Ecology, 93(5), 2012, pp. 974–980

Area-based assessment of extinction risk

FANGLIANG HE[1]

SYSU-Alberta Joint Lab for Biodiversity Conservation, State Key Laboratory of Biocontrol and School of Life Sciences,
Sun Yat-sen University, Guangzhou 510275 China
Department of Renewable Resources, University of Alberta, 114 St.–89 Ave., Edmonton, Alberta T6G 2H1 Canada

Abstract. Underpinning the International Union for Conservation of Nature (IUCN) Red List is the assessment of extinction risk as determined by the size and degree of loss of populations. The IUCN system lists a species as Critically Endangered, Endangered, or Vulnerable if its population size declines 80%, 50%, or 30% within a given time frame. However, effective implementation of the system faces substantial challenges and uncertainty because geographic scale data on population size and long-term dynamics are scarce. I develop a model to quantify extinction risk using a measure based on a species' distribution, a much more readily obtained quantity. The model calculates the loss of the area of occupancy that is equivalent to the loss of a given proportion of a population. It is a very simple yet general model that has no free parameters and is independent of scale. The model predicted well the distributions of 302 tree species at a local scale and the distributions of 348 species of North American land birds. This area-based model provides a solution to the long-standing problem for IUCN assessments of lack of data on population sizes, and thus it will contribute to facilitating the quantification of extinction risk worldwide.

Key words: area of occupancy; extent of occurrence; extinction; IUCN; Red List; species distribution; threatened categories.

INTRODUCTION

No other scientific activity is arguably more important and challenging than understanding the causes and consequences of the contemporary mass loss of species (Höglund 2008, Barnosky et al. 2011). The IUCN addresses this challenge by proposing quantitative measures for listing species in the categories of threat: Critically Endangered, Endangered, and Vulnerable (IUCN-SSC 2010). The IUCN Red List of Threatened Species is the most comprehensive and authoritative system available for assessing risk of extinction and for planning conservation on local, national, and global scales (Eken et al. 2004, Miller et al. 2007, Mace et al. 2008). Over the past nearly half century, the Red List has evolved from extinction risk assessments based on expert opinion to that driven by data and theory (Mace and Lande 1991, Rodrigues et al. 2006, Mace et al. 2008). The system has five quantitative criteria, and a species is designated to a threat category if it meets at least one of these (IUCN-SSC 2010). Underlying the five criteria are threat thresholds defined by measures related to population size or the spatial extent of species occurrence. The use of population size as a measure of extinction risk stems from the theory of population genetics and population dynamics (Mace and Lande 1991, Lande 1993, Caughley 1994). It assigns a species to the category of Critically Endangered, Endangered, or Vulnerable if its population size is reduced, respectively, by 80%, 50%, or 30% within 10 years or three generations, whichever is longer (up to a maximum of 100 years in the future), i.e., criterion A of the IUCN threat categories (IUCN-SSC 2010). Alternatively, measures of range size assign a species to a threat category if the area occupied by the species is smaller than a given (arbitrary) threshold and the species meets some further criteria (i.e., the criterion B of the IUCN threat categories).

It is recognized that there are theoretical and practical limitations to current Red List assessments (Possingham et al. 2002, Lamoreux et al. 2003, Robbirt et al. 2006, Mace et al. 2008). Of these, the most serious is the uncertainty associated with the implementation of the IUCN system due to the paucity of large-scale and long-term data on population size. Consequently, conservation decisions have to be made on the basis of limited information, making the assessment of extinction risk less reliable and subject to misuse (Mrosovsky 1997, Possingham et al. 2002, Lamoreux et al. 2003, Robbirt et al. 2006, Mace et al. 2008). Alternatively, area-based measures are employed by the IUCN to make use of the wealth of distribution maps of a wide range of taxa across broad scales (Mitchell-Jones et al. 1999, BirdLife International 2004, IUCN-SSC 2004). However, the area-based methods suffer from lacking a proven biological basis; little is understood about the quantitative relationship between occupancy and extinction risk.

Manuscript received 3 October 2011; revised 6 January 2012; accepted 10 January 2012. Corresponding Editor: B. D. Inouye.

