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Assessing extinction risk in the absence of species-level data: quantitative criteria for terrestrial ecosystems

RODRIGUEZ Jon Paul* (Balch J. K. and Rodriguez-Clark K.M.) Instituto Venezolano de Investigaciones Cientificas (Ivic). Centro de Ecologia Apdo. 21827 1020-A Caracas VENEZUELA ORIGINAL PAPER

Assessing extinction risk in the absence of species-level data: quantitative criteria for terrestrial ecosystems

Jon Paul Rodríguez · Jennifer K. Balch · Kathryn M. Rodríguez-Clark

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Abstract The conservation of individual plant and animal species has been advanced greatly by the World Conservation Union's (IUCN) development of objective, repeatable, and transparent criteria for assessing extinction risk, which explicitly separate the process of risk assessment from priority-setting. Here we present an analogous procedure for assessing the extinction risk of terrestrial ecosystems, which may complement traditional species-specific risk assessments, or may provide an alternative when only landscape-level data are available. We developed four quantitative risk criteria, derived primarily from remotely sensed spatial data, information on one of which must be available to permit classification. Using a naming system analogous to the present IUCN species-specific system, our four criteria were: (A) reduction of land cover and continuing threat, (B) rapid rate of land cover change, (C) increased fragmentation, and (D) highly restricted geographical distribution. We applied these criteria to five ecosystems covering a range of spatial and temporal scales, regions of the world, and ecosystem types, and found that Indonesian Borneo's lowland tropical forests and the Brazilian Atlantic rainforest were Critically Endangered, while South Africa's grasslands and Brazil's Mato Grosso were Vulnerable. Furthermore, at a finer grain of analysis, one region of Venezuela's coastal dry forests (Margarita Island) qualified as Vulnerable, while another (the Guasare River watershed) was Critically Endangered. In northern

J. P. Rodríguez (🖂) · J. K. Balch · K. M. Rodríguez-Clark

Centro de Ecología, Instituto Venezolano de Investigaciones Científicas, Apartado 21827, Caracas 1020-A, Venezuela e-mail: jonpaul@ivic.ve

e mani jonpaarennen

J. P. Rodríguez · J. K. Balch Provita, Apartado 47552, Caracas 1041-A, Venezuela

Present Address: J. K. Balch School of Forestry & Environmental Studies, Yale University, 205 Prospect Street, New Haven, CT 06511-2186, USA

Jon Paul Rodríguez and Jennifer K. Balch contributed equally to this work

Venezuela, deciduous forests were classified as Endangered, semi-deciduous forests Vulnerable, and evergreen forests of Least Concern. We conclude that adoption of such a standardized system will facilitate globally comparable, repeatable geographic analyses that clearly separate risk assessment (a fundamentally scientific process), from the definition of conservation priorities, which should take into account additional factors, such as ecological distinctiveness, costs, logistics, likelihood of success, and societal preferences.

Keywords Endangered · Extinction risk · IUCN Red Lists · Land cover change · Remotely sensed data · Terrestrial ecosystems · Threatened

Introduction

Given the perennially limited funds available for conservation of the world's biodiversity, a great deal of research effort has been invested in the process of setting conservation priorities (Avery et al. 1995; Dinerstein et al. 1995; Olson and Dinerstein 1998; Stattersfield et al. 1998; Margules and Pressey 2000; Myers et al. 2000; The Nature Conservancy 1997; Gregory et al. 2002; Polishchuk 2002; Keller and Bollmann 2004; Kuper et al. 2004; Rodrigues et al. 2004; Rodríguez et al. 2004a; Eaton et al. 2005; Kier et al. 2005). One factor often considered in this process, and which has received particular attention in the recent scientific literature, is extinction risk (Baillie et al. 2004; Butchart et al. 2004; Stuart et al. 2004; Butchart et al. 2005; Ricketts et al. 2005; Rodrigues et al. 2006). During the past decade, the World Conservation Union (IUCN) thoroughly revised its methods for assigning categories to threatened species, in an attempt to make classification more objective, repeatable and transparent, and to separate the determination of extinction risk from the definition of conservation priorities (Mace and Lande 1991; IUCN 2001, 2004). At present, red list categories are designed to solely reflect a taxon's extinction risk, while prioritization of conservation action is considered a second step in the process, which should take into account many additional factors (IUCN 2001, 2004).

While the IUCN system has greatly assisted conservation efforts at the individual species level (resulting in, for example, many taxon-specific Action Plans; Thorbjarnarson et al. 1992; Wilcove 1994; Servheen et al. 1999; Brooks and Strahl 2000; Snyder et al. 2000), complimentary assessment tools are needed for several reasons. First, individual species may be more or less threatened than the habitats they use (e.g. Bodmer and Robinson 2004; Brashares et al. 2004; Blom et al. 2005; Nijman 2005). Second, individual assessments cannot hope to keep pace with current levels of biodiversity loss (May et al. 1995; Baillie et al. 2004; Mace et al. 2005). Although the system has functioned well for many groups with a sufficient critical mass of specialists and researchers to produce the detailed data required for individual assessments (e.g., Thorbjarnarson et al. 1992; Servheen et al. 1999; Brooks and Strahl 2000; Snyder et al. 2000), it has lagged far behind for other less-well studied groups. To date, the IUCN has published 66 animal Species Action Plans, but 47 of these are for mammals and 11 for birds, while only five are for reptiles, two for invertebrates and one for fishes (IUCN 2006). Finally, the species-level focus of IUCN risk assessments does not translate directly into the landscape-level conservation strategies that may ultimately be most efficient and effective, especially in 🖉 Springer

data-poor regions of the world (Noss 1996; Ward et al. 1999; Ferrier 2002; Bonn and Gaston 2005).

One approach to overcoming these limitations to species-centered assessments is to develop criteria for assessing extinction risk at a higher level of biological organization: the ecosystem. Such an approach could take advantage of recent advances in geographical information systems (GIS)-more powerful computers, less expensive software packages, and increasingly available remotely sensed satellite data, spanning two to four decades—which allow quantification of land cover change. Rather than replacing the IUCN's species listing process, assessing ecosystem extinction risk could complement it or provide a useful alternative when only landscape-level data are available, and could offer at least three additional advantages. First, a holistic approach could lead to the creation of regional reserves, aimed not only on maintaining viable populations of species, but also at ensuring ecosystem services (Franklin 1993; Heal et al. 2001; Heinz Center 2002; Foley et al. 2005; Hassan et al. 2005). Second, an ecosystem focus could produce assessments more rapidly, allowing for the more proactive, preventative conservation strategies that are more cost-effective than rehabilitation or restoration (Orians 1993; Scott et al. 1993; Noss 1996). Third, with the rapid increase in GIS and remote-sensing analyses of land cover change, a focus on ecosystem extinction risk could provide a means to synthesize disparate local studies into a coherent global assessment.

