

On the use of connectivity measures in spatial ecology. A reply

Lutz Tischendorf, Busestrasse 76, D-28213 Bremen, Germany. – Lenore Fahrig (correspondence), Ottawa-Carleton Inst. of Biology, Carleton Univ., 1125 Colonel By Drive, Ottawa, Canada K1S 5B6 (fahrig@ccs.carleton.ca).

The purpose of our initial review on the “usage and measurement of landscape connectivity” (Tischendorf and Fahrig 2000a) was to clarify the concept of landscape connectivity. It was also our intention to stimulate discussion and to raise awareness among landscape ecologists about problems related to the interpretation of connectivity measures, and to encourage a more consistent use of terminology when referring to the concept of landscape connectivity.

However, connectivity is a concept and a term that is shared between two ecological disciplines – landscape ecology and metapopulation ecology. The two disciplines measure connectivity at different scales, landscape and patch scale respectively, and use these measures in different ways. Yet, the assumed underlying process – movement of organisms across landscapes – is the same. Our initial review was limited to issues associated with the concept of landscape connectivity and not to connectivity as it is used in metapopulation ecology.

Moilanen and Hanski (2001) extend our discussion and emphasize how connectivity is measured and used in metapopulation ecology. However, we take issue with some aspects of Moilanen and Hanski’s paper. In particular, they have not accurately represented the concept of landscape connectivity, largely because they appear to misunderstand the overall objectives of landscape ecology and the relationship between metapopulation ecology and landscape ecology. In this reply we attempt to clarify this relationship as well as the differences in the concept of connectivity as it is used in the two disciplines.

Relationship between metapopulation ecology and landscape ecology

Moilanen and Hanski state that landscape ecology suffers from a “lack of clear focus and theory” and that

landscape ecologists study “measures that just happen to be convenient to obtain using GIS-methods” that “have not necessarily been derived from first principles nor from some relevant theory”. This caricature of landscape ecology suggests that Moilanen and Hanski may not be aware of the objectives and approaches in this field. Since this bears on the issue of connectivity (below), we take this opportunity to clarify the relationship between these two disciplines.

Metapopulation ecology is primarily the study of the effects of habitat structure (patch number, patch sizes, and inter-patch distances) on the dynamics of a metapopulation (Hanski 1994). Landscape ecology is the study of the effects of landscape structure on ecological processes (Turner 1989). An important objective of both disciplines is to predict persistence of populations at a landscape scale. Since habitat structure is one aspect of landscape structure and since metapopulation dynamics is an ecological process, metapopulation ecology is in fact a subdiscipline of landscape ecology.

However, metapopulation ecologists and landscape ecologists have taken different approaches to predicting population persistence. Metapopulation ecology describes a population at the landscape scale (i.e. a metapopulation) in terms of the presence/absence of local populations in patches of actual or potential habitat. The objective is to predict the dynamics of the metapopulation based on local extinction and colonization rates, which are input parameters in metapopulation models (Hanski 1994). In contrast, landscape ecologists typically use spatially explicit population models (SEPM’s) to predict landscape-scale population persistence (e.g., Fahrig 1992, Pulliam et al. 1992, Anderson and Mahato 1995). In these models actual numbers of individuals and their spatial distribution over the landscape are studied, not just presence/absence of local patch populations. A SEPM may or may not character-

ize the landscape in terms of patches. Unlike metapopulation models, extinction and colonization of local populations are not defined by input variables but result from population processes (births, deaths, movement) (e.g., Fahrig 1998). Another important distinction between the metapopulation approach and the SEPM approach is that metapopulation models ignore the characteristics of the non-habitat ("matrix") portion of the landscape. In contrast, landscape models often assume that movement through matrix depends on attributes of the matrix, which may influence dispersal mortality and/or movement direction (e.g., Tischendorf and Fahrig 2000b). Therefore, in metapopulation ecology, movement between patches depends only on the distance between patches and the inherent "dispersal ability" of the organism (as captured in the colonization rate parameter). In landscape models, movement through the landscape is assumed to depend on the interaction between characteristics of the matrix and the movement behaviour of the organism.

Interestingly, Moilanen and Hanski (2001) suggest that "one central aim of current metapopulation research is to produce a generally applicable modelling approach of spatial population dynamics that could be applied to arbitrary landscapes and parameterized with a reasonable amount of empirical data". This is reflected in a recent trend toward including population size and matrix effects in so-called metapopulation models (e.g., Kean and Barlow 2000, Heino and Hanski 2001). Such models are in fact not correctly termed metapopulation models, because they are not based on the metapopulation framework of patch population presence/absence (colonization/extinction). In any event, the issues that must be dealt with for such a modelling objective to succeed are exactly the issues that landscape ecologists are already tackling in the context of landscape connectivity: effects of matrix structure and quality on movement through the landscape. Therefore, this trend in metapopulation ecology represents a shift toward the type of approach currently used by many landscape ecologists.

