

Continua and Umwelt: novel perspectives on viewing landscapes

A. D. Manning, D. B. Lindenmayer and H. A. Nix, Centre for Resource and Environmental Studies, The Australian National Univ., Canberra, ACT 0200, Australia (adrianm@cres.anu.edu.au).

The concept of habitat fragmentation has been central to conservation research and practice since the 1970s (Diamond 1975, Bunnell 1999, Haila 2002). The consequences of fragmentation have been researched worldwide (Saunders et al. 1991, Haila 2002). One of the original fragmentation models was adapted from the island biogeography theory developed by MacArthur and Wilson (1967) to explain differences in species richness on oceanic islands. The early fragmentation models applied the analogy of oceanic islands to terrestrial habitat "islands" resulting from the breaking up of formerly continuous habitat (Haila 2002). By the early 1990s it was recognised that these early models failed to describe the range of possible landscape configurations found in reality (Lord and Norton 1990, McIntyre and Barrett 1992, McIntyre and Hobbs 1999). These "schematic" fragmentation models have been extensively criticised for failing to reflect "multi-faceted empirical reality" (Haila 2002; summary in Table 1).

In this paper we discuss two key concepts that have major implications for the understanding of landscapes and landscape ecology (1) the concept of continua in nature; (2) the concept of *Umwelt* – individual species perception and response. We also outline the landscape continuum model proposed by McIntyre and Hobbs (1999) as an alternative to the fragmentation model. Finally, we conclude that there is a need to revise how we view landscapes and how we research, understand and manage those landscapes.

Continua

The concept of continua has been widely accepted in vegetation science for over 40 years (Austin 1999a). It arose as the antithesis to the community-unit theory in which plant communities were thought to have evolved into "homogenous, discrete, and recognisable units" (Austin 1985). Since its inception, much of the work on

fragmentation has been on vertebrates (Haila 2002). Fragmentation models often simply view vegetation as habitat for animals. Yet despite the importance of continua in vegetation science (Austin 1999a), continua have been largely ignored in both animal ecology (Lindenmayer et al. 2003) and schematic fragmentation models. In this paper we divide continua into two broad types: (1) environmental continua and (2) spatial continua.

Environmental continua

Austin (1999b) describes the continuum concept as follows:

"The continuum concept states that vegetation has gradually changing species composition along environmental gradients, with each species having an individualistic and independent distribution" (p. 170–171).

The concept is closely associated with H. A. Gleason's individualistic theory (Austin 1985). As such there are similarities with the concept of *Umwelt* (see below). Although largely ignored in animal ecology (see above), Austin (1999a) cites a number of early works (Bond 1957, Beals 1960, Sabo 1980) where the continuum was shown to be applicable to bird community composition. More recently a number of studies have examined vertebrate response along gradients (Braithwaite et al. 1989, Fisher 2001, Lindenmayer et al. 2003). Environmental gradients occur in abstract ecological space. Thus, sites can be close together in environmental space, but far apart in geographical space (Austin 1985).

Spatial continua

In contrast to environmental continua, spatial continua occur in geographical space. McIntyre and Hobbs (1999)

Table 1. Summary of criticisms of fragmentation model.

