of key habitats (e.g. farmland to forest)
Configuration: arrangement of habitat or elements within the landscape	
Patch area for individual habitat patches	**Juxtaposition** – position of habitat elements relative to other habitats
Patch shape the complexity of an individual patch, most easily quantified as edge to area ratio (or less intuitively, as fractal dimension)	**Edge contrast**, for example between forest abutting farmland or abutting shrubland
Patch isolation or **proximity**, may be quantified as the distance to nearest neighbouring patch, or to the nearest large patch exceeding a minimum threshold area, or the amount of potential source habitat within a buffer radius.	**Connectivity** – *Structural connectivity* is solely a physical attribute of landscapes (e.g. measures of continuity of linkage, contagion), independent of species attributes (e.g. gap-crossing ability, dispersal ability). Measures are contingent on measurement scale and resolution. *Functional connectivity* to a particular species depends on dispersal ability and behaviour (e.g. habitat-specific impedance or movement costs), imposed on the arrangement of habitat elements, expressed as a cost surface for movement or network analysis
Landscape grain and **contagion** measure aggregation – the degree of clumping or subdivision of a particular habitat into small parcels. Subdivision may be quantified as mean, SD, or median patch area within a landscape; as percentage of total contained within the largest (or *n* largest) patches; as the fractal measure lacunarity	**Landscape grain** of heterogeneous mosaics, may be measured by indices of contagion that consider increasing subdivision and interspersion (juxtaposition) of land-cover classes or patch types, giving a measure of overall 'clumpiness', or by fractal measures such as lacunarity. Metrics that measure configuration independently of extent, relate observed clumpiness to the maximum possible for the same overall extent and grain size (Langlois *et al*., 2001).

Appendix: E4.2 *Approaches to designing and conducting studies of landscape structure effects*

Many studies take a binary approach, conceptualising a single habitat type (often defined on the basis of suitability for particular species of interest) existing as scattered patches within an inhospitable matrix. 'Focal-patch studies' that take individual patches as the unit of replication have been able to examine responses to patch area or isolation. Distinguishing independent effects of habitat configuration from confounding and intercorrelated effects of extent is often problematic in such studies, as landscapes with greater habitat extent tend also to have larger and less-isolated patches (Askins *et al*., 1987; Trzcinski *et al*., 1999; Villard *et al*., 1999; Austen *et al*., 2001). Stratified sampling according to habitat extent in the surrounding landscape can help in identifying independent effects of configuration (Austen *et al*., 2001; Radford *et al*., 2005; Vergara and Armesto, 2009).

The binary island-matrix concept has limitations (Norton *et al*., 2000; Kupfer *et al*., 2006; Lindenmayer *et al*., 2007). Matrix composition and juxtaposition can influence edge effects, dispersal and colonisation, even for species restricted to habitat islands (Andrén, 1999; Vandermeer and Carvajal, 2001; Schmiegelow and Mönkkönen, 2002; Bennett *et al*., 2006; Kupfer *et al*., 2006). To examine this, patch area, configuration and edge effects have been compared among replicated focal-patch studies set in regional landscapes that differ in mosaic type or habitat extent (Sisk *et al*., 1997; Brotons *et al*., 2003; Watson *et al*., 2005). Not surprisingly, the number of replicate landscapes or contexts is often rather low in such studies (e.g. Andrén, 1992; Åberg *et al*., 1995; Edenius and Sjöberg, 1997; Sisk *et al*., 1997; Austen *et al*., 2001; Watson *et al*., 2005). Furthermore, species that are able to exploit diverse habitats may experience landscapes as a continuous heterogeneous mosaic, rather than as a series of patches set in an inhospitable matrix. Therefore, Bennett *et al*. (2006) advocate treating local landscape mosaics as the unit of sampling.

National bird atlas and monitoring schemes that use grid-based sampling lend themselves well to such analyses, allowing massive replication and stratification by extent or composition (Trzcinski *et al*., 1999; Boulinier *et al*., 2001; Robinson *et al*., 2001). Field studies designed to sample mosaics have used well-replicated grid-based sampling points (Barbaro *et al*., 2007), grid squares (Pino *et al*., 2000; Smith *et al*., 2001), or nested sampling of patches or plots within multiple landscapes that differ in structure or habitat extent (van Dorp and Opdam, 1987; Villard *et al*., 1999; Betts *et al*., 2006). In Chile, Vergara and Armesto (2009) adopted a well-replicated and spatially nested hierarchical design, allowing them to examine the relative strength of, and interactions among, effects at different scales. Sampling replicate landscape mosaics can also be used to examine effects of edge extent or edge density (Villard *et al*., 1999; Barbaro *et al*., 2007) or hedgerow density (Fuller *et al*., 1997), on species incidence or abundance; effects that are difficult to study using a focal patch approach.

Appendix: E4.3A *Patterns of assemblage and species responses to landscape structure, irrespective of underlying mechanisms. For each, key references are given, methodological issues in measurement are identified and the strength of supporting empirical evidence from empirical studies of Mediterranean, temperate and boreal bird species and or assemblages, is summarised. Examples of potential mechanisms underlying these patterns are highlighted in bold. The full range of mechanisms and supporting evidence for these, is summarised in Table 4.2, and detailed in Appendix E4.3B.*

Pattern	Explanation	Evidence
Edge sensitivity	Edge-sensitive (or 'interior') species occur at higher density further from edges, and have lower incidence or lower density in smaller patches. Edge sensitivity can reduce effective (core) patch area. Edge sensitivity as a pattern, may potentially arise through *passive displacement* or through mechanisms of active avoidance due to *reduced edge quality* or *edge truncation*. 'Edge species' occur at higher density at or close to edges, potential mechanisms include: *Edge-exploiters* or *complementing species*, but greater *territory packing* at edges (due to *phenotypic-based territorial compressibility*) can also result in greater density. Patterns of density with respect to edges therefore do not necessarily	*Strong support*: however, responses to edges can be variable, species-specific and context specific. In oak woodlands in California (Sisk *et al*., 1997) and in mixed pine-hardwood forest in Tennessee (Kroodsma, 1984), different species showed either positive (e.g. by *edge-exploiters* or *complementing species*), edge-neutral or -negative (edge sensitivity/edge avoidance) responses (either in terms of registrations or territory densities). Similarly, different shrubland birds in Missouri showed contrasting nest site preferences in relation to distance to edge (Woodward *et al*., 2001). *Edge-avoidance*: In Tennessee, territory mapping identified edge-avoiders (previously recognised as 'forest-interior' species) with effects penetrating > 200 m for ovenbird *Seiurus aurocapillus*. Other edge-sensitive species were Acadian flycatcher *Empidonax virescens* (effects > 60 m) and worm-eating warbler *Helmitheros vermivora* (Kroodsma, 1984). However, after the nesting period, radio-tagged adult male ovenbird were more often located close (< 50 m and < 25 m) to fragment edges than expected by chance, either suggesting post-breeding edge responses differ, or barrier effects and deflection along edges (Bayne and Hobson, 2001). In Iowa, Bobolink *Dolichonyx oryzivorus* density increased with distance from edge. Although territory size was similar at different types of edge, densities were much lower at edges abutting woodland than arable, and territory mapping supported active avoidance at woodland edges (Fletcher and Koford, 2003).

	reflect demographic or fitness effects of edges – and higher density at edges may occur despite lower quality and breeding productivity (Wilkin *et al*., 2007). It is therefore important to examine reproductive parameters. Edge sensitivity potentially underpins much landscape-scale distribution pattern (Andrén, 1994).	*Edge-positive species:* In studies of grassland fragments in North America, incidence of numerous ‘edge species’ was negatively related to area (Herkert, 1994; Vickery *et al*., 1994). In Tennessee, at least three woodland species had higher territory density close to the forest edge (cardinal *Cardinalis cardinalis*, rufous-sided towhee *Pipilo erythrophthalmus* and summer tanager *Piranga rubra*) (Kroodsma, 1984). In Texas higher woodland bird diversity and species abundance was found within 25m of forest edges adjacent to clearcuts (Strelke and Dickson, 1980).
Fine-grain-dependent species	Some *complementing* and *edge-exploiting* species (or edge specialists) have greater incidence or abundance in heterogeneous landscapes that are complex and fine-grained, relative to the scale of their home range or seasonal ranging movement, as such landscapes provide high edge density or juxtaposition of habitats.	*Some support:* For example, probability of buzzard *Buteo buteo* nesting incidence in grid cells within Argyll, Scotland, was positively related to the length of edges, particularly that between pre-thicket-stage forest and open ground (Austin *et al*., 1996)
Area sensitivity: incidence-area	Area-sensitive species were initially defined as those occurring more frequently in larger patches (Freemark and Collins, 1992). Species-specific area incidence is examined by logistic models of	*Strong support* for both forest and grassland birds. Species-specific area incidence is commonly found in woodland assemblages (van Dorp and Opdam, 1987; McCollin, 1993; Cieslak, 1985; Watson *et al*., 2005) particularly woodland specialists or interior species e.g. (Freemark and Collins, 1992; Hinsley *et al*., 1996). For example, in eastern England across 151 small woods (range 0.02–30 ha) most species did not

Appendix: E4.3A (*cont.*)

Pattern	Explanation	Evidence
	probability of incidence relative to area or log area, using data from focal-patch studies. However random placement (distribution of individual pairs randomly in relation to woodland area) may also give a significantly positive incidence-area function, so that observed incidence or abundance should be compared to a null model or use data from plots of standard area within patches of varying size (Coleman, 1981). While area sensitivity may arise due to *minimum area requirements* that relate to biological traits, such as home-range size, it may also result from mechanisms such as *area quality*, or edge-avoidance, for example due to *reduced edge quality* or perceived *nest predation* risk at edges.	conform to random placement either in all three years (seven species) or in at least one of three years (six species) (Hinsley *et al*., 1996). Area-sensitive incidence has commonly been found for grassland and shrubland bird species, in Europe and North America. Numerous North American grassland birds are area sensitive, in Illinois (*n* = 24 prairie fragments, ranging 0.5–600 ha) (Herkert, 1994), Maine (90 dwarf-shrub/grassland patches, 0.3 to 404 ha) (Vickery *et al*., 1994), and Nebraska (45 wet floodplain grasslands, 0.12 to 347 ha) (Helzer and Jelinski, 1999), and across restored northern plains grasslands in Montana, North Dakota, South Dakota and western Minnesota (303 grassland patches) (Johnson and Igl, 2001). Fewer species were found to be area sensitive in Missouri prairie, but in a study that examined a limited number of fragments with high variability in grassland structure (Winter and Faaborg, 1999). Species with greater incidence in larger patches included grasshopper sparrow *Ammodramus savannarum*, Henslow's sparrow *A. henslowii*, Baird's sparrow *A. bairdii*, savannah sparrow *Passerculus sandwichensis*, vesper sparrow *Pooecetes gramineus*, clay-colored sparrow *Spizella pallida*, bobolink, eastern meadowlark *Sturnella magna*, western meadowlark *S. neglecta*, dickcissel *Spiza americana*, sedge wren *Cistothorus platensis*, northern harrier *Circus cyaneus*, greater prairie-chicken *Tympanuchus cupido* and upland sandpiper *Bartramia longicauda*. Species-specific area thresholds differed among the regional grassland types: e.g. grasshopper sparrow reached 50% incidence

		at *c*.10 ha in Nebraska, at 30 ha in Illinois, but only at 100 ha in Maine; while upland sandpiper and bobolink reached 50% incidence at *c*.50 ha in Nebraska but only at 200 ha and *c*.1000 ha in Maine. In Portugal, male little bustard *Tetrax tetrax* only approached 100% occupancy in grassland fields of 100 ha (Silva *et al*., 2010). In complex forest mosaics in south-western France, of the ten open habitat specialists examined (in heathland or young plantations) abundance of eight was positively related to mean patch area, including linnet *Carduelis cannabina*, skylark, red-backed shrike *Lanius collurio*, cirl bunting *Emberiza cirlus*, grasshopper warbler *Locustella naevia*, Dartford warbler *Sylvia undata*, but not common stonechat *Saxicola torquatus* or melodious warbler *Hippolais polyglotta* (Barbaro *et al*., 2007). In the Massif Central, France, tawny pipit *Anthus campestris* and wheatear *Oenanthe oenanthe* showed minimum area thresholds of 7 ha and 23 ha, respectively (Caplat and Fonderflick, 2009).
Area sensitivity: abundance-area	Different species may exhibit either positive or inverse (negative) density–area relationship (Bellamy *et al*., 2000; Bender *et al*., 1998), compared to a null model of random settlement (that predicts abundance is proportional or linearly related to, increasing area).	*Strong support:* Meta-analysis of 12 avian density–area studies (Bender *et al*., 1998) showed that, for forest interior species, migrants had weaker area–density effects than residents, while for edge species, migrants showed stronger (larger magnitude of negative effect) than residents.

