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# Global synthesis of conservation studies reveals the importance of small habitat patches for biodiversity

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**Island biogeography theory posits that species richness increases with island size and decreases with isolation. This logic underpins much conservation policy and regulation, with preference given to conserving large, highly connected areas, and relative ambivalence shown toward protecting small, isolated habitat patches. We undertook a global synthesis of the relationship between the conservation value of habitat patches and their size and isolation, based on 31 systematic conservation planning studies across four continents. We found that small, isolated patches are inordinately important for biodiversity conservation. Our results provide a powerful argument for redressing the neglect of small, isolated habitat patches, for urgently prioritizing their restoration, and for avoiding simplistic application of island biogeography theory in conservation decisions.**

Zonation | fragmentation | complementarity | irreplaceability | prioritization

Island biogeography and subordinate theories from metapopulation ecology and landscape ecology indicate that species richness and individual species' population sizes in a habitat patch will depend on the degree of isolation of the patch (e.g., distance to nearest neighbor or mainland), the size of the patch, and the quality of the habitat contained within the patch (1). Theory underpinning metapopulation ecology also emphasizes the role of size in enhancing populations' robustness to stochastic perturbations, and the role of connectivity in increasing gene flow and the probability of rescue following local extinctions (2, 3). Many studies in landscape ecology focus on the role of large patches in avoiding negative edge effects arising from fragmentation (4, 5). Each of these drivers point to the importance of large, connected patches of habitat for ensuring the persistence of species and conserving species richness, and to the lower ecological value of landscapes comprising many small, isolated patches with extensive edge environments.

Conservation planning principles of representativeness and complementarity have been introduced into conservation practice (6) to provide a pragmatic basis for conserving biodiversity in rapidly changing, fragmented landscapes under pressure from threats such as land clearing or climate change. These principles are embodied in conservation decision support tools (7, 8) that can be used to identify areas that most cost-efficiently ensure the representation of at least some part of each species range in protected areas. Operationally, areas are identified for protection so as to complement existing conservation efforts. This approach has been applied to many conservation decision problems, such as rezoning marine parks in California and wilderness areas in Indonesia (9), assessment of large-scale urban expansion in Western Australia (10), evaluation of the coverage and comprehensiveness of the Natura 2000 network (11), and expansion of Madagascar's protected area network (12).

The predisposition toward larger and more connected areas has found its way into conservation and land use policy in many jurisdictions, sometimes in perverse or undesirable ways. In many jurisdictions, such as Australia, Canada, Brazil, and New Zealand, small patches of habitat may be cleared without significant regulatory impediment or requirements for compensation such as biodiversity offsetting (13). It is common to see strong conservation policy emphasis on the protection or enhancement of large, mostly intact landscapes (14) and avoidance of areas containing many small fragments (15). Most of these policies and approaches to setting conservation priorities are implemented without any particular consideration of the level of threat currently faced in those landscapes, or the degree to which conservation of the areas in question would complement existing conservation reserves and improve representation of species habitats that are currently poorly represented in conservation reserves (14).

Arguably, a greater emphasis on representativeness and complementarity has emerged in places where the influence of technical experts in conservation planning is greatest. This is the case in Australia, which has seen government policies that seek to create a "comprehensive, adequate and representative" reserve system (16). Nonetheless, in Australia, vegetation management and conservation policy continue to prioritize larger and more connected areas over smaller, more isolated fragments, and downplaying their value in offsets and vegetation loss regulations and policies. For example,

## Significance

**Expansive development for urbanization, agriculture, and resource extraction has resulted in much of the Earth's vegetation existing as fragmented, isolated patches. Conservation planning typically deprioritizes small, isolated patches, as they are assumed to be of relatively little ecological value, instead focusing attention on conserving large, highly connected areas. Yet, our global analysis shows that, if we gave up on small patches of vegetation, we would stand to lose many species that are confined to those environments, and biodiversity would decline as a result. We should rethink the way we prioritize conservation to recognize the critical role that small, isolated patches play in conserving the world's biodiversity. Restoring and reconnecting small isolated vegetation patches should be an immediate conservation priority.**

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Data deposition: All R code and raw data inputs (i.e., Zonation outputs and environmental layers) used in analyses are available at https://figshare.com/s/29477d872ea6ca2f9962.