Key assumption	Criticism
Human perspective equates to organism perspective	Human perceptions of landscapes are not necessarily the same as those of organisms (McIntyre and Hobbs 1999). The “experience” of fragmentation by different organisms and ecological systems is variable and sometimes contradictory (Haila 2002).
Habitat fragments are comparable to oceanic islands	The key to schematic fragmentation models is the ability to be able to identify discrete habitat patches or islands (Bunnell 1999). There are three difficulties with identifying discrete patches. (1) different organisms respond to landscapes differently (2) selection of areas that are sufficiently different is not always easy (especially considering point 1) (3) establishing if an area is truly isolated from its surrounds is problematic (Bunnell 1999).
Habitat islands are surrounded by a hostile “sea” of matrix	Schematic fragmentation models generally assume that the matrix surrounding habitat islands is hostile. However, in terrestrial environments this is rarely the case (Bunnell 1999, Haila 2002). Perception and usage of the matrix will also depend on the organism. Even in the highly agricultural areas some organisms forage outside forest remnants (Haila 2002). Most fragmentation studies have adopted a patch-centred approach, whilst ignoring the influence of the surrounding matrix (McGarigal and McComb 1995, Jokimäki and Huhta 1996, Bennett and Ford 1997, Saab 1999). There is little evidence that the results of patch-centred research can be extrapolated to the wider landscape (Wiens et al. 1993, McGarigal and McComb 1995). Multi-scale studies that have studied the wider landscape context have found that the matrix has a great influence on faunal occurrence (McGarigal and McComb 1995, Jokimäki and Huhta 1996, Saab 1999).
Natural pre-fragmentation conditions were uniform	The assumption in early fragmentation models that natural, pre-fragmentation landscapes were homogenous and temporally constant is erroneous (Haila 2002). Landscapes vary in both time and space. For this reason it is questionable whether results of patch-centred research can be extrapolated to whole landscapes (see above).
Inter-patch distance equals isolation	The hypothesis that spatial configuration of habitat is the primary factor regulating populations is largely theoretical and there is a paucity of empirical evidence to support it (Kareiva 1990, Wiens 1992, McGarigal and McComb 1995). The idea of inter-patch distance as a measure of patch isolation has been widely adopted. Yet linear distance can be a poor measure of connectivity and patch isolation (Haila 1999). This is because fragments with surroundings of high connectivity will be less isolated than those in a landscape of low connectivity (Haila 1999).
Fragmentation a unitary process	Many studies have confused the process of fragmentation (ie. the breaking of habitat into pieces) with the loss of habitat area (Bunnell 1999). However, habitat area loss and habitat fragmentation are separate phenomena (Lord and Norton 1990, Wiens 1994, Bunnell 1999, Haila 2002). For example, McGarigal and McComb (1995) investigated the effect of forest fragmentation on breeding birds in Oregon, USA and found that landscape structure (habitat fragmentation) explained less than 50% of variation in species abundance. The authors concluded that habitat loss has a larger effect than habitat fragmentation in that environment.

recognized that fragmentation was not a categorical process and that it occurred on a continuum. They believed that the binary view of landscape as either “habitat” or “non-habitat” was too simplistic and did not describe the complex and varied nature of landscapes. The authors also believed the fragmentation model reflected an anthropocentric view of the world and failed to account for organism-perception of landscapes (see below). On this basis, McIntyre and Barrett (1992) and McIntyre and Hobbs (1999) introduced the term “habitat variegation” which they defined as:

“landscapes [that] are dominated by original habitats that have been variously modified rather than extensively destroyed” (p. 1283, McIntyre and Hobbs 1999).

In the landscape continuum model, the authors categorise landscapes on a continuum from intact, to variegated, then fragmented and finally relictual (Fig. 1).

***Umwelt*: individual organism perceptions and response**

The concept of *Umwelt* potentially offers a bridge between environmental and spatial continua. Both the continuum concept of vegetation science and the landscape continuum emphasise individual response. The continuum concept of plant science has similarities with niche theory in animal community ecology (Austin 1985). The landscape continuum model emphasises individual species perception (McIntyre and Hobbs 1999). The concept of *Umwelt*, developed by the Estonian biologist Jakob von Uexküll in his seminal 1926 work “Theoretical biology”, encapsulates both individual species response and perception (von Uexküll 1926, 1957). The *Umwelt* is the ‘phenomenal world’ or ‘self world’ of an organism (von Uexküll 1957, Clemmons and Buchholz 1997). It is the environment that is perceived and used by that organism (Clemmons and

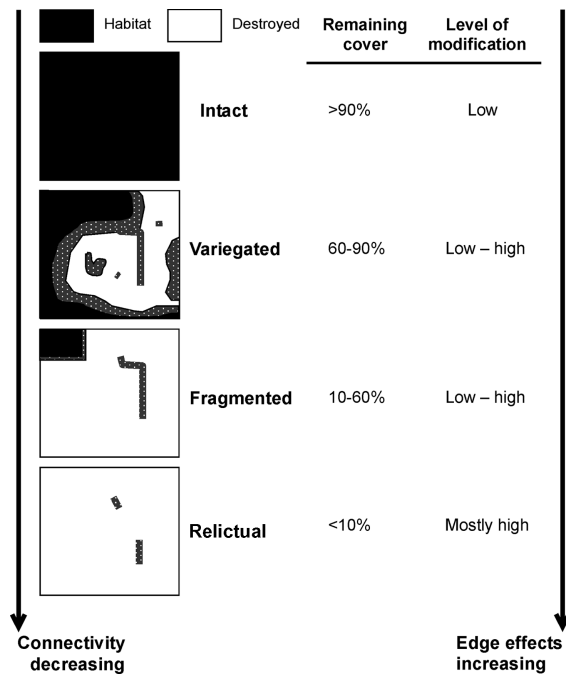


Fig. 1. The four alteration states of the landscape continuum model (sensu McIntyre and Hobbs 1999) with corresponding levels of cover and modification. From Lindenmayer and Franklin (2002).