[1] Present address: Department of Renewable Resources, University of Alberta, 114 St.–89 Ave., Edmonton, Alberta T6G 2H1 Canada. E-mail: fhe@ualberta.ca

In this study I develop a method that is based on the extinction theory derived from population genetics and ecology (Mace and Lande 1991, Lande 1993, Caughley 1994), but uses the area of occupancy as a measure of extinction risk. The method does not require any information on population size. It answers the question: How much loss of the area of occupancy is equivalent to the loss of a given percentage (e.g., 80%, 50%, or 30%) of a population? Therefore, the new method integrates criteria A and B of the IUCN system into a single method. It addresses the fundamental criterion A but uses occupancy rather than population abundance as a measure.

The model

The model that answers the question of the relationship between occupancy area loss and population loss is of the form

$$p_c = 1 - (1-p)^{(1-c)} \tag{1}$$

where p is the original area of occupancy of a species in a region and p_c is the resultant occupancy after c proportion of the population is removed from the region. This is a very general model that is scale invariant and holds true for species with a very broad range of spatial distributions, as derived below.

To derive Eq. 1, first consider a randomly distributed species in which the relationship between population size and area of occupancy in a region of size A has the following form (He and Gaston 2000):

$$p = 1 - \left(1 - \frac{a}{A}\right)^{N} \tag{2}$$

where a is the cell size (spatial resolution) at which the species is mapped, N is the population size of the species in A, and p is the proportion of the region occupied by the species.

If the population is reduced by a proportion c of its original size, occupancy becomes

$$p_c = 1 - \left(1 - \frac{a}{A}\right)^{(1-c)N}. \tag{3}$$

Substituting Eq. 2 into Eq. 3 gives Eq. 1: $p_c = 1 - (1 - p)^{(1-c)}$. This model predicts that, given the original occupancy p of a species, the removal of proportion c of its population from the landscape will reduce the occupancy from p to p_c. Although Eq. 1 is derived from the assumption of a random spatial distribution, it also holds for nonrandom species, as will be proven.

Species can be distributed in space in numerous configurations. There is no single occupancy–abundance model for nonrandom distributions (Gaston and He 2010). Among the many models for describing a species' aggregation, the negative binomial distribution (NBD) is the most general and widely used (Boswell and Patil 1970, Pielou 1977). Its occupancy–abundance relationship is the following (He and Gaston 2000):

$$p = 1 - \left(1 + \frac{aN}{Ak}\right)^{-k} \tag{4}$$

where k is a positive parameter indicating spatial aggregation. Aggregated species have small k, whereas randomly distributed species have large k.

Consider the change in occupancy p when population size N is reduced to $(1 - c)N$ in Eq. 4. The NBD has a well-known statistical property (Johnson et al. 1993) that if x follows an NBD with parameter k, $(1 - c)x$ is also an NBD but with the aggregation parameter becoming $(1 - c)k$. This leads to

$$\begin{aligned} p_c &= 1 - \left(1 + \frac{a(1-c)N}{A(1-c)k}\right)^{-(1-c)k} \\ &= 1 - \left[\left(1 + \frac{aN}{Ak}\right)^{-k}\right]^{(1-c)}. \end{aligned} \tag{5}$$

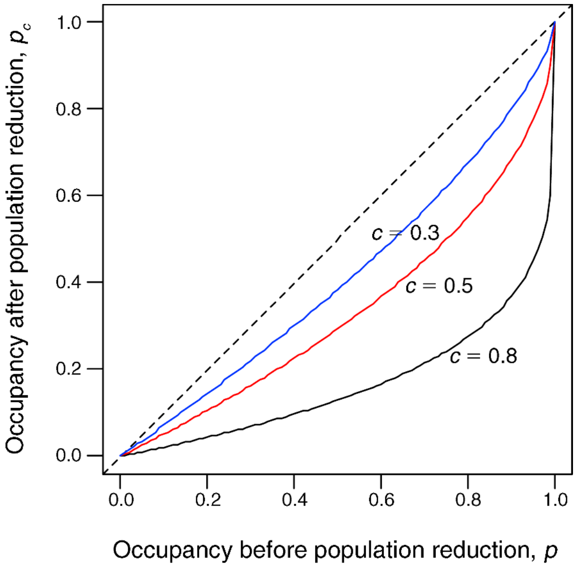
Substituting Eq. 4 into Eq. 5 again leads to Eq. 1.

Eq. 1 is remarkable. It provides a simple method to assess risk of extinction. From Eq. 1 we can easily calculate the percentage reduction in population size using occupancy as $c = 1 - [\log(1 - p_c)/\log(1 - p)]$ ($c \geq 0.8$ for Critically Endangered, $0.5 \leq c < 0.8$ for Endangered, and $c \geq 0.3$ for Vulnerable IUCN status). More importantly, the model does not have any free parameters and is independent of spatial scale. This means that it can be applied to species distributions of any mapping resolution or spatial extent. The scale-invariant property arises because the equation models relative (not absolute) changes in population size and occupancy. This property is especially desirable because the dependence of area-based measures on spatial scale is the major obstacle undermining the use of range data in the Red List assessments (Mace et al. 2008).

