Appreciating Ecological Complexity: Habitat Contours as a Conceptual Landscape Model

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Abstract: *Organisms respond to their surroundings at multiple spatial scales, and different organisms respond differently to the same environment. Existing landscape models, such as the "fragmentation model" (or patch-matrix-corridor model) and the "variegation model," can be limited in their ability to explain complex patterns for different species and across multiple scales. An alternative approach is to conceptualize landscapes as overlaid species-specific habitat contour maps. Key characteristics of this approach are that different species may respond differently to the same environmental conditions and at different spatial scales. Although similar approaches are being used in ecological modeling, there is much room for habitat contours as a useful conceptual tool. By providing an alternative view of landscapes, a contour model may stimulate more field investigations stratified on the basis of ecological variables other than human-defined patches and patch boundaries. A conceptual model of habitat contours may also help to communicate ecological complexity to land managers. Finally, by incorporating additional ecological complexity, a conceptual model based on habitat contours may help to bridge the perceived gap between pattern and process in landscape ecology. Habitat contours do not preclude the use of existing landscape models and should be seen as a complementary approach most suited to heterogeneous human-modified landscapes.*

Key Words: conceptual models, fragmentation, habitat contours, habitat suitability maps, landscape models, patch-matrix-corridor model, variegation

Valorando la Complejidad Ecológica: Contornos de Hábitat como un Modelo Conceptual del Paisaje

Resumen: *Los organismos responden a su entorno en múltiples escalas espaciales, y organismos diferentes responden de manera diferente al mismo ambiente. Modelos de paisaje existentes, como el "modelo de fragmentación" (o modelo parche-matriz-corredor) y el "modelo de variegación," pueden ser limitados en su habilidad para explicar patrones complejos para diferentes especies y en múltiples escalas. Un método alternativo es conceptuar a los paisajes como mapas sobrepuestos de contornos de hábitat especie-específicos. Las características clave de este método son que las diferentes especies responden diferencialmente a las mismas condiciones ambientales y en diferentes escalas espaciales. Aunque se están utilizando métodos similares en modelos ecológicos, hay mucho espacio para los contornos de hábitat como una herramienta conceptual útil. Al proporcionar una visión alternativa de los paisajes, un modelo de contorno puede estimular más investigaciones estratificadas con base en variables ecológicas distintas a los parches y límites de parche definidos por humanos. Un modelo conceptual de contornos de hábitat también puede ayudar a comunicar la complejidad ecológica a administradores de tierras. Finalmente, al incorporar complejidad ecológica adicional, un modelo ecológico basado en contornos de hábitat puede ayudar a reducir la brecha entre patrón y proceso en ecología del paisaje. Los contornos de hábitat no excluyen el uso de modelos de paisaje existentes y deben ser vistos como un método complementario mejor adecuado a paisajes heterogéneos modificados por humanos.*

Palabras Clave: contornos de hábitat, fragmentación, modelos conceptuales, mapas de aptitud de hábitat, modelos de paisaje, modelo parche-matriz-corredor, variegación

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Introduction

How we conceptualize landscapes influences how we study and manage biodiversity. Human-modified landscapes are commonly perceived as a mosaic of patches situated within a more or less hostile matrix (e.g., Saunders et al. 1991; Forman 1995). This predominant world view (here called the fragmentation model) has often led to an inappropriate neglect of small patches and habitat features not recognized as patches by humans (Joyal et al. 2001; Haila 2002). Partly because of this, McIntyre and Barrett (1992) suggested the variegation model as an alternative way of conceptualizing modified landscapes. Their model recognized gradients in habitat suitability and emphasized the complementary value of semi-isolated trees present throughout many Australian grazing landscapes (Barrett et al. 1994). We are not aware of other models designed explicitly to conceptualize modified landscapes.

