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REVIEW

Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal

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Abstract Landscape connectivity can be viewed from two perspectives that could be considered as extremes of a gradient: functional connectivity (refers to how the behavior of a dispersing organism is affected by landscape structure and elements) and structural connectivity (depends on the spatial configuration of habitat patches in the landscape like vicinity or presence of barriers). Here we argue that dispersal behavior changes with landscape configuration stressing the evolutionary dimension that has often been ignored in landscape ecology. Our working hypothesis is that the functional grain of resource patches in the landscape is a crucial factor shaping individual movements, and therefore influencing landscape connectivity. Such changes are likely to occur on the short-term (some generations). We review empirical studies comparing dispersal behavior in landscapes differing in their fragmentation level, i.e., with variable resource grain. We show that behavioral variation affecting each of the three stages of the dispersal process (emigration, displacement or transfer in the matrix, and immigration) is indeed likely to occur according to selective pressures resulting from changes in the grain of the landscape (mortality or deferred costs). Accordingly, landscape connectivity results from the interaction between the dispersal behavior of individuals and the grain of each particular landscape. The existence of this interaction requires that connectivity estimates (being based on individual-based models, least cost distance algorithms, and structural connectivity metrics or even Euclidian distance) should be carefully evaluated for their applicability with respect to the required level of precision in species-specific and landscape information.

Keywords Dispersal evolution · Behavioral syndrome · Life-history traits · Animal personalities · Habitat fragmentation · Landscape grain · Biological conservation · Ecological network · Landscape planning

Introduction

Connectivity is a key concept in spatial ecology, as it encompasses all aspects affecting the displacement of an individual among resource or habitat patches within landscapes. Since its introduction the concept of landscape connectivity generated enthusiasm from conservation biologists (e.g., Bennet 1999), develop-

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ment of mathematical supports (e.g., Hanski 1999) but also some controversies (e.g., Tischendorf and Fahrig 2000, 2001; Moilanen and Hanski 2001). Landscape connectivity was initially introduced as ‘‘the degree to which the landscape facilitates or impedes movements among resource patches’’ (Taylor et al. 1993, p. 571). Accordingly, connectivity can be viewed from two different perspectives, which could be considered as extremes of a gradient: at the organism side, connectivity depicts the influence of landscape on dispersing individuals; at the landscape side, connectivity is a global property approximating more or less closely the number of dispersing individuals produced or received per habitat patch. These two viewpoints support the two different aspects of landscape connectivity, usually presented as antagonist: functional connectivity refers to how the behavior of a dispersing individual is affected by landscape structure and elements, whereas structural connectivity depends on the spatial configuration of habitat patches in the landscape (vicinity and presence of barriers) (e.g., Baudry and Merriam 1988; Burel and Baudry 2003).

Landscape connectivity is increasingly used in decision making for fragmented landscape management (e.g., Jongman and Pungetti 2004), particularly in natural reserve design (Calabrese and Fagan 2004). Such exercises usually favor the use of the simplest connectivity metrics including spatial pattern indices, because those are considered to be much less data consuming than more sophisticated connectivity estimates requiring accurate description of individual movements (emigration or immigration rates and dispersal kernels or individual tracks) (Calabrese and Fagan 2004). However, Calabrese and Fagan (2004) point out rightly that structural connectivity metrics are meaningless if those are not compared to reliable data on dispersal ability of focal species, which is, however, often unknown or only poorly known. Besides, the comparison of simple connectivity metrics (including several weighted sum indices) to empirical derived dispersal estimates revealed that none of those metrics performed well in predicting dispersal rates (Winfree et al. 2005).

Landscape connectivity still remains an inconsistently mastered concept (Calabrese and Fagan 2004), and we suggest it is another example of a more general problem of having some knowledge about patterns but poor knowledge about the processes that are causing the pattern. The manipulation of landscape connectivity patterns for conservation or restoration purposes requires that we need to influence processes, and dispersal is the key process underlying landscape connectivity. However, dispersal is not a species-specific fixed trait, but must rather be regarded as an individual trait showing variation both within and among populations, according to various selective pressures (e.g., Clobert et al. 2004; Van Dyck and Baguette 2005). Differences in dispersal ability were indeed observed among populations of the same species living under different environmental regimes (e.g., Hanski et al. 2004; Mennechez et al. 2004; Schtickzelle et al. 2006), and also among different individuals (e.g., Barbaresi et al. 2004; Doerr and Doerr 2005). Admittedly, we suggest that taking into account dispersal variation would most often provide more precise assessment of landscape connectivity than simpler but unreliable measures based on Euclidian distances or the simplest connectivity metrics (see, e.g., Keyghobadi et al. 2005; Michels et al. 2001; Stevens et al. 2006a).