Equipped with Eq. 1, one can readily calculate the loss of occupancy for any given population removal and any given original area of occupancy (Fig. 1). The table in Fig. 1 presents a Red List-equivalent threat categorization for a given loss of occupancy. For example, given a species with an original area of occupancy $p = 0.4$, if its resultant occupancy after population removal becomes $p_c = 0.09$, the species should then be designated as Critically Endangered because $c = 1 - \log(1 - p_c)/\log(1 - p) = 0.815$ is greater than 0.8.

In application, data on area of occupancy are sometimes not available (Gaston 1994). Alternatively, the measure of extent of occurrence is used for assessing the endangered status of species (Mace et al. 2008, IUCN-SSC 2010). A risk model for extent of occurrence can also be derived. To derive that, habitats within a range of species distribution are classified into three types: occupied (with presence of species, denoted as m_1), unoccupied (suitable but not colonized habitats, m_2), and unsuitable habitats (m_3). In Eqs. 2–5, p is the proportion of occupied sites over the total number of suitable sites, i.e., $p = m_1/(m_1 + m_2)$. For extent of

Reports



p	p_c		
	$c = 0.8$	$c = 0.5$	$c = 0.3$
0.1	0.0208	0.0513	0.0711
0.2	0.0436	0.106	0.145
0.3	0.0688	0.163	0.221
0.4	0.0971	0.225	0.301
0.5	0.129	0.293	0.382
0.6	0.167	0.367	0.473
0.7	0.214	0.452	0.569
0.8	0.275	0.553	0.676
0.9	0.369	0.684	0.800

FIG. 1. (Top panel) The p–p_c relationship of Eq. 1, where p is the original area of occupancy of a species in a region and p_c is the resultant occupancy after c proportion ($c = 0.8$, 0.5, and 0.3, respectively) of the population is removed from the region. The dashed diagonal line is equivalent to $c = 0$ (no reduction of population size). (Bottom panel) Numerical tabulation of Eq. 1, showing the reduction in original proportion of area occupied, corresponding to (p_c), after the removal of 80% (Critically Endangered), 50% (Endangered), and 30% (Vulnerable) of a population.

occurrence, however, the proportion of occupancy is $p' = m_1/(m_1 + m_2 + m_3)$. It is easy to show that Eq. 1 for extent of occurrence is

$$p'_c = \frac{M}{M'}[1 - (1 - p)^{(1-c)}] \tag{6}$$

where M is the total number of suitable sites ($= m_1 + m_2$) and M' is the total number of sites within the extent area ($= m_1 + m_2 + m_3$). Proportion M/M' needs to be known (or estimated) for applying this model, i.e., data on the proportional area of unsuitable sites within the extent of a species' distribution are needed to apply this model to risk assessment.

Tests of the model

Data on the population size and spatial distribution of the species of interest are required for testing Eq. 1. Two sets of data are used here. The first is the distribution of tree species in a 50-ha (1000 × 500 m rectangle) stem-mapping plot on Barro Colorado Island (BCI), Panama. In the plot, trees and shrubs with diameter at breast height $\geq$1 cm were mapped and identified to species. There are >227 000 stems belonging to 302 species in the BCI plot (1980 census). The abundance for each of the 302 species is known. To construct the occupancy–abundance model, the plot is gridded into a lattice system at three cell sizes: $a = 10 \times 10$, 25×25, and 50×50 m, respectively. For a given cell size, the occupancy (p) of a species is the proportion of the number of occupied cells over the total number of cells for that species; see Fig. 2 for an example of how to convert a stem distribution into an occupancy map. Note that while p and p_c for the BCI species are conveniently calculated by gridding the plot, regular gridding is not necessarily in application. Any mapping method can be used as long as p and p_c can be accurately calculated.

