

MEASURING LANDSCAPE CONNECTIVITY: THE CHALLENGE OF BEHAVIORAL LANDSCAPE ECOLOGY

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Abstract. The recognition of behavior as a link between process and pattern in landscape ecology is exemplified by the concept of functional connectivity: the degree to which the landscape facilitates or impedes movement among resource patches. In this paper, I first argue that the actual operational definitions of this concept as applied to animal movement are not fully consistent with its formal definition. For instance, I question that a high likelihood of movement among the different points of primary habitat implies a high connectivity and contend that such a view can lead to misinterpretations. I also address two more hurdles to the measurement of functional connectivity: the fact that functional connectivity may not be equal along all axes and directions of movement and individual variation in functional connectivity within a given landscape. These points bring me to suggest that the concept of functional connectivity be bridged to the one of travel costs used in behavioral ecology. This would help define unequivocal operational definitions of functional connectivity as its measurement would then be dictated by its ecological role within specific models (e.g., travel costs within group membership models of foraging theory). I argue further that this ecological role shall in turn determine the motivation underlying the movement of individuals, implying that the latter should preferably be standardized when measuring functional connectivity in the field. I finally present some methods to do so. These include translocation and playback experiments, food-titration and giving-up densities experiments, and manipulating feeding and breeding site locations and success.

Key words: *behavioral ecology; cost function; dispersal; field experiments; functional connectivity; gap-crossing behavior; landscape anisotropy; movement; travel costs.*

BEHAVIOR: THE LINK BETWEEN PROCESS AND PATTERN

One of the main focuses of landscape ecology is to explain how ecological processes and patterns originate from or modify the composition and configuration of habitat patches within a given area. Although the actors involved in such spatial processes and patterns may be abiotic, most are living organisms that react to one another, as well as to landscape structure, through behavior. Recent studies on wintering parids illustrate well how landscape structure can influence the behavior of organisms, and thereby generate patterns at the patch and landscape scales. For instance, these small, resident forest birds venture further out into open habitat to obtain food as forest cover decreases within a 500-m radius (Turcotte and Desrochers 2003). Yet, when supplemented with food for some weeks, they barely enter the open to forage, and this, independently of forest cover within a 500-m radius (Turcotte and Desrochers 2003). This suggests that parids in landscapes with low

forest cover are energetically stressed and experience a greater predation risk to gain access to food. Along the same line, parids living in small forest patches show daily fattening patterns that indicate a trade-off between accumulating reserves to counter an unpredictable access to food and limiting their body weight to reduce predation risk (Tellería et al. 2001). The energy stress experienced by parids within highly fragmented landscapes may not only result from a lower resource density, but also from a greater exposure to adverse weather conditions that constrain individuals to feed and cache food towards the center of patches (Dolby and Grubb 1999, Brotons et al. 2001). On another front, parids have a high propensity to follow forest edges (Desrochers and Fortin 2000) and are reluctant to move among forest patches surrounded by open areas (St. Clair et al. 1998, Grubb and Doherty 1999). In addition, parids experience lower survival when moving within highly fragmented landscapes (Doherty and Grubb 2002). Taken together, these responses to conditions emanating from the landscape structure may explain why the incidence, density, and social structure of parids are influenced by the area and isolation of forest patches (Pravosudova et al. 1999, Doherty and Grubb 2000).

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The recognition of behavior as a link between process and pattern by landscape ecologists is exemplified by the concept of landscape connectivity: “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993:571). Because this formalization is associated to the ease with which processes such as dispersal can operate, it is often referred to as the functional connectivity of landscapes. This is to distinguish the latter from the structural connectivity or connectedness of landscapes, which refers to the degree to which some landscape elements of interest are contiguous or physically linked to one another (With et al. 1997, Tischendorf and Fahrig 2000a).

With respect to animal movement, the functional connectivity of a landscape is thought to depend on how an organism perceives and responds to landscape structure within a hierarchy of spatial scales. In fact, organisms are expected to alter their movements, as well as experience differential fitness benefits or costs, according to the nature, form, and spatial arrangement of habitat patches and ecotones (Tischendorf and Fahrig 2000a, Wiens 2001). Several behavioral constraints underpin this framework. For instance, the perception and response of individuals to landscape structure will be influenced by their state and their motivation, which will dictate their needs, how much risk they are willing to take in order to fulfill those needs, and possibly their specific destinations. Thus, factors such as the perceptual range of the organisms (*sensu* Lima and Zollner 1996), their susceptibility to competition and predation, as well as their level of conspecific attraction, will play an important role at determining the movements of individuals (Danielson 1992, Bélisle 1998, Fraser et al. 2001, Greene and Stamps 2001). It follows that the functional connectivity of a landscape is likely to be both species and context-dependent (Pither and Taylor 1998, Jonsen and Taylor 2000, D'Eon et al. 2002).