Buchholz 1997) rather than the physical “habitat” as perceived by humans. Von Uexküll (1926) wrote:

“The picture we get throughout is of a world that seems created exclusively for this animal. And so we are justified in assuming that there are as many surrounding worlds as there are animals” (p. 176).

Different organisms perceive and respond to the environment in different ways. The *Umwelt* will encapsulate not only perception and response to physical “habitat” continua, but also to environmental gradients in factors that influence biological processes such as light, heat, water and mineral nutrients (Mackey and Lindenmayer 2001). The useability of a landscape for a particular organism will often vary on a continuum rather than occur as either habitat or non-habitat (Lindenmayer et al. 2003). In addition, different organisms respond to different environmental factors at multiple and differing temporal and spatial scales (Holling 1992, Lindenmayer 2000). Hence, habitat useability for an organism will vary in both time and space (Law and Dickman 1998). The segmentation of landscapes by humans into elements such as patches, corridors and the matrix does not mean that other biota will perceive that landscape in the same way (McIntyre and Hobbs 1999). Rather than seeing discrete patches, some organisms may see continuous habitat (Enoksson et al. 1995).

Integration of perspectives

The landscape continuum model (sensu McIntyre and Hobbs 1999) is a significant improvement on schematic fragmentation models. The incorporation of continua and organism perception and response into our understanding of landscapes provide an opportunity to better reflect multi-faceted reality. However, the application of continua to a landscape requires further conceptual development to have wider applicability. In the following discussion we attempt to further develop this important post-schematic concept. The implications of continua and *Umwelt* will then be discussed.

(1) *Process*. The landscape continuum model is still essentially pattern-based and lacks a process dimension. For example, variegation, without ongoing natural regeneration, is a transitory artefact of earlier modification towards the fragmented-relictual end of the habitat continua. Isolated trees that make up the variegated pattern in some landscapes are what Janzen (1988) called the “living dead”. This is certainly the case in the semi-cleared grazing and cropping land of southeastern Australia, for which the model was originally developed, where trees are not regenerating on a landscape scale (Reid and Landsberg 2000).

(2) *Confounding continua*. The landscape continuum model does not make a distinction between spatial and environmental continua. This is important because while spatial pattern is categorized in the model, it is the environmental space experienced by individual organisms which determines habitat useability. Although similar in some respects, the continuum concept in plant science and the landscape continuum model differ in fundamental ways:

- the former deals with abstract environmental space
- the latter deals with geographical space

Reconciling abstract environmental space with geographical space requires further investigation. In a recent study of bird occurrence in eucalypt and pine plantations in southeast Australia, Lindenmayer et al. (2003) drew comparisons between the landscape continuum model and the continuum concept discussed by Austin (1999b). The authors surveyed for birds in landscapes that ranged from intact to relictual as defined from a human perspective. They found: a) a continuum of responses to landscape conditions that would have been overlooked if a traditional binary approach has been taken to habitat classification. For example, a number of species thought to be sensitive to vegetation modification were found

using the exotic pine “matrix”; b) that different species responded to (therefore perceived) the same landscape differently. That study highlighted possible experimental directions for incorporating continua and *Umwelt* into our understanding of landscapes.

(3) *Time*. The landscape continuum model lacks a temporal dimension. It is important to understand the landscape “trajectory” (sensu Hansen et al. 1992), which is a combination of:

- a) underlying ecological processes;
- b) time

An appreciation of the trajectory of landscapes is as important as the current habitat pattern and helps to inform landscape decision-makers of the resilience of the current landscape. As a static model, the landscape continuum model assumes a homogeneous and continuous “intact” habitat as the starting point of a landscape (as do the schematic fragmentation models). This fails to take into account the dynamic nature of ecosystems and responses to factors such as climatic variability through time (Sprugel 1991).

(4) *Scale*. Even when viewed from a human perspective, the identification of the four habitat conditions (intact, variegated, fragmented or relictual) is scale-dependent. Habitat that is intact at one scale could be fragmented at another. For example, at the local scale a habitat may be considered relatively large and intact, yet at a broader scale it may constitute a small fragment of formerly extensive ‘original’ habitat. In addition, identification of each category would be dependent on the *Umwelt* of the particular organism of interest. Functional usage of habitat is not only organism-specific, but is also dependent on broader-scale context. For example, variegated habitat, at one scale, which is surrounded by largely hostile, destroyed habitat at a broader scale could have a quite different functional usage by organisms to one that is variegated at multiple scales. Therefore, the *Umwelt* of individual organisms must not only be central to researching landscapes, but also needs to be multi-scaled for each organism of interest.

