Extending Models of Edge Effects to Diverse Landscape Configurations, with a Test Case from the Neotropics

JAY R. MALCOLM

The extent, timing, and spatial config-
uration of deforestation in the tropics
varies greatly from one region and
development activity to another. Typically,
forest loss proceeds through "perforation" or
"dissection," in which the original forest
dominates and connectivity is high, to frag-
mentation, where a shift in dominant cover
types occurs and secondary habitats come to
dominate the landscape, to shrinkage and
attrition, where individual primary forest
patches are eroded, become progressively
isolated, and may eventually disappear al-
together (Forman 1995). Superimposed on
this variation in primary forest cover and
connectivity is variation due to the spatial
grain of deforestation (Forman 1995). Aver-
age clearing sizes may vary by three or four
orders of magnitude among regions, even
though the total magnitude of canopy loss
may be similar. For example, at one extreme,
large-scale industrial agriculture such as in
northern Mato Grosso, Brazil, can result in
coarse-grained landscapes, where clearings
(and fragments) may be kilometers or tens of
kilometers across. At the other extreme, se-
lective logging results in a fine-grained mo-
saic of small clearings, treefall gaps, and
roads that are tens of meters across or less
(White 1994b). Although canopy loss in

both coarse-grained and fine-grained land-
scapes is known to have important implica-
tions for the flora and fauna of the remaining
forest (e.g., Laurance and Bierregaard 1997a;
Struhsaker 1997), possible parallels between
the two have rarely been investigated. The
identification of these links is of great im-
portance for conservation. In light of accel-
erating loss and disturbance of tropical
forests, and urgent needs for effective con-
servation guidelines and management tech-
niques, the ability to apply knowledge and
understanding from one type of landscape
transformation to another is welcomed.

Unfortunately, it is not yet clear what gen-
eralizations can be extended from one land-
scape configuration to another, nor is there a
general body of theory that applies to the
full range of landscape configurations. The
major body of theory available for frag-
mented landscapes, namely island biogeog-
raphy (MacArthur and Wilson 1967) and
metapopulation dynamics (Levins 1969,
1970; Hanski 1991), is not directly applica-
ble in perforated or "shredded" forests
(*sensu* Feinsinger 1997) where the remain-
ing primary forest is still broadly contiguous
and interconnected. For example, in an ide-
alized checkerboard landscape, where clear-
ings alternate with forest patches, island

biogeography offers few predictions with respect to fragmentation effects, because each patch is connected at its four corners to a neighboring patch and hence none is a true "island." At the same time, checkerboard landscapes can be expected to result in highly modified forest communities. Many studies in tropical forests have shown that a key effect of deforestation is alteration of the forest habitat close to newly created edges (e.g., Kapos 1989; Malcolm 1994; Ferreira and Laurance 1997; Kapos et al. 1997; Turton and Freiburger 1997; Didham 1997b). Thus, deforestation not only affects the spatial configuration of remnant patches, and hence probabilities of colonization and local extinction, but also results in changes within the forest itself under the influence of altered moisture, light, and wind regimes close to edges.

Because both edge and island processes may be operating simultaneously, the study of human-induced landscape change in the tropics becomes considerably more complicated. The two sets of processes are potentially confounded, for example, because both predict that fragment communities will vary as a function of patch size; in one case because smaller patches have greater perimeter:area ratios than do larger patches and hence have proportionally more edge-modified habitat (Levenson 1981); in the other because smaller populations may be subject to more frequent extinction than larger populations (MacArthur and Wilson 1967). In some cases, one of the two processes may be unimportant or absent. For example, island effects may be irrelevant where connectivity is high or where remnant patches are still close to large contiguous areas of rainforest and populations are periodically rescued by immigration (Brown and Kodric-Brown 1977). As an example, I was able to predict vegetation structure, in-

sect biomass, and the abundance of small mammal species in recently created forest fragments in the central Amazon based solely on information from the edge of continuous forest; effects due to insularization per se were not discernible (Malcolm 1991, 1995, 1997a, 1997b). Similarly, where edge effects are weak or extend only a relatively short distance into the forest, metapopulation dynamics may be of overriding importance in driving community change. Evidently, a comprehensive and quantitative theory of landscape transformation in the tropics must include both edge and island effects.

In this chapter I pursue the overall objective of developing landscape models that can be applied to a broad range of landscape configurations, and hence can be used to provide a firm basis for interlandscape comparisons and for management decisions. I focus on edge effects because of their potential importance in both perforated and fragmented landscapes. First, I examine several edge models that provide an increasingly realistic description of the additivity inherent in edge effects (Malcolm 1994). Second, I apply a recently developed model to the problem of grain size and model a set of hypothetical landscapes where grain size is systematically varied across several orders of magnitude, from scales similar to those in selective logging to those observed during large-scale agricultural development. I was particularly interested in testing agreement between this relatively sophisticated model and a simple nonadditive edge model based only on perimeter:area ratios. Finally, as a possible case study in the transfer of knowledge from one landscape configuration to another, I compared avian communities between two Neotropical sites where the potential importance of edge effects was high, but where the grain size of habitat dis-

turbance differed markedly (a selectively logged landscape versus a fragmented landscape).

