



# Measuring impacts on species with models and metrics of varying ecological and computational complexity

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**Abstract:** Approaches to assess the impacts of landscape disturbance scenarios on species range from metrics based on patterns of occurrence or habitat to comprehensive models that explicitly include ecological processes. The choice of metrics and models affects how impacts are interpreted and conservation decisions. We explored the impacts of 3 realistic disturbance scenarios on 4 species with different ecological and taxonomic traits. We used progressively more complex models and metrics to evaluate relative impact and rank of scenarios on the species. Models ranged from species distribution models that relied on implicit assumptions about environmental factors and species presence to highly parameterized spatially explicit population models that explicitly included ecological processes and stochasticity. Metrics performed consistently in ranking different scenarios in order of severity primarily when variation in impact was driven by habitat amount. However, they differed in rank for cases where dispersal dynamics were critical in influencing metapopulation persistence. Impacts of scenarios on species with low dispersal ability were better characterized using models that explicitly captured these processes. Metapopulation capacity provided rank orders that most consistently correlated with those from highly parameterized and data-rich models and incorporated information about dispersal with little additional computational and data cost. Our results highlight the importance of explicitly considering species' ecology, spatial configuration of habitat, and disturbance when choosing indicators of species persistence. We suggest using hybrid approaches that are a mixture of simple and complex models to improve multispecies assessments.

**Keywords:** biodiversity metrics, impact assessment, metapopulation capacity, metapopulation models

Medición de los Impactos sobre las Especies con Modelos y Medidas de Complejidad Ecológica y Computacional Variante

**Resumen:** Las estrategias para evaluar el impacto de los escenarios de perturbación de paisaje sobre la distribución de las especies van desde las medidas basadas en patrones de presencia o hábitat hasta los modelos integrales que incluyen explícitamente a los procesos ecológicos. La elección de medidas y modelos afecta la interpretación de los impactos y las decisiones de conservación. Exploramos los impactos de tres escenarios realistas de perturbación sobre cuatro especies con características ecológicas y taxonómicas diferentes. Usamos progresivamente modelos y medidas más complejas para evaluar el impacto relativo y la clasificación de los escenarios sobre las especies. Los modelos variaron desde aquellos de distribución de especies que dependen de las suposiciones implícitas acerca de los factores ambientales y la presencia de la especie hasta aquellos modelos poblacionales explícitos con una alta parametrización espacial que incluyen los procesos ecológicos y la estocasticidad. Las medidas tuvieron un desempeño uniforme en la clasificación de los diferentes escenarios de acuerdo a la gravedad, principalmente cuando la variación en el impacto fue causada por la cantidad de hábitat presente. Sin embargo, las medidas difirieron en la clasificación para los casos en los que las dinámicas de dispersión fueron significativas en la influencia de la persistencia metapoblacional. Los impactos de los escenarios sobre las especies con una habilidad

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reducida de dispersión estuvieron mejor caracterizados con el uso de modelos que capturaron explícitamente estos procesos. La capacidad metapoblacional proporcionó categorías de clasificación con la correlación más consistente a aquellas provenientes de los modelos ricos en datos y con una alta parametrización e incorporó información sobre la dispersión con un reducido costo adicional de cómputo y de datos. Nuestros resultados resaltan la importancia de la consideración explícita de la ecología de las especies, la configuración espacial del hábitat y la perturbación cuando se eligen los indicadores de la persistencia de una especie. Sugerimos que se usen estrategias híbridas que mezclen modelos simples y complejos para mejorar las evaluaciones realizadas a múltiples especies.

**Palabras Clave:** capacidad metapoblacional, evaluación de impacto, medidas de la biodiversidad, modelos metapoblacionales

**摘要:** 评估景观干扰情景对物种影响的方法包括基于物种出现格局或栖息地格局的指标和纳入生态过程的综合模型等。对指标和模型的选择会影响对物种所受影响的理解和保护决策。本研究探索了三种真实干扰情景对四种不同生态学特征和类群的物种的影响。我们使用了逐渐复杂化的模型和指标评估了干扰情景对物种的相对影响和影响等级。本研究涉及的模型包括依赖于环境因素和物种出现的隐式假设的物种分布模型, 以及明确包含生态过程和随机性的高度参数化的空间显式种群模型。当影响的变化是由栖息地数量驱动时, 各种指标对不同情景的影响严重程度排序的结果一致。然而, 当扩散动态对集合种群续存有重要影响时, 不同指标的排序结果不同。使用明确考虑了扩散过程的模型可以更好地描述干扰情景对扩散能力弱的物种的影响。集合种群承载力提供了与高度参数化和数据丰富的模型最为一致的排序, 并且可以在几乎没有额外计算和数据成本的情况下加入扩散的信息。我们的结果强调了选择物种续存指标时应清楚地考虑物种的生态特征、栖息地空间结构以及干扰。我们建议使用简单和复杂模型混合的方法来改进多物种评估。【翻译: 胡怡思; 审校: 聂永刚】