I implemented two ways of population removal that represent two extreme cases of habitat loss. The first is random removal, i.e., the population of each species is thinned by randomly throwing away $c = 80\%$, 50%, or 30% of the population (Fig. 2c). The second is systematic removal, e.g., the population of each species is reduced by sweeping from the left to the right side of the plot until $c = 80\%$, 50%, or 30% of the individuals are removed (Fig. 2d). Note that for the systematic removal, other directions of removal (e.g., from right to left or up to down) do not change the results. Although neither of these two extreme cases occurs in reality, because landscape destruction is often spatially aggregated, the first scenario might be more relevant for describing the effect of haphazard weather or climate, whereas the second may better reflect land-use change such as agricultural expansion or deforestation. More often though, the manners of disturbances probably fall between these two extremes, e.g., hunting and selective logging neither randomly nor systematically remove populations but are constrained by accessibility. For this reason, I used the occupancy (p_c) averaged over the p_c's of the two extreme cases of Fig. 2c and d to represent population removal. The results are shown in Fig. 3. The relationships between p and p_c for random and systematic removals are shown in the Appendix: Figs. A1 and A2, respectively. Random removal produces higher p_c than systematic removal, an expected outcome because random removal makes the distribution of the remaining population more scattered across the region than does the systematic removal. For example, after 80% of the population is removed, the remaining 304 trees in Fig. 2c are spread across the entire plot, as opposed to clustered on the right portion of the plot in Fig. 2d. The performance of Eq. 1 seems to become progressively poorer with an increase in cell size for the

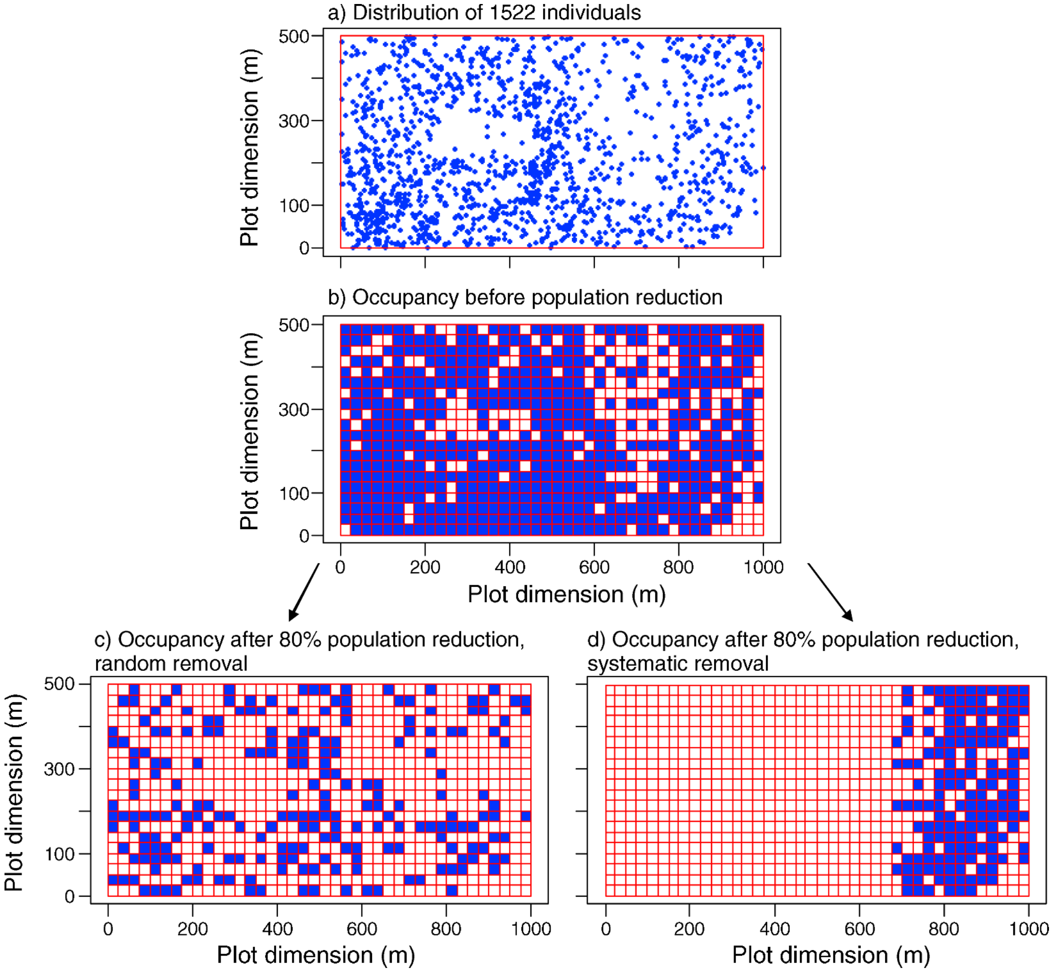


FIG. 2. (a) Distribution of 1522 individuals of an understory tree species, *Lacistema aggregatum* (Flacourtiaceae), in the 50-ha plot on Barro Colorado Island, Panama. (b) Occupancy before removal (cell size 25 × 25 m); proportion of cells occupied is $p = 0.748$. (c) Occupancy after randomly removing 80% of the population (304 individuals remain); $p_c = 0.274$. (d) Occupancy after systematically removing 80% of the population (304 individuals remain); $p_c = 0.200$.