Despite being considered as a key concept of landscape ecology, the actual study of functional connectivity requires dealing with complex phenomena difficult to sample, experiment on, and describe synthetically. This stems mainly from the multivariate nature of the processes involved as well as from the spatial and temporal scales at which they manifest themselves. In the remaining sections of the paper, I will discuss how functional connectivity can be operationally defined and measured in the field. After, I bring up two more aspects that should be considered in measuring landscape connectivity: the fact that functional connectivity may not be equal along all axes and directions of movement and that it may vary strongly among individuals within a given landscape. I then propose that we have much to gain from using a theoretical framework that stems from behavioral ecology to improve our measurement of functional connectivity. Specifically, I suggest that the concept of functional connectivity be linked to the one of travel costs found in

behavioral ecology models that predict how animals should use resources heterogeneously distributed in space. Within this framework, I finally present some approaches to measure functional connectivity in the field.

MEASURING FUNCTIONAL CONNECTIVITY

The lack of an operational definition

Landscape ecology recognizes the importance of movement with respect to habitat selection and gene flow, as well as population viability and stability. Yet, the limited empirical knowledge on how landscape structure influences the movement of animals has so far hindered the development of a strong theoretical framework around the concept of functional connectivity. This is partly reflected by the lack of consensus on how to measure landscape connectivity (Tischendorf and Fahrig 2000a, b, Moilanen and Hanski 2001, Goodwin 2003). For instance, Taylor et al. (1993:572) suggested that functional connectivity “can be measured for a given organism using the probability of movement between all points or resource patches in a landscape.” This operational definition is generally interpreted such that a high likelihood of movement among the different points of primary habitat implies a high functional connectivity. This interpretation, however, is hazardous if we stick to the conceptual definition of functional connectivity: “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor et al. 1993). Indeed, both dispersion and patch models in behavioral ecology sustain the possibility that two landscapes can have identical connectivity while the propensity of individuals to move can differ between the two landscapes. This claim, like the rest of the paper, assumes that animals tend to behave optimally (Krebs and Kacelnik 1991) and that the travel costs they incur reflect the level of functional connectivity. Here are two “thought experiments” that illustrate the rationale.

As a set up for both experiments, let's assume two landscapes, A and B, in which individuals experience the same ease of movement among resource patches (Fig. 1a). As a result, individuals incur the same travel costs (e.g., energy, predation risk) as they search for and sample resource patches in both landscapes. Moreover, the landscapes have the same number of resource patches. Furthermore, the frequency distributions of patch quality in the two landscapes have the same mean, variance, and kurtosis (Fig. 1b). On the other hand, although the frequency distributions of patch quality have the same skewness level, the distribution in landscape A is skewed to the left, whereas it is skewed to the right in landscape B. As a consequence, the quantiles of the two distributions will differ and the median patch quality will be higher in landscape A.

The first “thought experiment” considers a simple dispersion model whereby individuals attempting to