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offsetting requirements are more stringent for larger patches in Victoria and New South Wales (17, 18). Globally, the "bigger (and more connected) is better" logic continues to dominate conservation policy, and the scientific community appears largely to reinforce this view (2, 19), but not without dissent (15). The current focus of conservation scientists on conserving large intact landscapes may have the unintended consequence of downplaying the importance of small, isolated, remnant patches of habitat in fragmented landscapes in the eyes of policy makers, land planners, and conservation organizations (13).

There are pragmatic arguments against the default policy of focusing conservation effort predominantly or solely in large and connected patches of habitat. In human-dominated landscapes where past urban and agricultural development has favored flat, fertile environments, the remaining small and isolated patches of vegetation tend to host species and ecological communities notably different than those occurring on poor soils or steep locations where the majority of existing conservation areas are placed (20). The size of remnant patches of habitat is not the only consideration. The more isolated remnant patches are from large intact patches, the more likely they are to be different in species composition, based on the characteristic spatial autocorrelation observed in most environmental data (21). Finally, small and isolated patches, such as those in more-urbanized environments, tend to be disproportionately susceptible to processes such as weed and feral pest invasion or illegal clearing. Without protection and restoration, opportunities to incorporate these patches with unique species composition into a reserve system may disappear quickly, making immediate protective action necessary. Hence, the case for securing, protecting and restoring small patches may be more urgent, as they tend to be more threatened by clearing or degradation than larger patches.

Herein lies an important conceptual, practical, and sociological challenge for conservation practitioners: Should we focus conservation efforts on protecting large, less vulnerable patches of habitat that may contain species relatively well represented in existing conservation areas? Or should we focus efforts on preserving and restoring the often more degraded, but possibly more ecologically unique, small and isolated patches of habitat that could contain species less well represented in existing conservation areas?

While this question requires both practical (cost, logistics) and sociological (preferences for large wild areas versus protection of rare species habitats) considerations, we approach this problem from an ecological perspective by testing the hypothesis that small and isolated patches of remnant habitats in fragmented landscapes tend to contain unique biodiversity that is not well represented in large, contiguous conservation reserves. This is an important issue to resolve, because it determines how much effort conservation scientists should invest in moving the focus of policy makers toward conserving and restoring small and isolated patches of vegetation that are often quite degraded and threatened by many stressors, and potentially more costly to manage per unit area.

While a number of authors have explored the relationship between patch size, isolation, and species richness in fragmented landscapes, with mixed findings (2, 15, 22–30) (*SI Appendix*, section S1), we could find no studies that explicitly quantify the relationship between patch size, isolation, shape, and conservation value based on the principles of complementarity and representativeness.

We utilize a global synthesis of 31 spatial conservation studies, implemented using the spatial prioritization software Zonation (7), in 27 countries across four continents. We statistically synthesize the results of these studies by quantifying the relationship between conservation value and the size, shape, and isolation of habitat patches in each study landscape. Our synthesis allows us to draw significant empirical generalities about this relationship and provide evidence-based advice on the importance of small habitat patches for conservation.

## Results and Discussion

Our central result indicates a working hypothesis for land managers and policy makers: that small, relatively isolated habitat patches of high shape complexity in fragmented landscapes tend to be of higher conservation value according to a complementarity and representativeness criterion than a similar-sized habitat patch within contiguous tracts of intact vegetation of low shape complexity. The key finding of our analysis is that patch size, proportion of intact vegetation in a 5-km radius, and fractal dimension index had a statistically significant effect ($P < 0.01$) on conservation value across the 31 conservation prioritization case studies in our global data set. Our final fitted model indicates that conservation value tends to decrease as patch size increases and the intactness of the surrounding landscape increases. Conservation value also increases with increasing fractal dimension (a measure of patch shape complexity), but tends to decrease with increasing perimeter–area ratio (Fig. 1). A final model including an autocovariate term and cubic transformations of 4 of the 16 candidate patch variables provided the most parsimonious and interpretable explanation of spatial variation in Zonation conservation rank (a measure of conservation value and the dependent variable in our analysis). All variables and interactions in the final model were statistically significant ($P < 0.01$).