In recognition of the many advantages of an ecosystem focus, to date several attempts have been made to establish ecosystem-level conservation criteria. Prominent among these are: the World Wildlife Fund's (WWF) 'ecoregions' (Olson et al. 2001); Conservation International's 'hotspots' and 'wilderness areas' (Mittermeier et al. 1998; Myers et al. 2000); The Nature Conservancy's (TNC) focus on 'functional conservation areas' and 'conservation status ranks' (The Nature Conservancy 2001; Regan et al. 2004); the TNC-WWF joint effort to quantify the 'level of threat to the world's biomes' (Hoekstra et al. 2005); Blab et al.'s (1995) proposal for a 'national red data book of biotopes' in Germany; and most recently the smaller-scaled but very detailed work of Benson and his colleagues in New South Wales, Australia (Benson 2006; Benson et al. 2006). While these efforts represent important advances, they all share a similar constraint (that the IUCN categories also suffered initially, two decades ago; Mace and Lande 1991): among their criteria they include factors which, though important for *priority-setting*, are not directly relevant to *risk* (such as 'degree of legal protection,' Dinerstein et al. 1995; 'biological importance,' Mittermeier et al. 1998; 'regeneration ability,' Blab et al. 1995).

One alternative would be a system which focuses on extinction risk alone as measured by actual or projected land cover extent and changes, allowing for a clearer interpretation of the likelihood that a particular biological assemblage may disappear. After this risk has been determined in a scientific context, whether or not to invest limited conservation resources in that threatened ecosystem may then be made in a societal context, by including additional biological, social, economic, legal, logistical or cultural factors such as those listed above (Mace and Lande 1991; Gärdenfors et al. 2001; IUCN 2004).

Here we propose such a system for assessing relative ecosystem extinction risk, incorporating four quantitative criteria derived from landscape-level ecosystem characteristics, analogous to the present IUCN species-centered system. We then apply this system to six sets of previously published remotely sensed land cover data, covering a range of spatial and temporal scales (decades to centuries, and tens to millions of square kilometers), regions of the world (Brazil, Indonesia, South Africa, and Venezuela), and ecosystem types (from grasslands to tropical humid forests). Our central purpose is to present a conceptual framework and the first draft of a broadly applicable system, with all decisions explicitly presented to facilitate subsequent collaborative improvement, much as the present IUCN system was developed (Mace and Lande 1991; Mace et al. 1992; Mace and Stuart 1994; IUCN 1994, 2001).

Methods

The techniques we used to design a system for classifying ecosystem risk included considering the definition of an ecosystem and its extinction, the unit of analysis, the spatial scale of the analysis, the temporal scale of the analysis, and the actual risk criteria with their accompanying thresholds for different levels of threat. We then applied these quantitative criteria to Indonesian Borneo's lowland tropical forests, Brazil's Atlantic rainforests and Mato Grosso, two Venezuelan dry forest sites, the ecosystems of northern Venezuela, and South African grasslands.

Definition of an ecosystem and its extinction

Although shifting focus to a higher level of biological organization may initially seem to introduce new problems of definition ('What is an ecosystem?'), we are encouraged that the ongoing debate about how to define a species has not diminished the usefulness or widespread adoption of the present species-based IUCN system, which similarly declines to provide a universal species definition (Peterson and Navarro-Sigüenza 1999; Agapow 2005). Similarly, many valid definitions for an ecosystem have been proposed (e.g., Gleason 1926; Tansley 1935; Odum 1969; Whittaker 1975; Pickett and Cadenasso 2002), and although we prefer the traditional "unit of biological organization that encompasses a unique and relatively homogeneous composition of species and abiotic elements and their dynamic processes" (Odum 1969; Whittaker 1975), we emphasize that a universal definition is not necessary for successful classification. This definition is useful because it underscores that this *composition* of species and other elements which is worth preserving, because of its contribution to ecosystem function (Hassan et al. 2005). And although it has been difficult to prove experimentally, increasing evidence indicates that modification of original ecosystem composition can compromise function and resilience to natural and anthropogenic change (e.g., Dukes et al. 2005; Hooper et al. 2005; Spehn et al. 2005; Tilman et al. 2006). However, in practice, more simplified and practical definitions (based on delimiting ground-truthed areas with similar spectral properties) may be more readily applicable (much in the same way that the biological species concept is often theoretically preferred but the morphological species concept is more often applied). In the end, what is most important is that the definition used in any particular classification exercise be specified (McMahon et al. 2004).

As difficult as defining an ecosystem may be, defining the risk of its extinction presents an even greater challenge. If an ecosystem is defined by its composition at a given point in time, then at one extreme extinction may be any change (however slight) in that composition, while at another extreme it may occur only when all original components are completely gone. Between these extremes of infinitesimal and complete change, we find an intermediate definition to be more useful, particularly one that is quantifiable with the tools and information sources readily available for this task. Using remotely sensed data, we consider an ecosystem extinct if no intact land cover of the original ecosystem exists. Some components of the ecosystem may still exist, but the way in which all original components were organized no longer does. Under this definition of ecosystem extinction, if something resembling the original composition reappears (e.g. if secondary forests mature to old growth forests), the original ecosystem must still be considered extinct—although a critically endangered ecosystem may move to lower levels of risk if the small remaining patches of the unaltered original ecosystem expand and reconnect due to secondary growth over the long term. This assumes that if an ecosystem is severely degraded but still extant in some areas, sufficient original components may be present to recover most ecological functions. It is likely, however, that some functions such as those provided by top predators and other wide-ranging species, might be irreversibly lost (e.g. Laidlaw 2000; Sanderson et al. 2002).

The unit of analysis

Ideally, an ecosystem classification system should define the unit of analysis, a method for defining the 'original' ecosystem, and a method for delineating alternative (more recent) ecosystems. However, ecosystems are intrinsically complicated and dynamic, which makes these tasks difficult. Attempts to develop an accepted ecosystem classification system based on ecological theory started in the late 1800s and continue today (Orians 1993; McMahon et al. 2004). However, we agree with other authors who have observed that nearly any classification of ecosystems that is broad enough to encompass both species distributions and ecological processes, yet sufficiently discrete to allow repeatable mapping of ecosystems in time and space, may allow practical risk assessment and target-setting (Noss 1996). Ultimately, any ecosystem delineation is an abstraction—as is any defined species distribution—and any classification decision will have consequences for how extinction risk is determined.