Appendix: E4.3A (*cont.*)

Pattern	Explanation	Evidence
Both **inverse and positive density–area effects**	Distinguishing mechanisms underlying abundance–area patterns is challenging. Positive area sensitivity resulting from preference for larger patches, is most likely due to: *area quality*, edge-avoidance, or potentially *conspecific attraction* or *heterospecific attraction*. Inverse area sensitivity may occur through preferential settlement in small patches or near patch edges by *edge-exploiting* or *complementing* species or, hypothetically, due to *density compensation*. Apparent area sensitivity can be inferred from the scaling of abundance to patch area. However, greater density in small patches or near edges (giving appearance of inverse area sensitivity) may result from territory packing and edge truncation, either without an underlying preference, or	*Positive area sensitivity*: In Eastern England, evidence for positive area sensitivity was found for three woodland species: long-tailed tit *Aegithalos caudatus*, marsh tit *Poecile palustris* and chiffchaff *Phylloscopus collybita* (Hinsley *et al*., 1996; Bellamy *et al*., 2000), while nine showed apparent negative area sensitivity. In Finland, pied flycatcher *Ficedula hypoleuca* preferentially settled medium (>1 ha) or large forest stands in which breeding density was higher than in small stands (≤1 ha); stands ≤5 ha were occupied later and had a greater proportion of unpaired males, than larger stands (>5 ha) (Huhta *et al*., 1998; Huhta and Jokimäki, 2001). Similarly, redstart *Phoenicurus phoenicurus* settled later in patches <1 ha, with a greater proportion of unpaired males in patches <5 ha (Huhta and Jokimäki, 2001). In North America, territorial male ovenbird pairing success was lower in fragments than in nearby extensive forest (Villard *et al*., 1993), and area-sensitive density responses were found for neotropical migrant forest species across woodlots in Wisconsin (Ambuel and Temple, 1983). In Ohio, although all woodlots were settled in winter following removal, Carolina chickadee *Poecile carolinensis* were more likely to remain and breed in larger woodlots (Groom and Grubb, 2006). In south-eastern Australia, red-capped robin *Petroica goodenovii* occurred at higher density with a lower proportion of yearlings in large fragments (Major *et al*., 1999). In Belgium, crested tit *Lophophanes cristatus* fledglings from first broods settled on winter territories

despite a positive preference for larger patches (Hinsley *et al*., 1999; Bellamy *et al*., 2000). Conversely, demographic effects may occur without apparent preference (Winter and Faaborg, 1999).

Area preferences can be tested by comparing area–density relationships and mean area of occupied patches between years of high and low regional population abundance (Hinsley *et al*., 1996; Bellamy *et al*., 2000); or by relating relative timing of settlement (Lens and Dhondt, 1994; Huhta *et al*., 1998) or pairing success (Villard *et al*., 1993, Huhta *et al*., 1998) to patch area.

in fragments later than in continuous forest, and territories in fragments were more likely to be settled by second broods than in continuous forest (Lens and Dhondt, 1994).

In a meta-analysis of three Fennoscandian archipelago studies of forested islands surrounded by water, population densities of forest specialists were more sensitive to area than were forest generalists (Brotons *et al*., 2003), suggesting greater sensitivity to area quality, or less use of edges.

Positive area–density preferences have also been found for birds associated with grassland (Winter and Faaborg, 1999; Johnson and Igl, 2001; Renfrew and Ribic, 2008) and shrubland (Lehnen and Rodewald, 2009). For example, in Portugal male little bustard (Silva *et al*., 2010) occurred at higher density in larger fields, while across Northern Plains states, bird species showing positive area-sensitive incidence also tended to show significant area-sensitive density effects (Johnson and Igl, 2001). In oak-hickory forest in Ohio, three of six shrubland species examined (yellow-breasted chat *Icteria virens*, white-eyed vireo *Vireo griseus* and common yellowthroat *Geothlypis trichas*, but not blue-winged warbler *Vermivora pinus*, prairie warbler *Dendroica discolor* or indigo bunting *Passerina cyanea*) had greater abundance (capture rates) in larger regenerating clear-cuts (*n* = 13, ranging 4–16 ha) (Lehnen and Rodewald, 2009). In New Hampshire, chestnut-sided warbler *Dendroica pensylvanica* occurred at lower densities and had later nest initiation in smaller patches (total *n* = 29, varying 0.2–0.7 ha) (King and DeGraaf, 2004); in New England only one shrubland species of five tested (eastern towhee *Pipilo erythrophthalmus*) showed a positive area effect, with greater frequency in larger clear-cuts (total *n* = 34, varying 0.6–21 ha) (Askins *et al*., 2007).

Appendix: E4.3A (*cont.*)

Pattern	Explanation	Evidence
		Inverse area sensitivity: In an extensive meta-analysis, forest birds showed more frequent inverse abundance–area patterns than scrub, grassland or wetland species (Bayard and Elphick, 2010). In woodland fragments in eastern England, 9 of 16 species examined exhibited apparent inverse area sensitivity (Hinsley *et al*., 1996; Bellamy *et al*., 2000). However, examining patterns for years with varying regional abundance supported an actual preference for smaller woods for only two of these, blackbird *Turdus merula* and dunnock *Prunella modularis*, with apparent area sensitivity of other species, such as great tit *Parus major*, blue tit *Cyanistes caeruleus*, chaffinch *Fringilla coelebs* and robin *Erithacus rubecula*, likely to result from territory packing not preference (Bellamy *et al*., 2000). In Fennoscandia, in a meta-analysis of species density–area relationships across islands and forest fragments, most species showed no or positive area sensitivity, with little evidence of inverse area sensitivity (Brotons *et al*., 2003). In New England, a greater proportion of blue-winged warbler territories had evidence of nesting in small than in large forest openings (Askins *et al*., 2007) with some evidence of lower mating success.
Richness-area or 'area-related species density'	Random settlement proportionate to area may result in higher occupancy rates and thus greater species richness in larger patches (Coleman, 1981). The patch-size effect predicts	*Strong support* for both forest and grassland birds: For example, in North America grassland bird species richness in standard sized plots consistently increased with greater fragment or contiguous patch area (Herkert, 1994; Vickery *et al*., 1994; Helzer and Jelinski, 1999); for woodland birds richness of interior species increased with area (Freemark and

	that species richness in plots or samples of uniform area (‘species density’, to control for null hypothesis of random sampling) is greater in patches of greater contiguous area. Passive sampling may be an important process underlying the widespread species–area effect (Connor and McCoy, 1979). Possible mechanisms include: species-specific *minimum area requirements* (so that assemblages are nested in relation to patch size) and various mechanisms resulting in *area-sensitive* patterns of distribution (see below).	Collins, 1992) and richness of woodland birds increased with area in Britain (Bellamy *et al*., 1996a) and Australia (Watson *et al*., 2005).
Landscape diversity	Assemblage composition depends on landscape composition; landscapes with more diverse habitat composition support richer regional assemblages (greater beta diversity). See Andrén (1994). This may result from addition of species associated with novel habitats, but also from complex requirements of *complementing*	*Strong support*: e.g. (Pino *et al*., 2000; Jansson and Andrén, 2003; Tellería *et al*., 2003; Moreira *et al*., 2005; Bennett *et al*., 2006; Barbaro *et al*., 2007).

Appendix: E4.3A (*cont.*)

Pattern	Explanation	Evidence
	species that require multiple resources or landscape elements.	
Habitat extent	Fragmentation effects on richness and abundance primarily arise through the overall proportion of habitat remaining in a fragmented landscape, not through the arrangement of patches. See Andrén (1994).	*Strong support*: Most studies that have simultaneously examined the relative importance of landscape-scale extent, local extent, patch-scale area or configuration have concluded that extent has stronger effects, explaining more variation in abundance or incidence (Trzcinski *et al*., 1999; Fahrig, 2003; Bennett *et al*., 2006), though Vergara and Armesto (2009) found different bird species showed contrasting responses to different scales.
Non-linear fragmentation effects	Across both real and simulated landscapes, measures of configuration (e.g. patch area, isolation, contagion, structural connectivity) change progressively as overall habitat extent is reduced with marked non-linear thresholds at which connectivity deteriorates, irrespective of whether habitat is aggregated or randomly distributed (Andrén, 1994, 1999; Fahrig, 2003). Andrén (1994) proposed that initial effects of habitat fragmentation are due to loss of	*Strong support*: In a review of landscape-scale tests of the random sample hypothesis for birds and mammals, significant effects of configuration (patch area and/or isolation) were not found in any study where extent was >30%, in approximately a third of studies with extent 20–30%, and in the majority of studies with <20% of original habitat remaining (Andrén, 1994). In a meta-analysis of 25 avian, mammalian and invertebrate studies, abundance–area (density) effects were weaker with greater habitat extent (Bender *et al*., 1998), but this effect was lost when they controlled for location (western/eastern hemisphere) and migratory status. For forest interior birds across four regions of Ontario, the magnitude of effect of core patch area on species richness was greater in subregions (total *n* = 8) with less forest extent (Austen *et al*., 2001). Similarly, Radford *et al*. (2005) found greater influence of configuration and habitat aggregation in replicate landscapes (10 km × 10 km) containing less

habitat area, but configuration effects are important in landscapes of low habitat extent (e.g. <10–30%) where they contribute to species richness, incidence and population abundance. Thus at low habitat extent, species richness and total population size decline more rapidly than predicted by the null random sample hypothesis (that species richness and population size pooled across fragments is the same as predicted by a random sample of the same total area from the original continuous habitat (Connor and McCoy, 1979).	habitat extent. For long-tailed tits in Sweden, isolation effects on local incidence were stronger in boreal landscapes with less habitat extent (Jansson and Anglestam, 1999): when habitat cover was only 5%, a strong non-linear threshold in incidence (probability of occupancy declining from 0.8 to only 0.1) was found as interpatch distance increased from just 100 m to 500 m; but with 15% habitat coverage, a threshold in occupancy occurred as isolation increased from 500 m to 900 m. In a stratified study that controlled for independent effects of extent and configuration, ovenbird patch area effects were important only at low landscape level habitat extent (Betts *et al*., 2006). Black-throated blue warbler *Dendroica caerulescens* abundance increased with increasing territory-scale shrub density more strongly in fragmented than in contiguously forested landscapes (Cornell and Donovan, 2010).

Appendix E4.3B *Hypotheses for mechanisms underlying observed patterns of response to landscape structure described in Appendix E4.3A. For each hypothesised mechanism, key references are given, assumptions and predictions are detailed and the strength of supporting empirical evidence from empirical studies of Mediterranean, temperate and boreal bird species and or assemblages is summarised. Alternative mechanisms are highlighted in bold text. Mechanisms are considered at a hierarchy of biological scales, as processes at the scale of: (a) individual home ranges; (b) individual dispersal; (c) structured regional populations.*

Hypothesis	Assumption or prediction	Evidence
(a) Processes at the scale of individual home ranges		
Species-specific minimum area requirements	Species-specific minimum area requirements (Hinsley *et al*., 1996) of large-area species (Andrén, 1999) predict nested patterns of increasing species-richness with increasing patch area: with ubiquitous species found in most patches, but species with larger area requirements absent from smaller patches (Hinsley *et al*., 1996). Thus area requirements may filter avian assemblages in heavily fragmented landscapes.	**Strong support**: Species-specific area thresholds have been demonstrated for woodland bird assemblages in the Netherlands (van Dorp and Opdam, 1987), northern England (McCollin, 1993), Poland (Cieslak, 1985) south-eastern Australia (Watson *et al*., 2005). ‘Interior’ or woodland specialists often tend to have larger area requirements; for example, in eastern England across 151 small woods (range 0.02–30 ha) specialist woodland species (e.g. marsh tit *Poecile palustris* and treecreeper *Certhia familiaris*) only approached 100% probability of breeding in woods of 10 ha and more (Hinsley *et al*., 1996). Similarly, area thresholds for incidence have been found for forest interior species in North America, with few found in forests <10 ha (Freemark and Collins, 1992). Incidence–area thresholds are also commonly found in grassland and shrubland species (see Appendix E4.3A); however thresholds are often at scales much greater than that of a home range, suggesting other mechanisms (edge-avoidance, edge quality, area quality) may also be implicated.