(5) *Umwelt and the landscape continuum*. The landscape continuum model is contradictory in its use of terminology. McIntyre and Hobbs (1999) highlight the importance of individual organism perception but the proposed landscape continuum model uses a categorical typology to describe landscapes. The authors believe that:

“most of the habitat states relate to hypothesised thresholds in geometric characteristics of the landscape and to effects on biota” (p. 1285).

However, the idea of generalizable thresholds has been challenged because thresholds will be species-specific (Mönkkönen and Reunanen 1999, Lindenmayer et al. 2003). It is therefore difficult to reconcile individual species perception and response with the definition of alteration states based on generalizable thresholds. It is therefore important to be explicit about which organism the landscape continuum model is being applied to, even if it means defining multiple landscapes for the area targeted for investigation.

(6) *Wider applicability*. The landscape continuum model was originally proposed for the semi-cleared grazing and cropping land of southeastern Australia (Lindenmayer et al. 2003), but McIntyre et al. (1996) suggested that it could also apply to forest landscapes. McIntyre and Hobbs (1999) assume that the natural “baseline” habitat can be recognised. While this might be possible in southeast Australia, in many parts of the world, “natural” habitats were destroyed or modified hundreds, if not thousands, of years ago. Therefore, there are no intact or variegated habitats under these circumstances.

There are, however, some analogous habitats elsewhere. For example, patterns of vegetation cover of wood-pasture in Europe (Rackham 1986, Peterken 1996) are similar to variegation in southeastern Australia (but they differ in that the former is underpinned by regenerative processes). Recently, Vera (2000) proposed a controversial theory that has challenged thinking about natural vegetation in Europe. Vera (2000) argued that, due to grazing pressure by native herbivores, ancient forests had an open structure with solitary and small groups of trees rather than dense, tall forest. Peterken (1996, 2001 reprint only) believed that, while Europe was not covered in a natural type of wood-pasture as Vera (2000) proposed, there were probably more open areas than previously thought. This highlights three points:

- 1) European landscapes did not necessarily start in an intact, homogenous, spatially continuous state (for example, only ca 18000 years BP large parts of Europe were covered in ice or tundra);
- 2) A continuum of forest types from tall forest to wood-pasture may have existed naturally and therefore;
- 3) Variegation has applicability to European landscapes.

The landscape continuum model does address disturbance, but the emphasis is on human-induced destruction or modification (Fig. 1). Yet natural disturbance plays an important role in the genesis of both natural landscapes (Sprugel 1991) and human-modified landscapes. Not all landscapes necessarily begin in a spatially intact state and natural habitats can be highly disturbed.

Practical implications

Schematic fragmentation models have greatly influenced how ecological research has been conducted. As a consequence, many fragmentation studies have adopted a patch-centred approach, whilst ignoring the influence of the surrounding matrix (McGarigal and McComb 1995, Jokimäki and Huhta 1996, Bennett and Ford 1997, Saab 1999). It is understandable why landscapes were simplified in this way so as to make problems tractable. However, there is little evidence that the results of patch-centred research can be extrapolated to the wider landscape (Wiens et al. 1993, McGarigal and McComb 1995). This is not only because ecological processes and organism responses vary at different scales (Wiens et al. 1993), but also because schematic fragmentation incorrectly assumes that the pre-fragmentation ecosystems were homogenous and constant through time (Haila 2002). Multi-scale studies that have studied the wider landscape context have found that the matrix has a great influence on faunal occurrence (reviewed by Lindenmayer and Franklin 2002).

Research that looks at organism occurrence across continua or gradients can produce quite different results to those conducted according to schematic fragmentation model. For example, Fisher (2001) surveyed birds along a regeneration gradient near Bathurst, New South Wales. There was a decrease in the number of bird species along the gradient with time since disturbance. There was also a succession of bird fauna along the gradient. In another study, Newton et al. (1986) investigated the spacing of sparrowhawk nest sites in the UK in relation to food supply, elevation and soil productivity. Distance between nest sites increased by 0.1 km with every 20 m rise in elevation and 0.35 drop in soil productivity. Without the incorporation of continua or gradients in the above research, conclusions from both these studies could have been quite different. Conservation and landscape management could therefore benefit from research that samples the whole landscape as defined by the organism(s) of interest.

