

A framework for predicting species extinction by linking population dynamics with habitat loss

Andrew J. Tanentzap¹, Susan Walker¹, R. T. Theo Stephens², & William G. Lee^{1,3}

¹Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand

²Department of Conservation, Private Bag 1930, Dunedin 9054, New Zealand

³School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand

Keywords

Extinction crisis; fragmentation; island biogeography; metapopulations; sampling theory; species–area relationship.

Correspondence

Andrew J. Tanentzap, Landcare Research, Private Bag 1930, Dunedin 9054, New Zealand.
Tel: +64 3 470 7218; Fax: +64 3 470 7201.
E-mail: tanentzapa@landcareresearch.co.nz

Received

27 July 2011

Accepted

24 December 2011

Editor

Dr. Richard Zabel

doi: 10.1111/j.1755-263X.2011.00221.x

Abstract

Conservation policy requires reliable estimates of extinction rates that consider the interactions between population size (N) and habitat area. Current approaches to estimating extinction from the endemics–area relationship (EAR) estimate only the minimum number of species that can become extinct because of habitat loss (instantaneous extinction). EARs will therefore underestimate extinction if small populations and/or habitat area (SPHA) commit species to future extinction. We demonstrate this mathematically, by assuming species require a minimum population size of two individuals, and by randomly sampling habitat loss within stem-mapped forest plots. We then develop a general framework for incorporating SPHA effects into EARs that builds upon recent advances introducing N into estimates of extinction. By accounting for effects that modify N , our framework explains extinction debt and reduces the uncertainty associated with future estimates of extinction through carefully qualifying the spatial and temporal context of predictions.

Introduction

Species extinctions are accelerating as humans appropriate ever greater proportions of the earth's habitats (Myers 1989; MEA 2005). Policies seeking to halt or slow extinctions through conservation are controversial because they challenge the dominant contemporary economic paradigm, powerful vested development interests, and embedded norms of human enterprise and consumption (e.g., Parenteau 1998). It is therefore important for ecological science to provide policy with reliable predictions of the rates at which species extinctions will occur, and how conservation policies and actions will alter species persistence. However, the question of how best to estimate rates of extinction remains unresolved.

Traditional approaches for estimating extinction have used the species–area relationship (SAR), which describes the number of unique species that accumulate as a power of increasing area (Rosenzweig 1995). The reverse of the

power-law SAR, i.e., the backward SAR, has often been used to predict the numbers of unique species that will be lost as habitat area is increasingly eroded from a landscape but it can overestimate extinction compared with observed rates (Pimm & Askins 1995; Brooks *et al.* 1997, 1999). A prevailing explanation for this discrepancy is that there is a time lag before extinction reaches species that survive habitat loss with small and fragmented populations (Heywood *et al.* 1994; Brooks *et al.* 1999). The difference between instantaneous and future extinction has been termed “extinction debt” (Tilman *et al.* 1994).

The backward SAR will overestimate instantaneous extinction rates from habitat loss because of a feature of sampling: the area required to contact a species for the first time is always less than the area required to contact a species for the last time when species are nonrandomly distributed (He & Hubbell 2011). The number of species immediately lost if an area of habitat is removed is instead described by the endemics–area relationship (EAR),

which calculates the number of species whose individuals are confined to the lost habitat (Harte & Kinzig 1997; Kinzig & Harte 2000). By linking species distributions to sampling theory, the random placement model of He & Hubbell (2011) provides a simple and mechanistic explanation for the EAR that produces lower estimates of extinction than the backward SAR. Importantly, however, the EAR calculates only the number of species whose populations are entirely and immediately destroyed by habitat loss (He & Hubbell 2011), ignoring species that are committed to future extinction. These EAR-based estimates are therefore of limited value to policy makers concerned with future extinctions and not merely instantaneous effects (Brooks *et al.* 2011).

