University Library

MINERVA ACCESS

A gateway to Melbourne's research publications

Minerva Access is the Institutional Repository of The University of Melbourne

Author/s:
Hallam, CD;Wintle, BA;Kujala, H;Whitehead, AL;Nicholson, E

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

Date:
2020-12-01

Citation:
Hallam, C. D., Wintle, B. A., Kujala, H., Whitehead, A. L. & Nicholson, E. (2020). Measuring impacts on species with models and metrics of varying ecological and computational complexity. CONSERVATION BIOLOGY, 34 (6), pp.1512-1524. https://doi.org/10.1111/cobi.13524.

Persistent Link:
https://hdl.handle.net/11343/275732

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

Christopher D. Hallam: School of Bioscience, Building 122, University of Melbourne, Victoria 3010, Australia. challam@student.unimelb.edu.au

Brendan A. Wintle: School of Bioscience, Building 122, University of Melbourne, Victoria 3010, Australia.

Heini Kujala: School of Bioscience, Building 122, University of Melbourne, Victoria 3010, Australia.

Emily Nicholson: Deakin University, School of Life and Environmental Sciences, Centre for Integrative Ecology (Burwood Campus). 221 Burwood Highway, Burwood, VIC, 3125, Australia.

Amy L. Whitehead: National Institute of Water and Atmospheric Research, 10 Kyle Street, Riccarton, Christchurch 8011, New Zealand

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

Running head: Evaluating biodiversity metrics

Article impact statement: Not explicitly including ecological complexity in biodiversity metrics may result in misleading conclusions when assessing impacts.

This is the author manuscript accepted for publication and has undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/cobi.13524.

This article is protected by copyright. All rights reserved.

Author Manuscript

Abstract

Approaches to assessing the impacts of different landscape 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 may be interpreted, with flow-on effects on conservation decisions. We used a case study to explore the impact of three realistic disturbance scenarios on four 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. We found that 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 critical cases where dispersal dynamics influenced metapopulation persistence. Impacts of scenarios on species with low dispersal ability were better characterised using models that explicitly captured these processes. We found metapopulation capacity provided rank orders that most consistently correlated with those from highly parameterized and data-rich models, because it incorporated information about dispersal with little additional computational and data cost. Our work highlights the importance of explicitly considering species ecology, spatial configuration of habitat, and disturbance when choosing indicators of species persistence. We suggest hybrid approaches, using a mixture of simple and more complex models, may improve assessments for multi-species assessments.

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

This article is protected by copyright. All rights reserved.

Author Manuscript

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 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 non-habitat matrix through which species may disperse (Levins 1969; Hanski 1998). Mathematical shortcuts have been developed for metapopulation models, making it analytically simpler to estimate metrics related to species persistence in a given landscape. These include Frank and Wissel's approximation for the mean time to extinction (Frank & Wissel 2002), 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,

This article is protected by copyright. All rights reserved.

Author Manuscript

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 impacts how comprehensively they characterise impact. For example, population size can be estimated from a species distribution model (SDM) using a relationship between habitat quality and abundance (Freckleton et al. 2006) or from a more complex spatially explicit population model (McCarthy & Thompson 2001). While 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 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 two models may characterise impact significantly differently, with 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 characterising species impacts, and whether simpler metrics reliably approximate the behaviour 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

This article is protected by copyright. All rights reserved.

Author Manuscript

Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES 2016), it becomes more critical to understand the impact that the choice of model and metric has on assessments of biodiversity change.

In this study, we explored and compared the ranking of the impact for plausible landscape disturbance scenarios, as characterised by commonly used metrics of species persistence derived from increasingly complex underlying models. We explored the behaviour of five species-specific metrics for four species with different ecological traits and vulnerabilities to extinction. We used a case study in a 35,000 km^2 landscape in south-eastern Australia under three scenarios involving different levels of fire disturbance and urban and infrastructure development.

Methods

Study Area

The Greater Hunter region is in eastern New South Wales, Australia, and supports a variety of land uses including open-cut coal mining, urban infrastructure and residential areas, manufacturing industries, and agriculture, as well as species and ecosystems of national environmental importance. Over 65% of the area is native vegetation (Figure 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.

Development Scenarios

We created three development scenarios representing plausible future landscape changes and compared these to a baseline scenario with no habitat loss for each species, where current

This article is protected by copyright. All rights reserved.

Author Manuscript

habitat distribution remained static. The scenarios were designed to provide a gradient of impact from low to high, providing realistic variation between overall area of habitat and the degree of fragmentation and connectivity of habitat in the landscape (appendix 1) (Figure 1).

Study Species and key ecological traits

We selected four study species based on data availability, and to represent a variety of ecological traits, threat status and vulnerability to habitat disturbance. The greater glider (*Petauroides volans*), the tiger quoll (*Dasyurus maculatus maculatus*), the yellow-bellied glider (*Petaurus australis*), and the green and golden bell frog (*Litoria aurea*). The tiger quoll is listed as endangered whereas 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 (EPBC 1999). While our species do not represent an exhaustive representation of ecological traits, they contain variation in key traits which likely affects their vulnerability to the different habitat and fragmentation patterns of disturbance outlined in the scenarios above for this exploratory analysis.

While 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 (Johst et al. 2002; Reinhardt et al. 2005). Detailed descriptions of species biology and ecology can be found in appendix 2, with key ecological traits for the target species' vulnerability to habitat loss and fragmentation summarised in Table 1.

Measuring the species-specific impact of scenarios

We evaluated five species-specific metrics of impact from three broad model types: SDM, patch occupancy models and a spatially-explicit population model. We broadly categorised metrics

This article is protected by copyright. All rights reserved.

Author Manuscript

into "*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 explicitly include parameters accounting explicitly for dispersal at a minimum, but often including population parameters including survival and fecundity (Figure 2).

Species metrics

Species distribution models

All metrics were based on species distribution models (SDM). These models and their resultant distribution of habitat were not intended to be the best representations of distribution but rather as the base from which to build the subsequent metrics. We created SDM for each species using methods best suited to the available data (Wintle et al. 2005b; Phillips et al. 2006). Detailed description of the methods and outputs are found in appendix 3.

Pattern based Metrics

For each species and scenario we calculated a series of metrics to approximate persistence. We describe each metric briefly below and provide detailed descriptions and equations in appendix 4.

