Contributed Paper

Scaling range sizes to threats for robust predictions of risks to biodiversity

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Abstract: *Assessments of risk to biodiversity often rely on spatial distributions of species and ecosystems. Range-size metrics used extensively in these assessments, such as area of occupancy (AOO), are sensitive to measurement scale, prompting proposals to measure them at finer scales or at different scales based on the shape of the distribution or ecological characteristics of the biota. Despite its dominant role in red-list assessments for decades, appropriate spatial scales of AOO for predicting risks of species' extinction or ecosystem collapse remain untested and contentious. There are no quantitative evaluations of the scale-sensitivity of AOO as a predictor of risks, the relationship between optimal AOO scale and threat scale, or the effect of grid uncertainty. We used stochastic simulation models to explore risks to ecosystems and species with clustered, dispersed, and linear distribution patterns subject to regimes of threat events with different frequency and spatial extent. Area of occupancy was an accurate predictor of risk (0.81<|r|<0.98) and performed optimally when measured with grid cells 0.1–1.0 times the largest plausible area threatened by an event. Contrary to previous assertions, estimates of AOO at these relatively coarse scales were better predictors of risk than finer-scale estimates of AOO (e.g., when measurement cells are <1% of the area of the largest threat). The optimal scale depended on the spatial scales of threats more than the shape or size of biotic distributions. Although we found appreciable potential for grid-measurement errors, current IUCN guidelines for estimating AOO neutralize geometric uncertainty and incorporate effective scaling procedures for assessing risks posed by landscape-scale threats to species and ecosystems.*

Keywords: IUCN Red List of Ecosystems, IUCN Red List of Threatened Species, landscape modeling, risk assessment, spatial scale, species distribution, threatening process

Ampliación de Rangos de Distribución ante Amenazas para Predicciones Robustas de los Riesgos para la Biodiversidad

Resumen: *La evaluación de los riesgos para la biodiversidad generalmente depende de la distribución espacial de las especies y los ecosistemas. Las medidas del rango de extensión, como el área de ocupación (ADO), que se utilizan ampliamente en estas valoraciones son sensibles a la escala de medición, lo que genera propuestas para medirlas a escalas más finas o a diferentes escalas con base en la forma de distribución o en las características ecológicas de la biota. A pesar de su papel dominante en las valoraciones de listas rojas durante décadas, las escalas espaciales apropiadas del ADO para predecir el riesgo de extinción de las especies o el colapso de un ecosistema sigue siendo polémico y sin ser probado. No hay evaluaciones cuantitativas de la sensibilidad de escala del ADO como pronóstico de los riesgos, la relación entre la escala óptima del ADO y la*

escala de la amenaza, o el efecto de incertidumbre de cuadrícula. Utilizamos modelos de simulación estocástica para explorar los riesgos para los ecosistemas y las especies con patrones de distribución agrupada, dispersa y linear sujetos a regímenes de eventos amenazantes con frecuencias y extensiones espaciales diferentes. El área de ocupación fue un pronosticador preciso del riesgo (0.81<|r|<0.98) y actuó óptimamente cuando se midió con celdas de cuadrícula de 0.1 –1.0 veces la mayor área plausible amenazada por un evento. Contrario a aseveraciones previas, los estimados del ADO a estas escalas relativamente burdas fueron mejores pronosticadores del riesgo que los estimados del ADO a escalas más finas (p. ej. cuando las celdas de medición son <1% del área de la mayor amenaza). La escala óptima dependió de las escalas espaciales de las amenazas más que de la forma o el tamaño de las distribuciones bióticas. Aunque encontramos un potencial apreciable para los errores de medida de celda, las pautas actuales de la UICN para la estimación del ADO neutralizan la incertidumbre geométrica e incorporan procedimientos efectivos de modificación de escala para la valoración de los riesgos presentados por las amenazas a escala de paisaje para las especies y los ecosistemas.

Palabras Clave: distribución de especies, escala espacial, Lista Roja de la UICN de Ecosistemas, Lista Roja de la UICN de Especies Amenazadas, modelado de paisajes, proceso amenazante, valoración de riesgo

摘要: 确定分布区大小受到胁迫的尺度以用于稳健的生物多样性风险预测
对生物多样性面临风险的评估通常依赖于物种和生态系统的空间分布。在这类评估中广泛使用的分布范围大小的度量, 例如占有面积 (AOO), 对测量尺度很敏感, 这提示我们应基于分布区形状或生物区生态特性在更精细的尺度或不同尺度上进行测量。尽管几十年来 AOO 在红色名录评估中占有关键地位, 然而用于预测物种灭绝风险或生态系统崩溃的 AOO 合适的空间尺度还未得到检验且尚存在争议。AOO 作为风险预测指标的尺度敏感性、最适 AOO 尺度和胁迫尺度的关系, 以及网格不确定性的影响, 目前都没有进行定量评估。我们用随机模拟模型来探究生态系统和聚群分布、分散分布和线性分布的物种面临的风险, 同时考虑它们受到的不同频率和空间尺度的胁迫事件。占有面积是准确的风险预测指标 (0.81<|r|<0.98), 当在测量的网格单元大小为受胁迫影响的最大可能面积的 0.1-1.0 倍时, 预测效果最好。与之前的认识相反, AOO 估计值在相对粗糙的尺度上比在精细尺度上(如测量单元大小<1%最大胁迫面积时)可以更好地预测风险。最优尺度更多地依赖于胁迫的空间尺度, 而不是生物分布区的形状或大小。尽管我们发现网格测量有很大潜在的误差, 但当前 IUCN 估计 AOO 的指导原则抵消了几何不确定性, 且整合了确定尺度的有效程序, 来评估景观尺度的胁迫对物种和生态系统产生的风险。【翻译: 胡怡思; 审校: 胡义波 】

关键词: 风险评估 ,IUCN 濒危物种红色名录, IUCN 生态系统红色名录,物种分布,胁迫过程,景观建模,空间尺度

Introduction

As life on Earth erodes unabated, a reliable understanding of the risks to biodiversity becomes ever more imperative to inform effective conservation action. The spatial extent of biological distributions (range size) is widely recognized as a key predictor of risks across multiple levels of biological organization (Mace et al. 2008; Gaston & Fuller 2009; Keith et al. 2013). Accordingly, the International Union for Conservation of Nature (IUCN) Red List criteria for assessing risks to both species and ecosystems incorporate simple range-size metrics to identify what is most at risk. The evidence used to assess many red-listed species (57%) and ecosystems (38%) is based on range-size data, either entirely or in combination with other factors. Yet the reliance on general range-size metrics has been repeatedly questioned on the basis that they do not represent detailed, taxon-specific spatial patterns in habitat (e.g., Cardoso et al. 2011; Gigante et al. 2016; Ocampo-Peñuela et al. 2016).