To help interpret the size of the effect we are reporting, our result indicates that a land unit of around 1 ha selected at random from a small patch of habitat (<1,000 ha) with a complex shape that is predominantly surrounded by cleared or degraded area (e.g., <20% area in a 5-km radius under natural vegetation) will tend to have a substantially higher conservation value than a similar unit selected from a large habitat patch within a largely intact landscape. However, patches characterized by high perimeter–area ratio (often linear patches of habitat along road and river edges in cleared landscapes) tend to have lower conservation value, holding all other variables at their mean. In our case study regions, we would expect the conservation value to reduce by a factor of ∼3 with a doubling of the proportion of habitat in a 5-km radius or a doubling patch area, holding all other variables at their mean (Fig. 1 and *SI Appendix*, section S2).

Looking at species distribution maps (31) for rare or highly restricted species and comparing them to conservation priority maps in some of our case study regions allows us to further tease out the reasons for the statistical relationships observed across the multiple spatial prioritizations we examined. For example, the Perth–Peel region of southern Western Australia is highly representative of the more fertile and wet coastal regions of the Australian continent (Fig. 2). The region is characterized by a few large contiguous tracts of forest at a relatively large distance from urban and coastal areas, and many much smaller fragments of habitat embedded in a matrix of agriculture and urban development closer to the coast. For the bulk of species found in the larger, contiguous forest areas, loss of any particular hectare of that environment would generate a relatively small overall proportional loss in available habitat. Conversely, closer to the coast, the loss of any small patch of vegetation leads to a significant (and in some instances total) loss of suitable habitat for species confined to those patches, and hence those small patches are afforded a very high conservation value in a regional Zonation analysis. For example, the Western ringtail possum (*Pseudocheirus occidentalis*) is a Critically Endangered (Environment Protection and Biodiversity Conservation Act 1999) arboreal marsupial that has retracted to the few remaining fragments of the coastal plain of southwest Western Australia (Fig. 2*A*). The fragments of habitat in which it persists tend to be small and isolated; however, a conservation plan for the Perth region must include those patches if it is to ensure representation of the range of this species. Three other species—one migratory bird (red-necked stint, *Calidris ruficollis*) and two endemic plants (*Dillwynia dillwynioides* and the endangered glossy hammer orchid *Drakaea elastica*)—rely on the same small fragments of habitat close to Perth. These