**关键词:** 生物多样性指标, 影响评价, 集合种群模型, 集合种群承载力

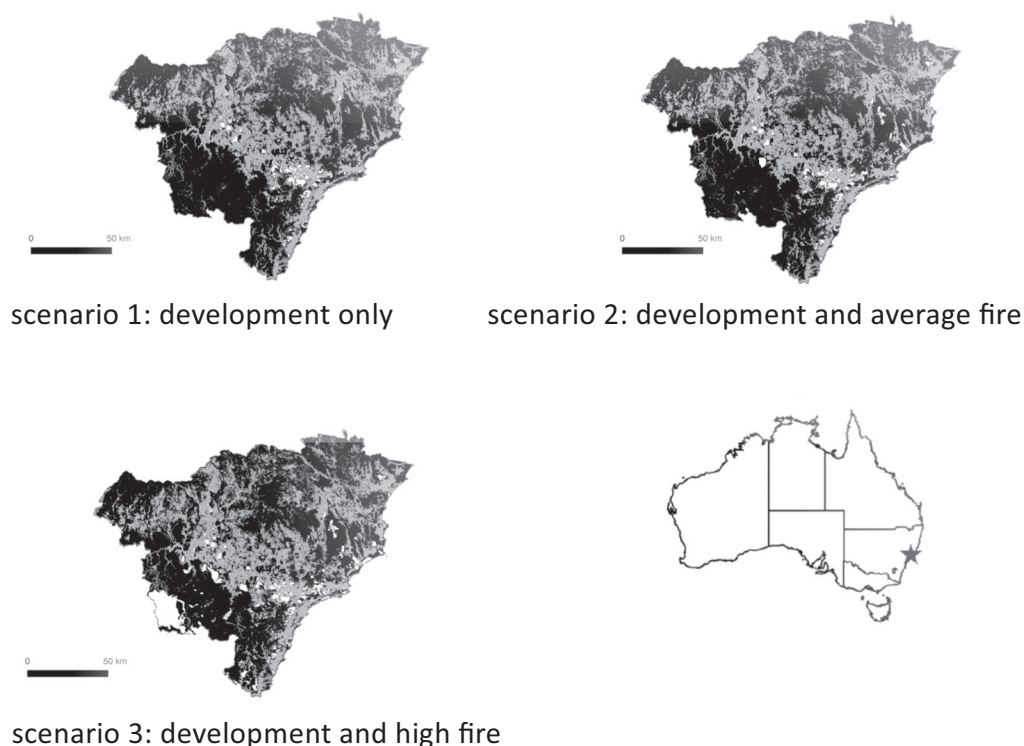
## Introduction

When evaluating the potential impacts of land-use or climate change on biodiversity, conservation practitioners look for cost-effective analytical approaches to support robust decisions to sustain species (Possingham et al. 2001; Guisan et al. 2013). Because complete biological and ecological complexity can never be fully captured in analysis, surrogates for species' persistence, such as habitat availability (Andelman & Fagan 2000; Nicholson & Possingham 2006; Guisan et al. 2013), and simple analytical measures of persistence, such as metapopulation capacity (Hanski & Ovaskainen 2000), are often used. More detailed population models can incorporate greater ecological complexity and spatial processes (Akcakaya 2000), but are data, time, and resource intensive to implement, need experts to contribute data and knowledge, and require a competent modeler to run them. This leads to trade-offs between the time and expertise cost of model development, model complexity, and capacity to account for key ecological processes (Beissinger et al. 2009).

A range of model types have been used to measure the impact of land-use and management options at varying spatial scales (Bekessy et al. 2009; Pereira et al. 2010; Sebastián-González et al. 2011). Species distribution models (SDM) implicitly include ecological processes by correlating observed patterns of occurrence with environmental variables (Phillips et al. 2006; Elith & Leathwick 2009) and are commonly used at larger spatial scales to characterize impact under different scenarios (Visconti et al. 2016). Patch occupancy models offer a

more comprehensive representation of ecological processes and are based on a metapopulation framework (Etienne et al. 2004); these models view a population as a network of discrete habitat patches of local populations within a nonhabitat matrix through which species may disperse (Levins 1969; Hanski 1998). Mathematical shortcuts have been developed for metapopulation models that make it analytically simpler to estimate metrics related to species persistence in a given landscape. These include Frank and Wissel's (2002) approximation for the mean time to extinction, which approximates a stochastic patch occupancy model and metapopulation capacity, a deterministic measure of metapopulation persistence (Hanski & Ovaskainen 2000). More complex still are metapopulation models that attempt to account for population processes including variation in individual mortality and fecundity, dispersal, and environmental and demographic stochasticity (Akcakaya et al. 2004; Wintle et al. 2005a; Franz et al. 2013).

Different models, and the metrics derived from them, fall on a spectrum of ecological complexity that affects how comprehensively they characterize impact. For example, population size can be estimated with an SDM, based on a relationship between habitat quality and abundance (Freckleton et al. 2006), or from a more complex spatially explicit population model (McCarthy & Thompson 2001). Although estimates from SDM implicitly assume abundance is directly related to habitat quantity and quality, abundance metrics derived from a spatially explicit population model will also explicitly include additional ecologically meaningful parameters and processes while also including stochasticity. Depending



**Figure 1.** Maps of study area showing extant native vegetation (black) and 3 impact scenarios (white): development only (indicates habitat lost due to current and planned urban development and potential mining areas), 422 km<sup>2</sup>; development and average fire, 594 km<sup>2</sup>; and development and high fire, 1717 km<sup>2</sup> (scale bar; 50 km).

on the pattern of disturbance (habitat loss, fragmentation, and scale of disturbance) and the relative importance of different ecological traits in mediating persistence, abundance estimates from these 2 models may characterize impact significantly differently and have potential flow-on effects to conservation decisions.

A key question for the application of models in conservation decision making is how complex does a model need to be to make a robust assessment of biodiversity outcomes under different management scenarios for a given species? It remains unclear whether more complex population models and metrics provide a substantial improvement over simpler models for characterizing species impacts and whether simpler metrics reliably approximate the behavior and predictions of fully parameterized population models. As global assessments of biodiversity become more formalized, integrated across sectors, and important for informing global policy (e.g., the United Nations Sustainable Development Goals [UN 2015] and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES 2016]), it will become more critical to understand the impact the choice of model and metric has on assessments of biodiversity change.

We explored and compared the ranking of the impact for plausible landscape disturbance scenarios, as

characterized by commonly used metrics of species persistence derived from increasingly complex underlying models. We explored the behavior of 5 species-specific metrics for 4 species with different ecological traits and vulnerabilities to extinction. We used a case study in a 35,000-km<sup>2</sup> landscape in southeastern Australia under 3 scenarios involving different levels of fire disturbance and urban and infrastructure development.

## Methods

### Study Area and Development Scenarios

The Greater Hunter region in eastern New South Wales, Australia, supports a variety of land uses, including open-cut coal mining, urban infrastructure, residential areas, manufacturing industries, and agriculture, as well as species and ecosystems of national environmental importance. Over 65% of the area is native vegetation (Fig. 1). Increasing urbanization is placing pressure on the region's natural environment, therefore assessing the impacts of these developments on biodiversity will be important for effective urban and regional planning.

We created 3 development scenarios representing plausible future landscape changes and compared these

**Table 1.** Four key traits potentially influencing vulnerabilities<sup>a</sup> of greater glider, green and golden bell frog, tiger quoll, and yellow-bellied glider to extinction.