Despite the dominant role of range-size metrics in red-list assessments since the 1990s, the factors that influence their performance as predictors of risk to biodiversity have not been evaluated systematically. We empirically assessed the performance of area of occupancy (AOO), the most contentious of the standard range-size metrics for predicting risks to biodiversity (Simaika & Samways 2010; Cardoso et al. 2011; Gigante et al. 2016). First, we reviewed the theoretical basis for range-size metrics in red-list criteria. We then used simulation models to explore the sensitivity of estimates of AOO to geometric uncertainty; the ability of AOO estimated at a given spatial scale to predict risks to biodiversity across a range of distribution types and threat regimes; how the predictive performance of AOO varies with the spatial scale at which it is estimated; and whether there is an optimal scale for estimating AOO that maximizes its predictive performance, taking into account the spatial properties of both biological distributions and threat regimes. Our analyses represent the first comprehensive assessment of scale-sensitivity in AOO as a predictor of risks to biodiversity.

Theoretical Basis of Range-Size Metrics in Red-List Criteria

Range size metrics are founded on empirical and theoretical generalizations about insurance effects or risk spreading (e.g., Loreau et al. 2003; Gaston & Fuller 2009;
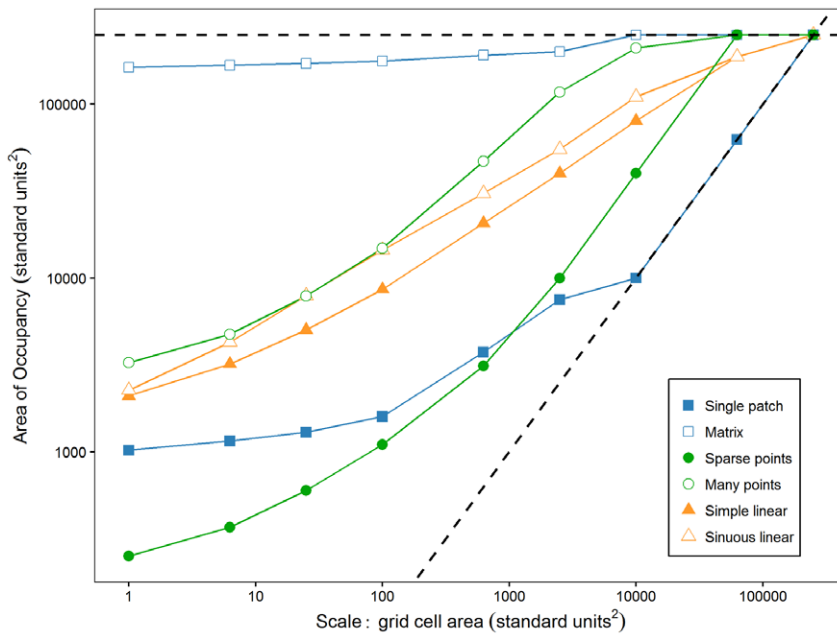
Figure 1. Median scale–area relationships for 5 replicates of distribution types for species or ecosystems (see Table 1) (dashed lines, theoretical limits of distribution within the size of the study area). Two distribution types (matrix and sparse points) span the theoretical extremes, whereas the other 4 types represent different shapes of distribution with comparable areas at the finest scale of measurement. See Methods and Table 1 footnote explanation of standard distance units.

Keith et al. 2013). Elements of biodiversity are more likely to persist and continue functioning if their distribution is large or dispersed relative to the footprint of the threats they face. Large or dispersed distributions therefore buffer species, ecosystems, and other elements of biodiversity from threats by spreading risks spatially across multiple locations. Conversely, elements of biodiversity that are restricted within small distributions are more prone to elimination by a small number of threat events. These insurance effects and their relationships are crucial to understanding the relative risks faced by different elements of biodiversity (Gaston & Fuller 2009).

The spatial interaction between threat and biota will determine the impact on biodiversity at organizational levels from species (Polaina et al. 2016) to ecosystems (Etter et al. 2011). Most threats to biodiversity are spatially explicit and autocorrelated, which affects portions of landscapes and seascapes in nonrandom spatial patterns (Sanderson et al. 2002; Halpern et al. 2008; Vorosmarty et al. 2010). For example, processes such as land conversion, chemical spills, biological invasions, disease outbreaks, fires, and other disturbances (Salafsky et al. 2008) all have characteristic nonrandom patterns of spatial expression that interact with the distribution of biodiversity, which is, itself, spatially structured (Evans et al. 2011).

Generic protocols for assessing risks to biodiversity, such as the IUCN Red List criteria for species (IUCN 2001; Mace et al. 2008) and ecosystems (Keith et al. 2013; IUCN 2016), employ standard spatial metrics to identify spatial symptoms associated with different levels of relative risk. The protocols in their entirety comprise ensembles of criteria (A–E) designed to allow qualitative evaluation of different symptoms of risk (Mace et al. 2008; Keith et al. 2013). The main spatial component (criterion B in both

protocols) focuses on small range sizes of species and ecosystems that may predispose them, respectively, to high risks of extinction and collapse. Two spatial metrics are employed in red-list protocols (Gaston 1994; IUCN Standards and Petitions Subcommittee 2016): extent of occurrence (EOO) (i.e., the area within the outermost geographic limits of the distribution), estimated using a minimum convex polygon enclosing all occurrences, and AOO (i.e., the area within the outermost limits over which a species or ecosystem actually occurs), estimated using a count of occupied grid cells of standard dimensions. Species and ecosystems are evaluated, in part, by comparing their estimated EOOs and AOOs with fixed thresholds that delineate ordinal categories of risk (critically endangered, endangered, vulnerable, and least concern). The inclusion of these simple spatial metrics and standard methods for their use reflects the importance of parsimony and generality as fundamental design principles in the development of IUCN Red List criteria (Keith et al. 2015). The two metrics are complementary in measuring different aspects of range size that may limit the persistence of biota (Gaston & Fuller 2009).

