Landscape Permeability: From Individual Dispersal to Population Persistence

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Abstract

Landscape permeability, usually known as connectivity in landscape ecology, defines to what degree organisms are capable of moving through a landscape. It is an important functional aspect linking landscape structure to the dynamics of populations, when these are at least in part determined by emigration and immigration of individuals. Landscape permeability is thus most relevant in landscapes with fragmented habitat and where populations are organised as metapopulations. This chapter briefly reviews how the two paradigms "habitat fragmentation" and "metapopulation dynamics" are related, which main effects of habitat fragmentation on populations have been found, and how structural landscape elements such as edges, matrices, barriers and corridors may determine landscape permeability for dispersing individuals. We use an example from our own work on capercaillie (*Tetrao urogallus*; Aves; Tetraonidae) to illustrate how the commonly used static approach of relating spatial population patterns to landscape structure is limited by the lack of empirical data on how dispersal actually takes place, and how the problem may be mitigated by studying the result of the unknown dispersal by genetic methods. We then follow the development leading from static distribution models to dynamic, spatially explicit population models and conclude that validation lags behind the theoretical development, again as a matter of lack of data on dispersal, particularly for vagile, large-bodied animal species. The chapter is concluded with some management-related observations regarding the restoration of landscape connectivity by means of movement corridors.

Keywords: connectivity, fragmentation, metapopulations, modelling, SEPM, dispersers, capercaillie, *Tetrao urgallus*

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Introduction

Ecological processes operating within a landscape can be seen in their most basic form as the flow of matter, energy and information between habitats (Turner *et al.* 2001). Flow strength is controlled by the permeability of the landscape, i.e. by the spatial configuration of landscape elements supporting or restraining flow. In landscape ecology, permeability is usually known as connectivity, defined by the degree to which the landscape facilitates or impedes flow among resource patches (Bélisle 2005; Taylor *et al.* 1993; Tischendorf and Fahrig 2000). The notion of resource patchiness may thus be seen as an equivalent of habitat fragmentation. In this chapter, we address recent progress in linking individual dispersal to population persistence in fragmented habitats, focusing on animals (for plants see Holderegger *et al.* 2007). The theme has been extensively dealt with in the literature, including a number of books (e.g. Gutzwiller 2002; Hanski 1999; McCullough 1996) and paper series (e.g. Villard 2002). We concentrate on the question of how landscape structure influences the dispersal of individuals and thus affects (meta-)population dynamics, how this has been explored in theoretical and modelling approaches, and what empirical data are available.

We begin with a brief look at how the two paradigms "habitat fragmentation" and "metapopulation dynamics" are related, and at the main effects habitat fragmentation can have on populations. We then briefly discuss the role of structural landscape elements for landscape permeability to dispersing individuals. An example from our own work on capercaillie (*Tetrao urogallus;* Aves; Tetraonidae) illustrates how the commonly used static approach of relating spatial population patterns to landscape structure is limited by the lack of data on dispersing individuals. In the following chapter, we look at how this problem has been tackled so far, and which challenges remain. We end with some management-related conclusions.

Habitat Fragmentation and Metapopulation Dynamics: Two Basic Paradigms

We prefer the term «habitat fragmentation» to «landscape fragmentation», since it is the habitat rather than the landscape that become fragmented by human activity. Habitat fragmentation and its effects on populations have been a key issue in ecology since the 1970s, but the concept has proven multifaceted (Fahrig 2003). Implications from modelling and empirical results are similarly manifold, depending on which organisms, habitats, and biogeographical areas are studied (Haila 2002; Villard 2002), and which temporal and spatial scales are addressed (Debinski and Holt 2000; Urban 2005). In general, increasing habitat fragmentation is coupled with decreasing habitat patch size and increasing inter-patch distances across the «non-habitat» matrix (Turner *et al.* 2001). Fragmentation also results in an increase of boundary lines between habitat units, which can act as obstacles to dispersing individuals. Hence, habitat connectivity as seen from a biological point of view is reduced by fragmentation but in effect strongly depends on the dispersal ability (D'Eon *et al.* 2002) of the organism in question.

At about the same time as landscape ecology emerged as a discipline, the theory of metapopulation dynamics was developed by population ecologists. It aims at understanding the overall persistence of an array of local populations that are spatially separated but loosely linked by dispersal (Hanski and Gilpin 1997). Thus, metapopulation theory is easily applicable to animal populations in fragmented habitats (With 2004; for plants see Freckleton and Watkinson 2002). The rate at which individuals (or genes) are exchanged between local populations is central to the concept, and here metapopulation theory is bound to the idea of landscape connectivity.

