

MODELING BIODIVERSITY DYNAMICS IN COUNTRYSIDE LANDSCAPES

HENRIQUE M. PEREIRA^{1,3} AND GRETCHEN C. DAILY²

¹*Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Lisboa, Edifício C2, Campo Grande, 1749-016 Lisboa, Portugal*

²*Center for Conservation Biology, Department of Biological Sciences, 371 Serra Mall, Stanford University, Stanford, California 94305-5020 USA*

Abstract. The future of biodiversity hinges to a great extent on the conservation value of countryside, the growing fraction of Earth's surface heavily influenced by human activities. How many species, and which species, can persist in such landscapes (and analogous seascapes) are open questions. Here we explore two complementary theoretical frameworks to address these questions: species–area relationships and demographic models. We use the terrestrial mammal fauna of Central America to illustrate the application of both frameworks. We begin by proposing a multi-habitat species–area relationship, the countryside species–area relationship, to forecast species extinction rates. To apply it, we classify the mammal fauna by affinity to native and human-dominated habitats. We show how considering the conservation value of countryside habitats changes estimates derived from the classic species–area approach. We also examine how the z value of the species–area relationship affects extinction estimates. Next, we present a framework for assessing the relative vulnerability of species to extinction in the countryside, based on the Skellam model of population dynamics. This model predicts the minimum area of contiguous native habitat required for persistence of a species, which we use as an indicator of vulnerability to habitat change. To apply the model, we use our habitat affinity classification of mammals and we estimate life-history parameters by species and habitat type. The resulting ranking of vulnerabilities is significantly correlated with the World Conservation Union (IUCN) Red List assessment.

Key words: *biased random-walk; countryside biogeography; critical patch; extinction; population growth rate; PVA; reaction-diffusion PDE; species–area relationship.*

INTRODUCTION

Historical change in the richness and variety of life has long held the fascination of scientists and philosophers, largely at the abstract conceptual level. Major elements of current understanding trace back to eighteenth-century scientists, and even to Aristotle (Brown and Lomolino 1998). Today, long-standing conceptual frameworks for forecasting biodiversity change are coming under careful reexamination (Lawton and May 1995, Daily et al. 2003).

Concerns over the societal impacts of biodiversity change are driving new research into a series of classic questions (Daily 2001). Assuming human impacts on the biosphere intensify as currently projected, how many, and which, constituents of Earth's biota might survive? What species traits confer a survival advantage? What time course of biodiversity change is likely to pertain at local, regional, and global scales?

Here, we explore two complementary theoretical frameworks for projecting how many and which species (with which attributes) might survive habitat alteration, the main driver of biodiversity loss today (Baillie et al. 2004, Sala et al. 2005). The first framework, the species–area relationship, has been widely employed to predict extinction rates (Reid 1992, May et al. 1995, Pimm et al. 1995). We briefly present the classic theory and then modify it to account for the potential conservation value of countryside habitat, areas whose ecosystem properties and processes are strongly influenced by humanity (Daily et al. 2001). While the species–area relationship predicts how many species are likely to be lost because of habitat alteration, it says nothing about which species will disappear. In order to address this second problem we explore a framework based on demographic population models, particularly the reaction–diffusion model originally proposed by Skellam (1951), and recently extended to incorporate individual behavior at habitat edges (Cantrell and Cosner 1999, Pereira et al. 2004).

We illustrate how these two modeling frameworks can be applied using the terrestrial mammal fauna of Central America, a region with high rates of habitat alteration (Global Forest Resources Assessment 2001) and a rich fauna for which we still have limited knowledge. The use of demographic models to assess the relative vulner-

Manuscript received 21 January 2005; revised 15 August 2005; accepted 22 August 2005. Corresponding Editor: O. E. Sala. For reprints of this Special Feature, see footnote 1, p. 1875.

³ Present address: Department of Civil Engineering, Instituto Superior Técnico, Av. Rovisco Pais, 1049-001 Lisboa, Portugal. E-mail: hpereira@stanfordalumni.org

ability of species has been limited by the difficulty in compiling the required life-history parameters (Pereira et al. 2004). We show how this can be overcome using allometric relationships to complement databases of life-history traits.

A FRAMEWORK BASED ON THE SPECIES–AREA RELATIONSHIP

One of the few relationships that has reached the status of a law in ecology is the species–area relationship or SAR (Brown and Lomolino 1998). It states that the number of species S in a sampling area of size A , is given by the following power law:

$$S = c \times A^z \quad (1)$$

where c is a constant that depends on the taxonomic group and the region being studied and z is a constant that depends on the sampling regime and scale (Rosenzweig 1995). When sampling different islands of an archipelago or other types of habitat isolates (mountaintops, forest fragments, etc.), z typically takes values from 0.25 to 0.35. The z value is lower when the sampling units are not isolated. In the case of samples coming from nested areas in a given region, z values typically range from 0.12 to 0.18 (but see Crawley and Harral 2001). By contrast, when the samples correspond to different biogeographic regions with separate evolutionary histories, z can be as high as one.

