FORUM
FORUM
FORUM

FORUM is intended for new ideas or new ways of interpreting existing information. It provides a chance for suggesting hypotheses and for challenging current thinking on ecological issues. A lighter prose, designed to attract readers, will be permitted. Formal research reports, albeit short, will not be accepted, and all contributions should be concise with a relatively short list of references. A summary is not required.

Connectivity is a vital element of landscape structure

Philip D. Taylor, Lenore Fahrig, Kringen Henein and Gray Merriam, Dept of Biology, Ottawa-Carleton Inst. of Biology, Ottawa, ON, Canada K1S 5B6

In a recent FORUM article, Dunning et al. (1992) put forward a framework of landscape processes that stimulated considerable discussion amongst us. We are in general agreement with their ideas, but feel that a more explicit recognition of the importance of movement as a component of landscape structure would add clarity and utility to the framework. We wish to build on their foundation by presenting some additional ideas.

Dunning et al. (1992) outline four ecological processes acting at the landscape scale: 1) landscape complementation; 2) landscape supplementation; 3) sources and sinks; and 4) neighbourhood effects. Each process depends upon the distribution of resources in the landscape. Resources are distributed in patches. Implicit in the definition of each process is that animals move among the resource patches. In the first two, animals move among resource patches to: 1) acquire a full complement of resources to meet their needs; and 2) supplement their existing resources with those in additional patches. In the third, movement from sources to sinks is required for the maintenance of sink populations. The fourth process, neighbourhood effects, implies that individuals move between patches, but focuses on the permeability of the boundaries between contiguous patches.

Dunning et al. (1992) assume that the ability of an organism to complement or supplement its resource requirements depends only on the distance to those resource patches. In a related paper, Pulliam et al. (1992) state: "When both landscape physiognomy and composition are incorporated into a population model, the dispersal of organisms across the landscape can be followed...". However, an animal's ability to utilize a resource patch will also be dependent upon its ability to get there. This ability will be determined not only by the distance between patches (i.e. physiognomy), but also by the biophysical nature of the route(s) between two patches and the biology and behaviour of the organism (Henein and Merriam 1990). Some routes facilitate or allow unimpeded movement among patches; others impede to varying degrees the amount, or success, of movement.

Because movement is so critical to animal population survival, we recognize a third measure of landscape structure (sensu Dunning et al. 1992) namely landscape 'connectivity' (Merriam 1984, Baudry and Merriam 1988, Merriam 1991). Landscape physiognomy and landscape composition measure the distribution of resource patches in a landscape (Dunning et al. 1992). Landscape connectivity is the degree to which the landscape facilitates or impedes movement among resource patches.

Each of the components of landscape structure (landscape physiognomy, landscape composition and landscape connectivity) can be measured. Turner (1989) pre-

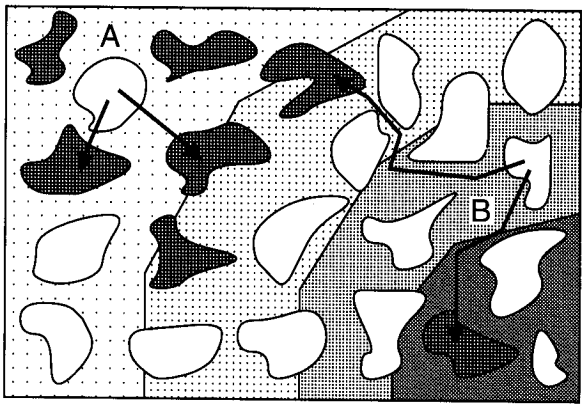

Fig. 1. Landscape complementation. Landscape connectivity underlies a mosaic of patches. Light and dark patches contain different resources required by the animal. Darker background areas have higher connectivity. Animals in area B can access patches more easily (arrows) and so will be able to complement their resource needs. Contrast with Fig. 1 of Dunning et al. (1992) where landscape connectivity is assumed to be homogenous over the landscape.

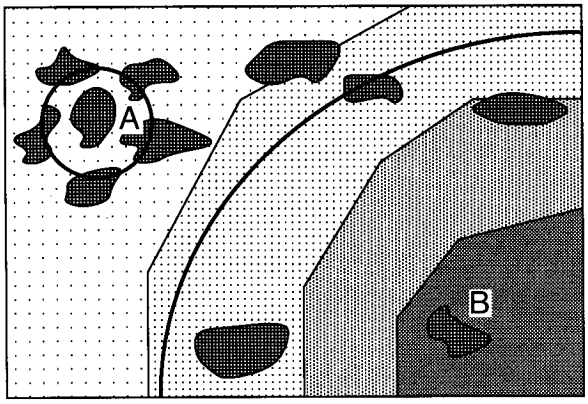

Fig. 2. Landscape supplementation. Landscape connectivity underlies a mosaic of patches. Darker background areas have higher connectivity. Animals in area B can access other patches more easily than animals in area A (areas within circle) and so will complement their resource needs. Contrast with Fig. 2 of Dunning et al. (1992) where landscape connectivity is assumed to be homogenous over the landscape, and the area of B is smaller.

sents methods for the first two. Landscape connectivity can be measured for a given organism using the probability of movement between all points or resource patches in a landscape. Fahrig and Paloheimo (1988) and Henein and Merriam (1990) have demonstrated the use of such measures in mathematical models of animal movement in landscapes.