Reduced edge quality	Settling birds may actively avoid lower habitat quality near edges, for example with reduced prey density due to altered habitat structure or microclimate e.g. desiccation at forest edges (McCollin, 1998; Ortega and Capen, 1999), resulting in edge sensitivity and area sensitivity.	**Some support**: Ovenbird pairing success was slightly less close to edges (n.s.) and territory size increased away from edge (effect continuing >200 m) suggesting edge habitat was lower quality, with reduced prey density suggested as a mechanism (Ortega and Capen, 1999). Great tit nesting further from edges (>200 m) nested earlier and had larger clutch size, indicating better-quality habitat (controlling for immigrant status, elevation and density) (Wilkin *et al*., 2007).
Passive displacement	Passive displacement due to constraints of placing a territory near abrupt edges, would reduce territory density close to edges, for species that do not use the external habitat (Kroodsma, 1984; McCollin, 1998; Lehnen and Rodewald, 2009), resulting in apparent (not active) edge sensitivity. However, this can be an artefact of mapping territories as roughly circular polygons (Kroodsma, 1984; King *et al*., 1997).	**Lacks support**: In Vermont, ovenbird had 40% lower territory density close to edges (0–150 m) than in forest interior (150–300 m), greater than simulated effects of passive displacement (Ortega and Capen, 1999).
Edge truncation	Truncation of territories placed near edges may reduce foraging efficiency during provisioning (i.e. for central-place foragers that do not exploit the external habitat) (Huhta *et al*., 1999), leading to avoidance of edges at settlement and lower density close to edges – resulting in apparent edge sensitivity and area sensitivity.	**Some support**: Early arriving male pied flycatcher preferentially settled nestboxes located 50–100 m from forest-clear-cut edges, and provisioning rates and nestling body mass were lower in nests moved to the edge than in nests moved into the stand interior (Huhta *et al*., 1999). Edge avoidance was attributed to foraging costs of territory truncation, though area quality or edge quality may also be implicated.

Appendix E4.3B (*cont.*)

Hypothesis	Assumption or prediction	Evidence
Edge- and patch-area effects on nest failure rates	Edge effects in fragmented landscapes elevate nest failure rates, due to higher rates of predation (by generalist predators from the matrix) or higher rates of nest parasitism (e.g. in North America by brown-headed cowbird *Molothrus ater*) close to habitat edges, or in small fragments (Gates and Gysel, 1978). Perception of increased risk can result in active edge avoidance at territory settlement, resulting in edge-sensitive and area-sensitive patterns of landscape effects. Can be tested by examining success rates of real (but not artificial) nests in relation to distance to edge, or patch size.	**Weak support**: In North America, edge and patch area effects on nest failure rates of forest birds have been detected (particularly for ground-nesting forest interior species and grassland specialists); however effects are region-, landscape-, habitat- and species-specific, (see Box 4.1). Local landscape effects may be more common in deciduous forests and marshes than in coniferous forest or fields (Bátary and Baldi, 2004) but have been found for grassland species, for example dickcissel and Henslow's sparrow (Winter and Faaborg, 1999; Winter *et al*., 2000), but not for shrubland birds (Woodward *et al*., 2001). In northern hardwood forest Flaspohler *et al*. (2001) found effects for two ground nesters, but not for six canopy-nesting species. No difference was found in the proportion of male ovenbirds producing fledglings close to or far from edges (Ortega and Capen, 1999); however in Minnesota ovenbird nest success (with failures mainly due to predation) was lower closer to internal clear-cut edges (Manolis *et al*., 2002). Studies of European woodland birds have often found no patch area or edge effects for nest predation rates: e.g. for cavity-nesting nuthatch *Sitta europaea* (Matthysen and Adriaensen, 1998) and middle-spotted woodpecker *Dendrocopus medius* (Robles *et al*., 2008). However,

		significant effects have been found for some European species: e.g. great tit nesting in wooden nest-boxes in Oxfordshire had higher rates of nest predation close (<25 m) to edges (Wilkin *et al*., 2007) and in Finland predation rates of treecreeper *Certhia familiaris* nests was related to local- (500m radius) rather than territory-scale forest fragmentation (200m radius) (Huhta *et al*., 2004).
Edge contrast	Increasing contrast between the patch and matrix is thought to increase edge effects. Thus, processes affecting forest fragments set in farmland may not apply to forests fragmented by clear-felling and regeneration, where old growth patches are set in a matrix of other forest growth stages (Schmiegelow and Mönkkönen, 2002).	**Some support**: Some evidence of greater edge effects on nest predation rates at forest-farmland than internal forest-clear-cut boundaries, but review confounded by inclusion of artificial nest studies (Schmiegelow and Mönkkönen, 2002) and potentially also confounded by differences in habitat extent. For indigo bunting *Passerina cyanea* in Illinois, nest predation rates were nearly twice as high at abrupt agricultural or other permanent edges than in more gradual complex edges (e.g. treefalls, streamsides, gaps created by selective logging) (Suarez *et al*., 1997). Food caching behaviour of black-capped chickadee *Poecile atricapillus* provides evidence of edge avoidance, thought to be due to wind exposure; edges adjacent to wide unforested areas were avoided more than those delimiting narrower unforested areas (Brotons *et al*., 2001).
Conspecific attraction	Initial territories may be settled randomly in proportion to habitat area (thus large patches have higher probability of	**Strong support**: Aggregated territory settlement of pied flycatcher *Ficedula hypoleuca* in Sweden was influenced

Appendix E4.3B (*cont.*)

Hypothesis	Assumption or prediction	Evidence
	settlement) or in response to habitat quality; subsequent settlement can be influenced by conspecific attraction (Svärdson, 1949) as a cue to habitat suitability (Smith and Peacock, 1990). Could potentially contribute to species (richness)–area, and for individual species, area-sensitivity patterns (both incidence–area and abundance–area relationships).	by conspecific attraction: new arrivals settled preferentially in experimental areas of vacant nest-boxes with song playback, while controls without playback remained unused (Alatalo *et al*., 1982). Unpaired woodlark *Lullula arborea* males establish territories adjacent to paired males (P.D. unpublished obs.). Higher frequency of unpaired male middle-spotted woodpecker in smaller patches was attributed to conspecific cues affecting female settlement, rather than underlying area quality, as reproductive parameters were similar (Robles *et al*., 2008). Black-throated blue warbler settled poor-quality territories in response to experimental exposure to singing in the post-breeding period the preceding year (Betts *et al*., 2008).
Heterospecific attraction	Residents have sampled the landscape or survived in better-quality patches; arriving migrants (that are assumed to be time limited) may then settle in response to the presence of residents as a cue to patch quality or safety (Mönkkönen *et al*., 1990, 1997). As with conspecific attraction, this could potentially contribute to species (richness)–area, and for individual species, area-sensitivity patterns (both incidence–area and abundance–area relationships).	**Strong support**: in Finland, densities of migrant passerines unexpectedly increased in response to manipulation of resident *Parus* spp. density on islands, with effects then responding to reversal of treatments (Mönkkönen *et al*., 1990). Similar responses to manipulation of *Parus* density were found by Thomson *et al*. (2003), with increased density of migrant foliage gleaners and generalists, particularly chaffinch. In Minnesota, resident bird numbers were manipulated on seven reservoir islands, reversing treatments the

		following year (Mönkkönen *et al*., 1997). Total density of migrant arboreal insectivores was greater on islands with resident addition; species-specific responses were significant for red-eyed vireo *Vireo olivaceus* and marginally for black-and-white warbler *Mniotilta varia* and yellow warbler *Dendroica petechia*.
Territory packing and **phenotypic-based territorial compressibility**	**Territory packing** at edges can result in greater density, despite lower edge quality (Wilkin *et al*., 2007). Similarly, territories may be more densely packed in small patches despite lower quality and reproductive success (Hinsley *et al*., 1996, 1999; Bellamy *et al*., 2000). This may occur if individuals of higher phenotypic quality that settle better-quality habitat (e.g. core, or larger patches) effectively defend territories that are consequently less elastic or compressible, than marginal territories occupied by lower-quality individuals that are compressed by intraspecific competition.	**Some support, but requires explicit testing**: In Oxfordshire, England, great tit breeding in extensive woodland had greater territory density within *c*. 100 m of woodland edge, at least partly due to settlement and greater packing of immigrants from the surrounding landscape (Wilkin *et al*., 2007). Density-dependent patterns of territory compressibility (Mallord *et al*., 2007) should be compared between low- and high-quality landscape elements.
Area-quality hypothesis	Larger patches support higher species-specific density (positive area sensitivity, see above) (Matter, 1997) because they are of better quality. This may be due to: ● **Resource concentration** (Brotons *et al*., 2003) through greater prey density, or greater habitat heterogeneity (Ambuel and Temple, 1983), or ● **Lower nest predation rates** (Askins and Philbrick, 1987), or	**Strong evidence in some studies, but not supported for all studies and species**: **Habitat and Resource effects**: In Wisconsin vegetation structure did not vary with forest area (from 3 ha to > 500 ha) though bird communities varied (Ambuel and Temple, 1983). Density of arthropod prey or other food resources is inconsistently related to patch area: with both positive (Burke and Nol, 1998; Zanette *et al*., 2000) and negative (Halme and Niemelä, 1993) area effects for

Appendix E4.3B (*cont.*)

Hypothesis	Assumption or prediction	Evidence
	● **Direct environmental effects** such as winter wind-chill or nestling survival (McCollin, 1998; Doherty and Grubb, 2002)	fragments versus large blocks or contiguous forest, but no area effect for small versus large regenerating clear-cuts (Rodewald and Vitz, 2005).
	Prey abundance may be an imprecise measure of resources; aggregate measures of invertebrate biomass are crude relative to specific resources exploited by specialists. Furthermore, biomass may not represent availability. Discriminating tests of area quality come from relating avian fitness and demographic parameters to configuration (Hinsley *et al*., 1999; Zanette *et al*., 2000). However, large sample sizes may be required to detect effects if there are high rates of stochastic nest failure (Mallord *et al*., 2008). Ideal free settlement and density dependence may obscure or reduce effects resulting from underlying differences in habitat quality.	**Breeding productivity**: For eastern yellow robins *Eopsaltria australis* in New South Wales, Australia, insect biomass in two small fragments (55 ha) was half that in two large forest blocks (>200 ha), foraging efficiency was reduced (females received 40% less food from males, and foraged independently more often), eggs were 7% lighter, nestling provisioning rate was less and nestlings were lighter (Zanette *et al*., 2000). In Missouri, dickcissels had lower breeding success in small grassland patches, although no area-sensitive incidence or density patterns were detected (Winter and Faaborg, 1999). In Britain, breeding success of blue tits and great tits was reduced in smaller woodlands (n = 43 woods ranging 0.1 to 157 ha) due to later breeding in small woods; for great tit, fledging mass was also smaller (Hinsley *et al*., 1999). Crested tit *Lophophanes cristatus* in mixed woodland in Belgium produced fledglings with lower body mass, and had delayed second attempts, in fragments ($n = 3$, ranging 9–50 ha) compared to continuous habitat (Lens and Dhondt, 1994).

Although positive area preference of pied flycatcher in Finland was attributed to area quality (Huhta *et al*., 1998); clutch size, brood size and nestling survival were independent of patch size (Huhta and Jokimäki, 2001). Similarly, nuthatch reproductive success, nestling mass, fledging date and recruitment did not differ between small oak woodlands (<30 ha) and two larger patches (>200 ha) (Matthysen and Adriaensen, 1998), and in north-western Spain, middle spotted woodpecker reproductive parameters (clutch size, nesting success, productivity per nest and fledgling mass) and juvenile survival did not differ with fragment size, despite lower male pairing success in smaller patches (Robles *et al*., 2007, 2008). In regenerating clear-cuts in Ohio, Lehnen and Rodewald, (2009) found no evidence that fitness (apparent survival, reproductive success) of shrubland birds was related to patch area despite apparent area preferences

Survival: In Ohio, Carolina chickadee, white-breasted nuthatch *Sitta carolinensis* and downy woodpecker *Picoides pubescens* had higher annual survival in larger woodlots (across 54 woodlots, ranging 0.1–60 ha, over five years) (Doherty and Grubb, 2002); high mortality of chickadee in small wood lots was attributed to wind-chill and food limitation (Doherty and Grubb, 2002). Nutritional condition (rate of growth of induced feathers) showed a significant interaction between supplemental feeding and woodlot size (Doherty and Grubb, 2003). In Spain, blue

Appendix E4.3B (*cont.*)

Hypothesis	Assumption or prediction	Evidence
		tits in small forest fragments increased vigilance as flock size reduced, while no such effect occurred in continuous forest (Telleria *et al*., 2001).
Edge exploitation	Preferentially settle at edges as these are high-quality habitats, and thus may have higher density near edges, or higher incidence or density in smaller patches (McCollin, 1998).	**Strong support**: In Texas, higher diversity of birds and greater abundance of great crested flycatchers *Myiarchus crinitus*, eastern wood pewee *Contopus virens* and Carolina chickadee occurred within 25 m of forest edge adjacent to clearcut stands; effects were attributed to well-developed foliage layers at edges that provided foraging and singing sites (Strelke and Dickson, 1980). In pine-dominated forest in Finland, arthropod abundance decreased with distance from forest edge, and was lower in large than small patches, primarily due to greater deciduous and shrub elements at edges (Jokimäki *et al*., 1998). See also Chapter 5.
Complementing species and **habitat juxtaposition**	Species that require contrasting resources from different habitats or landscape elements, termed ‘complementing species’ (Dunning *et al*., 1992), benefit from heterogeneous landscapes comprising a mosaic of patches of different habitats. Small habitat fragments (e.g. woodlands) set in a favourable matrix may therefore support greater species richness and greater density of	**Strong support** from mosaic and focal-patch studies and from autecological and telemetry studies: Many bird species require contrasting vegetation structures or habitats for nesting and foraging (Fuller *et al*., 2004). Complementing species nesting in tree holes or wood edge and feeding in adjacent open habitats may be classified as ‘edge species’; however, their incidence in

individual species, than those set in less favourable landscape contexts (Brotons *et al*., 2003).