Connectivity estimates should therefore have the potential to be altered according to evolutionary changes, when and where dispersal behavior of individuals is affected by landscape configuration. To support our plea for the use of such connectivity estimates in landscape planning, we focus on variation in dispersal relative to landscape fragmentation. More precisely, we propose a framework allowing sorting out which dispersal behavioral rules are affected by landscape structure and elements.

Dispersal is in fact a complex of behaviors (‘‘omnibus behavior’’: Clobert et al. 2005) that can be simplified as a three stage process: emigration, transfer in the matrix, and immigration (Ims and Yoccoz 1997; Bowler and Benton 2005). The dispersal behavior of an individual can thus be modeled by a vector reflecting its propensity to emigrate, and its ability to displace and to settle, respectively (Fig. 1). Interactions between biological and landscape processes are expected to occur at each of the three stages of the process (Fig. 1), which could generate variation in each term of the dispersal vector. In this paper, we focus on these variation components.

According to searching theory (Bell 1991), our working hypothesis is that the grain of the resource configuration in the landscape is a crucial factor

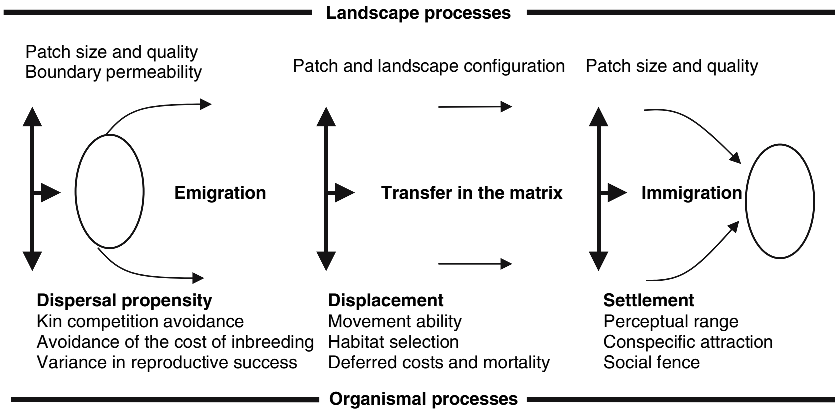

Fig. 1 Schematic representation of the interaction between biological and landscape processes at each of the three stages of dispersal (modified from Ims and Yoccoz 1997; Bowler and Benton 2005)

shaping individual movements. The grain size is the smallest spatial scale at which an organism recognizes spatial heterogeneity according to its perceptual range, which is the basic limitation of animal perception (Wiens 1989; Kotliar and Wiens 1990; Lima and Zollner 1996). We hypothesize that the interaction between organisms and landscapes should depend on whether or not the grain of resource patches matches the spatial scale of the perceptual range. To explore this hypothesis, we first review in a selective way empirical studies comparing dispersal behavior in landscapes differing in degree of fragmentation, i.e., with variable resource grain. We then discuss whether conclusions can be generalized relative to adaptive behavioral changes in dispersal and hence to landscape connectivity. Finally, we discuss which procedure allows best a reliable assessment of connectivity in real landscapes. As all these points are of both general ecological and conservation interest, we have tried to incorporate studies coming from a wide array of taxonomic groups, but our main input comes from insects, mainly butterflies, which are commonly used as model organisms in spatial ecology (Watt and Boggs 2003). However, it should be relatively simple to apply our findings to other study systems.

Landscape–dispersal interactions

Although dispersal patterns can be summarized relatively easily by dispersal rates (the number of individuals moving from patch *i* to patch *j*) or dispersal kernels (the probability distribution of individuals moving a certain distance), the processes behind these patterns are far less studied. As dispersal is a chain process; we discuss the three stages explained above separately.