The recent rapid development of tools for spatial analysis has directed much effort towards pattern analysis and development of landscape metrics or indices. As a result, landscape ecology has suffered from having neglected relationships between landscape patterns and ecological processes (Goodwin 2003; Li and Wu 2004; Wu and Hobbs 2002), although recent theoretical developments have helped to fill this gap (With 2002). Ironically, patch/matrix-oriented thinking in metapopulation theory has also given strong emphasis to patterns despite the fundamentally process-based nature of metapopulation models. Views thus differ on the general applicability of metapopulation models to natural systems (Baguette and Mennechez 2004; Shreeve *et al.* 2004). Most applications refer to small-bodied species such as arthropods and small mammals for which patch incidence is easily measured, but the concept should also be amenable to large mammals if dynamics of subpopulations are measured in terms of their demography (Elmhagen and Angerbjörn 2001). Modelling has steadily progressed in the last decade, but validation lags behind. There is an urgent need for empirical data on how organisms move through landscapes and thereby perceive and react to obstacles and resources (Bélisle 2005; Lidicker 2002; McGarigal and Cushman 2002), because metapopulation dynamics will ultimately be shaped by individual-based processes (see also paragraph "From structure to process: …", this chapter).

Effects of Fragmentation

Declining population size due to splitting up of contiguous habitats may simply reflect the decrease in habitat area, without any superimposed fragmentation effects (Fahrig 2003). Yet the reduction of population size associated with habitat fragmentation is often disproportionately larger than the proportion of habitat lost, especially when populations in small patches become extinct (Andrén 1994; Beier *et al.* 2002). Such immediate consequences of habitat fragmentation have primarily nurtured the scientific interest in this topic. Processes resulting in reduced fitness within isolated and small populations (Frankham *et al.* 2002; Young and Clarke 2000) are often related to increased amounts of boundaries (edge effects), which may alter regimes of predation, parasitism or disturbance (Hansson *et al.* 1995). Thus, habitat quality also decreases with decreasing patch size, and this may affect the persistence of populations. The probability that individuals from some other (source) patches immigrate will at the same time decrease, mainly because distances between patches have become larger and more difficult to overcome. Hence, size and number of habitat fragments and their spatial arrangement in a landscape play important roles in mortality/extinction and migration/colonisation rates. Matrix composition and quality are currently also being discovered as important factors in metapopulation research. Spatial aspects are now routinely incorporated in conservation modelling including viability analyses of vertebrate species with the aid of specialized software (Reed *et al.* 2002).

Genetic effects in small and isolated populations may additionally reduce reproductive success and lower population persistence (Lande 1999; Saccheri *et al.* 1998). Conservation genetic theory predicts that small population size tends to increase the probability of genetic drift (i.e. the random sampling of genetic variants), decreases genetic diversity (i.e. genetic erosion) and heterozygosity, increases breeding among related individuals (inbreeding), and reduces the fitness of inbred individuals (inbreeding depression; Young and Clarke 2000; Frankham *et al.* 2002). The viability of small populations may become reduced within only a few generations. On the other hand, diminished gene exchange among populations may lead to population differentiation (see paragraph "From structure to process: …", this chapter). Potential evolutionary differentiation as a consequence of habitat fragmentation reflects the fact that habitat fragmentation does not necessarily have a negative connotation *per se*.

Habitat islands can temporarily become safe from predators, parasitoids and diseases (Frankham *et al.* 2002) or temporarily support species that commute between different habitats, be it on a daily (e.g. feeding – shelter) or seasonal basis, or once in a life time (e.g. different juvenile and adult habitats). Generally, experimental fragmentation studies mainly show the immediate negative effects of habitat loss and habitat change during the first few years, i.e. the actual process of fragmentation (Zschokke *et al.* 2000), while long-term stabilising or even positive effects that might only come into play after years of community restructuring are often missed by shorter empirical studies.

Edges, Matrix, Barriers and Corridors: Requisites of Landscape Permeability

Because of increased edge length, the proportion of fragment area subject to influences originating in the surrounding land (i.e. the matrix) increases. Edge effects include both abiotic factors, such as wind or fire, and biotic factors, such as predators, parasites, disease vectors, or man (Laurance *et al.* 2002). Edge effects can often not be generalised (Lahti 2001). While edges may be penetrable from the outside, they may still act as barriers for many organisms living in the fragmented habitat but ready to disperse (Cale 2003). However, the strength of this effect may be more related to the contrast between habitat and matrix (Collinge and Palmer 2002; Holmquist 1998; Ricketts 2001) and the extent and structure of the matrix that has to be crossed (Haynes and Cronin 2003) than to the edge itself.