Estimates of EOO and AOO vary depending on the methods of estimation (Gaston & Fuller 2009). The sensitivity of EOO to exclusions of outlying occurrences and discontinuities is well known, whereas AOO is particularly sensitive to the scale of measurement (Keith et al. 2000; Hartley & Kunin 2003; Nicholson et al. 2009). The shape of scale–area relationships (Fig. 1) is a function of occurrence saturation and spatial clustering. For species or ecosystems that fully occupy a landscape at some fine spatial resolution (e.g., distribution in a contiguous matrix; Fig. 2b), the AOO is independent of scale at any coarser range of scales within the landscape (i.e., scale-area slope = 0). For those that occupy a single
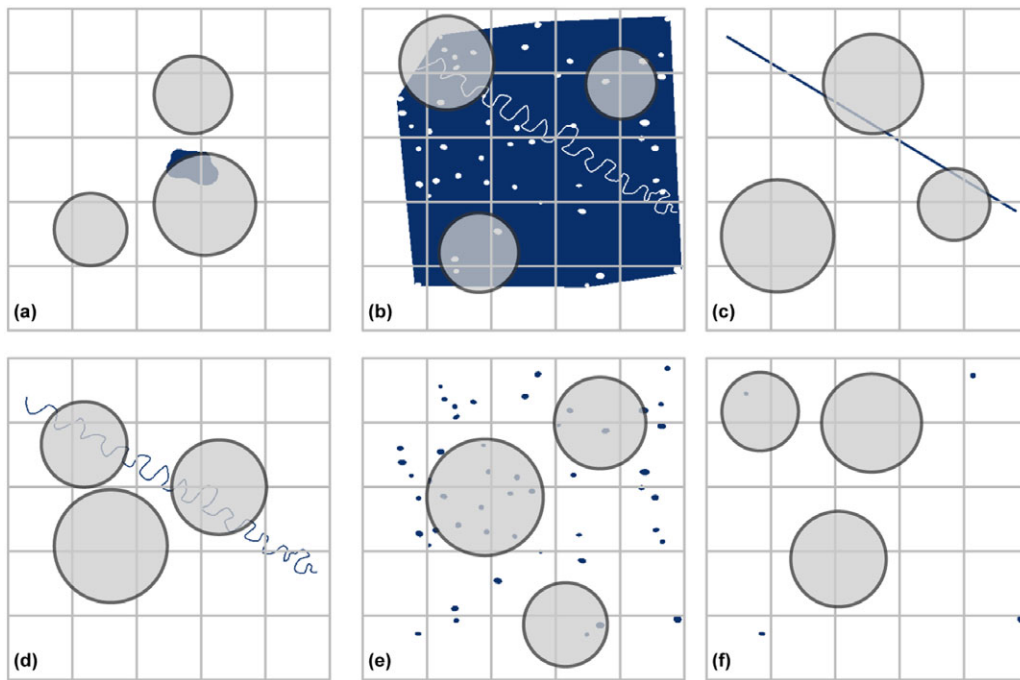
Figure 2. Simulated landscape showing 6 species or ecosystem distribution types (see Table 1): (a) single patch, (b) semicontinuous matrix, (c) simple linear, (d) sinuous linear, (e) many points, and (f) sparse points. Circles show example threat regimes comprising infrequent events (1–10 within the duration of the risk-assessment time frame) of medium size (radius 50–100 units) that were used in simulations. The grid-cell dimensions are 100 standard distance units (see Methods and Table 1 footnote).

point at some fine scale (e.g., distribution in a single small patch; Fig. 2a), the AOO increases predictably as measurement scales become coarser (scale-area slope = 1). Real biological distributions lie between these theoretical limits, and scale–area slope ranges from 0 to 1, depending on the degree of saturation, dispersion, and clustering at different scales, the causes of which may be abiotic (Porter & Kearney 2009) or biotic (Bulleri et al. 2016). Clustering may also be sensitive to sampling bias (Sheth et al. 2011), especially when access to habitat is limited.

If applied to risk assessments without standardization, such a range of measurement scales creates serious inconsistencies in red-list assessment outcomes. When estimated at fine grains, AOO will be small and more likely to meet thresholds delimiting high threat categories than if estimated at coarse grains. Conversely, coarse-grain estimates of AOO are likely to underestimate threat status (Nicholson et al. 2009). A second, less widely appreciated source of error involves uncertainty related to registration of the origin of the geometric reference grid used to estimate AOO—grids with different origins could produce different estimates of AOO depending on how they overlap with the same mapped biological distribution (IUCN Standards and Petitions Subcommittee 2016).

To minimize these methodological inconsistencies among assessments, guidelines for red-list assessments

of both species and ecosystems specify standard grains (grid cell sizes) for estimating AOO (IUCN Standards and Petitions Subcommittee 2003; Bland et al. 2016). Alternative approaches to this problem involve adjustments to thresholds or measurement grains depending on characteristics of the species or ecosystems under assessment. Concerns that the estimates of AOO resulting from standard grain sizes may not distinguish different types of distribution pattern (such as distributions along coastlines and across fragmented habitats) have led some authors to suggest that finer scales of measurement are needed to represent the detail of different biological distribution patterns according to species biology or habitat geometry: Simaika and Samways (2010), Cardoso et al. (2011), and Gigante et al. (2016). Authors of each of these studies claim that AOO measured at recommended scales under- or overestimate risks, but none attempt to quantify risks or explore how the spatial features of threats influence risks through their interactions with those of biological distributions. Such analyses are essential to resolve the performance of AOO as a predictor of risk and to quantify how this performance depends on scale. However, we know of no studies that quantify the relationship between AOO estimated at a range of scales and risks to biodiversity. Similarly, we found no published studies that evaluated the effect of geometric uncertainty (variations in grid origin) on estimates of AOO.