	Habitat specificity <sup>b</sup>	Home range size <sup>c</sup>	Dispersal ability <sup>d</sup>	Reproductive potential <sup>e</sup>	
Greater glider	specific (tall moist sclerophyll forest with hollows)	small approximately 2 ha	low (2 km)	low (1 offspring/year, sexually mature at 2 years)	Possingham et al. 1994; Nicholson et al. 2006; Maloney 2007
Green and golden bell frog	highly specific (reedy wetlands <100m asl)	very small (0.25 ha)	very low (0.25 km)	high (5000 average eggs, sexual reproduction approximately 2 years for females)	DEC 2005; Pickett 2012; Pickett et al. 2013
Tiger quoll	broad (from forested areas to more arid landscapes)	large (276 ha)	high (5 km)	medium (approximately 3–5 offspring/year, sexually mature at 1 year)	Belcher & Darrant 2004; Meyer-Gleaves 2008
Yellow-bellied glider	broad (tall eucalypt forest)	large (64 ha)	low (2 km)	low (1 offspring/year, sexually mature at 2 years)	Goldingay & Kavanagh 1991, 1993; Citroen 2006

<sup>a</sup>References: Jobst et al. 2002; Akcakaya 2005; Kallimanis et al. 2005; Reinhardt et al. 2005.

<sup>b</sup>Narrow habitat preference generally has a higher vulnerability to extinction.

<sup>c</sup>Species with larger home range size are more vulnerable to extinction because they occur in lower densities and have higher individual energetic requirement and naturally lower population density. Lower density populations will be more susceptible generally to demographic and environmental stochasticity.

<sup>d</sup>Low dispersal ability is generally associated with increased vulnerability to extinction. This vulnerability may be mediated by high reproductive potential. Ability to disperse long distances generally reduces vulnerability to extinction because it increases potential couplings between patches. However, this advantage can be mediated by low population growth rates.

<sup>e</sup>Species with high reproductive potential and short generations have greater ability to recover from disturbances (but see dispersal ability).

with a baseline scenario with no habitat loss for each species, where current habitat distribution remained static. The scenarios were designed to provide a gradient of impact from low to high and realistic variation between overall area of habitat and degree of fragmentation and connectivity of habitat in the landscape (Supporting Information & Fig. 1).

### Study Species and Key Ecological Traits

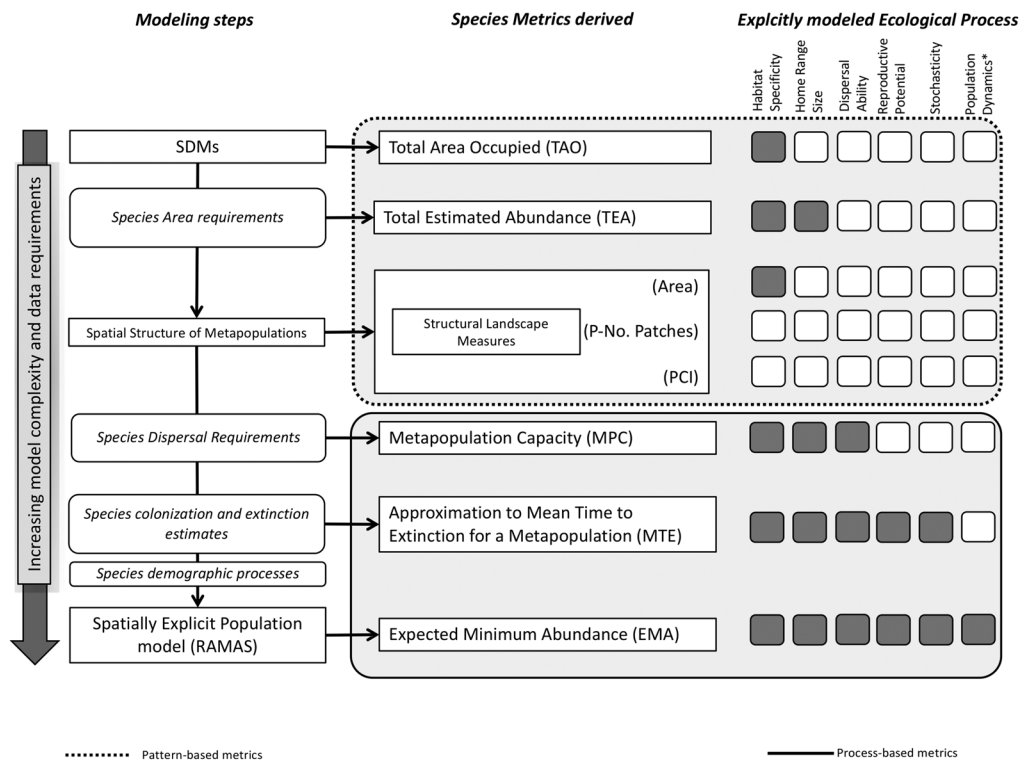
We selected 4 study species based on data availability and to represent a variety of ecological traits, threat status, and vulnerability to habitat disturbance: greater glider (*Petauroides volans*), tiger quoll (*Dasyurus maculatus maculatus*), yellow-bellied glider (*Petaurus australis*), and green and golden bell frog (*Litoria aurea*). The tiger quoll is listed as endangered and the greater glider, green and golden bell frog, and yellow-bellied glider are listed as vulnerable under the Australian Environment Protection and Biodiversity Conservation Act 1999 (Australian Government 1999). Although our species do not represent an exhaustive representation of ecological traits, they contain variation in key traits that likely affects their vulnerability to the different habitat and fragmentation patterns of disturbance outlined in the scenarios above.

Although spatial aspects of species traits are likely more decisive in influencing a species vulnerability to habitat fragmentation and loss (Curtis & Naujokaitis-Lewis 2008), combinations of traits together can exacerbate or mediate effects of habitat loss and fragmentation on a species' vulnerability to extinction (Jobst et al. 2002; Reinhardt et al. 2005). Detailed descriptions of these species' biology and ecology are in Supporting Information, and key ecological traits related to their vulnerability to habitat loss and fragmentation are summarized in Table 1.