The EAR will provide unbiased estimates of extinction rates if species are unaffected by small population and/or small habitat area (SPHA) after habitat loss, but this is unlikely to be a biologically realistic assumption. Habitat loss reduces the size of species populations, which increases their susceptibility to extinction from demographic, genetic, and environmental stochasticity (Lande 1988, 1993; Hubbell 2001). Communities in small, isolated fragments also receive fewer immigrant species, as predicted by island biogeography theory (MacArthur & Wilson 1967), and the persistence of individual species populations is reduced by changes associated with habitat fragmentation, e.g., increased edge effects; disrupted competitive, reproductive, and trophic interactions; and lower resistance and resilience to disturbance (Laurance 2008 and references therein). Habitat loss, fragmentation, and the loss of some but not all individuals within a population can thus commit a species to extinction before all individuals in a population have died. Often, species require a minimum number of hundreds or thousands of individuals to avoid extinction arising from such SPHA effects (Shaffer 1981; Traill *et al.* 2007). EARs that ignore SPHA effects, and assume that extinction occurs only instantaneously (e.g., He & Hubbell 2011), will systematically underestimate future extinction; i.e., they estimate the minimum number of species that will become extinct.

Here, we demonstrate mathematically how predictions of species loss from random placement EARs underestimate species loss in the presence of SPHA effects. We first sample five stem-mapped forest plots and compare predictions from the EAR without SPHA effects to those derived from the backward power-law SAR. We then test two specific SPHA scenarios that assume species are committed to extinction when: (1) population size falls below a minimum threshold; or (2) individuals are separated from their nearest conspecific neighbor by a given distance. Our approach demonstrates how the EAR can be extended to incorporate SPHA effects, providing a robust framework for calculating future extinction rates.

Methods

Derivation of generalized EAR

The probability of encountering the last individual of a species at a random location can be derived from sampling theory to calculate a random placement EAR (He & Hubbell 2011). If we assume that species occur randomly, then their distributions can be described by a Poisson probability distribution, of which the binomial is a special case when a finite area is studied. The binomial model describes the probability of a sampling area of size a containing at least n individuals of species i when N_i individuals are located within the total area A (Eberhardt 1967)

$$F_{i,n}(a) = \sum_{j=n}^{N_i} \left[\binom{N_i}{j} \left(\frac{a}{A}\right)^j \left(1 - \frac{a}{A}\right)^{N_i-j} \right], \quad (1)$$

where $F_{i,n}(a)$ is a function of a for species i summed across each potential population size from n to the species-specific N_i and varying from 0 to 1 as a increases from 0 to A . The random placement model for multiple species all containing at least n individuals in an area a is then the sum of $F_{i,n}(a)$ across species i to S

$$S_{a,n} = \sum_{i=1}^S F_{i,n}(a), \quad (2)$$

where $S_{a,n}$ is the expected number of species with n individuals remaining in an area of size a . To sample all N_i individuals of a species i within an area a , which will result in extinction if that area is lost, $n = N_i$ and Equations (1) and (2) respectively simplify to

$$F_{i,N_i}(a) = \left(\frac{a}{A}\right)^{N_i}, \quad (3)$$

and

$$S_{a,N_i} = \sum_{i=1}^S \left(\frac{a}{A}\right)^{N_i}. \quad (4)$$

Although we assume species are distributed at random, despite evidence that they are generally not, predictions from Equation (1) will be remarkably similar to those from a negative binomial model that captures spatial aggregation. Broadly, as the size of the sampling area used to count individuals increases, the negative binomial for a finite area approaches the binomial function (Zillio & He 2010), and so the EAR based on random sampling distributions, i.e., Equation (4), will be invariant to spatial aggregation (He & Hubbell 2011). The negative binomial model also requires prior knowledge of spatial distributions for all species, which is impractical at large scales, and so will limit the generality of the EAR derived from this function.

The remarkable advantage of the random placement model is that it simplifies to a form that estimates extinction by considering species' population sizes (N_i) in addition to traditional measures of habitat area (a and A ; Equation (4)). Consequently, ecological processes that affect N_i can now be incorporated into estimates of extinction.

