

## ***Beyond fragmentation: the continuum model for fauna research and conservation in human-modified landscapes***

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Animal distribution patterns in human-modified landscapes are often examined from the basis of the “fragmentation model”, which recognises habitat patches located within an inhospitable matrix. The fragmentation model can establish correlations between landscape pattern and animal distribution patterns. However, it is limited in its ability to generate a process-based understanding of species distribution patterns. Here we propose a process-based conceptual landscape model. The “continuum model” is derived from continuum theory, and recognises the importance of space-related ecological variables alongside other factors, such as the availability of suitable food, shelter, and climatic conditions. The continuum model allows for gradual changes in these variables through space, and assumes species respond individualistically to their environment. We contrast the continuum model with the fragmentation model, and outline how it can be used to interpret and design empirical studies. While the fragmentation model may provide a satisfactory description of ecological patterns where many species are confined to human-defined “patches”, the continuum model can help to establish links between fundamental ecological processes and individualistic species distribution patterns. Conservation guidelines arising from the fragmentation model will emphasise the importance of large and well-connected pre-defined “habitat” patches. Conversely, the continuum model recognises potentially large discrepancies between different species’ ecological requirements. Conservation guidelines arising from the continuum model therefore will focus on habitat heterogeneity at multiple spatial scales to enhance the number of niches available to different species.

The conservation management of modified landscapes requires a sound understanding of how organisms are distributed through space. In this context, conceptual landscape models can be useful tools (McIntyre and Hobbs 1999, Lindenmayer et al. 2003, Manning et al. 2004). We define a landscape model as a theoretical framework that explains how organisms are distributed through space and that can be explored with empirical data.

In the context of fauna research and conservation in human-modified landscapes, the most frequently used landscape model (both implicitly and explicitly) is the “fragmentation model”, which recognises habitat

patches scattered throughout a matrix of non-habitat (Haila 2002). Although the destruction and sub-division of natural ecosystems are important drivers of biodiversity decline (Saunders et al. 1991, Fahrig 1997, 2003, McGarigal and Cushman 2002), many factors other than the spatial distribution of remnants of natural ecosystems also influence animal distribution patterns. Many “fragmentation” studies establish correlations between landscape pattern and species distribution patterns, but shed little light on the ecological processes underlying such correlations. Understanding how ecological processes shape species distribution patterns is a key challenge for landscape ecology, and an important prerequisite for successful biodiversity conservation (Wiens et al. 1993, Hobbs 1997). Because of its strong emphasis on landscape pattern, but limited consideration of ecological processes, the fragmentation model is unlikely to be satisfactory in all situations. Specifically, an over-reliance on the fragmentation model may lead to (1) a limited predictive ability of actual animal distribution patterns (Lindenmayer et al. 2003), and (2) simplistic conservation recommendations that ignore important threatening processes (Manning et al. 2004).

Here, we outline a conceptual model that creates an explicit link between ecological processes and species distribution patterns. First, we briefly review the fragmentation model, including its origin, assumptions, and relationship to other existing landscape models. We then introduce the “continuum model” as a tool to investigate the causal links between key ecological processes and species distribution patterns. We explore the conceptual value of the continuum model in the context of the Tumut fragmentation “natural experiment” in south-eastern Australia, and briefly outline how it may be applied in an empirical context.

## The fragmentation model

### Definition and assumptions

The fragmentation model originates from the theory of island biogeography (MacArthur and Wilson 1967) and was recently reviewed in depth by Whittaker (1998) and Haila (2002). The model considers a range of habitat “patches” located within a less inhabitable or hostile “matrix” that dominates the landscape (Saunders et al. 1991, Harrison and Bruna 1999, Debinski and Holt 2000, Fahrig 2003). The fragmentation model makes several implicit assumptions. Three key ones are:

- Assumption 1. There is a clear contrast between human-defined patches and the remainder of the landscape.
- Assumption 2. Multiple organisms perceive the same human-defined patches as suitable “habitat patches”.
- Assumption 3. The correlation between landscape pattern (e.g. patch sizes and their spatial configuration) and species distribution patterns is of interest, and is a reasonable proxy for the ecological processes that are causally related to species distribution patterns.