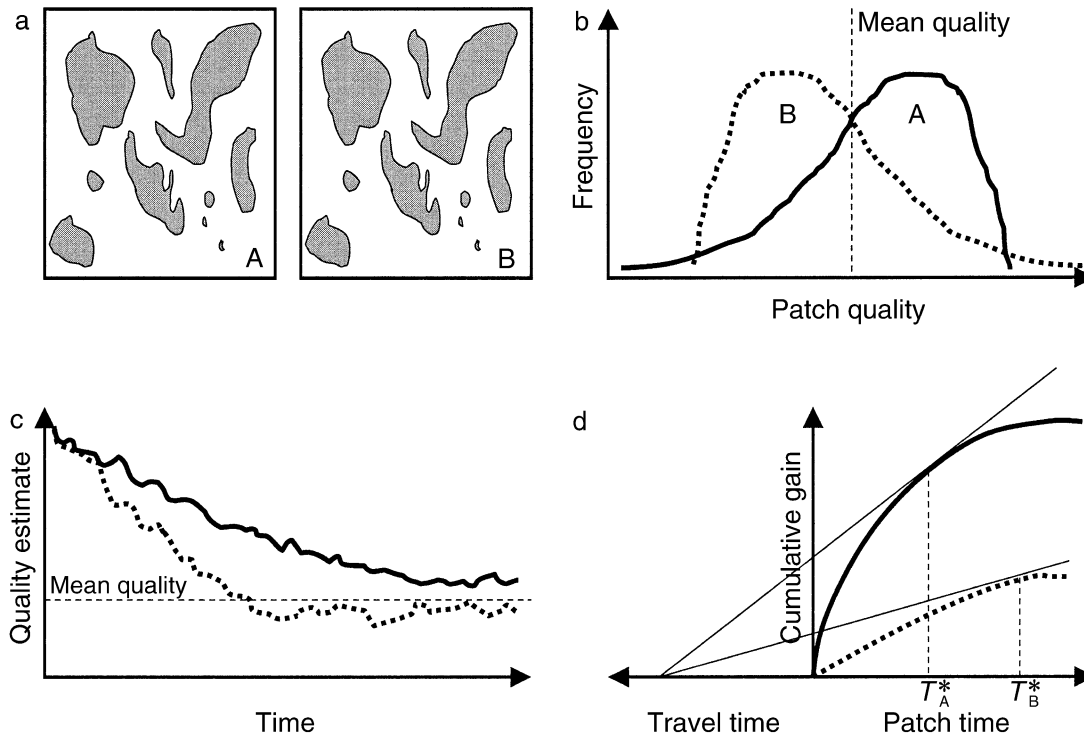


FIG. 1. Main aspects of the two thought experiments showing that two landscapes with identical functional connectivity can lead to different movement rates or propensities in animals that attempt to maximize their gain rate. (a) Two landscapes (A and B) with “identical” structures (i.e., composition [forest vs. nonforest] and configuration) with respect to movement costs. (b) Although the two landscapes are composed of habitat patches of the same mean quality, the frequency distribution of patch qualities is skewed to the left in landscape A (solid line) and to the right in landscape B (dotted line). (c) The estimate of the average quality of the environment, as learned through sampling by foraging individuals, will decrease more rapidly in landscape B (dotted line) than in landscape A (solid line). Hence, individuals in landscape A will, on average, sample more habitat patches before they settle down into a patch to exploit its resources. (d) Once in a patch, individuals in landscape A (solid line) will, on average, gain benefits more rapidly than in landscape B (dotted line). Because travel time is identical in both landscapes, individuals should, on average, leave patches sooner in landscape A (T_A^*) than in landscape B (T_B^*).

maximize their rate of gain must distribute themselves among resource patches of unknown quality (Bernstein et al. 1991, Beauchamp et al. 1997). These individuals will settle in or exploit resource patches showing a better quality than their current estimate of the average quality of the environment, which they must learn. To avoid settling in a patch of poor quality, individuals must initially be optimistic. Yet, as they sample, they devalue past experiences and their current estimate of the average quality of the environment turns out to be mostly influenced by the qualities of recently encountered patches (Giraldeau 1997). Frequently encountered patch qualities will therefore have a substantial effect on their current estimate. All other things being equal, then one is likely to observe more (sampling) movement in landscape A than in landscape B, as individuals would, on average, maintain a higher estimate of the average quality of the environment in landscape A (Bernstein et al. 1991, Beauchamp et al. 1997: Fig. 1c). Based on the widely accepted operational definition which equates a high likelihood of movement among the different points of primary hab-

itat with a high functional connectivity, one would conclude that landscape A has greater functional connectivity. This conclusion is, however, wrong if we stick to Taylor's et al. (1993) conceptual definition; it is as easy for individuals to move in both landscapes.

The second “thought experiment” considers patch models whereby individuals attempting to maximize their rate of gain must decide when to stop exploiting a resource patch and search for a new one (Stephens and Krebs 1986, Giraldeau and Caraco 2000). Not having perfect information about the location and quality of resource patches, individuals are expected to exploit patches in accord to the marginal-value theorem. Encountering resource patches of higher quality more frequently, individuals in landscape A will thus be more likely to leave a resource patch early and resume searching (i.e., move) compared to individuals in landscape B, all other things being equal (Stephens and Krebs 1986, Giraldeau and Caraco 2000: Fig. 1d). Movement probabilities or rates will thus depend on the rate at which individuals gain benefits through time within resource patches, not on functional connectivity.