Incorporation of SPHA effects into the EAR

Following from Equation (1), it is easy to incorporate an effect that assumes species become extinct when population size falls below a minimum threshold. To illustrate, we use a simple scenario that assumes a species is committed to extinction when its population falls to less than two individuals, i.e., species reproduce sexually, there are no reproductive barriers, and there is no immigration. Under this condition, the expected number of species in a given area with less than two individuals (S_{a, N_i-1}) is the sum across all species i to S in a sample area a for which n is exactly equal to either N_i or $N_i - 1$. By substituting $n = N_i - 1$ into Equation (2)

$$S_{a, N_i-1} = \sum_{i=1}^S a^{-1} \left(\frac{a}{A} \right)^{N_i} (AN_i - N_i a + a). \quad (5)$$

Larger extinction estimates will always be obtained from Equation (5), which includes an SPHA effect, than from Equation (4), which assumes that extinction occurs when the last individual of a species is removed. This can be demonstrated mathematically by the inequality for a single species between Equations (4) and (5): $a^{-1} \left(\frac{a}{A} \right)^N (AN - Na + a) > \left(\frac{a}{A} \right)^N$. The inequality simplifies to $A > a$, which will always be true because by definition a is a subsample of A .

SPHA effects with empirical datasets

We analyzed five publicly available datasets ranging in area from 2 to 50 ha. Plots were from temperate and tropical forests and contained mapped coordinates of live trees, such that each species was represented by at least two individuals (Table S1). We superimposed 25 m \times 25 m grid cells onto each plot and randomly sampled cells ranging in area from 625 m² to the full extent of the plot, without requiring cells to be nested within each other (i.e., cell congruency). Within each sample of grid cells, we counted species: (1) entirely confined to a sampling area (EAR without SPHA effects); (2) with <2 individuals outside the sampling area (EAR with SPHA scenario 1); and (3) with pairwise distances among individuals outside the sampling area all >100 m (EAR with SPHA scenario 2); and repeated sampling 50 times. SPHA scenarios 1 and 2 respectively incorporate into the EAR assump-

tions that species are committed to extinction when their populations fall below a minimum threshold of viability or are separated from their nearest neighbor such that they become reproductively isolated, giving rise to inbreeding depression (Angeloni *et al.* 2011), which subsequently elevates extinction risk (Spielman *et al.* 2004). We also assume: (1) habitat loss renders a patch permanently unavailable for species establishment, so extirpated species cannot reinvade it; and (2) each plot is isolated, such that populations in remaining habitat do not receive immigrants (after He & Hubbell 2011). Local patches exposed to habitat loss within a larger matrix are unlikely to have global endemics or experience strong SPHA effects because of the ability of species to recolonize remaining area, so EARs are inapplicable in these contexts.

We also calculated the SAR by averaging counts of endemic species within all grid cells superimposed on each plot, and increasing the sizes of grid cells in increments of 25 m along each axis. We fitted the power-law SAR, $S = cA^z$, to species counts using maximum-likelihood to estimate c and z (*nlme* function in R ver 2.13; R Development Core Team 2011), and reversed this relationship to plot the backward SAR. The power-law model overestimates z values at small spatial scales, so we fitted our model only to areas >0.2 ha (He & Hubbell 2011).

Finally, for each site, we plotted the theoretical EAR: (1) without SPHA effects (Equation (4)); and (2) with the effect of SPHA scenario 1 (Equation (5)). We only present results from random sampling and not a theoretical expectation for SPHA scenario 2; its mathematical incorporation into an EAR is relatively intractable because it assumes that species are not distributed at random, i.e., variation in distances among individuals.

Results

The EAR underestimates extinction in the presence of SPHA effects when it is assumed that extinction occurs when the last individual of a species dies. Differences in predicted species loss between the theoretical-derived EAR with and without SPHA scenario 1, which assumed that species required a minimum population size of two individuals to persist, were greatest between 25% and 90% habitat loss (gray vs. green lines; Figure 1). SPHA scenarios also predict greater species loss than the EAR without SPHA effects (gray lines beneath overlapping colored regions; Figure 1). Although the backward SAR based on the power-law lacks a theoretical basis for estimating extinction because of habitat loss, its predictions are surprisingly similar to the EAR that incorporates SPHA effects (Figure 1).