Table 1. Six types of species or ecosystem distribution used in simulations with mean (minimum and maximum) values of area of occupancy (AOO) expressed as the number of the smallest simulated grid cells in the landscape (1 × 1 standard unit).

Type[a]	AOO mean and range[b] (standard units^2)	Examples of ecosystem type and species' habitat
1 Single patch	65926, (10230−174590)	lake, wetland, oceanic island, mountain top
2 Matrix (semicontinuous)	1383750, (1089680−1628550)	grassland plains, lowland forests, tundra, submarine abyssal plains
3 Simple linear	38336, (12190−86420)	straight coastlines and streamlines, continental shelves
4 Sinuous linear	56526, (22630−127740)	cave systems, meandering streams, complex coastlines
5 Many points (micropatches)	34010, (22880−59420)	rocky outcrops, island archipelagos, insular wetlands
6 Sparse points (micropatches)	2448, (1480−3680)	as above but with few widely scattered outcrops, islands, wetlands

[a]*Five replicates per type were selected from a uniform distribution between maximum and minimum values.*
[b]*Spatial dimensions of the simulated landscape are 500 × 500 standard distance units. Standard units can be multiplied by a constant to represent real distances and areas (e.g., if 1 standard unit = 20 m, the landscape is 10 × 10 km).*

We used a spatially explicit simulation model (Murray et al. 2017), applicable to both species and ecosystems, to explore the performance of AOO as a predictor of risks to biodiversity with varied distribution patterns subject to a range of threat regimes across varied spatial scales. We generated a suite of exemplar biological distribution patterns and characterized their scale–area relationships to provide context for interpreting simulation outcomes. We then exposed each distribution to threat regimes that varied in the size and frequency of individual threat events.

Methods

We simulated a landscape with 6 distribution patterns designed to represent the range of variation in spatial occupancy that is commonly encountered in nature among species and ecosystems (Table 1 & Fig. 2). This enlarged upon 3 distribution types proposed by Gigante et al. (2016). The spatial dimensions of the simulated landscape were set at 500 × 500 standard distance units. These standard units can be multiplied by a constant to represent real distances and areas (e.g., if 1 standard unit = 20 m, the landscape is 10 × 10 km). For each distribution type, we simulated 5 replicates from a uniform distribution within a specified range of distribution sizes (see Supporting Information for the resulting 30 distributions). Four of our distribution types were designed to have similar AOOs at the finest scale of measurement (i.e., based on cells with dimensions of 1 × 1 standard unit), and replicates were thus selected from the same range of sizes (Table 1).

To provide context for interpreting our results, we characterized scale–area relationships by calculating AOO based on the summed area of grid cells intersected by each distribution; the dimensions of grid cells increased in a roughly geometric series across 3 orders of magnitude (1, 2.5, 5, 10, 25, 50, 100, 250, 500 units). The shapes of scale–area relationships varied markedly between distribution types (Fig. 1). The most saturated

distribution (matrix) had a slope of approximately zero, the theoretical minimum value, indicating that AOO remained relatively independent of measurement scale. Conversely, the least saturated distribution (sparse point) had a slope approaching the theoretical maximum value of 1 because cell sizes became large enough to cover entire patches. The scale–area relationship for many points was similar, but slope values were less extreme. The distribution with the most variation across scales (sparse points) had a low slope (~0) at fine scales and a maximal slope (~1) at coarse scales. The 2 linear distributions (simple and sinuous) had similar scale–area relationships overall but diverged slightly at intermediate scales (Fig. 1). The 4 distributions that had similar AOOs at the finest scale (single patch, simple and sinuous linear, and many points) diverged at coarser scales, and their rank-order varied with scale.

We used the methods of Akçakaya and Root (2007) to explore uncertainty in estimates of AOO due to variation in the grid origin (geometric uncertainty). We calculated AOO for each distribution type based on grids with cell dimensions of 100 × 100 standard units. We randomly moved the location of the origin by a distance of up to 100 standard units in both dimensions and recalculated AOO for each of 1,000 iterations.

Finally, we used simulated circular footprints of threat events to estimate the risk of extinction or collapse for each distribution type. We assumed a threat eliminated the species or ecosystem everywhere the threat footprint intersected the distribution and that dispersal did not lead to recolonization during the life of the simulation. We applied 9 different threat regimes to the landscape based on factorial combinations of size and frequency. Thus, threat regimes were simulated in 3 size categories—small (events of radius 20-50 standard units), medium (radius 50-100 standard units), large (radius 100-200 standard units)—and 3 frequency categories—infrequent (1-10 events), occasional (11-50 events), and frequent (51-100 events). In each case, we ran the model for 2000 iterations, drawing the number of events from a uniform distribution across the range specified
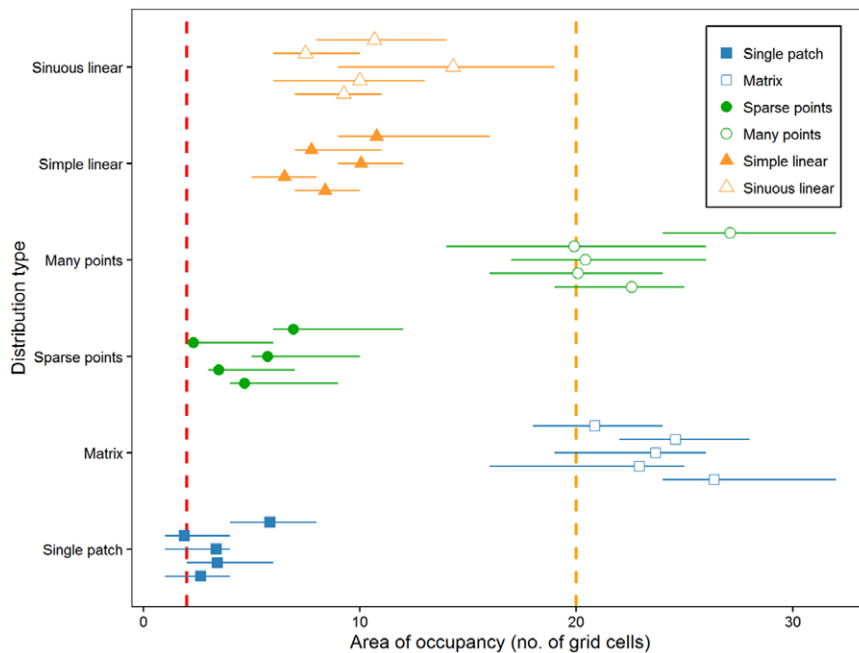
Figure 3. Variation in estimates of area of occupancy due to variation in the origin of the grid used to estimate it for 6 species or ecosystem distribution types (see Table 1 and Fig. 2). Data are mean estimates with error bars showing maximum and minimum. Area of occupancy is measured with a grid size of 100 × 100 standard units. Assuming each spatial unit is 100 m, the dashed vertical lines mark the thresholds for critically endangered (left) and endangered (right) ecosystems at 10-km grid cell size.

