

Native vegetation cover thresholds associated with species responses

D.B. Lindenmayer *, J. Fischer, R.B. Cunningham

Centre for Resource and Environmental Studies, Building 43, The Australian National University, Canberra ACT 0200, Australia

Abstract

We examined data on bird and reptile assemblages in a plantation landscape in southern New South Wales, south-eastern Australia, for evidence of threshold responses to the amount of native eucalypt vegetation in circular areas of 2000 and/or 1000 m around field survey sites. These circular areas contained varying proportions of native *Eucalyptus* and exotic radiata pine *Pinus radiata* forest thereby providing a basis for examining potential threshold effects in relation to the area of native vegetation cover. For bird species richness or the probability of detection of individual bird species we found no empirical evidence of a threshold response to the area of native vegetation cover, or any other potential explanatory variables. All relationships were characterised by considerable variability in the response data. “Broken-stick” relationships which involved sudden change points did not fit the response data better than smooth relationships obtained from generalised additive or linear models. As with birds, there was no evidence that a threshold model between lizard richness and the amount of native vegetation within 1000 m described the relationship any better than a smooth, continuous or other type of relationship. Several related factors may explain our results. An important one is that species-specific responses to landscape conditions mean that marked thresholds will not be seen for an aggregate measure like species richness at a given value for a given landscape variable. Another is that factors other than the amount of native vegetation may significantly influence underlying patterns of species occurrence. This highlights a need to be aware of the potential effects of various ecological processes, even when a substantial amount of native vegetation cover remains.

Our findings do not rule out the possibility of the existence of threshold relationships. However, irrespective of the choice of measure of predictor variable (e.g., the amount of native vegetation cover), it will often be difficult to detect and estimate threshold responses due to high inherent variability – a characteristic of the vast majority of ecological datasets. Furthermore, even if it is possible to estimate functional (threshold) forms and although they might be useful from an explanatory perspective, in most instances they are likely to be of limited value in a predictive sense. This calls into question the practical significance of the threshold concept. © 2005 Elsevier Ltd. All rights reserved.

Keywords: Thresholds; Vertebrates; Birds; Reptiles; Landscape “natural experiment”; Habitat fragmentation; Conservation

1. Introduction

Several forms of threshold responses have been identified in ecology (see Huggett, this volume). One is the Allee effect where patterns of social behaviour are dysfunctional below a given population size (Allee, 1931). Another example is the relationship between plant species diversity and island size published by MacArthur and Wilson (1967) (Fig. 1).

More recently and in a conservation biology context, With and King (1999) broadly defined thresholds as abrupt, non-linear changes that occur in some measure (such as the rate of loss of species) across a small amount of habitat loss. It has been hypothesised that where a threshold response occurs, below a critical amount of habitat cover, the loss of species and populations is greater than can be predicted from a smooth relationship with habitat cover alone (Rolstad and Wegge, 1987; Andrén, 1994, 1999; Enoksson et al., 1995; With and Crist, 1995; With and King, 1999). In a review of studies on birds and mammals, Andrén (1994) calculated that

* Corresponding author. Fax: +11 61 2 6125 0757/6249 0654.
E-mail address: davidl@cres.anu.edu.au (D.B. Lindenmayer).

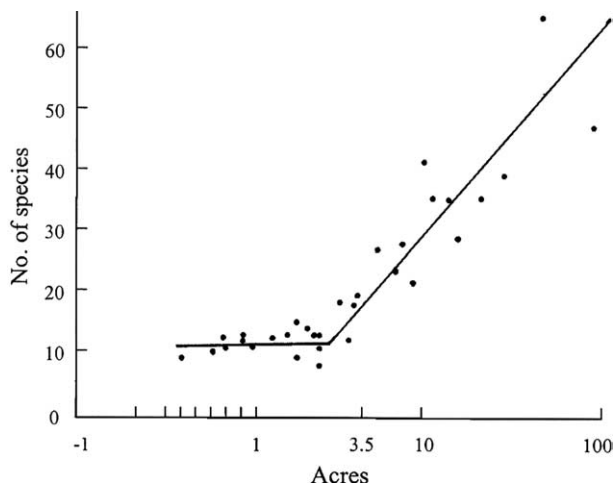


Fig. 1. The form of the relationship between higher plant species richness and island area for the islands of the Kapingamarangi Atoll, Micronesia. The relationship is suggestive of a 'broken-stick' model on a log scale (redrawn from MacArthur and Wilson, 1967).