Habitat patches and surrounding matrices are usually considered to be binary systems of suitable and unsuitable habitat (Turner *et al.* 2001). Crossing ability and propensity are species- and often also sex-specific, but generally increase with body mass (Grubb and Doherty 1999). Many species are reluctant to cross even small expanses of unsuitable land, although they would be able to do so physically (Bélisle *et al.* 2001; Laurance *et al.* 2002; Gobeil and Villard 2002; Creegan and Osborne 2005). Independent of animal size, (behavioural) barriers may thus restrict movements across the landscape (Harris and Reed 2002). However, a rising number of studies on the dispersal behaviour of a wide range of animals provide evidence that the matrix does not simply consist of unsuitable «desert» between habitat islands, but that it can have some habitat quality of its own (Enoksson *et al.* 1995; Haynes and Cronin 2004; Bender and Fahrig 2005). Such quality will enhance the permeability of the matrix. Permeability may also depend on the spatial structure of the matrix, with some species using certain elements in preference to others when dispersing (Cale 2003). In heterogeneous landscapes, dispersal patterns are significantly affected by edge mediated behaviour (Ovaskainen 2004). When moving across boundaries, the strength of the contrast at boundaries determines the direction of movements of animals: low contrast boundaries exhibit net immigration, and high contrast boundaries experience net emigration (Collinge and Palmer 2002). While moving through different habitat types, the animals experience high variation in mortality risk and thus highly variable matrix permeability (Hein *et al.* 2003).

Linear landscape structures such as roads or rivers often act as barriers for many terrestrial animals; whereas for aquatic organisms, rivers function as dispersal corridors. Such linear landscape structures can therefore either reduce or increase species-specific landscape permeability (Forman and Alexander 1998). Animals may not cross a linear structure because of either physical or behavioural inability, or they simply avoid areas bordering linear man-made structures (Nellemann *et al.* 2001). Thus, road networks simultaneously fragment habitats and produce edge effects (Mech *et al.* 1988; Forman *et al.* 2003). Strips of remnant (or restored) habitat linking larger expanses of the same habitat (e.g. forest patches in an agricultural matrix) can work as corridors enhancing dispersal or migrational movements, particularly for larger ground-dwelling animals. There is still some controversy about how effectively corridors enhance connectivity of habitat patches (Beier and Noss 1998), as applications of the corridor concept in biological conservation have hardly been evaluated with respect to their capacity of defragmenting habitats at regional scales (Vos *et al.* 2002). Additionally, corridors are likely to favour groups of species with particular life histories more than other groups (Hudgens and Haddad 2003; see also paragraph "Managing landscape permeability", this chapter). For smaller organisms such as insects, strips of (semi-)natural vegetation often have significance as habitat *per se* rather than as movement corridor, and may even represent the last refuges for rare species (e.g. «road reserves», Saunders and Hobbs 1991). On the other hand, corridors, *sensu stricto*, may not be a prerequisite for successful dispersal of mobile species as long as a series of smaller habitat patches can function as «stepping stones» between larger habitat expanses and thus become a functional corridor (With 2002).

Landscape Permeability: Lessons from Capercaillie

The capercaillie *(Tetrao urogallus)*, one of the largest forest-dwelling galliform birds, serves to illustrate the importance of a detailed understanding of spatial landscape aspects in the conservation biology of endangered species. Habitats of capercaillie in Central Europe have become strongly fragmented, and most populations show recent decreasing trends (Klaus and Bergmann 1994; Storch 2000). Population decline and fragmentation have been particularly severe in the Swiss Alps after 1970 (Mollet *et al.* 2003). The remnants apparently form metapopulations (Segelbacher and Storch 2002). Here the contemporary spatial pattern of occupied forest areas resembles islands within a matrix of unsuitable woodland or open montane-subalpine farmland (Fig. 1). Conservation measures to halt the overall decline have rarely succeeded, probably because they were local in scope and neglected population processes operating at the landscape scale (i.e. hundreds of km^2; Storch 2002). A complex interplay of local habitat quality at the forest stand scale, regional habitat fragmentation, and large-scale climatic factors such as cold and wet summers is suspected to have caused the decline (Lindström *et al.* 1996). Since capercaillie possesses characteristics of an umbrella species, conserving the capercaillie will also benefit a wider array of bird species (Suter *et al.* 2002) and generally improve the habitat of subalpine forest communities.

