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Empirical explorations of landscape connectivity

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Abstract

Movement plays a fundamental role in the dynamics of populations, and is influenced by differences in the patterning of resources on the landscape. The interaction between the ability of an organism to move through different types of landscapes and the relative size and positioning of resources in the landscape is termed landscape connectivity. Experimental manipulations have been made to measure landscape connectivity for two species of damselflies (*Calopteryx maculata* and *Calopteryx aequabilis*) in completely forested, completely open and mixed landscapes. Experimentally, individuals have been translocated between landscapes to measure aspects of how they move through the different types of landscapes. I present an overview of these experiments and results and then discuss their importance as methods for further exploring the important concept of connectivity.

Introduction

At least since Andrewartha and Birch (1954) we have known that movement plays a crucial role in the dynamics of many populations. Movement is critical at an individual level in allowing animals to access heterogeneously distributed resources. At a population level, it is necessary for the establishment and re-establishment of local populations. The increase in our understanding about the importance of movement has been primarily responsible for much of the development of our current conceptual framework of both metapopulation dynamics (Hanski 1996) and the dynamics of other types of spatially-structured populations (Harrison 1994).

An essential part of the development of this body of theory was the notion that the degree to which local populations were joined, or connected, had an influence on the persistence of the metapopulation (e.g. Fahrig and Merriam, 1985; Lefkovich and Fahrig, 1985). These ideas emerged from empirical work on the movements of small mammals in fencerows that showed that patches of habitat connected by linear elements improved the probability of regional population survival for some species (Henderson *et al.* 1985; Henein and Merriam 1990).

From these early explorations came at least two important ideas. First, the work suggested that links between habitats, or corridors, were a potential conservation tool for aiding the persistence of spatially structured populations (Merriam 1991). Second, and more generally, the work demonstrated, through a series of modelling and empirical surveys, that the extent to which patches of habitat were connected, and the 'quality' of those connections, positively influenced the probability of metapopulation persistence (Fahrig and Merriam,

1985; Merriam 1991; Fahrig and Merriam 1994). Considerable controversy subsequently surrounded the first idea (e.g. Simberloff *et al.* 1992) but, at least in part, such controversy rested on the false understanding that the connectivity of a landscape was equivalent to the establishment of corridors (e.g. Forman 1995). The second idea has gained more general acceptance in the current literature, even though it seems to have an even weaker base in empirical study. As a consequence, I have focussed my research over the past three years on empirically exploring and determining how to measure landscape connectivity using insect systems.

In this paper I present my views of the current understanding of connectivity in the literature together with an overview of some empirical work my students and I are undertaking to enhance that understanding. I end the paper highlighting some important areas for further work.

What are the elements of connectivity?

Merriam (1984), and Henein and Merriam (1990) define connectivity as the extent to which an organism is able to move through the landscape to access resources vital to its survival. Taylor *et al.* (1993) generalized the concept to include it as a component of landscape structure (*sensu* Dunning *et al.* 1992). Most authors follow from this earlier work and include in definitions of connectivity two important elements: those related to the physical structure of the landscape and those related to behavior. Henein and Merriam (1990) recognized that ability to use resource patches was directly a function of both distance between patches (a measure of landscape structure) and the biology and behavior of the organism. With *et al.* (1997) define connectivity as a 'functional' link among habitats. They highlight the importance of the habitat elements and the dispersal capabilities of the organism. Schippers *et al.* (1996), and Hof and Flather (1996) consider connectivity to be a measure of the probability of individuals successfully immigrating to a new patch. Hof & Flather (1996) succinctly define connectivity mathematically using three parameters: the distance between patches and the nature of the matrix between patches, (both of which are measures of landscape structure) and the capability of dispersal in the species, a measure of behavior that interacts with structure.