Note that the arguments presented in the two “thought experiments” would have been much stronger if there had been greater discrepancies in the likelihood of encountering patches of high quality between the two landscapes. It is also important to realize that the above arguments are not restricted to a foraging context or to “local” processes, but can also be applied to dispersal (Danielson 1992). Resources can be very diverse and include food, mates, and territories, and these can be exploited from a central place to which individuals periodically return (e.g., nest or roost) or not. Moreover, similar critiques could be addressed to other operational definitions that were attributed to functional connectivity. Those include, among others, the proportion of individuals that immigrate into a new habitat patch within a given amount of time and the time required to settle in a new habitat patch (reviewed by Tischendorf and Fahrig 2000*a, b*, Goodwin 2003). Hence, it must be concluded that neither high probabilities of moving among points of primary habitat or high movement rates imply high functional connectivity.

The lack of an operational definition based on established theories in behavioral ecology has probably led to the notion that a lot of “moving around” by individuals (e.g., high patch immigration rate) is profitable with respect to habitat selection and population viability. It is indeed intuitive to equate an ease of movement among resource patches with a propensity to move. From this standpoint, and without precisely knowing how much movement is necessary to maintain processes, a high level of functional connectivity is often considered as a desirable property of landscapes. This notion, which was often implied or referred to in studies on wildlife corridors (Beier and Noss 1998) and population viability (e.g., Thomas 2000), should nevertheless be applied carefully. For instance, favoring a landscape structure where high levels of dispersal occur may result in recommending a landscape structure in which individuals experience poor breeding success and thus exhibit low philopatry, all other things being equal (Switzer 1997, Doligez et al. 2002). This example illustrates the potential for misinterpretation, and may be more importantly, the possibility of committing errors when applying the concept of functional connectivity in its actual form to conservation issues.

Two more hurdles: landscape anisotropy and individual variation

Whereas landscape ecologists are interested in the connectivity of entire landscapes, metapopulation ecologists are interested in the connectivity of single habitat patches (Moilanen and Hanski 2001, Tischendorf and Fahrig 2000*a*). In metapopulation ecology, connectivity is restricted to the modeling of migration rates among habitat patches, which directly points towards clear operational definitions amenable to field measurements and statistical modeling: e.g., the probability

that an empty patch will be colonized during a dispersal event (Moilanen and Nieminen 2002). Implicit to this patch-based approach is the fact that not all patches are assumed to be of equal connectivity. The flow of dispersing individuals may accordingly be polarized along certain axes and in certain directions within a given landscape (Gustafson and Gardner 1996, Ferreras 2001, Ovaskainen 2004). Polarized or anisotropic flows of individuals may not only result from different abundances of dispersers that depend on the structure of the landscape, but also from variations in the ease of movement along the different axes and directions of movement. Bélisle and St. Clair (2001) have illustrated this possibility with an experiment where they translocated territorial, mated male forest birds within a valley characterized by several parallel, linear strings of open habitat. Overall, the birds translocated across the valley floor, such that they would repeatedly encounter movement barriers, took longer to return to their territories than birds translocated along the valley floor. They also found variation in response among species, suggesting that life-history characteristics may modulate how individuals perceive and respond to movement barriers. Such landscape anisotropy with respect to movement certainly deserves to be taken into account given its potential impacts on the structure and dynamics of populations and communities (Wiegand et al. 1999, Sherratt et al. 2003).

The fact that the ease of movement can vary among different axes within a landscape, as well as in opposite direction along a given axis, certainly complicates the derivation of synthetic measures of functional connectivity (Gustafson and Gardner 1996, Bélisle and St. Clair 2001). For that matter, it certainly proscribes summarizing functional connectivity by a single number that would originate from a simple integration or average over all patches of “patch-based connectivities” as suggested by some authors (e.g., Tischendorf and Fahrig 2000*a, b*). In its simplest expression, functional connectivity should be characterized by a magnitude and a direction (i.e., a vector), which would integrate measurements taken along different axes and in different directions. And depending on the theoretical framework in which functional connectivity is being used, it might even prove better to use a matrix of directionally explicit, patch-to-patch measures. Note that metapopulation ecologists have been able to synthesize the information of such a matrix into a single measure relevant to population viability, namely metapopulation capacity (Hanski and Ovaskainen 2000).