Ecological factors driving population processes in capercaillie have been shown to operate on different spatial scales, from local stands to entire regions (10 ha to 100 km^2; Andrén 1994; Kurki *et al.* 2000; Storch 1997, 2002, 2003). For example, at least three spatial scales have to be considered to understand habitat requirements (Storch 1997): vegetation structure (small scale), stand mosaic (intermediate scale) and spatial arrangement of forests in the landscape (large scale). A habitat area described at the intermediate scale usually comprises stands both used and unused by capercaillie. Used stands are characterised by intermediate canopy cover, rich field-layer and low-branched solitary trees (Bollmann *et al.* 2005a). Graf *et al.* (2005) applied a habitat suitability model of the capercaillie for the central and eastern Prealps and Alps and produced a map of discrete distribution patches resembling a metapopulation pattern (Fig. 1). The total area of the patches (1,187 km^2) was much larger than the area actually occupied by capercaillie, but coincided with the former distribution of capercaillie in the seventies, when total Swiss population size was at least twice as large as it is today (Mollet *et al.* 2003).

According to a stochastic model of Grimm and Storch (2000), the minimum viable size for an isolated capercaillie population in the Alps is 470 individuals. This figure corresponds

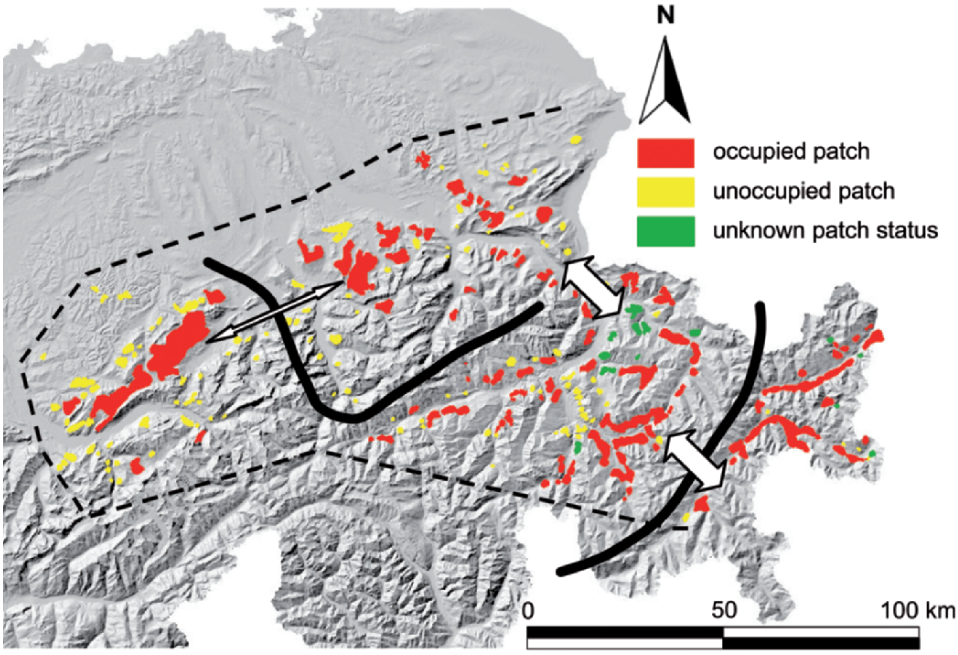

Fig. 1. Distribution and occupation of potential habitat patches by capercaillie *(Tetrao urogallus)* in the Central and Eastern Alps of Switzerland. Gene flow (arrows) among regions is derived from genetic analyses (Jacob *et al.*, WSL Birmensdorf, unpubl. data). Arrow sizes represent the relative amount of gene flow. The patches were predicted and derived from the habitat models of Graf *et al.* (2006). Areas believed to act as barriers to dispersal (Mollet *et al.* 2003) are depicted with thick lines. The dashed line denotes the study area.

to a minimum area requirement of 250 km², although in a metapopulation arrangement, patches of 50–100 km² might suffice as long as they allow the exchange of dispersers (Grimm and Storch 2000). Only four of the Alpine populations in Switzerland inhabit forest areas ≥100 km². We assume that these forests are the hubs of a habitat network of core populations which are spatially linked with smaller populations via dispersing individuals. Such metapopulations may thus manage with considerably less than 250 km² of forest area to be viable, but the dispersal rate between occupied patches would therefore be a key factor for the persistence of local capercaillie populations (Segelbacher and Storch 2002; Storch and Segelbacher 2000). Dispersal rate should depend on parameters related to the patches (patch area, patch quality and local population size) as well as parameters defining the gap (inter-patch distance, matrix quality, topography, anthropogenic barriers etc.). In the Swiss Alps, patches were occupied only if they were larger than 54 ha and less than 10 km away from the next occupied patch (Bollmann *et al.* 2005b). These results are in line with dispersal distances of 5–10 km determined by field observations and telemetric studies (review in Storch and Segelbacher 2000). Currently no empirical data are available for parameters that potentially influence dispersal rates in capercaillie.