In turn, the behavior of an organism at any given time is a function of the structure of the landscape; that is, animals will respond differently to different types of habitat elements within landscapes (Wiens *et al.* 1997). Behavior will also interact with landscape structure at different spatial scales; these scales necessarily define the types of behavior and the types of interactions that we may observe (Holling, 1992). It is important to note that behavioral decisions at fine spatial or temporal scales may translate into differences in connectivity at larger-scales. In other words, the implications of a behavioral decision of an individual in a landscape at a fine scale may have consequences that extend far beyond that scale (Levin, 1992). Recently, some have recognized that there is room for fruitful interaction among the fields of landscape and behavioral ecology (e.g. Lima and Zolner, 1996). Another way of considering this proposition is that there is an important need to consider how the effect of spatial and temporal scale influences measures of connectivity.

Connectivity then, is an element of landscape structure; a function of the composition and configuration of the landscape, and a function of the relative ease by which an organism

moves through elements in that landscape. It is a probabilistic measure that is determined by both fine-scale and large-scale patterns of behavior of the organism, that in turn are a response to fine and large-scale aspects of the physical structure of the landscape. Conceptually, it is a measure of the ease with which an organism moves through the landscape, taking into account that landscapes are heterogeneous mosaics of resources and non-resources. It incorporates both the amount of movement (the relative probability of an individual moving) and success of movement (the relative probability of an animal successfully moving between two points).

Measuring connectivity

Connectivity can be inferred, modelled, or assessed empirically. As spatial scale increases, and the distances that organisms are capable of moving increases, the empirical assessment of the connectivity of landscapes becomes more difficult. As a consequence, most work has proceeded conceptually (Dunning *et al.*, 1992; Taylor *et al.*, 1993), using simulation modelling (Schumaker, 1996) or null-model studies (With and Crist, 1996) or indirectly, through inference. Hjermand & Ims (1996), for example, measured connectivity for a European bush cricket as equivalent to the relative density of dispersing animals. Roland & Taylor (1997) inferred from meso- and large-scale surveys that connectivity differed among a group of four parasitoid species since the rate of parasitism by each species was influenced by forest structure (the relative proportion of the landscape that was forested) at different spatial scales.

Connectivity has been empirically assessed for only a few groups of animals, and usually at relatively small spatial and temporal scales (e.g. Wiens *et al.* 1995). Rarely has the concept been explicitly studied at the meso-scales that are relevant to population processes (Kareiva and Wennergren, 1995; May, 1994). Exceptions include the work on small mammals described above (Merriam) and the work of Ilkka Hanski and his colleagues who have inferred, or directly measured connectivity in populations of the butterfly *M. cinxia* (e.g. Hanski *et al.*, 1994). Considerable additional work on colonization of patches has been undertaken by numerous researches, but rarely with an explicit view to examining the process of movement through heterogeneous landscapes.

Empirical measures using damselflies as examples.

We are working on measuring connectivity in a group of Calopterygid damselflies that inhabit streams as nymphs, and along which they mate and oviposit. During preliminary studies, these nominally forest damselflies were observed to fly from streams that wound through relatively open landscapes, across several hundred meters of open pasture to nearby forest. These early observations suggested that the damselflies were linking resource patches together (stream and forest) by flying across open pasture. We considered these open landscapes (consisting of patches of forest and pasture) as fragmented; the resources necessary for damselfly survival were distributed heterogeneously within them, and separated by inhospitable, or at least neutral, habitat.

These observations also suggested that connectivity might be an important component of the population dynamics of these organisms. Surveys of their distribution in the vicinity of the streams confirmed that individuals were using both types of habitat. On average, animals were distributed farther from the streams in the pasture landscapes than they were in the forest

landscapes (Taylor and Merriam, 1995). That is, in the mixed landscapes, where resource patches (forest and stream) were separated by intervening pasture, the animals moved readily through the pasture to link the resource patches.

The observed distributions in the mixed landscape suggested that connectivity might be enhanced in these moderately fragmented landscapes. Enhanced connectivity would imply that in mixed landscapes, animals from different local populations (groups of damselflies found along individual streams) would interact (exchange genetic material) more frequently than in non-fragmented, forest landscapes. Therefore, we addressed the question of whether, in this system, damselflies were impeded, aided, or not affected, by travelling through pasture elements in the fragmented landscape. In other words, we wished to assess connectivity for damselflies within a range of types of landscapes. To answer the question, we designed and performed a manipulative field experiment. The field experiment was used to assess the relative ability of the organisms to move through two different elements in the landscape: forest and pasture, and to assess whether that ability differed as a function of the sex of the animal, and its natal landscape.