for each threat regime (combination of threat size and frequency). Thus, the total number of simulations was 540,000 (6 distribution types × 5 distribution sizes × 9 threat regimes × 2000 iterations) (Fig. 2 has an example iteration). We calculated the probability (risk) of extinction or collapse for each combination of distribution type and threat regime as the ratio of the number of iterations in which distributions were completely covered by threat events to the total number of iterations (2000). To examine the efficacy of AOO as a predictor of risk across different spatial scales, we calculated Spearman rank correlation coefficients between AOO and risk, for each combination of AOO measurement scale and threat regime.

The simulated distribution types encompass a wide range of realistic cases summarized in Table 1. For example, a unique lake ecosystem and its endemic fish species threatened by water extraction would be represented by the single-patch distribution exposed to a large frequent threat regime. Mammalian predators in an extensive savanna ecosystem threatened by poaching and trophic disruption would be represented by the matrix distribution exposed to small frequent threat regimes. A fringing coral reef ecosystem and its endemic species threatened by oil spills or polluted runoff would be represented by the simple-linear distribution exposed to a medium infrequent threat regime. To illustrate relationships between risk and AOO in a realistic landscape, we examined scenarios in which 1 standard unit = 20 and 100 m. At these scales, the events we simulated corresponded to a wide but realistic range of sizes, from 0.5 to 1260 km^2, consistent with the spatial footprints of a wide range of threat events reviewed by Murray et al. (2017). The largest simulated threats approximated the extent

of documented examples such as meteorite strikes and unregulated mines.

The modeled parameter space of distribution types and threat regimes produced risk estimates spanning the full range from 0 to 1, inclusive of the most and least threatened real species and ecosystems.

Results

Geometric Uncertainty

There was substantial uncertainty in estimated AOO for all 6 distribution types due to variation in the location of the grid origin (Fig. 3). The difference between minimum and maximum estimates generally increased with the mean AOO. Proportionately, estimates of AOO could be up to 73% larger (single patch) or 63% smaller (sparse points) than the mean value. Moreover, the statistical distribution of AOO estimates differed depending on the pattern and extent of a biological distribution. For example, for species or ecosystems occupying sparse points (Fig. 3), there was a long tail of overestimates above the mean and minimum estimates. For those occupying many points (Fig. 3), mean AOO tended to be evenly positioned between the minimum and maximum estimates, although AOO estimates could be skewed either way for other distribution types. To illustrate the consequences of this uncertainty for outcomes of red-list assessments, we interpreted the distribution types as ecosystem types and defined 1 standard distance unit as 100 m. In that scenario, the range of AOO estimates for 11 of the 30 simulated distributions spanned thresholds that delimited different categories of risk.
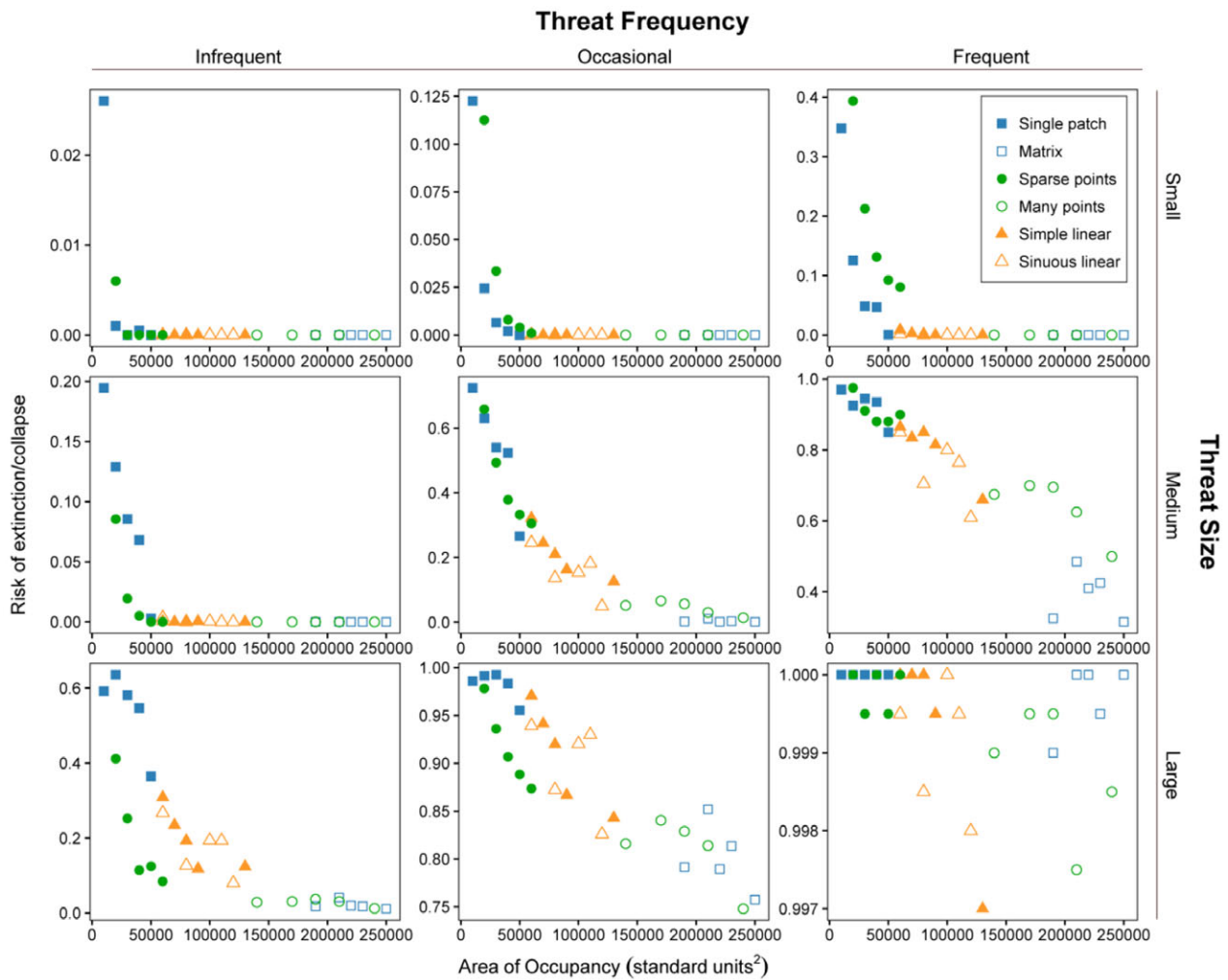
Figure 4. Relationship between risk of extinction or ecosystem collapse and area of occupancy estimated from grid cells with dimensions of 100 standard distance units (see Methods or Table 1 footnote) for 6 distribution types (Table 1 and Fig. 2) exposed to 9 different threat regimes based on factorial combinations of frequency (infrequent, occasional, frequent) and size (small, medium, large). See Methods for details. Each panel has a different y-axis scale.