Incorporating Additivity into Edge Models

Perhaps the simplest edge model is to imagine a strip of edge-modified habitat parallel to an edge, wherein the edge effect declines with increasing distance from the edge, perhaps in a linear or curvilinear fashion (e.g., Laurance and Yensen 1991). These models are useful in coarse-grained landscapes but are unable to treat the additive effects that must occur in small fragments or fine-grain landscapes where edge effects from neighboring edges overlap extensively (e.g., Kapos 1989; Struhsaker 1997). Thus, they are of little use in many fine-grained tropical landscapes that result from such activities as selective logging and small-scale shifting agriculture. In an earlier paper I developed a more realistic model that incorporated additivity from all nearby edges (Malcolm 1994). I assumed that the total edge effect at a location in the interior of a patch was the sum of "point" edge effects along the edges of the patch, weighted by the distance of the edge points to the location. Symbolically, we denote a fragment as a region Ω on the x-y plane with boundary δ. Defining the vector $\mathbf{b}$ as a point on the boundary, and $\mathbf{i}$ as a point in the interior, the function $g(\mathbf{b}, \mathbf{i})$ gives the point edge effect on whatever community characteristic is being considered at $\mathbf{i}$ due to an edge at $\mathbf{b}$. The total edge effect (E) at $\mathbf{i}$ due to the edge effects is obtained by summing $g(\mathbf{b}, \mathbf{i})$ along the boundary δ, which is accomplished by using line integrals:

$$E = \int_{\delta} g(\mathbf{b}, \mathbf{i}) \, ds$$

where ds is the differential of arc length along the boundary δ.

This model is one-dimensional in that the point edge function is evaluated solely over the fragment perimeter; clearings that abut edges are not directly incorporated. Thus, although a significant improvement over non-additive strip models (Malcolm 1994), the model does not describe edge effects in the most general sense because it fails to directly incorporate variation in clearing widths. A logical extension therefore is to extend the model to two dimensions and to imagine that each point in the surrounding clearings (instead of just the points on boundaries) exerts a "point" edge effect. Thus, a narrow road will have less of an edge effect than a large pasture, because the summation will be over fewer points. For this case, we define a region Σ of clearings in the landscape surrounding Ω, $\mathbf{c}$ as a point in Σ and $h(\mathbf{c}, \mathbf{i})$ as the point edge effect. To accomplish the summation we use a surface integral:

$$E = \iint_{\Sigma} h(\mathbf{c}, \mathbf{i}) \, dS$$

where dS is the differential of surface area over the surface Σ. For an application of this model, see Struhsaker (1997).

An alternate approach to these empirical ones is to directly model the abiotic and biotic processes that are altered at edges (which may not result in simple gradients [Chen, Franklin, and Lowe 1996; Kapos et al. 1997]). Heat conduction is a useful physical process to model because it is a simple, diffusion-like process, incorporates the two-dimensional additivity that realistic edge models must incorporate, and is an important component of a forest's thermal balance (other main components are latent heat and convection). Perhaps equally important, process-based models can serve as potential proxy measures of other processes. From a biodiversity standpoint, heat flow models might be useful because they may be able to capture the approximate spatial behavior of several other types of edge-induced habitat

changes, such as changes in understory density and insect biomass. They may prove useful as statistical models with parameters that can be estimated in one landscape and subsequently used to predict edge effects in others. Thus, rather than being restricted to the study of the forest temperature or its role in ecosystem processes, heat conduction may serve as a useful proxy measure of edge-induced disturbance gradients and associated community change.

Briefly, in a model of heat conduction, a landscape is envisioned as a two-dimensional grid composed of cells with various thermal properties (Malcolm 1998). If we consider heat flow across a single cell, the rate of heat transfer, Q, from the hotter side of the cell to the cooler side is directly proportional to: (1) the surface area of the cell, A (which is normal to the direction of heat flow); (2) the temperature difference across the cell, $(T_i - T_0)$; and (3) the inverse of the wall thickness, L (Karlekar and Desmond 1977). That is

$$Q \alpha \frac{A(T_i - T_0)}{L} \quad \text{or} \quad Q = \frac{kA(T_i - T_0)}{L}$$

where k is a proportionality constant equal to the thermal conductivity of the cell. Heat flow through a composite of two cells with differing conductivity is obtained in a straightforward way (Malcolm 1998).