Recent work suggests that the fragmentation and variegation models by themselves are a weak conceptual foundation for conservation research and management in heterogeneous human-modified landscapes. For example, studies on countryside biogeography in Costa Rica demonstrated that a large number of birds, moths, and butterflies persist, and that they responded differently in a severely modified tropical landscape and in areas outside remnant patches (e.g., Daily et al. 2001; Ricketts et al. 2001; Hughes et al. 2002; Horner-Devine et al. 2003). Similarly, studies in the Nanangroe grazing landscape of southeastern Australia show that different species responded to their environment and to different habitat attributes at different scales (Lindenmayer et al. 2001; Fischer et al. 2004a, 2004b). Given the range of possible responses by different organisms to a given set of environmental conditions, we believe a new conceptual landscape model is needed that guides our thinking to be less anthropocentric and that can accommodate species-specific characteristics.

We sought to present an alternative conceptual model of biodiversity patterns in heterogeneous human-influenced landscapes. Our approach is based on habitat contours and as such has similarities with recent quantitative habitat modeling approaches (Guisan & Zimmerman 2000; Guisan et al. 2002). Despite these similarities, our primary objective was not to provide a quantitative modeling approach. Rather, we hope our conceptual model will facilitate change in the way ecologists and land managers perceive modified landscapes. We briefly review the fragmentation and variegation models and then outline a new conceptual model based on habitat contours. We highlight potential uses of this model as a research and communication tool and use a brief case study on the greater glider (*Petauroides volans*) in the Central Highlands of Victoria, Australia, to demonstrate parallels to modern empirical modeling approaches.

The Fragmentation and Variegation Models

The fragmentation model is derived from the theory of island biogeography (MacArthur & Wilson 1967). Despite its original focus on true island systems, the theory is often applied to terrestrial ecosystems (Haila 2002). In the 1970s and 1980s, island biogeography formed the basis for a range of guidelines for the design of reserve networks (Diamond 1975; Davey 1989). By the 1990s, the fragmentation paradigm had gained considerable momentum, and the existence of patches embedded within a somewhat hostile matrix was a widely accepted way of conceptualizing modified environments (Haila 2002; Table 1). Users of the fragmentation model often define habitat patches on the basis of their vegetation cover and refer to the dominant background patch type as the matrix (Forman & Godron 1986). Although some have emphasized that within-patch conditions can be heterogeneous (e.g., Forman 1995), in practice, the distinction between patches and the matrix can often lead to a binomial classification of land into habitat and nonhabitat (e.g., Vos et al. 2001; Westphal & Possingham 2003). This classification can be powerful in some environments—especially for organisms that are totally restricted to certain vegetation types and in landscapes where vegetation occurs in neatly delineated areas (e.g., Sarre et al. 1995). However, in some cases, organisms are not tightly related to predefined patches of different vegetation types, and the fragmentation model may be overly simplistic.

McIntyre and Barrett (1992) recognized the limitations of the fragmentation model in the New England Tablelands of New South Wales, Australia. They found that the density of vegetation cover changed gradually, which made it difficult to delineate "patches" in a meaningful way. On this basis, they suggested an alternative approach to conceptualizing landscapes (i.e., the variegation model). McIntyre and Barrett (1992) believed that a variegated landscape was characterized by a gradual change in vegetation cover, which matched the distribution of some fauna, such as woodland birds (Table 1). Although the variegation model has received less attention than the fragmentation model, several authors found it a useful alternative to fragmentation (e.g., Ingham & Samways 1996; Fischer & Lindenmayer 2002). McIntyre and Hobbs (1999) further examined the relationship between the fragmentation and variegation models, and suggested that there was a temporal component to landscape change. Different landscape alteration states meant that landscapes could be classified as intact, variegated, fragmented, or relictual, and this temporal sequence corresponded to a decrease in available habitat and an increase in disturbance and edge effects.

The most important difference between the fragmentation and variegation models is their ability to deal with spatial continua in habitat quality or vegetation type. The fragmentation model does not generally deal with gradual

Table 1. Comparison of key characteristics of the fragmentation, variegation, and contour-based landscape models (based on Forman & Godron 1986; McIntyre & Barrett 1992; Forman 1995; Wiens 1995; McIntyre & Hobbs 1999; this article).