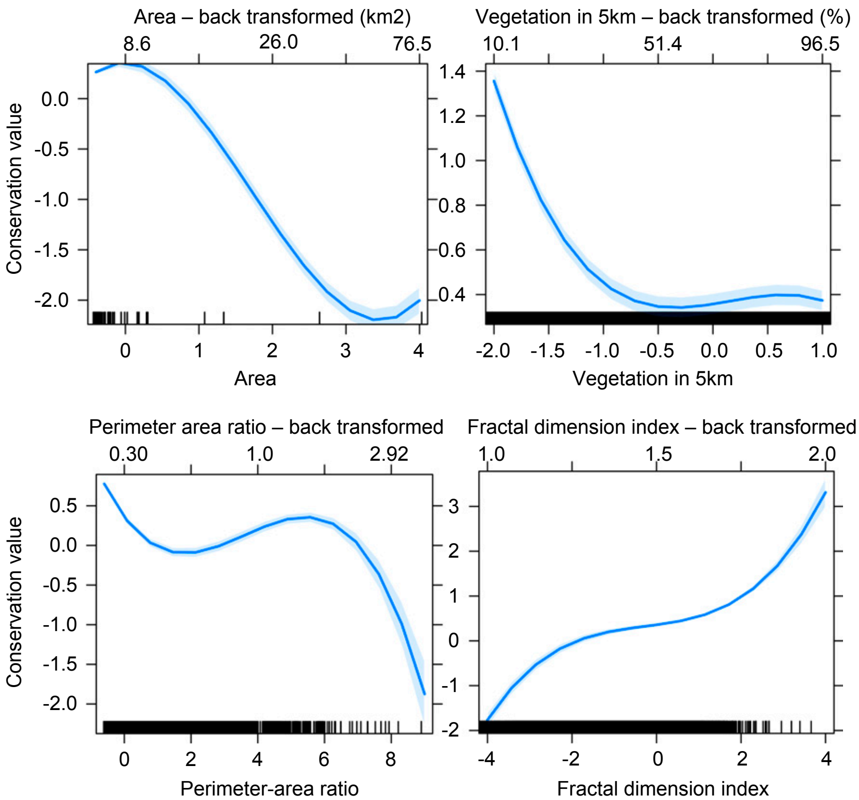


**Fig. 1.** Relationship between conservation value (logit-transformed) and the four patch-level independent variables from the global model. Independent variables presented are patch area, proportion of cells containing natural vegetation in a 5-km radius, the fractal dimension of the habitat patch, and the perimeter–area ratio of the patch in which the cell is located. The *x* axes along the bottom of the plots give standardized values of independent variables used in the regression. Equivalent raw values are given on the upper *x* axes. The conservation value of a landscape unit (a single raster cell) is defined by its conservation importance rank, as determined by a Zonation analysis (*y* axis), that takes into account the proportion of species' ranges contained within each cell. Cells with a high conservation rank will tend to be ones that constitute a larger proportion of the remaining range of a species. Zonation conservation values that range on the scale [0,1] were logit-transformed to allow linear modeling (43). All independent variables were standardized, so the scale on the *x* axes represents SDs from the mean. Each of the relationships depicted here were statistically significant at $P < 0.01$. Each of the independent variables was fitted as a cubic polynomial. An interaction between patch area and fractal dimension was included in the AIC-best model (*SI Appendix*, section S2). An autocovariate term was fitted to reduce spatial autocorrelation in model residuals (see *SI Appendix*, section S2 for details).



species are "driving" the prioritization (32) of those small habitat fragments midway down the coast in the Perth region (Fig. 2*A*).

A similar situation can be observed in the Pacific Northwest United States case study (Fig. 2*B*). The large central area of the region around the Willamette River has a very high conservation value rank (Fig. 2*B*, *Left*), despite being an area of high urbanization and agricultural impact. The environmental conditions that made the fertile valley a place to settle, farm, and build cities also make it suitable for a particular set of grassland birds such as the Threatened streaked horned lark (*Eremophilia alpestris strigata*) (Endangered Species Act 1973), and the declining western meadowlark (*Sturnella neglecta*) that have relatively little suitable habitat elsewhere in the region. The fact that much of their habitat is severely altered or destroyed by agriculture and urbanization means that what remains is crucial for preventing these species from going locally extinct and for halting the loss of regional biodiversity. Here, as in the fragmented regions around Perth and the other case studies in our dataset, high conservation value coincides with lower native vegetation extent distributed in smaller patches with complex shapes characteristic of the fragmented parts of those landscapes.

This result provides quantitative evidence and a powerful argument that small remnant patches of habitat should, by default, be highly valued, more than they currently are in many jurisdictions. Indeed, we may be gravely mistaken in deprioritizing small, isolated patches, as their continued loss will almost certainly lead to local, and in some instances global, extinctions. Small intact patches of vegetation in areas otherwise largely cleared of vegetation tend to support the last individuals of species that have been eliminated from other parts of the landscape due to systematic destruction of similar habitat types (33). This study systematically analyzes and statistically quantifies this effect across diverse landscapes globally, reinforcing the need to avoid the continued loss of small isolated patches of habitat, even when concerns exist about the long-term viability of species in such patches.

The landscapes analyzed in this study have been cleared or heavily modified for as little as 80 y (Australia), and, in many cases (in Europe), for hundreds of years. For most animal species, even 80 y is enough for extinction debts to play out (34). The same can be said for the bulk of the threatened plants included in these studies, although, for long-lived tree species, it may take hundreds of years for extinction debts to be realized. Our results show that large conservation gains could be achieved by protecting, restoring, and increasing the size and connectedness of small remnant patches, where many rare and threatened animals and plants still survive. International agreements such as the Bonn Challenge (35), and associated regional initiatives such as Africa's Great Green Wall (36) and China's Grain for Green project (37), are providing impetus to restore habitats. These are catalyzing ambitious national restoration goals, with a current focus on forests and the numerous ecological and carbon sequestration benefits. There remain significant challenges to introducing biodiversity into such initiatives. Nonetheless, with a growing interest in broad-scale restoration for multiple social and environmental benefits, taking more of a restoration perspective to identifying conservation priorities is becoming a very realistic strategy.