To model two-dimensional unsteady heat flow in the full landscape, a finite difference grid is established for time as well as for space, and the rate of heat flow during a small interval of time (Δt) is modeled among cells that have centers spaced at regular intervals of Δx. According to the principle of energy conservation, the net rate of energy arriving at a cell center during Δt is equal to the rate of change of internal energy of the cell, which is a function of the temperature of the center at time $t+\Delta t$, the temperature at time t, and the mass density and specific

heat of the cell. Therefore, the temperature of a cell at time $t+\Delta t$ can be expressed as a function of: (1) Δx; (2) temperature differences with the surrounding cells at time t; (3) the thermal conductivities of the surrounding cells; and (4) the mass density, specific heat, and thermal conductivity of the cell (see Malcolm [1998] for details). Thus, the temperature in the landscape can be followed over time.

Edge Effects as a Function of Landscape Grain

METHODS

To design hypothetical landscapes, I used cells that were 10 m on a side (Δx) within grids that encompassed 10,000 ha (1,000 × 1,000 cells). Three grain sizes were simulated by varying the size of the clearings in a landscape. To approximate individual treefall gaps, the finest-grained landscapes had clearings that were 10 × 20 m (i.e., two adjacent grid cells). Clearing sizes in the other two grain sizes were 100 × 100 m and 1000 × 1000 m. Clearings were oriented either north-south or east-west and were created at randomly determined locations on the grid until the total area of cleared forest comprised 10, 20, 30, 40, or 50 percent of the whole grid. Fifteen landscape grids were created in total (three clearing sizes for each of five levels of deforestation). Because of the relatively large size of the grids, one per combination of clearing size and deforestation extent was sufficient to provide a precise description of temperature changes.

Cells in the clearings were assumed to have the thermal diffusivity and conductivity of air ($\alpha = 0.2$ m²/s, $k = 0.02$ W/°C [Karlekar and Desmond 1977]). Thermal diffusivity and conductivity in forested cells were set to 0.053 m²/s and 0.075 W/°C, respectively (see Malcolm 1998). Over the

course of a day (see below), these parameters resulted in pronounced edge effects up to 100 m deep along the borders of large gaps, in general agreement with experiments in the central Amazon (see Malcolm 1994).

Heat conduction was simulated during the course of a single day from 0600 to 1800 h. Shading served to control radiative input and was incorporated by assuming that the sun rose at 0600 h in the east and set at 1800 h in the west and moved only in the east-west dimension (zero declination). Thus, shading occurred only in the east-west dimension. The forest was assumed to be 30 m high and to act as a complete barrier to radiative heat input. At the start of each clock interval, clearing cells that were at least partly in the sun were "turned on" to 35° C —i.e., they acted as heat sources. All cells were set to 20° C at the start of the simulation, and except for unshaded cells that were reset to 35° C at the start of a clock interval, cell temperatures were allowed to freely vary. To calculate shading along the periphery of the landscape grid, I assumed that the grid was surrounded by forest. For heat conduction calculations, forested cells outside the grid were neutral—i.e., they had the same temperature as adjacent grid cells. In all simulations, the time interval (Δt) was 120 s. For analysis, cell temperatures at the start of the time intervals were averaged over the 360 intervals in the day.

Results

Edge effects in the simulations varied both quantitatively and qualitatively as a function of the extent and grain of deforestation. Average forest temperature (and hence the proportion of edge-modified habitat) increased with the extent of deforestation, but decreased with increasing grain size (fig. 27.1a). Deforestation of only 10 percent of the landscape using 1 ha clearings resulted in average forest temperatures equivalent to

50 percent deforestation using 100 ha clearings. Similarly, 10 percent deforestation using 0.02 ha clearings resulted in average forest temperatures equivalent to 40 percent deforestation using 1 ha clearings. In addition to these relative effects, grain size also had a strong effect on the absolute amount of edge-modified habitat in the remaining forest. For example, holding deforestation constant at 10 percent, the amount of forest that remained at less than 21° C ("interior" habitat) varied from approximately 8,400 ha under coarse-grained deforestation, to approximately 7,000 ha under medium-grained deforestation, to less than 3,700 ha under fine-grained deforestation (fig. 27.2). In other words, at least 3,000 ha of interior habitat could be maintained under approximately 50 percent deforestation in the coarse-grained landscape, 30 percent deforestation in the medium-grained landscape, and 10 percent deforestation in the fine-grained habitat. These results make intuitive sense because, given the same amount of deforestation, finer-grain landscapes will have more forest edges and hence more pervasive edge effects.