	Fragmentation model	*Variegation model*	*Contour model*
Features and terminology	patches; matrix; corridors	gradual changes from habitat to nonhabitat	peaks and troughs; contour spacing
Model summary	patches of habitat located in a somewhat hostile matrix of nonhabitat; patches may be connected through corridors	gradual changes from habitat to nonhabitat; may be related to vegetation cover (e.g., gradual decline in tree density)	each species has its own habitat contour map with peaks and troughs; spacing of contours represents the change of habitat suitability through space
Degree of realism	high to low, depending on species and landscapes	high to low, depending on species and landscapes	high
Degree of complexity	low	medium	high
Ability to deal with multiple species	low, unless species are very similar	low, unless species are very similar	high, even if species are very different
Ability to deal with multiple spatial scales	high, can consider the area covered by patches at multiple spatial scales	medium, model deals primarily with gradual changes in woodland vegetation	high, nested contours and choices about contour resolution are possible
Ease of quantifying patterns	high, presence or abundance data need to be collected from patches and the matrix	medium, presence and abundance data need to be collected across a gradient	low, detailed data on multiple habitat features and species are required at multiple spatial scales
Ease of communication	high	medium	medium

changes (apart from edge effects that may extend deeply into a patch; see Laurance 1991, 2000), whereas the variegation model was developed explicitly to incorporate gradients (Table 1). Neither the fragmentation nor the variegation model, however, can easily deal with species-specific differences in response to a given landscape because both models are based on biophysical patterns deemed relevant by humans. Indeed, McIntyre and Hobbs (1999) conceded that many landscape models were somewhat biased toward an anthropocentric perspective of the world.

Some workers have attempted to overcome this problem by labeling species according to their use of a modified landscape—such labels include "forest-interior species" (Tang & Gustafson 1997; Zanette et al. 2000); "edge species" (Bender et al. 1998; Euskirchen et al. 2001); and "generalist species" (Andrén 1994; Williams & Hero 2001). Others have more generally captured the notion that different species utilize areas between patches to different extents (Andrén et al. 1997). Similarly, attempts have been made to describe the matrix in more detail because in some cases, labeling it as nonhabitat was considered simplistic. Gascon and Lovejoy (1998) considered that the likelihood of a given species to move through the matrix depends on the vegetation structure in the matrix. They likened the matrix to a filter with a certain pore size that influences its permeability (see also Forman 1995). Although refinements in labeling species or matrix types will sometimes be sufficient to explain ecological patterns in modified landscapes, in some cases it may be useful to start from more neutral grounds and consider a more flexible landscape model. Such a conceptual

model is explained in the next section, and it may be particularly useful in heterogeneous landscapes and when multiple species are considered simultaneously.