As a result of this recognition, most classification systems to date have taken a more pragmatic mapping approach, rather than using theoretical definitions (McMahon et al. 2004). In this spirit, we advocate a variation on this practical approach: first define arbitrary units on the landscape, and then quantify land cover change within them. According to the needs of the user, these units may be natural divisions (such as watersheds or land cover types), political boundaries (such as counties, states or nations), or fully arbitrary units (such as grid cells). In all cases, the unit of analysis is a delimited portion of the landscape, and the extinction risk reflects the degree of land cover change that has taken or is projected to take place within it. Such a process has the advantage of flexibly producing risk estimates for landscape units that are either biologically meaningful (e.g., watersheds), meaningful for human planning (e.g. political boundaries, watersheds), or at least easy to define (e.g. a square, 100 km \times 100 km grid).

As with the ecosystem itself, what is most important is that the unit of analysis be defined clearly, because the interpretation of the risk category assigned to a portion of the landscape is intimately dependent on how this portion relates to the rest. A similar problem is faced by assessors when they implement IUCN species red listing at the regional level (Gärdenfors et al. 2001; IUCN 2003). In these analyses, assessors

quantify the risk of extinction of a population that is arbitrarily defined by political boundaries, but are required to report other data such as the global risk category, and the proportion of the global population that the regional population represents. While the global risk status of an ecosystem might not influence local extinction risk directly, it is still a fundamental piece of information for policymakers interested in using red list categories as one of the inputs for conservation priority setting.

The temporal scale of analysis

Another element required by a transparent and repeatable risk classification system is an explicit time scale (Mace and Lande 1991). In the present species-focused IUCN system, one temporal issue is the period of time over which extinction risk must be considered into the future, to assign risk categories. This is solved with a combination scale, which in some cases considers the horizon over which human activities can be reasonably planned (e.g. risk of extinction in 10 years), and in others considers the time frame set by demographic processes within the species in question (e.g. risk of extinction in three generations)—although future projections are never allowed to exceed 100 years (IUCN 2001). At an ecosystem level, we consider a fixed time interval to be more relevant, given that the widely varying demographic characteristics of the constituent species of an ecosystem preclude a more biologically based timescale. On the longer evolutionary time scales over which such biologically based measures might converge, issues of conservation become trivial: extinction of species and ecosystems moves from probabilistic to certain, since given enough time all life forms go extinct and are replaced by others. We therefore propose a ~ 30-year time frame into the future, as this interval falls within the scope of human planning and policy-setting cycles. It is sufficiently long to reflect slow human-driven change, but not so long as to increase uncertainties in model predictions.

As in the case with species-level analyses (IUCN 2001), at the ecosystem level an additional temporal issue becomes important: at what point in the past to set the baseline, to define 'original' ecosystems. Again, we feel that the actual choice here is less important than the fact that it be made explicit, and propose two different time frames for baselines. In the case of Criteria A and C (see below), which consider the amount of change in or fragmentation of the original ecosystem, the choice of the baseline may be flexible in order to encompass a time interval relevant to anthropogenic disturbance in that ecosystem in that landscape (and to take advantage of 'older' datasets such as aerial photographs or written accounts). In the case of Criterion B, which focuses on the rate of change of ecosystem cover, we suggest that analyses focus again on an interval of ~ 30 years, with a baseline at approximately 1970. This is for the reasons given above, as well as the fact that the availability of global quantitative land cover change data is greatest during this period. Furthermore, even if data were available, trends calculated from baselines set too far in the past might not reflect more recent human-caused land cover change patterns and result in an incorrect estimate of current extinction risk.

The spatial scale of analysis

The spatial scale of any mapping task is composed of two aspects: the grain or resolution at which the area is examined, and the total extent of the area considered (Savitsky and Lacher Jr. 1998). To select the resolution of analysis, several factors

are important: the scale at which species interactions relevant for ecosystem processes occur; the scale at which human modification has taken place and in which conservation efforts can proceed; and practical limitations imposed by the raw data and the equipment available. Species interactions and ecological processes of course occur at various spatio-temporal resolutions (Levin 1992). However, research to date suggests that fewer processes appear to be captured at the patch scale than at the landscape scale. Using data on the distributions of British plants and animals mapped on a 10 km \times 10 km grid (i.e., at a 'patch' scale), Prendergast et al. (1993) found that species-rich areas frequently do not coincide for different taxa, nor do they coincide with the distributions of many rare species. Using data on Australian birds, mapped on a 100 km \times 100 km grid (a 'landscape' scale), Curnutt et al. (1994), however, found that the second pattern dissolves, and that rarity overlaps with species richness to a greater extent. Also, habitat fragmentation is more likely to have significant effects on bird nesting success and predation at a landscape scale, rather than edge or patch scales (Stephens et al. 2003).

Human modification can occur in areas ranging from entire countries (e.g., vegetation change across Madagascar; Green and Sussman 1990), to individual neighborhoods and houses (e.g., steady human encroachment in the cloud forests of Venezuela's Cordillera de la Costa; Llamozas et al. 2003). Similarly, the spatial extent of conservation efforts (as well as their resolution) may vary greatly depending on the conservation entity's priorities, targets, and resources. In a study of 21 different conservation approaches, Redford et al. (2003) found that the extent of activities ranged from 10 km² to over a billion km² (and the resolution of activities ranged from 100 m² to over 10^{6} km²). In the end, however, the remote-sensing imagery analysis essential to any ecosystem risk assessment may impose the most important scale on the classification process. The size of satellite images available and their pixel resolution is often fixed; for example, a Landsat Thematic Mapper image has a width of 186 km and a grain size of 30×30 m (Savitsky and Lacher Jr. 1998). There also may be practical limitations to the number of images that can be processed and analyzed by any one research group, given the length and amount of typical funding cycles.

Rather than recommending a single resolution and extent for the analysis of ecosystem extinction risk, we propose that this should be determined by the assessor, according both to the geographical extent of the area of interest and to the type of data available. To illustrate this, the examples that we selected to test the system below cover a wide range of spatial (and temporal) scales.

