Landscape Characterization and Biodiversity Research

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INTRODUCTION

Rapid deforestation often produces landscape-level changes in forest characteristics and structure, including area, distribution, and forest habitat types. Changes in landscape pattern through fragmentation or aggregation of natural habitats can alter patterns of abundance for single species and entire communities (Quinn and Harrison 1988). Examples of single-species effects include increased predation along the forest edge (Andreas and Angelstam 1988), the decline in the number of species with poor dispersal mechanisms, and the spread of exotic species that have deleterious effects (e.g., gypsy moth). A decrease in the size and number of natural habitat patches increases the probability of local extirpation and loss of diversity of native species, whereas a decline in connectivity between habitat patches can negatively affect species persistence (Fahrig and Merriam 1985). Thus, there is empirical justification for managing entire landscapes, not just individual habitat types, in order to insure that native plant and animal diversity is maintained (McGarigal and Marks 1993).

A landscape is defined as an area composed of a mosaic of interacting ecosystems, or patches (Forman and Godron 1986), with the heterogeneity among the patches significantly affecting biotic and abiotic processes in the landscape (Turner 1989). Patches comprising a landscape are usually composed of discrete areas of relatively homogeneous environmental conditions (McGarigal and Marks 1993) and must be defined in terms of the organisms of interest. For example, in a landscape composed of equal parts of forest and pasture, a photophilic butterfly species would perceive the pasture areas as suitable habitat whereas a shade-tolerant species would prefer the forest. In addition, both landscapes and patches are dynamic and occur on a variety of spatial and temporal scales that vary as a function of each animal’s perceptions (McGarigal and Marks 1993). For instance, a long-lived and far-ranging bird will view its environment at broader spatial and temporal scales than a short-lived, wingless insect (Allen and Starr 1982, Urban et al. 1987). These differences must be incorporated and used in landscape analysis by changing the spatial or temporal resolution.
of a database or simulation model.

Simulation experiments of species with different life history patterns on heterogeneous landscapes (Gardner et al. 1993) have shown that natural disturbance and forest management practices interact with existing landscape pattern to dramatically affect the risk of species loss. Those species which are most vulnerable are ones that become isolated as a result of landscape fragmentation and are also restricted to specific habitat types. Simulation results have also shown that policies for land management that change the degree of landscape fragmentation will result in a change in the competitive balance between species, further exacerbating the maintenance of native species diversity.

A large body of theoretical work in landscape ecology has provided a wealth of methods for quantifying spatial characteristics of landscapes (e.g., Baker and Cai 1992, Gardner and O’Neill 1991, Gustafson and Parker 1992, Krummel et al. 1987, O’Neill et al. 1988, Plotnick et al 1993). Recent advances in remote sensing and geographic information systems (GIS) allow these methods to be readily applied over large areas. One of today’s challenges is to relate quantitative measures of landscape characteristics to changes in biodiversity of animals dependent on the landscape structure. The current paucity of spatially-explicit ecological field data makes exploring this relationship difficult.

The objectives of this paper are to present a brief overview of common measures of landscape characteristics, to explore the new technology available for their calculation, to provide examples of their application, and to call attention to the need for collection of spatially-explicit field data. The paper focuses on spatial issues related to macroscopic tropical fauna, although the ideas are in theory applicable to temporal analysis and other biotic groups.

MEASURES OF LANDSCAPE CHARACTERISTICS

Landscapes can be quantified in terms of area, diversity, and pattern. Area measures include total
area of habitat suitable for a particular species, maximum patch size, and mean patch size and are often the simplest to calculate and interpret. For instance, species decline is often correlated with a decrease in the total area of habitat available (Wilson 1988, Saunders et al. 1991). Similarly, information on maximum patch size may provide insight into long-term population viability because populations are unlikely to persist in landscapes where the largest patch is smaller than that species’ home range.

Traditional diversity indices such as the Shannon Index and Simpson Index quantify diversity rather than pattern. These indices first gained popularity as measures of plant and animal diversity and are easily applied to landscape diversity (O’Neill et al. 1988). Unfortunately, these indices convey no information about the structure and arrangement of patches within the landscape. For instance, a landscape composed of 90% forest and 10% pasture would yield the same diversity index value as a landscape of 10% forest and 90% pasture. In addition, these diversity indices combine patch richness and evenness information, although these components are often more useful when considered separately. Richness refers to the number of patch types present; because many organisms are associated with a single type, patch richness may correlate well with species richness (McGarigal and Marks 1993). Following this line of reasoning, Stoms and Estes (1993) outline a remote sensing agenda for mapping and monitoring biodiversity which focuses almost exclusively on species richness. Evenness, on the other hand, refers to the distribution of area or abundance among patch types.