We derived two metrics directly from the SDM. The total area occupied (TAO) and the total estimated abundance (TEA). While TAO include an indication of the area of habitat only, TEA incorporates heterogeneity in habitat quality by relating species abundance to habitat

This article is protected by copyright. All rights reserved.

Author Manuscript

suitability as approximated by the SDM. TEA is also used in the population models described below and appendix 2 to calculate initial patch abundance for spatially explicit population models and metrics.

Creating species-specific metapopulation structure

The remaining metrics relied on defining a metapopulation structure, with suitable 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 using RAMAS GIS 5.0 (Akcakaya 2005). The program uses information on the distribution of suitable habitat, as defined by the SDM, together with 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 appendix 2.

Structural landscape measures

From this metapopulation structure we calculated three 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 realised for each species by the development scenarios. We followed Fahrig 2003 and 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

Patch occupancy approximation metrics

Again using the metapopulation structure above we calculated the metapopulation capacity (Hanski 1998; Schnell et al. 2013) (MPC) and Fank and Wissel's (2002) approximation of mean time to extinction for a metapopulation (MTE) based on a stochastic patch occupancy model.

This article is protected by copyright. All rights reserved.

Author Manuscript

MPC provides a deterministic measure of how the spatial configuration of patches contributes to long-term metapopulation persistence (Hanski & Ovaskainen 2000), while MTE provides a stochastic approximation of the mean time to extinction.

Spatially-explicit population model and metric

Using the metapopulation structure developed above as a base, we used RAMAS GIS (Akcakaya 2005) to develop stage-based population models that represented vital rates at different life stages for our species and evaluated persistence using population simulations. We specified density-dependence functions, fecundity and survival, and constructed stage-based population matrices for each species by reviewing species lifecycles, published models and consultation with species experts. From this we calculated expected minimum abundance (EMA). We chose this over probability of extinction because: (i) it provides a more nuanced indication of the propensity for decline than the risk of extinction especially when the risk of extinction is small, and (ii) it is regarded as a more robust metric for ranking scenarios than the risk of extinction (McCarthy & Thompson 2001). The main functions and parameters, used in RAMAS along with justifications for parameter choice are outlined in appendix 2, while details of all metrics are described in appendix 4.

Measuring and characterizing the predicted impact of environmental changes

Relative Impact and Rank

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: $I_{sk}=(X_s-X_b)/X_b*100$. An I_{sk} value of zero indicates there is no difference in the scenario relative to baseline, while negative and positive values indicate both direction and magnitude of

This article is protected by copyright. All rights reserved.

Author Manuscript

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, EMA was the only one to include error estimates around the values. We defined differences in EMA between scenarios that were smaller than the estimated standard error as insignificant in terms of rank and impact. When ranking using the structural landscape measures we made the assumption that more habitat area was preferable, fewer patches were preferable and that increasing PCI was preferable to the alternatives.

Sensitivity Analysis

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 analysis 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, re-calculating 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.

In addition, 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.

This article is protected by copyright. All rights reserved.

Author Manuscript

Results

General patterns of habitat loss and fragmentation and relationship with species traits

Each scenario resulted in different species habitat availability and fragmentation patterns, creating twelve realisations of the disturbance scenarios, three for each species. For all species we observed the greatest impacts arising under scenario 3 where habitat loss and fragmentation were most severe (Figure 3).

Scenarios 1 and 2 resulted in varying patch number and local aggregation in sub-populations (PCI increases), accompanied by a small loss of habitat in peripheral isolated patches for green and golden bell frog. For these cases we may reasonably expect an increase in overall probability of persistence, especially if in aggregating sub-populations, new sites are within the dispersal ability of the species, as 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, while for greater glider and yellow-bellied glider there was negligible habitat loss and fragmentation for scenario 1 and 2, but scenario 3 indicated considerable fragmentation and habitat loss for both species (Figure 3).

Impacts by species and metric

The results for the ranking and relative impact of each scenario on each species as quantified by the different metrics, are shown in Figures 4 and 5 respectively.

This article is protected by copyright. All rights reserved.

Author Manuscript

We found that MTE showed contrasting behaviour to all other metrics when used 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 ($+1.36x10^{6}$ % and $+2.97x10^{16}$ % increase in MTE from baseline in scenario 3, respectively, for the green and golden bell frog and greater glider). These results suggested that the formula was unable to approximate realistic values with the combination of landscape and model parameters in our case study, and that it is not a reliable measure of impact for the scenarios presented here (Figure 4). Results for all species, metric and scenario combinations are included in appendix 5 - Table 1.

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

For scenarios 1 and 2 metrics gave identical rank order for two species, tiger quoll and yellow-bellied glider, while the pattern-based metrics (TAO and TEA) disagreed with process-based metrics (MPC and EMA) for green and golden bell frog and greater glider. MPC and EMA were the only metrics to agree in their rank order for all species (Figure 4).

For greater glider, both MPC and EMA ranked scenario 1 and 2 as equal, while 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 (Figure 3). For green and golden bell frog TAO and TEA ranked scenario 1 as preferential to scenario 2. Conversely,

This article is protected by copyright. All rights reserved.

Author Manuscript

process-based metrics, rank scenario 2 as preferential over scenario 1. Rank was challenging to discern for the structural landscape measures, as there were confounding signals between changes in patch numbers, habitat area and PCI (Figure 4).

Generally, for all species, pattern-based metrics provided similar assessments of impact to one another (±5%), but MPC and EMA showed marked variation in their individual characterisations of impacts, and on occasions 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 (Figure 5).

Sensitivity to metric parameters

For cases where ranks diverged or where there were marked differences in impact measured, we examined how key parameters in the different models influenced impact and ranks by systematically adjusting underlying model parameters to either include or exclude specific ecological parameters (appendix 5).

We found that 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 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.

Author Manuscript

This article is protected by copyright. All rights reserved.

For yellow-bellied glider we noted the marked difference in impact between EMA and MPC in scenario 3 was best explained by a difference in scaling between the two metrics rather than by dispersal, stochasticity or correlation in vital rates. For example we noted the key patch affected in scenario 3 (Figure 4d and Figure 5d) accounted for ~94% of the metapopulation persistence as measured by MPC while the relative contribution of the effected patch accounted for ~ 63% of the total EMA 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 is ensured in scenario 1 and 2 for greater glider (appendix 5).