Proposed criteria: principles

Once the units and spatio-temporal scales of analyses have been defined, the final step in ecosystem risk assessment is to assess observed ecosystem changes against unambiguous, predetermined risk criteria. In defining these criteria for ecosystem threat levels, we have adhered to some general principles to maintain consistency and promote wide applicability. Following Mace and Lande's (1991) suggestions for the IUCN species red listing process, we chose criteria to be as intuitive as possible. We deliberately selected variables that were relatively easy to quantify, with thresholds that were straightforward. Each criterion captured different information about the system in question, which is important for any set of measures trying to characterize the overall status of an ecosystem (Riitters et al. 1995). When possible,

our criteria were directly parallel to existing criteria for species and were relevant not only to ecosystem characteristics (e.g., area) but also ecosystem processes (e.g., rate of land cover change).

We designed four quantitative criteria (Fig. 1); evaluation within any one criterion was held as sufficient to estimate risk (thus allowing, but not requiring, evaluation of more than one criterion). Within each criterion, we then set thresholds based on fundamental principles of ecological theory, field studies, and meaningful time frames, in order to reflect eight categories of risk: Extinct (EX, defined above), Critically Endangered (CR), Endangered (EN), Vulnerable (VU), Near Threatened (NT), Least Concern (LC), Data Deficient (DD), and Not Evaluated (NE). By analogy to IUCN Red List categories (IUCN 2001), CR, EN and VU corresponded to the *threatened* ecosystem categories, and were assigned on the basis of the quantitative criteria discussed below. They had the quality of being inclusive, such that an ecosystem meeting a criterion for CR, also met those for EN and VU, and



Fig. 1 Schematic representation of the process for assigning *threatened* ecosystem categories (CR, EN and VU), illustrating their inclusive nature (e.g. if an ecosystem qualifies for CR, it also qualifies for EN and VU). The remaining categories: Near Threatened (NT), Least Concern (LC), Data Deficient (DD), and Not Evaluated (NE) are not assigned according to quantitative thresholds (as in the current IUCN system for species). An ecosystem is considered Extinct (EX) if no intact land cover of the original ecosystem exists

one meeting a criterion for EN also qualified as VU. Although all of the cases presented below fall within these three categories, we briefly note that an additional four categories (besides EX) are necessary to cover the full spectrum of possibilities when classifying a large number of ecosystems. NT applies to ecosystems that do not qualify as threatened at present, but may be close. LC applies to ecosystems that do not qualify (and are not close to qualifying) as threatened or NT. DD and NE do not reflect the current risk status, and instead apply to ecosystems for which there is not sufficient information to make a sound quantitative assessment (DD), or which have not yet been assessed against the criteria (NE).

Following the example of the IUCN Red Lists, we used ecological 'rules of thumb' to select the criteria and to determine the thresholds between the ecosystem threat categories of CR, EN, and VU. For example, we assumed that increased fragmentation as a result of human modification represented increased risk (see below), because several different general mechanisms are known to contribute to the decline of ecosystem remnants which are small and isolated—including increased edge effects, decreased dispersal of ecosystem-maintaining species, inbreeding and loss of gene diversity, and increased susceptibility to stochastic events, among others (Wilcove et al. 1986; Laurance et al. 2002; Frankham 2005). Finally, we tried to select criteria that could be applied both to previously published data (as we have done below) as well as to novel data collected expressly for assessing relative extinction risk.

The four quantitative criteria and their thresholds

Our four quantitative criteria were designed to be analogous to the present speciesbased system, but are based on measures of ecosystem 'quantity' and its change rather than population size and its change (IUCN 2001). These are encompassed by four landscape attributes: (A) reduction of land cover and continuing threat, (B) rapid rate of land cover change, (C) increased fragmentation, and (D) highly restricted geographical distribution. In general, we found that previously published data were more readily available for Criteria A and B than for C and D; however, advances in remote sensing technology will make evaluations of fragmentation patterns increasingly feasible for Criterion C. In particular, the FRAGSTATS software package will be useful to make calculations of spatial characteristics, since it performs particularly well for homogenous ecosystems (McGarigal et al. 2002).

Criterion A: Reduction of land cover and continuing threat

We defined the proportion of intact land cover remaining to be the area of the ecosystem that remained relative to its baseline extent, or the total amount of land cover change, as determined by the land cover classification system used in the analysis. For this criterion, extinction risk is conceptually based on the expected non-linear decline in species numbers with habitat conversion, based on theoretical species–area relationships (Wilson 1992; Tilman et al. 1994; Rosenzweig 1995). Field studies show that species numbers indeed decline with a decrease in area (Brook et al. 2003; Ferraz et al. 2003), and that the time lag inherent in this process means that present habitat losses impose an 'extinction debt,' such that more species are lost in the future, even if no further habitat loss occurs (Tilman et al. 1994). We

assume that as these species are lost, the composition of the ecosystem changes and therefore extinction risk of the assemblage as a whole increases.

To determine thresholds for this criterion, we combined a generalized form of this species-area relationship (as it is impossible to empirically determine the relationship for every ecosystem) with estimates of the minimum proportion of suitable habitat needed to maintain species and ecosystems (Table 1). We set thresholds of the reduction of original habitat to fall within the range of original habitat remaining found in a variety of ecosystem studies concerned with conservation and future risk (5–80%; Environmental Law Institute 1999), and spaced these thresholds throughout the range using approximately a doubling rule, in order to reflect the non-linear impact of habitat loss on species extinction described above.

The species–area relationship provides a means to predict the expected species extinctions in a given ecosystem that will result from observed reductions at each threshold, if the species–area relationship for that ecosystem has been empirically determined. For example, if a tropical wet forest is categorized as CR, EN, or VU, the species–area relationship published in Wilson (1992) for this ecosystem predicts that it will eventually lose at least 50%, 31%, or 7% of its species, respectively. It is important to note that even if these values are calibrated to a focal ecosystem, predictions may not match observed extinction rates because anthropogenic land cover conversion does not occur at random (as the species–area model assumes). Conversion tends to be spatially aggregated, and rates of species loss are also linked with local species richness (Seabloom et al. 2002; Tucker and Townshend 2000). Rather, as with present species-based assessments, accurate predictions will be of *relative* and not *absolute* risk (IUCN 2004).

Because Criterion A highlights the risk to ecosystems that have experienced a large reduction in their size, but does not make any assumption about the time scale involved, the assessor must demonstrate that the threat to the focal ecosystem continues for it to qualify as CR, EN, or VU—just as in Criterion A of the present IUCN (2001) species-based system. This is because if a given ecosystem type currently covers a small fraction of its original extent, but it is not facing any known threat at present, its extinction risk in the foreseeable future may be very low. Among the factors that could be considered to represent continuing threats are the documented spread of invasive plant species, the degree of human contamination, the presence of industrialized agriculture or forestry, the expansion of urban areas, or other processes that may decrease the hospitability of the matrix surrounding the remaining focal ecosystem.