Population genetic methods have the potential to significantly improve estimates of dispersal, where traditional field methods reach their limits. An evaluation of genetic differentiation of capercaillie populations in the European Alps revealed only low to moderate structuring, although populations at the northern edge of the Alps were clearly distinct from central Alpine populations (Segelbacher and Storch 2002). Genetic distances between different edge populations correlated significantly with geographic distances (isolation by distance), while central Alpine populations showed a higher degree of genetic differentiation from each other, irrespective of distance (Segelbacher and Storch 2002). Our own data (G. Jacob *et al.* unpubl., WSL Birmensdorf) provide evidence of some dispersal across mountain ridges dividing the central Swiss Alps and between the central Alps and the northern edge of the Alps. Surprisingly, there is much less exchange of individuals between central and eastern edge populations (Fig. 1). This is contrary to the common belief that the mountain chain stretching between the central Alpine populations and edge populations in eastern Switzerland forms a major barrier to dispersal, whereas the gap between the edge populations is only of recent origin. In summary, there seems to be still a considerable but varying level of dispersal, and hence connectivity, in the Swiss Alps. Finding discrepancies between estimates of dispersal made by telemetric methods and genetic investigations is a common experience. It may reveal the fact that telemetry measures the contemporary gene flow and genetic methods provide surrogates of the historic dispersal ability of the species. The discrepancies also illustrate well the need for a better understanding of how landscape structures promote or impede dispersal events. Judging landscape permeability is crucial for the effective conservation of capercaillie, but important questions remain unanswered, for example: which topographical features really function as dispersal barriers (see above); what role matrix characteristics play in dispersal; or how patch size and quality influence the dispersal ability and propensity of individual birds.

From Structure to Process: Current and Future Challenges

Understanding, modelling and predicting population dynamics and persistence in a spatially explicit context is a challenging task and a hot topic of current and possibly, future research. In Figure 2, we have tried to illustrate how we perceive linkages between approaches that are mainly landscape-, individual-, or population-based.

A starting point on the long way to understand the dynamics of populations in space is the understanding of landscapes and populations in terms of their structures. Landscape ecological work has originally been concerned with landscape metrics to describe, analyse and measure the structural units which form a landscape. Along with a growing interest in the functional understanding of landscape structure (Tischendorf and Fahrig 2000), more complex metrics such as measures of fragmentation or connectivity/cohesion (e.g. Chardon *et al.* 2003; Jaeger 2000; Opdam *et al.* 2003; Fig. 2 A1) were developed.

Landscape metrics, together with spatial information on species occurrence, are the raw material for modelling species distributions in relation to habitat quality and configuration, matrix resistance, corridors or barriers, and for modelling landscape connectivity and suitability for given species (Fig. 2 B1). Some studies have modelled ecological connectivity at the regional scale without referring to particular organisms (e.g. Marulli and Mallarach 2005), but in general the concept of landscape functioning needs an organismal reference in order to be meaningful. Most studies use empirical data on the occurrence of species (or entire communities; e.g. Perault and Lomolino 2000), whereas in the assessment of landscape permeability for a focal species, assumptions on how the species perceive landscape elements such as barriers might be used (Hunter *et al.* 2003). There are a wide range of modelling approaches for a wealth of species. These models are generally static and often probabilistic in nature (Burgman *et al.* 2005; Guisan and Zimmermann 2000). They have a