Scale Effects on Risk

Risks depended on AOO, the spatial pattern of distribution of biota, and the spatial properties of the threats (Fig. 4). Risks were greater for distributions with smaller AOO; distributions with different shapes but similar AOO often exhibited similar risk under the same threat regime. Thus, distribution shape, independent of size, did not have a major influence on risk.

Risks to biodiversity were greater when both the size and frequency of threat events were larger but were more sensitive to frequency than size (Fig. 4). Risks were highest under a regime of frequent large threats, followed by regimes of occasional large threats and frequent medium threats. The lowest risks occurred under a regime of infrequent small threats, followed by regimes of occasional small threats and infrequent medium threats.

The risk of extinction or collapse was inversely related to AOO (Fig. 4); however, the strength of this relationship varied depending on the size and frequency of threat events and scale of AOO measurement (Fig. 5a). For 7 of the 9 threat regimes, AOO was a very strong predictor of risk ($0.81 < |r| < 0.98$). Predictive performance was strongest for medium-sized threat events of occasionally frequent occurrence (Fig. 5a). Even when risks were almost uniformly low (small infrequent threats) or uniformly high (large frequent threats), AOO was a reasonable predictor of relative risks ($0.44 < |r| < 0.57$).

The performance of AOO as a predictor of relative risk varied nonlinearly with its measurement scale. For all 9 threat regimes, AOO performed best when measured at grid cell sizes in the range of 25×25 to 100×100 standard units (625–$10,000$ standard units^2). Performance declined rapidly when AOO was measured at coarser
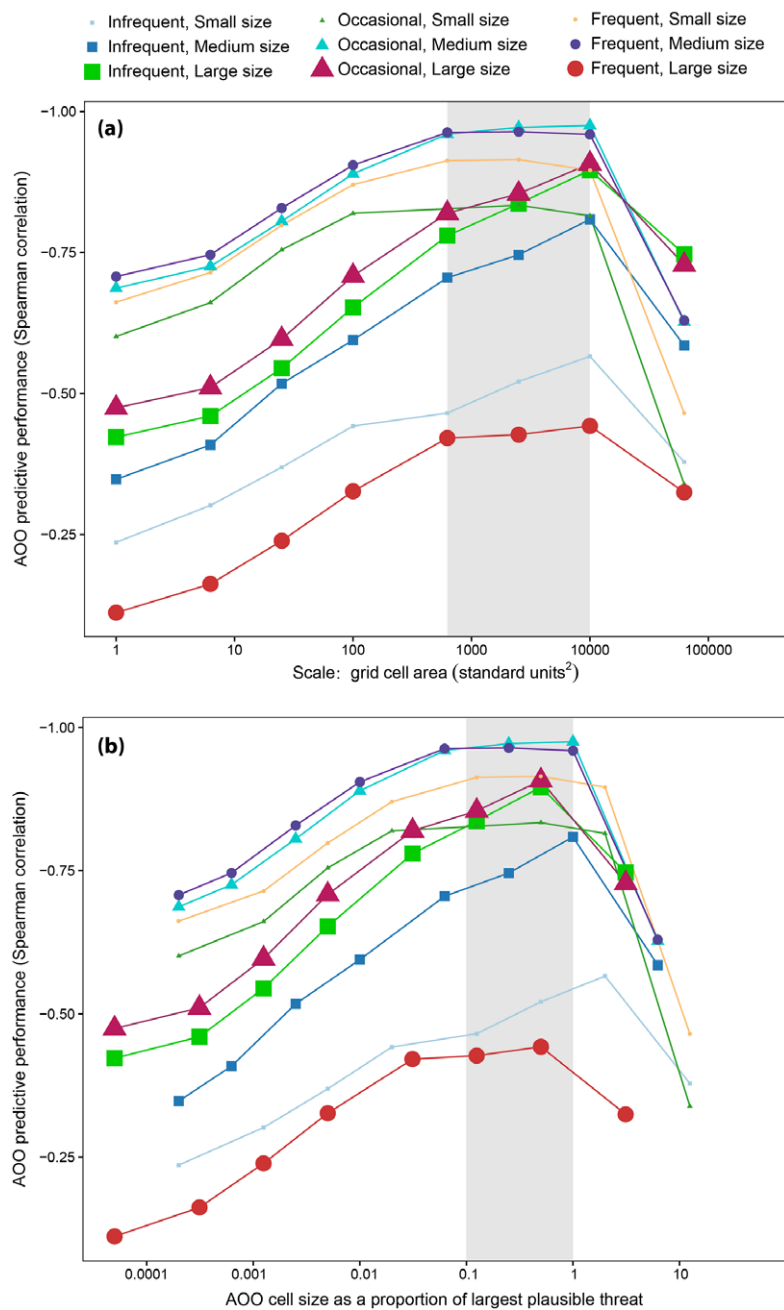
Figure 5. Performance of area of occupancy (AOO) at different scales of measurement as a predictor of risk of species extinction or ecosystem collapse. Predictive performance (y-axis) is measured by Spearman rank correlation coefficients between estimated AOO and risk. Measurement scale is represented by (a) area of grid cells in standard distance units and (b) area of grid cells relative to the spatial extent of the largest possible threat event in each of the simulated threat regimes (see Methods for details) (shading, approximate range of measurement scales for optimal predictive performance). The proportional shaded zone in (b) is a rounded approximation of the absolute values in (a).