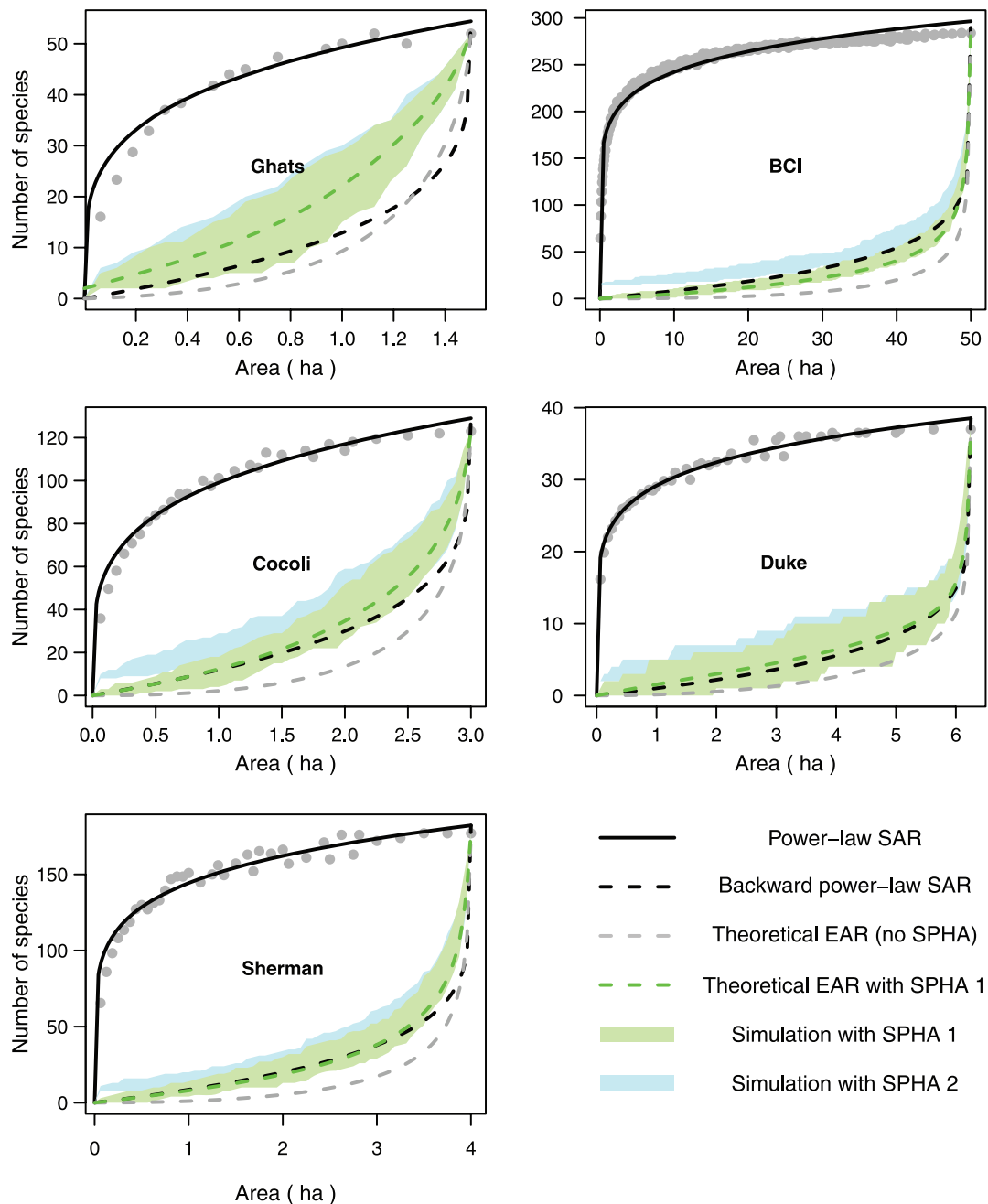


Figure 1 Species– and endemics–area curves for five mapped forest plots (Table S1). Dots represent species accumulation within contiguous grid cells 25 m × 25 m; solid and dashed black lines are forward and backward maximum-likelihood fit of the power-law SAR. The gray line is random placement EAR without SPHA effects (Equation (4)), whereas the green

line considers SPHA scenario 1 (extinction = <2 individuals; Equation (5)). Shaded green and blue regions are observed ranges for 50 samples of random habitat loss under SPHA scenarios 1 and 2 (extinction = pair-wise distances among individuals of a species > 100 m), respectively.