Our models explain a small amount of the spatial variation in conservation value across our global data sets. While our main effects were all statistically significant (*SI Appendix*, section S2) and ecologically sensible in the responses they represent, there are clearly other environmental and social processes not included in our models that drive spatial variation in conservation value. Patchiness in species distributions due to competition, disease, and other ecological processes will drive spatial variation in conservation value that cannot be easily mapped and modeled at a global scale. While it was impossible to sample the full range of environments in this study, we have sampled a wide range of geographies, climates, and land use histories. Areas such as The Netherlands, with only 16% of the landscape comprising natural or seminatural vegetation cover, contrast with relatively intact

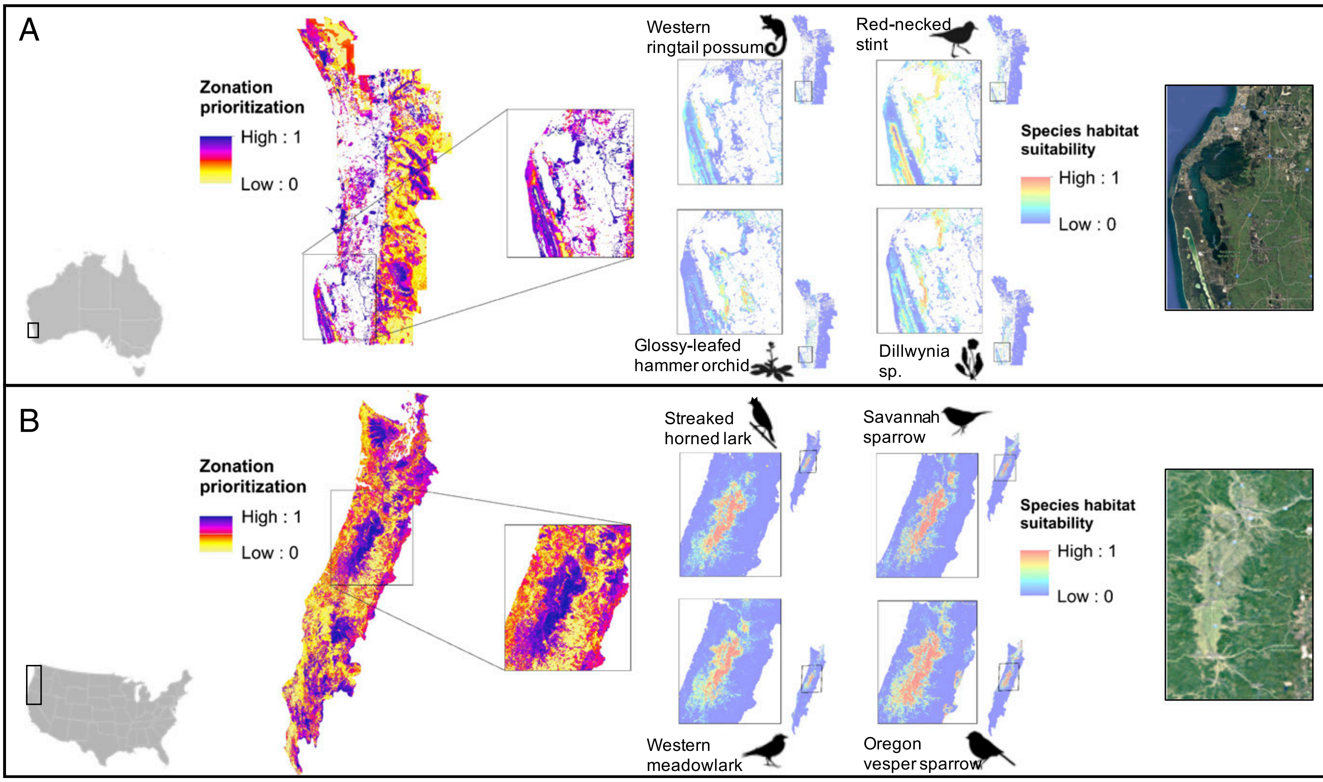


**Fig. 2.** Zonation priority rank maps (*Left*) are provided for two case studies: (*A*) Perth Australia and (*B*) Pacific Northwest United States showing the lowest (yellow) and highest (purple) conservation priority areas. Enlarged portions of the map (*Middle*) highlight fragmented parts of the study area that contain habitat patches of very high conservation value. The species icons indicate the species that have ranges primarily in those small, isolated patches. Maps adjacent to each species icon give SDM predictions for each of those species. Satellite images (*Right*) provide a bird's-eye view of the level of habitat fragmentation in the featured case study subregions.

landscapes in western Australia and North America, where ∼70% of the landscape contains intact forests and grasslands. The primary bias in this study is toward areas with relatively high-quality biodiversity data suited to Zonation-style analyses.