Indices which represent the spatial arrangement of landscapes have been developed from theoretical work in landscape ecology. Three of the more common indices are dominance, contagion, and fractal dimension (O’Neill et al. 1988). Dominance, which is the complement of evenness, provides a measure of how common one land cover is over the landscape (fig. 1). Its value indicates the degree to which species dependent on a single habitat can pervade the landscape (e.g., koala bears dependent on eucalyptus groves). The contagion index measures the extent to which land
covers are clumped or aggregated (fig. 2). Contagion is a useful metric for those species which require large contiguous areas of a particular land cover (e.g., euglossine bees requiring closed-canopy forest). Fractal dimension uses perimeter-to-area calculations to provide a measure of complexity of patch shape (fig. 3). Natural areas tend to have a more complex shape and a higher fractal value, whereas human-altered landscapes have more regular patch structure and a lower fractal dimension (Krummel et al. 1987). This difference can influence the diversity of species which inhabit edges or require multiple habitats (e.g., elk require both forests for cover and open fields for forage).

**RECENT APPROACHES FOR QUANTIFYING LANDSCAPE PATTERN**

Spatial indices and other landscape-level measures can be painstakingly calculated by hand from maps but are typically calculated digitally from a grid of numeric values which represent the map of a landscape. Both field work and aerial photography can provide spatial data, but satellite-borne sensors automatically collect and store such data in a digital grid-cell format. This format is ideal for quantifying spatial characteristics of landscapes or as input to geographic information systems (GIS) and computer simulation models.

Satellite remote sensing offers several other advantages over traditional field work. First, data can be collected simultaneously over large areas. Whereas it might take two years of field work to map the vegetation over a 1000 km² area, a satellite can obtain an image of the same area in a few seconds. In addition, satellites collect data for multiple time periods and at multiple spatial and spectral resolutions using a repeatable and non-destructive sampling method.

Finally, satellite images have a very high information content, and the prices for both images and computer equipment are dropping rapidly. Free public domain software is available for image analysis and the quantification of the results maps (McGarigal and Marks 1993). These features combine to make remote sensing, and satellite imagery in particular, one of the important tools for
ecological monitoring and quantitative assessment at the landscape level.

The utility of remotely sensed data is increased by integration with computerized geographic information systems (GIS) and simulation models that project changes in spatial cover under specific scenarios. GIS allows the efficient layering of many types of data (e.g., vegetation, hydrology, elevation) by referencing all data to a common denominator: geographic location. This multilayered data set can be used to examine causes and effects of changes in the spatial arrangement of each layer by using spatially-explicit simulation modelling. The theoretical and technical groundwork has been laid to allow efficient quantification of landscapes for biodiversity research. Nevertheless, the ties between theory, technology, and reality are tenuous at best. Dale et al. (in press) used the Dynamic Ecological-Land Tenure Analysis (DELTA) model to explore the implications of various land management alternatives on Amazonian diversity as discussed below. This case study demonstrates how spatially-explicit ecological data can be used to strengthen the ties between theory, technology and reality.

CASE STUDY: LINKING LANDSCAPE MEASURES WITH ECOLOGICAL DATA

Background

Amazonian diversity is being negatively impacted by large scale forest clearing. The case study focuses on the Brazilian state of Rondônia which is located in the central Amazon Basin (fig. 4) and is dominated by mature neotropical forests. Government initiatives produced an extensive network of roads (an 18-fold increase in the total length of roads occurred between 1979 and 1988 (Frohn et al. 1990)) which opened the interior forest areas to colonization. Colonists used slash and burn techniques to clear the forest for agriculture, producing a dynamic mosaic of agricultural fields, pasture, regrowth, and mature forest, with most of the clearing originating along and near roads.
Between 1978 and 1988, 17,717 km² of Rondônia's forest were cleared, and an additional 1,417 km² of forest were isolated from the contiguous forest into small (<100 km²) patches (Skole and Tucker 1993).

Changing patterns of forest clearance and isolation can be simulated by the Dynamic Ecological-Land Tenure Analysis (DELTA) model (Southworth et al. 1991, Dale et al. 1993, 1994). The model uses side-looking radar imagery, GIS, field estimates of biomass in forests, and socio-economic data to simulate changes in the area, biomass, and pattern of land-cover types. DELTA is a stochastic spatially-explicit model which combines a decision model of farmers' land-use choices with ecological information about changes in biomass.