Discussion

SPHA effects are pervasive in ecological systems (Shaffer 1981; Lande 1988, 1993; Andrén 1997; Hubbell 2001; Laurance 2008), and our results show that failure

to incorporate them into the EAR leads to underestimates of future extinction. We also demonstrate that incorporating SPHA effects into the EAR explains the lag between instantaneous and future extinction from habitat loss (Simberloff 1992; Hanski & Ovaskainen 2002; Bulman

et al. 2007). Although the random placement method that links sampling theory to species distributions is a theoretical advance on traditional power-law approaches for predicting extinction, incorporation of SPHA effects into an EAR produces similar predictions of future extinction to those derived from a backward power-law SAR. We emphasize that this finding is entirely coincidental and should not be taken as support for the backward power-law SAR method, which clearly lacks any theoretical basis and should not be used in predicting extinction (He & Hubbell 2011). However, it cannot be automatically assumed that all previous studies have overestimated future extinction by reversing the power-law SAR (e.g., Pimm & Askins 1995; Brooks & Balmford 1996; Brooks *et al.* 1997, 1999), contrary to the claim by He & Hubbell (2011) that SARs “always” overestimate extinction.

Fragmentation elevates extinction of small populations at intermediate habitat loss

Our finding that in the presence of SPHA effects more extinction arises at intermediate habitat loss (i.e., 25–90%) than predicted by the EAR without SPHA effects (e.g., He & Hubbell 2011) is consistent with known effects of fragmentation. Increasing habitat fragmentation creates habitat islands that are progressively smaller and more distant from mainland source populations, ultimately reducing population sizes of species (after MacArthur & Wilson 1967). For the simple case of no SPHA effects, the probability of extinction (p_i) of a single species i with loss of habitat of area a is equal to the EAR in Equation (3). The change in p_i as habitat area is proportionally lost, defined by $h = a/A$, is then $dp_i/dh = N_i h^{N_i-1}$. Because the slope of the EAR, i.e., dp_i/dh , depends on N_i and h , reductions in N_i that arise from habitat loss will lead to relatively larger slopes at all but the largest values of h , causing p_i to increase more rapidly when relatively less area is lost (Figure 2). Conversely, in larger populations, slopes will be less than 1 and approach zero at all but the highest levels of habitat loss, so p_i will increase rapidly only where h is large (Figure 2). The EAR without SPHA effects, however, ignores how habitat loss affects population size, i.e., N_i is independent of h , and so underestimates extinction of rare species at intermediate h . Our results do demonstrate an increase in p_i compared with the EAR without SPHA effects at between ca. 25% and 90% habitat loss as $dp_i/dh \rightarrow 1$, lending support to the argument that smaller populations have a greater probability of extinction as habitat loss fragments a landscape into progressively smaller increments (Laurance 2008).

Although our example shows the greatest variation in extinction occurs from $N_i = 1$ –5 (Figure 2), N_i implicitly represents relative population size ($N_{r,i}$), and so will vary