BCI species (the first three rows of Fig. 3), although the deterioration appears to be small as judged by the values of R^2 (lowest $R^2 = 0.952$).

The second data set is a subset of the 372 species used in Hurlbert and White (2005). It describes the distribution of population sizes for 348 land bird species (excluding nocturnal, crepuscular, and raptorial species) on 4950 routes of the North American Breeding Bird Survey (BBS). The population size of each species in each route is a sum of a 5-year period (2003–2007). The use of 5-year sum is a common practice in the literature to avoid inadequate sampling (Hurlbert and White 2005). Not all of the 4950 routes are suitable for colonization of every species. For each species, the routes located within its distribution range are considered suitable, based on its NatureServe range map (*available online*).[2] To test Eq. 1, I again implemented random removal and systematic removal of populations. For random removal, individuals of a bird population across routes had the same chance to be thrown away. For systematic removal, a route was first randomly selected and then all of the individuals within the selected route were discarded until the required percentages (80%, 50%, and 30%) of a bird population were removed. The averaged results for the random and systematic removals are shown in Fig. 3. Results of the respective random and systematic removals are shown in the Appendix: Fig. A3.

RESULTS

As expected, Eq. 1 predicts very well the change in occupancy resulting from the reduction of population size (Fig. 3; Appendix: Figs. A1–A3). The correlation coefficients between the reduced occupancy (p_c) and the model prediction are consistently larger than 0.85 across all the threatened levels and