Now the definitions of the four fundamental ecological processes can be re-stated by considering that each process results from the interacting effects of patch configuration and level of connectivity in a given landscape. We re-present the figures from Dunning et al. (1992) to illustrate our point. Fig. 1 shows landscape complementation and Fig. 2 shows landscape supplementation but in each figure, we have overlaid the resource patches on a map of differential landscape connectivity. It is no longer clear (as stated by Dunning et al. 1992) that area B will support fewer individuals than area A. Since animals in area B can move around the landscape more easily than those in area A, they are able to overcome the problems imposed by resource distribution. Both processes are fundamentally dependent upon the landscape connectivity because that determines the animal's ability to get to the resource patches. By adding landscape connectivity to the picture, we arrive at a conclusion different from Dunning et al. (1992) for the same landscape.

The source-sink process has a more complex interaction with landscape connectivity. A sink that is easily accessed from one or more sources may 'draw off' more animals than one that is poorly connected. Similarly, a poorly connected source will contribute fewer individuals to sinks than a well-connected one. The importance of landscape connectivity to this process is evident from studies showing delayed recolonization of local extinctions (e.g. Verboom and Lankester 1991, Villard et al. 1992). Recolonization of patches is delayed because animals are unable to get to them, not because the patches are unsuitable. Again, the degree to which populations behave as sources or sinks also depends on the landscape connectivity.

Finally, landscape connectivity is vital to the concept of neighbourhood effects. Dunning et al. (1992) state: "A species' abundance in a particular focal patch may be more strongly affected by characteristics of contiguous patches than by those of more distant parts of the landscape". We contend that defining a patch as a neighbour depends not only on its physical distance from the focal patch but also on the landscape connectivity. A distant patch in a landscape with high connectivity will exert stronger neighbourhood effects than a closer patch within a landscape with lower connectivity. Where connectivity is zero, the neighbourhood is restricted to the focal patch itself. In other words, connectivity defines the neighbourhood of the focal patch.

The inclusion of landscape connectivity as an explicit component of landscape structure increases the utility of the framework put forward by Dunning et al. (1992). If we do not explicitly incorporate movement into such a framework, landscape managers and planners will continue to ignore its importance. Several studies have demonstrated that movement is as fundamental to population viability as resource distribution (e.g. Saunders and Ingram 1987, Fahrig and Paloheimo 1988) but maps produced by planners are usually of resource distribution, not movement patterns. Ignoring movement can lead to incorrect and potentially devastating consequences for conservation (e.g. Peterson 1985, Harris and Gallagher 1989). Recognizing all three components of landscape structure assists our efforts in offering prescriptive solutions to ecological problems at the landscape scale.

References

Baudry, J. and Merriam, G. 1988. Connectivity and connectedness: Functional versus structural patterns in landscapes. – In: Schreiber, K.-F. (ed.), Connectivity in landscape ecology. Proc. 2nd International Association for Landscape Ecology. Münstersche Geogr. Arbeiten 29, pp. 23–28.

Dunning, J. B., Danielson, J. B. and Pulliam, H. R. 1992. Ecological processes that affect populations in complex landscapes. – Oikos 65: 169–175.

Fahrig, L. and Paloheimo, J. 1988. Determinants of local population size in patchy habitats. – Theor. Popul. Biol. 34: 194–213.

Harris, L. D. and Gallagher, P. B. 1989. New initiatives for wildlife conservation. The need for movement corridors. – In: Preserving communities and corridors. Defenders of Wildlife, Washington, pp. 11–34.

Henein, K. and Merriam, G. 1990. The elements of connectivity where corridor quality is variable. — Landscape Ecol. 4: 157–170.

Merriam, G. 1984. Connectivity: A fundamental ecological characteristic of landscape pattern. – In: Brandt, J. and Agger, P. (eds), Proceedings First international seminar on methodology in landscape ecological research and planning.

Theme I. International Association for Landscape Ecology. Roskilde Univ., Roskilde, pp. 5–15.
– 1991. Corridors and connectivity: animal populations in heterogeneous environments. – In: Saunders, D. A. and Hobbs, R. J. (eds), Nature conservation 2: The role of corridors. Surrey Beatty & Sons, Chipping Norton, pp. 133–142.
Peterson, B. 1985. Extinction of an isolated population of the middle spotted woodpecker *Dendrocopus medius* (L.) in Sweden and its relation to general theories on extinction. – Biol. Conserv. 32: 335–353.
Pulliam, H. R., Dunning, J. B. and Liu, J. 1992. Population dynamics in complex landscapes: a case study. – Ecol. Appl. 2: 165–177.
Saunders, D. A. and Ingram, J. A. 1987. Factors affecting survival of breeding populations of Carnaby's cockatoo *Calyptorhynchus funereus latirostris* in remnants of native vegetation. – In: Saunders, D. A., Arnold, G. W., Burbidge, A. A. and Hopkins, A. J. M. (eds), Nature conservation: The role of remnants of native vegetation. Surrey Beatty & Sons, Chipping Norton, pp. 249–258.
Turner, M. G. 1989. Landscape ecology: the effect of pattern on process. – Annu. Rev. Ecol. Syst. 20: 171–197.
Verboom, J. and Lankester, K. 1991. Linking local and regional dynamics in stochastic metapopulation models. — Biol. J. Linn. Soc. 42: 39–55.
Villard, M.-A., Freemark, K. E. and Merriam, G. 1992. Metapopulation dynamics as a conceptual model for neotropical migrant birds: an empirical investigation. – In: Hagan, J. M. and Johnston, D. W. (eds), Ecology and conservation of neotropical migrant landbirds. Smithsonian Inst. Press, Washington, DC.