Discussion

Using models of varying sophistication, we compared five metrics of persistence for four species, across three scenarios of varying habitat loss and fragmentation. We found metrics performed consistently in ranking different scenarios in order of severity under circumstances where variation in population size is driven by habitat amount. However, where inter-patch 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 (Figure 4). In contrast, we found MTE to be unreliable for our study species and context.

The landscape configurations in this study rendered Frank & Wissel's (2002) MTE formula unworkable. Frank & Wissel (2002) and Frank (2005) identify four key conditions under which their approximation is likely to fail: 1) the population includes isolated sub-networks of patches; 2) the metapopulation patch size is very heterogeneous; 3) metapopulation persistence is

This article is protected by copyright. All rights reserved.

Author Manuscript

driven by several large patches; and 4) the number of patches falls below approximately five (Frank & Wissel 2002; Frank 2005). At least one of these conditions were met in our landscape patch configurations. We suggest similar arrangements are likely to occur frequently in many larger scale assessments of biodiversity impact, restricting the formula's use to smaller, more classically structured metapopulations (see, for example, Levins 1969).

Measures of landscape structure (percentage area loss, PCI and change in number of Patches) (Figure 4) failed to capture the species-specific ecological impact and ranks were difficult to discern with 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 to act as a proxy for assessing impacts on biodiversity.

The species-specific metrics in this study did perform 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 metapopulation as a whole, such that pattern-based metrics were a reasonable proxy for MPC and EMA in terms of rank.

Author Manuscript

This article is protected by copyright. All rights reserved.

Where changes in landscape configuration were more nuanced, critical differences in rank order occurred between pattern-based 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, may not for other situation where, for example asynchronous colonization and extinction in sub-populations are decisive for maintaining persistence (Hanski 1998). Including dispersal is likely particularly important for range-restricted species (Cardillo et al. 2005), like the green and golden bell frog, and indeed using MPC in systematic spatial prioritisation 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 while our initial results suggested dispersal was a decisive factor in altering rank between pattern and process-based metric, 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 such as EMA in spatially realistic landscapes across different disturbance scenarios and for different species are needed to discern any patterns or scaling relationships.

Although not critical to rank order for our cases, sensitivity analysis uncovered additional parameters that may have been decisive to 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

This article is protected by copyright. All rights reserved.

Author Manuscript

the disturbance scenarios (spatially auto-correlated, large, small or fractal), and the configuration of the species habitat (size of patches, inter patch distance and patch aggregation) (Kallimanis et al. 2005).

Firstly, 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 (Akcakaya 2000). The same can be said for 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 (see Frank 2005). For species with restricted ranges, relying on colonization dynamics or with naturally low densities, metrics including stochasticity in representations of impact, along with dispersal, will further increase the relevance of the metrics in characterising impact.

Secondly, 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, then deterministic and stochastic models and indeed pattern- and process-based metrics will likely rank impact similarly. If however disturbance is spatially autocorrelated on important sub-populations, metrics including dispersal and stochasticity are likely to be critical for obtaining meaningful characterisations of impact. This is likely compounded as disturbances become larger, or more heterogeneous (Kallimanis et al. 2005). For most real landscapes, spatially autocorrelated

This article is protected by copyright. All rights reserved.

Author Manuscript

patterns of disturbance are likely (Hanski 2009). As 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, where different patterns of density-dependence are important or where including density-dependent dispersal is likely 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.

Our exploratory analysis suggests 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).

This article is protected by copyright. All rights reserved.

Author Manuscript

Although our exploratory analysis suggests MPC provided 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 are 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). MPC is also asymptotic, and thus where persistence is assured in a landscape it may not be particularly sensitive to small scale and localised 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 et al. 2011). While 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 multi-species 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 with elucidating 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).

Author Manuscript

This article is protected by copyright. All rights reserved.

Although not comprehensively dealt with in our assessment, sensitivity and uncertainty to parameter estimates are critical to address where using metrics 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 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 explore above. If we are 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 are needed, especially in how it scales to more complex metrics such as EMA in spatially realistic landscapes across different disturbance scenarios and for different species.

Acknowledgments: This work was made possible with funding from the Australian Government's National Environmental Research Program (NERP) and NESP Threatened Species Recovery Research Hub. We also thank The Hunter and Central Coast Environmental Strategy and their staff for their data contributions and support. CH was supported by Australian Post Graduate Award, HK and AW were supported by an Australian Research Council (ARC) Discovery grant (DP160101003) and the Australia Government's National Environmental

This article is protected by copyright. All rights reserved.

Author Manuscript

Science Program. EN was supported by ARC Discovery DP170100609. CH also thanks the many colleagues who have fielded questions and queries and provided inputs on countless drafts and coding problems. Especially Natasha Cadenhead for discussions on tiger quoll models, Michael Mahoney, Trent Penman, Geoff Heard and Tracy Regan for discussions and information on green and golden bell frog models and SDMs.

Author Manuscript

This article is protected by copyright. All rights reserved.

References

Akcakaya HR. 2000. Population viability analyses with demographically and spatially structured models. Ecological Bulletins:23–38.

Akcakaya HR. 2005. RAMAS GIS: Linking Spatial Data with Population Viability Analysis (v.5.0). Applied Biomathematics, New York, USA.

Akcakaya HR, Radeloff VC, Mladenoff DJ, He HS. 2004. Integrating Landscape and Metapopulation Modeling Approaches: Viability of the Sharp-Tailed Grouse in a Dynamic Landscape. Conservation Biology **18**:526–537.

Alkemade R, Oorschot M, Miles L, Nellemann C, Bakkenes M, ten Brink B. 2009. GLOBIO3: A Framework to Investigate Options for Reducing Global Terrestrial Biodiversity Loss. Ecosystems **12**:374–390.

Andelman SJ, Fagan WF. 2000. Umbrellas and flagships: efficient conservation surrogates or expensive mistakes? Proceedings of the National Academy of Sciences **97**:5954–5959.

Beissinger SR, Nicholson E, Possingham HP. 2009. Application of population viability analysis to landscape conservation planning. Pages 33–49 in J. J. Millspaugh and F. R. Thompson, editors. Models for planning wildlife conservation in large landscapes. Academic Press, Elsevier Science, Burlington, MA, USA.

Bekessy SA, Wintle BA, Gordon A, Fox JC, Chisholm R, Brown B, Regan T, Mooney N, Read SM, Burgman MA. 2009. Modelling human impacts on the Tasmanian wedge-tailed eagle (*Aquila audax fleayi*). Biological Conservation **142**:2438–2448.