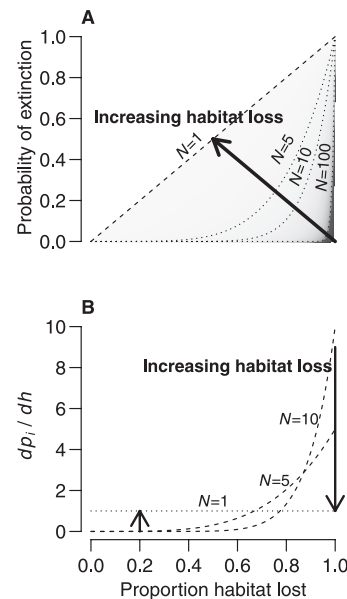


Figure 2 Effects of increasing habitat loss on species extinction. (A) EAR for one species i without SPHA effects when population size (N_i) varies from 1 to 100. For the single-species case, the EAR (Equation (4)) corresponds to the probability of extinction p_i . (B) Change in the probability of extinction with habitat loss, equal to the slope dp_i/dh in (A). Increasing habitat loss that simultaneously reduces N_i will change the slope of the plotted curves; arrow in (A) shows direction of change in curves with decreasing N_i . Reduced N_i in (B) causes p_i with habitat loss (h) to increase: (1) faster when little area in the landscape is destroyed (small values of h , positive arrow) and (2) slower when most of the landscape is lost (large values of h , negative arrow). dp_i/dh estimated for species with N_i of 1, 5, or 10; $N_i = 100$ omitted for clarity.

with assumptions of the number of individuals required to commit a species to extinction. For example, characteristics of each species i reproductive potential, such as sex ratios (R_i), age-specific fecundity (F_i), and propagule pressure from the surrounding landscape (P_i), along with their respective effects α , β , and γ , may be linear predictors of $N_{r,i}$, such that $N_{r,i} = N_i + \alpha R_i + \beta F_i + \gamma P_i$. By substituting N_i for $N_{r,i}$ in $dS_E/dh = N_i h^{N_i-1}$ (Figure 2), variation in extinction may arise over much larger absolute population sizes than 1–5 individuals.

Placing the EAR into spatial and temporal contexts

An EAR excluding SPHA effects is misleading because it captures only instantaneous and not eventual (i.e., future) extinction, thereby ignoring the spatial and temporal contexts that influence species' persistence. Specifically, instantaneous extinction underestimates future extinction because it excludes species that are committed to extinction while immigration and extinction rates reach

a new equilibrium state (Rosenzweig 1995). Our framework advances the work of He & Hubbell (2011) that links sampling theory to species' distributions by also demonstrating how the EAR can explicitly incorporate spatial and temporal context into predictions of species loss that account for future species loss. The EAR and SAR fundamentally depend on the size of species' populations (N_i), so modifications of these relationships that allow N_i to vary in specific contexts will offer better predictions of species loss than those derived simply from considering instantaneous extinction.

The EAR framework can readily incorporate spatial context to better predict extinction rates. Specifically, we can assume that species' population sizes N_i are a direct function of habitat area, whereby the population size of species i follows a power function with the area of a landscape after habitat destruction ($A - a$)

$$N_i(a) = \alpha_i (A - a)^{\beta_i}, \quad (6)$$

where α_i and β_i are estimated coefficients. The EAR is then: $S_{a,N_i} = \sum_{i=1}^S \left(\frac{a}{A}\right)^{\alpha_i(A-a)^{\beta_i}}$. This formulation also allows us to consider how spatial processes, such as composition of the matrix surrounding habitat patches, nonrandom habitat loss, edge effects, and patch isolation, can accelerate extinction (Seabloom *et al.* 2002; Laurance 2008; Koh & Ghazoul 2010). For example, if A is the total area of a landscape, and is equal to the sum of the individual areas of H habitats ($A = \sum_{k=1}^H A_k$), then N_i can be expressed for each species i as a function of the favorability (γ_k) and amount of area lost (a_k) of each habitat type k :

$$N_i(A, a) = \beta_i + \alpha_i \sum_{k=1}^H \frac{\gamma_{i,k}(A_k - a_k)}{\sum_{k=1}^H (A_k - a_k)}.$$

The EAR can then be rewritten as:

$$S_{a,N_i} = \sum_{i=1}^S \left(\frac{a}{A}\right)^{N_i(A,a)}.$$

Such an approach allows the EAR to be extended beyond estimates of extinction arising from the conversion of habitat into inhospitable matrices to predict how particular land-use changes and conservation initiatives will influence species loss (e.g., Koh & Ghazoul 2010).