### Conservation implications

Conservation prescriptions arising from the fragmentation model include: (1) large patches are usually more important than small patches, (2) patches are more important than the matrix, (3) corridors can enhance connectivity, and (4) a dense array of patches is preferable to widely spaced patches (Diamond 1975). Thus, conservation management based on the fragmentation model tends to focus on a mosaic of patches and corridors with emphasis on the total amount of pre-defined “habitat”, patch shapes and sizes, and the spatial arrangement of patches (Andrén 1994, Fahrig 2003).

### Limitations of the fragmentation model and existing alternatives

In some high-contrast regions, it may be reasonable to assume that pre-defined “habitat patches” are relevant to the conservation of many species. The wheatbelt in Western Australia is a good example of such a region. Over 90% of native *Eucalyptus* woodland vegetation has been cleared in this region. Most remaining woodland patches are relatively small (<20 ha), and are situated on private land within an intensively grazed or cropped landscape context (Saunders et al. 1993). Both ecological research and conservation management in the wheatbelt have been driven by the fragmentation model. For example, much research has focused on the relationships

between the size and connectivity of woodland patches and various measures of biodiversity (Kitchener et al. 1982, Arnold and Weeldenburg 1998, Brooker 2002), and the focal species approach was developed in this region to guide conservation on the basis of variables like patch size and isolation (Lambeck 1997). Given the high contrast between areas of native vegetation and the remainder of the landscape, the fragmentation model may be a reasonable starting point for conservation management in this region (Freudenberger and Brooker 2004, but see Lindenmayer and Fischer 2003).

In other landscapes, it is more obvious that the assumptions made by the fragmentation model are sometimes overly simplistic. For example, in south-eastern Australia, the lack of a clear contrast between woodland patches and grazed pastures led McIntyre and Barrett (1992) to suggest the “variegation model” as an alternative to the fragmentation model. The variegation model suggests viewing landscapes as habitat gradients rather than patches within a matrix, thereby relaxing the assumption of clearly delineated patches located within a hostile matrix. However, like the fragmentation model, the variegation model does not explicitly recognise species-specific differences or highlight underlying ecological processes.

To overcome these limitations, Manning et al. (2004) suggested the “continua-umwelt” model. Like the variegation model, this model recognises spatial gradients. However, in addition, it recognises that (1) species differ in their perception of what constitutes suitable habitat, and (2) a range of ecological processes may affect habitat suitability for different species through time, in a spatially continuous and potentially complex way. The continua-umwelt model comes significantly closer to linking landscape pattern with ecological processes than both the fragmentation and the variegation models. However, while acknowledging the importance of considering ecological processes, it provides little guidance with respect to which ecological processes may be particularly important; and how the link between pattern and process may be achieved in practice. Further refinement of the link between pattern and process is the objective of the “continuum model” discussed below.

## The continuum model

### Definition

Continuum theory is widely accepted in vegetation ecology, but has received little attention from animal ecologists (Austin 1999a, 1999b). “The continuum concept states that vegetation has a gradually changing species composition along environmental gradients, with each species having an individualistic ... distribution” (Austin 1999b, p. 170-171). Thus, the theory shows clear parallels with Gleason’s (1939) “individualistic concept

of plant association". Environmental gradients can be direct (e.g. temperature), indirect (e.g. latitude) or resource-related (e.g. nutrients) (Austin and Smith 1989). Because they are process-based, direct and resource-related gradients are likely to be particularly robust as explanatory variables in statistical distribution models (Austin 2002).

To apply continuum theory to animal ecology, it will be useful to focus on direct and resource and environmental gradients that are likely to be relevant to a wide variety of animal species. Four such gradients are: (1) food, (2) shelter, (3) space, and (4) climate. We consider these gradients over other possible candidates for a conceptual framework because they are closely linked to ecological processes that affect animals and therefore should be related to their distribution patterns. The direct quantification of these gradients often will be difficult. In such cases, indirect variables may need to be used to approximate ecological processes. It is important to recognise species-specific responses to some of these gradients, and define them fairly broadly. Space, for example, may relate to an individual's home range or "patch size", or it may relate to the juxtaposition of certain habitat attributes across a landscape. Similarly, depending on the organism and landscape of interest, shelter may relate to shrub cover, the abundance of tree

hollows, or may include the availability of breeding locations. Fig. 1 summarises how, thus framed, the continuum model may be useful for explaining animal distribution patterns.