The opposite patterns held true for temperatures in forest clearings (figs. 27.1b, 27.3). Relative to the other landscapes, clearings in the fine-grained landscape on average had cooler conditions more typical of the closed forest environment. Thus, the fine-grained landscape on average had highly edge-modified (warm) forest, but relatively moderated (cool) clearings due to shading. In an absolute sense, average forest temperatures in the fine-grained landscape closely approximated average temperatures in the clearings; hence in comparison to the other landscapes, its average temperature profile was the most homogeneous. However, this homogeneity over the whole landscape belied significant heterogeneity within the forest and clearings themselves (figs. 27.2 and
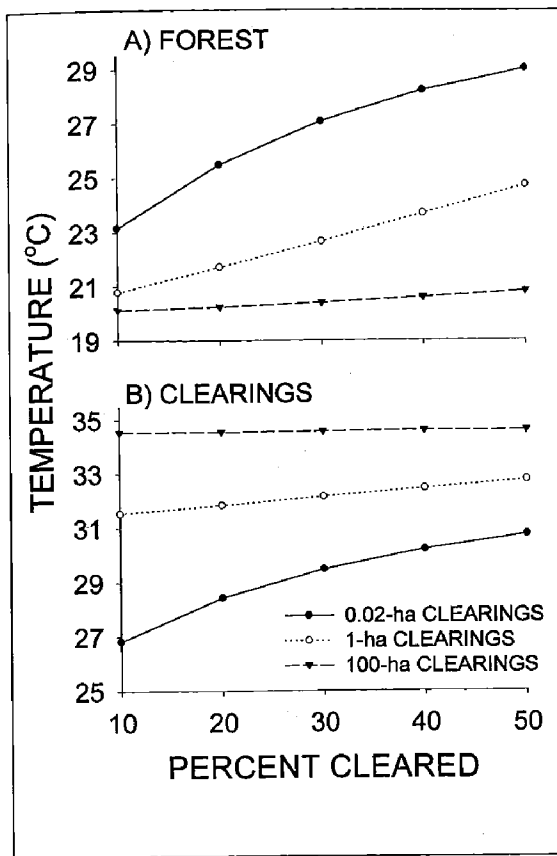
Fig. 27.1. Average temperatures of grid cells in forest (A) and clearings (B) in simulated tropical landscapes. Clearings of one of three sizes were used to deforest 10, 20, 30, 40, or 50 percent of the landscape. Heat conduction was simulated during the course of a 12 h day, with unshaded grid cells in clearings acting as heat sources. Cell temperatures were recorded at 120 s intervals, and were averaged over the 360 intervals in the day.
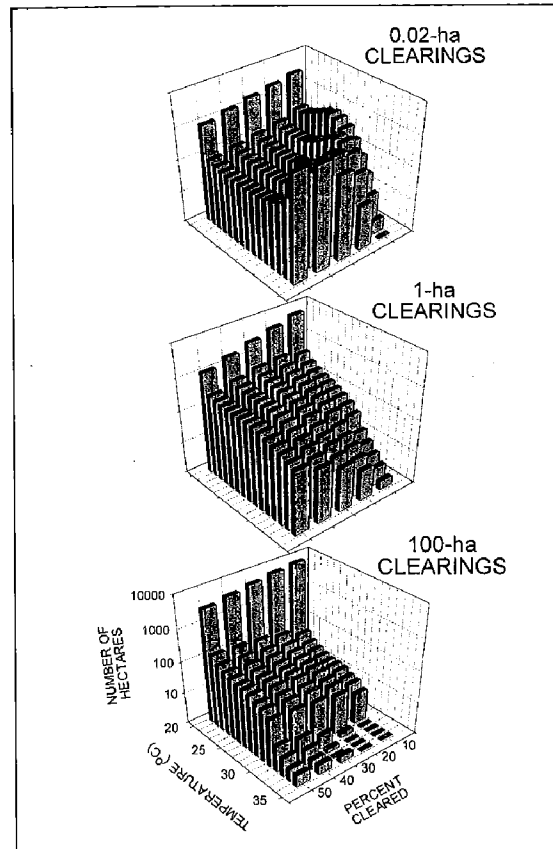

Fig. 27.2. Frequency distribution of temperatures of forested land in simulated landscape grids. Temperature values were truncated to create the plot intervals (e.g., 20.9 = 20° C). For each clearing size, deforestation varied from 10 to 50 percent. Each grid consisted of 10,000 ha in total.

27.3). At medium (20 to 30 percent) levels of deforestation in the fine-grained landscape, primary forest was composed of approximately equal areas of highly edge-modified forest and interior forest, whereas at these levels of deforestation in the coarser-grained landscape, the primary forest was mostly interior forest. Similarly, cells in forest clearings in the fine-grained landscape were about evenly split between hot and cold conditions, whereas clearings in the coarser-grain landscapes were characterized by hot conditions. Thus, the variance among tem-

peratures within either forest or clearings in the fine-grained landscape was greater than in the other landscapes.