Change in dispersal propensity

Crossing or not crossing the boundary of suitable habitats is the first behavioral component leading to dispersal. Avoidance of, or reluctance to boundary crossing, have been reported in several taxa including insects, fish, amphibians, birds, and mammals (e.g., Bayne and Hobson 2001; Schultz and Crone 2001; Belisle and Desrochers 2002; Morales 2002; Bakker and Van Vuren 2004; Bosschieter and Goedhart 2005; Rittenhouse and Semlitsch 2006). On the other hand, some experimental studies reported full permeability of habitat boundaries in their study systems (Goodwin and Fahrig 2002; Schooley and Wiens 2004). The nature of the landscape component and the degree of contrast on the other side of the boundary may of course mediate boundary permeability, depending on the perceptual abilities of the organism to perceive habitat boundaries (Haynes and Cronin 2006). However, such studies have rarely considered that this behavioral response could also be mediated by the grain size of the landscape (but see Bayne and Hobson 2001). The grain size of the landscape is typically used as structural measure of heterogeneity, like ''the average, and the variability in, diameter or area of the landscape element present'' (Forman and Godron 1986). Individuals may differ considerably in the distance and area to which they are sensitive to gather information that may affect their behavior and space-use. So, functional grain follows from a spatially explicit, organism-centered view on landscape structure (e.g., Wiegand et al. 1999)

An integrated study on this subject was performed using the bog fritillary butterfly (*Proclossiana eunomia*) as model organism. It is a narrow habitat specialist that is confined to zones where its unique host plant occurs in clumped spatial patches. Hence, habitat boundaries are easy to delineate accurately in the field (Baguette and Mennechez 2004). In other butterfly systems with different resource distribution settings, the recognition of such discrete habitat patches and boundaries can be more difficult, or even problematic (Dennis et al. 2003). First, it was addressed whether the behavior of adult butterflies differed at habitat boundaries according to the grain size of the landscape. Movements of *P. eunomia* were recorded in two habitat networks located in the same landscape, but differing in their degree of fragmentation: a highly fragmented and a aggregated system of habitat patches (Schtickzelle and Baguette 2003). Tracking movements of butterflies within habitat patches showed that movement parameters (length of flight bouts and turning angles) changed close to habitat boundaries. More interestingly, boundary behavior was not the same as in the two habitat networks: the distributions of turning angles were significantly different, whereas the length of flight bouts was similar. The distribution of turning angles peaked at 180° in the highly fragmented network, corresponding to a tendency to return at habitat boundaries, whereas the distribution of turning angles was not significantly different from the circular equivalent of the normal distribution in the aggregated network.

Second, changes in emigration propensity with habitat fragmentation were quantified in the same species from capture-mark-recapture (CMR) data analyzed with the virtual migration model (VM, Hanski et al. 2000). VM allows estimating various dispersal parameters from multi-site CMR data, including dispersal propensity (the probability to disperse) and within or between patch mortality. CMR data on *P. eunomia* were collected using a standardized method in four landscapes showing different levels of habitat fragmentation: a highly fragmented network, a fragmented network, an aggregate network and a large site with continuous habitat (Schtickzelle et al. 2006). The analysis of a large data set indicated that the dispersal propensity showed a significant monotonal decrease according to an increase in landscape fragmentation, from the continuous landscape (94 km^2 with 48% suitable habitats) to the highly fragmented landscape (1,050 km^2 with 0.4% suitable habitats). All four dispersal propensity estimates were significantly different.

Although using different methods, both the behavioral and the modeling approach converge to the same conclusion of decreasing dispersal propensity with increasing level of fragmentation. The active avoidance of habitat boundary crossing showed by empirical studies dissecting butterfly behavior is likely to be the proximate factor leading to the decrease of dispersal propensity quantified by the VM. The experimental study of Merckx et al. (2003) goes further as it suggests a heritable basis for dispersal propensity. They compared the behavior of laboratory reared speckled woods (*Pararge aegeria*) from landscapes that differed in degree of fragmentation (continuous woodland landscape versus agricultural and fragmented landscape) in an experimental arena with woodland and open land conditions (i.e., outdoor cages). Both types of *P. aegeria* had the same habitat selection as they preferred the wooded parts of the cage, but there were significant differences in dispersal propensity. The latter was measured as the frequency of crossing the open area between the two wooded parts in the experimental outdoor cage. Individuals born from woodland ascendants were more prone to cross the open area and thus traveled more often between the wooded parts of the cage than conspecifics from the fragmented landscape. Such evidence for a genetic background to changes in dispersal propensity at habitat boundaries suggest that selective pressures against dispersal occur in fragmented landscapes. Earlier work on *Calopteryx* damselflies had indicated evidence for selection for increased mobility in fragmented landscapes as reproduction habitat (river) and foraging habitat (woodland) became spatially separated in agricultural landscape compared to continuous woodland (Taylor and Merriam 1995).