### Conservation implications

Given the emphasis the continuum model places on species-specific differences and gradual changes through space, the following generic implications for conservation strategies arise: (1) heterogeneity at the landscape scale (e.g. topography, mix of patch sizes and vegetation types) and microhabitat scale (e.g. structural complexity) should create additional niches and thus enhance species richness (e.g. Tews et al. 2004). (2) Unmodified or "original" habitats are likely to be beneficial for most native and endemic species which have co-evolved with such habitats. However, even highly modified locations may provide habitat for some native species. Hence, conservation enhancement can take place throughout entire landscapes. (3) Given species-specific differences, no single conservation action can benefit all species. This implies a choice is needed regarding which species are most deserving of conservation efforts (Daily 2001).

The continuum model is likely to be a significant improvement over the fragmentation model in landscapes

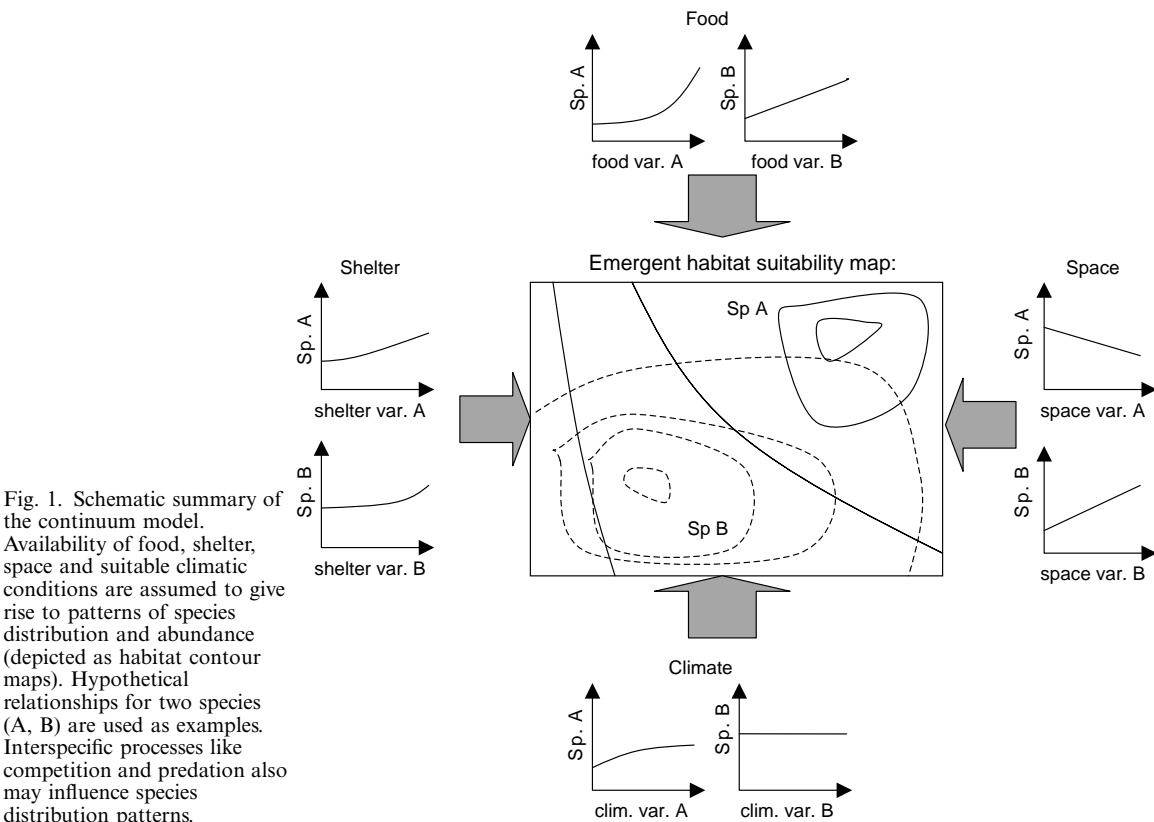


Fig. 1. Schematic summary of the continuum model. Availability of food, shelter, space and suitable climatic conditions are assumed to give rise to patterns of species distribution and abundance (depicted as habitat contour maps). Hypothetical relationships for two species (A, B) are used as examples. Interspecific processes like competition and predation also may influence species distribution patterns.