Complementing species are often grouped with other ‘edge species’.

Complementing species will be favoured by landscapes that are **fine-grained** relative to territory or home range extent.

Complementarity may be tested in a number of ways:

- Within general linear models of species-habitat association (i.e. incidence, density), testing whether terms for interactions between habitats are significant, or strongly supported.
- Within grid-based mosaic landscape studies, examining whether the species richness of assemblages associated with particular habitats (e.g. cropland) is affected by wider landscape diversity.
- Examining whether patch or territory settlement is related to proximity to another habitat.
- By detailed analysis of foraging movements, for example through radio-telemetry.

woodland patches is dependent on landscape context and composition (Hinsley *et al*., 1996). In forest mosaic in south-western France, some complementing species were associated with mosaics, breeding in woodlands, but foraging in adjacent grasslands, road verges or firebreaks, including turtle-dove *Streptopelia turtur*, hoopoe *Upupa epops*, mistle thrush *Turdus viscivorus*, red-backed shrike, common starling *Sturnus vulgaris* and cirl bunting (Barbaro *et al*., 2007). In Norway, both yellowhammer *Emberiza citrinella* and ortolan bunting *E. hortulana* nesting in burnt forest commuted to forage in adjacent farmland, with ortolan bunting commuting up to 2.7 km (Dale and Manceau, 2003).

In Spain, greater landscape diversity enhanced richness of cropland and crop-forest birds (Pino *et al*., 2000). In Britain 5 of 15 farmland species tested (greenfinch *Carduelis chloris*, house sparrow *Passer domesticus*, yellowhammer, robin, common whitethroat *Sylvia communis*) had greater abundance with greater local cover of cereal, but only at low regional extent (<20%); when regional extent was large (>60%) increasing local extent reduced abundance (Robinson *et al*., 2001). In analysis restricted to local scales, abundance of yellowhammer was non-linearly related to cereal extent – a positive effect with an initial increase in extent, but reduced benefits of further increase. Hooded crow *Corvus cornix* density in south-central Sweden was

Appendix E4.3B *(cont.)*

Hypothesis	Assumption or prediction	Evidence
		higher in landscapes composed of a mixture of farmland and forest, than in landscapes dominated by either one (Andrén, 1992). In southern France, breeding density of displaying male little bustard was higher in semi-natural pasture close to modified (improved) pasture (Wolff, 2004, 2005); in other studies little bustard density was positively related to landscape diversity (Martinez and Tapia, 2002; Morales *et al*., 2005; García *et al*., 2007); however, in Portugal male density was greater in larger fields (Silva *et al*., 2010). In southern France, densities of tawny pipit and skylark within natural grasslands were positively affected by proximity of agricultural habitats (hayfields, improved pastures such as fallows and grazed crops) (Brotons *et al*., 2005). Golden plover *Pluvialis apricaria* nesting on heather moorland in northern England, commuted 1.1–3.7 km to feed in enclosed fields during incubation, but broods supplemented at finer scales and fed in grazed mires and patches of calcareous grassland within the moorland (Whittingham *et al*., 2000). Similarly twite *Carduelis flavirostris* nesting in moorland fringes in the South Pennines commuted 1.3–3.5 km to forage in meadows and pastures (Raine, 2006). Within moorland, curlew

		Numenius arquata lapwing *Vanellus vanellus* and snipe *Gallinago gallinago* were positively associated with intensive grassland in the surrounding landscape (750m) (Dallimer, 2010)
Supplementing species	If individual patches are too small to provide sufficient resources, gap-insensitive species may be able to supplement resource needs by exploiting multiple patches (Dunning *et al*., 1992). The scale of the home range or territory will be large relative to landscape grain (Rolstad, 1991; Andrén, 1994). Some large-area species foraging across scattered patches may be insensitive to finer-scale grain. Reduced patch–matrix contrast may enhance local persistence if birds in small fragments are able to utilise resources from the surrounding matrix (habitat supplementation) (Brotons *et al*., 2003).	**Strong support**: But largely anecdotal examples. In Sweden, goshawk *Accipiter gentilis* had home range sizes of 3400–8000 ha, though most patches of old forest were smaller than 30 ha (Widén, 1989). In Finland, black woodpecker *Dryocopus martius*, had the same density per woodland patch in a forest-farmland landscape (comprising 26% forest) as in forest patches within forest-dominated landscape (80% extent), but territories included many forest patches (mean 76 per territory); neither reproduction or survival differed among landscapes (Tjernberg *et al*., 1993). Similarly, in managed boreal forests of western Canada, pileated woodpecker, *Dryocopus pileatus* include multiple patches of preferred habitat within territories (Schmiegelow and Mönkkönen, 2002)
Gap-sensitive species and **perforation-insensitive species**	For some species, gap-crossing increases foraging costs, reducing effective habitat quality. Predation risk imposes costs to gap-crossing that differ among species. Gap-sensitive species may be sensitive to fine-grained habitat perforation within home ranges. Conversely, some large-area species, with large home-range sizes, may be mosaic- or perforation-insensitive	**Strong support** for gap-sensitive species: For woodland songbirds in Scotland, gap-crossing in response to predator threat, scaled with body size from 46 m for goldcrest *Regulus regulus* to 150 m for chaffinch (Creegan and Osborne, 2005). In Quebec black-capped chickadee and yellow-rumped warbler *Dendroica coronata* detoured twice as far

Appendix E4.3B (*cont.*)

Hypothesis	Assumption or prediction	Evidence
	when landscapes are fine-grained (at a scale less than that of their home range) within extensive areas of preferred habitat (Andrén, 1994).	through forest cover rather than cross gaps (Desrochers and Hannon, 1997). In Alberta black-capped chickadee were reluctant to cross gaps >50 m when a forested route was available, but sometimes crossed gaps up to 200 m when no alternative forested route was available; white-breasted nuthatch, hairy woodpecker *Picoides villosus* and downy woodpecker were less willing to traverse any gap (St. Clair *et al*., 1998). Radio-telemetry of male ovenbirds showed successful breeders readily crossed narrow gaps (<25 m), but rarely crossed larger gaps (100–300 m), perhaps due to energetic constraints when provisioning, or vulnerability of offspring (Bayne and Hobson, 2001). In contrast, males without young readily crossed farmland of 100–300 m separating forest fragments and moved up to 5.6 km. In Sweden, matrix-crossing, edge-crossing and group cohesion were affected by habitat-mediated predation risk for crested tit, willow tit *Poecile montanus*, coal tit *Periparus ater* and goldcrest (Rodríguez *et al*., 2001). Movement rates between old forest patches were strongly restricted by open matrix (farmland and clearcuts) and young plantations, suggesting fine-grained fragmented landscapes have substantially lower quality than contiguous habitat. For great tit an energetic

model showed that thresholds of gap size that could be regularly crossed without exceeding maximum sustainable daily energy expenditure (DEEmax), and time costs of gap-crossing, differed greatly with brood size (for large broods gap threshold 50–100 m, and time costs 6 h day^{-1}; for smaller broods 300–550 m and 1 h day^{-1}) (Hinsley, 2000); distances that can be crossed without exceeding DEEmax were greatly increased for adults with lower body size. In Oxfordshire, England, great tit nesting close to internal woodland clearings nested later, but had similar clutch size egg mass and recruitment rates (Wilkin *et al*., 2007); narrow gaps within territories had no effect.

Some support for perforation-insensitive species: In Oregon, spotted owl *Strix occidentalis* utilising old growth and mature timber, used territories (550–3380 ha) although perforated by fine-grained clear-cuts (10–20 ha) (Forsman *et al*., 1984). In Norway, capercaillie *Tetrao urogallus* males (territory size *c*. 50 ha) prefer old-growth forest, but accepted fine grained clear-cuts (0.3 ha) within home ranges (Rolstad, 1989), but increased territory size (Wegge and Rolstad, 1986).

In eastern England, green woodpecker *Picus viridis* and great-spotted woodpecker *Dendrocopos major* were more likely to cross open fields than follow wooded boundary features (Bellamy and Hinsley, 2005). Other European forest birds exploiting scattered resources within extensive mosaics, that are mobile and readily

Appendix E4.3B (*cont.*)

Hypothesis	Assumption or prediction	Evidence
		cross gaps and so are likely to be perforation insensitive, or at larger scales to act as supplementing species, may include siskin *Carduelis spinus*, crossbill *Loxia curvirostra*, and hawfinch *Coccothraustes coccothraustes*.
(b) Processes at the scale of individual dispersal		
Patch isolation impedes dispersal	Isolation of habitat patches from other source patches is predicted to reduce rates of local occupancy through impeded dispersal (Hanski, 1994). A prediction of metapopulation theory, but importance of isolation is also a general prediction of spatially structured populations for species with limited dispersal – due to reduced rescue effect, impeded territory settlement, and re-colonisation of vacant patches. Gap-sensitive individuals in low-quality isolated fragments may be prevented from dispersing by ‘barrier-effects’, becoming ‘gap-locked’, with important fitness consequences.	**Strong support** Incidence of dispersal-limited species may be lower in isolated patches. Long-tailed tit habitat occupancy in a boreal landscape in Sweden was positively related to the amount of habitat within 1 km, and negatively related to the distance between habitat patches; together these explained 78% of local patch occupancy (Jansson and Anglestam, 1999). For boreal forest fragments (21–61 ha) set in farmland in Sweden, willow tit and crested tit incidence was significantly higher closer to continuous forest (over scales of 100–200 m and up to 1 km, respectively); for the more mobile coal tit and goldcrest no isolation effects were found (Rodríguez *et al*., 2007). Similarly, isolation effects were found for forested islands set in water (Brotons *et al*., 2003). In, eastern England, woodlark occupancy was lower in clearfells located in outlying forest blocks, than in a central core block, over a scale 2–3 times that of mean

natal dispersal (Evans, 2002; Wright, 2006). Similarly for Bachman's Sparrow *Aimophila aestivalis*, occupancy of ephemeral salvage clear-cuts within pine forest was related to distance from a large source population in the first year of colonisation in one landscape (patches 0–5 km from source) and in both years of study in a second landscape (patches 1.4–9.5 km from source) with a strong threshold effect on colonisation probability at 6 km (Dunning *et al*., 1995). In Chile, Austral thrush *Turdus falcklandii* responded to forest patch isolation more strongly than to local or regional extent (Vergara and Armesto, 2009). In south-eastern Australia, isolation affected patch incidence of a number of forest bird species for fragments in a farmland matrix, with thresholds of 200–2600 m (Watson *et al*., 2005).