Risk category	Quantitative threshold
Critically Endangered (CR)	An observed or estimated reduction of >90% of the original extent of the ecosystem, with evidence that the threat has not ceased
Endangered (EN)	An observed or estimated reduction >70% of the original extent of the ecosystem, with evidence that the threat has not ceased
Vulnerable (VU)	An observed or estimated reduction of >30% of the original extent of the ecosystem, with evidence that the threat has not ceased

Table 1 Criterion A-reduction of the land cover and continuing threat

Criterion B: Rapid rate of land cover change

The rate of ecosystem change is the pace at which land cover conversion occurs, rather than the total amount that has occurred. (Table 2). The theoretical foundation and the thresholds for each category follow from the reasoning used in Criterion A; however, here the focus is process rather than state. Therefore, the rates of change, as determined, for example, from a time series of at least two satellite images spanning at least 10 years, may be used to project the proportion of land cover which existed 30 years ago or will remain in the next 30 years.

For future studies using these criteria, we encourage the use of Markov chain models to predict transition rates, and ultimately to estimate when the focal ecosystem will go extinct, in the same way that quantitative assessments are currently used for individual species (IUCN 2001). Markov models use transition rates between different land cover types over an observed time period to make predictions about future transition rates (Horn 1975; Hall et al. 1991; Eastman 2003). The assumption is that the observed rates approximate future rates of change. To refine thresholds of extinction risk using these methods, we recommend investigating the transition rates of the ecosystem of interest to all other land cover types and using these transition probabilities to determine when in the future the ecosystem will go extinct. If within the next 30 years more then 90% of the original ecosystem is predicted to disappear, for example, the ecosystem would be considered Critically Endangered (Table 2).

Criterion C: Increased fragmentation

Anthropogenic fragmentation of ecosystems may lead to shifts in water regimes, wind patterns, radiation balances, and other flows which sustain ecosystem function (Forman 1995). We therefore posit that anthropogenic fragmentation necessarily leads to a change in forces affecting the composition of the original ecosystem, and thus compromises its functioning and longevity (Henle et al. 2004). Fragmentation can be conceived of as having three central measurable effects: decreasing the size of remaining patches, changing the shape of the remaining patches, and decreasing connectivity among them (Laurance et al. 2002). We therefore combine these three

Risk category	Quantitative thresholds
Critically Endangered (CR)	Observed, estimated, or inferred rate of change is sufficiently high that a reduction of >90% of the original ecosystem took place over the last 30 years or is projected to take place within the next 30 years
Endangered (EN)	Observed, estimated, or inferred rate of change is sufficiently high that a reduction of >70% of the original ecosystem took place over the last 30 years or is projected to take place within the next 30 years
Vulnerable (VU)	Observed, estimated, or inferred rate of change is sufficiently high that a reduction of >30% of the original ecosystem took place over the last 30 years or is projected to take place within the next 30 years

Table 2 Criterion B-rapid rate of land cover change

elements—patch size, conformation, and connectivity—to determine an ecosystem's risk of extinction in Criterion C (Fig. 2).

Following from island biogeography theory (MacArthur and Wilson 1967; Wilcox 1980), species–area relationships (Preston 1962a, b; Rosenzweig 1995), and metapopulation theory (Levins 1969; Hanski 1991, 1994), we assumed that a decrease in area will increase the number of global species' extinctions, and that increasing isolation will decrease the rate of species' movements between patches, increasing the likelihood of local extinctions. This was undoubtedly a simplified view of a fragmented landscape, as the matrix surrounding ecosystem remnants, albeit disturbed, can in fact have great value for maintaining ecosystems (Franklin 1993; Forman 1995). However, following the precautionary principle (Precautionary Principle Project 2005), assuming that the matrix is relatively inhospitable will cause the assessor to err in favor of the degraded ecosystem.

To incorporate the first two aspects of fragmentation (patch size and shape), we focused on what we define as the 'core area' remaining within patches—the area of the patch minus the area influenced by edge effects (Fig. 2). This is because, in addition to the theories mentioned above predicting increased extinctions with decreased area, there is substantial evidence suggesting that edge effects decrease the value of remaining patches for ecosystem longevity (Laurance et al. 2002). For example, empirical evidence indicates that edge effects for many processes extend ~250 m into fragments of a wide variety of ecosystems (Environmental Law Institute 1999; Laurance et al. 2002).

We set the thresholds for core area by noting that the amount of habitat necessary to maintain populations and ecosystems varies depending on the species or process of interest. Viable populations of some birds, small mammals, plants and invertebrates



Fig. 2 Quantitative thresholds for Criterion C—increased fragmentation

may be able to survive in patches 1–10 ha in size, whereas larger mammals may need hundreds to thousands of hectares (Environmental Law Institute 1999; Laurance et al. 2002; Laidlaw 2000). We therefore set 10 km² (1,000 ha) as a threshold for the minimum patch size in this sub-criterion, which should capture the majority of species and processes vital for maintaining ecosystems (in a 10 km² circular patch, assuming a 250 m edge, the core area occupies roughly 75% of the patch). Ecosystems which consist of less than 10 km² at the start of the time period considered will therefore need to be assessed using only Criteria A, B or D, since C will be irrelevant. The composition of the fragmented landscape, another aspect of the 'shape' component of Criterion C, was furthermore considered by quantifying the proportion of fragments <10 km²: the larger the proportion of fragments below this 10 km² threshold, the higher the expectation of extinction risk (Fig. 2).

The final component of the fragmentation criterion, connectivity, refers to the degree "to which the landscape facilitates or impedes movement among resource patches" (Taylor et al. 1993). Despite the widely recognized importance of landscape connectivity (e.g., Naiman et al. 1993; Lindenmayer and Possingham 1996; Beier and Noss 1998; Trakhtenbrot et al. 2005; Williams et al. 2005), it remains an imprecise term, and is difficult to measure because any particular landscape has multiple connectivities, depending on the organism or process of interest (Wiens and Milne 1989; Tischendorf and Fahrig 2000; McGarigal and Cushman 2002). There are consequently a plethora of proposed connectivity measures (Forman 1995; Gustafson 1998; Calabrese and Fagan 2004), and indeed, a major current goal in landscape ecology is to understand the relationship between landscape pattern and ecological processes (Wiens et al. 1993; Winfree et al. 2005). Currently, however, no measures of landscape connectivity exist that can be applied to many species across a single ecosystem and still have biological significance—ideally what is required by an ecosystem risk classification system (Tischendorf and Fahrig 2000; Calabrese and Fagan 2004). Many present connectivity measures have the additional disadvantage of being data intensive and unintuitive to a non-specialist audience (Calabrese and Fagan 2004).