with pronounced ecological gradients, and when species of conservation concern differ strongly in their ecological requirements (Table 1). Examples of such situations include heterogeneous farming landscapes in Europe (Benton et al. 2003), Central America (Mayfield and Daily 2005), and south-eastern Australia (Fischer et al. 2004); and situations involving both terrestrial and aquatic or semi-aquatic organisms (Zimmerman and Bierregaard 1986, Semlitsch and Bodie 1998, Joyal et al. 2001).

**Summary: strengths and limitations of the continuum model**

The continuum model relaxes several assumptions made by the fragmentation model, and to a lesser extent the variegation model (Table 1). Key strengths of the continuum model are that it recognises gradients in space and species-specific differences; and that it links ecological processes to species distribution patterns. One limitation of the continuum model is that its increased realism comes at the cost of reduced simplicity. A second limitation is that despite its increased complexity, the continuum model still is a highly simplified model of reality. As a result, synergistic effects, cross-scale effects, and complex species interactions, may be difficult to explain from the basis of the continuum model. However, other frameworks exist to explore such complexity, such as complex adaptive systems theory (Holling 2001, Folke et al. 2004, Walker et al. 2004). Notably, the purpose of the continuum model is not to explain all ecological patterns in all landscapes. Rather, it is a tool that can help to focus the interpretation and design of empirical work in modified landscapes. Unlike other landscape models, the continuum model encourages the exploration of ecological processes rather than restrict the analysis to establishing correlations between landscape pattern and species distribution patterns.

**Interpretation and design of empirical studies**

The continuum model can assist (1) the interpretation of existing empirical data on animal distribution patterns, and (2) the design of empirical studies in modified landscapes.

**Interpreting field data from the Tumut “natural experiment”**

The continuum model can help to interpret ecological findings from empirical studies in human-modified landscapes, like the Tumut fragmentation “natural experiment” (sensu Diamond 1986) in south-eastern Australia. The Tumut study was established in 1995, and is one of the world’s largest natural experiments to investigate ecological questions related to “fragmentation” (reviewed by Lindenmayer 2000, Lindenmayer and Franklin 2002). The “experiment” focuses on Buccleuch State Forest, approximately 100 km to the west of Canberra, Australia. Buccleuch State Forest is located between 700 m and 1100 m above sea level, and covers approximately 100 000 ha. Roughly half of the state forest is comprised of native forest (primarily swamp gum *Eucalyptus camphora*, ribbon gum *E. viminalis* and narrow-leaved peppermint *E. radiata*, with less widespread occurrences of other eucalypt species). The other half is dominated by a plantation of the introduced radiata pine *Pinus radiata*. Throughout the pine plantation, patches of native eucalypt forest have been retained, ranging from <1 ha to >100 ha. A range of ecological studies have been completed on vertebrates (Table 2) and other organisms, including bryophytes (Pharo et al. 2004), invasive weeds (Lindenmayer and McCarthy 2001), and invertebrates (Smith et al. unpubl.).

The landscape pattern of the Tumut landscape suggests it is a clearly “fragmented” mosaic of native forest patches within an intensively managed exotic pine plantation. Empirical work to date has established a range of relationships between patch sizes and levels of

Table 1. Assumptions made by the fragmentation model, and how they are relaxed in the continuum model.

	Fragmentation model	Continuum model
Landscape pattern	assumes clear contrast between patches and areas outside patches	allows landscapes with gradually changing patterns
The notion of “patches”	requires human-defined patch boundaries to correspond closely with animal-perceived patch boundaries; patches are assumed to be internally homogeneous	human-defined patches are not of primary interest, and no assumptions are needed about their internal homogeneity
Identity of species	restricted to single species or multiple species with similar requirements	allows consideration of multiple species with vastly different requirements
Species distributions	requires species to be restricted to patches, ideally as metapopulations	species can be distributed through space in complex and continuous ways
Ecological processes	assumes that landscape pattern is a reasonable proxy for a multitude of interacting ecological processes	attempts to study ecological processes directly

Table 2. Summary of findings on vertebrate distribution patterns in the Tumut fragmentation “natural” experiment. Fragmentation-related findings are listed near the top of the table. A range of additional findings listed towards the bottom of the table highlighted species-specific differences, gradual changes through space, and suggested causal links between the availability of suitable food, shelter and climatic conditions, and animal distribution patterns.