Author Manuscript

This article is protected by copyright. All rights reserved.

Cadenhead NCR, Kearney MR, Moore D, McAlpin S, Wintle BA. 2016. Climate and Fire Scenario Uncertainty Dominate the Evaluation of Options for Conserving the Great Desert Skink: Resolving uncertainty in fire management. Conservation Letters **9**:181–190.

Cardillo M, Mace GM, Jones KE, Bielby J, Bininda-Emonds ORP, Sechrest W, Orme CDL, Purvis A. 2005. Multiple Causes of High Extinction Risk in Large Mammal Species. Science **309**:1239–1241.

Curtis JMR, Naujokaitis-Lewis I. 2008. Sensitivity of population viability to spatial and nonspatial parameters using grip. Ecological Applications **18**:1002–1013.

Drechsler M. 2009. Predicting metapopulation lifetime from macroscopic network properties. Mathematical Biosciences **218**:59–71.

Elith J, Leathwick JR. 2009. Species Distribution Models: Ecological Explanation and Prediction Across Space and Time. Annual Review of Ecology, Evolution, and Systematics **40**:677–697.

EPBC. 1999. Environment Protection and Biodiversity Conservation Act 1999.

Etienne RS, ter Braak CJF, Vos CC. 2004. Application of stochastic patch occupancy models to real metapopulations. Pages 105–133 in I. Hanski and O. E. Gaggiotti, editors. Ecology, genetics, and evolution of metapopulations. Elsevier, Burlington, MA.

Eyre TJ, Kelly AL, Neldner VJ, Wilson BA, Ferguson DJ, Laidlaw MJ, Franks AJ. 2015. BioCondition: A Condition Assessment Framework for Terrestrial Biodiversity in Queensland. Assessment Manual. Version 2.2. Queensland Herbarium, Department of Science, Information Technology, Innovation and Arts, Brisbane.

This article is protected by copyright. All rights reserved.

Author Manuscript

Fahrig L. 2003. Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics **34**:487–515.

Frank K. 2004. Ecologically differentiated rules of thumb for habitat network design–lessons from a formula. Biodiversity & Conservation **13**:189–206.

Frank K. 2005. Metapopulation persistence in heterogeneous landscapes: lessons about the effect of stochasticity. The American Naturalist **165**:374–388.

Frank K, Wissel C. 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. The American Naturalist **159**:530–552.

Franz KW, Romanowski J, Johst K, Grimm V. 2013. Ranking Landscape Development Scenarios Affecting Natterjack Toad (*Bufo calamita*) Population Dynamics in Central Poland. PLoS ONE **8**. Available from http://www.ncbi.nlm.nih.gov/pmc/articles/PMC3667123/ (accessed February 12, 2015).

Freckleton RP, Noble D, Webb TJ, Chase AEJM, Losos EJB. 2006. Distributions of Habitat Suitability and the Abundance-Occupancy Relationship. The American Naturalist **167**:260–275.

Grilli J, Barabás G, Allesina S. 2015. Metapopulation Persistence in Random Fragmented Landscapes. PLOS Computational Biology **11**:e1004251.

Guisan A et al. 2013. Predicting species distributions for conservation decisions. Ecology Letters **16**:1424–1435.

Hanski I. 1998. Metapopulation dynamics. Nature **396**:41–49.

Author Manuscript

This article is protected by copyright. All rights reserved.

Hanski I. 2009. Chapter II.4: Metapopulations and Spatial Population Processes. Pages 177–185 Princeton Guide to Ecology. Princeton University Press.

Hanski I. 2010. Incorporating the spatial configuration of the habitat into ecology and evolutionary biology. Pages 167–188 in R. S. Cantrell, C. Cosner, and S. Ruan, editors. Spatial ecology. CRC Press, Boca Raton, FL. Available from http://www.crcnetbase.com/isbn/9781420059854 (accessed September 18, 2014).

Hanski I, Ovaskainen O. 2000. The metapopulation capacity of a fragmented landscape. Nature **404**:755–758.

Hanski I, Zurita GA, Bellocq MI, Rybicki J. 2013. Species–fragmented area relationship. Proceedings of the National Academy of Sciences **110**:12715–12720.

Henle K, Davies KF, Kleyer M, Margules C, Settele J. 2004. Predictors of species sensitivity to fragmentation. Biodiversity & Conservation **13**:207–251.

IPBES. 2016. Summary for policymakers of the methodological assessment of scenarios and models of biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Secretariat of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services.

Johst K, Brandl R, Eber S. 2002. Metapopulation persistence in dynamic landscapes: the role of dispersal distance. Oikos **98**:263–270.

Kallimanis AS, Kunin WE, Halley JM, Sgardelis SP. 2005. Metapopulation Extinction Risk under Spatially Autocorrelated Disturbance. Conservation Biology **19**:534–546.

Levins R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America **15**:237–240.

This article is protected by copyright. All rights reserved.

Author Manuscript

McCarthy MA, Thompson C. 2001. Expected minimum population size as a measure of threat. Animal Conservation **4**:351–355.

Naujokaitis-Lewis IR, Curtis JMR, Arcese P, Rosenfeld J. 2009. Sensitivity Analyses of Spatial Population Viability Analysis Models for Species at Risk and Habitat Conservation Planning. Conservation Biology **23**:225–229.

Nicholson E, Possingham HP. 2006. Objectives for Multiple-Species Conservation Planning. Conservation Biology **20**:871–881.

Pereira HM et al. 2010. Scenarios for Global Biodiversity in the 21st Century. Science **330**:1496–1501.

Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species geographic distributions. Ecological Modelling **190**:231–259.

Possingham H, Andelman SJ, Noon BR, Trombulak S, Pulliam HR. 2001. Making smart conservation decisions. Pages 1–18 in M. E. Soule and G. H. Orians, editors. Conservation biology: research priorities for the next decade. Island Press, Washington, [D.C.].

Reinhardt K, Köhler G, Maas S, Detzel P. 2005. Low dispersal ability and habitat specificity promote extinctions in rare but not in widespread species: the Orthoptera of Germany. Ecography **28**:593–602.