A second difference between metapopulation ecology and landscape ecology is the scale of empirical analysis. In empirical metapopulation studies a single data point represents data from a single patch, and data analyses relate patch size and isolation (predictor variables) to population presence/absence at the patch scale (response variable). These results are then combined in a model to predict metapopulation persistence (Hanski 1994). In contrast, in landscape ecological studies, each individual data point represents data from a landscape (e.g., McGarigal and McComb 1995, Trzcinski et al. 1999, Villard et al. 1999, Pope et al. 2000). Data analysis involves relating indices of landscape structure (e.g., mean patch size, total edge) for different landscapes to a population response variable such as landscape connectivity (e.g., Tischendorf 2001) or

population spatial distribution (e.g., With et al. 1997) or population presence/absence on the landscapes. These landscape indices are not simply measures that can be easily obtained through GIS (as suggested by Moilanen and Hanski) but are indices that, for theoretical reasons or reasons based on the organism's biology, are thought to be related to population density or presence/absence at the landscape scale. Each data point in a landscape-scale analysis therefore represents data from an individual landscape, and data from several landscapes are required for the analyses. To summarize this point, in metapopulation ecology data analysis is conducted at the patch scale (multiple patches) whereas in landscape ecology data analysis is conducted at the landscape scale (multiple landscapes).

Patch connectivity vs landscape connectivity

Connectivity is a shared term with different meanings in different contexts. It is therefore necessary to be clear about the context in which it is used. This can be done by stating the context whenever the term is used. However, the author must then rely on the readers' ability to associate this term with the relevant context, when comparing the paper with other studies. A better way to clarify the context is to provide a modifier (e.g., "landscape" or "patch") for connectivity, which clearly identifies the intended meaning. The literature reveals both approaches. There are at least six different terms for connectivity: "landscape connectivity", "patch connectivity", "connectivity", "connectedness", "habitat connectivity" and "patch isolation". The term "landscape connectivity" refers to the landscape ecological perspective in which connectivity is seen as a property of an entire landscape. "Patch connectivity" identifies connectivity as an attribute of a patch and is typically used in metapopulation ecology. "Patch isolation" has been used as an antonym of "patch connectivity". Most landscape ecologists associate patch isolation with patch connectivity. The other three terms can only be interpreted unambiguously within a clearly demarcated context. To summarize, the inconsistent use of at least six different terms for two concepts in two related scientific disciplines has hindered communication and is responsible for some misunderstandings, which are reflected in the current debate. We therefore suggest using the terms "patch connectivity" (or patch isolation) and "landscape connectivity". Other terms should be avoided since their meaning is ambiguous.

Patch connectivity, as used in metapopulation ecology, is usually measured as the distance to the next nearest patch or the next nearest occupied patch (or the weighted mean of the distances to the next nearest n patches or next nearest n occupied patches). Inter-patch distance is assumed to be directly related to the colo-

nization rate of a patch. Patch connectivity is part of a metapopulation model (through its effect on the patch colonization term), which describes population dynamics at the landscape scale, i.e. a metapopulation. Hence, metapopulation ecology defines connectivity at the patch scale and the dynamics of a metapopulation at the landscape scale. There is no explicit transformation or aggregation of the patch connectivity measures to the landscape scale. Instead, this aggregation is done implicitly, since the individual patch connectivity values in the metapopulation model influence the metapopulation dynamics at the landscape scale.

This approach is different from landscape connectivity, which is a species-specific attribute of a landscape and not of a habitat patch. Since landscapes are often described in terms of the habitat patches they contain, it has been convenient to derive landscape connectivity measures based on some combination of immigration into habitat patches. Landscape connectivity measures such as mean dispersal success or mean search time (e.g. Doak et al. 1992, Demers et al. 1995, Schippers et al. 1996, Schumaker 1996, Tischendorf and Fahrig 2000b) are typical examples of this approach.

However, as we pointed out in our initial review (Tischendorf and Fahrig 2000a), such averages are problematical, in particular when used in landscapes with a few large habitat patches. For this reason, we argued for careful interpretation of patch-based landscape connectivity measures. We also suggest that non-patch-based measures of landscape connectivity, such as cell immigration (Tischendorf and Fahrig 2000a, b) or the frequency of boundary crossings (Wiens et al. 1985), may be preferable to patch-based measures. This should, however, not be mistaken for a general criticism of patch connectivity or patch isolation. Both patch connectivity and landscape connectivity are useful (though different) concepts.

The concepts of landscape and patch connectivity were formulated based on the insight that movement of organisms across a heterogeneous landscape results in population linkages across the landscape. However, movement is incorporated in very different ways in these two approaches. The metapopulation approach focuses on colonization of empty patches. High patch connectivity implies a high probability of (re)colonization of that patch. Patch connectivity is assumed to result from movement through a landscape, but this movement is not explicitly modelled. In contrast, landscape connectivity is based directly on rates of movement through the landscape. Not all emigrants from habitat will reach other habitat, but may die or return. Movement rates are not necessarily uniformly distributed across a landscape. Individual perception combined with external forces, such as wind or road mortality, may alter movement paths or kill dispersers, resulting in different immigration rates than predicted by distance alone. All of these effects determine the rate

of movement through the landscape (landscape connectivity). Moilanen and Hanski refer to landscape connectivity as one among many indices that are used to characterize entire landscapes. In fact, landscape connectivity is not like other landscape indices because it is not based on landscape structure but rather on organism response to structure, i.e., successful movement through the landscape. The effects of the interactions between individual movement and landscape structure can only be understood using a landscape scale examination.