Several studies have used the SAR to predict extinction rates from tropical deforestation rates (Reid 1992, May et al. 1995, Pimm et al. 1995). These estimates are based on a local analysis of the SAR, where Eq. 1 is Taylor-expanded in relation to area:

$$S(A - \delta A) \approx c \times A^z \times (1 - \delta z). \quad (2)$$

For a given proportional decrease in tropical forest area δ , the proportional decrease in the number of species is given by

$$\frac{S(A) - S(A - \delta A)}{S(A)} = \delta z. \quad (3)$$

A z value of 0.25, typical of the island SAR, has been used in most estimates of extinction rates (Reid 1992, May et al. 1995, Pimm et al. 1995). Current annual rates of tropical deforestation are about 0.6–0.8% (Global Forest Resources Assessment 2001, Achard et al. 2002). We thus arrive at an annual rate of species extinctions of 0.1–0.25%. Considering that about two-thirds of the extant ~5000 species of terrestrial mammals are endemic to biogeographic realms covering tropical regions (Baillie et al. 2004), the SAR approach yields an estimated rate of committing three to eight mammal species to extinction per year. This is much higher than the one to two mammal extinctions per thousand years observed in the Cenozoic fossil record (Regan et al. 2001), and higher than the 83 mammal extinctions

registered in the last four centuries (Groombridge and Jenkins 2002).

Two primary assumptions of the SAR approach are that remaining native habitat is uniform (i.e., species are distributed at random within it) and continuous (i.e., unfragmented). The first assumption can cause an underestimate of extinction rates when the habitat loss occurs predominantly in high diversity areas (e.g. biodiversity hotspots) and the habitat that remains has low species diversity. The second assumption causes an underestimation of extinction rates because of nestedness patterns (Boecklen 1997), which imply that a set of habitat fragments has lower species diversity than a single habitat patch which has an area equal to the sum of those fragments. The underestimation of extinction rates that these assumptions cause is doubtless offset, to an unknown degree, by a third primary assumption, that modified habitat is uniformly hostile and sterile. The SAR approach is limited in assuming equilibrium, revealing an expected eventual number of extinctions but nothing about the dynamic time-course of extinction. Further, it assumes that all species are equal, thus revealing nothing about the relative vulnerabilities of species to extinction. In spite of these and other limitations (Reid 1992; also Simberloff 1992, Rosenzweig 2001), with judicious tailoring to specific regions in the world, the SAR approach has proved remarkably accurate in predicting the disappearance or endangerment of locally endemic species, particularly those restricted to native habitat (e.g., Pimm and Askins 1995, Brooks and Balmford 1996, Cowlishaw 1999).

In the next subsections, we discuss how to improve SAR-based estimates of extinction rates by examining how to include the conservation value of human-dominated habitat, and the implications of different z values choices.

The countryside species–area relationship

Calculation of extinction rates based on Eq. 3 assumes that no native species can survive outside of native forest habitats. However, we know that many native species use nonnative (e.g., agricultural) habitats. For instance, at least half of terrestrial Costa Rican bird species and non-flying mammal species use agricultural habitats (Daily et al. 2001, 2003). In this section, we propose a generalization of the SAR, the countryside SAR, that accounts for a differential use of habitats by different species groups.

Let m be the number of species groups in our province. Each group of species is characterized by having similar habitat preferences. Let h_{ij} be the affinity of species group i to habitat type j . We propose that the countryside SAR for the group i is

$$S_i = c_i \times \left(\sum_j h_{ij} A_j \right)^z \quad (4)$$

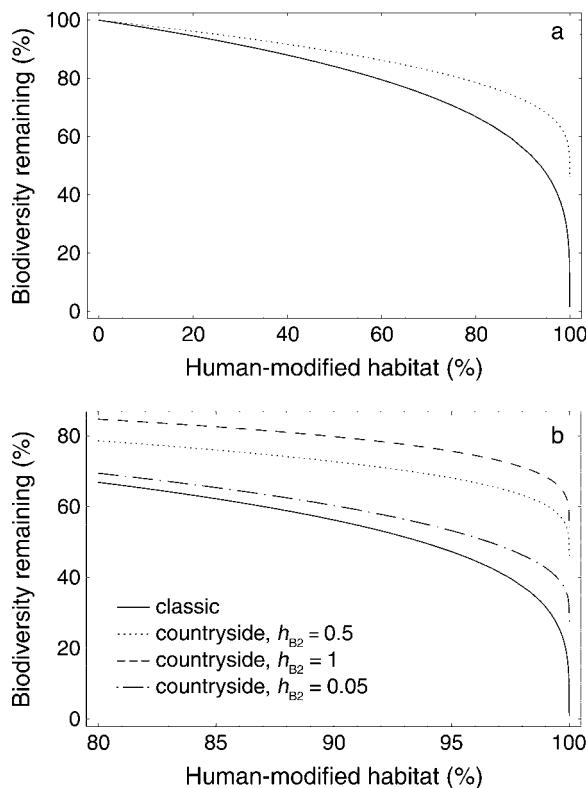


FIG. 1. Comparison of predictions of biodiversity loss based on the countryside SAR (species–area relationship) and the classic SAR. Other parameters are $z = 0.25$, $h_{A1} = 1$, $h_{A2} = 0$, $h_{B1} = 1$, $h_{C1} = 1$, $h_{C2} = 1$, $c_1 = 46\%$, $c_2 = 51\%$, and $c_3 = 3\%$. See *A framework based on the species–area relationship: The countryside species–area relationship* for a description of the species groups A–C.

where A_j is the area covered by habitat j . Note that the affinity h_{ij} can be seen as the proportion of area of habitat j that can be effectively used by group i . The total number of species in the landscape is then

$$S = \sum_{i=1}^m S_i. \quad (5)$$

To illustrate how the countryside SAR modifies the estimates of extinction rates, we apply it to the terrestrial non-volant mammals of Central America ($N = 178$). Using the descriptions of habitat and habits of Reid (1997), and observations reported in Daily et al. (2003), we classified all but nine of the mammals of Central America and Southeast Mexico into three habitat affinity groups (Appendix):

Group A.—Mammals that use only native habitats (78 species). In ambiguous cases, we classified species conservatively, so that any bias in assessing their vulnerability is in the direction of more vulnerable. Thus, strictly arboreal species that nonetheless occur (i.e., can be seen) in heavily deforested regions are included in this group. Species that occur in secondary

forest are also included if all other habitat types they use are unambiguously native.