A Contour-Based Landscape Model

Ecological complexity is difficult to summarize in simple graphical representations, which often form a useful basis for conceptual tools. Multiple species, multiple spatial scales, and a wide range of ecological processes interact in complex ways to give rise to emergent patterns. Humans are inherently inept at conceptualizing continua (Anderson 2001). In the ecological sciences, this is highlighted by many cases in which continua have been broken up into seemingly discrete units to help communication. Examples include landscape alteration states (from intact to relictual; McIntyre & Hobbs 1999); edge versus forest-interior species and area-sensitive species (Villard 1998); generalists versus specialists (e.g., McIntyre & Martin 2002); or the core of a bioclimatic domain versus the remainder of the bioclimatic domain (e.g., Nix 1986). All these entities are extreme points along continua that are segmented to reduce complexity. Although the reduction of complexity is an important characteristic if any model, concept, or theory is to be widely accepted (Hoffman 2003), we are concerned that oversimplifying ecological complexity in heterogeneous landscapes can have undesired consequences for conservation (e.g., by neglecting key habitat attributes that are not part of human-defined patches). For this reason, we believe that a new conceptual landscape model should convey more complexity than previous approaches.
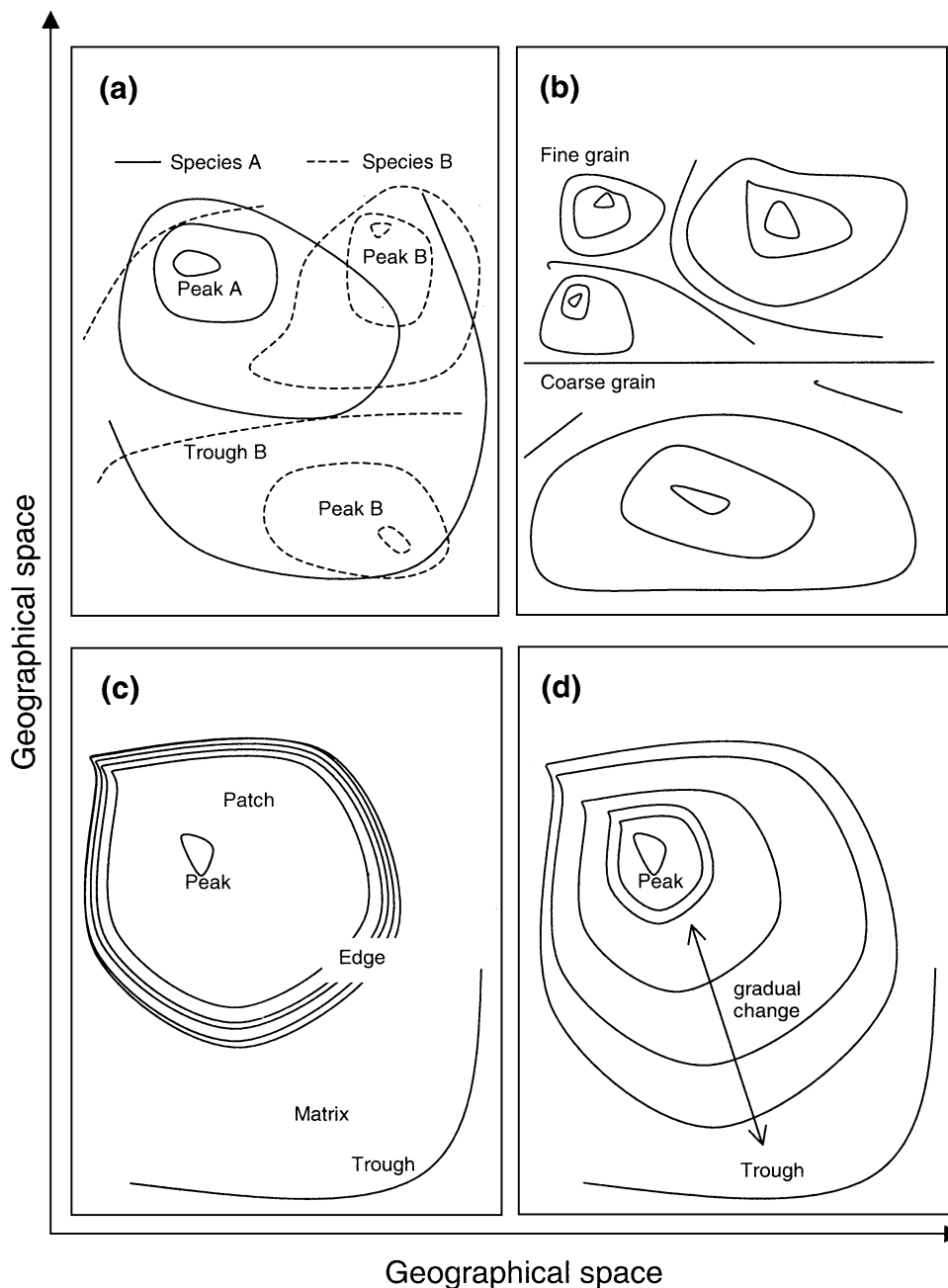
Figure 1. Graphical presentation of a conceptual landscape model based on habitat contours. Key model features are that it (a) allows for species to differ in what constitutes suitable habitat, (b) recognizes differences in the spatial grain of species, (c) contains the fragmentation model, and (d) contains the variegation model. Further characteristics and limitations are outlined in the text.