Conservation priorities are driven by more than the spatial distribution of biodiversity. Acquisition and management costs, social and political constraints, threats to biodiversity, and data uncertainty all play into conservation decisions. Our analysis indicates that an emphasis on larger, cheaper conservation areas may compromise biodiversity conservation objectives. If larger patches are cheaper to manage than small or isolated ones, then an explicit cost−benefit analysis could compare the efficiency gained by choosing larger patches to the cost of losing unique biodiversity values in small patches. Our aim here is not to argue for thoughtlessly prioritizing protection of small and isolated habitats, but rather to prompt a reassessment of assumptions about their lack of worth. When setting conservation priorities, application of rules that penalize small and isolated patches as a matter of course, without adequate assessment of value, should be avoided.

Our findings raise important questions for conservation practitioners. Our results are driven by our use of a biodiversity measure that emphasizes representativeness and complementarity (6). Does that mean that island biogeography and metapopulation theories are not relevant in conservation? Obviously not. However, the relative emphasis given to these two bodies of theory should reflect the specific objectives of a conservation program. A program seeking to ensure long-term persistence of particular species would aim to preserve larger, more intact habitats for those species. However, if the aim is to ensure representation of a large number of species with diverse habitat needs, then it is appropriate to secure poorly represented environments, even if they comprise small and isolated patches, and especially if those patches face destruction. Biogeography and metapopulation theories underpin conservation and restoration efforts that seek species persistence, but they must be reconciled against the objective of achieving a representative and cost-effective conservation estate.

Our unique attempt to draw some generality from spatial prioritizations conducted in diverse landscapes across the planet has provided insights into the relative importance of small and isolated habitat patches, and a statistical predictive framework for analyzing conservation importance. Our work provides a hypothesis that is testable and falsifiable with further evidence: that small and isolated patches of remnant habitat are likely to contain disproportionately more unique or rare biodiversity values that may be irreplaceable, compared with equivalent sized areas in highly intact landscapes. We encourage synthetic analyses such as ours to explore big questions of high practical relevance for the conservation of biodiversity.

## Methods

**Spatial Conservation Prioritization Case Studies.** We synthesized and analyzed the results of 31 multispecies spatial conservation prioritization case studies from 28 countries around the globe, including case studies from Australia, North America, Africa, and Europe (*SI Appendix*, Table S1). The case studies presented in this study were all implemented using the systematic spatial prioritization software Zonation (7). Drawing on case studies that utilized a single decision support package allowed us to take a consistent approach to the definition of the "biodiversity value" across all studies. Landscape units were defined as raster map cells of 1 ha in size. A key criterion for inclusion in our synthesis was that studies must not have used arbitrary weighting of patches based on their size or level of fragmentation, such as the edge-to-area, patch-size, or connectivity penalties commonly applied in conservation prioritization studies (38), as this would confound our attempts to understand the representativeness value of small isolated patches. The case studies analyzed conservation value across multiple biomes. All studies ranked conservation priorities across landscape units, using individual species distributions as the currency of conservation significance (*SI Appendix*, Table S1). No studies incorporated land acquisition or management costs in their Zonation prioritization. Based on these criteria, we identified four other studies that were not included in our analysis because authors could not be contacted or were not able to provide the necessary Zonation output files. Our aim was to achieve a geographically representative sample of Zonation studies, not a comprehensive analysis of the almost 1,000 studies that have utilized Zonation since 2005. We anticipate that many other studies could be added to our analysis in the future.

**Conservation Value.** The conservation value of a given landscape unit (raster cell) was defined in terms of its conservation priority rank, as determined by a Zonation analysis, that is based on the proportion of remaining species distributions contained within each cell. The ranking of cells in the landscape is created through a cell removal process whereby the Zonation software first assumes all cells in the landscape to be protected and then progressively removes cells that cause the smallest marginal loss in overall conservation value. This is repeated until no cells are left, with the least valuable grid cells being removed first and the most valuable cells being retained until the very end. The cell removal order provides the relative ranking. The critical component of the algorithm is the definition of marginal loss (6) that dictates which grid cell is removed at each step of the process. There are multiple marginal loss functions that can be used in Zonation. The commonly used "core-area" marginal loss function aims to balance the solution across all features (species and/or ecosystem types) at each removal step, retaining the high-quality locations for all features as long as possible. Mathematically, the marginal loss in core-area Zonation is defined as