The basic design of the experiment was as follows. In each of two replicates, 20 male and 20 female *Calopteryx maculata* were collected from the edge of the stream in a forest and an adjacent pasture landscape for a total of 80 animals. Each animal was marked by writing a unique alphanumeric on its wings using thinned liquid paper. The animals were placed in 1 x 1m cages (according to the design outlined below) to acclimatize for 1h, then released. The main treatment was to displace animals from the edge of the stream (where mating and oviposition take place) by approximately 300m prior to release, testing their ability to move through either a forest or a pasture habitat. The expected number to be re-observed in each landscape were provided by releasing half of the animals at the edge of the stream. Both natal and release landscape were controlled for by translocating half the individuals between landscapes. The design is shown graphically in Figure 1. The objective is not to determine the homing abilities of the animals, but to assess their ability to move through the different elements of the landscape as a function of their landscape of origin and their sex.

The results of the experiment were inconclusive. In brief, more than the expected number of displaced animals was re-observed in the pasture landscape than in the forest landscape but the result was only marginally significantly different from what would be expected by chance (logistic regression; Treatment x landscape term; $p(\chi^2) = 0.116$). Subsequently, we have repeated these experiments for both *C. maculata* and a congeneric species, *Calopteryx aequabilis* (Pither, 1997) and have shown that there is a significant effect (logistic regression; $p(\chi^2) = 0.002$) of the release landscape on the re-observation rate of *C. maculata*, but not for *C. aequabilis*; pasture facilitates movement for *C. maculata*, but neither facilitates nor impedes movement for *C. aequabilis*.

These findings raise additional questions about whether extensive flights across pasture are simply an extension of existing behavior, or are new behaviors that arise as a function of the new type of landscape. To begin to assess the importance of these finer-scale behaviors, we have been performing experiments to explore more fully the behavioral elements of landscape connectivity.

In particular, we are interested in the role of fine-scale decisions in the measurement of connectivity, and the impact that these decisions have on the landscape connectivity. The