Santini L, Di Marco M, Visconti P, Baisero D, Boitani L, Rondinini C. 2013. Ecological correlates of dispersal distance in terrestrial mammals. Hystrix, the Italian Journal of Mammalogy **24**. Available from http://www.italian-journal-of-mammalogy.it/article/view/8746/0 (accessed October 30, 2013).

Author Manuscript

This article is protected by copyright. All rights reserved.

Schnell JK, Harris GM, Pimm SL, Russell GJ. 2013. Estimating Extinction Risk with Metapopulation Models of Large-Scale Fragmentation: Metapopulation Analyses of Large-Ranged Species. Conservation Biology **27**:520–530.

Sebastián-González E, Sánchez-Zapata JA, Botella F, Figuerola J, Hiraldo F, Wintle BA. 2011. Linking cost efficiency evaluation with population viability analysis to prioritize wetland bird conservation actions. Biological Conservation **144**:2354–2361.

Strimas-Mackey M, Brodie JF. 2018. Reserve design to optimize the long-term persistence of multiple species. Ecological Applications **28**:1354–1361.

Sutherland GD, Harestad AS, Price K, Lertzman KP. 2000. Scaling of natal dispersal distances in terrestrial birds and mammals. Conservation Ecology **4**:16.

UN. 2015. 70/1. Transforming our world: the 2030 Agenda for Sustainable Development. UN General Assembly.

Van Houtan KS, Pimm SL, Halley JM, Bierregaard RO, Lovejoy TE. 2007. Dispersal of Amazonian birds in continuous and fragmented forest. Ecology Letters **10**:219–229.

Visconti P et al. 2016. Projecting Global Biodiversity Indicators under Future Development Scenarios: Projecting biodiversity indicators. Conservation Letters **9**:5–13.

Wintle BA, Bekessy SA, Venier LA, Pearce JL, Chisholm RA. 2005a. Utility of Dynamic-Landscape Metapopulation Models for Sustainable Forest Management. Conservation Biology **19**:1930–1943.

Wintle BA, Elith J, Potts JM. 2005b. Fauna habitat modelling and mapping: a review and case study in the Lower Hunter Central Coast region of NSW. Austral Ecology **30**:719–738.

This article is protected by copyright. All rights reserved.

Author Manuscript

This article is protected by copyright. All rights reserved.

Author Manuscript

Table 1: Description of key traits potentially influencing vulnerabilities of species to extinction (top row) and a description of where each species sits on along each trait axis relative to the other species (columns) for (a)greater glider, (b)green and golden bell frog, (c) tiger quoll and (d) yellow-bellied glider.

	Habitat specificity Narrow habitat preference generally has a higher vulnerability to extinction	**Home range size-** Species with larger home range size are more vulnerable to extinction as they occur in lower densities, have higher individual energetic requirement and naturally lower population density. Lower density populations will be more susceptible generally to demographic and environmental stochasticity.	**Dispersal ability-** Low dispersal ability is generally associated with increased vulnerability to extinction. This vulnerability may be mediated by high reproductive potential. Longer dispersal ability generally reduces vulnerability to extinction as it increases potential couplings between patches. However, this advantage can be mediated by low population growth rates.	**Reproductive Potential**- species with higher reproductive potential and short generations will have greater ability to recover from disturbances (but see dispersal ability)	**References (Johst et al. 2002; Akcakaya 2005; Kallimanis et al. 2005; Reinhardt et al. 2005)**
(a) 	Specific- Tall moist sclerophyll forest with hollows	Small ~2ha	Low- 2km	Low (1 offspring/year, Sexually mature at 2 years)	(Possingham et al. 1994; Nicholson et al. 2006; Maloney 2007)

Author Manuscript

This article is protected by copyright. All rights reserved.

(b) 	Highly Specific- Reedy Wetlands <100m asl	Smallest (0.25ha)	Lowest- 0.25km	Highest (5000 average eggs sexual reproduction ~2years for females)	(DEC 2005; Pickett 2012; Pickett et al. 2013)
(c) 	Broadest- From forested areas, to more arid landscapes	Largest (276ha)	Highest- 5km	Medium (~3-5 Offspring/year, sexually mature at 1 year)	(Belcher & Darrant 2004; Meyer-Gleaves 2008)
(d) 	Broad- Tall Eucalypt Forest	Large(64ha)	Low- 2km	Low (1 offspring/year, Sexually mature at 2 years)	(Goldingay & Kavanagh 1991, 1993; Citroen 2006)

Author Manuscript

This article is protected by copyright. All rights reserved.

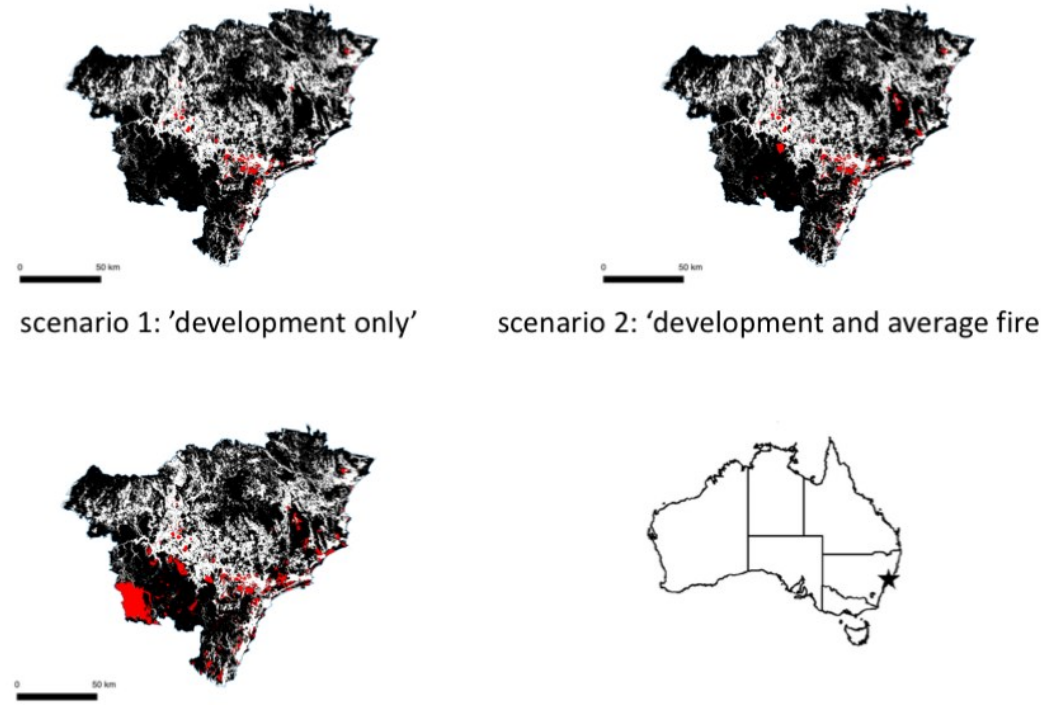


Figure 1: Map of study area showing extant native vegetation (black) with impact scenarios (red). scenario 1: 'development only' - indicates habitat lost due to current and planned urban development and potential mining areas(422km^2); scenario 2: 'development and average fire'(594km^2); and scenario 3: 'development and high fire'(1717km^2). Scalebar represents 50km

Author M

This article is protected by copyright. All rights reserved.