Group B.—Mammals that use both native and human-modified habitats (86 species). Species in this group occur in at least one native habitat and one human-modified habitat. We conservatively assigned to this group all species that occur both in unambiguously human-modified habitats (such as cropland) and in secondary forest, but in no other native habitat types.

Group C.—Mammals that use only human-modified habitats (five species). Species that use secondary forest are not included.

We conservatively assume zero affinity of group A for human-modified habitat. For group B, we generally assume that the affinity for human-modified habitat is half of the affinity for native habitat, and then test other values. Finally, we assume that the affinity of group C for human-modified habitat is at least as large as for native habitat. This last assumption is equivalent to saying that the number of species in group C is independent of the amount of native habitat lost.

The classic SAR predicts that no biodiversity remains when all native habitat is lost (Fig. 1). By contrast, the countryside SAR predicts that considerable diversity remains after all native forest is lost (Fig. 1a). The amount remaining depends on the proportions of species in each group and on their affinity for human-modified habitats. In the extreme case of equal affinities of group B for native and human-modified habitats, about 54% species remain after all native forest is lost (Fig. 1b). At the other extreme, if the affinity of group B for human-modified habitats is only 5% of the affinity for native habitats, only 27% of the original species remain (Fig. 1b). There is a nonlinear relationship between the reduction in group B's affinity for the agricultural lands and maximum biodiversity loss: a reduction in the affinity for human-modified habitat of 50% reduces equilibrium species diversity by only 11%.

The differences between the two curves are relatively small for moderate native habitat losses (Fig. 1a). However, as the amount of native habitat remaining approaches zero, the countryside SAR departs from the classic SAR significantly. Note that both in the classic SAR and in the countryside SAR, as the proportion of human-modified habitat increases more species are lost for the same absolute amount of habitat converted (more species are lost when the landscape goes from 80% to 90% human-modified habitat than when the landscape goes from 0% to 10% conversion), meaning that the last fragments of remaining habitat have an extremely high value for the conservation of biodiversity. The conservation value of the remaining habitat is the negative of the derivative of the SAR curves, and it increases faster than exponentially with decreasing native habitat.

The choice of a z value

We do not know which type of SAR best describes biodiversity loss caused by habitat conversion. Rosen-

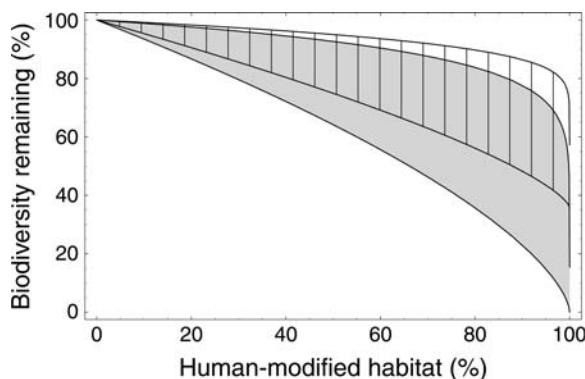


FIG. 2. The effect of the uncertainty of the z values on the predictions of the biodiversity loss based on the countryside SAR (region with vertical lines) and the classic SAR (gray region). For each type of SAR, we calculated the upper and lower boundaries of the SAR based on the 95% CI for island z values, $z_{95\%} = [0.11, 0.64]$, reported by Sala et al. (2005). Other parameters are: $h_{A1} = 1$, $h_{A2} = 0$, $h_{B1} = 1$, $h_{B2} = 0.5$, $h_{C1} = 1$, $h_{C2} = 1$, $c_1 = 46\%$, $c_2 = 51\%$, and $c_3 = 3\%$.

zweig (2001) has recently proposed that extinctions caused by habitat loss proceed in three stages. The first stage corresponds to the loss of endemics, and is described by continental z values. The second stage corresponds to the loss of sink species (those restricted to marginal habitats) and is described by island z values. The first and second stages occur on ecological scales of decades to thousands years (Rosenzweig 2001, Sala et al. 2005). The third stage, occurring over an evolutionary time scale, leads to a decrease in speciation rates, results in a lower equilibrium diversity, and is described by the interprovincial z value. It may be argued that the evolutionary time scale is not relevant for decision making, and that we should focus on the ecological time scales. But even if we focus on the island and continental SARs, a significant uncertainty still exists. A recent review (Sala et al. 2005) of the published SARs in literature found that for plants, a 95% confidence interval for continental z values ranges from 0.14 to 0.45 with a mean of 0.25, much higher than the 0.15 to 0.18 range reported by Rosenzweig (1995). Similarly, they found that a 95% confidence interval for island z values ranges from 0.11 to 0.64 with a mean of 0.34.

In order to ascertain the variability caused by the uncertainty of the z values on the predictions of the countryside SAR and the classic SAR, we calculated the biodiversity loss predicted for the extreme z values of 0.11 and 0.64 (Fig. 2). The z value has a large effect on the prediction of biodiversity loss. For a conversion of 95% of forest to cultivated land, the classic SAR predictions of species loss range from 28% to 85%. A narrower range occurs for the countryside SAR, from 16% to 57% species loss.