Evidence of barrier effects has been found for gap-sensitive species. In Belgium, dispersal away from natal territory by juvenile crested tit was delayed in fragments (Lens and Dhondt, 1994); dickcissels move further in larger patches suggesting barrier effects in smaller patches (Berkeley *et al*., 2007); nuthatches were less likely to move to a new territory following initial settlement in fragments compared to continuous forest suggesting they were 'gap-locked' (Matthysen *et al*., 1995); over-wintering black-capped chickadees were more mobile (both immigration and emigration) in continuous forest (Turcotte and Desrochers, 2005) and Carolina chickadees

Appendix E4.3B (*cont.*)

Hypothesis	Assumption or prediction	Evidence
		had higher mortality in small wood lots with low food availability (Doherty and Grubb, 2002).
Physical connectivity enhances dispersal	Connecting elements and or enhanced matrix permeability are predicted to enhance functional connectivity and thus: ● facilitate movement of gap-sensitive species, ● reduce patch isolation effects, ● increase probability of local occupancy through enhanced re-colonisation rates or rescue effects, ● reduce the probability of local and thus regional population extinction in metapopulation systems (Harrison, 1994; Dolman and Fuller, 2003). Whether or not bird dispersal and patch colonisation are enhanced by linear elements (corridors), or by greater matrix permeability (landscape composition and cost surface analysis) depends on dispersal behaviour, gap-crossing ability and species-specific response to matrix composition and structure. Evidence can be provided by studies that examine movement behaviour (e.g. by direct observation, ringing-re-capture or telemetry), by examining patterns of patch	**Some support from behavioural studies, limited evidence of demographic effects**: In eastern England smaller songbirds including goldcrest, *Parus* tits, long-tailed tit and *Sylvia* warblers exclusively used woody boundary features rather than crossing open fields when moving between woodland fragments; furthermore, the number of individuals moving between paired woods was positively related to woody cover in boundary features rather than distance between the woods (Bellamy and Hinsley, 2005). Larger species such as chaffinch and blackbird readily crossed open fields, while great-spotted woodpecker and green woodpecker did not use boundary features (Bellamy and Hinsley, 2005). In Alberta black-capped chickadees were as likely to use corridors as continuous forest, but white-breasted nuthatch, hairy woodpecker and downy woodpecker were less willing to travel in narrow linear forest corridors (<10 m wide) than through continuous forest, in response to mobbing/alarm calls (St. Clair *et al*., 1998). *Patch incidence*: In The Netherlands, incidence of woodland specialists showed effects of landscape composition (amount of woodland, distance to large

	incidence or by analysing population synchrony in relation to local landscape structure.	woodland), but no effects of connectivity (density of wooded banks) (van Dorp and Opdam, 1987). In a removal experiment in Ohio, although all wood lots were eventually re-occupied, wood lots in less-forested landscapes that were connected to other woodland by habitat corridors were re-occupied by Carolina chickadees sooner than unconnected wood lots (Groom and Grubb, 2006). However, connectivity may increase effective area quality, as well as allowing dispersal and settlement. *Population dynamics relative to connectivity*: For some ubiquitous western European species that exploit edges (wren *Troglodytes troglodytes*, blackbird, dunnock), local population synchrony among small woodlands in Eastern England was greater among patches in more connected landscapes (Bellamy *et al*., 2003). This could represent functional connectivity facilitating dispersal and re-colonisation of patches after local stochastic or weather-related losses (Dolman *et al*., 2007). However, linear connecting elements used as breeding habitat (Hinsley and Bellamy, 2001) may also contribute to patch occupancy through habitat–area effects or greater local source populations (rescue effects) (Bellamy and Hinsley, 2005), so effects on synchrony cannot be solely attributed to connectivity (Dolman *et al*., 2007).
Matrix quality hypothesis	Reduced patch–matrix contrast with less hostile matrix habitats may enhance dispersal, reducing isolation	**Some support**: At assemblage scale, evidence is provided by the extreme contrast of island archipelagos

Appendix E4.3B (*cont.*)

Hypothesis	Assumption or prediction	Evidence
	effects (Moilanen and Hanski, 1998, Pither and Taylor, 1998; Vandermeer and Carvajal, 2001; Brotons *et al*., 2003; Kupfer *et al*., 2006). Matrix quality can affect individual movement and dispersal and thus metapopulation colonisation–extinction dynamics; this can lead to greater species richness for small fragments set in a more favourable matrix (Brotons *et al*., 2003; Vandermeer and Carvajal, 2001).	set in large lakes or sea, versus mature growth forest fragments set in forest age–structure mosaics (Brotons *et al*., 2003). In a meta-analysis of studies of Fennoscandian forest fragments (Brotons *et al*., 2003) islands surrounded by water ($n = 3$ studies, 13–44 islands) showed stronger species-specific population density–area relationships than mature forest fragments surrounded by cut-over or regenerating forest (6 studies, 12–56 fragments); combined correlations were significant on islands, but did not differ from zero in fragments embedded in forest mosaics. However, this may result from birds using resources from the matrix (i.e. **complementation, supplementation**), not solely dispersal effects. Similarly, in different Mediterranean landscapes, species responses to decreasing open habitat extent differed between farmland-forest landscapes and farmland-shrubland landscapes (Vallecillo *et al*., 2008), but again complementation, supplementation or compensation may occur rather than matrix-mediated dispersal. In Mediterranean *Pinus halapensis* forest fragments set in shrubland, forest-canopy species responded positively to fragment shape and edge density, which had a stronger effect than patch area, interpreted as a lack of

		detrimental fragmentation effects in this matrix (Herrando and Brotons, 2002). Contrasting isolation effects with landscape context have been found for individual species. For willow tit and crested tit, significant isolation effects occurred for boreal forest fragments set in farmland, but not for old-forest fragments in a mosaic of young forest and clear-cuts (Rodríguez *et al*., 2007). Similarly, in Sweden, hazel grouse *Bonasa bonasia* incidence in forest patches was strongly influenced by isolation in an agricultural landscape, with no patches occupied further than 100 m from continuous forest edge, while in a forested landscape incidence in deciduous patches set in a matrix of non-habitat coniferous forest was negligibly affected by distance (Åberg *et al*., 1995).
(c) Processes at the scale of regional populations		
Island biogeography	Richness and composition of species assemblage in local patches is determined by area- and isolation-dependent rates of species arrival, local population extinction and re-colonisation (MacArthur and Wilson, 1967).	**Relevant to regional archipelagos**: Regional populations in extensive source habitat and scattered outlying fragments may act as an archipelago (see ‘mainland-island effects’ below). However, species replacement through turnover of local populations within patchy terrestrial landscapes is rarely at the timescales considered by island biogeography theory.
Density compensation	Hypothesis predicted from island biogeography, whereby individual species have higher densities on smaller patches (inverse area sensitivity) as a	Untested at landscape scales?

Appendix E4.3B *(cont.)*

Hypothesis	Assumption or prediction	Evidence
	consequence of lower species richness and thus reduced inter-specific competition (MacArthur *et al*., 1972).	
Metapopulation theory	Regional species populations persist by stochastic extinction/re-colonisation dynamics of local populations in fragments of habitat (Hanski, 1998, 1999). Semi-isolated populations have independent dynamics and are linked by infrequent dispersal. Levins' idealised metapopulation model (Levins, 1969, 1970) assumes colonisation and extinction rates are equal across patches. However, in spatially explicit or realistic metapopulation models, that consider distance among patches or model explicit landscapes, colonisation rate is inversely related to isolation and extinction probability is inversely related to patch area. Predictions are: ● Occupancy is positively related to patch area, and is negatively related to isolation. ● Connectivity is important to occupancy and regional persistence. ● Regional persistence is dependent on regional-scale extent of source patches (as this affects colonisation rate). Many predictions of metapopulation theory cannot be distinguished from patterns arising by other population mechanisms. The matrix is assumed to be homogeneous	**Not supported**: Patchy populations distributed across numerous small fragments can have high rates of local patch-scale turnover (i.e. single species extinction/re-colonisation in terms of occupancy) (Haila *et al*., 1993; Villard *et al*., 1995; Bellamy *et al*., 1996b; Foppen *et al*., 2000) similar to a metapopulation. Despite this superficial similarity, turnover is generally at the scale of territories, not isolated subpopulations and most patchily structured bird populations are continuous demes linked by frequent dispersal at a scale greater than patches (Andrén, 1994; Hinsley *et al*., 1994; Bellamy *et al*., 1996b); see Box 4.2. The metapopulation model (of independent local subpopulations linked by infrequent dispersal) is particularly inappropriate for seasonal re-settlement of long-distance migrants across small patches of habitat. For generalists (defined as species that did not show a preference for, or avoidance of, forest edges) the lack of any area–density effects (i.e. mean slope = zero) in a meta-analysis across 12 avian studies (Bender *et al*., 1998) suggests these species are not subject to area-dependent extinction or colonisation rates, in contrast to assumptions of spatially explicit metapopulation theory.

	and ecologically unimportant; although lacking the resources to support a local population it is generally considered sufficiently benign to allow dispersal (Vandermeer and Carvajal, 2001).	
Rescue effects	Large source populations are important to both regional and local persistence, through immigration and reinforcement that reduces extinction probability of vulnerable small local subpopulations (Brown and Kodric-Brown, 1977; Hanski and Gyllenberg, 1993).	**Some support**: Across 145 woodlands in eastern England (ranging from 0.02 ha to 10.30 ha) over three years, chaffinch had more ‘extinctions’ in woodlands with less woodland within 1 km, suggesting a rescue effect (Bellamy *et al*., 1996b). Reduced probability of ‘extinction’ with greater neighbourhood woodland area was also found in just one of two year-to-year models, for wren and robin. For blue tit fewer extinctions occurred in woodlands connected to more hedges, possibly suggesting rescue effects, but confounded by greater effective habitat area of the focal wood. Across 235 small wood lots in the Netherlands (ranging from 0.1 to 39 ha), woodland extent in the local landscape influenced the number of woodland species found, in addition to strong primary effects of patch area (van Dorp and Opdam, 1987). For reedbed patches, the distance-weighted sum of habitat extent within 10 km affected incidence and ‘extinction probability’ of reed warbler *Acrocephalus scirpaceus* (Foppen *et al*., 2000).

Appendix E4.3B (*cont.*)

Hypothesis	Assumption or prediction	Evidence
Mainland-island metapopulation and **key patch theory**	Repeated re-colonisation of ephemeral subpopulations in small patches by individuals dispersing from a persistent source population in a large habitat fragment ('mainland'). Islands are largely irrelevant to regional persistence that depends on the mainland population (Harrison, 1994). A single-species version of the island biogeography model of MacArthur and Wilson. Similarly, Verboom *et al*. (2001) expressed this as the 'key patch' approach to network design. Regional population persistence is enhanced by creation of one or more key patches – large enough to support a persistent local population semi-indefinitely in the absence of immigration. For forest interior birds, these would comprise large forest fragments with extensive core habitat.	**Some support** for archipelago effects, but often semi-anecdotal or poorly replicated. In a spatially explicit, individual-based simulation model of nuthatch (a sedentary forest specialist with poor dispersal ability), in a landscape of small woodland fragments in eastern England, persistence was attributed to immigration from a neighbouring regional source population; in the absence of immigration the modelled population did not persist (Alderman *et al*., 2005). Across 16 fragmented woodland patches in a sparsely wooded region (mean 2.6% cover) of North Humberside, England (McCollin, 1993), species richness of woodland birds was strongly related to the distance to the boundary of an adjacent 'wooded archipelago' (with >4% woodland cover) as well as to woodland area; however, the number of replicate woodlands was low relative to the number of predictors considered. **Strong theoretical support for key patch theory, but lacks empirical tests for birds**: For most metapopulation systems (including territory models with individual dispersal), resilience is best enhanced by creation of core patches, not investment in buffering small fragments, stepping stones or connectivity. In the

		nuthatch metapopulation model (Alderman *et al*., 2005), buffering all small patches did not prevent regional extinction, buffering the single largest patch prevented extinction, for less area of habitat creation. Vermaat *et al*. (2008) applied a key patch assumption to a metapopulation analysis of wetland bird species across 14 wetland complexes (3–55 km^2) in the Netherlands; however, findings depended on assumptions with no test of whether key patches or dispersal among networks contributed to local or regional persistence.
Regional population effects	Local occupancy requires a large extent of source habitat, reduction in habitat extent leads to local and regional extinction (Virkkala, 1991). Metapopulation theory provides a similar prediction, but regional population effects are not restricted to metapopulation dynamics among extinction-prone local subpopulations).	**Strong support** from Finland (see Box 4.3). For resident low-density species, regional population effects may be important at surprisingly large scales (>> 100s km^2). In England, persistence of strong regional populations of whinchat *Saxicola rubetra* in Salisbury Plain (SPA area 197 km^2), in contrast to wider declines may similarly indicate the importance of regional habitat extent.
Filtering of assemblages	Local assemblages in regions with reduced habitat extent are expected to be filtered, with loss of low-density, large-area specialists (Virkkala, 1991; Dolman *et al*., 2007).	**Strong support** from Finland (Virkkala, 1991) (see Box 4.3), and from meta-analysis of European area-richness studies of woodland birds (Tellería *et al*., 2003).
Regional landscape structure affects nest failure rates	Nest failure rates of forest birds are greater in fragmented landscapes with more non-forest and farmland habitats, due to greater abundance of generalist mobile predators that permeate through all habitats irrespective of local edge proximity. Can be tested by measuring nest success rates of real (not artificial) nests and the	**Strong support**: Provided by studies of nest success in relation to forest extent in the Midwestern USA (Robinson *et al*., 1995) and for forest grouse in Finland (Kurki *et al*., 1998, 2000), also from studies of activity and abundance of generalist predators (Donovan *et al*., 1997) and in fragmentation studies conducted at landscape rather