Vertebrate group	Finding
Fragmentation-related findings	
Birds	<ul style="list-style-type: none"> <li>• distribution patterns of sacred kingfisher <i>Todiramphus sanctus</i> predicted well by metapopulation model (Lindenmayer et al. 2001)</li> </ul>
Marsupials	<ul style="list-style-type: none"> <li>• bird species richness highest in large patches and continuous native forest (Lindenmayer et al. 2002)</li> <li>• greater glider <i>Petaurus volans</i> and common brushtail possum <i>Trichosurus vulpecula</i> more likely in large patches (Lindenmayer et al. 1999a)</li> <li>• yellow-bellied glider <i>Petaurus australis</i> only in continuous native forest (Lindenmayer et al. 1999a)</li> </ul>
Rodents	<ul style="list-style-type: none"> <li>• brown antechinus <i>Antechinus stuartii</i> more likely in well connected patches (Lindenmayer et al. 1999b)</li> <li>• bush rat <i>Rattus fuscipes</i> may use native streamside vegetation as corridors (Lindenmayer and Peakall 2000)</li> </ul>
Lizards	<ul style="list-style-type: none"> <li>• bush rat more likely in large patches (Lindenmayer et al. 1999b)</li> <li>• maccoy's skink <i>Nannoscincus maccoyi</i> more likely in less isolated patches (Fischer et al. 2005)</li> <li>• coventry's skink <i>Niveoscincus coventryi</i> more likely in large patches (Fischer et al. 2005)</li> </ul>
Frogs	<ul style="list-style-type: none"> <li>• lizard species richness highest where context was dominated by eucalypt forest (Fischer et al. 2005)</li> <li>• only two frog species in the pine matrix (Parris and Lindenmayer 2004)</li> </ul>
Findings better explained by the continuum model	
Birds	<ul style="list-style-type: none"> <li>• laughing kookaburra <i>Dacelo novaeguineae</i> may move frequently between patches (Lindenmayer et al. 2001)</li> <li>• pre-defined patch boundaries may not apply to the white-throated treecreeper <i>Cormobates leucophaea</i> (McCarthy et al. 2000)</li> <li>• different bird species perceived the same landscape as fragmented, variegated or continuous (Lindenmayer et al. 2003)</li> </ul>
Marsupials	<ul style="list-style-type: none"> <li>• common ringtail possum <i>Pseudecheirus peregrinus</i> more likely in forest patches than in continuous native forest (Lindenmayer et al. 1999a)</li> <li>• common wombat <i>Vombatus ursinus</i> and swamp wallaby <i>Wallabia bicolor</i> regularly in pine forest (Lindenmayer et al. 1999b)</li> <li>• arboreal marsupials feeding on insects, pollen, plant and animal exudates more common in continuous forest (i.e. explicit link with food) (Lindenmayer et al. 1999a)</li> </ul>
Rodents	<ul style="list-style-type: none"> <li>• bush rat may use streamside vegetation for dispersal because it offers shelter and wet microclimate (Lindenmayer and Peakall 2000)</li> </ul>
Lizards	<ul style="list-style-type: none"> <li>• lizard occurrence related to invertebrate abundance (i.e. food availability) (Fischer et al. 2005)</li> <li>• different lizard species had different altitudinal preferences, presumably in response to climate (Fischer and Lindenmayer 2005)</li> <li>• garden skink <i>Lampropholis guichenoti</i> and Coventry's skink more abundant at plots with a high volume of old logs to shelter under (i.e. patches were not homogeneous) (Fischer et al. 2005)</li> <li>• distribution patterns of several lizard species extended into the pine forest (Fischer et al. 2005)</li> <li>• maccoy's skink avoided canopy gaps, presumably in response to microclimate (i.e. patches were not homogeneous) (Fischer et al. 2005)</li> </ul>
Frogs	<ul style="list-style-type: none"> <li>• garden skink highly abundant at some recently clearcut pine sites (Fischer et al. 2005)</li> <li>• frogs responded to moisture regime and vegetation structure, rather than patch size (Parris and Lindenmayer 2004)</li> </ul>