Movement across the landscape matrix

We move to the second step of dispersal, being the displacement or the transfer in the landscape matrix. Many empirical studies on various taxa reported that searching behavior using explorative-type of movements within habitats differ from movements observed in the matrix, between suitable resource or habitat patches (e.g., Baars 1979; Schultz 1998; Doncaster et al. 2001; Goodwin and Fahrig 2002; Johnson et al. 2002; Baguette 2003; Hein et al. 2005; Schtickzelle et al. 2007). Mechanistic studies dissecting inter-patch movements reported that when resources and habitats are scattered in the landscape, individuals moving between patches adopt faster and straighter displacements than their usual slow and tortuous trajectories associated to resource searching (e.g., foraging associated movements). Simulation models of various displacement types in virtual landscapes showed that straighter moves provide the best solution when energy resources are limited and dispersing individuals incur predation risks (Zollner and Lima 1999). Consequently, landscape has two main effects on dispersing individuals.

First, the ability to move depends on both the nature of the substrate in which the displacement occurs and the decision taken by the dispersing individuals at the boundaries between landscape components; this is intuitively especially important to ground-dwelling animals, in comparison with flying organisms (but see, e.g., Haddad 1999; Dover and Fry 2001; Haddad and Tewksbury 2005 for landscape component effects on butterflies). Variation in displacement speed among landscape components is indicative of their resistance to movements (e.g., Schooley and Wiens 2004; Stevens et al. 2004), which in turn may influence the shape of the movement paths (Goodwin and Fahrig 2002). Moreover, recent experimental studies showed that the choice to move in one or another landscape component is not straightforward, as it cannot be inferred from its resistance (Haynes and Cronin 2006; Stevens et al. 2006b). Admittedly, displacements in the landscape matrix are constrained by both habitat selection by the dispersing individual and resistance of each landscape component to animal's movement.

Second, the time spent by dispersing individuals in the matrix depends on both the distribution and the configuration of resource or habitat patches in the landscape, which in turn entails that movements outside suitable resource or habitat patches bear a cost. Whatever the exact shape of the relation, we predict that the longer the time, the higher the cost. Two main sources of costs are usually separated, mortality and deferred costs (e.g., Zollner and Lima 1999; Stamps et al. 2005).

Mortality of dispersing individuals might occur by energetic reserve exhaustion, or predation, whereas deferred costs are those that reduce the fitness of immigrants after they have traveled in the matrix. Several empirical studies document that dispersing individuals suffered from higher predation mortality than residents (e.g., Vanvuren and Armitage 1994; Sakai and Noon 1997; Smith and Batzli 2006), and that mortality risks during dispersal increase with the distance between suitable resource or habitat patches in the landscape (e.g., Matter et al. 2004; Schtickzelle et al. 2006). We have recently suggested that special dispersal movements could have evolved in response to higher mortality risks in the matrix (Van Dyck and Baguette 2005). Accordingly, the application of the VM model to inter-patch movements of bog fritillaries in the four landscapes mentioned above showed that overall dispersal mortality increased with habitat fragmentation. However, landscape structural connectivity at which half of the dispersing individuals die decreased with habitat fragmentation. This finding indicates that individuals better survived dispersal in more fragmented landscapes, for a given structural connectivity value (Schtickzelle et al. 2006). It hence supports the hypothesis of adaptive changes in movements according to the landscape grain (Schtickzelle et al. 2007). From a mechanistic viewpoint, metabolic differences were recorded among individuals coming from recently founded populations (i.e., with high proportion of mobile individuals) or from ancient populations (i.e., with lower proportion of mobile prone individuals) in the butterfly *Melitaea cinxia* (Hanski et al. 2004), which were in line allelic variation allowing different flight performance (Haag et al. 2005). Such evidence that both landscape structure and composition may influence the outcome of dispersal has strong evolutionary implication on the physiology and behavior of dispersing individuals. Moreover, the selection of special directed movements when resources are scattered in the landscape is expected to have consequences on other life history traits.