threshold levels for remaining habitat often were approximately 10–30% of original levels of native vegetation cover. That is, species richness and populations of individual species declined more rapidly when less than 10–30% of habitat cover remained, than expected under a simple linear model. Threshold levels are predicted to vary among landscape types and species (Andrén, 1999; Mönkkönen and Ruenanen, 1999); from 60% for some taxa to 10% for others (Bennett and Ford, 1997). They also have been thought likely to vary according to the number and spatial arrangement of patches in fragmented environments (Lamberson et al., 1994; Doncaster et al., 1996; Jansson and Angelstam, 1999), the movement capabilities of the group of species targeted for investigation (Andrén, 1994, 1999), and the spatial scale at which organisms use the landscape (Pearson et al., 1996).

The search for threshold responses for biota in relation to native vegetation cover has become a topic of increasing interest in biological conservation (e.g., McAlpine et al., 2002; Radford and Bennett, 2004). Much of the work on threshold responses for biodiversity has been derived from theoretical landscape cover models (With and Crist, 1995) and population models (e.g., Doncaster et al., 1996; see the review by Huggett, this volume). In Australia, McIntyre et al. (2000, 2002) have focussed considerable effort in this arena, with much of their thinking based on work showing that the prevalence of eucalypt dieback was most pronounced in landscapes supporting less than 30% of the original eucalypt woodland cover. Other workers have examined threshold relationships for individual species (van der Ree et al., 2003; Homan et al., 2004; Radford and Bennett, 2004) and species assemblages (Drinnan, this volume; Radford et al., this volume). Given the upsurge of interest in stud-

ies of thresholds, in this paper we report on results of a statistical analysis to empirically explore threshold relationships between species diversity and individual bird and lizard taxa and the amount of native vegetation cover. We chose to focus our work on the total amount of native vegetation cover because it has been found to be important in other studies (Andrén, 1994; Bennett and Ford, 1997) and secondly, because some authors have recommended using threshold levels of native vegetation cover as a benchmark for land clearing and restoration programs (Brown et al., 1999; McAlpine et al., 2002; see Lindenmayer and Luck, this volume).

2. Data

2.1. Study area

The study area was a 50,000 ha radiata pine (*Pinus radiata*) plantation at Tumut in south-eastern Australia which contained 192 patches of remnant eucalypt (*Eucalyptus* spp.) forest of varying sizes, shapes and forest types. These were the remains of the original native forest cover that was cleared to establish the plantation between the 1930s and 1980s. The landscape context (*sensu* Enoksson et al., 1995) of the eucalypt remnants varied. Some were surrounded by extensive stands of uniform-aged radiata pine and were remote from other eucalypt remnants, whereas others were close to neighbouring remnants with only 200–300 m of softwood forest separating them. The extent of the road network in the forests surrounding the eucalypt remnants, the extent of patchiness of native vegetation cover and other landscape measures also varied across the study area. Further information on the study area such as climatic conditions, the history of landscape change and other details are presented in Lindenmayer et al. (1999, 2002a).

2.2. Birds

For birds, our data were obtained from sites within a randomised selection of 86 eucalypt remnants in the study area. The remnants varied in size from 1 to 124 ha (Lindenmayer et al., 2002a). Field counting of birds were completed by repeated 5 min point interval counts at seven stations spaced 100 m apart along a 600 m transect that had been established within 63 remnants that were 3 ha or larger. A 400 m long transect (with five point interval counting stations spaced at 100 m intervals) was used to count birds in 14 eucalypt remnants measuring 2–3 ha in size. A 200 m transect (with three point interval counting stations spaced at 100 m intervals) was used to count birds in nine eucalypt remnants measuring 2–3 ha in size. Counts were undertaken by experienced observers in the spring breeding seasons of 1996 and 1997 (Cunningham et al., 1999; Lindenmayer et al., 2002a).