isolation, and the presence or abundance of individual species, as well as species richness (Table 2). Thus, the fragmentation model has helped to describe distribution patterns of various vertebrate groups. In addition, the fragmentation model has highlighted the importance of some space-related ecological processes like dispersal of the bush rat along creek lines (Lindenmayer and Peakall 2000), or metapopulation dynamics of the sacred kingfisher (Lindenmayer et al. 2001).

Despite these benefits of the fragmentation model, its three main assumptions have repeatedly been shown to be overly restrictive. Many vertebrate species were not restricted to pre-defined “habitat patches” (cf. assumption 1 above in “Definition and assumptions” of the fragmentation model); species within a given taxonomic group differed in their response to landscape pattern (cf. assumption 2 above); and variables related to food, shelter or climate were often equally important to variables

describing landscape pattern (cf. assumption 3 above; Table 2). The limitations of the fragmentation model were particularly apparent with respect to lizard distribution patterns (Fischer et al. 2005). There was clear evidence that lizards responded individually to gradients of landscape modification and climate (Fig. 2). Given the limitations of the fragmentation model in the Tumut landscape, the continuum model offers an alternative, more holistic, conceptual framework from which to interpret vertebrate distribution patterns.

Notably, the continuum model does not suggest that fragmentation-related ecological processes are irrelevant. Rather, it highlights the potential for additional ecological complexity in human-modified landscapes that is not adequately captured by the fragmentation model. Adequately capturing ecological complexity in conceptual models is key to successful conservation management (Manning et al. 2004).

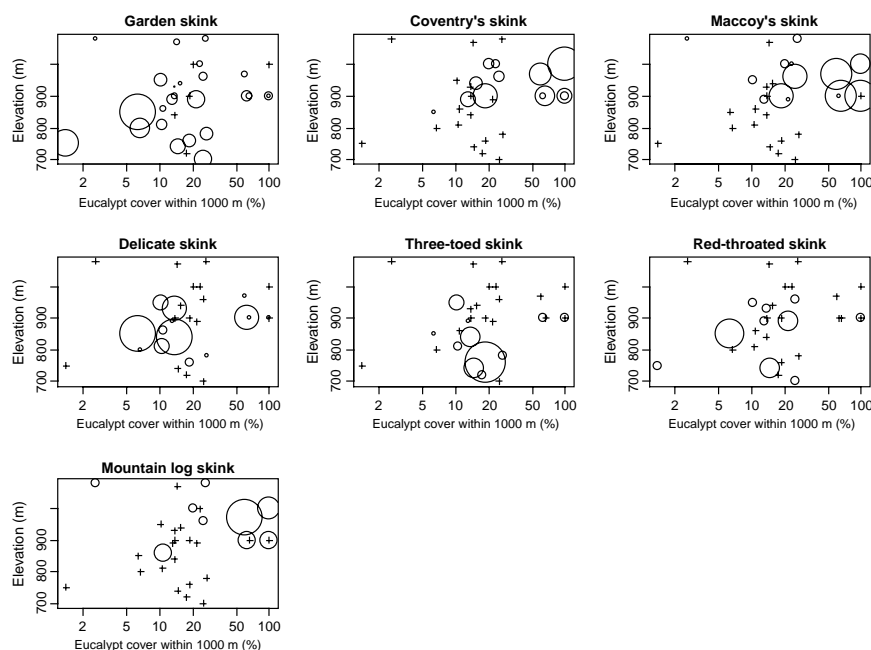


Fig. 2. Graphical summary of the response of the seven most common lizard species in the Tumut area to two key environmental gradients – elevation (indirect climatic gradient) and proportion of eucalypt forest within 1000 m (spatial gradient). Thirty sites were surveyed (Fischer et al. 2005). Here, sites are plotted in environmental space, and a given species' presences are shown as circles and absences are shown as crosses. The size of the circle is proportional to a species' abundance at a particular site. The graph summarises individualistic responses by different species to the two selected environmental gradients. (Scientific names row by row from top left are *Lampropholis guichenoti*, *Niveoscincus coventryi*, *Nannoscincus maccoyi*, *L. delicata*, *Hemiergis decresiensis*, *Bassiana platynota*, *Pseudemoia entrecasteauxii*).