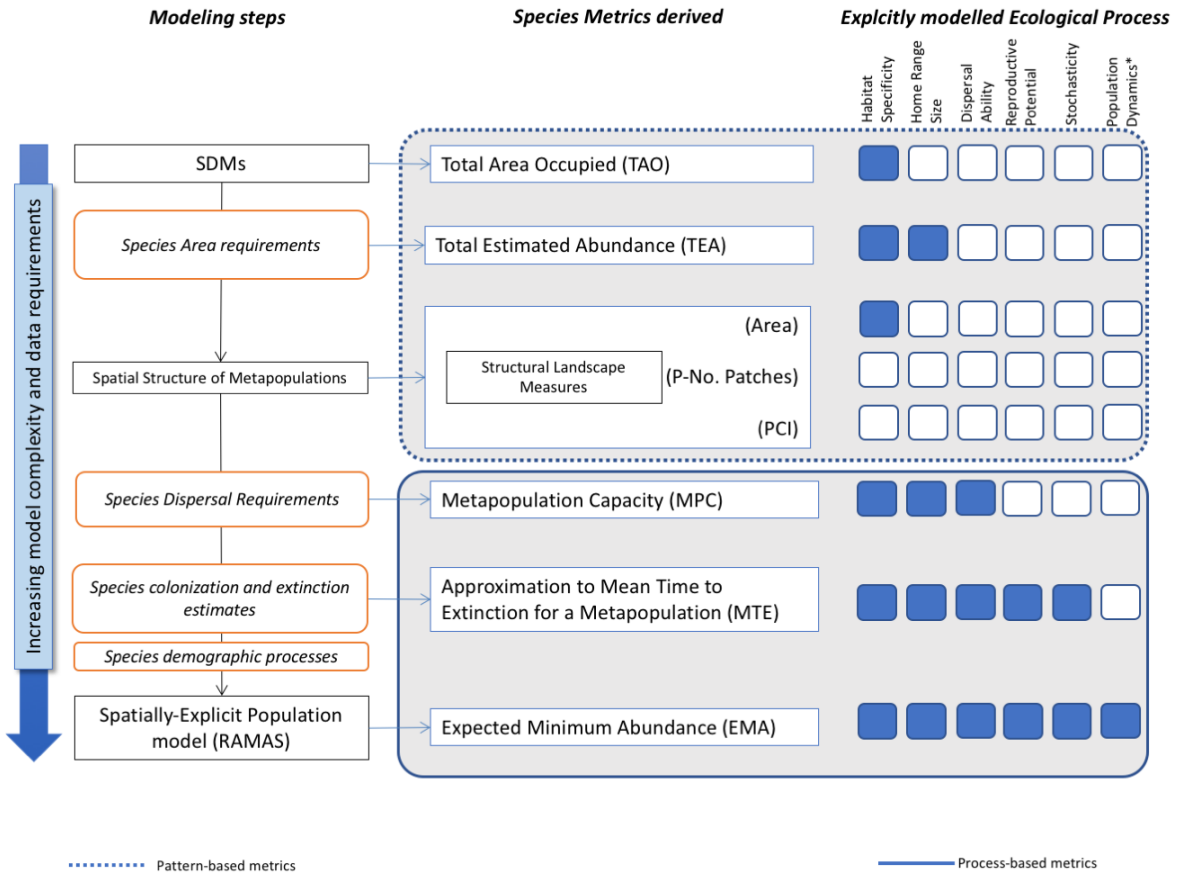


Figure 2: Schematic illustrating increasing model complexity and explicit inclusion of ecological processes in metrics. Species distribution models (SDMs) rely only on the correlation between observed patterns of occupancy and environmental variables to predict where suitable habitat may exist in the landscape. This habitat suitability can be converted to an estimate of the total area of occupancy (TAO) for any individual species. By combining this information with data on the area requirements of individuals of a species and the average density, an overall total estimate of abundance (TEA) is obtained. These data can then be combined with information on daily movement to identify patches, from which several other structural measures can be obtained including the area of habitat, the number of patches of habitat (P-No. Patches) and the Patch Cohesion Index (PCI: see Equation 3 Appendix 4). The metapopulation capacity is calculated from this patch structure and includes species-specific dispersal to give a deterministic measure of persistence. Again, using the metapopulation structure and using an established formula to approximate a stochastic patch occupancy model (Frank & Wissel 2002) we include species-specific information on rates of colonization, extinction and fecundity to provide a stochastic approximation of mean time to extinction of a metapopulation (MTE).