### Measuring Species-Specific Impact of Scenarios

We evaluated 5 species-specific metrics of impact from 3 broad model types: SDM, patch occupancy models, and a spatially explicit population model. We broadly categorized metrics as pattern based—those metrics based primarily on patterns of species occurrence that do not explicitly include ecological processes, such as dispersal, population vital rates, and stochasticity—and process based—those that include parameters accounting explicitly for dispersal at a minimum, but often including population parameters, including survival and fecundity (Fig. 2).





**Figure 2.** Illustration of increasing model complexity and explicit inclusion of ecological processes in impact metrics (SDM, species distribution model; P-no. patches, number of patches of habitat; PCI, patch cohesion index [eq. 3 Supporting Information]). Each metric explicitly includes varying degrees of modeled ecological processes that approximate different ecological traits for a species and therefore explicitly include how these traits will mediate or exacerbate the effect of changes in habitat configuration.

### Species Metrics

All metrics were based on SDM. These models and their resultant distribution of habitat were not intended to be the best representations of distribution, but rather the base from which to build the subsequent metrics. We created an SDM for each species with methods best suited to the available data (Wintle et al. 2005b; Phillips et al. 2006). Detailed description of methods and outputs are in Supporting Information.

For each species and scenario, we calculated a series of metrics to approximate persistence. We derived 2 metrics directly from the SDM: total area occupied (TAO) and total estimated abundance (TEA). TAO includes an indication of the area of habitat only, whereas TEA incorporates heterogeneity in habitat quality by relating species abundance to habitat suitability as approximated by the SDM. Total estimated abundance is also used in the population models described below and in Supporting Information to calculate initial patch abundance for spatially explicit population models and metrics. Detailed descriptions and equations for each metric are in Supporting Information.

### Creating Species-Specific Metapopulation Structure

The remaining metrics relied on defining a metapopulation structure, with habitat patches within which a population exist, and unsuitable areas that must be traversed during dispersal events. We defined our metapopulation structure for each species with RAMAS GIS 5.0 (Akçakaya 2005). The program uses information on the distribution of habitat, as defined by the SDM, and species-specific parameters to identify clusters of cells that represent distinct habitat patches. The patch identification algorithm, parameters used, and procedure are described in detail in Supporting Information.

### Structural Landscape Measures

From this metapopulation structure, we calculated 3 structural landscape measures commonly used to assess and monitor landscape condition and inform management decisions (Eyre et al. 2015). These measures are also illustrative of the effect of the disturbances pattern realized for each species under the development scenarios. Following Fahrig (2003), we examined habitat area loss and fragmentation separately for each species. We calculated the number of patches ( $P$ ), percentage of

habitat lost from baseline, and the patch cohesion index (PCI), a measure of patch aggregation.

### Process-Based Metrics

Again using the metapopulation structure, we calculated the metapopulation capacity (MPC) (Hanski 1998; Schnell et al. 2013) and Frank and Wissel's (2002) approximation of mean time to extinction for a metapopulation (MTE) based on a stochastic patch occupancy model. The MPC provides a deterministic measure of how the spatial configuration of patches contributes to long-term metapopulation persistence (Hanski & Ovaskainen 2000), and MTE provides a stochastic approximation.

Using the metapopulation structure developed above as a base, we used RAMAS GIS (Akçakaya 2005) to develop stage-based population models that represented vital rates at different life stages for our species and evaluated persistence with population simulations. We specified density-dependence functions, fecundity, and survival and constructed stage-based population matrices for each species by reviewing species life cycles and published models and consulting with experts on the species. From this, we calculated expected minimum abundance (EMA). We chose this over probability of extinction because it provides a more nuanced indication of the propensity for decline than risk of extinction, especially when risk of extinction is small, and it is regarded as a more robust metric for ranking scenarios than risk of extinction (McCarthy & Thompson 2001). The main functions and parameters used in RAMAS, justifications for parameter choice, and details of all metrics are described in Supporting Information.

### Measuring and Characterizing the Predicted Impact of Environmental Changes

For consistency and interpretation, we measured impact for a species ( $k$ ) and scenario ( $s$ ),  $I_{sk}$ , as the proportional difference between a given scenario ( $X_s$ ) and the baseline scenario ( $X_b$ ) for each metric:  $I_{sk} = (X_s - X_b)/X_b \times 100$ . An  $I_{sk}$  value of 0 indicated there was no difference in the scenario relative to baseline, whereas negative and positive values indicated both direction and magnitude of the impact for a scenario relative to the baseline for a given metric, species, and scenario. We used the direction and magnitude of change to rank the scenarios from least to most negative impact for each species and metric. Of the metrics used, only EMA included error estimates around the values. We defined differences in EMA between scenarios that were smaller than the estimated SE as insignificant in terms of rank and impact. When ranking based on structural landscape measures, we assumed that more habitat area, fewer

patches, and increasing PCI were preferable to the alternatives.

### Sensitivity Analyses

To investigate critical cases where metrics diverged in their rank or where there were marked differences in impact for the same scenario and species, we performed sensitivity analyses by varying parameters in metrics thought to be decisive. Depending on the species and metrics in question, we varied dispersal by either including or excluding it from the metric, recalculating, and comparing the results. To test the impact of stochasticity on the outputs from the stage-based model, we also ran the model in a deterministic mode, excluding demographic and environmental stochasticity and any spatial correlation in vital rates. Further details are in Supporting Information.

Where the above investigations proved unhelpful in revealing decisive parameters, we examined the pattern of the disturbance itself and difference in scaling of the metrics for affected patches. We examined the value of affected patches as measured by different metrics by iteratively calculating the metric with and without the affected patches and comparing results. This allowed comparison of the relative importance placed on the patches affected by the different metrics.