---

[2] www.natureserve.org/getData/birdMaps.jsp

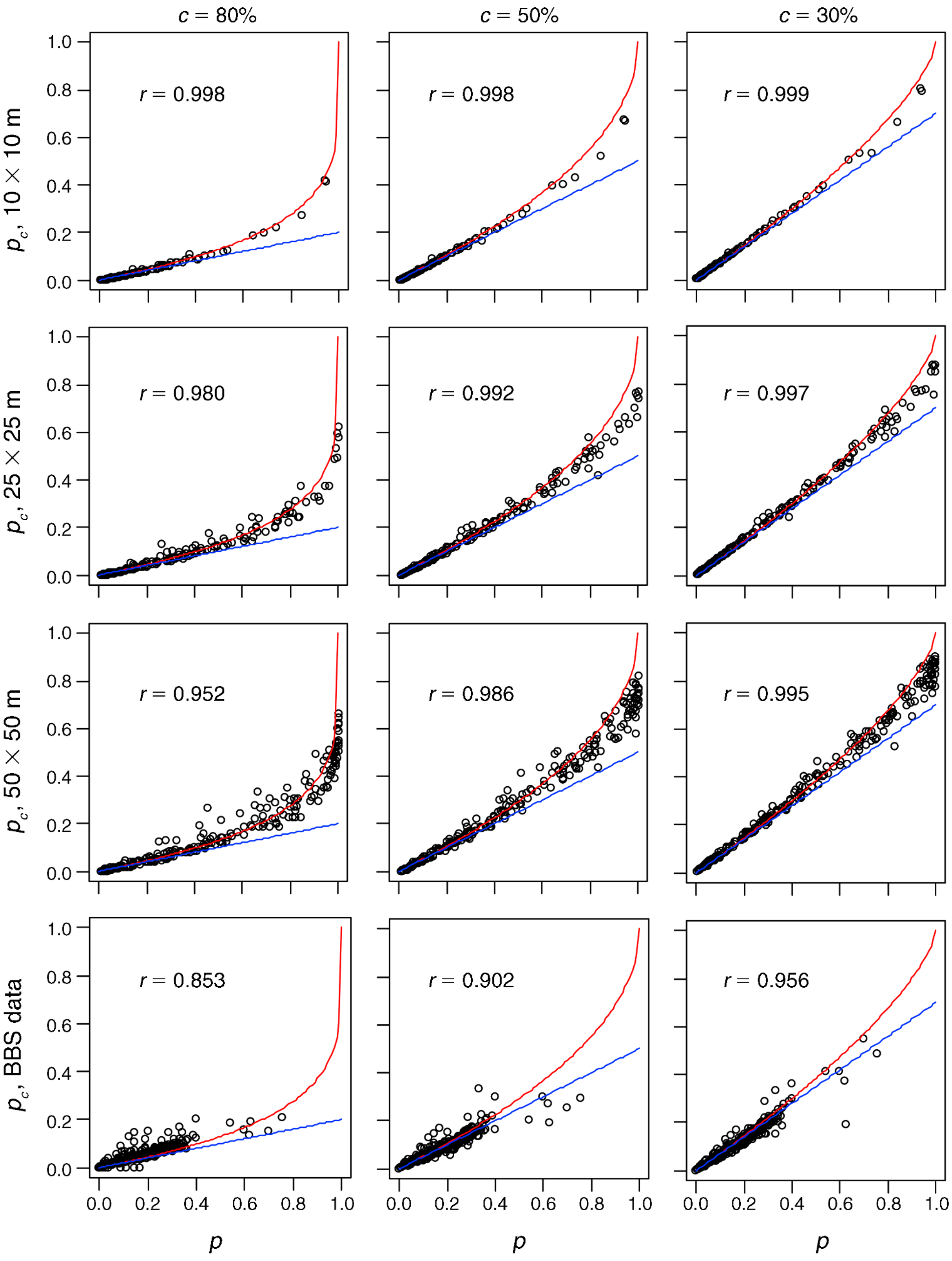


FIG. 3. The p–p_c relationship for three Red List threat levels ($c = 80\%$, 50%, and 30%) for 302 tree species in the 50-ha BCI plot, Panama (at three different spatial scales, $a = 10 \times 10$, 25×25, and 50×50 m; first 3 rows) and for 348 land bird species of the North American Breeding Bird Survey (BBS, bottom row). Dots are the averaged occupancy of random and systematic removal. Red curves are Eq. 1, whereas the blue lines are the linear approximation of Eq. 1: $p_c = (1 - c)p$. Pearson's correlation coefficient (r) describes how well Eq. 1 predicts the empirical p–p_c relationship.

scales (Fig. 3). Note that the model works especially well for small values of p (e.g., <0.40). Following a Taylor expansion, Eq. 1 can be approximated by $p_c = (1 - c)p$ for small p or c. This linear approximation is shown in Fig. 3 (also in Appendix: Figs. A1–A3) and can be useful because, in practice, what most concerns IUCN risk assessments are those species with small occupancies.

DISCUSSION

Eq. 1 integrates criteria A and B of the IUCN system into a single method. With the aid of Eq. 1, assessment of endangerment can now be made based on the concept of criterion A, but using the occupancy measure of criterion B. This overcomes a dilemma in application of the IUCN system: criterion A is biologically sound but requires labor-intensive data on population size, while occupancy data for criterion B are easier to collect but the criterion lacks biological justification. Eq. 1 is a simple yet general model that has no free parameters and is independent of spatial scale. With the wealth of data on species' distributions, the model could significantly facilitate the assessment of extinction risks worldwide.

A striking feature of Eq. 1, as shown in Fig. 3 and the Appendix, is its scale independence: the same model equally applies to different map resolutions (e.g., across three resolutions of the BCI data) and different map extents (e.g., across the BCI and the BBS data). The Red List is primarily designed for assessing extinction risk at the global level. Nonetheless, since the original publication and rapid expansion of the Red List, there has been a widespread demand for applying the IUCN system to regions within countries (Eken et al. 2004, Miller et al. 2007, Mace et al. 2008). The extent-independence of Eq. 1 allows adapting the IUCN system to any designated area. It is, however, worth noting that although Eq. 1 applies to species that have distributions of different extents and resolutions, the extent and resolution of the distribution of a given species must be kept constant during the period of assessment (10 years or three generations, whichever is longer). Otherwise, the occupancy data are invalid for IUCN assessment; this requirement also applies to Eq. 1.

Another useful property of Eq. 1 is that it reinforces the use of spatial distributions as a measure of extinction risk. As shown by the North American birds, global data on the trend of population density or change in global distribution are not necessary for IUCN threat assessment; what is needed for applying Eq. 1 is the change in species occurrence in multiple sites. Practically, this property is very useful because a simple measure of variation in population size might not reflect the difference in spatial distribution: two species of the same size can have very different occupancies (Gaston 1996, He and Condit 2007). Species with a small range area in which all individuals are clustered in one location could face a higher extinction risk than species occupying multiple sites forming a metapopulation. This difference can be easily represented by Eq. 1. For example, suppose two species have the same population size, but one has occupancy $p = 0.2$ and the other $p = 0.3$. A reduction of 80% of the population will lead to the reduction of range areas of the two species to $p_c = 0.0436$ and 0.0688, respectively.