Topographic contour maps are a noteworthy tool for representing spatial continua. Many scientists and land managers are familiar with topographic maps that summarize a large amount of complex spatial information (e.g., elevation, slope, aspect, and catchment area) in a simple graphical representation. A similar approach may be useful for conceptualizing landscapes in a conservation context. A landscape can be visualized as a map of overlaid habitat suitability contours for different species (or in the case of many species, parallel habitat suitability contours) (Fig. 1). The properties of a contour-based landscape model can then be summarized in six key characteristics (see also Table 1).

1. Habitat is a species-specific concept. Hence, areas of high suitability for one species do not necessarily coincide with areas of high suitability for another species (Fig. 1a).
2. The spatial grain at which species respond to their environment, and at which species abundance will reach peaks and troughs, can vary between species (Kotliar & Wiens 1990). This realization can be translated onto a contour map through different spacing of contours for different species (e.g., species may have densely spaced contours with many peaks and troughs [fine spatial grain] or widely spaced contours with few peaks and troughs [coarse spatial grain; Fig. 1b]).

3. Species respond to ecological phenomena at a range of spatial scales (Forman 1964). Spatially nested contours can be represented, and different resolutions of contours can be used to represent responses at different spatial scales. If only the continental scale is of interest, the interval between contours can be somewhat coarse. If microhabitats are of interest, contour intervals will need to be finer.

4. A contour model can be simplified to correspond to the fragmentation model and variegation model where appropriate. The fragmentation model translates into a contour model if contours are spaced widely within a given patch (continuously high suitability), undergo a rapid transition from high suitability to low suitability at the edge of a human-defined patch, and are widely spaced and indicate low habitat suitability within the matrix (Fig. 1c). The variegation model also can be represented through habitat contours, but the "edge zone" of gradually changing contours would take up a much larger area to indicate a more gradual change (Fig. 1d). Habitat contours, then, are an extension of, not a replacement for, existing landscape models.

5. A given species' habitat contour map is the emergent pattern arising from myriad ecological processes operating at multiple spatial scales. Knowing a species' habitat contour map does not allow direct conclusions about the processes that are causing the pattern in species distribution or abundance.

6. A given contour map is set in geographical space and does not have a temporal component. This may require the consideration of multiple snapshots of contour maps at various different times (e.g., some species have changing habitat requirements at different stages of their life cycle [Palomares et al. 2000; Lehtinen et al. 2003]).

Four Potential Uses of Habitat Contours as a Conceptual Model

Facilitating Change in the Way We Think about Landscapes

The primary usefulness of habitat contours is that they provide an alternative—and potentially more holistic—way of thinking about ecological complexity, especially in human-influenced landscapes. It is clear that an exclusive focus on patches is not sufficient to conserve many species in many modified landscapes (e.g., Semlitsch & Bodie 1998; Joyal et al. 2001; Fischer & Lindenmayer 2002; Luck & Daily 2003), and the variegation model alone is unlikely to be a viable alternative in all situations. A more holistic way of thinking about ecological complexity may improve the design of future research projects and communication among scientists and land managers.

Realistic Experimental Design and Interpretation of Field Studies

Many ecological studies in modified landscapes are centered on a paradigm of fragmentation. Some ecological questions can be answered well on this basis (e.g., for species that are closely associated with human perceptions of patches). Other ecological questions would be better addressed with a more flexible approach. This is especially the case when various species are considered simultaneously or when anthropocentric scales are meaningless. For example, Hazell et al. (2001) examined landscape use by frogs in an agricultural landscape in southeastern Australia. The occurrence of frog species was related to moisture gradients in the landscape and to woodland patches. Because factors other than vegetation cover affected the occurrence of frogs, Hazell (2002) concluded that landscape models useful for mammals or birds may be of limited value for frogs. Clearly, considering a priori the limitations of predefined patches to reflect all species' habitat requirements will be useful in many landscapes.