We therefore propose that, at present, the best proxy measure available to capture the connectivity aspect of the fragmentation criterion was a simplified 'nearestneighbor distance' metric. Modified from the Euclidean nearest-neighbor distance, and one of the most widely used measures of patch isolation (Moilanen and Nieminen 2002; Bender et al. 2003; Calabrese and Fagan 2004), this metric examines the proportion of patches which are a threshold distance from their nearest neighbor (Fig. 2). Unfortunately, it remains unclear whether nearest-neighbor distance captures true isolation from the perspective of organisms and ecosystem processes; for example, a recent meta-analysis failed to find statistically significant effects associated with nearest-neighbor measures (Moilanen and Nieminen 2002). Recognizing these limitations, we highlight the need for additional work developing a metric which is both intuitive and relevant at the scale of community or ecosystem-level functioning.

To set the thresholds in this sub-criterion of Criterion C, we selected a distance beyond which many organisms and processes were assumed to be unable to maintain functioning (e.g., dispersal, foraging, pollination). Unfortunately, we found few studies to guide our selection. However, several suggest that in the order of 1 km may be appropriate for some small organisms, certain invertebrates, amphibians, mammals, and birds, for example, do not cross distances greater than several hundred meters (Mader 1984; Saunders and de Rebeira 1991; Bowne et al. 1999; Lehtinen et al. 1999; Norris and Stutchbury 2001; Laurance et al. 2002).

Criterion D: Highly restricted geographical distribution

We used Criterion D to highlight ecosystems that exist in few, small geographical areas, in the same way that Criterion D highlights restricted-range species in the current species-based system (IUCN 2001). We included it for ecosystems that are not decreasing but are characterized by an acute restriction in their geographical extent. We did not apply it to ecosystems that have undergone a process of fragmentation and which are presently restricted in extent (which should be assessed using Criterion C; Fig. 2)—but rather those that have not existed in large areas in recent geological history and are thus vulnerable to catastrophes (IUCN 2004). To define the thresholds for Criterion D, we used the concept of minimum patch size of Criterion C (Fig. 2), and assumed that ecosystems existing naturally as 1–10 patches <10 km² in size should be considered threatened (Table 3).

Results

Extinction risk for Indonesian Borneo's lowland tropical forests

The threat to Indonesian Borneo's (*Kalimantan*) lowland tropical forests by logging, conversion, and fire has been well-documented in research that carefully defines the extent, composition, and natural dynamics of this ecosystem (Curran et al. 1999; Siegert et al. 2001; Holmes 2002; Wikramanayake et al. 2002; Curran et al. 2004). Remotely ensed data (30- and 250-m spatial resolution satellite images) and field observations show that, of the ~52,000 km² of formally protected Kalimantan lowland forest present in 1986, 56% had been transformed by 2001, and that the replacing matrix (particularly logged areas and oil palm plantations), holds little value for many lowland forest species (Curran et al. 2004). This finding is consistent with a coarser, more extensive report on the three major islands of Indonesia (Sumatra, Sulawesi, and Kalimantan) which estimates that 60% of lowland forests were lost between 1985 and 1997 (Holmes 2000). The detailed Curran et al. (2004) study area encompasses nearly half (47%) of Kalimantan's and nearly a third (30%) of the three large islands' lowland forests originally present in 1985 (Holmes 2000). Furthermore, the threat to this forest is expected to continue, as logging is projected

Risk category	Quantitative thresholds
Critically Endangered (CR)	Entire original geographical distribution of the ecosystem is comprised of one fragment <10 km ²
Endangered (EN)	Entire original geographical distribution of the ecosystem is comprised of three of fewer fragments $<10 \text{ km}^2$
Vulnerable (VU)	Entire original geographical distribution of the ecosystem is comprised of ten or fewer fragments <10 km ²

Table 3 Criterion D-very small geographical distribution

2004). Extrapolations suggest that Kalimantan's non-swampy lowland forests will be reduced to <10% of their original extent soon after 2010, (Holmes 2002).

Using these published data, we were able to evaluate this ecosystem using Criteria A and B (Table 4). Although Curran et al. (2004) do provide data concerning the area and isolation of fragments, they were insufficient to apply Criterion C as specified (i.e. Data Deficient). Assessments in different criteria suggested different extinction risks (Table 4), so, following the principles used for species (IUCN 2004), we chose the highest extinction risk category. We therefore designated Indonesian Borneo's low-land tropical forests as Critically Endangered. This example demonstrates how a more refined regional-level analysis within the context of a coarser national-level study can contribute to understanding ecosystem extinction risk across scales.

Brazil's Atlantic rainforests

It is thought that, before European colonization, Atlantic rainforests formed a narrow ribbon of vegetation spanning 4000 km along Brazil's eastern coast, covering 1.0–1.5 million km² (da Fonseca 1985). Today, somewhere between 1% and 12% of that original expanse is estimated to remain (Brown and Brown 1992; Fearnside 1996; Morellato and Haddad 2000; Myers et al. 2000; Saatchi et al. 2001). Most of the Brazilian Atlantic forest had been converted to pasture or agriculture by the early 1980s (da Fonseca 1985). Over the past few centuries, deforestation rates have varied in different states, leading to a mosaic of fragmentation on a temporal as well as a spatial scale. For example, peak deforestation rates hit São Paulo between 1925 and 1935, whereas rates peaked in Espírito Santo between 1975 and 1980 (Viana et al. 1997). Some suggest that most of the Atlantic forest remains in small, isolated, and highly disturbed fragments; in the Piracicaba region of São Paulo, for example, small fragments of less the 50 ha each constitute nearly 90% of remaining oldgrowth patches (Viana et al. 1997). In the state of Pernambuco, however, 48% of forest fragments are less than 10 ha (and 7% are greater than 100 ha), but small fragments are relatively close together (Ranta et al. 1998).

Using these data and the designation of ecosystem, the units and scales of interest, and the changes as defined by the authors, we classified Brazil's Atlantic rainforests as Critically Endangered using Criterion A (Table 4). Synthesizing all authors' data forms a consensus for the entire ecosystem and this designation is therefore a global classification. Although convincing evidence is available on the diminished size, there is conflicting evidence on the isolation of remaining fragments from different regions (Viana et al. 1997; Ranta et al. 1998). Furthermore, the analysis of connectivity in these studies has not yet been synthesized in a way which is compatible with the methods outlined above for Criterion C, and thus Data Deficient was assigned for that criterion. Again, however, quantification of the required metrics could be carried out within the context of these groups' research objectives.