A FRAMEWORK BASED ON A DEMOGRAPHIC MODEL

The classic SAR tells us how many species are likely to be lost for a given land use change but tells us nothing

about which species are going to be lost. The countryside SAR goes a step further in separating species into groups with different affinities for native and human-modified habitats, but it does not discriminate between species within each of these groups. In order to make species by species predictions, we use a demographic model to characterize the dynamics of each species. We first derive the model and determine the equation that predicts the minimum habitat size needed for a species to survive. We then estimate the demographic model parameters for each non-volant mammal species of Central America and produce a relative ranking of vulnerabilities to habitat conversion.

A demographic model

We start with the reaction–diffusion model proposed by Skellam (1951) to describe population dynamics in a landscape with two types of habitat. We assume a circular patch of native habitat with diameter L , surrounded by human-modified habitat. To investigate whether a species can survive habitat modification, we assume exponential growth. Further, we assume a random walk, where the probability that each individual disperses a distance $d = \sqrt{x^2 + y^2}$ in a small time interval δt is given by a bivariate Gaussian distribution:

$$P(d) = \frac{1}{2\pi\sigma^2\delta t} \exp\left(-\frac{d^2}{2\sigma^2\delta t}\right) 2\pi d \quad (6)$$

where σ^2 is the dispersal variance. Let $N(\rho, t)$ denote the population size at time t at distance ρ from the center of the patch of native habitat, and let r_1 and r_2 denote the population growth in the native and modified habitat, respectively. Then the population dynamics is described by

$$\frac{\partial N}{\partial t} = \frac{\sigma^2}{2} \times \left(\frac{\partial^2 N}{\partial \rho^2} + \frac{1}{\rho} \times \frac{\partial N}{\partial \rho} \right) + r_i N \quad (7)$$

where $i = 1$ if $\rho < L/2$ and $i = 2$ otherwise. The boundary conditions impose continuity on the population densities and the population fluxes and are

$$N\left(\frac{L^-}{2}\right) = N\left(\frac{L^+}{2}\right) \quad (8a)$$

$$\frac{\partial N}{\partial t}\left(\frac{L^-}{2}\right) = \frac{\partial N}{\partial t}\left(\frac{L^+}{2}\right). \quad (8b)$$

However, it is increasingly clear that animals actively choose where to move and disperse in countryside habitats (Desrochers and Hannon 1997, Belisle et al. 2001). In order to accommodate this reality, Ovaskainen and Cornell (2003) modified the boundary condition of Eq. 8a to incorporate selective dispersal at the habitat edge. If the probability that an individual moves outside at the native habitat edge is α , then the boundary condition for the densities is

$$\alpha N\left(\frac{L^-}{2}\right) = (1 - \alpha) \times N\left(\frac{L^+}{2}\right). \quad (9)$$

TABLE 1. Regression results with body mass (*m*) in grams for each of the model parameters.

Variable	Symbol	Units	Estimate	<i>r</i> ²	<i>N</i>	<i>s</i> ² _{<i>y,x</i>}
Mortality rate	μ	yr ⁻¹	2.8 <i>m</i> ^{-0.37}	0.76	16	0.40
Age at first breeding	β	yr	0.050 <i>m</i> ^{0.37}	0.73	45	0.40
Inter-litter interval	Δ	yr	0.15 <i>m</i> ^{0.23}	0.37	41	0.50
Dispersal median	σ _{<i>m</i>}	km/generation	0.0046 <i>m</i> ^{0.72}	0.72	20	2.33

Notes: A linear regression equation $\log y = a + b \log x + \varepsilon$, corresponds to the allometric relationship $y = e^a x^b e^\varepsilon$. The allometric relationships in this table are the raw estimates from linear regression and need to be multiplied by $\exp(s^2_{y,x}/2)$ to correct for bias (Sprugel 1983).

The solution to this model is derived elsewhere (Pereira et al. 2004) and can be summarized as follows. If the species has a positive growth rate in the human-modified habitat ($r_2 > 0$) then the species persists. If the species has negative growth rates in both types of habitats ($r_1 < 0$ and $r_2 < 0$) then the species goes extinct. If the species has a positive growth rate in the native habitat but negative growth rate in the human-modified habitat, the species persists if the size of the native habitat patch is greater than a critical patch size L^* . The critical patch size L^* is the implicit solution of

$$i \frac{I_0[\sqrt{r_1/(2\sigma^2)}L^*]}{I_1[\sqrt{r_1/(2\sigma^2)}L^*]} = \frac{1 - \alpha}{\alpha} \frac{\sqrt{-r_1} K_0[\sqrt{-r_2/(2\sigma^2)}L^*]}{\sqrt{-r_2} K_1[\sqrt{-r_2/(2\sigma^2)}L^*]} \tag{10}$$

where I_n and K_n are modified Bessel functions of the first and second kind of order n , respectively. Eq. 10 can be solved numerically. The critical patch size decreases with increasing population growth rates in either of the two habitats, and increases with increasing dispersal.

Applying the demographic model to Central American mammals

In order to calculate the critical patch size, we have to estimate the three parameters of the demographic model (r_1 , r_2 , and σ^2) for each mammals species of Central America. We start by calculating the maximum population growth rates r . The maximum population growth rate is the solution to the Euler equation (Roughgarden 1996):

$$\int_0^\infty e^{-rx} l(x) m(x) dx = 1 \tag{11}$$

where $l(x)$ is the survivorship at age x and $m(x)$ is the fecundity at age x . Because mammals differ so much in generation times, it is cumbersome to utilize the discrete version of Eq. 11 or a Leslie matrix. To approximate the survivorship and fertility functions we assume that (1) the mortality rate μ is constant (i.e., $l_x = e^{-\mu x}$); (2) fecundity is zero before the breeding age β ; (3) after the breeding age, fecundity equals the number of female offspring b (50% of the litter size) at regular birth pulses intervals; and (4) the birth pulse intervals are spaced by the mean interval between litters, Δ . Therefore, Eq. 11 simplifies to the following:

$$b \times \int_0^\infty \sum_{y=0}^\infty \delta(x - y\Delta - \beta) e^{-(r+\mu)x} dx = 1 \tag{12}$$

where $\delta(x)$ is the birth pulse function, which has a value of $1/T$ for x between 0 and T and 0 elsewhere. For computational purposes, we approximated by zero the survivorship after five mean life spans, and assumed that the birth pulse had the duration of one day (1/365 of a year).