Quantifying modelled landscapes

DELTA model simulations suggest that different scenarios of land management result in unique land-cover patterns (Dale et al. 1994) (fig. 5). Land-use activities that are typical for colonists in Rondônia (Coy 1987, Dale and Pedlowski 1992, Leite and Furley 1985) involve rapid clearing of the forest and almost complete deforestation within 18 years. The worst case scenario (taken from the extreme of the Transamazon Highway experience as reported by Moran 1981 and Fearnside 1980, 1984, and 1986) results in total clearance in the first 10 years. On the other hand, a best case scenario can be simulated in which forest clearance stabilizes at about 40% by year 20. The best case scenario involves some clearing, but no burning, of the virgin forest and planting of perennial trees. Using the model to simulate different scenarios of land management permits evaluation of causes of specific land cover changes. The worst and best case model projections are hypothetical, but the typical model scenario is meant to replicate recent land management activities in central Rondônia.

Comparing model projections to satellite imagery over recent years provides a way to verify
the modeled projections. Frohn et al. (in prep.) compare the percent of forest cleared, contagion and fractal indices from the three model scenarios to those obtained from Landsat imagery for 1978, 1980 and 1986 (fig. 6). The clearing pattern for 1978 and 1980 are similar to the typical simulation projections (Fig. 6a). However, the model overestimates the amount of clearing for the 1986 scene.

Initially, contagion is high for both the simulation and the Landsat estimate (Fig. 6b) because the landscape consists primarily of large contiguous patches of forest. Contagion decreases in both estimates as the number of small forest clearings increases and the landscape is less dominated by large patches of forest. In the simulations, contagion increases as larger patches of cleared forest dominate the landscape. However, this pattern has not been verified by Landsat data. The fractal dimension (Fig. 6c) also shows a similar pattern between the typical simulation and the Landsat images indicating that the model predicts landscape patch complexity similarly to that determined from remote sensing.

The comparison shows that the typical scenario simulation is consistent with both the amounts and patterns of forest clearing for central Rondônia for the years tested. This comparisons provides greater confidence in the use of model estimates for later years and for prediction of biodiversity changes in response in landscape patterns.

Modelling faunal response to landscape pattern

In order to relate these landscape-level changes to changes in faunal abundance and distribution, spatially-explicit data were collected for 9 taxonomically diverse groups of neotropical forest animals (table 1) (Dale et al. in press). Examples of spatially-explicit data include the maximum gap width between habitat patches that an animal is physically able to cross; the minimum patch area required to maintain normal behavioral patterns (e.g., including special habitats for breeding); the spatial distribution of rare or patchily distributed resources vital to a particular species' survival; and the
width of the "buffer zone" at a forest edge where climatic or ecological edge effects render the area uninhabitable for a particular species.

The spatial land-cover data was used to define landscape and patch characteristics for the study. DELTA typically runs on an area of ~3000 km². This scale represents an intermediate landscape size for the macroscopic, mobile fauna selected. Model output data was stored in a grid with 37.5 m resolution, because field observations of maximum gap width crossed between habitat patches was most easily divided into multiples of 37.5. In other words, those animals that could not cross a distance greater than 37.5 m were assigned a low gap-crossing ability. Patches were defined simply as areas covered by forest, because the selected groups of animals were all primarily forest-dwellers.

For each model year, the area of forest habitat suitable for each animal group was measured. First, "connected" clusters of habitat cells were identified. A cluster is connected if an animal in one cell can move to any other cell in that cluster (i.e., gaps between cells in a cluster are not wider than the maximum gap width that animal is able to cross). Next, clusters with areas less than the minimum area required by an individual or group (for those that only occur in groups) were discarded. Further discussion of this technique can be found in Pearson et al. (in press).

The result of this analysis is that changes in available habitat are similar for animals that have their gap-crossing ability proportional to area requirements (fig. 7a), regardless of taxonomic affiliation (Dale et al., in press). For instance, the model suggests that species with large gap-crossing abilities and large area requirements (e.g., jaguars) respond in a similar fashion as species with small gap-crossing abilities and smaller area requirements (e.g., sloths). In contrast, animals with gap-crossing ability disproportionately small in comparison to their area requirements (e.g., scarab beetles) decline more rapidly (fig. 7b). Few animals larger than insects seem to fall into this latter group; therefore landscape-level analysis using simply gap-crossing ability and area requirements may provide a swift preliminary identification of the animals most susceptible to rapid decline and possible
extirpation.