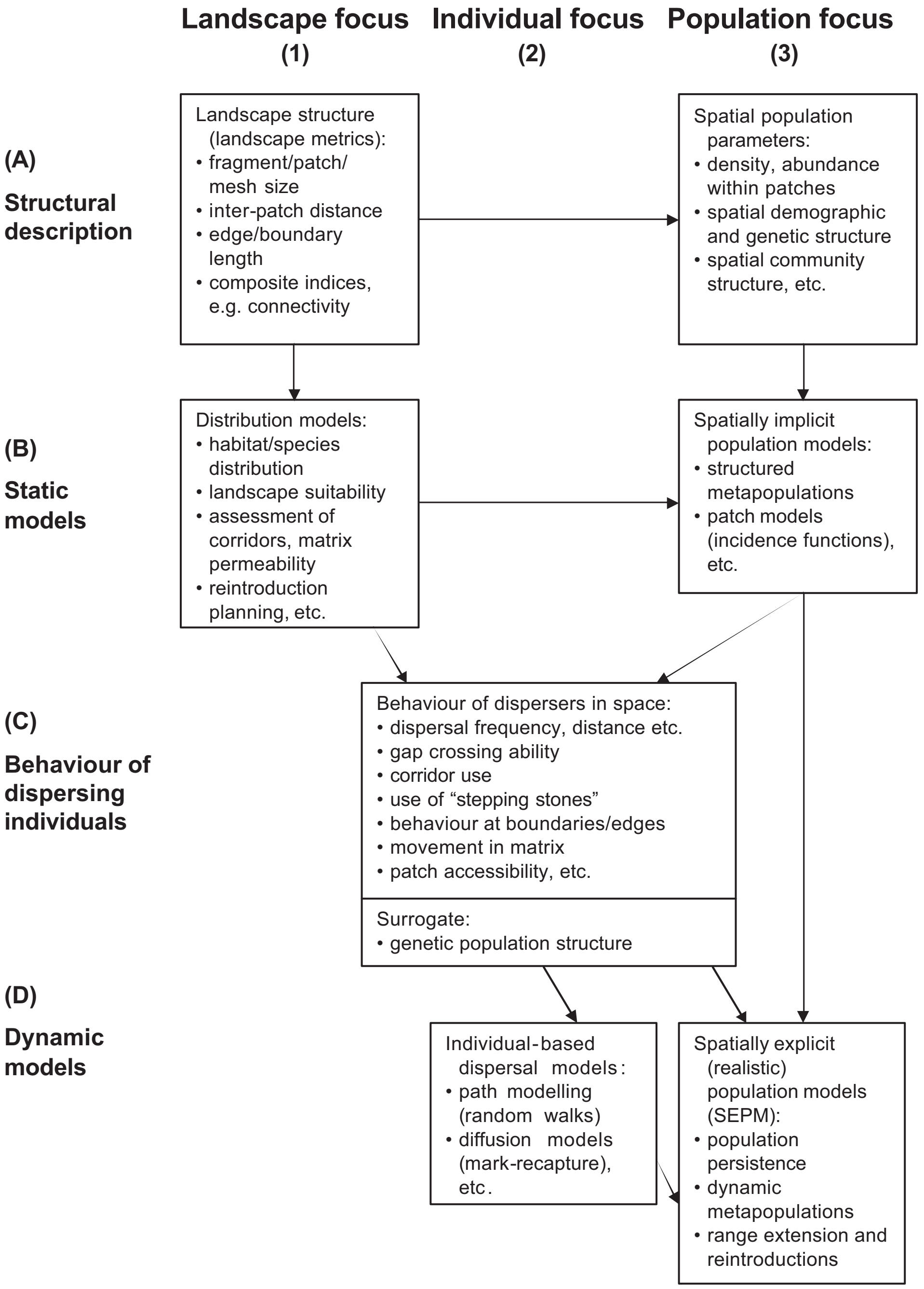

Fig. 2. Graphical representation of ways and linkages leading from structural information on landscapes and animal populations to spatially explicit (= realistic; Hanski and Gaggiotti 2004) population models (see text for explanations).

strong emphasis on landscape structural data, while data regarding the focal species are often rather crude measurements, such as presence/absence (incidence; e.g. Verbeylen *et al.* 2003). This is why we list them as "landscape-based" models. Many of these studies, however, are done in a conservation-related context. Our model of capercaillie distribution summarised above is a typical example, and it exemplifies the limits of this type of approach for understanding the viability of fragmented populations when demographic data are not available.

The way to progress beyond static models and eventually to understand how population dynamics are moulded by their landscape context starts by linking population parameters to landscape metrics (Fig. 2 A3). The variety of population parameters lending themselves to analysis ranges from measures of species abundance to temporally explicit demographic data but may also include approaches of studying the genetic structure of populations in space (see below). There is now a plethora of papers exploring spatial population structure in relation to landscape metrics, although a preponderance of studies using smaller vertebrates (small mammals, birds, amphibians etc.) is obvious. However, working with invertebrates on smaller spatial scales allows experimental approaches to be used (Grez *et al.* 2004; Haddad and Baum 1999) and provides insight into scale-dependence of species responses to landscape structure (Krawchuk and Taylor 2003).

Analogous to the landscape-based approach, modelling the distribution of populations in space will first produce a static model, which for fragmented landscapes is usually within the metapopulation framework (Hanski 1999; Hanski and Gaggiotti 2004; Hanski and Gilpin 1997). Our label "static" for structural metapopulation models in Figure 2 B3 simply means that the inherently dynamic aspect of patch extinction/colonisation is often based on assumptions about the dynamics of subpopulations rather than empirical data. In this case, the distribution pattern of a metapopulation as it is seen ("snapshot") is the outcome not only of population processes within the patch but also of unknown behavioural decisions of individual dispersers moving across a landscape (Andreassen *et al.* 2002; Sutherland 1996). The distinction between approaches classified as B1 or B3 in Figure 2 is thus small in many published examples.