Predictions of extinction from the backward SAR also have no theoretical basis for incorporating the timescale over which species will be lost, but the EAR again allows this to be estimated explicitly. Returning to the example of the EAR in the absence of SPHA effects, Equation (6) can be modified to express the size of species' populations (N_i) as a function of time t in addition to remaining habitat. If we assume, e.g., that N_i increases linearly as a function of t for each species i , such that $N_i(\alpha, t) = t\alpha_i(A - \alpha)^{\beta_i}$ and α_i and β_i are estimated coef-

ficients, then the EAR will be: $S_{a,t,N_i} = \sum_{i=1}^S \left(\frac{a}{A}\right)^{t\alpha_i(A-a)^{\beta_i}}$. Models from population ecology and conservation genetics of how N_i varies with t and a can provide estimates of α_i and β_i , enabling the EAR to provide more realistic predictions of timescales of extinction arising from habitat loss.

Policy implications of predicting extinction with SPHA effects

Estimates of species extinction enter a contested political context (Parenteau 1998), and vested interests may exploit scientific uncertainty to stall and prevent implementation of controversial policies, such as those related to biodiversity conservation (Oreskes & Conway 2010). He & Hubbell (2011) asserted that the backward SAR based on the power-law "always" overestimates extinction from habitat destruction, casting doubt on previous estimates. Here, we show that performance of the backward SAR depends on the temporal context of predictions, which is not always explicitly identified. Our findings agree that the backward power-law SAR overestimates instantaneous extinction, but show that its alternative, a random placement EAR, poorly estimates future extinction unless it is modified to incorporate the ecological effects that commit species to extinction in SPHA. The random placement model does, however, provide a robust framework for incorporating SPHA effects, allowing distinction of instantaneous and future extinction. Temporally and spatially explicit predictions of extinction derived from the EAR that incorporates SPHA effects are ultimately needed to guide conservation policy.

Adding SPHA effects to the random placement EAR also reveals approaches for minimizing extinction debt in response to habitat loss. Specifically, the model demonstrates that population sizes within remaining fragments, in addition to habitat area, influence whether a species is committed to extinction. Interventions that increase species' populations will thus complement interventions focused on habitat area, e.g., protection and restoration (Kuussaari *et al.* 2009), thereby reducing future extinctions.

Conclusions

Underestimates of extinction may harm biodiversity by understating the need for, and urgency of, conservation intervention, whereas overestimates may brand scientists as alarmists. Our results demonstrate that the EAR provides a robust foundation for estimating extinction, but that it will underestimate future extinction unless it is modified to incorporate the ecological effects that commit species to extinction in small populations and/or

small areas of habitat. Predictions of future extinction that are needed to guide policy will require incorporation of spatiotemporal context and empirical data into the EAR from fields such as conservation genetics (Lande 1988), population ecology (Traill *et al.* 2007), and spatial ecology (Andrén 1997; Matter *et al.* 2002; Koh & Ghazoul 2010), and we have demonstrated how this might be achieved.

Acknowledgments

We thank the Center for Tropical Forest Science of the Smithsonian Tropical Research Institute for making data freely available online (<http://www.ctfs.si.edu>), and A. Monks, D.M. Tompkins, C. Bezar, F. He, R. W. Zabel, and an anonymous reviewer for improving an earlier draft.

Supporting Information

The following supporting information is available for this article:

Table S1: Five publicly available stem-mapped forest plot datasets used to simulate endemics–area relationships with the effects of small population and/or habitat area.

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.