We compiled information on the life-history parameters of Eq. 12 and body mass for each mammal species of Central America (Appendix) from Ried (1997) and Nowak (1999). For litter size and body mass, whenever data were not available for a species (14 species for body mass and 47 species for litter size), the mean of the genus (available in most cases) or the family was used. For the remaining life-history parameters (Table 1), allometric relationships were established based on the compiled data for Central America mammals, and then used to estimate the life-history parameters for species for which data were lacking.

Next we estimated the population growth rates on native habitat and on human-modified habitat (Appendix). We used the aforementioned classification of mammals in three groups of habitat affinities: group A, species that use only native habitats; group B, species that use both native and human-modified habitats; group C, species that use only human-modified habitats. We assume that species in groups A and B attain the maximum population growth rate in the native habitat, i.e., $r_1^A = r_1^B = r$. We assume that human-modified lands are lethal for species in group A, $r_2^A = -\infty$, and are unable to support breeding activities of species in group B, $r_2^B = -\mu$. This latter assumption is equivalent to saying that species in group B can occur in human-modified habitat but cannot persist exclusively in that habitat. For species in group C, we assume that the maximum population growth rate is attained in human-modified habitat $r_2^C = r$. Note that for group C, $r_2^C \geq r_1^C$ which implies that a sufficient condition for persistence is the maximum population growth rate to be positive.

Dispersal data were not available for most species, so we had to resort to the work of Sutherland et al. (2000). They compiled information on median natal dispersal for non-volant terrestrial mammals across the world, including two species occurring in Central America. We first calculated an allometric relationship based on their

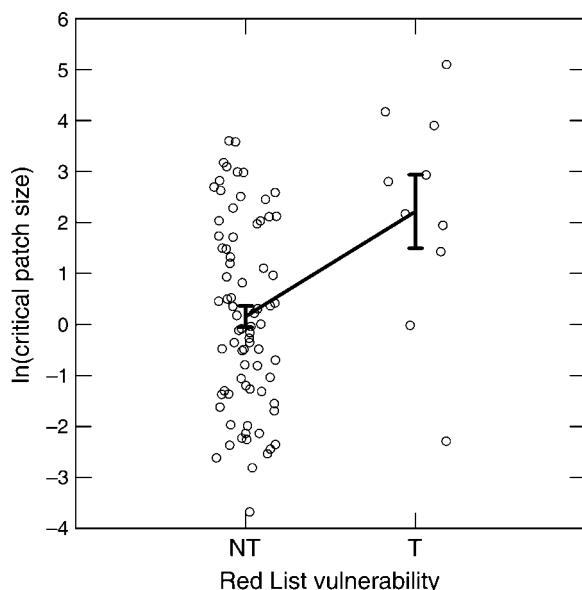


FIG. 3. Critical patch sizes of native habitat (diameter; \log_e -transformed) for Costa Rican mammals vs. World Conservation Union (IUCN) vulnerability classification (NT, not threatened; T, threatened). The line connects mean patch sizes for each group; error bars indicate \pm SE.

data (Table 1). Assuming Gaussian dispersal, the annual dispersal variance σ^2 , was then obtained from the natal dispersal medians σ_m as follows:

$$\sigma^2 = \frac{\sigma_m^2}{(1.18)^2} \times \frac{1}{1/\mu}. \quad (13)$$

Note that the division by the mean life span ($1/\mu$) is a conversion of the natal dispersal from units of $\text{km}^2/\text{generation}$ to units of km^2/year . An alternative would be to divide by the age at first breeding β , but that would result in overly high dispersal distances over the lifetime of an individual in the demographic model.

Next, we estimated the critical patch sizes for each mammal by solving Eq. 10 using the estimates for r_1 , r_2 , and σ^2 . In these calculations, we assumed unbiased dispersal at the habitat edge ($\alpha = 0.5$) because we do not have an empirical basis to estimate this parameter for each species. Later in the paper, we examine the consequences of biased dispersal. The ranking of critical patch sizes (Appendix) is a ranking of vulnerability to land-use change. Species with higher critical patch sizes require larger areas of native habitat to persist. Note, however, that the ranking of the critical patch sizes provides an index of vulnerability that is more than a simple ordinal ranking of vulnerabilities. That is, the vulnerabilities of two species that are one rank apart may be very different if the critical patch sizes are dissimilar.

Testing the model results

In order to assess the performance of the demographic model, we compared the critical patch sizes with the

World Conservation Union (IUCN) 2003 Red List, which provides a classification of vulnerability for the vast majority of Central American mammals. We grouped all the species classified by IUCN as vulnerable, endangered, or critically endangered in the threatened group, and all the remaining species in the nonthreatened group. A Kruskal-Wallis test shows that species classified as threatened by the IUCN have significantly larger critical patch sizes than nonthreatened species ($P = 0.038$, $N_1 = 142$, $N_2 = 22$). If we restrict the analysis to the Costa Rican mammals (Rodrigues and Chinchilla 1996), a subset of species for which we have more life-history data and where inferences using allometric relationships are not needed as often, the contrast in the critical patch sizes between threatened species and nonthreatened species is even more significant ($P = 0.0035$, $N_1 = 81$, $N_2 = 10$; Fig. 3).