$$\delta_i = \max_j \frac{w_j p_{ij}}{c_i \sum_{k\in S} p_{kj}}, \quad [1]$$

where $p_{ij}$ is the occurrence level of feature $p_j$ in cell $i$, and $\Sigma_{k\in S} p_{kj}$ is the sum of occurrence levels (usually relative likelihood, probabilities of occurrence or population density) of species $j$ in cells $k$ that are included in the remaining set of cells $S$ at each point of the cell removal process; $w_j$ is the weight given to species $j$ in the analysis, which is commonly set as uniform across all species or linked to species threat level, endemicity, or some other factor of conservation relevance (39). For completeness, we also include $c_i$, the cost of adding cell $i$ to the reserve network. As cost was not used in the case studies incorporated in our analyses, this receives a value of 1 (equal cost for all grid cells). Using Eq. **1**, the software calculates the relative importance of each cell for each feature (species or vegetation type) during the prioritization process. Then, for each cell, it identifies the maximum value across species and finally removes (ranks) the cell that has the smallest maximum value and, hence, the lowest marginal loss.

In most Zonation analyses, including those presented here, the currency of benefit is based on maps of habitat value for each species or vegetation community of interest. These are usually derived from observation data, species distribution models (SDMs), and/or maps of vegetation communities. Other values may be included, such as human social or economic values placed on particular places (e.g., refs. 7 and 40). However, here we focus on analyses conducted only with biodiversity features, predominantly species distributions derived from SDMs (31). Zonation can account explicitly for connectivity when prioritizing sites for conservation (38), including identifying suitable and efficient corridors for maintaining connectivity between core areas of suitable habitat (39). Here we avoided studies that prioritized connectivity, to avoid confounding our statistical analysis. The top priority sites identified in the studies that underpin our analyses represent areas assumed to be necessary to ensure habitat representation for all species and vegetation communities.

**Vegetation Patch Size, Shape, and Isolation Variables.** Vegetation mapping of case study regions was used to define habitat patch size, shape, and isolation metrics for each region (*SI Appendix*, Table S2). Based on vegetation mapping, patches of habitat generally comprised areas of natural forest, woodland, shrubland, or grassland embedded in a matrix of human-modified agricultural land thought to be unsuitable for the species included in each case study. In some case studies, habitat was considered more broadly as any type of native or natural vegetation that could serve as habitat for species in the analysis (11), including agricultural areas with important natural features such as large scattered trees (35). Areas under intensive agriculture, industrial and urban areas, large water bodies, and transport corridors were considered nonhabitat for the purposes of our analysis. All species considered in case studies were terrestrial. Vegetation mapping and patch level variables were processed at 1-ha (100 m) grid cell resolution for all case study areas using patch delineation and size, shape, and isolation computation algorithms implemented in the R packages *raster* (v2.6-7) (41) and *SDMTools* (v1.1-221) (42) (see *SI Appendix*, Table S2 for definitions of patch variables computed and used in the analysis and *SI Appendix*, section S2 for R code to generate all patch variables). The original vegetation mapping included raster maps at resolutions ranging from 0.25-ha (50 m) to 6.25-ha (250 m) grid cell resolution, and some vector maps at mapping resolution ranging from 1:10,000 to 1:100,000. All vegetation maps not at 1-ha grid cell resolution were resampled to that resolution in R *raster*.

**Analyzing Conservation Value in Relation to Patch Size, Shape, and Isolation Variables.** The original grid cell resolution of Zonation case study analyses varied from 0.25 ha (New South Wales, Australia) to 1.5 km$^2$ (Europe) (*SI Appendix*, Table S2). For consistency, Zonation outputs in all case study regions were resampled to 1-ha resolution and clipped using the R package *raster* to exactly match the grid cell resolution and extent of the vegetation mapping used to compute patch metrics.

Preliminary graphical exploration of the relationship between conservation value, patch size, and landscape fragmentation was conducted at a case study/country level to provide some insights into likely global-level patterns. Zonation priority rank values were plotted against the patch variables planned for use in the statistical analysis, using box plots and scatter plots. Observed relationships were then explored in more detail using statistical modeling.