Considering different species and spatial scales presents a challenge to the statistical design of ecological studies. Patches lend themselves to a rigorous stratification. However, other ecological variables can also be used as the basis of a sound experimental design, such as aspect, topographic position, or habitat structure in a certain area (e.g., Fischer et al. 2004a). In addition, a contour model highlights the importance of incorporating multiple spatial scales, especially (but not only) if a range of different species is considered. A range of tools is available for studying multiple spatial scales (summarized in Meentemeyer & Box 1987; Mackey & Lindenmayer 2001). Although we focused largely on the landscape scale (e.g., tens of square kilometers), the inherent ability of a contour model to incorporate multiple scales means that it may also incorporate larger or smaller scales. At least in the first instance, considering landscapes or regions as overlaid species-specific contour maps may be a better way of thinking about ecological complexity than considering them as mosaics of patches. If it is decided that other, simpler landscape models adequately describe the patterns and processes of interest, it may be preferable to revert to a simpler model (see Table 1 for trade-offs between realism and simplicity).

Communication between Different Strands of Ecology

By acting as a communication tool, the habitat contours model may help to bridge the perceived gap between pattern and process in landscape ecology (Hobbs 1997). Wu and Hobbs (2002) argue that landscape ecologists who focus on those patterns have made little progress in relating emergent patterns to ecological processes. Similarly, studies that investigate processes directly have had only limited success in applying their findings to real landscapes.
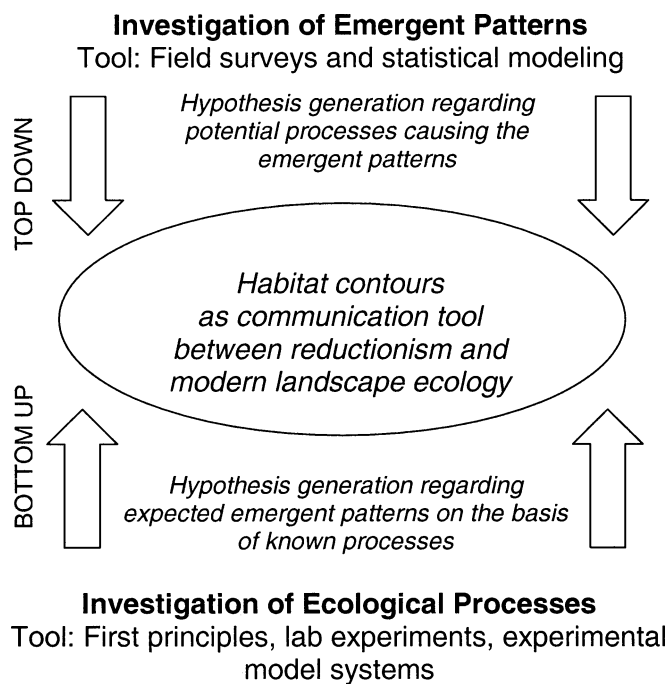
Investigation of Emergent Patterns
Tool: Field surveys and statistical modeling

TOP DOWN

Hypothesis generation regarding potential processes causing the emergent patterns

Habitat contours as communication tool between reductionism and modern landscape ecology

BOTTOM UP

Hypothesis generation regarding expected emergent patterns on the basis of known processes

Investigation of Ecological Processes
Tool: First principles, lab experiments, experimental model systems

Figure 2. Graphical representation of how a conceptual model of habitat contours may assist communication between traditional reductionist science and pattern-based landscape ecology.

This may be partly because the traditional reductionist goal of focusing on smaller and smaller scales (Meentemeyer & Box 1987) may be in stark contrast to landscape-scale research and conservation management. On this basis, Hobbs (1997) argued that linking pattern and process was an important requirement for landscape ecology to prove itself as a useful science.

A contour-based landscape model may be a useful tool for generating spatially explicit hypotheses, which may be tested with respect to patterns and processes (Fig. 2). A contour-based landscape model may be built from first principles on the basis of known ecological processes (bottom-up approach). This approach is compatible with the ideas of Wiens (1995), who suggests visualizing space as cost-benefit contours, and it may lead to testable predictions of likely emergent patterns for one or multiple species. Conversely, large-scale field studies may be used to generate maps of known emergent patterns and to create hypotheses with respect to potential ecological processes that may have caused these patterns (top-down approach; see case study that follows). A contour model, then, may be a possible starting point to aid communication between traditional reductionist science and more pattern-based field research in landscape ecology.