Of the three types of parameters estimated for the model, demographic parameters, habitat affinity, and dispersal, only the latter seems not be contributing for the model explanatory power of the IUCN Red List. When the same r_1 is used for all species ($r_1 = \bar{r}$) and the same r_2 is used in each habitat affinity category ($r_2^A = -\infty$, $r_2^B = -\bar{\mu}$, $r_2^C = \bar{r}$), the difference in critical patch sizes between nonthreatened and threatened species is no longer significant ($P = 0.11$, $N_1 = 142$, $N_2 = 22$). Similarly, when all species are assumed to be restricted to native habitat ($r_2^A = r_2^B = r_2^C = -\infty$) the difference between nonthreatened and threatened species is not significant ($P = 0.09$, $N_1 = 142$, $N_2 = 22$). In contrast, if a constant dispersal variance is used ($\sigma = \bar{\sigma}$), the difference between nonthreatened and threatened species remains significant ($P = 0.005$, $N_1 = 142$, $N_2 = 22$).

Species in the threatened group have significantly lower population growth rates than nonthreatened species ($P = 0.039$, $N_1 = 142$, $N_2 = 22$), but this difference is only partially due to larger bodied species having slower population growth rates (log-log regression, $r^2 = 0.56$), and depends also on other life-history parameters (age at first breeding, litter size, inter-litter interval, and mortality rate).

In order to examine the sensitivity of our results to the unexplained variance in the allometric relationships, we performed Monte Carlo simulations. We added normally distributed errors to the allometric estimates of all species, with variance equal to the unexplained variance s_{y-x}^2 of each allometric relationship (Table 1), and estimated a set of sensitivity measures: the mean patch size, the standard deviation of the patch sizes and the Spearman rank correlation with our baseline estimates. Only species in groups A and B were considered for this analysis, and negative values of the maximum population growth rate were excluded. We performed 1000 simulations and report the mean values for the sensitivity statistics (Table 2) and 95% confidence intervals for the critical patch size for each species (Appendix). The confidence intervals for the critical patch size of each species suggest that errors can be of

TABLE 2. Sensitivity analysis of the probability of moving outside at the native habitat edge (α), of the population growth rates in human-modified habitats of species that use only native habitats (r_2^A), and of the unexplained variance ($s_{y,x}^2$) in the allometric relationships.

Parameter values	Mean L (km)	SD L (km)	Rank correlation
$\alpha = 0.50, r_2^A = -\infty$ (baseline)	5.63	15.5	
$\alpha = 0.50, r_2^A = -10$	4.58	10.4	0.96
$\alpha = 0.15, r_2^A = -10$	2.04	5.08	0.95
$s_{y,x}^2$	5.09	31.3	0.72

Notes: This analysis was performed using species in groups A and B only. See *A framework based on the species–area relationship: The countryside species–area relationship* for a description of the species groups.

† L is the diameter of a circular patch of native habitat.

one to two orders of magnitude. However, the Monte Carlo simulated rankings are still good predictors of the baselines ranks (Spearman rank correlation, $P < 0.001$), implying that the rankings are robust to the uncertainty in the allometric relationships.

We also examined the effect of two assumptions in our estimates: the population growth rate in human-modified habitats of species that use only native habitats (r_2^A) and the dispersal behavior of individuals at the habitat edge (Table 2). Again, the relative rankings are insensitive to these assumptions, but the mean patch sizes and the variance of the patch sizes are dependent on our particular choices for those parameters. Therefore, while an absolute interpretation of the critical patch size, as the minimum area of native habitat needed to support a viable population, is assumption dependent, the relative rankings are robust measures of vulnerability.

DISCUSSION

Mitigating the drivers causing biodiversity loss requires understanding how each driver affects biodiversity and ecosystem function. Here we have presented two frameworks that model the impacts of the main driver, habitat alteration, on biodiversity. The first framework, species–area relationships, allows us to estimate how fast we are losing biodiversity in a region, provided that we know the rates of habitat alteration. The second framework, demographic models, allows us to identify which species are most vulnerable to habitat conversion, provided that basic life-history data are available.

We show that the conservation value of the remaining native habitat increases as the landscape becomes more and more humanized. This is even more the case if we consider extinction debt (Brooks and Balmford 1996, Cowlishaw 1999), the fraction of species held temporarily by an area not yet in the equilibrium predicted by the species–area relationship. Biodiversity will eventually decline on an ecological time scale of decades to millennia to the equilibrium predicted by the species–area relationship (Rosenzweig 2001, Sala et al. 2005),

but, in the meantime, there will be an opportunity to restore the conservation value of habitats and landscapes. It is important to note however, that restoration may not come in time for the most sensitive species and ecosystems.

Many species occur in human-modified habitats (Daily et al. 2001, 2003) and some are even adapted to particular agricultural practices (Bignal and McCracken 1996). We extended the classic species–area relationship to accommodate this reality by proposing a model for the species diversity in landscapes with multiple habitats, which we name the countryside species–area relationship. The precise shape of the species–area relationship in landscapes with multiple habitats is an open question. Tjorve (2002) and Triantis et al. (2003) have recently proposed models for the multi-habitat SAR that differ from ours, but only a careful empirical test comparing the three models will determine which best describes nature. Whatever multi-habitat SAR is used, the predictions of biodiversity loss should not differ much from the countryside SAR (Fig. 1), which are much more optimistic than the predictions of the classic SAR.