Our focus was on exploring relationships between: (1) bird species richness (excluding birds that used pine stands) and (2) the probability of detection of individual birds and the amount of native (eucalypt) vegetation cover. We defined the amount of native vegetation cover as the area of native vegetation within circles of 2000 m radius around the centroid of each remnant. Statistical analysis involved fitting generalised additive models (see Hastie and Tibshirani, 1990) and ‘broken-stick’ models (two intersecting lines of different slope).

2.3. Lizards

In the case of lizards, the logistics of pitfall trapping meant that fewer locations could be sampled than for birds. Thirty sites were sampled, and they included 24 eucalypt sites, ranging from 1 ha in size to continuous forest, three sites in pine forest >20 years of age, and three sites in recently clearcut pine forest. Each site contained 12 pitfall traps (total number of traps = 360) and was sampled on 12 separate days throughout the summer of 2002/2003. For lizards, the amount of native vegetation cover within a circle of 1000 m radius was used as the potential explanatory variable in investigations of potential threshold relationships. We also assessed data from a range of other radii, but here we only report results from 1000 m because it produced the most significant results for both species richness and several individual species.

3. Results

3.1. Birds

No strong empirical evidence of threshold relationship (e.g., a ‘broken-stick’ model; see Fig. 1 for an example) between bird species richness (excluding pine-using species) and the total area of native vegetation within a circle of 2000 m radius around the 86 sites was found (Fig. 2). Indeed, there was an insufficient signal in our data to distinguish between many alternative plausible models (such as straight line and curvilinear functions).

Furthermore, there was no empirical evidence for a change point or threshold relationship between the probability of detection of individual bird species and the area of native vegetation cover. Our findings for the red wattlebird (*Anthochaera carunculata*) (Fig. 3) are indicative of those for other bird taxa, we analysed.

We further explored the potential, for threshold relationships for bird species richness and individual bird species responses, using a range of other landscape variables including the density of roads within a landscape area (the sum of all 20 × 20 m cells bisected by a road), the mean area of native vegetation patches within a landscape area (a measure of spatial sub-division),

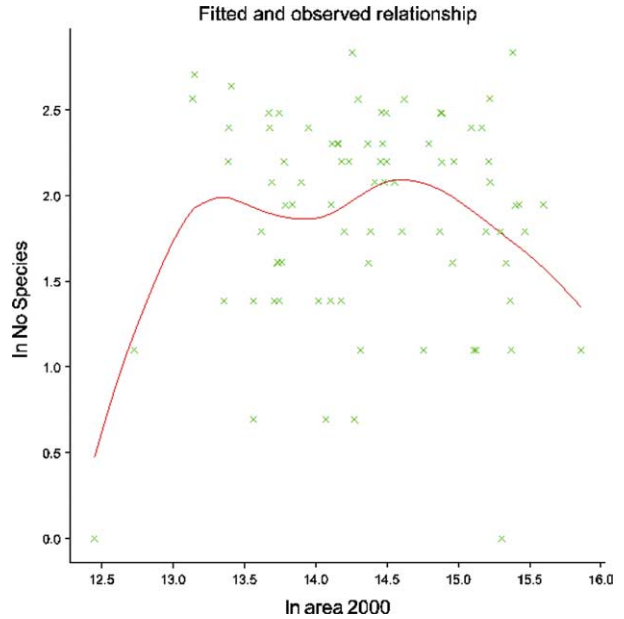


Fig. 2. Relationship between bird species richness and the natural logarithm of the area of native vegetation within a circle of 2000 m radius. The solid line is the fitted relationship estimated using a general non-parametric spline smoother, which was not statistically significant (see Hastie and Tibshirani, 1990).