The effects of additivity were especially evident in the fine-grained landscape. In the coarser-grained landscapes, average forest temperate was a linear function of gap perimeter:forest area ratios, indicating that simple strip-based edge models were sufficient to describe the overall patterns (fig. 27.4). In contrast, in the fine-grain landscape, where edge effects from neighboring gaps often overlapped, the relationship be-
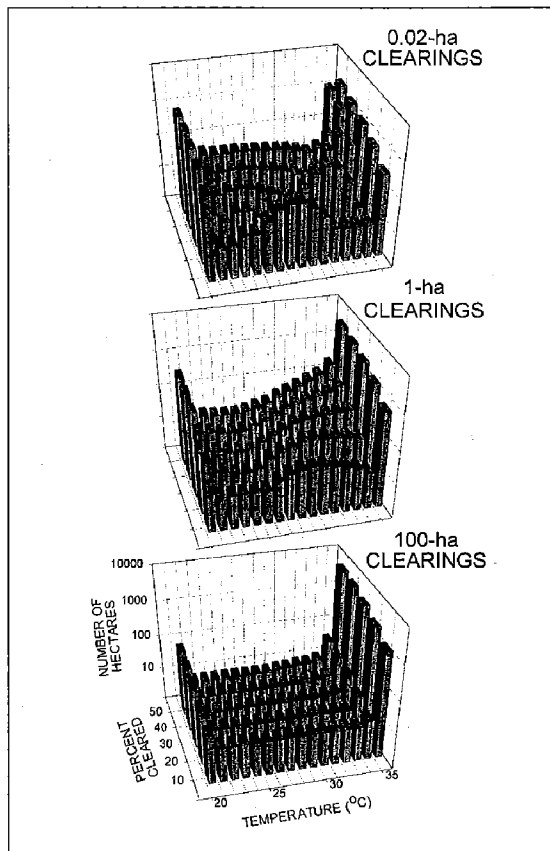
Fig. 27.3. As fig. 27.2, except that temperatures are of clearings.

tween forest temperature and perimeter:area ratios was curvilinear. In addition, the curve for the fine-grained landscape was below an extrapolation of the coarser-grained curves, indicating that for equal perimeter:area ratios, the fine-grained landscape had more extensive heating (i.e., more severe edge effects). The shape of the curve (concave downward) indicated that the increase in edge effects with increasing deforestation was disproportionately high when the absolute amount of deforestation was low. I have noted the serious conservation implications of this relationship before (Malcolm 1998); it suggests, for example, that the most rapid changes in the forest environment as a function of increased logging intensity will be at low harvest intensities.

Forest Bird Communities in Selectively Logged and Fragmented Landscapes

METHODS

The dimensions of the forest clearings in Thiollay (1992) and Bierregaard and Love-joy (1989) differed by nearly two orders of magnitude. In the selectively logged landscape studied by Thiollay, gaps were usually 25 m across or less, although they were often long (access roads) (see fig. 1 in Thiollay [1992]). At the BDFFP in the agricultural landscape of the central Amazon, clearings were 2,000 m or more across, and the 1 and 10 ha fragments censused were at least 100–800 m from other forest (see fig. 4.1; also see fig. 2 in Malcolm [1994], which included many of the same sites that Bierregaard and Lovejoy [1989] censused).

Despite this difference in the grain size of canopy openings, plots in both studies were in areas that were presumably strongly influenced by edge effects. In the BDFFP study, obvious biotic and abiotic edge effects extended at least 100 m into fragments, and the centers of 1 ha fragments were influenced by additivity from all four edges (see fig. 29.1; Kapos 1989; Malcolm 1994; Laurance, Bierregaard, et. al 1997). Assuming a 100 m wide strip of edge-modified forest, 10 ha fragments contained only 1.35 ha of "interior" forest. I have argued that changes in small mammal communities in these fragments in the first ten years after deforestation were entirely attributed to edge effects (Malcolm 1997a). Although no information on the magnitude of edge effects is available in Thiollay's (1992) study, all of the forest in his illustration was within 100 m of a road, log-gathering area, or treefall gap. Although the logging was highly selective, it resulted in considerable damage (Thiollay 1992). On average, 3.04 trees were cut per hectare, but at one to two years later, an additional 10 to 43/ha had fallen (versus 0.7–1.2 treefalls/ha/yr in nearby primary
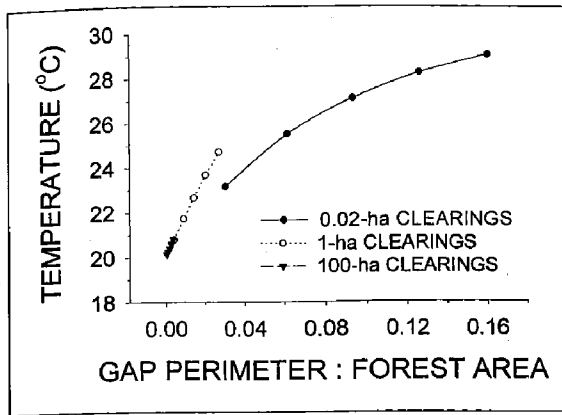
Fig. 27.4. Average temperatures in forested grid cells as a function of the gap perimeter/forest area ratios in the landscape. Results are shown for fifteen landscape grids (five levels of deforestation for each of three clearing sizes).

forest). At ten years after logging, transects in logged forest consisted of 41.9 percent gaps (versus 12.8 percent in primary forest). Thus, the potential for additive edge effects was high.