References

- Andrén, H. (1997) Habitat fragmentation and changes in biodiversity. *Ecol Bull* **46**, 171–181.
- Angeloni, F., Ouborg N.J., Leimu R. (2011) Meta-analysis on the association of population size and life history with inbreeding depression in plants. *Biol Conserv* **144**, 35–43.
- Brooks, T., Balmford A. (1996) Atlantic forest extinctions. *Nature* **380**, 115–115.
- Brooks, T.M., Brook B.W., Koh L.P. *et al.* (2011) Extinctions: consider all species. *Nature* **474**, 284.
- Brooks, T.M., Pimm S.L., Collar N.J. (1997) Deforestation predicts the number of threatened birds in insular southeast Asia. *Conserv Biol* **11**, 382–394.
- Brooks, T.M., Pimm S.L., Kapos V., Ravilious C. (1999) Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. *J Anim Ecol* **68**, 1061–1078.
- Bulman, C.R., Wilson R.J., Holt A.R. *et al.* (2007) Minimum viable metapopulation size, extinction debt, and the conservation of a declining species. *Ecol Appl* **17**, 1460–1473.
- Eberhardt, L.L. (1967) Some developments in “distance sampling.” *Biometrics* **23**, 207–216.
- Hanski, I., Ovaskainen O. (2002) Extinction debt at extinction threshold. *Conserv Biol* **16**, 666–673.
- Harte, J., Kinzig A.P. (1997) On the implications of species-area relationships for endemism, spatial turnover, and food web patterns. *Oikos* **80**, 417–427.
- He, F., Hubbell S.P. (2011) Species-area relationships always overestimate extinction rates from habitat loss. *Nature* **473**, 368–371.
- Heywood, V.H., Mace G.M., May R.M., Stuart S.N. (1994) Uncertainties in extinction rates. *Nature* **368**, 105.
- Hubbell, S.P. (2001) *The unified neutral theory of biodiversity and biogeography*. Princeton University Press, Princeton, NJ.
- Kinzig, A.P., Harte J. (2000) Implications of endemics-area relationships for estimates of species extinctions. *Ecology* **81**, 3305–3311.
- Koh, L.P., Ghazoul J. (2010) A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. *Conserv Biol* **24**, 994–1001.
- Kuussaari, M., Bommarco R., Heikkinen R.K. *et al.* (2009) Extinction debt: a challenge for biodiversity conservation. *Trends Ecol Evol* **24**, 564–571.
- Lande, R. (1988) Genetics and demography in biological conservation. *Science* **241**, 1455–1460.
- Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am Nat* **142**, 911–927.
- Laurance, W.F. (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biol Conserv* **141**, 1731–1744.
- MacArthur, R.H., Wilson E.O. (1967) *The theory of island biogeography*. Princeton University Press, Princeton, NJ.
- Matter, S.F., Hanski I., Gyllenberg M. (2002) A test of the metapopulation model of the species–area relationship. *J Biogeogr* **29**, 977–983.
- MEA [Millennium Ecosystem Assessment]. (2005) *Ecosystems and human well-being: biodiversity synthesis*. World Resources Institute, Washington, D.C.
- Myers, N. (1989) Extinction rates past and present. *BioScience* **39**, 39–41.
- Oreskes, N., Conway E.M. (2010) *Merchants of doubt: how a handful of scientists obscured the truth on issues from tobacco smoke to global warming*. Bloomsbury Press, New York, NY.
- Parenteau, P.A. (1998) Rearranging the deck chairs: endangered species act reforms in an era of mass extinction. *Wm. & Mary Envtl. L. & Pol’y Rev.* **22**, 227–311.
- Pimm, S.L., Askins R.A. (1995) Forest losses predict bird extinctions in eastern North America. *P Natl Acad Sci USA* **92**, 9343–9347.
- R Development Core Team (2011) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.

- Rosenzweig, M.L. (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge, U.K.
- Seabloom, E.W., Dobson A.P., Stoms D.M. (2002) Extinction rates under nonrandom patterns of habitat loss. *P Natl Acad Sci USA* **99**, 11229–11234.
- Shaffer, M.L. (1981) Minimum population sizes for species conservation. *BioScience* **31**, 131–134.
- Simberloff, D. (1992) Do species-area curves predict extinction in fragmented forest? Pages 75–88 in T.C. Wihtmore, J. Sayer, editors. *Tropical deforestation and species extinction*. Chapman and Hall, London, U.K.
- Spielman, D., Brook B.W., Frankham R. (2004) Most species are not driven to extinction before genetic factors impact them. *P Natl Acad Sci USA* **101**, 15261–15264.
- Tilman, D., May R.M., Lehman C.L., Nowak M.A. (1994) Habitat destruction and the extinction debt. *Nature* **371**, 65–66.
- Traill, L.W., Bradshaw C.J.A., Brook B.W. (2007) Minimum viable population size: a meta-analysis of 30 years of published estimates. *Biol Conserv* **139**, 159–166.
- Zillio, T., He F. (2010) Modeling spatial aggregation of finite populations. *Ecology* **91**, 3698–3706.