Appendix E4.3B *(cont.)*

Hypothesis	Assumption or prediction	Evidence
	abundance and activity of known nest predators, in relation to regional- or landscape-scale habitat composition.	than at finer scales (Chalfoun *et al*., 2002; Stephens *et al*., 2003). See Box 4.1.
Source–sink population dynamics	Subpopulations in poor-quality habitats, local landscape elements or regional landscapes are non-viable and are only maintained by immigration from viable source patches, habitats or landscapes (Pulliam, 1988; Robinson *et al*., 1995) . A special case of the **buffer effect**, with demographic rates in poor-quality landscape elements having per capita population growth <1.	**Some support**: Avian populations in fragmented landscapes are often discussed in terms of source–sink dynamics; for example in models or discussion of edge effects or fragmentation effects on nest success rates (Robinson *et al*., 1995; Donovan and Lamberson, 2001; Perkins *et al*., 2003; Vergara and Hahn, 2009) or analyses that assume a metapopulation structure (Foppen *et al*., 2000). However, this does not yet appear to be supported by examination of both demography and movement rates among landscapes or landscape elements, or experimental tests. Source–sink dynamics among territories within a local population (Manolis *et al*., 2002) are best considered in the context of buffer effects mediating population-scale per capita productivity (below).
Buffer effect	Density dependence arising through sequential settlement of habitats or landscape elements of varying quality, where patch use or settlement is constrained by competition or territoriality (Kluijver and Tinbergen, 1953; Brown, 1969)	**Strong evidence at habitat scale, very likely important for landscape structure effects**: Buffer effects through breeding habitat heterogeneity have been demonstrated in a wide range of bird species, including waders (Ens *et al*., 1992; Gunnarsson *et al*., 2005), raptors (Newton,

	Buffer effects can potentially operate through landscape composition effects if demographic rates differ among habitats, but also though landscape configuration effects if area or shape of landscape elements affects their demographic quality. See Fig. 4.4.	1991; Ferrer and Donazar, 1996; Krüger and Lindström, 2001), corvids (Andrén, 1990) and passerines (Kluijver and Tinbergen, 1953; Brown, 1969; Krebs, 1971; Dhondt *et al*., 1992; Brown, 1969; Sherry and Holmes, 1989; van den Berga *et al*., 2001; Burskiĭ, 2008). Far fewer studies have demonstrated demographic buffer effects through landscape configuration. Survival and productivity rates of grasshopper sparrow in dry prairie fragments in central Florida suggested core areas (> 400 m from habitat edges) were sources, compared to sink habitat along wide fragment borders (Perkins *et al*., 2003). Large fragments (possibly >4000 ha) were considered necessary to maintain local populations; however, number of sites and duration (three years) were limited. For ovenbird territories <100 m from forest edge, productivity was less than mortality, suggesting that this is a sink habitat (Manolis *et al*., 2002). In eastern England, for some woodland species, patch-area incidence functions differed significantly between years with greater and lower regional population abundance (Bellamy *et al*., 2000). For example, chiffchaff occupied relatively fewer small patches when regional abundance was low (Hinsley *et al*., 1996); if patch-area preferences affect productivity this will form the basis for a buffer effect.

References to Electronic Appendices E4.1 to E4.3

Åberg, J., Jansson, G., Swenson, J. E. and Anglestam, P. (1995). The effect of matrix on the occurrence of hazel grouse (*Bonasa bonasia*) in isolated habitat fragments. *Oecologia*, **103**, 265–269.

Alatalo, R. V., Lundberg, A. and Björklund, M. (1982). Can the song of male birds attract other males? An experiment with the Pied Flycatcher *Ficedula hypoleuca*. *Bird Behav*., **4**, 42–45.

Alderman, J., McCollin, D., Hinsley, S. A., Bellamy, P. E., Picton, P. and Crockett, R. (2005). Modelling the effects of dispersal and landscape configuration on population distribution and viability in fragmented habitat. *Landscape Ecol.*, **20**, 857–870.

Ambuel, B. and Temple, S. A. (1983). Area-dependent changes in the bird communities and vegetation of southern Wisconsin. *Ecology*, **64**, 1057–1068.

Andrén, H. (1990). Despotic distributions, unequal reproductive success and population regulation in the jay *Garrulus glandarius L*. *Ecology*, **71**, 1796–1803.

Andrén, H. (1992). Corvid density and nest predation in relation to forest fragmentation: a landscape perspective. *Ecology*, **73**, 794–804.

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

Andrén, H. (1999). Habitat fragmentation, the random sample hypothesis and critical thresholds. *Oikos*, **84**, 306–308.

Askins, R. A. and Philbrick, M. J. (1987). Effects of changes in regional forest abundance on the decline and recovery of a forest bird community. *Wilson Bull.*, **99**, 7–21.

Askins, R. A., Philbrick, M. J. and Sugeno, D. S. (1987). Relationship between the regional abundance of forest and the composition of forest bird communities. *Biol. Conserv.*, **39**, 129–152.

Askins, R. A., Zuckerberg, B. and Novak, L. (2007). Do the size and landscape context of forest openings influence the abundance and breeding success of shrubland songbirds in southern New England? *For. Ecol. Manage*., **250**, 137–147.

Austen, M. J. W., Francis, C. M., Burke, D. M. and Bradstreet, W. (2001). Landscape context and fragmentation effects on forest birds in southern Ontario. *Condor*, **103**, 701–714.

Austin, G. E., Thomas, C. J., Houston, D. C. and Thompson, D. B. A. (1996). Predicting the spatial distribution of buzzard *Buteo buteo* nesting areas using a Geographical Information System and remote sensing. *J. Appl. Ecol.*, **33**, 1541–1550.

Barbaro, L., Rossi, J. P., Vetillard, F., Nezan, J. and Jactel, H. (2007). The spatial distribution of birds and carabid beetles in pine plantation forests: The role of landscape composition and structure. *J. Biogeogr.*, **34**, 652–664.

Bátary, P. and Baldi, A. (2004). Evidence of an edge effect on avian nest success. *Conserv. Biol.*, **18**, 389–400.

Bayard, T. S. and Elphick, C. S. (2010). How area sensitivity in birds is studied. *Conserv. Biol.*, **24**, 938–947.

Bayne, E. M. and Hobson, K. A. (2001). Movement patterns of adult male ovenbirds during the post-fledging period in fragmented and forested boreal landscapes. *Condor*, **103**, 343–351.

Bellamy, P. E. and Hinsley, S. A. (2005). The role of hedgerows in linking woodland birds populations. *Planning, People and Practice: The Landscape Ecology of Sustainable Landscapes. Proceedings 13th Annual IALE(UK) Conference*, ed. D. McCollin and J. I. Jackson, pp. 99–106. Northampton: University of Northhampton.

Bellamy, P. E., Hinsley, S. A. and Newton, I. (1996a). Factors influencing bird species numbers in small woods in south-east England. *J. Appl. Ecol.*, **33**, 249–262.

Bellamy, P. E., Hinsley, S. A. and Newton, I. (1996b). Local extinctions and recolonisations of passerine bird populations in small woods. *Oecologia*, **108**, 64–71.

Bellamy, P. E., Rothery, P. and Hinsley, S. A. (2003). Synchrony of woodland bird populations: the effect of landscape structure. *Ecography*, **26**, 338–348.

Bellamy, P. E., Rothery, P., Hinsley, S. A. and Newton, I. (2000). Variation in the relationship between numbers of breeding pairs and woodland area for passerines in fragmented habitats. *Ecography*, **23**, 130–138.

Bender, D. J., Contreras, T. A. and Fahrig, L. (1998). Habitat loss and population decline: A meta-analysis of the patch size effect. *Ecology*, **79**, 517–533.

Bennett, A. F., Radford, J. Q. and Haslem, A. (2006). Properties of land mosaics: Implications for nature conservation in agricultural environments. *Biol. Conserv.*, **133**, 250–264.

Berkeley, L. I., McCarty, J. P. and Wolfenbarger, L. L. (2007). Postfledging survival and movement in Dickcissels (*Spiza americana*): implications for habitat management and conservation. *Auk*, **124**, 396–409.

Betts, M. G., Forbes, G. J., Diamond, A. W. and Taylor, P. D. (2006). Independent effects of habitat amount and fragmentation on songbirds in a forest mosaic. *Ecol. Appl.*, **16**, 1076–1089.

Betts, M. G., Hadley, A. S., Rodenhouse, N. and Nocera, J. J. (2008). Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proc. R. Soc. B*, **275**, 2257–2263.

Boulinier, T., Nichols, J. D., Hines, J. E. *et al.* (2001). Forest fragmentation and bird community dynamics: inference at regional scales. *Ecology*, **82**, 1159–1169.

Brotons, L., Desrochers, A. and Turcotte, Y. (2001). Food hoarding behaviour of black-capped chickadees (*Poecile atricapillus*) in relation to forest edges. *Oikos*, **95**, 511–519.

Brotons, L., Mönkkönen, M. and Martin, J. L. (2003). Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *Am. Nat.*, **162**, 343–357.

Brotons, L., Wolff, A., Paulus, G. and Martin, J.-L. (2005). Effect of adjacent agricultural habitat on the distribution of passerines in natural grasslands. *Biol. Conserv.*, **124**, 407–414.

Brown, J. H. and Kodric-Brown, A. (1977). Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology*, **58**, 445–449.

Brown, J. L. (1969). The buffer effect and productivity in tit populations. *Am. Nat.*, **103**, 347–354.

Burke, D. M. and Nol, E. (1998). Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk*, **115**, 96–104.

Burskiĭ, O. V. (2008). [Habitat selection and metapopulation structure: a multi-year study of distribution of the Hodgson's pipit, *Anthus hodgsoni* Richm. (Aves, Passeriformes)]. *Zh. Obshch. Biol.*, **69**, 323–343.

Caplat, P. and Fonderflick, J. (2009). Area mediated shifts in bird community composition: a study on a fragmented Mediterranean grassland. *Biodivers. Conserv.*, **18**, 2979–2995.

Chalfoun, A. D., Thompson, F. R. III, and Ratnaswamy, M. J. (2002). Nest predators and fragmentation: a review and meta-analysis. *Conserv. Biol.*, **16**, 306–318.

Cieslak, M. (1985). Influence of forest size and other factors on breeding bird species number. *Ekol. Polska*, **33**, 103–121.

Coleman, B. D. (1981). On random placement and species-area relations. *Math. Biosci.*, **54**, 191–215.

Connor, E. F. and McCoy, E. D. (1979). The statistics and biology of the species-area relationship. *Am. Nat.*, **113**, 791–833.

Cornell, K. L. and Donovan, T. M. (2010). Effects of spatial habitat heterogeneity on habitat selection and annual fecundity for a migratory forest songbird. *Landscape Ecol.*, **25**, 109–122.

Creegan, H. P. and Osborne, P. E. (2005). Gap-crossing decisions of woodland songbirds in Scotland: An experimental approach. *J. Appl. Ecol.*, **42**, 678–687.

Dale, S. and Manceau, N. (2003). Habitat selection of two locally sympatric species of *Emberiza* buntings (*E. citrinella* and *E. hortulana*). *J. Ornithol.*, **144**, 58–68.

Dallimer, M., Marini, L., Skinner, A. M. J., Hanley, N., Armsworth, P. R. and Gaston, K. J. (2010). Agricultural land-use in the surrounding landscape affects moorland bird diversity. *Agric. Ecosyst. Environ.*, **139**, 578–583.

Desrochers, A. and Hannon, S. J. (1997). Gap crossing decisions by forest songbirds during the post-fledging period. *Conserv. Biol.*, **11**, 1204–1210.

Dhondt, A. A., Kempenaers, B. and Adriaensen, F. (1992). Density-dependent clutch size caused by habitat heterogeneity. *J. Anim. Ecol.*, **61**, 643–648.

Doherty, P. F., Jr. and Grubb, T. C., Jr. (2002). Survivorship of permanent resident birds in a fragmented landscape. *Ecology*, **83**, 844–857.

Doherty, P. F. J. and Grubb, T. C. J. (2003). Relationship of nutritional condition of permanent-resident woodland birds with woodlot area, supplemental food, and snow cover. *Auk*, **120**, 331–336.

Dolman, P. M. and Fuller, R. J. (2003). The processes of species colonisation in wooded landscapes: a review of principles. *The Restoration of Wooded Landscapes*, ed. J. Humphrey, A. Newton, J. Latham, H. Gray, K. Kirby, E. Poulsom and C. Quine, pp. 25–36. Edinburgh: Forestry Commission.

Dolman, P. M., Hinsley, S. A., Bellamy, P. E. and Watts, K. (2007). Woodland birds in patchy landscapes: the evidence base for strategic networks. *Ibis*, **149** (Suppl. 2), 146–160.

Donovan, T. M., Jones, P. W., Annand, E. M. and Thompson, F. R., III. (1997). Variation in local scale edge effects: mechanisms and landscape context. *Ecology*, **78**, 2064–2075.

Donovan, T. M. and Lamberson, R. H. (2001). Area-sensitive distributions counteract negative effects of habitat fragmentation on breeding birds. *Ecology*, **82**, 1170–1179.