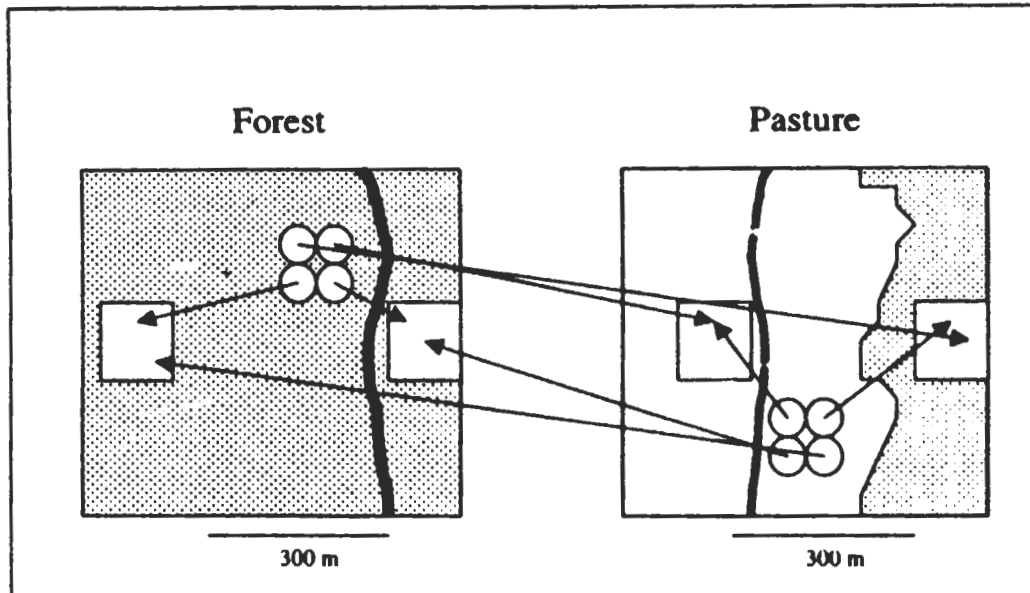


Figure 1. Schematic diagram of experimental manipulation to test the effect of source and release landscapes on the ability of damselflies to move through pasture and forest elements. Stippled areas are forested and open areas are pasture. The dark line represents the stream. Each circle represents 10 male and 10 female damselflies. Squares represent the cages that were situated at the streams, or 300m distant from the stream. Arrows indicate how damselflies were moved within and between landscapes

experiments to elucidate these decisions have been conducted in a similar fashion to the translocation experiments described above. Three types of landscapes are examined: those that are completely forested, those where forest is disjunct from the edge of the stream as in the experiments above and landscapes with little, or no forest. In these experiments we are testing how release landscape, natal landscape, and sex influence the probability that an animal leaves the stream, and the pathways they take. We have experimentally translocated and released over 100 damselflies of two species (*C. maculata* and *C. aequabilis*) in each of 15 different landscapes, of the three types. Experimental damselflies are marked and released in the target landscape then tracked for up to 30 minutes.

Preliminary results (not shown) indicate that, for both species, the probability of animals leaving the stream is highest in the forest and mixed landscapes and lowest (near zero) in the non-forested landscapes (Jonsen 1997). We predict then that moderately fragmented landscapes are more connected than both non-fragmented landscapes and completely fragmented landscapes, perhaps implying a metapopulation-like population structure in forest and completely fragmented landscapes but not in moderately fragmented landscapes.

A third way we have used to approach the measurement of connectivity is to examine the patterns of distribution of organisms in the landscape, and examine how simple measures of landscape structure influence those distributions, at multiple spatial scales. Such an approach was used by Roland & Taylor (1997) to demonstrate that the proportion of forest in a landscape influenced rates of parasitism by four species of forest-tent caterpillar (*Malacosoma disstria*) parasitoids. We have shown for damselflies, that both local habitat

characteristics (the physical characteristics of the streams and the amount of oviposition material present) and landscape characteristics (distance to nearby forest) influence the incidence of damselflies at streams (Pither, 1997). We are now in the process of testing, using simulation models, whether these fine-scale habitat characteristics and behavioral decisions, coupled with the different levels of connectivity within a landscape, are sufficient to predict patterns of distribution at larger spatial scales. Preliminary tests of these models show that at least some of the variance in distribution at large spatial scales can be predicted by the meso scale behaviors, but considerable unexplained variance remains.

What important questions remain?

As with any new field of study, there are important questions unanswered. One important area of further study is to examine how such responses to structure vary across taxa. For example, other studies we are undertaking focus on asking similar questions as outlined above, but using amphibians as models. Amphibian populations are similar to the damselfly system in that important resource requirements include both terrestrial and aquatic habitats. The rationale is to look at how ecological processes such as movement differ across the two very different taxa. The results from a range of such studies will begin to address important questions about which kinds of species are most susceptible to anthropogenic changes in landscape structure.

A second important area, only partially addressed in this paper, is how spatial scale influences connectivity. Earlier definitions of landscape connectivity do not deal explicitly with how connectivity varies with scale.

A third important area of increasing interest is to determine when connectivity is important to population persistence. Our research has shown us that the Calopterygid damselflies are able to persist within moderately fragmented landscapes by linking together spatially separate resource patches. However, our initial results suggest that in highly fragmented landscapes, damselflies must switch to new resource patches for foraging, as sufficient forest no longer exists close to the streams along which they must mate, oviposit and develop. What are the critical amounts and distributions of resources within landscapes below which persistence begins to decline? Andr n (1994) suggested such a threshold effect may exist for birds and small mammals, but it remains to be discovered how such concepts can be more generally applied to other important landscape ecological processes.

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