I examined two aspects of the bird community: bird species richness (as reported by the authors) and abundances of the fifty-three species in common to the two studies (see appendices in Thiollay [1992] and Bierregaard and Lovejoy [1989]). I classified each species as showing positive, negative, or no change in abundance in response to the landscape modification, and the agreement in classification between the two studies was compared with a null model based on chance agreement. A positive response was assigned if a species was more abundant in both of the disturbed habitats in a study (1 and 10 ha fragments in the case of Bierregaard and Lovejoy [1989] and 1- and 10-year-old forest in the case of Thiollay [1992]) than in undisturbed primary forest. A negative response was assigned if the species was less abundant in both disturbed habitats than in continuous forest. A species was judged to have shown no response if abundance in undisturbed forest was inter-

mediate between that in the two disturbed habitats.

RESULTS

In both studies, the landscape transformation resulted in a marked decline in species richness (fig. 27.5). Moreover, individual species tended to respond in the same way in the two sites (fig. 27.6). Most species (44 of 53) showed a negative response to the landscape transformation in at least one of the studies (hence the decline in species richness), but more important, of the 24 species affected by the landscape transformation in both studies, the sign of the impact (either positive or negative) was the same for 17 ($P = 0.06$, two-tailed binomial test).

DISCUSSION

The additive edge models described here are an improvement over previous models because they can be more easily applied to a broader range of landscape configurations. Simple strip-based models are inaccurate whenever edge effects overlap, which is a common occurrence where forest clearings are relatively close to one another (as investigated here) or where edge effects extend far into the forest (as investigated by Malcolm [1998]). These results suggest that edge effects may provide a useful metric of grain size. A relatively coarse-grained landscape under one edge environment will be considered finer-grained when edge effects are stronger, and vice versa. In turn, a given landscape configuration may have different grain sizes from the perspective of different processes and organisms, depending on the depths of edge effects.

The similar responses of the bird community under two different grains of deforestation support the possibility that edge effects in some cases may provide a common
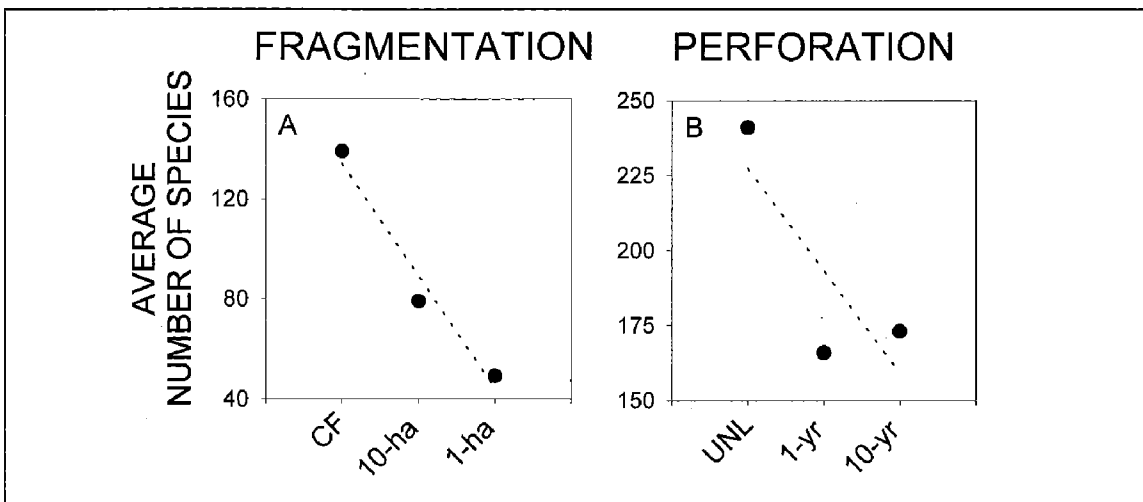
Fig. 27.5. Avian species richness in continuous forest (CF) and 10 and 1 ha forest fragments in the central Amazon (Bierregaard and Lovejoy 1989) and in French Guiana (UNL = unlogged; 1 yr = 1 year after logging; 10 yr = 10 years after logging [Thiollay 1992]). In each graph, edge-modified sites are to the right of undisturbed forest sites.

currency for understanding the impacts of diverse landscape change. Thus, edge models may provide a quantitative framework for transferring understanding and empirical results from one landscape to another. I did not undertake a quantitative test here because I did not have information on the spatial context of all of the individual plots. However, as a rough approximation, fragments in the large agricultural clearings at the BDFFP site in the central Amazon probably corresponded in size to residual forest in the simulated medium-grained, high deforestation landscape, whereas edge effects at the selectively logged sites probably corresponded to the fine-grained, low deforestation simulation. In my simulations, average forest temperatures in these two situations were approximately equal (see fig. 27.1), suggesting that if census sites randomly sampled the forest, similar magnitudes of community change would be observed in the two landscapes. More detailed predictions would require detailed information on census locations.