Communication with Land Managers and Land-Use Planning

Conceptual models are vital to communicating ideas among scientists and land managers. The fragmentation model is a successful communication tool. For example, general principles such as "a bigger patch is better for biodiversity conservation than a smaller patch" (e.g., Diamond 1975) are widely accepted among land managers, such as Australian farmers (e.g., Bennett et al. 2000). Although general principles based on traditional landscape models have helped conservation in many modified landscapes (e.g., large patches may be targeted for exclusion from grazing), some conservation issues cannot be adequately addressed from the basis of the fragmentation (or variegation) model. For example, several endangered lizard species in eastern Australia are reliant on grasslands (e.g., Osborne et al. 1995; Dorrough & Ash 1999; Milne & Bull 2000). Native grasslands, however, are rarely conceptualized as patches, and as a result, surveys of farmers have shown that grasslands are not highly valued for conservation, unlike clearly recognizable patches of trees (Williams & Cary 2001). Exploring ecological complexity with land managers through the use of a contour-based landscape model may be helpful because the simple analogy of topographic maps helps to explain why whole landscapes need to be managed instead of certain patches in isolation. As a result, the focus of conservation practices in some modified landscapes may be more successfully targeted to the requirements of species of concern and will be more likely to simultaneously consider a wide range of organisms with different habitat requirements. In this context, hands-on attempts at habitat contour mapping may be of direct practical value. For example, in a planning context, existing maps or aerial photographs may form the background for actual attempts to draw possible habitat relationships for various species. Although the direct quantification of contour lines will often be impossible because of a lack of empirical data, the very process of thinking about species-specific continua may be a useful exercise in visualizing the complexity of ecological systems—as opposed to seeing them as a patchwork of neatly delineated habitat patches or one-way habitat gradients.

Making the Link to Quantitative Ecological Modeling

Predicting habitat suitability through the use of quantitative models (empirical or nonempirical) has been an important aspect of ecological modeling for some time. There are many different approaches to modeling habitat suitability for one or several species (e.g., Guisan & Zimmermann 2000; Guisan et al. 2002; Ohmann & Gregory 2002; Zaniewski et al. 2002). In the next section, we use a case study to illustrate parallels and possible future connections between the conceptual model described previously and empirical investigations.
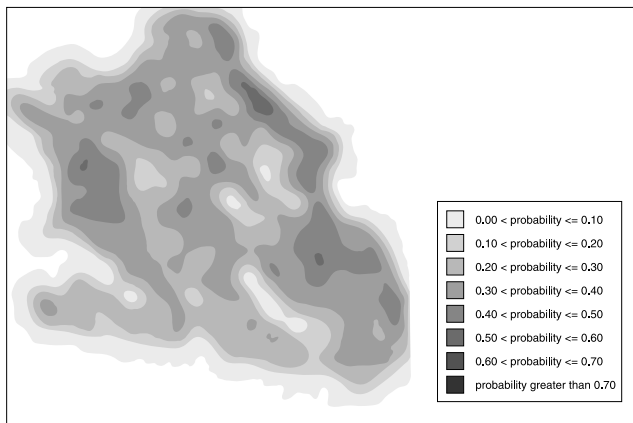
Figure 3. The predicted probability of detecting the greater glider in the Ada Forest Block (6700 ha) in the Central Highlands of Victoria, Australia.

The Greater Glider in the Victorian Central Highlands

The greater glider is a forest-dependent arboreal marsupial, and has been the target of a range of ecological studies in a 6700-ha wood production block in the Central Highlands of Victoria (Lindenmayer 2002). To establish habitat associations for the species, more than 150 field sites were surveyed throughout the montane ash forests of the Central Highlands. These sites covered a broad range of environmental conditions (Lindenmayer et al. 1990, 1995). Numerous measures of vegetation structure and plant species composition were gathered at the survey sites. Logistic regression analysis showed that the presence of the greater glider was related to two habitat attributes. The species was significantly more likely to occur in old-growth stands and in stands characterized by large numbers of trees with hollows.