From this point onwards, however, progress in understanding how populations behave under the constraints set by real landscapes cannot be achieved without taking the behaviour of dispersing individuals into account. Dispersal, particularly in an evolutionary context or in terms of geographical patterns (Bullock *et al.* 2002; Clobert *et al.* 2001), has been well studied. However, dispersal as an individual-based process, in which organisms move through a landscape, navigate, and make decisions in response to habitat and landscape structures encountered (Fig. 2 C2), has received much less attention (Lidicker 2002). Empirical studies have focused on small species with limited mobility such as arthropods (often butterflies and beetles), small mammals (almost exclusively small rodents), reptiles, amphibians, and some birds (see Bowne and Bowers 2004 for a review of interpatch movements). When empirical data are lacking, one can look at the genetic structure in a metapopulation and infer movement rates between patches and the role that barriers, corridors, and the matrix might play therein. A number of studies already used this landscape-genetic approach (Coulon *et al.* 2004; Manel *et al.* 2003). We complemented our static capercaillie distribution model with a genetic analysis and found that gene flux between patches was not entirely in agreement with conclusions drawn from interpreting the patch distribution map and intermediary corridors and barriers as they presented themselves to the human eye (previous chapter).

Another way to explore behaviour of dispersers in the landscape is by means of individual-based models (Fig. 2 D2). Movement analysis often employs random walk techniques or related diffusion modelling (Ovaskainen 2004), but several other approaches have also been taken. Recent simulation studies using virtual organisms have investigated patch reachability as a function of various landscape metrics as well as behavioural tradeoffs for dispersers (Hein *et al.* 2004; Tischendorf *et al.* 2003; Zollner and Lima 2005). Several authors have concluded that dispersal may be adequately captured by simple depictions or algorithms (King and With 2002; Zollner and Lima 2005) whereas others have pointed out that modelling outcome regarding patch accessibility or colonisation probability may heavily depend on how movement is modelled, at what grain size landscape is represented, and how realistically behaviour is implemented in the model (Jepsen *et al.* 2005). Results from data-driven individual-based models support the notion that the main challenge lies in dealing with behavioural complexity rather than the spatial structure of the landscape (Morales and Ellner 2002; Ovaskainen 2004; Whittington *et al.* 2004).

The final step in exploring of how population dynamics work in a specific landscape configuration leads to spatially explicit population models (SEPM; Fig. 2 D3). These models differ from other landscape models in that they allow modelling movements of individuals within a heterogeneous landscape and an estimation of how this movement influences (meta) population dynamics (Dunning *et al.* 1995). SEPMs are increasingly used by both researchers and managers (Dunning *et al.* 1995; Etienne *et al.* 2004). They have tremendous potential for application in species conservation and management and are able to address questions regarding population viability in fragmented landscapes, effects of landscape change or direct human impact on species distribution, whether parks can sustain populations of focal species, or how to plan reintroduction schemes, among others. Recent examples include models for space-demanding medium- to large-sized wildlife species such as raptors (Lawler and Schumaker 2004) or mammalian carnivores (Carroll *et al.* 2003, 2006; Macdonald and Rushton 2003; Wiegand *et al.* 2004a). Many of these models addressing large spatial scales use relatively coarse parameters for estimating dispersal movements. Concern has repeatedly been expressed that uncertainties due to assumptions or overt simplifications in parameterising movements or patch-specific demography may severely affect the usefulness of SEPMs for management purpose (Beissinger *et al.* 2006; Doak and Mills 1994; Wiegand *et al.* 2004b; Zollner and Lima 2005). Current progress with theoretical SEPMs has shown ways of how to mitigate a lack of empirical data in some cases (Parvinen *et al.* 2003; Wiegand *et al.* 2004b), but ultimately, there is no substitution for real data when it comes to validate these "data-hungry" models.

Most of the papers cited above make some mention of which types of field data are especially scarce, and we subscribe to most of them. Nonetheless, we would like to conclude this section with an eclectic list of aspects that are particularly data-deficient in our view.