The above very approximate analysis begs the question: What sort of information is required in order to develop more quantitative

predictions of the extent of edge-induced habitat change? Previously, I used one landscape configuration to provide the parameters for an edge model that was subsequently applied to other landscape configurations (Malcolm 1994). In that study, I used the linear edges of continuous forest to provide the parameters for the model and then used the resulting parameter estimates to predict edge effects in 1 and 10 ha fragments. To apply this approach to the two-dimensional model described here, information on a more diverse array of clearing sizes is desired. An ideal experimental design would be one in which censuses are undertaken in forest strips of various widths isolated by clearings of various widths (including narrow roads and large clearings). A further refinement would be to extend the univariate approach in Malcolm (1994), where I examined understory and overstory vegetation density as a function of the edge gradient, to a multivariate community approach.

Detailed predictions of edge effects provide a baseline from which to investigate other processes acting in the landscape. Up to approximately 10 years after deforestation, and perhaps beyond, small mammal
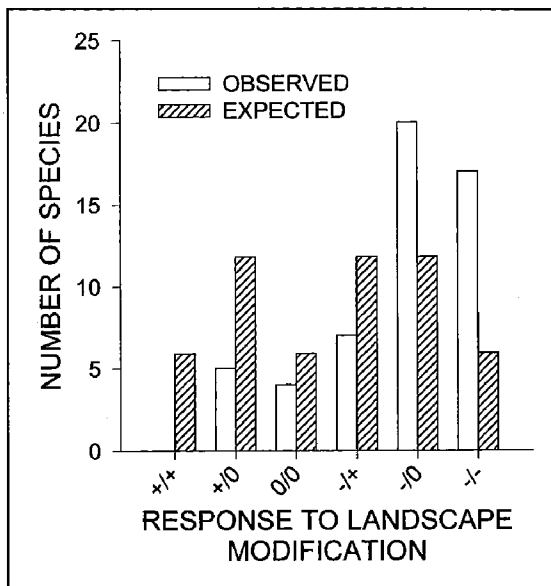
Fig. 27.6. Frequency of fifty-three bird species in common to Bierregaard and Lovejoy (1989) and Thiollay (1992) that showed a positive response to landscape modification in both studies (+/+), one study but not the other (+/0), neither study (0/0), a negative response in one study but a positive response in the other (+/-), etc. Shaded histograms are null expectations under the assumption that any response is equally likely.

populations at the BDFFP site appear to be at levels expected solely from edge-induced habitat change, presumably because the fragments periodically received immigrants from nearby continuous forest (Malcolm 1991). With time, as the fragments become further isolated, their communities can be expected to evolve not only as a function of direct and indirect edge-based change within the fragments, but also because of decreased possibilities for colonization from source populations in primary forest. Thus, species that avoid secondary and edge habitats (such as the wooly opossum [Caluromys philander] and the rice rat [Oryzomys macconnelli]) can be expected to eventually disappear from the fragments (Malcolm 1991). Simplification and loss of secondary forests in the matrix can be expected to lead to simplification in the matrix small-mammal community (Malcolm 1995) and to further changes in the pool of immigrants. This deterioration in the original small-mammal community may have already taken place in the Atlantic rainforest of Brazil, an ecosystem that has been highly modified by human activities (see Fonseca 1988). A predominance of marsupials, even in large primary forest tracts, may be indicative of these changes on a landscape level (Fonseca 1988).

Similar expectations with regard to changes in fragment communities may apply in Africa as well. Indications are that African rainforests are strongly convergent with Neotropical ones, both in the importance of vegetation structure as a correlate of small mammal community structure and with respect to the apparent paucity of small mammal interior-forest specialists (Malcolm 1997a; Malcolm and Ray, in press). In addition to edge-induced habitat changes and altered immigration and extinction probabilities comes the possibility of invasion by savanna species and other exotics as modern human-created "savannas" interconnect naturally occurring ones. The extent to which these invasions will occur in the Neotropics is unknown, but in Africa degradation of primary forest habitats is frequently accompanied by a decrease in the primary-forest rodent fauna and increases in taxa associated with anthropogenic and savanna habitats (e.g., Rahm 1972; Happold 1975, 1977; Adam 1977; Iyawe 1989; Okia 1992; Struhsaker 1997; Malcolm and Ray, in press).

The simulations presented here show that the grain size of clearings (as defined relative to the depth that edge effects extend) has important implications for the resultant spatial distribution of edge-modified habitats, both in forest and in clearings. In fine-grained landscapes, such as those resulting from selective logging and small-scale shifting agriculture, the overall shift in the forest environment is to conditions more typical of

clearings. At the same time, despite the overall convergence in forest and gap environments, both cover types come to contain habitat extremes that are rare in coarser-grained landscapes. On one hand, the relatively benign conditions in some clearings hold out hope for the regeneration of shade-tolerant forest tree species. However, because of additive neighborhood effects, areas of extremely edge-modified forest are also common.