Note that the accurate application of Eq. 1 relies on the quality of data. The BCI and BBS data are exceptional in that both the total area and the spatial resolution of occurrences are well defined. For real species of concern, occurrence data usually do not have that level of quality. To minimize the uncertainty associated with messy data in application, decisions need to be made regarding (1) what occurrence data should be used (e.g., occurrences over 5 years, 10 years, or longer; for the BBS data, 5-years occurrence is used), and (2) what grid size should be used to evaluate occurrence (data quality usually decreases with increasing grid size). Another limitation of Eq. 1 is that it does not account for dynamic variation in species distributions driven by potentially many mechanisms, particularly Allee effects and demographic, environmental, and genetic stochasticities that can accelerate the extinction risk of small (endangered) populations. These processes, together with others (e.g., lagged response of population abundance to habitat loss, recolonization of destroyed habitats), can have important effects on the relationship between habitat loss and population reduction and, in turn, on the outcome of endangerment assessment (IUCN-SSC 2010: section 5.7). For these reasons, Eq. 1 should be used with caution and in alignment with the IUCN criteria that rely on the net change in distribution (or population size) over the period of assessment (10 years or three generations). Further tests of Eq. 1 are needed to evaluate its reliability in the face of poor data quality and dynamic change in distribution and population abundance.

The impact of the Red List on the conservation community is so profound that it has fundamentally changed the way biological conservation is studied, legislated, and practiced (Hutton and Dixon 2000, Lamoreux et al. 2003, Rodrigues et al. 2006). Simplicity, flexibility, consistency, and ease of implementation of the measures of extinction risk are crucial to the global effort of Red List assessments (Lamoreux et al. 2003, Mace et al. 2008). These principles are important for minimizing geographical and taxonomic biases in the Red List and for making the best use of the limited information to inform conservation decisions. This study contributes to the quantification of extinction risk in general and to the IUCN assessments in particular by providing a simple, yet general, model for standardizing the assessment of extinction risk using distributional data. Expansion of the taxonomic coverage of Red List assessments has been identified as the highest priority of the IUCN Red List, which currently covers only ~2.7% of known species (Rodrigues et al. 2006, Barnosky et al. 2011). With the wealth of data (Mitchell-Jones et al. 1999, BirdLife International 2004, IUCN-SSC 2004) and increasingly realistic models for species' distributions (Raxworthy et al. 2003, Guisan et al. 2006), the method developed here will contribute significantly to achieving this goal.

Acknowledgments

I thank Corey Bradshaw, Thomas Brooks, Kevin Gaston, Georgina Mace, and three anonymous reviewers for their constructive comments on early drafts which substantially improved this paper. Allen Hurlbert generously provided the Breeding Bird Survey data for use in this study. This work was supported by Sun Yat-sen University, the NSERC (Canada), and GEOIDE (Canada).

Literature Cited

Barnosky, A. D., N. Matzke, S. Tomiya, G. O. U. Wogan, B. Swartz, T. B. Quental, C. Marshall, J. L. McGuire, E. L.

Lindsey, K. C. Maguire, B. Mersey, and E. A. Ferrer. 2011. Has the Earth's sixth mass extinction already arrived? Nature 471:51–57.

BirdLife International. 2004. Threatened birds of the world 2004. CDROM BirdLife International. www.birdlife.org/datazone/species/index.html

Boswell, M. T., and G. P. Patil. 1970. Chance mechanisms generating the negative binomial distributions. Pages 3–22 *in* G. P. Patil, editor. Random counts in models and structures. Pennsylvania State University Press, University Park, Pennsylvania, USA.

Caughley, G. 1994. Directions in conservation biology. Journal of Animal Ecology 63:215–244.

Eken, G., et al. 2004. Key biodiversity areas as site conservation targets. Bioscience 54:1110–1118.

Gaston, K. J. 1994. Measuring geographic range sizes. Ecography 17:198–205.

Gaston, K. J. 1996. The multiple forms of the interspecific abundance–distribution relationship. Oikos 76:211–220.

Gaston, K. J., and F. He. 2010. Species occurrence and occupancy. Pages 141–151 *in* A. Maguran and B. McGill, editors. Biological diversity: frontiers in measurement and assessment. Oxford University Press, Oxford, UK.