Dunning, J. B., Borgella, R., Clements, K. and Meffe, G. K. (1995). Patch isolation, corridor effects and colonization by a resident sparrow in a managed pine woodland. *Conserv. Biol.*, **9**, 542–550.

Dunning, J. B., Danielson, B. J. and Pulliam, H. R. (1992). Ecological processes that affect populations in complex landscapes. *Oikos*, **65**, 169–175.

Edenius, L. and Sjöberg, K. (1997). Distribution of birds in natural landscape mosaics of old-growth forests in northern Sweden: relations to habitat area and landscape context. *Ecography*, **20**, 425–431.

Ens, B. J., Kersten, M., Brenninkmeijer, A. and Hulscher, J. B. (1992). Territory quality, parental effort and reproductive success of oystercatchers (*Haematopus ostralegus*). *J. Anim. Ecol.*, **61**, 703–715.

Evans, M. D. (2002). *GIS-based Modelling of Woodlark* (Lullula arborea) *and Nightjar* (Caprimulgus europaeus) *Habitats in a Forested Landscape*. PhD Thesis, University of East Anglia, Norwich.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. *Annu. Rev. Ecol. Syst.*, **34**, 487–515.

Ferrer, M. and Donazar, J. A. (1996). Density-dependent fecundity by habitat heterogeneity in an increasing population of Spanish imperial eagles. *Ecology*, **77**, 69–74.

Flaspohler, D. J., Temple, S. A. and Rosenfield, R. N. (2001). Species specific edge effects on nest success and breeding bird density in a forested landscape. *Ecol. Appl.*, **11**, 32–46.

Fletcher, R. J. Jr. and Koford, R. R. (2003). Spatial responses of Bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. *Auk*, **120**, 799–810.

Foppen, R. F. B., Chardon, J. P. and Liefveld, W. (2000). Understanding the role of sink patches in source-sink metapopulations: reed warbler in an agricultural landscape. *Conserv. Biol.*, **14**, 1881–1892.

Forsman, E. D., Meslow, E. C. and Wight, H. M. (1984). Distribution and biology of the spotted owl in Oregon. *Wildlife Monogr.*, **87**, 1–64.

Freemark, K. E. and Collins, B. (1992). Landscape ecology of birds breeding in temperate forest fragments. In *Ecology and Conservation of Neotropical Migrant Landbirds*, ed. J. M. Hagan and D. W. Johnston, pp. 443–454. Washington DC: Smithsonian Institution Press.

Fuller, R. J., Hinsley, S. A. and Swetnam, R. D. (2004). The relevance of non-farmland habitats, uncropped areas and habitat diversity to the conservation of farmland birds. *Ibis*, **146** (suppl. 2), 22–31.

Fuller, R. J., Trevelyan, R. J. and Hudson, R. W. (1997). Landscape composition models for breeding bird populations in lowland English farmland over a 20 year period. *Ecography*, **20**, 295–307.

García, J., Suárez-Seoane, S., Miguélez, D., Osborne, P. E. and Zumalacárregui, C. (2007). Spatial analysis of habitat quality in a fragmented population of little bustard (*Tetrax tetrax*): implications for conservation. *Biol. Conserv.*, **137**, 45–56.

Gates, J. E. and Gysel, L. W. (1978). Avian nest dispersion and fledging success in field-forest ecotones. *Ecology*, **59**, 871–883.

Groom, J. D. and Grubb, T. C. Jr. (2006). Patch colonization dynamics in Carolina chickadees (*Poecile carolinensis*) in a fragmented landscape: A manipulative study. *Auk*, **123**, 1149–1160.

Gunnarsson, T. G., Gill, J. A., Petersen, A., Appleton, G. F. and Sutherland, W. J. (2005). A double buffer effect in a migratory shorebird population. *J. Anim. Ecol.*, **74**, 965–971.

Haila, Y., Hanski, I. and Raivio, S. (1993). Turnover of breeding birds in small forest fragments: the “sampling” colonization hypothesis corroborated. *Ecology*, **74**, 714–725.

Halme, E. and Niemelä, J. (1993). Carabid beetles in fragments of coniferous forest. *Ann. Zool. Fenn.*, **30**, 17–30.

Hanski, I. (1994). A practical model of metapopulation dynamics. *J. Anim. Ecol.*, **63**, 151–162.

Hanski, I. (1998). Metapopulation dynamics. *Nature*, **396**, 41–49.

Hanski, I. (1999). *Metapopulation Ecology*. Oxford: Oxford University Press.

Hanski, I. and Gyllenberg, M. (1993). Two general metapopulation models and the core-satellite species hypothesis. *Am. Nat.*, **142**, 17–41.

Harrison, S. (1994). Metapopulations and conservation. In *Large-Scale Ecology and Conservation Biology*, ed. P. J. Edwards, R. M. May and N. R. Webb, pp. 111–128. Oxford: Blackwell Scientific Publications.

Helzer, C. J. and Jelinski, D. E. (1999). The relative importance of patch area and perimeter-area ratio to grassland breeding birds. *Ecol. Appl.*, **9**, 1448–1458.

Herkert, J. R. (1994). The effects of habitat fragmentation on Midwestern grassland bird communities. *Ecol. Appl.*, **4**, 461–471.

Herrando, S. and Brotons, L. (2002). Forest bird diversity in Mediterranean areas affected by wildfires: a multi-scale approach. *Ecography*, **25**, 161–172.

Hinsley, S. A. (2000). The costs of multiple patch use by birds. *Landscape Ecol.*, **15**, 765–775.

Hinsley, S. A. and Bellamy, P. E. (2001). The influence of hedge structure, management and landscape context on the value of hedgerows to birds: A review. *J. Environ. Manage.*, **60**, 33–49.

Hinsley, S. A., Bellamy, P. E. and Newton, I. (1994). Persistence, loss and replacement of woodland birds in habitat patches in an arable landscape. In *Fragmentation in Agricultural Landscapes* ed. J. W. Dover, pp. 161–167. Aberdeen: IALE(UK).

Hinsley, S. A., Bellamy, P. E., Newton, I. and Sparks, T. H. (1996). Influences of population size and woodland area on bird species distributions in small woods. *Oecologia*, **105**, 100–106.

Hinsley, S. A., Rothery, P. and Bellamy, P. E. (1999). Influence of woodland area on breeding success in Great Tits *Parus major* and Blue Tits *Parus caeruleus*. *J. Avian Biol.*, **30**, 271–281.

Huhta, E., Aho, T., Jantti, A., Suorsa, P., Kuitunen, M., Nikula, A. and Hakkarainen, H. (2004). Forest fragmentation increases nest predation in the Eurasian treecreeper. *Conserv. Biol.*, **18**, 148–155.

Huhta, E. and Jokimäki, J. (2001). Breeding occupancy and success of two hole-nesting passerines: The impact of fragmentation caused by forestry. *Ecography*, **24**, 431–440.

Huhta, E., Jokimäki, J. and Rahko, P. (1998). Distribution and reproductive success of the pied flycatcher *Ficedula hypoleuca* in relation to forest patch size and vegetation characteristics; the effect of scale. *Ibis*, **140**, 214–222.

Huhta, E., Jokimäki, J. and Rahko, P. (1999). Breeding success of pied flycatchers in artificial forest edges: the effect of a suboptimally shaped foraging area. *Auk*, **116**, 528–535.

Jansson, G. and Andrén, H. (2003). Habitat composition and bird diversity in managed boreal forests. *Scand. J. For. Res.*, **18**, 225–236.

Jansson, G. and Anglestam, P. (1999). Threshold levels of habitat composition for the presence of the long-tailed tit (*Aegithalos caudatus*) in a boreal landscape. *Landscape Ecol.*, **14**, 283–290.

Johnson, D. H. and Igl, I. D. (2001). Area requirements of grassland birds: a regional perspective. *Auk*, **118**, 24–34.

Jokimäki, J., Huhta, E., Itämies, J. and Rahko, P. (1998). Distribution of arthropods in relation to forest patch size, edge, and stand characteristics. *Can. J. For. Res.*, **28**, 1068–1072.

King, D. I. and DeGraaf, R. M. (2004). Effects of group-selection opening size on the distribution and reproductive success of an early successional shrubland bird. *For. Ecol. Manage.*, **190**, 179–185.

King, D. I., Griffin, C. R. and DeGraaf, R. M. (1997). Effect of clearcut borders on distribution and abundance of forest birds in northern New Hampshire. *Wilson Bull.*, **109**, 239–245.

Kluijver, H. N. and Tinbergen, L. (1953). Territory and the regulation of density in titmice. *Arch. Neérl. Zool.*, **10**, 266–287.

Krebs, J. R. (1971). Territory and breeding density in the great tit, *Parus major L. Ecology*, **52**, 2–22.

Kroodsma, R. L. (1984). Effect of edge on breeding forest bird species. *Wilson Bull.*, **96**, 426–436.

Krüger, O. and Lindström, J. (2001). Habitat heterogeneity affects population growth in goshawk *Accipiter gentilis*. *J. Anim. Ecol.*, **70**, 173–181.

Kupfer, J. A., Malanson, G. P. and Franklin, S. B. (2006). Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecol. Biogeogr.*, **15**, 8–20.

Kurki, S., Nikula, A., Helle, P. and Lindén, H. (1998). Abundances of red fox and pine marten in relation to composition of boreal forest landscapes. *J. Anim. Ecol.*, **67**, 874–886.

Kurki, S., Nikula, A., Helle, P. and Lindén, H. (2000). Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. *Ecology*, **81**, 1985–1997.

Langlois, J. P., Fahrig, L., Merriam, G. and Artsob, H. (2001). Landscape structure influences continental distribution of hantavirus in deer mice. *Landscape Ecol.*, **16**, 255–266.

Lehnen, S. E. and Rodewald, A. D. (2009). Investigating area-sensitivity in shrubland birds: Responses to patch size in a forested landscape. *For. Ecol. Manage.*, **257**, 2308–2316.

Lens, L. and Dhondt, A. A. (1994). Effects of habitat fragmentation on the timing of crested tit *Parus cristatus* natal dispersal. *Ibis*, **136**, 147–152.

Levins, R. (1969). Some demographic and genetic consequences of environmental heterogeneity for biological control. *B. Entomol. Soc. Am.*, **15**, 237–240.

Levins, R. (1970). Extinction. In *Lectures on Mathematics in the Life Sciences, Vol 2: Some*

Mathematical Questions in Biology, ed. M. Gerstenhaber, pp. 75–107. Providence, Rhode Island: American Mathematical Society.

Lindenmayer, D., Hobbs, R. J., Montague-Drake, R. *et al*. (2007). A checklist for ecological management of landscapes for conservation. *Ecol. Lett.*, **10**, 1–14.

MacArthur, R. H., Diamond, J. M. and Karr, J. R. (1972). Density compensation in island faunas. *Ecology*, **53**, 330–342.

MacArthur, R. H. and Wilson, E. O. (1967) *The Theory of Island Biogeography*. Princeton University Press, Princeton.

Major, R. E., Christie, F. J., Gowing, G. and Ivison, T. J. (1999). Age structure and density of red-capped robin populations vary with habitat size and shape. *J. Appl. Ecol.*, **36**, 901–908.

Mallord, J. W., Dolman, P. M., Brown, A. F. and Sutherland, W. J. (2007). Linking recreational disturbance to population size in a ground-nesting passerine. *J. Appl. Ecol.*, **44**, 185–195.

Mallord, J. W., Dolman, P. M., Brown, A. F. and Sutherland, W. J. (2008). Seasonal trends in the breeding success of the multi-brooded woodlark *Lullula arborea* – late nests produce fewer recruits. *Bird Study*, **55**, 145–151.

Manolis, J. C., Andersen, D. E. and Cuthbert, F. J. (2002). Edge effect on nesting success of ground nesting birds near regenerating clearcuts in a forest-dominated landscape. *Auk*, **119**, 955–970.

Martinez, C. and Tapia, G. G. (2002). Density of the Little Bustard *Tetrax tetrax* in relation to agricultural intensification in central Spain. *Ardeola*, **49**, 301–304.

Matter, S. F. (1997). Population density and area: the role of between- and within-patch processes. *Oecologia*, **10**, 533–538.

Matthysen, E. and Adriaensen, F. (1998). Forest size and isolation have no effect on reproductive success of Eurasian nuthatches (*Sitta europaea*). *Auk*, **115**, 955–963.

Matthysen, E., Adriaensen, F. and Dhondt, A. A. (1995). Dispersal distances of nuthatches, *Sitta europaea*, in a highly fragmented forest habitat. *Oikos*, **72**, 375–381.

McCollin, D. (1993). Avian distribution patterns in a fragmented wooded landscape (North Humberside, UK): the role of between-patch and within-patch structure. *Global Ecol. Biogeogr. Lett.*, **3**, 48–62.

McCollin, D. (1998). Forest edges and habitat selection in birds: a functional approach. *Ecography*, **21**, 247–260.