Author

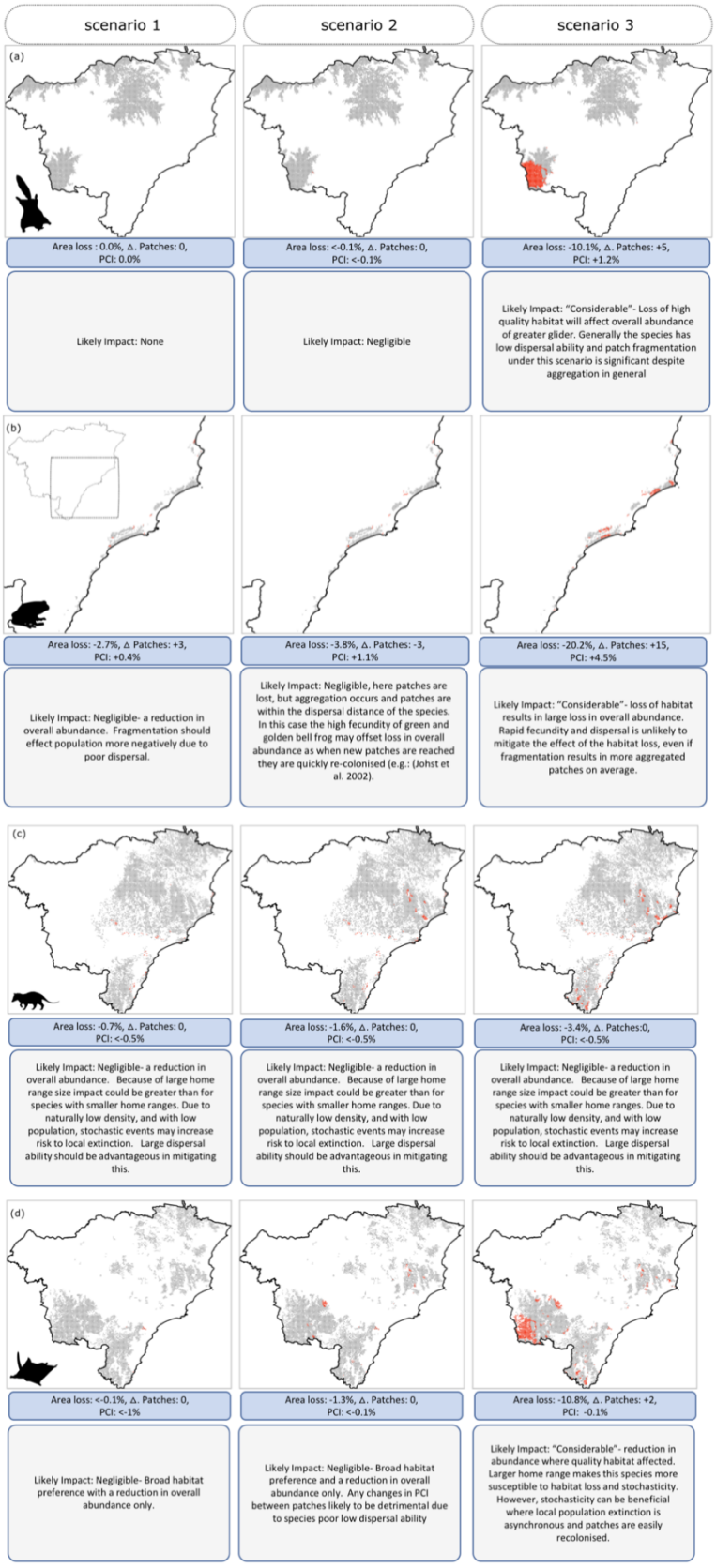
This article is protected by copyright. All rights reserved.

Finally, also based on the same metapopulation structure, we use stage-based population models and simulations that explicitly include the above ecological complexity and also include *population dynamics-referring to stochastic population processes such as variation in vital rates, spatial correlation in vital rates, different patterns of density-dependence and dispersal to provide an estimate of "expected minimum abundance" (EMA). Each metric explicitly includes varying degrees of modelled ecological processes that approximate different ecological traits for a species and therefore explicitly include how these traits will play out to mediate or exacerbate the effect of changes in habitat configuration.

Author Manuscript

This article is protected by copyright. All rights reserved.

Author Manuscript



This article is protected by copyright. All rights reserved.

Figure 3: Pattern of disturbance for each species and scenario and likely impact given species ecology and resultant changes in habitat configuration and quantity. Available habitat, shown in grey, with area lost in red for each species and scenario. (a) greater glider; (b) green and golden bell frog; (c) tiger quoll; (d) yellow-bellied glider. Relative change in habitat and PCI was calculated as a percentage loss from baseline. Δ Patches numbers are reported as change from baseline.

Author Manuscript

This article is protected by copyright. All rights reserved.