1. *Motivation and results of emigration:* How does emigration rate relate to patch characteristics and quality (which includes population size or density in a patch), i.e. what patch parameters make some subpopulations to sources and others to sinks? To what degree does immigration enhance subpopulation persistence? Are there thresholds of self-sustaining populations (Alderman *et al.* 2005)? How important is long-distance dispersal in animals (and plants; Nathan *et al.* 2002)?
2. *Behaviour and navigation of dispersers:* How do dispersing individuals navigate in the landscape (Andreassen *et al.* 2002; Schooley and Wiens 2003), and how do they interact with landscape features or quality gradients between patches and matrix (Haynes and Cronin 2004)? How do connectivity measurements relate to dispersal rate and distances in different organisms? There is much space for better understanding individual paths across the landscape in terms of behavioural tradeoffs (Zollner and Lima 2005) or travel costs (Bélisle 2005).
3. *Measurement of multiple aspects in the same study:* Almost all papers focus on one or two major aspects such as dispersal, patch occupancy or patch demography in relation to

landscape features. For very few species have multiple aspects such as reproduction, survivorship and movement of individuals between habitat patches been measured simultaneously (Smith and Hellmann 2002). This field is wide open to future research.

4. *Data for large-bodied, vagile species are needed:* We have repeatedly pointed to the fact that much work on metapopulations has used small organisms at small spatial scales (m^2 to hectares rather than hundreds or thousands of km^2). Size matters (Lawton 1999), and results obtained from small organisms cannot easily be upscaled to yield meaningful results in population viability models of far-dispersing, large-bodied organisms. Data for such species generally remain in short supply, although these species are often of great conservation concern. For example, most existing models on large carnivores so far had to substitute inexistent data on dispersal behaviour with simple assumptions on landscape permeability.

Managing Landscape Permeability

In man-altered landscapes, connectivity can be restored. This fact has quickly been taken up by managers and conservationists, and fragmentation theory has found its way into conservation practice. Since – as we have argued earlier in this chapter – empirical evidence is rather scarce at the scale relevant to landscape management (Niemelä 2001; Simberloff *et al.* 1992), it probably was the intuitive appeal of landscape connectivity that made legislation and conservation practice overtake empirical research (Soulé and Terborgh 1999). In fact, if people ranging from grass-root conservationists to international NGO leaders have one common idea about what is needed most in conservation, it is the conviction that habitats have to be reconnected. The idea is more and more converted into action at local, regional, or even continental scales (Soulé and Terborgh 1999). Local solutions often are technical measures such as passage-ways or crossing structures to mitigate barrier effects of roads (mostly for mammals) or barrages (for fish). On a slightly larger scale, habitat patches may be linked by habitat corridors, which is the underlying idea for building networks of hedgerows in Central Europe (Schuller *et al.* 2000). At an international and continental scale, networks of protected areas are created to ensure long-term survival of populations of animal species demanding extensive spaces (Bennett 1994; Large Herbivore Initiative LHI). The European Union's «Natura 2000» program now attempts to achieve "connectedness" across different scales (Kleyer *et al.* 1996). While the contribution of technical constructions to enhance landscape permeability is firmly established in terms of passage rates of wildlife (Clevenger and Waltho 2000; McDonald and St. Clair 2004), their roles in actually maintaining long-distance migration (Berger 2004) or dispersal are less clear. Regional or even nation-wide schemes to restore wildlife migration routes, at least in the form as they are currently *en vogue* in Central Europe (Woess *et al.* 2002), are often based on expert opinion rather than solid data on wildlife movements. The same is true for habitat corridors, i.e. linear habitat structures such as hedges or forest strips that are also created for enhancing connectivity. Criticism on the basis of a possibly unfavourable cost-benefit ratio has pointed out the paucity of empirical support (Simberloff *et al.* 1992; Noss and Beier 2000), but there are now examples which tested and confirmed the functionality of large corridors for long-ranging species (Dixon *et al.* 2006).

"Ecological compensation" or set-aside schemes that come into effect for farmland in many European countries can potentially improve the landscape for dispersing organisms by creating more habitat patches, reducing inter-patch distances, and ameliorating matrix hostility. With respect to biodiversity of plants and taxa of small animals, these schemes, in general, are improvements over the former situation (van Buskirk and Willi 2004), but there is usually little concern for spatial aspects of restored habitats accounting for the needs of moving individuals. However, proper placement of restored patches can improve restoration success for focal species (Huxel and Hastings 1999), but best practice may not follow from easy rules of thumb (Schultz and Crone 2004). Thorough assessments of schemes that have been implemented for several years are still few and recent results show that success is often limited or untestable, either because schemes had no proper planning or because ecological data prior to instalment are not available (Vos *et al.* 2002). There is an urgent need for controlled, quasi-experimental set-ups in order to come up with recommendations and measures with clearly stated objectives. Success of directed management has to be assessed in order to evaluate the effectiveness of measures taken and, if necessary, to adapt future management.

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