In the past, landscapes have been categorised according to human perceptions and land uses, such as forestry or agriculture. This has led to the artificial and arbitrary separation of the landscapes into land use types. However, the results from studies that have looked at both

forestry and agricultural land at the same time are quite informative. Tjernberg et al. (1993) found that the total density of black woodpecker (*Dryocopus martius*) territories in forests was higher than in agricultural landscapes. However, when density was calculated for the available forest area in each type of landscape, densities were the same. In another study, Norton et al. (2000) found that while deciduous and conifer forests in northern Alberta, Canada, were managed differently by different timber companies, they found overlap and connectedness in the bird communities using them.

A key challenge for much of the research in landscapes is to determine how individual organisms perceive and respond to the landscape continuum rather than discrete, human-defined management units. If landscape management, as well as research, were conducted on a continuum, the results are more likely to be more successful in terms of conservation and our understanding of landscapes.

In response to human-induced habitat loss and fragmentation worldwide, conservation strategies have focused largely on the creation of spatially fixed conservation reserves (Wiens 1994, Recher 1997, Norton 2000). This approach is underpinned, in part, by the schematic fragmentation model and the “principles” of island biogeography theory (Wiens 1994, Haila 2002). However, it has been increasingly recognised that while reserves are important, reserve-based conservation alone will not achieve all conservation goals (Wiens 1994, Recher 1997, Norton and Miller 2000, Lindenmayer and Franklin 2002). In response to this, there have been increasing calls for the integration of conservation and production in the same landscape (Hobbs and Saunders 1991) and whole landscapes approaches to research and conservation (Recher 1997, Norton and Miller 2000). The application of the fragmentation model to the conservation of native vegetation that is modified, but not destroyed, could be highly damaging. For example, fragmentation models would prescribe that patches have to be a certain size, must be a certain distance from each other and, where possible, should be connected by corridors. There is no place for continua, small patches or variegation. (It is worth noting that continua do not sit comfortably with cadastral boundaries, but patches and corridors often do). Yet variegation, such as isolated remnant trees in the matrix often have great value for biota (Law et al. 2000). Consolidation of vegetation according to the schematic fragmentation paradigm could potentially become a self-fulfilling prophecy. For example, if it is inappropriately assumed that conservation measures in the matrix are unnecessary, important elements such as small patches and isolated trees will be lost.

The fragmentation model may appear to reflect reality in some landscapes. As many landscapes are increasingly degraded towards the fragmented/relictual end of the

continuum, human perceptions of discrete landscape elements and the critical thresholds of many organisms may converge. Critical thresholds are abrupt, non-linear changes that occur as a result of small amounts of habitat loss (With and King 1999, Lindenmayer and Franklin 2002). Such thresholds, where they exist, are species-specific (Mönkkönen and Reunanen 1999). In the process of critical thresholds converging with increasing habitat loss, many organisms become extinct, so only biota that can survive in those landscapes persist. Under these circumstances, the fragmentation model may appear to reflect the reality of modern landscapes because all of the non-conforming organisms have already gone. In contrast by viewing landscapes using continua and *Umwelt*, and by incorporating factors such as time and processes into models, it may be possible to improve our understanding of whole landscapes and species responses to them.

In areas where vegetation is modified, but not destroyed, continua and *Umwelt* are a more appropriate way of viewing landscapes than the fragmentation model. Yet even in highly degraded landscapes, an appreciation of continua and *Umwelt* may better reflect reality. Many forest organisms live in landscapes considerably more fragmented than those in which they evolved and such landscapes are an evolutionary novelty to many (Lima and Zollner 1996). McIntyre and Hobbs (1999) call for fragmented landscapes to be returned to a variegated state. However, variegation must be underpinned by regenerative processes. For example, in long-

cleared and modified grazing landscapes, this could involve the establishment of new wood-pasture (sensu Peterken 1996, Vera 2000). In places where variegation currently exists, kick-starting regenerative processes and new types of wood-pasture could be developed (for example, through management of grazing intensity).

The continua-*Umwelt* approach

Figure 2 illustrates the differences between a continua-*Umwelt* approach and the schematic fragmentation model. The continua-*Umwelt* approach reflects processes and change through time, while the fragmentation model reflects the present and a human-based perception of the landscape. Processes such as vegetation regeneration, nutrient cycling or hydrological regimes can be incorporated through time. Unlike the fragmentation model, the continua-*Umwelt* approach reflects spatial gradients, including physical reality, and environmental gradients through the incorporation species-specific *Umwelten*. For example, species A was confined to an open area in the past, in the present it has been able to expand to all the open areas including the variegated areas. In the future it will expand further as the woodland diminishes. Species B, a woodland species, is the opposite of species A and through time sees continuous habitat become small fragments. Species C perceives a gradient that is completely unperceived by humans and this does not change through time. In the