scales than the optimal range and more gradually when measured at finer scales (Fig. 5a). Within the optimal range, grid cells of 10,000 standard units^2 performed best for several threat regimes, including occasional large, infrequent large, infrequent medium, and infrequent small (Fig. 5a). The AOO was very marginally a better predictor of risk when measured with cells of 2,500 standard units^2 for regimes of frequent or occasional small threats than when measured with cells of 10,000 standard units^2.

For a scenario in which 1 standard unit = 100 m, the extent of our landscape was 50×50 km (2500 km^2), and the area affected by individual threat events varied from 12.6 to 1260 km^2 across all simulations. In this scenario, AOO best predicted relative risk across most of the 30

biological distributions when measured with 10×10 km grid cells. The AOO was a poor predictor of risk when cells were smaller than 2.5×2.5 km and larger than 10×10 km. When 1 standard unit = 20 m, the extent of our landscape was 10×10 km, the area affected by individual threat events varied from 0.5 to 50 km^2, and AOO performed best as a predictor of risk when measured with 2×2 km grid cells and poorly when cells were smaller than 0.5×0.5 km and larger than 2×2 km.

In general, AOO performed optimally as a predictor of risk when measured with grid cells that are similar to, or slightly smaller than (one-tenth), the area affected by the largest plausible threat event, but its performance waned when the scale was much finer or coarser (Fig. 5b). This

rule of thumb was largely insensitive to the frequency of threat events within the range of values explored (1–100 events per 50 years for ecosystems and 1–100 events per 10 years or three generation lengths, whichever was longer, for species).

Discussion

Area of Occupancy, Risk Assessment, and Spatial Scaling

Our results confirm the value of AOO as an indicator of risks to biodiversity and for the first time show how the performance of AOO as a risk indicator varies with the spatial scale at which it is estimated and, most importantly, the spatial features of threat regimes. When AOO is measured using cells of 2 × 2 to 10 × 10 km, it produces good predictions of risk in the face of threat events that varied from <1 to >1,000 km^2 in area. This range encompasses realistic scenarios of land conversion, chemical spills, biological invasions, disease outbreaks, fires, and other disturbance regimes (Murray et al. 2017). The size of threat footprints therefore appear to be critical in determining the optimal measurement scale for AOO to be used in risk assessments, and this underscores the need to improve spatial data sets on threats to biodiversity (Joppa et al. 2016).

Although fine-grain estimates of AOO offer more precise estimates of the area occupied by a species or ecosystem, they are not the optimal scale for estimating risks of species extinction or ecosystem collapse as measures of risk-spreading or insurance effects. Very coarse-grain estimates of AOO also perform poorly as predictors of risk. Area of occupancy performed best for this purpose when estimates were based on grid cell sizes that were commensurate with (i.e., approximately 0.1–1 times the size of) the spatial extent of events that threatened the persistence of species and ecosystems.

The threshold values of AOO that delineated ordinal categories of threat in IUCN Red Lists were set with measurement scales that implied consideration of landscape-scale threats. Consequently, the respective application guidelines recommend standard scales (2 × 2 km and 10 × 10 km grid cells for species and ecosystems, respectively) for estimating AOO (IUCN Standards and Petitions Subcommittee 2003; Bland et al. 2016). Without this spatial scaling, estimates of AOO will be inconsistent with the thresholds specified in criterion B and may result in overestimation or underestimation of risk (i.e., the red-list category). Spatial scaling in criterion B, like temporal scaling based on generation length in criterion A of the IUCN Red List of Threatened Species (Mace et al. 2008), is therefore an essential standardization step for valid application of the criteria to different taxa and data types.

The use of coarse-grain estimates of AOO such as those recommended by IUCN for risk assessment may seem counterintuitive because large grid cells may include a high proportion of unoccupied habitat or unsuitable area. Much of the previous criticism directed at the application of AOO in IUCN Red List criteria is founded on mistaken beliefs that more precise estimates of area occupied are better indicators of risk than coarse-grain estimates. This has led to calls for use of finer-grained AOO estimates than those recommended in IUCN guidelines and adjustments to AOO thresholds based on taxonomic groups or habitat geometry (Simaika & Samways 2010; Cardoso et al. 2011; Gigante et al. 2016). Gaston and Fuller (2009) note "significant confusion in the literature over the measurement and interpretation of geographic ranges, and ... that [spatial metrics used in red listing] should not be regarded as more or less accurate ways of measuring range size." The evidence from our risk analyses should help resolve confusion between the application of AOO on one hand as a measure of occupied habitat in biogeographic analysis and on the other hand as an indicator of risk in red-list assessments. Relatively coarse-grain estimates commensurate with landscape-scale threats and IUCN Red List (criterion B) thresholds are appropriate for risk assessment, whereas a range of scales, including fine-grain scales may be appropriate for biogeographic analyses.