On another front, because individuals are likely to show different levels of motivation when it comes to move, we should expect individual variation in the functional connectivity of a given landscape. This amount of individual variation in functional connectivity may depend on landscape structure. If this were the case, then we should not only pay attention to mean values of functional connectivity, but also to their var-

iance, especially when the matrix is highly heterogeneous (Fraser et al. 2001, Ricketts 2001). If we assume that dispersal processes depend upon functional connectivity, then variation in functional connectivity certainly merits attention given that variance in demographic rates can influence population dynamics (Kendall and Fox 2002).

Incorporating behavior into functional connectivity

In spite of the above problems, I strongly believe that ecologists should not abandon the functional connectivity concept as defined by Taylor et al. (1993). Functional connectivity conceptualized as the ease of movement among points or resource patches is already used in several behavioral ecology models that address the spatiotemporal distribution of individuals. Addressing functional connectivity under the framework offered by these models would certainly help link process and pattern. For example, behavioral ecologists have developed several models predicting the duration that an individual should spend exploiting a resource patch as a function of travel time among patches (e.g., the marginal value theorem) for individuals that exploit resources solitarily (Stephens and Krebs 1986) or in groups (Giraldeau and Caraco 2000). Travel time is likely to be strongly correlated with the ease of movement among resource patches as it integrates the rate of movement and the detours that landscape structure may impose on individuals (Jonsen and Taylor 2000, Bélisle and Desrochers 2002). Hence, measuring the residence time within resource patches of known quality and abundance could provide an indication of the travel time experienced by moving individuals. Patch residence time would be especially useful to assess functional connectivity for species whose movements are difficult to track. Moreover, once properly adapted, patch models could be used to relate residence time to functional connectivity in terms of "integrative" fitness currencies (e.g., an integration of travel time and predation risk as perceived by individuals).

Group size models (Bélisle 1998, Giraldeau and Caraco 2000) could also prove to be useful to assess functional connectivity. These models essentially predict how individuals should distribute themselves among resources patches (or territories) that vary in quality. Because it is assumed that individuals behave in a way that maximizes their fitness and that the fitness experienced by individuals depends on patch attendance, a stable distribution is reached when individuals do not benefit from unilaterally changing position. In the absence of travel costs, this stable distribution is mostly dictated by patch quality. Yet, in the presence of travel costs, individuals often cannot afford reaching the resource patches that would convey the best returns upon exploitation. As a result, poor quality patches tend to be overused (Bernstein et al. 1991, Beauchamp et al. 1997). The level of discrepancies between observed and predicted distributions under the assumption of no

travel costs could therefore be used to assess functional connectivity. The implementation of such an approach should be greatly facilitated by recent developments in social foraging theory. For instance, the stringent assumptions whereby ideal free distribution (IFD) models could only be applied to very small and simply structured landscapes are starting to be relaxed. Models can now address the distribution of individuals among resource patches at large spatial scales (Tyler and Hargrove 1997), among resource patches embedded within a hierarchy of spatial scales (Beauchamp et al. 1997, Bélisle 1998), and along smoothly changing resource gradients (Stephens and Stevens 2001).

By equating functional connectivity with travel costs, landscape ecologists would benefit from a stronger theoretical framework to study the influence of landscape structure on ecological processes and their emerging patterns. As behavioral ecology models already consider the influence of several factors other than travel costs on movement, merging the notion of functional connectivity with the latter shall limit equivocal interpretations of quantitative measures of functional connectivity. Such a transition should be relatively straightforward as many behavioral ecology models, especially the ones in foraging theory, are spatially implicit [see Stephens and Stevens (2001) for a spatially explicit, IFD model]. It goes without saying that this joint venture would also improve how behavioral ecologists treat landscape heterogeneity in their models and scale-up their predictions. Nevertheless, measuring functional connectivity within the context of complex models will bring its share of problems, especially regarding their structure and parameterization (e.g., South et al. 2002). It may necessitate field-intensive studies in order to assess, among other things, the quality and distribution of resource patches and how different fitness currencies vary with patch attendance. In addition, both the physiological state of individuals and the fitness currencies that they may be maximizing will have to be considered (Turcotte and Desrochers 2003). At last, the measure of functional connectivity that will be obtained will likely be model specific. Yet, the ways in which functional connectivity should be measured must be dictated by its ecological role within specific models or theories. This ecological role shall in turn dictate the kind of motivation underlying the movement of individuals.