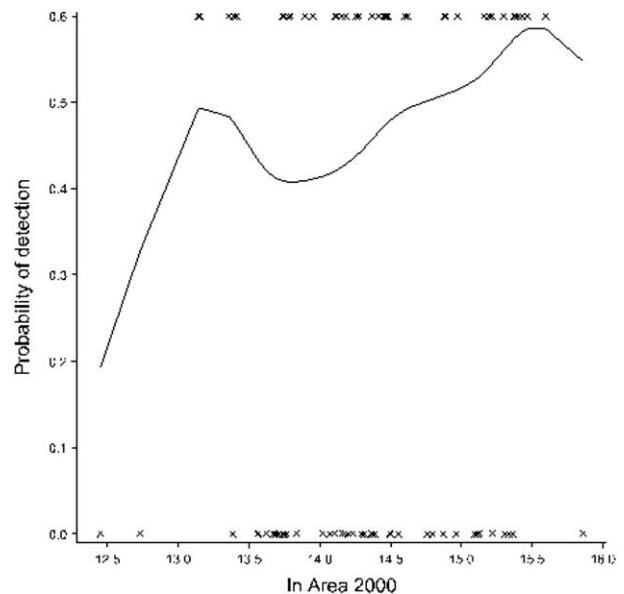


Fig. 3. The probability of occurrence of the red wattlebird and the natural logarithm of the amount of native vegetation within a surrounding landscape area of 2000 m. The solid line is the fitted relationship estimated using a general non-parametric spline smoother, which was not statistically significant (see Hastie and Tibshirani, 1990).

variability in patch size within a landscape area, minimum distance to native vegetation of all cells within a landscape area (a measure of isolation), and native vegetation cover data for the 1000 m circle around each remnant. Again there was no evidence for threshold relationships in any of these analyses (data not shown).

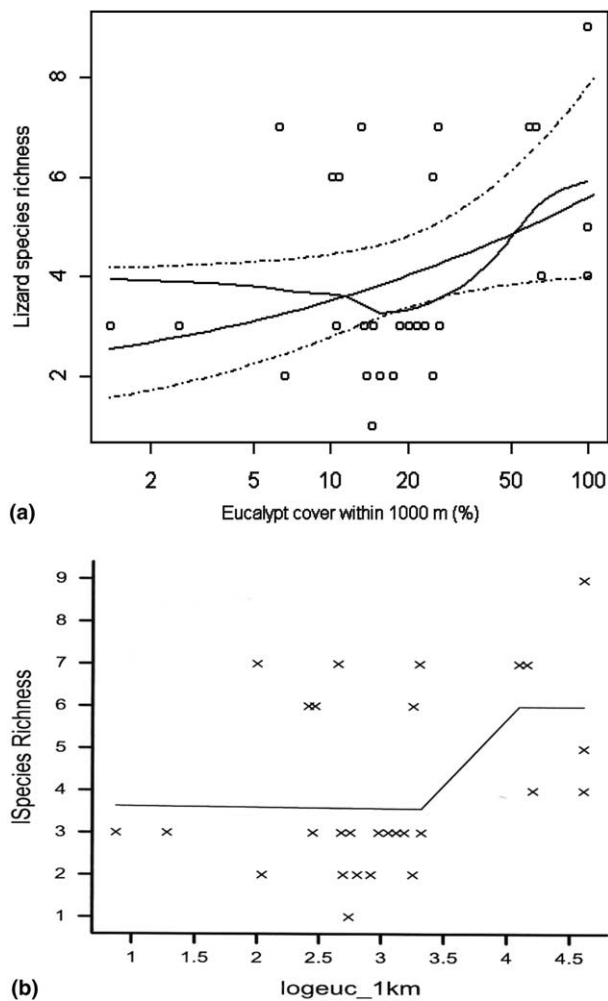


Fig. 4. Lizard species richness and the amount of native vegetation in the surrounding landscape: (a) shows a conventional generalised linear model, where the solid line is the fitted relationship and dotted lines indicate 95% confidence intervals around the mean. A non-parametric smoothing spline is also shown; (b) shows the predicted species richness from a broken-stick model.

3.2. Reptiles

Lizard species richness significantly increased with the proportion of native vegetation within 1000 m (Fig. 4). However, as with birds, there was no evidence that a threshold relationship described this relationship any better than a smooth, continuous or other type of relationship. Forcing a threshold relationship onto the data resulted in two change points in the data, rather than one. Neither change point was ecologically meaningful.