Once sensitive species have been identified, additional spatial data may be incorporated to improve the accuracy of the assessment. For example, when possible edge effects and breeding habitat requirements are included in the assessment of suitable habitat available for the tropical frog (Chiasmocleis shudikarensis), the amount of suitable habitat is decreased to 39% of the original area defined by gap-crossing and area requirements alone (Dale et al., In press).

Case study results

Spatially-explicit land-cover data are vital to the assessment of landscape-level change and the ecological implications of that change. These data can be derived from remote sensing data and in situ information (which measure actual patterns) and be integrated with models that simulate the cause and effect of changes in spatial pattern. A combination of area and pattern measures is useful in identifying species sensitive to landscape-level habitat modifications. Spatial indices can be used to represent the changes in land cover pattern to which species respond. Species response to these modifications may be based on spatial-explicit behavioral characteristics rather than taxonomic classification. The major implication of the Rondônia study is that a "balance" between gap-crossing ability and minimum area requirements allows species to maintain themselves under varied land cover conditions.

CONCLUSIONS AND FUTURE RESEARCH OPPORTUNITIES

The theory and technology currently exist to perform rapid, large-scale quantitative analysis of real and modelled landscapes. Policymakers request this type of analysis whenever decisions must be made which influence millions of dollars of public and private money (e.g., the issue of harvesting old-growth forests of the United States' Pacific northwest while protecting the spotted owl).
However, the current paucity of spatial-explicit field data makes it difficult to verify the link between real-world phenomena and the statistical phenomena seen in the landscape indices.

Policymakers require the linkage between indices and diversity be firmly established in the scientific community before the indices can be used to define policy. The urgency of biodiversity conservation issues, therefore, suggests first that field-based research agendas should focus less on taxonomy and morphological description, and more on collection of spatial data; and second, that researchers with remote sensing, GIS, and modelling capabilities should quantifiably the link between measures of landscape characteristics and the observed ecology of species occupying those landscapes.

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Table 1. Relative gap-crossing ability and area requirements for selected tropical fauna (modified from Dale et al. in press). The first seven species have their gap-crossing ability proportional to area requirements; the last two species have low gap-crossing ability and large area requirements.

<table>
<thead>
<tr>
<th>Species or species groups</th>
<th>Gap-crossing ability</th>
<th>Area requirement</th>
<th>Source of information</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jaguar (Felis onca)</td>
<td>High</td>
<td>High</td>
<td>Emmons, pers. commun., Parker 1990</td>
</tr>
<tr>
<td>Bare-tailed woolly opossum (Caluromys philander)</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Bierregaard et al. 1992, Malcolm 1990 and 1991</td>
</tr>
<tr>
<td>Mixed-species bird flock</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Bierregaard et al. 1992, Bierregaard and Lovejoy 1989</td>
</tr>
<tr>
<td>Ant-following bird flock</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Bierregaard 1990</td>
</tr>
<tr>
<td>Tropical frog (Chiasmocleis shudikarensis)</td>
<td>Moderate</td>
<td>Moderate</td>
<td>Zimmerman and Bierregaard 1986, Zimmerman pers. commun.</td>
</tr>
<tr>
<td>Black and white saki monkey (Pithecia pithecia)</td>
<td>Low</td>
<td>Low</td>
<td>Schwarzkopf and Rylands 1989, Rylands and Keuroghlian 1988</td>
</tr>
<tr>
<td>Three-toed sloth (Bradypus variegatus)</td>
<td>Low</td>
<td>Low</td>
<td>Montgomery and Sunquist 1975 and 1978</td>
</tr>
<tr>
<td>Scarab beetles</td>
<td>Low</td>
<td>High</td>
<td>Klein 1989, Howden pers. commun.</td>
</tr>
<tr>
<td>Euglossine bees</td>
<td>Low</td>
<td>High</td>
<td>Becker et al. 1991, Powell and Powell 1987</td>
</tr>
</tbody>
</table>

*aWidth of pasture which begins to inhibit movement between forest fragments: high is greater than 500 m, medium is 50 to 500 m, and low is less than 50 m.*

*bArea requirement: high is greater than 1000 ha, medium is 10 to 1000 ha, and low is less than 10 ha.*
INDICES: CONTAGION

- extent to which land cover types are aggregated or clumped.
INDICES: DOMINANCE

- degree to which one land cover type dominates the landscape.

HIGH

LOW
INDICES: FRACTAL DIMENSION

- a measurement of the complexity of patch shape.
A. Gap-crossing ability proportion to area requirements

B. Gap-crossing ability less than area requirement.