Finally, Moilanen and Hanski provide an example to “prove” that lower landscape connectivity should result in higher metapopulation persistence. The argument is that if we enlarge a landscape by adding a number of isolated habitat patches beyond the former bounds of the landscape, these isolated habitat patches will result in lower landscape connectivity (when calculated as an average over all habitat patch connectivities) but enhanced metapopulation persistence. We view this argument as specious and unrealistic. In any real situation the total area under consideration (e.g., for management) is predetermined. Changes in patch number and landscape connectivity will occur through addition or loss of habitat within this area. For example, if an existing landscape becomes more fragmented through habitat loss, both lower landscape connectivity and lower metapopulation persistence will result.

In summary, we disagree with the statement of Moilanen and Hanski that “connectivity is primarily a measure of a habitat patch, . . . , rather than a measure of an entire landscape”. In fact, there are two concepts of connectivity, one at the patch scale and one at the landscape scale. We hope that this reply has clarified and corrected some misapprehensions about landscape ecology in the paper by Moilanen and Hanski.

Acknowledgements – We thank Jochen Jaeger for his comments on a draft of this paper.

References

- Anderson, M. C. and Mahato, D. 1995. Demographic-models and reserve designs for the California spotted owl. – *Ecol. Appl.* 5: 639–647.
- Demers, M. N., Simpson, J. W., Boerner, R. E. J. et al. 1995. Fencerows, edges, and implications of changing connectivity illustrated by two contiguous Ohio landscapes. – *Conserv. Biol.* 9: 1159–1168.
- Doak, D. F., Marino, P. C. and Kareiva, P. M. 1992. Spatial scale mediates the influence of habitat fragmentation on dispersal success: implications for conservation. – *Theor. Popul. Biol.* 41: 315–336.
- Fahrig, L. 1992. Relative importance of spatial and temporal scales in a patchy environment. – *Theor. Popul. Biol.* 41: 300–314.
- Fahrig, L. 1998. When does fragmentation of breeding habitat affect population survival? – *Ecol. Model.* 105: 273–292.
- Hanski, I. 1994. A practical model of metapopulation dynamics. – *J. Anim. Ecol.* 63: 151–162.

- Heino, M. and Hanski, I. 2001. Evolution of migration rate in a spatially realistic metapopulation model. – *Am. Nat.* 157: 495–511.
- Kean, J. M. and Barlow, N. D. 2000. The effects of density-dependence and local dispersal in individual-based stochastic metapopulations. – *Oikos* 88: 282–290.
- McGarigal, K. and McComb, W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon Coast Range. – *Ecol. Monogr.* 65: 235–260.
- Moilanen, O. and Hanski, I. 2001. On the use of connectivity measures in spatial ecology. – *Oikos* 95: 147–151.
- Pope, S. E., Fahrig, L. and Merriam, H. G. 2000. Landscape complementation and metapopulation effects on leopard frog populations. – *Ecology* 81: 2498–2508.
- Pulliam, H. R., Dunning, J. B. and Liu, J. 1992. Population dynamics in complex landscapes: a case study. – *Ecol. Appl.* 2: 165–177.
- Schippers, P., Verboom, J., Knaapen, P. and van Apeldoorn, R. C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. – *Ecography* 19: 97–106.
- Schumaker, N. H. 1996. Using landscape indices to predict habitat connectivity. – *Ecology* 77: 1210–1225.
- Tischendorf, L. 2001. Can landscape indices predict ecological processes consistently? – *Landsc. Ecol.* 16: 235–254.
- Tischendorf, L. and Fahrig, L. 2000a. On the usage and measurement of landscape connectivity. – *Oikos* 90: 7–19.
- Tischendorf, L. and Fahrig, L. 2000b. How should we measure landscape connectivity? – *Landsc. Ecol.* 15: 633–641.
- Trzcinski, M. K., Fahrig, L. and Merriam, G. 1999. Independent effects of forest cover and fragmentation on the distribution of forest breeding birds. – *Ecol. Appl.* 9: 586–593.
- Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. – *Annu. Rev. Ecol. Syst.* 20: 171–197.
- Villard, M.-A., Trzcinski, M. K. and Merriam, G. 1999. Fragmentation effects on forest birds: relative influence of woodland cover and configuration on landscape occupancy. – *Conserv. Biol.* 13: 774–783.
- Wiens, J. A., Crawford, C. S. and Gosz, J. R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. – *Oikos* 45: 412–427.
- With, K. A., Gardner, R. H. and Turner, M. G. 1997. Landscape connectivity and population distributions in heterogeneous environments. – *Oikos* 78: 151–169.