4. Discussion

We found no strong empirical evidence of threshold responses to native vegetation cover in our analyses. Evidence from earlier work on birds at Tumut (Lindenma-

yer et al., 2002a,b), indicated that each bird species responded differently to landscape conditions. For example, while some were area-sensitive, several other species were more likely to occur in more (rather than less) human-modified parts of the landscape (Lindenmayer et al., 2002b). Species-specific responses to landscape conditions at Tumut were not unique to birds. For example, although Coventry's skink (*Niveoscincus coventryi*) was more abundant in relatively unmodified parts of the landscape, the garden skink (*Lampropholis guichenoti*) was more abundant in these areas (Fischer et al., in press). Such differences between species could be related to the fact that what constitutes suitable habitat is a species-specific concept (Block and Brennan, 1993) and they mean it is unlikely many species in an assemblage will respond in the same way to the same landscape variable (e.g., exhibit a sudden change point at 30% of native vegetation cover). Rather, some might be lost at higher levels and some at lower levels of native vegetation cover (see also Radford et al., 2005). Hence, it is likely that, in some circumstances marked thresholds will not be seen for an aggregate measure like species richness (see also Mönkkönen and Ruenanen, 1999).

The lack of threshold responses in this study, is consistent with some other empirical studies such as the recent empirical work on invertebrates by Parker and Mac Nally (2002). It is possible that threshold responses for measures such as species richness may not exist in some ecosystems. For example, a major investigation underway on an array of forest-dependent species in western Canada has shown the vast majority of species richness relationships and species-specific response relationships were smooth or curvilinear and few, if any, displayed characteristics of threshold functions (Bunnell et al., 2003). On this basis, we believe it is unlikely there will be generic rules for critical change points or threshold levels of vegetation or habitat cover (e.g., 10%, or 30%, or 70%) that can be applied broadly across different landscapes and different biotic groups (see also Parker and Mac Nally, 2002; but cf. Drinnam, this volume). Rather, in cases where thresholds can be established empirically they will depend on the landscape in question (a forest–forest or forest–agriculture system), the assemblages or particular species of interest, and the ecological processes in question (the extent of tree health or the extent of landscape-wide clearing).

A final issue associated with the application of the threshold concept is that of scale. The case of Fig. 5 (reproduced from Fahrig, 2003) is a useful example. Here, the “threshold” response is a curve which shows no abrupt critical change point (compared with the “broken stick” model depicted in Fig. 1). The perception that the curve in Fig. 5 is a threshold one can easily be removed by changing the scales on the graph's axes. For example, a straight line relationship at a scale appropriate for statistical analysis (e.g., logit linear scale for

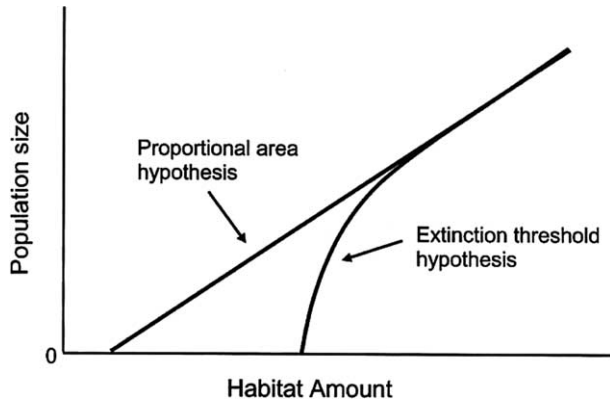


Fig. 5. Comparison of rates of species loss proportional to the remaining amount of habitat and the threshold hypothesis (redrawn from Fahrig, 2003).

binary data) may suggest a threshold type response on the natural or backtransformed scale. It is therefore important to consider the measurement scale of both the response and predictor variables because the true underlying functional form of the relationship will depend on the scale of both. Hence, it is important to be aware that the concept of thresholds is not scale invariant.

The findings of our study do not rule out the possibility of the existence of threshold relationships. Clearly our results are dependent on our choice of response variable as well as our choice of predictor variable. Nevertheless, it is our belief that irrespective of the choice of measures, it will often be difficult to estimate threshold responses due to high inherent variability. Indeed, considerable inherent variability was a key characteristic of our data. Such variability is common to the many ecological studies and resulting data, and it may obscure the detection of threshold relationships (where they exist). Indeed, this becomes clear if confidence intervals are included in graphical representations of trends – although many authors simply plot mean values without also showing relevant measures of uncertainty.