For global-level statistical modeling, the dependent variable—conservation value (Zonation rank)—which ranges on a [0,1] scale, was transformed using a logit transformation to allow linear modeling assumptions to apply (43). Independent variables (*SI Appendix*, Table S2) representing aspects of patch size, shape, fragmentation, and isolation were standardized to improve model parameter estimation. A Pearson's correlation matrix for all candidate independent variables was computed to allow identification of highly correlated pairs of independent variables, with the purpose of eliminating highly correlated variables being offered within the one statistical model; again, the purpose was to improve model coefficient estimation stability (*SI Appendix*, section S2) (44). From each pair of variables showing high correlations ($\rho > 0.6$), one variable was retained for further modeling on the basis of univariate (a single independent variable) regressions against the dependent variable (44). The variable from each correlated pair that most substantially reduced residual deviance in a univariate regression model (on conservation value) was the one that was retained. This resulted in a final set of four candidate patch-level independent variables retained for potential inclusion in the final multiple regression model: patch area, patch fractal dimension, patch perimeter-to-area ratio, and proportion of intact vegetation in a 5-km radius. Patch area is simply the area, measured in hectares, of contiguous natural vegetation that makes up the patch. Patch fractal dimension describes the shape complexity of each patch, with high values indicating high shape complexity. Patch perimeter-to-area ratio is used as an index of how much "internal" area of a patch exists relative to the amount of "edge." High ratios usually indicate long, thin strips of natural vegetation that are largely edge, with little internal area. The proportion of vegetation in a 5-km radius is computed by summing all of the 1-ha cells classed as natural vegetation in a 5-m radius around a focal cell (see *SI Appendix*, Table S2 for details of all patch variables, including those that made it to the final model selection stage).

Because ~290 million raster cells were available for regression modeling, we were forced to use a sparse sample of the available data to produce statistical models that converged with acceptable levels of spatial autocorrelation in model residuals (45). Using 10,000 random samples per case study region or country substantially reduced spatial autocorrelation in model residuals and provided sufficient data for stable inference. With 10,000 samples obtained from each case study region, the total sample for modeling was $n \approx 275{,}000$. Random sampling of the available data was repeated 10 times using an unweighted sampling scheme (10,000 from each region) to test for stable inference. Stable inference is defined here as low (<10%) coefficient of variation in estimates of coefficients (from models of the same structure) between independent samples obtained from each case study. Random samples from each case study region were obtained using the function *sampleRandom* in the R package *raster* (v2.6-7) (41). In all fitted models, residual autocorrelation was reduced to negligible levels by introducing an autocovariate term (45). The autocovariate was produced from the Zonation prioritization raster maps from each of the 31 studies using the R package *spdep* (v.0.6-5) (46) with a neighborhood radius of 20,000 cells and all other settings default (*SI Appendix*, section S2).

Global multivariable models were fitted as generalized linear models (GLMs) with a Gaussian link function (47). Nonlinear relationships observed in preliminary graphical explorations of relationships between conservation value and patch metrics using smoothing terms (44) were accommodated in the global GLMs using quadratic or cubic polynomial terms. The final model structure (variables included and shapes of the responses) was determined utilizing backward selection implemented in the *StepAIC* function available in the *Mass* library in R (48). The backward selection function compares the full model (all terms included with cubic transformations and interactions between some independent variables) to smaller subsets on the basis of Akaike's Information Criteria (AIC) (49). AIC supports model selection based on a trade-off between deviance reduction (explanatory power) and parsimony (50). The AIC-best model arising from that process included a cubic transformation on all terms except interactions (essentially the full model) (*SI Appendix*, section S2). All variables included in the AIC-best model were significant at $P < 0.01$ (*SI Appendix*, section S2). The tendency toward large models in this study is driven by the large sample of data used to fit each model. This is of little consequence, however, as smaller models (with fewer variables) give the same shape fits as larger models with respect to our main variables of interest (the patch-level indices). Plots of independent variable effects on conservation value were produced using the *effects* package (51) (v4.0-1) in R (52).

**Data and Software Availability.** All statistical analyses were undertaken in R 3.3.3. All R code and raw data inputs (i.e., Zonation outputs and environmental layers) used in analyses are available (52) and via a weblink in *SI Appendix*, section S2.

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