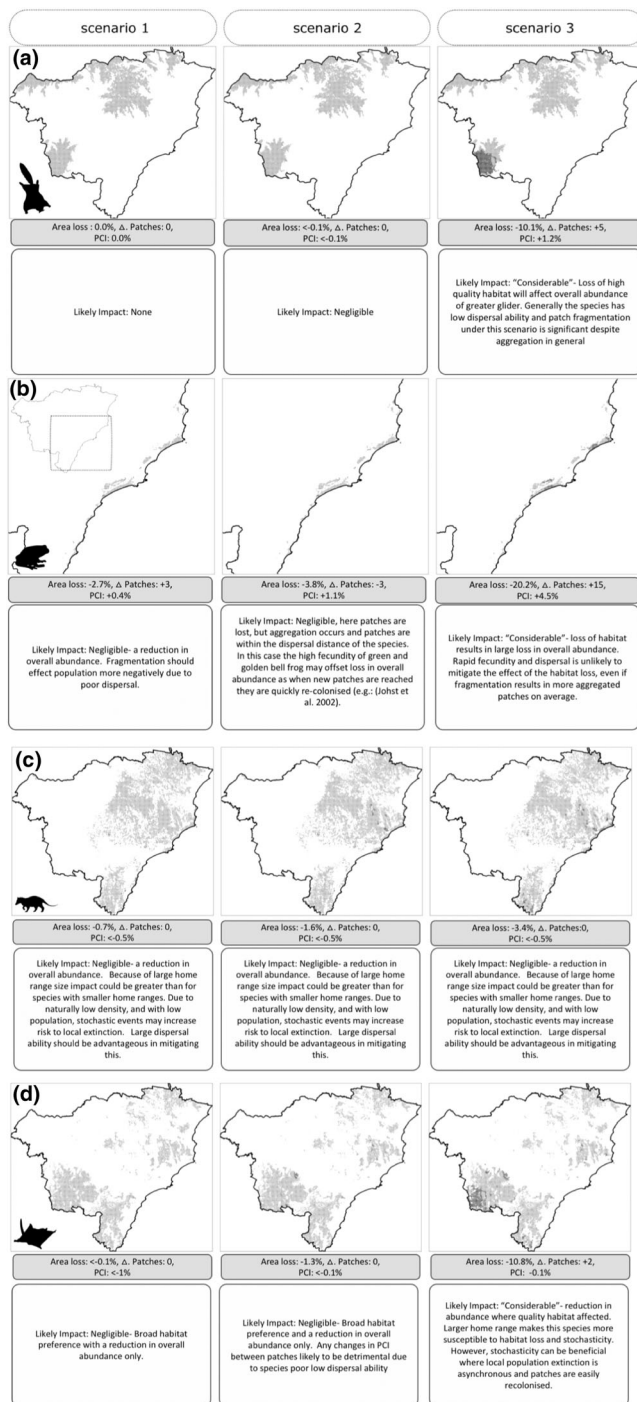
## Results

### General Patterns of Habitat Loss and Fragmentation and Relationship with Species Traits

Each scenario resulted in different species habitat availability and fragmentation patterns, resulting in 12 realizations of the disturbance scenarios, 3 for each species. For all species, we observed the greatest impacts under scenario 3, where habitat loss and fragmentation were most severe (Fig. 3)

Scenarios 1 and 2 resulted in varying patch number and local aggregation in subpopulations (PCI increases), accompanied by a small loss of habitat in peripheral isolated patches for green and golden bell frog. For these cases, one would reasonably expect an increase in overall probability of persistence, especially if in aggregating subpopulations new sites are within the dispersal ability of the species, because nearby sites emptied by local extinction are more rapidly recolonized for this highly fecund species.

Habitat loss and fragmentation were negligible for tiger quoll, and there was no reduction in the number of patches. For greater glider and yellow-bellied glider, there was negligible habitat loss and fragmentation for scenarios 1 and 2, but scenario 3 indicated



**Figure 3.** Pattern of disturbance for 4 species and scenario and likely impact given species' ecology and resultant changes in habitat configuration and quantity (gray, habitat; dark gray, area lost for each species and scenario; PCI, patch cohesion index; Δ patches values, change from baseline): (a) greater glider, (b) green and golden bell frog, (c) tiger quoll, and (d) yellow-bellied glider. Relative change in habitat and PCI was calculated as percent loss from baseline.

considerable fragmentation and habitat loss for both species (Fig. 3).

### Impacts by Species and Metric

The MTE behaved differently from all other metrics when we used it to rank and assess impact of the development scenarios. For example, this metric ranked scenario 3 as providing the best outcome for greater glider and green and golden bell frog, despite the scenario being the most destructive to available habitat. The magnitude of impact as indicated by this metric also differed markedly from the other tested metrics ( $1.36 \times 10^6$  % and  $2.97 \times 10^{16}$  % increase in MTE from baseline in scenario 3, respectively, for the green and golden bell frog and greater glider); thus, the formula did not approximate realistic values with the combination of landscape and model parameters in our case study and was not a reliable measure of impact for the scenarios (Fig. 4). Results for all species and metric and scenario combinations are in Supporting Information.

The 4 remaining species-specific metrics all ranked scenario 3 as the worst scenario.