Deferred costs are not yet convincingly documented, even if (1) apterous females of wing-dimorphic insect species lay more eggs than full-winged individuals and (2) fully winged female fruit flies that were forced to provide locomotive efforts mimicking dispersal displacements laid less egg than control females from the same strain (Roff 1977).

Both those ultimate and proximate effects correspond to the oogenesis-flight syndrome (Johnson 1969; Rankin et al. 1984), which was coined to depict the trade-off between movement ability and female fecundity. Further experiments challenged the generality of this syndrome: in some insect species, the relation between movement ability and female fecundity was not significant or even positive, indicating the existence of physiological adaptations to reduce flight costs (e.g., Rankin and Burchsted 1992). Besides, there is mounting evidence that the ability to move is not a single trait, but should be rather considered as the result of a suite of inter-related traits, each with their own genetic basis and correlation with other life-history traits (Roff and Fairbairn 2001). Butterflies provide good examples of this intricacy: the understanding of the relationship between dispersal and fecundity has to take into account the nature of female reproductive strategies (like capital versus income breeding strategies), which themselves depend on factors like larval and resource availability, or parasitoid avoidance strategies. Females laying a few large batches during their lifetime typically emerge with a high load of mature eggs which usually limits initial flights before first oviposition; this situation contrasts with single-egg laying females, which are immediately able to fly long distances after mating (Baguette and Schtickzelle 2006).

Habitat detection, arriving, and settlement: immigration

Until now, this final part of the dispersal chain process has been the least studied. Immigration in fragmented landscape systems implies the detection of habitats, arriving, and finally settle in this zone of (un)occupied habitat. The distance at which an individual is able to detect suitable habitat using its sensory organs defines its perceptual range. We might expect that in highly fragmented systems with small proportion of habitats and hence high-dispersal costs, any increase in perceptual range should represent a benefit for the dispersing individual. A theoretical model indeed suggests that when energy is limited, the ability to detect suitable habitat from a distance is the best strategy in comparison to random search or even to the use of information collected nearby (Vuilleumier and Perrin 2006). The effect of historical behavior (Pither and Taylor 1998) associated with landscape differing in grain size was tested on the perceptual range of the butterfly *P. aegeria* (Merckx and Van Dyck in press). They compared the behavior of butterflies originating from continuous forest landscape with conspecifics from fragmented agricultural landscape with some woodlots and hedgerows (<5% suitable habitat). Butterflies from both landscapes were released in an unfamiliar area at various distances from a forest edge. Their results show that ''agricultural landscape butterflies'' were able to orient to forest from a significantly wider distance than were ''woodland butterflies.'' This striking difference indicates the evolutionary potential of perceptual range changes relative to landscape structure.

Locating suitable habitat is only the first challenge within the immigration phase of the dispersal process. Little is known about the fitness of immigrants relative to residents once they have settled. However, some empirical studies show that at least in some cases immigrants may perform better than residents (e.g., Belichon et al. 1996; Altwegg et al. 2000; Gundersen et al. 2002; Le Galliard et al. 2005). Rigorous experimental analyses of such differences are hard to perform: the direct comparison of fitness components between immigrants and residents could be interesting, but may suffer from a fundamental problem if the two sets of individuals are distinctly different in other aspects of behavior, physiology and morphology contributing also to fitness differences (Lin and Batzli 2004). Based on this argument, the fitness prospects of immigrants if they stayed home remain the most critical, still unknown, and reference point.