Most importantly, high variability will reduce the predictive ability of threshold relationships and hence their usefulness for on-ground management (even when such relationships are statistically significant). Thus, even if it is possible to estimate functional (threshold) forms and although they might be useful from an explanatory perspective, in most instances they are likely to be of limited value in a predictive sense. This calls into question the practical significance of the threshold concept.

Acknowledgements

Work at Tumut has been supported by major grants from Land and Water Forest Research and Development Corporation, Forest and Wood Products Research and Development Corporation, Rural Industries Research

and Development Corporation, the Australian Research Council, and the NSW Department of Land and Water Conservation. Other supporting bodies for various projects in the Tumut regions NSW include National Parks and Wildlife Service, State Forests of NSW, Environment Australia, Brookfield Zoo (Chicago), The Pratt Foundation, Jim Atkinson and Di Stockbridge (private donation), the Ecological Society of Australia (J.F.), the Linnean Society of NSW (J.F.), and the Royal Zoological Society of NSW (J.F.). Mr. C. MacGregor, Mr. M. Crane, Mr. D. Michael and the Canberra Ornithologists Group assisted with the collection of data on birds at Tumut. Several people helped with the collection of pitfall data, and we particularly thank E. Flowers. Ms. N. Munro and Ms. M. Ruibal kindly assisted in the collection of scientific articles on the topics addressed in this paper. Comments from the other contributors to this series of papers on thresholds (particularly Jim Radford and Gary Luck) as well as very perceptive comments from Peter Cale and Denis Saunders greatly improved earlier versions of this manuscript. Work on the reptile fauna at Tumut was sanctioned by Animal Experimentation Ethics Committee of The Australian National University.

References

- Allee, W.C., 1931. *Animal Aggregations. A Study in General Sociology*. University of Chicago Press, Chicago.
- Andrén, H., 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. *Oikos* 71, 355–366.
- Andrén, H., 1999. Habitat fragmentation, the random sample hypothesis and critical thresholds. *Oikos* 84, 306–308.
- Bennett, A.F., Ford, L.A., 1997. Land use, habitat change and the conservation of birds in fragmented rural environments: a landscape perspective from the Northern Plains, Victoria, Australia. *Pacific Conservation Biology* 3, 244–261.
- Block, W.M., Brennan, L.A., 1993. The habitat concept in ornithology. Theory and applications. In: Power, D.M. (Ed.), *Current Ornithology* 11. Plenum Press, New York, pp. 35–91.
- Brown, J.R., Herrick, J., Price, D., 1999. Managing low-output agroecosystems sustainability: the importance of ecological thresholds. *Canadian Journal of Forest Research* 29, 1112–1119.
- Bunnell, F., Dunsworth, G., Huggard, D., Kremsater, L., 2003. *Learning to sustain biological diversity on Weyerhaeuser's coastal tenure*. Weyerhaeuser Company, Vancouver, British Columbia.
- Cunningham, R.B., Lindenmayer, D.B., Nix, H.A., Lindenmayer, B.D., 1999. Quantifying observer heterogeneity in bird counts. *Australian Journal of Ecology* 24, 270–277.
- Doncaster, C.P., Micol, T., Plesner Jensen, S., 1996. Determining minimum habitat requirements in theory and practice. *Oikos* 75, 335–339.
- Drinnan, I.N., 2005. The search for fragmentation thresholds in a Southern Sydney suburb. *Biological Conservation*, in press, doi:10.1016/j.biocon.2005.01.040.
- Enoksson, B., Angelstam, P., Larsson, K., 1995. Deciduous forest and resident birds: the problem of fragmentation within a coniferous forest landscape. *Landscape Ecology* 10, 267–275.
- Fahrig, L., 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* 34, 487–515.