Guisan, A., A. Lehmann, S. Ferrier, M. Austin, J. M. C. C. Overton, R. Aspinall, and T. Hastie. 2006. Making better biogeographical predictions of species' distributions. Journal of Applied Ecology 43:386–392.

He, F., and R. Condit. 2007. The distribution of species: occupancy, scale and rarity. Pages 32–50 *in* D. Storch, P. L. Marquet, and J. H. Brown, editors. Scaling biodiversity. Cambridge University Press, Cambridge, UK.

He, F., and K. J. Gaston. 2000. Estimating species abundance from occurrence. American Naturalist 156:553–559.

Höglund, J. 2008. Evolutionary conservation genetics. Oxford University Press, Oxford, UK.

Hurlbert, A. H., and E. P. White. 2005. Disparity between range map- and survey-based analyses of species richness: patterns, processes and implications. Ecology Letters 8:319–327.

Hutton, J., and B. Dixon. 2000. Endangered species, threatened convention: the past, present and future of CITES. Earthscan Publications, London, UK.

IUCN-SSC. 2004. Global amphibian assessment. IUCN-SSC, Conservation International, and NatureServe. International Union for Conservation of Nature, Standards and Petitions Subcommittee, Gland, Switzerland.

IUCN-SSC. 2010. Guidelines for using the IUCN Red List categories and criteria. Version 8.1. International Union for Conservation of Nature, Standards and Petitions Subcommittee, Gland, Switzerland. intranet.iucn.org/webfiles/doc/SSC/RedList/RedListGuidelines.pdf

Johnson, N. L., S. Kotz, and A. W. Kemp. 1993. Univariate discrete distributions. John Wiley, New York, New York, USA.

Lamoreux, J., et al. 2003. Value of the IUCN Red List. Trends in Ecology and Evolution 18:214–215.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Mace, G. M., N. J. Collar, K. J. Gaston, C. Hilton-Taylor. H. R. Akçakaya, N. Leader-Williams, E. J. Milner-Gulland, and S. N. Stuart, editors. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. Conservation Biology 22:1424–1442.

Mace, G. M., and R. Lande. 1991. Assessing extinction threats: towards a reevaluation of IUCN threatened species categories. Conservation Biology 5:148–157.

Miller, R. M., J. P. Rodríguez, T. Aniskowicz-Fowler, C. Bambaradeniya, R. Boles, M. A. Eaton, U. Gärdenfors, V. Keller, S. Molur, S. Walker, and C. Pollock. 2007. National threatened species listing based on IUCN criteria and regional guidelines: current status and future perspectives. Conservation Biology 21:684–696.

Mitchell-Jones, A. J., W. Bogdanowicz, B. Krystufek, P. J. H. Reijnders, F. Spitzenberger, C. Stubbe, J. B. M. Thissen, V. Vohralík, and J. Zima. 1999. The atlas of European mammals. Poyser, London, UK.

Mrosovsky, N. 1997. IUCN's credibility critically endangered. Nature 389:436.

Pielou, E. C. 1977. Mathematical ecology. John Wiley, New York, New York, USA.

Possingham, H. P., S. J. Andelman, M. A. Burgman, R. A. Medellin, L. L. Master, and D. A. Keith. 2002. Limits to the use of threatened species lists. Trends in Ecology and Evolution 17:503–507.

Raxworthy, C. J., E. Martinez-Meyer, N. Horning, R. A. Nussbaum, G. E. Schneider, M. A. Ortega-Huerta, and A. T. Peterson. 2003. Predicting distributions of known and unknown reptile species in Madagascar. Nature 426:837–841.

Robbirt, K. M., D. L. Roberts, and J. A. Hawkins. 2006. Comparing IUCN and probabilistic assessments of threat: Do IUCN Red List criteria conflate rarity and threat? Biodiversity and Conservation 15:1903–1912.

Rodrigues, A. S. L., J. D. Pilgrim, J. F. Lamoreux, M. Hoffmann, and T. M. Brooks. 2006. The value of the IUCN Red List for conservation. Trends in Ecology and Evolution 21:71–76.

SUPPLEMENTAL MATERIAL

Appendix

Figures showing relationships between occupancies before and after population removal for the 302 species in the 50-ha BCI plot, Panama, and the 348 land bird species of the North American Breeding Bird Survey with random removal and systematic removal, respectively (*Ecological Archives* E093-086-A1).