On the other hand, we have a limited knowledge of how to correct the SAR for habitat fragmentation. Should the SAR be applied just to the largest fragment of native habitat, or to the sum of the native habitat patches? Which z value should be used, the lower z values of continental SARs or the higher z values of the island SAR? Even in each of these categories, z values vary widely in different studies (Sala et al. 2005) and at different scales in the same study (Crawley and Harral 2001). An interesting related question is to ask if the z value across time for a habitat fragment that progressively decreases in size is the same as the z value across space in a landscape with habitat fragments of different size.

Both in terms of conservation value (Daniels 1991) and in terms of predicting impacts on ecosystem functioning (Loreau 2001), it is important to know which species are most vulnerable to habitat loss. There is now a large literature on using population viability analysis (PVA) models to predict the persistence of a population (Possingham et al. 2001). These models typically require a large number of parameters related to the species’ life history and to the spatial distribution of the habitat fragments, and therefore have not been applied to assess the vulnerability of large sets of species (for an exception, see Belovsky 1987). Here we used a simple demographic model that requires only three parameters, the population growth rate in native habitat, the population growth rate in human-modified habitats, and the dispersal variance, to assess the vulnerabilities of Central American mammals. We showed that these parameters can be calculated from existing life-history data complemented by the use of allometric relationships (Table 1). The results are promising, with our assessment of vulnerabilities identifying many of the species classified as threatened by the IUCN (Fig. 3).

Our assessments of vulnerability could be improved both by gathering more life-history data, particularly on demographic parameters, in human-modified habitats (Table 2), and by refinements of our model, such as by incorporating demographic stochasticity. But dispersal behavior, the key component of our model, is probably where there is more opportunity for improvement from a theoretical perspective. We have assumed that dispersal occurs at a steady state throughout an individual's lifetime. However, an integro-difference model could be used to account for differential dispersal of juveniles and adults (Lewis 1997). More complicated is the issue of directed dispersal, when individuals actively choose where to disperse in the landscape and can move towards the habitat patch even when they are far away from the habitat patch. This is different from the biased random walk used in our model, where the individual chooses where to move only at the habitat edge. Individual-based models or metapopulation models (Hanski 1999) may be better approaches in cases where dispersal behavior cannot be approximated by the biased random walk.

There is a subtle but important difference between the countryside SAR approach and the demographic model relative to what happens to species that use both human-modified and native habitats when all native habitat disappears. While, in the countryside SAR, some of these species will still persist (the relative number depending on how high is the habitat affinity of those species for human-modified habitat), in the demographic model, those species become extinct. Therefore, in the demographic model a species can occur in human-modified habitats even when it cannot persist exclusively in those habitats. This is the result of the source-sink structure (Pulliam 1988) of the demographic model, where the native habitat acts as a source and the human-modified habitat as a sink.

In conclusion, we have presented improved tools that allow us to estimate how much and which biodiversity will be lost as a consequence of habitat alteration. These tools give more optimistic predictions of biodiversity loss than classic tools because they incorporate the conservation value of the countryside. Nevertheless, many uncertainties remain and the exact dimension of the extinction crisis we are facing is still unclear.

ACKNOWLEDGMENTS

We thank Paul Armsworth for inspiring discussions and comments, Joan Schwan for data entry, and Vania Proença for help with proofing. Henrique Pereira was supported by a PRAXIS fellowship BPD/9395/2002 and by a grant to Gretchen Daily by the McDonnell Foundation. We are also indebted to the Winslow Foundation and Peter and Helen Bing for support.

LITERATURE CITED

- Achard, F., H. D. Eva, H.-J. Stibig, P. Mayaux, J. Gallego, T. Richards, and J.-P. Maingreau. 2002. Determination of deforestation rates of the world's humid tropical forests. *Science* **297**:999–1002.
- Baillie, J. E. M., C. Hilton-Taylor, and S. N. Stuart, editors. 2004. 2004 IUCN Red List of threatened species. a global species assessment. World Conservation Union (IUCN), Gland, Switzerland.
- Belisle, M., A. Desrochers, and M. J. Fortin. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* **82**:1893–1904.
- Belovsky, G. E. 1987. Extinction models and mammalian persistence. Pages 35–57 in M. E. Soulé, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, UK.
- Bignal, E. M., and D. I. McCracken. 1996. Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology* **33**:413–424.
- Boecklen, W. J. 1997. Nestedness, biogeographic theory, and the design of nature reserves. *Oecologia* **112**:123–142.
- Brooks, T. M., and A. Balmford. 1996. Atlantic forest extinctions. *Nature* **380**:115.
- Brown, J. H., and M. V. Lomolino. 1998. *Biogeography*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Cantrell, R. S., and C. Cosner. 1999. Diffusion models for population dynamics incorporating individual behavior at boundaries: applications to refuge design. *Theoretical Population Biology* **55**:189–207.
- Cowlishaw, G. 1999. Predicting the pattern of decline of African primate diversity: an extinction debt from historical deforestation. *Conservation Biology* **13**:1183–1193.
- Crawley, M. J., and J. E. Hurrell. 2001. Scale dependence in plant biodiversity. *Science* **291**:864–868.
- Daily, G. C. 2001. Ecological forecasts. *Nature* **411**:245.
- Daily, G. C., G. Ceballos, J. Pacheco, G. Suzán, and A. Sánchez-Azofeifa. 2003. Countryside biogeography of Neotropical mammals: conservation opportunities in agricultural landscapes of Costa Rica. *Conservation Biology* **17**(6):1814–1826.
- Daily, G. C., P. R. Ehrlich, and G. A. Sánchez-Azofeifa. 2001. Countryside biogeography: utilization of human-dominated habitats by the avifauna of southern Costa Rica. *Ecological Applications* **11**:1–13.
- Daniels, R., M. Hegde, N. Joshi, and M. Gadgil. 1991. Assigning conservation value: a case study from India. *Conservation Biology* **5**:464–475.
- Desrochers, A., and S. J. Hannon. 1997. Gap crossing decisions by forest songbirds during the post-fledging period. *Conservation Biology* **11**:1204–1210.
- Global Forest Resources Assessment. 2001. *Global forest resources assessment 2000: main report*. FAO forestry papers, volume 140. Food and Agriculture Organization, Rome, Italy.
- Groombridge, B., and M. D. Jenkins. 2002. *World atlas of biodiversity*. University of California Press, Berkeley, California, USA.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, Oxford, UK.
- Lawton, J. H., and R. M. May, editors. 1995. *Extinction rates*. Oxford University Press, Oxford, UK.
- Lewis, M. A. 1997. Variability, patchiness, and jump dispersal in the spread of an invading population. Pages 46–69 in D. Tilman and P. M. Kareiva, editors. *Spatial ecology: the role of space in population dynamics and interspecific interactions*. Princeton University Press, Princeton, New Jersey, USA.
- Loreau, M., S. Naem, P. Inchausti, J. Bengtsson, J. P. Grime, A. Hector, D. U. Hooper, M. A. Huston, D. Raffaelli, B. Schmid, D. Tilman, and D. A. Wardle. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science* **294**:804–808.
- May, R. M., J. H. Lawton, and N. E. Stork. 1995. Assessing extinction rates. Pages 1–24 in J. H. Lawton and R. M. May, editors. *Extinction rates*. Oxford University Press, Oxford, UK.