The implications of this intimate juxtaposition of extremes in fine-grained habitats is unknown, but because of the potential for changes in species interactions at small spatial scales, it does not bode well for many forest species. The counterintuitive loss from selectively logged forests of species that specialize on treefall gaps in primary forest (e.g., Iyawe 1989; Thiollay 1992) may be a result of this juxtaposition—although suitable gaps are present, suitable nearby forest is not. The nonlinear nature of the change in habitat characteristics with increasing deforestation moreover suggests an especially rapid change in interior (cool) conditions at low absolute quantities of deforestation (*contra* Johns 1997). Highly edge-modified forest as a result becomes widespread throughout the landscape. Struhsaker (1997) suggested that these areas of intense edge effects may act as foci for further deterioration in the forest environment. In even moderately logged African forests, elephants and rodents were attracted to areas where gap densities were high, which may have resulted in a positive feedback that led to further deterioration of the forest environment. Thus, although small clearings may seem benign (e.g., Dale et al. 1994), the edge effects that they create can quickly sum up to create disproportionate change.

Although the simulations here seem to suggest that with respect to edge effects in the remaining primary forest, coarse-grained deforestation is preferable to fine-grained deforestation, two critical factors must be kept in mind. First, although the idea of large forest remnants is an attractive one, rarely do they remain large for long. Instead, a frequent progression in coarse-grained landscapes is shrinkage and attrition of the remaining fragments until only heavily edge-affected, isolated fragments remain—a worst-case scenario from a conservation viewpoint. Second, compared to coarse-grained landscapes, conditions in the clearings of fine-grained landscapes are benign. These clearings will be more easily colonized by forest-dwelling species than the radically altered habitats created during large-scale clear-cutting. The conservation message of this paper instead is to point out the potential dangers of edge effects, even in fine-grained landscapes. A key conservation and management tool is to reduce edge effects whenever and wherever possible, by maintaining large reserves and corridors (on the order of tens or hundreds of kilometers in width), and by reducing canopy damage during selective logging, through low harvesting volumes and careful logging techniques (Johns, Barreto, and Uhl 1996).

The model presented here provides a starting point for simulations of edge effects under a broad range of landscape configurations. It is an improvement over existing models (e.g., Chen, Franklin, and Spies 1993; Chen, Franklin, and Lowe 1996) because it incorporates the additivity that is critical in fine-grained landscapes. My comparisons of avian communities between the two Neotropical sites suggest that edge models such as this one will be useful in extending knowledge from one landscape configuration to others. These models provide an important addition to metapopulation models, which for convenience often break landscapes into "suitable" or "unsuitable" patches (e.g., Bascompte and Solé 1996). In reality, processes such as edge effects create a gradient of habitat conditions and a complex

mosaic of abiotic and biotic change (Chen, Franklin, and Lowe 1996). Models based solely on the configuration of canopy cover that do not incorporate abundances of certain habitat types such as interior habitat may lead to incorrect estimates of extinction thresholds.

Conservation Lessons

1. An important conservation strategy appears to be to reduce edge effects wherever and whenever possible. This can be accomplished by establishing reserves and corridors that are at least tens of kilometers across. In fine-grained landscapes (many small clearings and fragments), the number and sizes of canopy gaps should be minimized; for example, by harvesting small timber volumes and by practicing careful logging techniques.

2. Edge effects are additive and can be particularly strong near corners of fragments or in thin corridors. Additivity is especially important in fine-grained landscapes, such as in selectively logged forests where clearing and fragment sizes are small, but where edge effects from neighboring gaps overlap. In these landscapes, simple edge models based on perimeter:area ratios are inaccurate — they underestimate the magnitude of edge effects.

3. A model of heat conduction can be used as a proxy to investigate additive edge-based disturbances in tropical landscapes. Edge effects in simulated landscapes varied both quantitatively and qualitatively as a function of the extent and grain of deforestation. The proportion of edge-modified forest habitat increased with the extent of deforestation, but decreased with increasing grain size. However, relative to other landscapes, clearings in the fine-grained landscapes on average had conditions more typical of the closed forest environment. In comparison to the other landscapes, average conditions in forest and clearings in fine-grained landscapes were more similar.

4. This homogeneity over the whole fine-grained landscape belied significant heterogeneity within the forest and clearings themselves. The variance among conditions within either forest or clearings was greater in the fine-grained landscapes than in the other landscapes. The results of this intimate juxtaposition of extremes are unknown but may have important conservation implications.

5. In fine-grained landscapes, the relationship between the average magnitude of edge effects and the magnitude of deforestation indicated that the increase in edge effects with increasing deforestation was disproportionately high when the absolute amount of deforestation was low. Thus, the most rapid changes in the forest environment as a function of increased logging intensity may be at low harvest intensities. Edge effects from neighboring gaps may quickly sum up to create disproportionate change.

6. Additive edge models provide an important addition to metapopulation models. Estimates of habitat connectivity based solely on the configuration of canopy cover may seriously overestimate connectivity for species that rely on interior forest conditions.

Acknowledgments