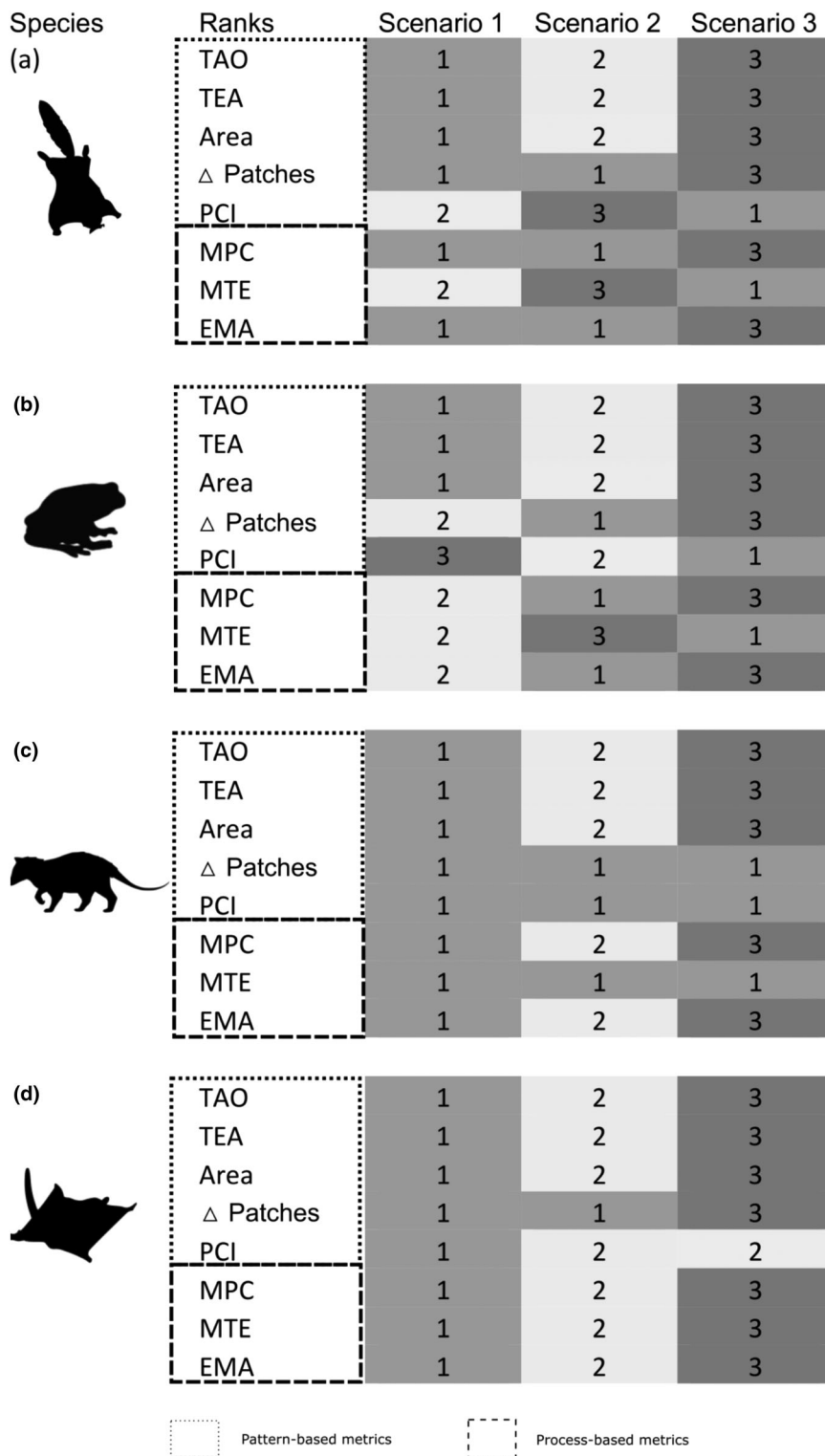
For scenarios 1 and 2, metrics gave identical rank order for tiger quoll and yellow-bellied glider, whereas the pattern-based metrics (TAO and TEA) contrasted with process-based metrics (MPC and EMA) for green and golden bell frog and greater glider. The MPC and EMA were the only metrics for which ranked order for all species matched (Fig. 4).

For greater glider, both MPC and EMA ranked scenarios 1 and 2 as equal, whereas pattern-based metrics ranked scenario 1 as preferential to scenario 2. This diverged from our expectations based on the landscape structural measures and species' ecology (Fig. 3). For green and golden bell frog, TAO and TEA ranked scenario 1 as preferential to scenario 2. Conversely, process-based metrics ranked scenario 2 as preferential over scenario 1. Rank was challenging to discern for the structural landscape measures because there were confounding signals among changes in patch numbers, habitat area, and PCI (Fig. 4).

Generally, for all species, pattern-based metrics provided similar assessments of impact to one another ( $\pm 5\%$ ), but MPC and EMA showed marked variation in their individual characterizations of impacts, and on occasion diverged markedly from pattern-based metrics. The differences in magnitudes of impact between metrics became more pronounced as the amount of habitat loss and fragmentation became more acute (Fig. 5).

### Sensitivity to Metric Parameters

Rank differences between pattern- and process-based metrics were most sensitive to the explicit inclusion or exclusion of dispersal in metrics for greater glider and



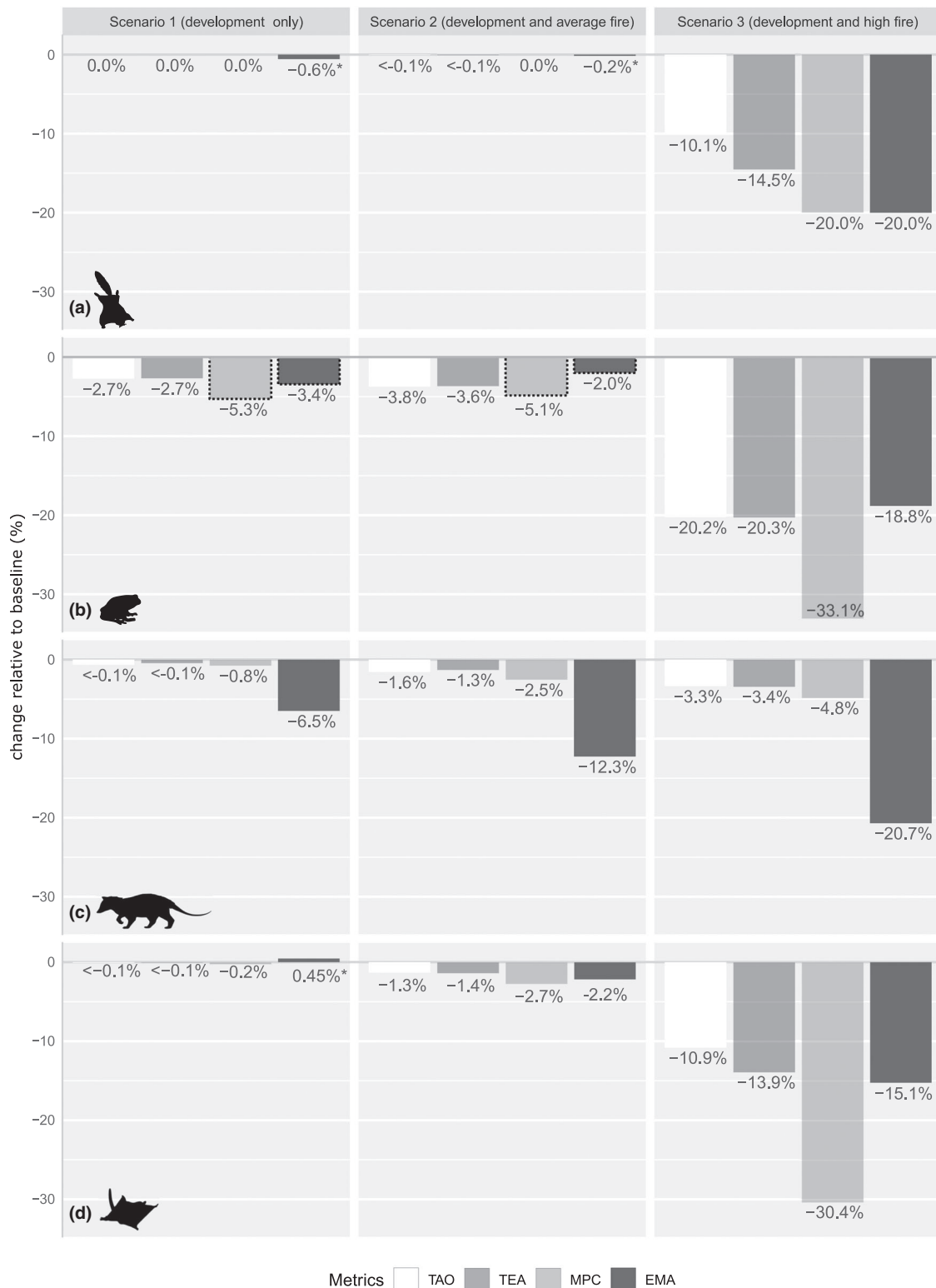
**Figure 4.** Rank order of scenario impact for target species based on different species' metrics: (a) greater glider, (b) green and golden bell frog, (c) tiger quoll, and (d) yellow-bellied glider (TAO, total area of occurrence; TEA, total estimated abundance; area, percent area loss; Δ patches, change in number of patches; PCI, patch cohesion index; MTE, mean time to extinction; MPC, metapopulation capacity; EMA, expected minimum abundance).