## Designing empirical studies

Fig. 3 outlines how the continuum model can be used as a conceptual basis for statistical distribution modelling (Austin 2002). Essentially, instead of focusing studies largely around fragmentation-related variables, other explanatory variables related to food, shelter and climate may be explicitly incorporated into the design of ecological surveys and subsequent data analysis. The

primary response variables in statistical models arising from the continuum approach will be single species or measures of community composition. In contrast, species richness at any given location will receive less attention than it would under the fragmentation approach. Fig. 3 also highlights that interspecific processes can affect animal distribution patterns. However, such processes can be difficult to quantify because they may be contingent on the environment (extensively discussed

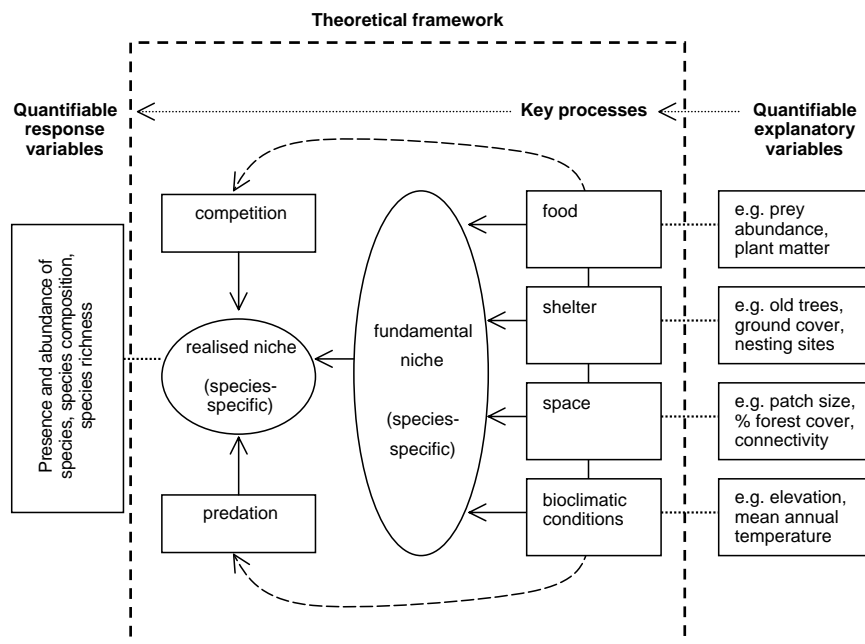


Fig. 3. Illustration of how the continuum model may be applied to empirical studies aimed at modelling the distribution of fauna. Although the theoretical framework is based on direct and resource and environmental gradients, in practice, quantifiable explanatory variables may sometimes need to be indirect (Fischer et al. 2005).

in Leathwick and Austin 2001). A key difference between the framework in Fig. 3 and many fragmentation modelling approaches is that the continuum model has a directly causal and process-based conceptual model at its core, rather than focusing on pre-defined landscape patterns as ecological explanations in their own right.

## Conclusion

Many studies have addressed how fragmentation affects biodiversity (reviewed by Fahrig 2003). As a result, conservation biologists now have a fairly well developed understanding of how the spatial arrangement of vegetation correlates with the distribution patterns of many organisms. However, beyond the facilitation of a deeper understanding of spatial processes, the fragmentation model cannot address the challenge of linking ecological processes with emergent animal distribution patterns. The continuum model outlined in this paper is an attempt to embed the understanding of spatial processes derived from the fragmentation model within a broader framework that recognises (1) the importance of other ecological processes, (2) species-specific differences in response to ecological processes, and (3) the value of landscape heterogeneity for biodiversity conservation. The continuum model creates an explicit link between ecological processes and species' distribution patterns, and can be used as a conceptual basis for statistical distribution modelling. This will be particularly useful in heterogeneous modified landscapes, where a sound understanding of species distribution patterns is a fundamental prerequisite for successful biodiversity conservation.

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