- Nowak, R. M. 1999. Walker's mammals of the world. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Ovaskainen, O., and S. J. Cornell. 2003. Biased movement at boundary and conditional occupancy times for diffusion processes. *Journal of Applied Probability* **40**:557–580.
- Pereira, H., G. C. Daily, and J. Roughgarden. 2004. A framework for assessing the relative vulnerability of species to land-use change. *Ecological Applications* **14**:730–742.
- Pimm, S. L., and R. A. Askins. 1995. Forest losses predict bird extinctions in eastern North America. *Proceedings of the National Academy of Sciences (USA)* **92**:9343–9347.
- Pimm, S. L., G. J. Russell, J. L. Gittleman, and T. M. Brooks. 1995. The future of biodiversity. *Science* **269**(5222):347–350.
- Possingham, H., D. B. Lindenmayer, and M. A. McCarthy. 2001. Population viability analysis. Pages 831–843 in S. Levin, editor. *Encyclopedia of biodiversity*. Academic Press, San Diego, California, USA.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *American Naturalist* **132**:652–661.
- Regan, H. M., R. Lupia, A. N. Drinnan, and M. A. Burgman. 2001. The currency and tempo of extinction. *American Naturalist* **157**:1–10.
- Reid, F. A. 1997. A field guide to the mammals of Central America and Southeast Mexico. Oxford University Press, New York, New York, USA.
- Reid, W. V. 1992. How many species will there be? Pages 53–73 in T. C. Whitmore and J. A. Sayer, editors. *Tropical deforestation and species extinction*. Chapman and Hall, London, UK.
- Rodríguez, J., and F. Chinchilla. 1996. Lista de mamíferos de Costa Rica. *Revista de Biología Tropical* **44**:877–890.
- Rosenzweig, M. L. 1995. *Species diversity in space and time*. Cambridge University Press, Cambridge, UK.
- Rosenzweig, M. L. 2001. Loss of speciation rate will impoverish future diversity. *Proceedings of the National Academy of Sciences (USA)* **98**:5404–5410.
- Roughgarden, J. 1996. *Theory of population genetics and evolutionary ecology*. Second edition. Prentice Hall, Upper Saddle River, New Jersey, USA.
- Sala, O. E., D. van Vuuren, H. M. Pereira, D. Lodge, J. Alder, G. Cumming, A. Dobson, W. Volters, M. Xenopoulos, and A. S. Zaitsev. 2005. Biodiversity across scenarios. Pages 375–408 in S. Carpenter, L. P. Prabhu, E. M. Bennet and M. B. Zurek, editors. *Ecosystem and human well-being: scenarios*. Island Press, Washington, D.C., USA.
- Simberloff, D. 1992. Do species area curves predict extinction in fragmented forest? Pages 75–89 in T. C. Whitmore and J. A. Sayer, editors. *Tropical deforestation and species extinction*. Chapman and Hall, London, UK.
- Skellam, J. G. 1951. Random dispersal in theoretical populations. *Biometrika* **38**:196–218.
- Sprugel, D. G. 1983. Correcting for bias in log-transformed allometric equations. *Ecology* **64**:209–210.
- Sutherland, G. D., A. S. Harestad, K. Price, and K. P. Lertzman. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. *Conservation Ecology* **4**(1):16 (<http://www.consecol.org/vol4/iss1/art16/>)
- Tjorve, E. 2002. Habitat size and number in multi-habitat landscapes: a model approach based on species-area curves. *Ecography* **25**:17–24.
- Triantis, K. A., M. Mylonas, K. Lika, and K. Vardinoyannis. 2003. A model for the species-area-habitat relationship. *Journal of Biogeography* **30**:19–27.

APPENDIX

Life history data and model parameters for all species considered in this analysis (*Ecological Archives* E087-118-A1).