green and golden bell frog. For tiger quoll, although ranks for all metrics concurred, the marked difference in impact between MPC and EMA was best explained by the explicit inclusion or exclusion of demographic stochasticity.

For yellow-bellied glider, the marked difference in impact between EMA and MPC in scenario 3 was best ex-

plained by a difference in scaling between the 2 metrics rather than by dispersal, stochasticity, or correlation in vital rates. For example, the key patch affected in scenario 3 (Figs. 4d and 5d) accounted for approximately 94% of the metapopulation persistence as measured by MPC, whereas the relative contribution of the effected patch accounted for approximately 63% of the total EMA





**Figure 5.** Change relative to baseline for species under 3 scenarios, as measured by the different metrics: (a) greater glider; (b) green and golden bell frog; (c) tiger quoll; (d) yellow-bellied glider (TAO, total area occupied; TEA, total estimated abundance; MPC, metapopulation capacity; EMA, expected minimum abundance; dashed line around bars, marginal increase in EMA and metapopulation capacity between scenarios 1 and 2; \*, no significant differences between scenarios when accounting for SE in EMA). Mean time to extinction is omitted for clarity. Full results are in Supporting Information. Structural landscape metric relative change is summarized in Fig. 4.

value. Also of note was the difficulty in interpreting any definitive difference due to stochasticity in the case of EMA or the asymptotic nature of MPC where metapopulation persistence was ensured in scenario 1 and 2 for greater glider (Supporting Information).

## Discussion

Our metrics performed consistently in ranking different scenarios in order of severity under circumstances where variation in population size was driven by habitat amount. However, where interpatch dynamics were important for maintaining metapopulation persistence, divergence in ranks occurred between pattern-based and process-based metrics. Despite differences in assessment of impact magnitude, MPC ranked scenarios most consistently with those from highly parameterized and data-rich spatial population models (Fig. 4). In contrast, MTE was unreliable for our study species and context.

The landscape configurations in this study rendered Frank and Wissel's (2002) MTE formula unworkable. Frank and Wissel (2002) and Frank (2005) identify 4 key conditions under which their approximation is likely to fail: the population includes isolated subnetworks of patches; the metapopulation patch size is very heterogeneous; metapopulation persistence is driven by several large patches; and the number of patches falls below approximately 5 (Frank & Wissel 2002; Frank 2005). At least one of these conditions was met in our landscape patch configurations. We suggest similar arrangements are likely to occur frequently in many large-scale assessments of biodiversity impact, restricting the formula's use to smaller, more classically structured metapopulations (e.g., Levins 1969).

Measures of landscape structure (percent area loss, PCI, and change in number of patches) (Fig. 4) failed to capture the species-specific ecological impact, and ranks were difficult to discern where there were confounding signals between changes in patch numbers, habitat area, and the PCI. We therefore caution use of these structural landscape measures in assessing the condition of a landscape related to suitability for a given species or as proxies for assessing impacts on biodiversity.

The species-specific metrics in this study performed consistently in identifying the worst scenario (scenario 3) for all species. For yellow-bellied glider and tiger quoll, pattern-based metrics concurred with the rank order of the most complex models and metrics. In these cases, the disturbance pattern and ecological traits of the species meant that persistence was driven by a few large patches or supported by the species' good dispersal capability. Although changes in habitat and area may have still affected population processes in smaller patches, this did not appear to significantly affect the metapop-

ulation as a whole, such that pattern-based metrics were a reasonable proxy for MPC and EMA in terms of rank.

Where changes in landscape configuration were more nuanced, critical differences in rank order occurred between pattern- and process-based metrics. For green and golden bell, the aggregation of patches in scenario 2 was beneficial, which was best accounted for in the metrics that explicitly included dispersal parameters (MPC and EMA). Including dispersal was more decisive than including stochasticity in our case; however, this may not hold for other situations where, for example, asynchronous colonization and extinction in subpopulations are decisive for maintaining persistence (Hanski 1998). Including dispersal is likely particularly important for range-restricted species (Cardillo et al. 2005), such as the green and golden bell frog, and indeed using MPC in systematic spatial prioritization has been shown to benefit range-restricted species over more traditional pattern-based approaches (Strimas-Mackey & Brodie 2018). Such a change in rank order of scenarios could affect decisions based on such assessments.