Evolution of dispersal according to the landscape grain

Our working hypothesis is that when the landscape grain is smaller than the perceptual range of the individual, there is no real difference between movements within and between habitats; dispersal occurs as a by-product of routine, explorative movement. When the landscape grain is tight, searching individuals moving between continuous resource patches might accomplish the equivalent of dispersal. In this case, we expect that there is no specific behavioral decision triggering dispersal (Van Dyck and Baguette 2005). Contrarily, if the grain of resources is larger than the perceptual range of the animal, dispersal bears larger costs for the individual: as searching time increased, predation or other mortality risks, and deferred costs become higher. According to this hypothesis, the spatial scale determining the functional landscape grain depends on the perceptual range of the individuals, which itself may vary according to landscape structure and configuration. Anyway, the precise assignation of observed movements to the spatial scale shaping the landscape grain is an essential prerequisite that should allow to avoid the problematic confusion between routine movements and special dispersal movements (see, e.g., Bowne and Bowers 2004; Casula 2006; Hanski et al. 2006).

Altogether, the recent studies reviewed above demonstrate that behavioral variation affecting each of the three stages of the dispersal process is subject to evolutionary changes in changing landscapes (Fig. 2). We believe that consequences of this evolutionary dimension of dispersal and functional connectivity have not yet been widely recognized and integrated in landscape ecology. Dispersal mortality was shown to increase with the degree of landscape fragmentation. Comparative studies of the same species in differently fragmented landscapes suggest the existence of several behavioral responses across the dispersal chain aiming at decreasing this cost: increased return behavior at habitat boundaries (i.e., reduced dispersal propensity), the use of special displacement movements (i.e., efficient transfer across the matrix) or an increase in the perceptual range (i.e., improved habitat detection ability). The time lag leading to those behavioral changes certainly deserves further investigation. Although anecdotal, two lines of evidence indicate that such responses are likely to occur on the short term. First, changes in dispersal propensity were observed in only one generation in the bug *Oncoptelus fasciatus* after intense selection experiments (Dingle 1968). Second, analysis of land cover change revealed that the current highly fragmented landscape in *which P. eunomia* is currently living (see above) was much less fragmented than three decades ago–which corresponds to *ca.* 30 generations of the butterfly (Baguette et al. 2003).

Central to our selective review is the idea that selective pressures on dispersal traits are different in continuous and fragmented landscapes. Admittedly, we should expect that certain levels of habitat fragmentation lead to the coexistence of both resident and dispersing strategies. This balance is essential for metapopulation persistence in dynamic landscape, particularly for species living in early succession stages (e.g., Olivieri and Gouyon 1997). When dispersing and resident individuals have different demographic properties, both strategies were indeed predicted to be evolutionarily stable by a theoretical model under particular condition of dispersal rates, themselves constrained by landscape grain (Lemel et al. 1997). Although empirical examples remain rather scarce, evidence grows that dispersing individuals are a non-random sample of their source population, and not low-quality individuals kicked out by others, competitively superiors (the Chitty–Krebs hypothesis). In some cases dispersing individuals seem at least for a fraction to be ‘‘super-dispersers,’’ whose fitness is unaffected, or even positively

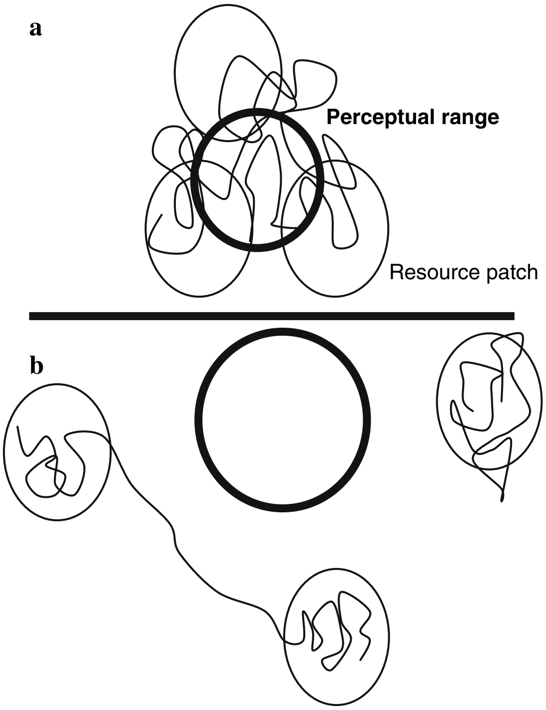

Fig. 2 Schematic representation of animal movements shaped by the inter-play between the grain of the landscape and the perceptual range: (**a**) when the grain of the landscape is of the same magnitude than the perceptual range, dispersal bears no cost and should occur a by-product of routine movements; (**b**) when the grain of the landscape is larger than the perceptual range, dispersal bears a cost and behavioral responses aiming at decreasing that cost are likely to occur

affected by their travel in the unsuitable matrix and their settlement in unknown habitats (e.g., Belichon et al. 1996; Altwegg et al. 2000; Gundersen et al. 2002; Lin and Batzli 2004; Le Galliard et al. 2005). Such results suggest that several behavioral syndromes (Sih et al. 2004a, b) submitted to uncoupled selection regimes could be implied for the evolution of dispersal in response to habitat fragmentation.