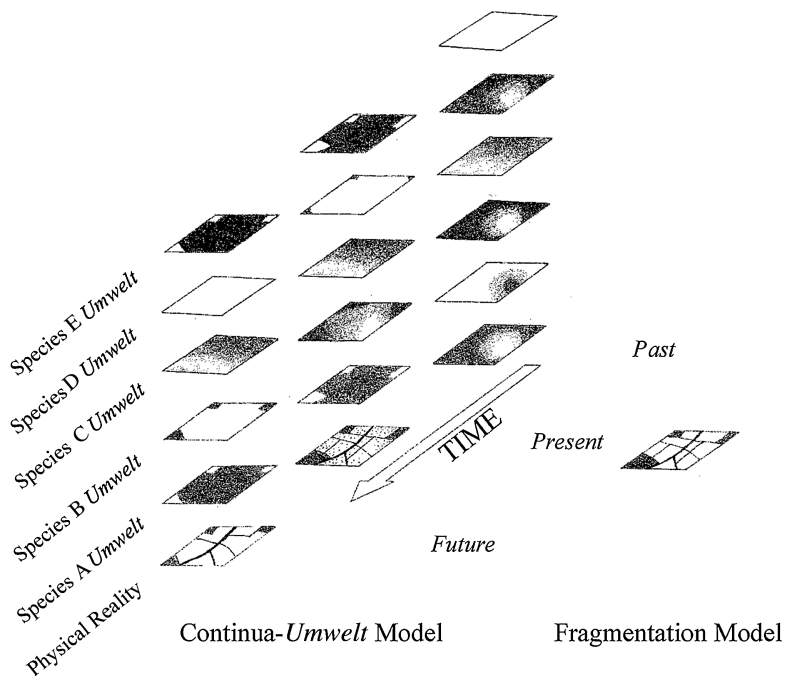


Fig. 2. The continua-*Umwelt* model.

past species D perceived almost continuous habitat except the most open area. In the present it views the open matrix as hostile, despite variegation. In the future it perceives no habitat and disappears from the landscape. Species E is the opposite, and is not present when the habitat is woodland, but arrives and expands as open habitats dominate. As the landscape degrades through time, only species that conform to the fragmentation model remain. Incorporation of time allows a better understanding of the trajectory of the landscape and the temporal response of species. In addition, the scale of a landscape in the continua-*Umwelt* approach would vary with the different species.

Possible ways of experimentally comparing the schematic fragmentation model and the continua-*Umwelt* approach could include methods such as those employed by Lindenmayer et al. (2003) where they sampled different parts of the spatial continua and looked at the differing response of different organisms. Another approach could be to sample a landscape using both a “traditional” patch-centred approach and a whole-landscape sampling approach and then compare the different results for each organism and between organisms.

Conclusion

Landscape fragmentation models have undoubtedly been useful tools for communicating concepts about landscapes. All models are, by definition, simplifications of that reality. As outlined above, application of these simplifications to real landscapes for research, conservation and land management can be problematic. The landscape continuum model, through the introduction of continua and species perception, has made great progress in finding ways of reflecting “multi-faceted reality”. In both research and management we must be explicit about the organisms of interest and avoid single-size-fits-all models. Research and management should reflect the *Umwelt* of the organisms, not just human perceptions and land use. Accordingly, research should be multi-scaled. This approach would incorporate many continua and *Umwelten* and would take the form of a multi-layered view of the same landscape. We realise that the daunting implication of this is that there are as many landscapes as there are organisms. However, if society is truly committed to the maintenance and restoration of native biota, our perspectives of landscapes must attempt to reflect ecological reality. If it is the ecology of landscapes that is of interest, it is logical to use the ecosystems, biota and ecological processes to scale our framework of understanding; not human activity. Rather than simplifying reality then communicating it, ecologists and conservationists must communicate such landscape complexity to the wider public (Harrison 1991).

Acknowledgements – ADM would like to thank S. Barry, J. Dargavel, A. Gilmore, B. Newell, D. Saunders and R. Tipping for helpful discussions. ADM would also like to thank Environment ACT, New South Wales National Parks and Wildlife Service, the Canberra Birds Conservation Fund, the Stuart Leslie Bird Research Award and CSIRO Sustainable Ecosystems for financial support. Thanks to P. Enckell and Y. Haila for helpful comments on an earlier draft.