Standardizing the motivation to move

Movement implies many decisions (Grubb and Bronson 2001, Stamps 2001). An individual must first leave an area, then adjust its course and rate of travel, and ultimately, settle somewhere. Those actions result from motivations that are influenced by the state of the individual. The motivation underlying the movement of individuals must therefore be taken into account when measuring functional connectivity. For instance, it is legitimate to ask whether a forest bird moving along a

forest edge indicates that open areas are barriers to movement or that the forest edge is a prime foraging habitat (Desrochers and Fortin 2000). Analogously, the likelihood that Red-eyed Vireos (*Vireo olivaceus*) cross gaps in forest habitat depends on whether individuals were lured by a mobbing scene or an intruding conspecific (Desrochers et al. 2002). At last, the fact that movement may serve more than one need and that those may vary across individuals can complicate field measurements.

Since the cause of movement (or lack thereof) will be difficult to identify under field conditions, especially at large spatial scales and during long time frames, experimental manipulations coupled with precise tracking methods may offer the best option for obtaining meaningful measures of functional connectivity (reviewed by Desrochers et al. 1999). For instance, translocating animals allows standardizing motivation across individuals, and if the latter happen to be site tenacious, it also provides the individuals' most likely destination. Being aware of the potential destinations that individuals are trying to reach may be advantageous for determining the level of anisotropy of a landscape with respect to its functional connectivity (Bélisle and St. Clair 2001). The relevance of translocation experiments for studying movement with respect to landscape structure is starting to be recognized and applied to various taxa such as insects (Pither and Taylor 1998), amphibians (M. J. Mazerolle and A. Desrochers, *unpublished manuscript*), birds (Bélisle et al. 2001, Cooper and Walters 2002, Gobeil and Villard 2002), and mammals (Bowman and Fahrig 2002, McDonald and St. Clair 2004). Playbacks to lure individuals to a specific destination have also been used successfully as another means to standardize the motivation of birds and address the permeability of various landscape elements to movement in different seasons (Harris and Reed 2001, Bélisle and Desrochers 2002, Desrochers et al. 2002).

On another front, food-titration experiments could help push the envelope further by allowing us to assess the cost of reaching certain destinations (Todd and Cowie 1990, Abrahams and Dill 1998). To my knowledge, this method has been used in landscape ecology only once (Turcotte and Desrochers 2003). Analogously, measuring giving-up densities (GUDs) in resource patches embedded in landscapes of varying structures is yet another means by which travel costs could be assessed (Kohlmann and Risenhoover 1998, Price and Correll 2001). Manipulating the location of nesting places or burrows with respect to landscape structure and known food sources (of similar or different quality) would also prove particularly useful to assess the travel costs implied when provisioning or hoarding food within heterogeneous landscapes (Huhta et al. 1999, Hinsley 2000). Although manipulations such as food-titration experiments can be difficult to apply at spatial scales relevant to dispersal movements,

we could still induce individuals to leave or remain within their home range or territory by altering their breeding success (e.g., Doligez et al. 2002).

Studying movement is strongly hampered by the difficulty of tracking animals over large expanses and during long time intervals. This is exacerbated by the temporal and financial constraints too often faced by ecologists. Beside the sound option of pooling resources and working within experimental landscapes (e.g., Haddad et al. 2003), part of the challenge of measuring functional connectivity will thus depend upon our ability to design experiments addressing travel costs within standardized motivational contexts. As good ideas will eventually proliferate, it will become of interest to correlate the results obtained by different methods, in different contexts, and across species with different life-histories (Desrochers et al. 1999).

CONCLUSION:

ECOLOGISTS SHOULD GET ON THE MOVE

By questioning the actual operational definitions given to landscape connectivity, I do not condemn the use of this concept, but call for research within a stronger theoretical framework. Behavioral ecology provides such a framework. Many of its models already use a concept analogous to the one of functional connectivity, namely travel costs, to describe the degree to which the environment facilitates or impedes movement among resource patches. Because these models predict how animals should use resources in space and time within spatially-implicit landscapes, they offer a great opportunity to link process and pattern. Landscape ecologists should be proactive and approach behavioral ecologists to improve the models of the latter to the spatially-explicit nature of their own object of study: the influence of landscape structure on the abundance and distribution of organisms. By quantifying functional connectivity within a stronger theoretical framework, landscape ecologists will certainly reduce the likelihood of obtaining equivocal results that may have negative implications not only for their science, but also for biological conservation. I hope that this paper will help favor a behavioral ecology of ecological landscapes as advocated by Lima and Zollner (1996).

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