Venezuelan dry forests

Tropical dry forests have been described as the most threatened, and perhaps underappreciated ecosystems in the world (Janzen 1988; Murphy and Lugo 1995; Sánchez-Azofeifa et al. 2005a, b; Miles et al. 2006). We used data and definitions from a recent assessment of Venezuelan dry forests (Fajardo et al. 2005) to classify the dry

Ecosystem	Extent in yea	r (km ²)	Change	0	30-year projection		Trend in threat?	Cate, criter	gory 1 ion	inder	1
			Loss (%)	Rate (km ² /y)	Loss (%)	% <10 km ²		А	в	C	D
Kalimantan lowland forests	1986	2001					Logging within protected areas	VU	CR	DD	n/a
Brazilian Atlantic forests	52,000 XV Century	23,000 1990–1998	56	1,930	>100	n/a	Forest continues to be	CR	n/a	DD	n/a
	$1-1.5 \times 10^{6}$	n/a	88-99	n/a	n/a	n/a	converted to pastures				
venezueian ury ioresis Margarita Island	1986	1999					Urbanization and	LC	N	DD	n/a
	230	190	17	ŝ	40	n/a					
Guasare River watershed	1986	2001	i	à	2		Agriculture and cattle ranching continue	ΝŪ	CR	DD	n/a
	328	198	39	6	>100	n/a	C				n/a
Mato Grosso's tropical	1973	2003					Forest continues to be	N	N	DD	n/a
ary rotests	322,526	205,525	36	5,000-12,000	50-75*	n/a	convertion tot agrinushiess				
Northern Venezuela	1986	2001									
Evergreen forest	397	385	e	1	9	n/a	Not on a major scale	ГC	ГC	DD	n/a
Semi deciduous forest	1190	1,037	13	10	30	n/a	Urbanization and fire	ГC	Ŋ	DD	n/a
Deciduous forest	2,252	1,585	30	44	84	n/a	Urbanization and fire	Ν	EN	DD	n/a
South African Grasslands	Original	1994-1995									
	n/a	n/a	45	n/a	n/a	77	Yes: biome with greatest conservation need	N	n/a	EN/DD	n/a
Sources indicated in the tex criterion is not applicable to next three decades. The cat smaller than 10 km ²	tt. Category abl the specific case egory indicated	oreviations for e. Projections l in bold is th	ollow Ta s were e he prop	able 1: ''n/a'' ii stimated assum osed category	idicates that ing that the for each eco	t the data a annual ave osystem (%	tre not available for that particul rage rate of decline (km^2/y_T) rem <10 km ² : proportion of remain	ılar ass mained ining eo	essme const cosyst	nt or that ant during em in patc	the thes

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*50-year projection

These two regions share a similar dry forest ecosystem, but have experienced slightly different types of threats. Margarita Island, located 38 km off the Venezuelan coast and covering 934 km², extends from sea level to 910 m. Using recent aerial photographs and satellite images from 1986 and 2001, Fajardo et al. (2005) estimate that 17% of dry forest cover was lost in this period, and that if current trends persist, 60% will remain within 30 years. The principal cause of land cover change, which continues at present, is urbanization and infrastructure development to support seasonal national and international tourism. In contrast, between 1986 and 2001, forest cover in the Guasare river watershed (Zulia State) declined more than twice as much, by 39%. And, if current trends persist, all of the Guasare forest will disappear within 30 years (Table 4). The principal causes of land cover change in this area, which also continue, are agriculture and cattle ranching (Portillo 2004).

These data allowed us to classify both of these dry forests according to Criteria A and B. Margarita qualified as Vulnerable according to Criterion B, and although it was not close to meeting any risk threshold for Criterion A, it was classified as Vulnerable following the precautionary principle. In contrast, the Guasare watershed qualified as Vulnerable by Criterion A and Critically Endangered by Criterion B. Therefore, we designated the Guasare region as Critically Endangered. Data for classification according to Criterion C were unavailable: Fajardo et al. (2005) present data on fragment size, but not on distance from the nearest neighbor.

Brazil's Mato Grosso tropical dry forests

Mato Grosso tropical dry forests (420,000 km²)—located in the southern part of the Amazon basin between the Brazilian *cerrado* to the south and more humid forests to the north—are experiencing combined threats from logging, agriculture, cattle ranching, and fire (Ivanauskas et al. 2003; Alencar et al. 2004; Cochrane et al. 2004). In Mato Grosso state, the rates of deforestation over the past decade, ranging from 5000 km²yr⁻¹ to 12,000 km²yr⁻¹, have been among the highest in the entire Brazilian Amazon (INPE 2006). More than a third of these ecotonal forests (36%) had been deforested by 2003 (Soares-Filho et al. 2006). Projections into the future predict that 75% will be converted by 2050 if current rates of deforestation continue (Soares-Filho et al. 2006). Even under optimistic assumptions of future governance, only half of these forests will remain in the next 50 years due to the combined threats from frontier expansion (due to cattle ranching and mechanized agriculture; Alencar et al. 2004) and the lack of protected areas (Soares-Filho et al. 2006).

Using published data, we were able to evaluate this ecosystem—at its global extent—using Criteria A and B (Table 4); data provided were insufficient to apply Criterion C (i.e. Data Deficient). Assessments using both Criteria A and B designated Mato Grosso's tropical dry forests as Vulnerable (Table 4).

Ecosystems of northern Venezuela

Northern Venezuela presents a major challenge for conservationists, as it is both important for biodiversity and for people: three of the largest cities in the country (Caracas, Maracay and Valencia) are located within a region that is key for both nationally and globally threatened species (Rodríguez and Rojas-Suárez 1996;

Rodríguez et al. 2004a). For this region, trends in land cover change were assessed for an area of approximately 6000 km^2 , delineated politically rather than ecologically, again using previously published data. These data, based on interpretation of aerial photographs and Landsat Thematic Mapper and Enhanced Thematic Mapper satellite images (30×30 m resolution), combined with extensive ground truthing, allowed the authors to quantify the conversion rates of evergreen, semi-deciduous and deciduous forests between 1986 and 2001 (PROVITA 2004; Fajardo et al. 2005). We were able to classify the three ecosystem types defined by the study according to Criteria A and B (Table 4).