References

- Austin, M. P. 1985. Continuum concept, ordination methods and niche theory. – *Annu. Rev. Ecol. Syst.* 16: 39–61.
- Austin, M. P. 1999a. The potential contribution of vegetation ecology to biodiversity research. – *Ecography* 22: 465–484.
- Austin, M. P. 1999b. A silent clash of paradigms: some inconsistencies in community ecology. – *Oikos* 86: 170–178.
- Beals, E. W. 1960. Forest bird communities in the Apostle Islands of Wisconsin. – *Wilson Bull.* 72: 156–181.
- Bennett, A. F. and Ford, L. A. 1997. Land use, habitat change and conservation of birds in fragmented rural environments: a landscape perspective from the Northern Plains, Victoria, Australia. – *Pacific Conserv. Biol.* 3: 244–261.
- Bond, R. R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. – *Ecol. Monogr.* 27: 351–384.
- Braithwaite, L. W., Austin, M. P., Clayton, M. et al. 1989. On predicting the presence of birds in *Eucalyptus* forest types. – *Biol. Conserv.* 50: 33–50.
- Bunnell, F. L. 1999. What habitat is an Island? – In: Rochelle, J. A., Lehman, L. and Wisniewski, J. (eds), *Forest fragmentation: wildlife and management implications*. Brill Academic Publishers, pp. 1–31.
- Clemmons, J. R. and Buchholz, R. 1997. Linking conservation and behavior. – In: Clemmons, J. R. and Buchholz, R. (eds), *Behavioral approaches to conservation in the wild*. Cambridge Univ. Press, pp. 3–22.
- Diamond, J. M. 1975. The island dilemma: lessons of modern biogeographic studies for the design of natural reserves. – *Biol. Conserv.* 7: 129–146.
- Enoksson, B., Angelstam, P. and Larsson, K. 1995. Deciduous forest and resident birds: the problem of fragmentation within a coniferous forest landscape. – *Landscape Ecol.* 10: 267–275.
- Fisher, A. M. 2001. Avifauna changes along a *Eucalyptus* regeneration gradient. – *Emu* 101: 25–31.
- Haila, Y. 1999. Islands and fragments. – In: Hunter, M. L. (ed.), *Maintaining biodiversity in forest ecosystems*. Cambridge Univ. Press, pp. 234–264.
- Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. – *Ecol. Appl.* 2: 321–334.
- Hansen, A. J., Urban, D. L. and Marks, B. 1992. Avian community dynamics: the interplay of landscape trajectories and species life histories. – In: Hansen, A. J. and di Castri, F. (eds), *Landscape boundaries: consequences for biotic diversity and ecological flows*. Springer-Verlag, pp. 170–195.
- Harrison, S. 1991. Metapopulations and conservation. – In: Edwards, P. J., May, R. M. and Webb, N. R. (eds), *Large-scale ecology and conservation biology*. Blackwell Scientific Publications, pp. 111–128.
- Hobbs, R. J. and Saunders, D. A. 1991. Re-integrating fragmented landscapes – a preliminary framework for the Western Australian Wheatbelt. – *J. Environ. Manage.* 33: 161–167.
- Holling, C. S. 1992. Cross-scale morphology, geometry and dynamics of ecosystems. – *Ecol. Monogr.* 62: 447–502.