The two significant explanatory variables in the regression were mapped spatially from aerial photographs and stored in a geographic information system (GIS) database. The habitat model was then linked to spatial data for the two attributes to predict the probability of occurrence of the greater glider throughout the entire Ada Forest Block (6700 ha), an area designated for wood production (Fig. 3; see Lindenmayer et al. 1995 for more details). Although Fig. 3 shows spatial predictions based on mean probability values, it is also possible to make predictions based on values for the upper and lower bounds of the 95% confidence interval associated with the mean.

The statistical relationship was based on significant explanatory habitat attributes and did not consider other ecological variables that may also affect the probability of detecting the greater glider. Such variables may include predation by large forest owls, the presence of parasites, the spatial juxtaposition of suitable habitat, and other factors. Habitat suitability, represented by contours of occurrence probability, represents the potential distribution of the target species in a given area, whereas other factors (such as those listed previously) may further limit the species' actual occurrence on the ground.

Spatial patterns of animal distribution are necessarily dynamic. For example, patches of forest, if undisturbed, may eventually reach a stage of maturity where they would provide suitable habitat for the greater glider. Therefore, a spatial prediction of suitable habitat now may be quite different from that made in 100 years as some forest stands age and others are logged. Similarly, the collapse of hollow trees will also lead to temporal changes in habitat suitability (Lindenmayer et al. 1997). In this case, both these changes in the significant explanatory habitat attributes of the greater glider can be tracked by aerial mapping, and it would be possible to produce contour maps of the predicted probability of occurrence at regular intervals in the future.

Potential Future Applications of Empirical Modeling

The greater glider case study demonstrated clear parallels between the conceptual model we proposed and existing empirical modeling approaches. There is ample scope to expand current modeling approaches to examine the relationships between biodiversity and environmental variables in more detail. Two key areas for future work include the consideration of multiple species simultaneously to identify groups of species with similar responses and species with different responses (see also Vos et al. 2001) and the investigation of relevant scenarios of habitat change and their effect on predicted habitat suitability maps (e.g., Schröder 2000). Together, these two areas for future work may result in mapped predictions of future occurrence patterns for various groups of organisms under different management regimes, thus providing usable scientific input for scenario planning as a conservation tool (Peterson et al. 2003).

Conclusions

Concepts such as the contour model can be useful in facilitating a transformation in the way we perceive ecological complexity. We acknowledge that there are obvious limitations to representing the contour model in diagrammatic form (e.g., it is difficult to imagine that dozens of parallel habitat contour maps for different species will ever actually be drawn). Similarly, the data required for quantification of the contour model will often be unavailable. However, these limitations do not preclude the usefulness of habitat contours as a tool for generating hypotheses, communicating ecological complexity, and changing the way scientists and land managers think about landscapes.

Metapopulation theory is an interesting analogy in the usefulness of concepts to instigate a different way of thinking (e.g., Hanski & Simberloff 1997). Although there

are many quantitative examples of metapopulation modeling (e.g., Lindenmayer & Possingham 1996; Vos et al. 2001), an important contribution of metapopulation theory to conservation has been its ability to act as a conceptual tool (e.g., Telfer et al. 2001). Because the theory is fairly easy to understand at a generic level, it has been taken up readily outside the academic community (Stinchcombe et al. 2002) and has successfully changed the way in which practitioners and others perceive populations and landscapes. As a result, in parts of the United Kingdom, it is now more widely accepted that a landscape-scale approach is needed to achieve effective conservation outcomes (I. Fazey, personal observation).

The way we think about human-influenced landscapes affects which research we deem to be important, how we communicate ecological complexity, and which conservation strategies are considered most effective. In many landscapes, the fragmentation paradigm will be overly simplistic, and the variegation model alone is unlikely to provide a satisfactory alternative in all situations. Habitat contours may be a flexible way of thinking about and planning for biodiversity conservation in heterogeneous landscapes.

Acknowledgments

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