The northern Venezuelan evergreen forest in this region did not meet the thresholds for any of the risk categories, thus qualifying it for the designation Least Concern (Table 4; probably because these have been included in effective protected areas since before the time of the assessment baseline; Rodríguez et al. 2004b). On the other hand, semi-deciduous forests were Vulnerable according to Criterion B (although they qualified as Least Concern for Criterion A). Finally, deciduous forests met the threshold for Vulnerable under Criterion A, and for Endangered under Criterion B, and were therefore classified as Endangered. Data were not available for classification of any of these ecosystems under criterion C.

South African grasslands

South African grasslands are considered the biome of greatest conservation priority in that country (Rebelo 1997). They occupy 16.5% ($349,174 \text{ km}^2$) of the land surface, and are home to the majority of South Africans, while also containing large coal reserves and the world's richest goldfields. Neke and Du Plessis (2004) present a definition of these South African grassland ecosystems and a quantitative analysis of their change based on Landsat Thematic Mapper satellite imagery and predictive modeling, showing that by 1994–1995 ~45% of this biome had been replaced by agriculture. They report that invasive species are present (but occupy a small proportion of the landscape), and that only 23% of remaining grassland fragments are >10 km² in size.

These analyses allowed us to classify this ecosystem as Vulnerable according to Criterion A, and to consider two alternative categories under Criterion C (Table 4). To fully classify an ecosystem according to Criterion C, two pieces of information are needed: patch area and connectivity (Fig. 2). However, data were only available concerning the first characteristic (Neke and Du Plessis 2004). Given the small total patch area remaining, application of the precautionary principle suggested that South African grasslands may be considered Endangered under Criterion C. Due to the uncertainty in this designation, however, one could argue it to be more appropriate to classify this ecosystem as Data Deficient in this criterion, leaving the overall assessment as Vulnerable in accordance with Criterion A.

Discussion

The classification system presented in this paper permitted us to assess the relative extinction risk of six disparate ecosystems, using data already available in the literature. Because these assessments were carried out in a systematic and transparent manner, in the context of explicit spatial and temporal scales, they represent

the first assessments of ecosystem extinction risk which are repeatable, readily comparable, and yet flexible in the face of varied data sources—in a manner exactly analogous to the presently globally accepted system for species-level assessments. Although the particular details of the system we present may need refinement, we feel that these advances provide the basis for transforming ecosystem risk assessment, and demonstrate that the benefits of a transparent, repeatable, and comparable system, clearly outweigh its costs.

We expect that both the particular criteria and the thresholds we have selected here will be hotly debated, and modified, as were the thresholds as initially proposed in the species-focused system (Mace and Lande 1991; Mace et al. 1992, Mace and Stuart 1994; IUCN 1994, 2001). For example, we expect that Criterion C will be much debated as consensus on defining and assessing fragmentation varies widely and thus fitting this spatial variable into a broad classification system proves difficult. However, the potential for fragmentation to contribute to definitions of extinction risk is great, as many authors have provided or are working to provide some measure of fragmentation. In terms of criteria selection, we followed the IUCN's red list example and focused on both flexibility and comparability as central goals. This presented us with a trade-off between selecting few criteria (which may leave some ecosystems un-assessable, but all the rest easily comparable), and selecting a large number of criteria (which permits the assessment of all ecosystems, but may hinder their comparison). We tried to balance these factors, arriving at a system with four categories, within any one of which assessment is required, but with each sufficiently broad that, even when some criteria cannot be applied at all, others will be straightforward to assess. For example, ecosystems which are naturally interspersed among other ecosystems may only be possible to assess using Criteria A and B (e.g. wetlands, with a mosaic of land cover types that are constantly changing, or some riparian ecosystems). We advocate the precautionary principle to resolve conflicts among the assessments resulting from alternate criteria, as presently applied by the IUCN (2004) to species, and suggest that the criterion leading to a higher risk classification be used. For example, we showed that Indonesian protected lowland forests could be classified as either Vulnerable or Critically Endangered, using different criteria, and in the end selected the Critically Endangered designation (Table 4). With respect to our threshold choices, we note that any values selected will be arbitrary to a certain extent; what is essential is that such thresholds be made clear, with their application supported by actual data. And since our system seeks to estimate *relative*, not absolute, extinction risk, 'mistakes' in locating thresholds 'properly' will be applied equally in all cases, and thus should not affect assessments.

An important issue that is likely to arise in assessing ecosystem extinction risk, which parallels the application of IUCN Red List categories at the regional level (Gärdenfors et al. 2001; IUCN 2003), is that assessments may occur over portions of ecosystems that are a subset of their global distribution. As the size of the unit assessed decreases, the likelihood that it will be considered threatened will also increase (IUCN 2004). However, even if the objective extinction risk of a small landscape unit (e.g. a municipality) is high, that does not mean that its loss would represent a major impact to global biodiversity, and that conservation action in that unit is of high priority (though people in such a municipality might think otherwise). The relative importance of a local assessment must always be placed in the context of its global significance in an independent process of priority-setting. Following the

recommendations for regional species assessments, we suggest that future ecosystem assessors must provide: (1) the regional extinction risk category, (2) the global extinction risk category, if known, or at the least documented information on how representative this region is of the entire habitat, and (3) what proportion (%) of the entire habitat this region represents (Gärdenfors et al. 2001).

While the choice of the overall extent of analysis is an issue faced by current species assessments, the importance of the grain or resolution of analysis is an issue unique to ecosystem assessments. These matters of scale are, of course, related: there may be practical tradeoffs between analyzing at the finest grain possible (and perhaps thereby limiting the area examined) and quantifying the largest area possible (which may decrease the grain too much to be useful). We propose, however, that just as an explicit report of the extent of the analysis ('global' versus 'regional') allows users to compare relative risks of different ecosystems within these categories, an explicit report of the grain of analysis will allow comparisons within categories of resolution. In the end, it should be stakeholders who decide at which scale to apply the system, according the data available, their financial and human resources, and the objectives of their analysis.

By building on the experience of the IUCN with animal and plant species as a model for the development of a 'red list' category system for terrestrial ecosystems, we have tried to solidify a framework in which to explore what extinction means in the context of ecosystems, in a way that engages the international conservation community and fosters work building upon that which we have presented here. Our examples demonstrate that this system may be applied transparently to a great diversity of scales and ecosystem types, and that in many cases, the necessary data to conduct classifications are already available. What remains is to confront this system with the world's diversity of ecosystems, and, piece by piece, construct a truly global picture of habitat extinction risk.

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