Moilanen, A. and Hanski, I. (1998). Metapopulation dynamics: effects of habitat quality and landscape structure. *Ecology*, **79**, 2503–2515.

Mönkkönen, M., Helle, P., Niemi, G. J. and Montgomery, K. (1997). Heterospecific attraction affects community structure and migrant abundances in northern breeding bird communities. *Can. J. Zool.*, **75**, 2077–2083.

Mönkkönen, M., Helle, P. and Soppela, K. (1990). Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? *Oecologia*, **85**, 218–225.

Morales, M. B., García, J. T. and Arroyo, B. (2005). Can landscape composition changes predict spatial and annual variation of little bustard male abundance? *Anim. Conserv*, **8**, 167–174.

Moreira, F., Beja, P., Morgado, R., Reino, L., Gordinho, L., Delgado, A. and Borralho, R. (2005). Effects of field management and landscape context on grassland wintering birds in Southern Portugal. *Agric. Ecosyst. Environ.*, **109**, 59–74.

Newton, I. (1991). Habitat variation and population regulation in Sparrowhawks. *Ibis*, **133** (suppl.), 76–88.

Norton, M. R., Hannon, S. J. and Schmieglow, F. K. A. (2000). Fragments are not islands: patch vs. landscape perspectives on songbird presence and abundance in a harvested boreal forest. *Ecography*, **23**, 209–223.

Ortega, Y. K. and Capen, D. E. (1999). Effects of forest roads on habitat quality for Ovenbirds in a forested landscape. *Auk*, **116**, 937–946.

Perkins, D. W., Vickery, P. D. and Shriver, W. G. (2003). Spatial dynamics of source-sink habitats: effects on rare grassland birds. *J. Wildlife Manage.*, **67**, 588–599.

Pino, J., Roda, F., Ribas, J. and Pons, X. (2000). Landscape structure and bird species richness: implications for conservation in rural areas between natural parks. *Landscape Urban Plan.*, **49**, 35–48.

Pither, J. and Taylor, P. D. (1998). An experimental assessment of landscape connectivity. *Oikos*, **83**, 166–174.

Pulliam, H. R. (1988). Sources, sinks and population regulation. *Am. Nat.*, **132**, 652–661.

Radford, J. Q., Bennett, A. F. and Cheers, G. J. (2005). Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biol. Conserv.*, **124**, 317–337.

Raine, A. F. (2006). *The Breeding Ecology Of Twite* Carduelis flavirostris *And The Effects of Upland Agricultural Intensification*. PhD Thesis. University of East Anglia, Norwich.

Renfrew, R. B. and Ribic, C. A. (2008). Multi-scale models of grassland passerine abundance in a fragmented system in Wisconsin. *Landscape Ecol.*, **23**, 181–193.

Robinson, R. A., Wilson, J. D. and Crick, H. Q. P. (2001). The importance of arable habitat for farmland birds in grassland landscapes. *J. Appl. Ecol.*, **38**, 1059–1069.

Robinson, S. K., Thompson, F. R., III, Donovan, T. M., Whitehead, D. R. and Faaborg, J. (1995). Regional forest fragmentation and the nesting success of migratory birds. *Science*, **267**, 1987–1990.

Robles, H., Ciudad, C., Vera, R. and Baglione, V. (2007). No effect of habitat fragmentation on post-fledging, first-year and adult survival in the middle spotted woodpecker. *Ecography*, **30**, 685–694.

Robles, H., Ciudad, C., Vera, R., Olea, P. P. and Matthysen, E. (2008). Demographic responses of middle spotted woodpeckers (*Dendrocopos medius*) to habitat fragmentation. *Auk*, **125**, 131–139.

Rodewald, A. D. and Vitz, A. C. (2005). Edge and area-sensitivity of shrubland birds. *J. Wildlife Manage.*, **69**, 681–688.

Rodríguez, A., Andrén, H. and Jansson, G. (2001). Habitat-mediated predation risk and decision making of small birds at forest edges. *Oikos*, **95**, 383–396.

Rodríguez, A., Jansson, G. and Andrén, H. (2007). Composition of an avian guild in spatially structured habitats supports a competition-colonization trade-off. *Proc. R. Soc. B*, **274**, 1403–1411.

Rolstad, J. (1989). Effects of logging on capercaillie (*Tetrao urogallus*) leks. I. Cutting experiments in southeastern Norway. *Scand. J. For. Res.*, **4**, 99–109.

Rolstad, J. (1991). Consequences of forest fragmentation for the dynamics of bird populations: conceptual issues and the evidence. *Biol. J. Linn. Soc.*, **42**, 149–163.

Schmiegelow, F. K. A. and Mönkkönen, M. (2002). Habitat loss and fragmentation in dynamic landscapes: Avian perspectives from the boreal forest. *Ecol. Appl.*, **12**, 375–389.

Sherry, T. W. and Homes, R. T. (1989). Age-specific social dominance affects habitat use by breeding American redstarts (*Setophaga ruticilla*): a removal experiment. *Behav. Ecol. Sociobiol.*, **25**, 327–333.

Silva, J. P., Palmeirim, J. M. and Moreira, F. (2010). Higher breeding densities of the threatened little bustard *Tetrax tetrax* occur in larger grassland fields: Implications for conservation. *Biol. Conserv.*, **143**, 2553–2558.

Sisk, T. D., Haddad, N. M. and Ehrlich, P. R. (1997). Bird assemblages in patchy woodlands: modelling the effects of edge and matrix habitats. *Ecol. Appl.*, **7**, 1170–1180.

Smith, A. A., Redpath, S. M., Campbell, S. T. and Thirgood, S. J. (2001). Meadow pipits, red grouse and the habitat characteristics of managed grouse moors. *J. Appl. Ecol.*, **38**, 390–400.

Smith, A. T. and Peacock, M. M. (1990). Conspecific attraction and the determination of metapopulation colonization rates. *Conserv. Biol.*, **4**, 320–323.

St. Clair, C. C., Bélisle, M., Desrochers, A. and Hannon, S. J. (1998). Winter responses of forest birds to habitat corridors and gaps. *Conserv. Ecol. [online]*, **2**, 13.

Stephens, S. W., Koons, D. N., Rotella, J. J. and Willey, D. W. (2003). Effects of habitat fragmentation on avian nesting success: a review of the evidence at multiple spatial scales. *Biol. Conserv.*, **115**, 101–110.

Strelke, W. K. and Dickson, J. G. (1980). Effect of forest clear-cut edge on breeding birds in east Texas. *J. Wildlife Manage.*, **44**, 559–567.

Suarez, A. V., Pfennig, K. S. and Robinson, S. K. (1997). Nesting success of a disturbance-dependent songbird on different kinds of edges. *Conserv. Biol.*, **11**, 928–935.

Svärdson, G. (1949). Competition and habitat selection in birds. *Oikos*, **1**, 157–174.

Tellería, J. L., Baquero, R. and Santos, T. (2003). Effects of forest fragmentation on European birds: implications of regional differences in species richness. *J. Biogeogr.*, **30**, 621–628.

Tellería, J. L., Virgos, E., Carbonell, R., Pérez-Tris, J. and Santos, T. (2001). Behavioural responses to changing landscapes: flock structure and anti-predator strategies of tits wintering in fragmented forests. *Oikos*, **95**, 253–264.

Thomson, R. L., Forsman, J. T. and Mönkkönen, M. (2003). Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis. *Oecologia*, **134**, 431–438.

Tjernberg, M., Johnsson, K. and Nilsson, S. G. (1993). Density variation and breeding success of the black woodpecker *Dryocopus martius* in relation to forest fragmentation. *Ornis Fennica*, **70**, 155–162.

Trzcinski, M. K., Fahrig, L. and Merriam, G. (1999). Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. *Ecol. Appl.*, **9**, 586–593.

Turcotte, Y. and Desrochers, A. (2005). Landscape-dependent distribution of northern forest birds in winter. *Ecography*, **28**, 129–140.

Vallecillo, S., Brotons, L. and Herrando, S. (2008). Assessing the response of open-habitat bird species to landscape changes in Mediterranean mosaics. *Biodivers. Conserv.*, **17**, 103–119.

van den Berga, L. J. L., Bullock, J. M., Clarke, R. T., Langston, R. H. W. and Rose, R. J. (2001). Territory selection by the Dartford warbler (*Sylvia undata*) in Dorset, England: the role of vegetation type, habitat fragmentation and population size. *Biol. Conserv.*, **120**, 137–143.

van Dorp, J. and Opdam, P. F. M. (1987). Effects of patch size, isolation and regional abundance on forest bird communities. *Landscape Ecol.*, **1**, 59–73.

Vandermeer, J. and Carvajal, R. (2001). Metapopulation dynamics and the quality of the matrix. *Am. Nat.*, **158**, 211–220.

Verboom, J., Foppen, R., Chardon, P., Opdam, P. and Luttikhuizen, P. (2001). Introducing the key patch approach for habitat networks with persistent populations: an example for marshland birds. *Biol. Conserv.*, **100**, 89–101.

Vergara, P. M. and Armesto, J. J. (2009). Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. *Landscape Ecol.*, **24**, 25–38.

Vergara, P. M. and Hahn, I. (2009). Linking edge effects and patch size effects: Importance of matrix nest predators. *Ecol. Model.*, **220**, 1189–1196.

Vermaat, J. E., Vigneau, N. and Omtzigt, N. (2008). Viability of meta-populations of wetland birds in a fragmented landscape: testing the key-patch approach. *Biodivers. Conserv.*, **17**, 2263–2273.

Vickery, P. D., Hunter, M. L. Jr. and Melvin, S. M. (1994). Effects of habitat area on the distribution of grassland birds in Maine. *Conserv. Biol.*, **8**, 1087–1097.

Villard, M.-A., Martin, P. R. and Drummond, C. G. (1993). Habitat fragmentation and pairing success in the ovenbird (*Seiurus aurocapillus*). *Auk*, **110**, 759–768.

Villard, M.-A., Merriam, G. and Maurer, B. A. (1995). Dynamics in subdivided populations of Neotropical migratory birds in a temperate fragmented forest. *Ecology*, **76**, 27–40.

Villard, M.-A., Trzcinski, M. K. and Merriam, G. (1999). Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. *Conserv. Biol.*, **13**, 774–783.

Virkkala, R. (1991). Population trends of forest birds in a Finnish Lapland landscape of large habitat blocks: Consequences of stochastic environmental variation or regional habitat alteration? *Biol. Conserv.*, **56**, 223–240.

Watson, J. E. M., Whittaker, R. J. and Freudenberger, D. (2005). Bird community responses to habitat fragmentation: how consistent are they across landscapes? *J. Biogeogr.*, **32**, 1353–1370.

Wegge, P. and Rolstad, J. (1986). Size and spacing of capercaillie leks in relation to social behavior and habitat. *Behav. Ecol. Sociobiol.*, **19**, 401–408.

Whittingham, M. J., Percival, S. M. and Brown, A. F. (2000). Time budgets and foraging of breeding golden plover *Pluvialis apricaria*. *J. Appl. Ecol.*, **37**, 632–646.

Widén, P. (1989). The hunting habitats of goshawk *Accipiter gentilis* in boreal forests of central Sweden. *Ibis*, **131**, 205–213.

Wilkin, T. A., Garant, D., Gosler, A. G. and Sheldon, B. C. (2007). Edge effects in the great tit: Analyses of long-term data with GIS techniques. *Conserv. Biol.*, **21**, 1207–1217.

Winter, M. and Faaborg, J. (1999). Patterns of area sensitivity in grassland-nesting birds. *Conserv. Biol.*, **13**, 1424–1436.

Winter, M., Johnson, D. H. and Faaborg, J. (2000). Evidence for edge effects on multiple levels in tallgrass prairie. *Condor*, **102**, 256–266.

Wolff, A. (2004). (Influence of the habitats mosaic on the ecology and distribution of the little bustard in the Crau). *Ecol. Mediterranea*, **30**, 111–132.

Wolff, A. (2005). Influence of landscape and habitat heterogeneity on the distribution of steppe-land birds in the Crau, southern France. In *Ecology and Conservation of Steppe-land Birds*, ed. G. Bota, M. B. Morales, S. Mañosa and J. Camprodon, pp. 141–168. Barcelona: Lynx Edicions and Centre Tecnològic Forestal de Catalunya.

Woodward, A. A., Fink, A. D. and Thompson, F. R., III. (2001). Edge effects and ecological traps: Effects on shrubland birds in Missouri. *J. Wildlife Manage.*, **65**, 668–675.

Wright, L. (2006). *Demography and Productivity of Woodlarks* Lullula arborea *in Breckland*. PhD Thesis. University of East Anglia, Norwich.

Zanette, L., Doyle, P. and Tremont, S. M. (2000). Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology*, **81**, 1654–1666.