- Janzen, D. H. 1988. Tropical ecological and biocultural restoration. – *Science* 239: 234–244.
- Jokimäki, J. and Huhta, E. 1996. Effects of landscape matrix and habitat structure on a bird community in northern Finland: a multi-scale approach. – *Ornis Fenn.* 73: 97–113.
- Kareiva, P. 1990. Population dynamics in spatially complex environments: theory and data. – *Philos. Trans. R. Soc. Lond. B* 330: 175–190.
- Law, B. S. and Dickman, C. R. 1998. The use of habitat mosaics by terrestrial vertebrate fauna: implications for conservation and management. – *Biodiv. Conserv.* 7: 323–333.
- Law, B. S., Chidel, M. and Turner, G. 2000. The use by wildlife of paddock trees in farmland. – *Pacific Conserv. Biol.* 6: 130–143.
- Lima, S. L. and Zollner, P. A. 1996. Towards a behavioural ecology of ecological landscapes. – *Trends Ecol. Evol.* 11: 131–135.
- Lindenmayer, D. B. 2000. Factors at multiple scales affecting distribution patterns and their implications for animal conservation – Leadbeater's possum as a case study. – *Biodiv. Conserv.* 9: 1535.
- Lindenmayer, D. B. and Franklin, J. F. 2002. *Conserving forest biodiversity: a comprehensive multi-scaled approach.* – Island Press.
- Lindenmayer, D. B., McIntyre, S. and Fischer, J. 2003. Birds in eucalypt and pine forests: landscape alteration and its implications for research models of faunal habitat use. – *Biol. Conserv.* 110: 45–53.
- Lord, J. M. and Norton, D. A. 1990. Scale and the spatial concept of fragmentation. – *Conserv. Biol.* 4: 197–202.
- Mackey, B. G. and Lindenmayer, D. 2001. Towards a hierarchical framework for modelling the spatial distribution of animals. – *J. Biogeogr.* 28: 1147–1166.
- MacArthur, R. H. and Wilson, E. O. 1967. *The theory of island biogeography.* – Princeton Univ. Press.
- McGarigal, K. and McComb, W. C. 1995. Relationships between landscape structure and breeding birds in the Oregon coast range. – *Ecol. Monogr.* 65: 235–260.
- McIntyre, S. and Barrett, G. W. 1992. Habitat variegation, an alternative to fragmentation. – *Conserv. Biol.* 6: 146–147.
- McIntyre, S. and Hobbs, R. J. 1999. A framework for conceptualizing human effects on landscapes and its relevance to management and research models. – *Conserv. Biol.* 13: 1282–1292.
- McIntyre, S., Barrett, G. W. and Ford, H. A. 1996. Communities and ecosystems. – In: Spellerberg, I. F. (ed.), *Conservation biology.* Longman, pp. 154–170.
- Mönkkönen, M. and Reunanen, P. 1999. On critical thresholds in landscape connectivity: a management perspective. – *Oikos* 84: 302–305.
- Newton, I., Wyllie, I. and Mearns, R. 1986. Spacing of sparrowhawks in relation to food supply. – *J. Anim. Ecol.* 55: 361–370.
- Norton, D. A. 2000. Conservation biology and private land: shifting the focus. – *Conserv. Biol.* 14: 1221–1223.
- Norton, D. A. and Miller, C. J. 2000. Some issues and options for the conservation of native biodiversity in rural New Zealand. – *Ecol. Manage. Restor.* 1: 26–34.
- Norton, M. R., Hannon, S. J. and Schmiegelow, F. K. A. 2000. Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. – *Ecography* 23: 209–223.
- Peterken, G. F. 1996. *Natural woodland: ecology and conservation in northern temperate regions.* – Cambridge Univ. Press.
- Rackham, O. 1986. *The history of the countryside.* – Dent.
- Recher, H. F. 1997. Conservation priorities: myths and realities. – *Pacific Conserv. Biol.* 3: 81.
- Reid, N. and Landsberg, J. 2000. Tree decline in agricultural landscapes: what we stand to lose. – In: Hobbs, R. J. and Yates, C. J. (eds), *Temperate eucalypt woodlands in Australia: biology, conservation, management and restoration.* Surrey Beatty & Sons, pp. 127–166.
- Saab, V. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. – *Ecol. Appl.* 9: 135–151.
- Sabo, S. R. 1980. Niche and habitat relations in sub-alpine bird communities of the white mountains of New Hampshire. – *Ecol. Monogr.* 50: 241–259.
- Saunders, D. A., Hobbs, R. J. and Margules, C. 1991. Biological consequences of ecosystem fragmentation: a review. – *Conserv. Biol.* 5: 18–32.
- Sprugel, D. G. 1991. Disturbance, equilibrium, and environmental variability: what is “natural” vegetation in a changing environment? – *Biol. Conserv.* 58: 1–18.
- Tjernberg, M., Johnsson, K. and Nilsson, S. G. 1993. Density variation and breeding success of the black woodpecker *Dryocopus martius* in relation to forest fragmentation. – *Ornis Fenn.* 70: 155–162.
- Vera, F. W. M. 2000. *Grazing ecology and forest history.* – CABI Publishing
- von Uexküll, J. 1926. *Theoretical biology,* Kegan Paul, Trench, Trubner & Co. Ltd.
- von Uexküll, J. 1957. A stroll through the worlds of animals and men. – In: Schiller, C. H. (ed.), *Instinctive behaviour: the development of a modern concept.* Methuen & Co Ltd.
- Wiens, J. A. 1992. What is landscape ecology, really? – *Landscape Ecol.* 7: 149–150.
- Wiens, J. A. 1994. Habitat fragmentation: island vs landscape perspectives on bird conservation. – *IBIS* 137: S97–S104.
- Wiens, J. A., Stenseth, N. C., Van Horne, B. et al. 1993. Ecological mechanisms and landscape ecology. – *Oikos* 66: 369–380.
- With, K. A. and King, A. W. 1999. Dispersal success on fractal landscapes: a consequence of lacunarity thresholds. – *Landscape Ecol.* 14: 73–82.