It is tempting to relate these behavioral registers to the bold and shy dichotomy, which captures well the extremes of personalities in vertebrates. Bold individuals are proactive and aggressive, take rapid decisions, are weakly influenced by external stimuli and easily form routine behaviors. Shy individuals are more passive, cautious in decisions and sensitive, and adjustable (reactive) to external stimuli (e.g., Wilson et al. 1994; Drent et al. 2003). Two empirical studies document that bolder individuals show ‘‘super-dispersers’’ characteristics and disperse further than shyer ones (Fraser et al. 2001; Dingemanse et al. 2003). If mortality or deferred costs change according to habitat loss and fragmentation, the balance between those two strategies should disappear and shy, resident individuals should be favored (McDougall et al. 2006). We expect that this selection of one particular behavioral syndrome would decrease the adaptive differences existing between individuals within populations (Wilson 1998) and generate unknown consequences on their evolutionary potential (see, e.g., Van Dyck and Matthysen 1999).

Assessment of functional connectivity: toward a toolbox for landscape planners

Landscape connectivity results from a complex interaction between the dispersal behavior of each particular individual and the grain of each particular landscape. As this process is still poorly understood it offers intriguing research perspectives. This message could also be interpreted as discouraging for end-users in conservation and landscape management. Simple structural metrics that deny within-species variation in dispersal are attractive to be used in conservation applications at the landscape level, but as we are dealing with a complex phenomenon we need to warn against oversimplifications. Moreover, we have to admit that we adopted here a simplifying approach by considering that the complex of dispersal behaviors was mainly affected by the grain of the landscape, i.e., its fragmentation level. We just briefly mentioned that the nature of the intervening matrix could affect the dispersal chain. The nature of landscape elements is undoubtedly important in modifying dispersal costs and benefice. In particular, habitat selection by dispersing individuals, including their perceptual abilities toward suitable habitat boundaries, should be of the significance to reduce mortality and deferred costs. It is therefore essential that the most precise landscape connectivity estimates take into account this variation (see also Belisle 2005). Two modeling approaches could be used to bypass this difficulty: cost-distance modeling and individual-based models.

Cost-distance modeling is currently increasingly used to select the best route that dispersing individuals should follow between suitable resource patches or habitat patches. Cost-distance modeling is a GIS tool that allows for the evaluation of the costs generated by the intervening elements. The cost of each landscape component reflects the degree to which that element facilitates or impedes dispersal movements for the studied organism (Adriaensen et al. 2003). Depending on the hypothesis tested, the cost of dispersal may be expressed by various parameters (e.g., speed of movement, resource availability, and survival). If necessary, various sets of parameter values may be used according to different types of individuals (e.g., sex and age or other features). Accurate data on habitat selection and movement ability in the various landscape components are therefore needed to estimate functional connectivity through a cost-distance modeling analysis. Unfortunately costs are most often estimated by the best values fitting empirical data to the least cost model (e.g., Sutcliffe et al. 2003), or even more indirectly by using expert opinion (e.g., Verbeylen et al. 2003). Such hints, however, are often imprecise and unable to account for evolution of dispersal behaviors and they blur inter-individual variability. Some recent studies go further by assessing costs from experimental data (Stevens et al. 2004, 2006b; Castellon and Sieving 2006), which could be useful to investigate effects of habitat fragmentation if tested animals come from landscapes showing contrasted levels of resource and hence habitat grains. The major drawback of the use of least cost models remains their lack of validation: the end product of such studies is a selection of one or several routes allowing dispersal in spatially explicit landscapes, usually without more confirmation of their real use than their additive explanatory value to Euclidean distances between populations in landscape occupancy models. Moreover, cost-distance models are based on two biologically improbable assumptions: (1) dispersers have complete knowledge of their surroundings, and (2) they do select the least cost route from this information. As dispersing individuals usually do not have such a global insight into their environment, some of them would be exhausted by their efforts to settle in their new habitat or even could die en route. The confrontation of cost-distance dispersal routes to the number of effective migrant as inferred from the population genetic structure depicted by neutral variable markers, offers a promising validation step (Coulon et al. 2004; Vignieri 2005; Stevens et al. 2006b). The use of the number of effective dispersal events not only validate the least cost route(s) but also circumvents the lack of data on deferred costs and dispersal mortality because only the surviving individual contributing to successful reproduction. Therefore, the combination of experimental measurements of movement costs and habitat selection, validated by genetic estimates of effective dispersal offers a first solution to parameterize the connectivity of a real landscape using cost-distance modeling, provided that individual tested in the experiments and genetic dispersal estimates came from the same landscape. This condition is essential to capture the landscape-dispersal behavior interaction we discussed here.