- Fischer, J., Lindenmayer, D.B., Barry, S., Flowers, E., 2005. Lizard distribution patterns in an Australian plantation landscape. *Biological Conservation* (in press).
- Hastie, T.J., Tibshirani, R.J., 1990. *Generalized Additive Models*. Chapman & Hall, London.
- Homan, R.N., Windmiller, B.R., Reed, J.M., 2004. Critical thresholds associated with habitat loss for two vernal pool-breeding amphibians. *Ecological Applications* 14, 1547–1553.
- Huggett, A.J., 2005. The concept and utility of 'ecological thresholds' in biodiversity conservation. *Biological Conservation*, in press, doi:10.1016/j.biocon.2005.01.037.
- Jansson, G., Angelstam, P., 1999. Threshold levels of habitat composition for the presence of the long-tailed Tit (*Aegithalos caudatus*) in a boreal landscape. *Landscape Ecology* 14, 283–290.
- Lamberson, R.H., Noon, B.R., Voss, C., McKelvey, R., 1994. Reserve design for territorial species: the effects of patch size and spacing on the viability of the northern spotted owl. *Conservation Biology* 8, 185–195.
- Lindenmayer, D.B., Cunningham, R.B., Pope, M., Donnelly, C.F., 1999. The response of arboreal marsupials to landscape context: a large-scale fragmentation study. *Ecological Applications* 9, 594–611.
- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Nix, H.A., Lindenmayer, B.D., 2002a. The distribution of birds in a novel landscape context. *Ecological Monographs* 72, 1–18.
- Lindenmayer, D.B., Cunningham, R.B., Donnelly, C.F., Lesslie, R., 2002b. On the use of landscape indices as ecological indicators in fragmented forests. *Forest Ecology and Management* 159, 203–216.
- Lindenmayer, D.B., Luck, G.A., 2005. Synthesis: thresholds in conservation and management. *Biological Conservation*, in press, doi:10.1016/j.biocon.2005.01.041.
- MacArthur, R.H., Wilson, E.O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- McAlpine, C.M., Fensham, R.J., Temple-Smith, D.E., 2002. Biodiversity conservation and vegetation clearing in Queensland: principles and thresholds. *Rangelands Journal* 24, 36–55.
- McIntyre, S., McIvor, J.G., MacLeod, N.D., 2000. Principles for sustainable grazing in eucalypt woodlands: landscape-scale indicators and the search for thresholds. In: Hale, P., Moloney, D., Sattler, P. (Eds.), *Management for Sustainable Ecosystems*. Centre for Conservation Biology, The University of Queensland, Brisbane, Australia, pp. 92–100.
- McIntyre, S., McIvor, J.G., Heard, K.M. (Eds.), 2002. *Managing and Conserving Grassy Woodlands*. CSIRO Publishing, Melbourne.
- Mönkkönen, M., Ruenanen, P., 1999. On critical thresholds in landscape connectivity: a management perspective. *Oikos* 84, 302–305.
- Parker, M., Mac Nally, R., 2002. Habitat loss and the habitat fragmentation threshold: an experimental evaluation of impacts on richness and total abundances using grassland invertebrates. *Biological Conservation* 105, 217–229.
- Pearson, S.M., Turner, M.G., Gardner, R.H., O'Neill, R.V., 1996. An organism perspective of habitat fragmentation. In: Szaro, R.C., Johnston, D.W. (Eds.), *Biodiversity in Managed Landscapes: Theory and Practice*. Oxford University Press, New York, pp. 77–95.
- Radford, J.Q., Bennett, A.F., 2004. Thresholds in landscape parameters: occurrence of the white-browed treecreeper *Climacteris affinis* in Victoria, Australia. *Biological Conservation* 117, 375–391.
- Radford, J.Q., Bennett, A.F., Cheers, G.J., 2005. Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation*, in press, doi:10.1016/j.biocon.2005.01.039.
- Rolstad, J., Wegge, P., 1987. Distribution and size of capercaillie leks in relation to old forest fragmentation. *Oecologia* 72, 389–394.
- van der Ree, R., Bennett, A.F., Gilmore, D.C., 2003. Gap-crossing by gliding marsupials: thresholds for use of isolated woodland patches in an agricultural landscape. *Biological Conservation* 115, 241–249.
- With, K.A., Crist, T.O., 1995. Critical thresholds in species' responses to landscape structure. *Ecology* 76, 2446–2459.
- With, K.A., King, A.W., 1999. Extinction thresholds for species in fractal landscapes. *Conservation Biology* 13, 314–326.