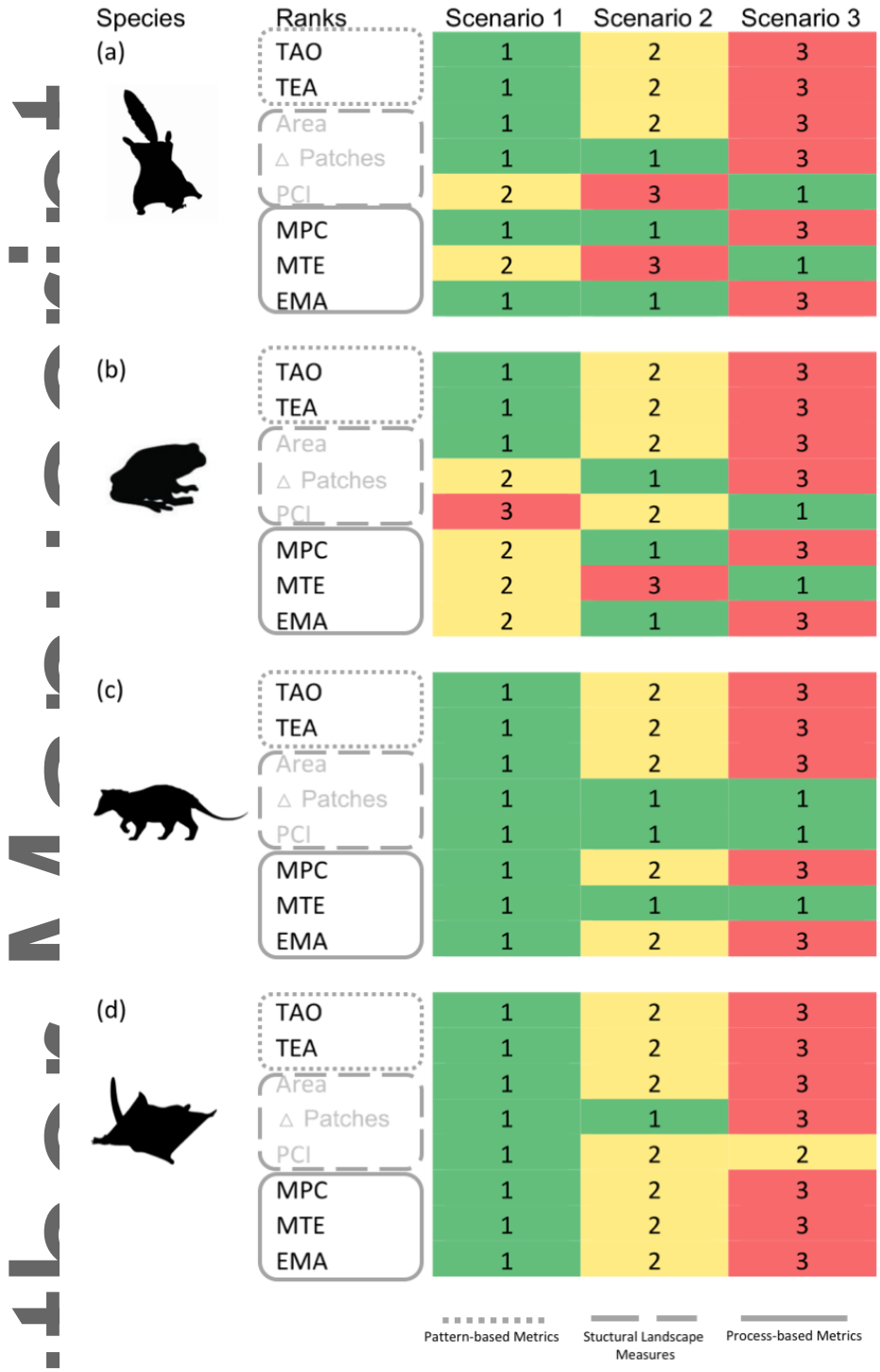


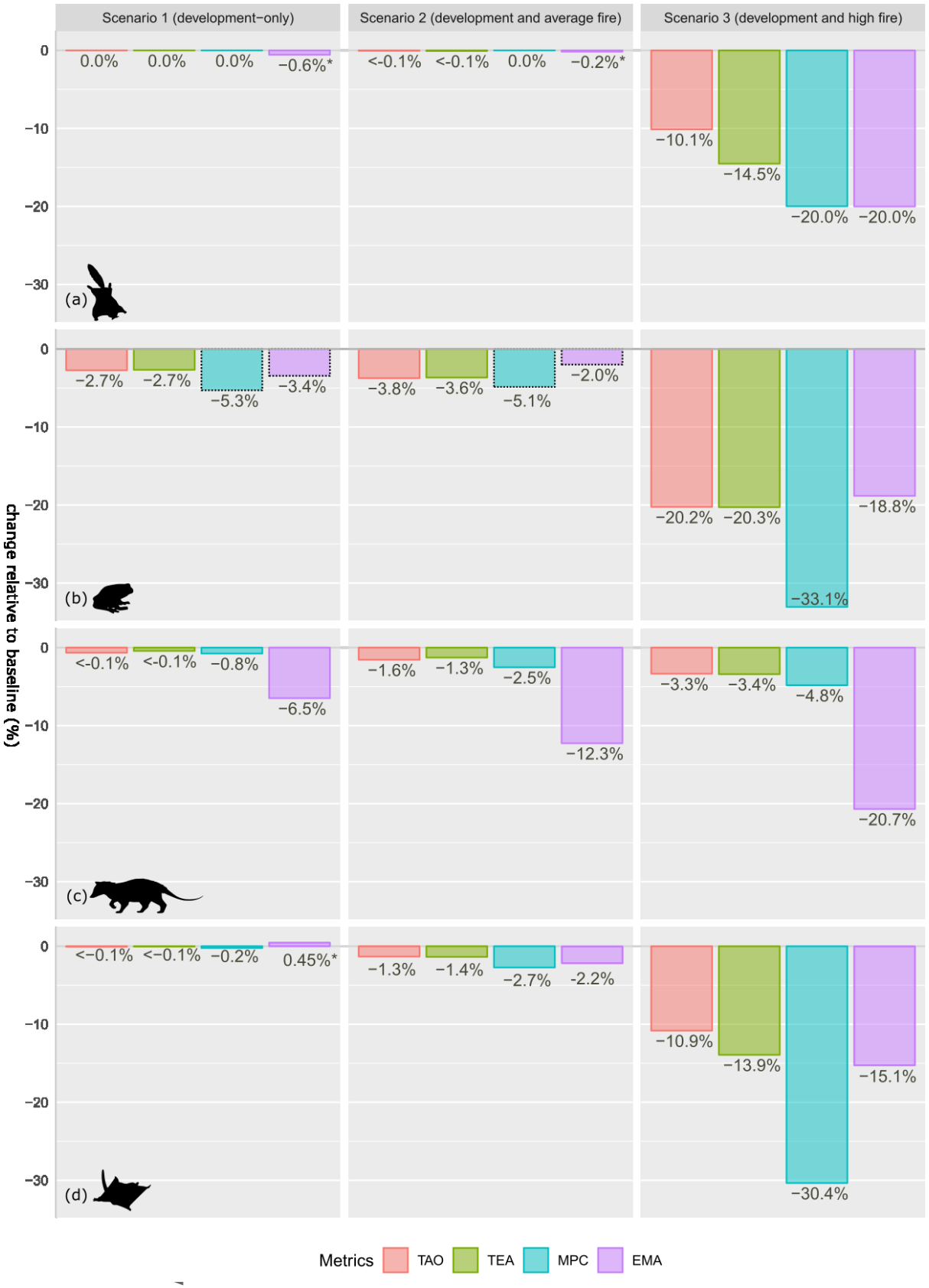
Figure 4: Rank order of scenarios for target species as established by impact measured by different species metrics (a) greater glider, (b) green and golden bell frog, (c) tiger quoll and (d) yellow bellied glider. TAO = total area of occurrence, TEA = Total estimated abundance, Area = % area loss, Δ Patches= Change in patch

This article is protected by copyright. All rights reserved.

number, PCI= Patch Cohesion Index, MTE= Mean Time to Extinction, MPC = metapopulation capacity and EMA = expected minimum abundance.

Author Manuscript

This article is protected by copyright. All rights reserved.



This article is protected by copyright. All rights reserved.

Figure 5. Change relative to baseline (y-axis) for species (a-d) in the three 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. Note MTE is omitted for clarity, but full results are listed in Annex 3. The dashed line around the bars in (b) highlights the marginal increase in EMA and metapopulation capacity between Scenarios 1 and 2. The asterisk (*) indicates insignificant differences between scenarios when accounting for standard error in EMA. Structural landscape metric relative change is summarized in figure 4.

Author Manuscript

This article is protected by copyright. All rights reserved.