Ranks also differed for the greater glider, but although our initial results suggested dispersal was a decisive factor in altering rank between pattern- and process-based metrics, we also caution that differences may be hidden in the stochastic noise of EMA or the asymptotic scaling of MPC. The results of the sensitivity analysis for yellow-bellied glider also pointed to differences in scaling between EMA and MPC. We suggest further investigations of how MPC scales to more complex metrics; for example, EMA in spatially realistic landscapes is needed to discern patterns or scaling relationships.

Although not critical to rank order for our cases, sensitivity analysis uncovered additional parameters that may have been decisive in altering ranks under slightly different landscape or disturbance patterns. These differences in impact were a function of the metrics and their underlying models (deterministic and stochastic) (Frank 2005), the pattern and configuration of the disturbance scenarios (spatially autocorrelated, large, small, or fractal), and the configuration of the species habitat (size of patches, interpatch distance, and patch aggregation) (Kallimanis et al. 2005).

First, including demographic and environmental stochasticity and spatial correlation drastically altered the magnitude of impact measured for tiger quoll. In similar species with naturally low-density populations, demographic stochasticity can drive populations to local extinction purely by random or correlated fluctuations in vital rates (Akçakaya 2000). The same can be said for range-restricted species, especially those that rely on colonization and extinction dynamics to maintain metapopulation persistence (Hanski 1998). Although for tiger quoll excluding stochasticity was insufficient to alter rank, this will not always be the case, especially for species with high sensitivity to stochasticity (Frank

2005). For species with restricted ranges or with naturally low densities relying on colonization dynamics, including stochasticity in representations of impact and dispersal will further increase the relevance of the metrics in characterizing impact.

Second, as species become more susceptible to stochastic events the pattern of the disturbance itself also becomes increasingly important to consider in metric choice. Where disturbance is fine scaled and affects only isolated patches, deterministic and stochastic models and indeed pattern- and process-based metrics will likely rank impact similarly. If, however, disturbance is spatially autocorrelated on important subpopulations, metrics, including dispersal and stochasticity, are likely to be critical for obtaining meaningful characterizations of impact. This will likely be compounded as disturbances become larger or more heterogeneous (Kallimanis et al. 2005). For most real landscapes, spatially autocorrelated patterns of disturbance are likely (Hanski 2009). Because patterns of disturbance are difficult to predict, to err on the side of caution, metrics with dispersal at a minimum, ideally with stochastic processes included, will provide more meaningful metrics. For poorly dispersing species in particular, the effect of the pattern of disturbance on species habitat may have as much bearing on metric choice and measuring a reliable impact as the biology and ecology of the species.

In our case, it appears the additional detailed parameters describing population dynamics, density dependence, survival, and fecundity included in EMA were not decisive enough to alter rank with the next most complex metric, MPC. However, where source-sink dynamics are present, Allee effects are probable, different patterns of density-dependence are important, or inclusion of density-dependent dispersal is required, these more complex parameters and metrics may prove essential. However, including meaningful parameter values for these may be difficult for all but the most well-studied species.

Results of our exploratory analysis suggest that including dispersal is the next important parameter to account for after amount and quality of habitat in obtaining more meaningful representations of impact. This is followed closely by the addition of stochasticity properties in population processes. Where dispersal accounts for configuration of habitat in a species-specific way, including stochasticity in ecological processes accounts for, and better captures, extinction risk to a species due to natural variation. Both dispersal and population structure are likely susceptibility to stochastic events and may be inferred from body size and general species traits (Sutherland et al. 2000; Van Houtan et al. 2007; Santini et al. 2013).

Although our results suggest MPC provides a useful shortcut for the most complex metric (EMA), it

does have its shortcomings and limitations. The deterministic character of MPC may make it unreliable in small patch networks, especially where extinction-colonization stochasticity is decisive or where the population dynamics are highly spatially correlated (Frank 2005; Hanski 2010). It is also limited in cases where habitat is mostly linear (Hanski et al. 2013). The MPC is also asymptotic and thus where persistence is assured in a landscape, it may not be particularly sensitive to small-scale and localized changes.

The choice of metric, and how comprehensively it represents the species of interest, will always be traded off against data availability and resources (Jones . 2011). Although rules of thumb for choosing metrics of performance have been suggested (Frank 2004; Henle et al. 2004; Drechsler 2009; Grilli et al. 2015), these are often based on hypothetical landscapes and scenarios. Significant further research is required before such rules and guidelines can be safely used in multispecies impact assessment over large, spatially realistic, and heterogeneous landscapes. Further simulations investigating realistic disturbance scenarios, the pattern of the disturbance itself, and a broader range of species may help elucidate these rules. In the meantime, where knowledge of outcomes for multiple species over a range of ecological traits is required, hybrid approaches to performance assessment based on a combination of pattern-based metrics and more sophisticated models that incorporate some aspects of dispersal and species' ecology may present a better way forward (Sebastián-González et al. 2011).

Although not comprehensively dealt with in our assessment, sensitivity and uncertainty to parameter estimates are critical to address where metrics are used to inform decisions or assess impact. Specifically, spatial parameters including population configuration, number of patches, carrying capacity, dispersal survival, and dispersal rates are likely most influential (Naujokaitis-Lewis et al. 2009). Importantly, the assumptions and uncertainties of our base SDM have the ability to propagate through to all metrics. In their creation, we assumed a linear relationship between habitat quality and density; however, altering the functional form of the response can significantly change assessments (Cadenhead et al. 2016).

Biodiversity assessments should be used to guide policy at continental or global scales (UN 2015; IPBES 2016). However, our results suggest that the consequences of not explicitly including ecological complexity, including dispersal as a bare minimum, may result in misleading conclusions as in the examples we explored. If conservation is to move beyond coarse approximations of biodiversity, such as mean species abundance (Alkemade et al. 2009), MPC offers an appealing shortcut. However, additional investigation of its properties is needed.

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## Supporting Information

Description of the development scenarios and how they were created (Appendix S1), detailed species parameters and methods used for creation of population models (Appendix S2), methods for creation of species distribution models (Appendix S3), detailed description of metrics and equations (Appendix S4), and full results for impact by species and metrics and for the sensitivity analysis (Appendix S5). 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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