Individual-based models coupled to dispersal rates between local populations obtained by CMR and/or as inferred from population genetic structure, is an alternative to cost-distance modeling. Basically, the idea is to include detailed information on landscape and individual processes into spatially explicit individual-based, stochastic model that simulate dispersal on a real spatial and temporal frame (e.g., Wiegand et al. 1999; Revilla et al. 2004) and test how closely these patterns fit those observed in the field, as inferred from individual capture histories or genetic dispersal estimates. The simulation models are constructed with data from short temporal scale, whereas model predictions represent the system at wider temporal scales, allowing comparison with empirical data of long-term dispersal rates obtained by CMR and/or inferred from population genetic structure. Behavioral rules of movements and habitat selection are assessed either in the field, by closely monitoring individual displacements, or in experimental conditions, with a focus on intra-specific variation in those traits relative to landscape of origin, sex, age, and phenotypic traits. A set of rules is applied to each individual, describing their searching behavior, dispersal propensity, displacement ability, and perceptual range, including individual- and landscape-mediated variation as inferred from observational and experimental data. Closeness of fit between individual-based model predictions and dispersal pattern is an indicator of the adequacy of the underlying movement rules, especially if individual-based model predictions can successfully be transferred to new landscape settings. So far only but a few studies used such functional connectivity estimates derived from individual-based models (e.g., Wiegand et al. 1998; Schadt et al. 2002; Revilla et al. 2004). However, this approach appears to be highly promising, given that individual-based models are flexible in design (e.g., Grimm and Railsback 2005) and can easily be altered to account for differences in behavioral rules between species and/or landscapes, including the evolutionary aspects of dispersal relative to landscape dynamics. In particular, this approach allows bypassing problems related to modeling mortality during dispersal if simulation procedures closely fit field protocols used to assess dispersal patterns at population scale, by simulating at each time interval the fate of the same number of individuals as they were monitored in the field. With this setting, it is possible to remove the effect that demography (mainly mortality of dispersing and resident individuals, but also the differential recruitment time of adults in local populations) would have on model predictions, as those model predictions are directly comparable with field data.

Conclusions

We suggest that least cost modeling, individual-based models or even simpler metrics can be useful tools to estimate landscape connectivity and hence to explore the functionality of ecological networks, provided that such exercises remain restricted to each population-environment system under investigation. We plea, however, for more precaution, particularly to generalize among landscapes and species. We suggest to use a procedure starting first from complex landscape connectivity estimates and then turn progressively to simpler metrics. During this procedure, the key point is the evaluation of the acceptability of the information loss on connectivity regarding to the simplification of data collection and analyses. Collecting comprehensive dispersal data on the population-landscape study system should be the first step aiming at providing the reference point. Next, individual-based models could be implemented with behavioral rules of decreasing complexity. The closeness of fit between individual-based model predictions and dispersal patterns would then be an indicator for the mechanistic understanding of the underlying behavioral process and hence of connectivity. The empirical reference data set and individual-based model predictions could also be compared with predictions of less data demanding models like cost distance algorithms or even structural landscape parameters such as Euclidean distances between patches, presence or length of corridors, or various connectivity measures that require less species-specific knowledge but are also likely to make less precise predictions. All the concurrent models should finally be evaluated for their applicability with respect to the required level of precision in species-specific information on landscape connectivity.

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