The use of different AOO measurement scales and thresholds for red-list assessment of different species, habitats and ecosystems, as suggested for example by Gigante et al. (2016), is problematic for 2 reasons. First, the performance of AOO as a risk indicator depends on the spatial scale of threats more than on the pattern of distribution. Proposals to adjust thresholds based on taxonomic groups or habitat geometry therefore ignore a key consideration (threats) in setting the relativity of AOO measurement scale and thresholds. Furthermore, the identity of threats (and hence their spatial properties) vary between locations and through time. To ensure generality and sensitivity to pervasive threat types, the IUCN Red List criteria embody a calibration of AOO measurement scale and thresholds that reflects landscape- and seascape-scale threats (Keith et al. 2015). Examples include land-use change driven by regional socioeconomic factors, chemical spills, disease outbreaks, exploitation of biota or habitats driven by regional markets, disturbances such as wildland fires, or tropical storms that may affect areas of a few square kilometers up to thousands of square kilometers in a small number of events (Murray et al. 2017).

Second, use of different AOO thresholds for different species or ecosystems runs counter to parsimony, one of the fundamental design principles for development of IUCN Red List criteria for both species and ecosystems (Mace et al. 2008; Keith et al. 2015). An approach based on variable scales of measurement would introduce a significant additional source of uncertainty into red-list assessments because different assessors may reach different conclusions about which scales and thresholds should be applied to particular cases. Regan et al. (2002)

defined this type of uncertainty as "vagueness" because the boundary between 2 or more categories (e.g., linear vs. area distributions) can never be specified with absolute precision. Inconsistencies stemming from vagueness could be reduced through explicit user guidelines, but the current system that applies a single standard measurement scale to fixed thresholds for all species or ecosystems avoids them altogether.

Dealing with Uncertainty

Our results suggest that variation in AOO estimates due to geometric uncertainty (uncertainty in the location of the origin of a grid used to estimate AOO) can be appreciable and may differ depending on the pattern and extent of a biological distribution. This can affect the outcome of red-list assessments, typically by underestimating the risk category. Different red-list outcomes could be assigned in one-third of our small sample of distributions, depending on the location of the grid origin. Compared with other sources of uncertainty (Regan et al. 2002), however, geometric uncertainty is easily dealt with. The IUCN guidelines for both species and ecosystems recommend that the estimate of AOO to be used in red-list assessments should be the minimum value produced by any placement of the grid. For simple distributions, a near-optimal grid position can be determined by eye. For more complex distributions Akçakaya and Root (2007) produced software to calculate the correct AOO from points. In Supporting Information, we provide a generalized R script that produces estimates from spatial distribution data. Sampling bias can also be an appreciable source of scale sensitivity in range-size estimation. Sheth et al. (2011), for example, found that dispersion and symmetry of the interspecific distribution of proportional bias in AOO estimates decreases as AOO increases. Although an investigation of sampling bias was beyond the scope of our study, our model could be adapted to explore the effect of detectability or spatially structured access constraints on the location of observed occurrences.

Learning About Real Landscapes From Simulations

The use of simulations enabled us to quantify risks of species extinction and ecosystem collapse across contrasting scenarios (Burgman et al. 1993). It is unlikely that any data set of real species or ecosystems could support such a direct and powerful comparison of observed and predicted risks. Nonetheless, it is prudent to examine assumptions and question how well our simulated landscapes represent real ones. For example, we did not model dispersal. However, adding dispersal among unaffected patches would not change any of the extinction risks unless we also modeled extinction from causes other than the disturbance we are simulating, which would have increased the complexity of the model

beyond what is required to answer the stated questions. Thus, the critical assumption we make is that dispersal, if any, occurs in affected patches and will not lead to recolonization. In effect, disturbances we simulated were similar to habitat loss such that restoration of the habitat to a state in which recolonization is possible takes longer than 3–5 generations for species or 50 years for ecosystems, which are the time frames of IUCN assessments. This is a reasonable assumption for many of the anthropogenic threats considered in red-list assessments. When recolonization is significant (typically over longer time frames), extinction risks are less strongly influenced by interactions between the pattern of clustering in the distribution and spatial autocorrelation in the threat (Vuilleumier et al. 2007).

Certain spatial attributes of the species distributions and threats we simulated (square grid cells, circular threats, uniform severity of threats within their footprint) were abstractions of reality and may appear simplistic. However, they were designed to uncover general relationships among range size, measurement scale, and extinction risk and to make robust recommendations about applications of the red-list criteria. Additional model complexity may enable more specific conclusions about particular types of distribution and threat but involves trade-offs in the breadth of general scenarios that could be explored and a clear overview of the major relationships. Our simulated distribution types spanned a range of variation that should encompass most distributions of real species and ecosystems (see Table 1 and examples in Methods). Our simulated threats involve simplified spatial footprints that could be expanded to consider other threat types with different patterns of spatial expression. Nonetheless, the key properties of extent and frequency of threat events are likely to be important irrespective of the shape of threat events. Furthermore, recent research has shown that relationships between AOO and extinction risk are relatively robust to types of threat footprints and to random versus clustered patterns of occurrence, although edge effects produce different responses (Murray et al. 2017). We therefore expect our general conclusions about the scale-sensitivity of AOO as a predictor of risk and the importance of threats in defining the optimal scales for measuring AOO to be robust when more complex distribution patterns and threats are analyzed.

Policy Implications

Our study provides empirical evidence that AOO is a strong predictor of risks to biodiversity for biota with a wide range of distribution types including patches, matrices, and linear patterns. The spatial characteristics of threats emerged as key to scaling estimates of AOO to optimize its performance for predicting risks to biodiversity and underscores a policy imperative to improve spatial data on threats (Joppa et al. 2016). These insights

from simple modeling should help resolve long-standing confusion about concepts, sources of uncertainty, and standardization procedures in red-list methods. Consistent application of these methods underpins the reliability of meta-analyses that form a crucial basis for future development and implementation of conservation policy.

Acknowledgments

Supporting Information

Maps of the 30 simulated distributions (Appendix S1) and R code for estimating area of occupancy accounting for uncertainty in the location of grid origin (Appendix S2) are available online. The data supporting the results are archived at https://figshare.com/s/ 61cba4c92c90b749a92f (https://doi.org/10.6084/m9. figshare.5139505). The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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