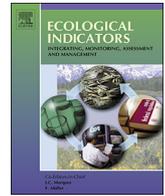


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Using ecological niche theory to avoid uninformative biodiversity surrogates

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ABSTRACT

Surrogates and indicators of biodiversity are used to infer the state and dynamics of species populations and ecosystems, as well as to inform conservation and management actions. Despite their widespread use, few studies have examined how ecological theory can guide the selection of surrogates and indicators, and thus reduce the likelihood of failure or cost of validation. We argue that ecological niche theory and knowledge of the extent to which particular limiting factors (e.g. physiological tolerances, limits to growth rates, or competitive exclusion) affect species distributions, abundance and coexistence could inform the choice of potential surrogates. Focusing on the environmental characteristics that define species niches makes it possible to identify situations where surrogates are likely to be *ineffective*, such as when there is no mechanistic basis for a candidate surrogate to be related to a biodiversity target. We describe two case studies where different candidate surrogate variables are shown to have contrasting potential as indicators of sustainable farming. Variables not mechanistically linked to the driver of change or responsive over appropriate timeframes or spatial scales are suggested *a priori* to be uninformative. The niche concept provides a framework for exploring ecological relationships that can inform the selection or exclusion of potential biodiversity surrogates. We think that this new approach to integrating ecological theory and application could lead to improved effectiveness of biodiversity monitoring and conservation.

1. Surrogates provide a way to monitor the state and dynamics of biodiversity

Biodiversity surrogates are used widely to make inferences about the status or trend of a biodiversity target of interest that cannot be measured easily or directly (Hunter et al., 2016; Lindenmayer et al., 2015b; O'Loughlin et al., 2018). Here, we define a biodiversity surrogate as an ecosystem attribute (the surrogate) that is intended to provide useful and reliable information about some aspect of biodiversity of interest (the target), but which is too costly or difficult to measure directly (Hunter et al., 2016; Lindenmayer and Likens, 2011). Strong demand exists for surrogates to inform decisions about the management of species of conservation concern (Caro, 2010), to design reserve networks that efficiently protect biodiversity (Rodrigues and Brooks, 2007), or to track biotic responses to anthropogenic disturbances (Hunter et al., 2016). Consequently, the use of biodiversity surrogates has increased rapidly in recent years (Caro, 2010; Lindenmayer et al.,

2015b; Mellin et al., 2011; Niemi and McDonald, 2004; Westgate et al., 2014). In response to this growth, many frameworks have been developed to assist in selecting biodiversity surrogates and indicators while considering practical constraints, different surrogate applications, or taxon-specific requirements (e.g. Lindenmayer et al., 2015a; McGeoch, 1998; Noss, 1990; van Oudenhoven et al., 2012). Yet there have been very few studies that have explicitly examined ecological theory and how it might be used to inform or prioritise the selection of surrogates (Lindenmayer and Likens, 2011; Muller and Lenz, 2006; Sætersdal and Gjerde, 2011). Closing this knowledge gap is critical because there is insufficient time to test the utility or validity of the vast array of potential surrogates identified using these existing frameworks. We suggest there are important opportunities to explore the ways in which ecological theory can provide conceptual guidance to the selection of biodiversity surrogates.

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Table 1

Three kinds of ecological phenomena that fall under the niche concept, and could contribute to the establishment of *a priori* expectations for when surrogate-target relationships are plausible or not. All three phenomena and their limiting parameters will interact to define a species niche via key mechanisms, thus providing a boundary around where a surrogate will and will not provide useful information about a biodiversity target.

Ecological phenomena	Example limiting parameter	Mechanism(s)
Species distributions	Climatic characteristics	Physiological tolerances
Species abundance	Resources	Growth rate, carrying capacity
Species interactions	Ecological similarity	Competition, predation, mutualism

2. Ecological theory and biodiversity surrogates

Ecological theory spans individual organisms, populations, communities, and ecosystems, as well as their interactions, behaviour, and responses to perturbations (Scheiner and Willig, 2011). Meanwhile, the application of surrogates in biodiversity conservation and environmental management are as diverse as there are problems and species (Hunter et al., 2016; Lindenmayer et al., 2015b). This means the starting point for improved use of theory in evaluating potential surrogates remains unclear, and there is no framework to guide work in this area. To date, there has only been one review of theory in biodiversity; Sætersdal and Gjerde (2011) looked at whether different classes of species-based surrogates were supported by niche and neutral models of community assembly. Their key finding was that focal species (sensu Lambeck, 1997) and surrogates of species richness (e.g. Fleishman et al., 2005) were not supported by either neutral or niche models, but that complementarity and cross-taxon congruence (e.g. Margules and Pressey, 2000) was supported by niche models when applied in the context of strong environmental gradients (Sætersdal and Gjerde, 2011). This suggests that there is substantial room for improvement in the use of theory to justify or test assumptions about many kinds of surrogates.

One way that theory could be useful is by identifying quickly what surrogates are likely to be ineffective. Rather than searching for theoretical support for proposed surrogates, theory could be used to rule out surrogates and to narrow down a potential pool of candidate variables, thus helping to focus effort and further examination. A starting point for theory and surrogates is to give greater attention to the causal mechanisms that might influence surrogate effectiveness and identify the contexts in which associations between a surrogate and its target are likely to be strong (Barton et al., 2015; Sætersdal and Gjerde, 2011). In contrast, surrogates chosen only because of empirical correlations with a target, even if easier to measure, may not provide useful information about the target in all circumstances (Barton et al., 2019). This is a problem because surrogates that perform well in changing environments, or in multiple spatial or temporal contexts (e.g. following ecological disturbance), are critical for effective management and conservation. Surrogacy built from purely correlative associations, such as cross-taxonomic surrogates (Heino, 2010; Lovell et al., 2007; Westgate et al., 2014; Yong et al., 2018) or focal indicator species (Lambeck, 1997; Lindenmayer et al., 2014b) has an important role in prioritising some taxa over others, and this might lead to reduced cost or effort in biodiversity management. Surrogates based on correlative associations in one context, however, may be weak or ineffective at another location or different time, resulting in poor decision making about surrogates or where to allocate scarce resources (Westgate et al., 2017).

Ecological constraints or limits to species abundances and distributions are often found to be causal, and represent a kind of relationship that has received little attention in the literature on biodiversity surrogates. Despite the plethora of studies of limits on ecological phenomena, like population growth rates, carrying capacity and species distributions (e.g. Abrams, 1983; Austin, 2007; Danger et al., 2008; Scheiner and Willig, 2011; Tilman, 1990), very few have explicitly examined ecological constraints to guide the selection of biodiversity

surrogates. We suggest that niche theory is useful for establishing clearer expectations and boundaries concerning when and where ecological relationships hold. Niche theory therefore provides an *a priori* set of principles to guide the selection of robust surrogates. Theory concerning ecological constraints provides valuable shortcuts for improved effectiveness of biodiversity monitoring and conservation. This is because a constraining relationship between a surrogate and its target can, for example, be identified intuitively (such as a limiting resource or habitat requirement), and then examined critically (in a range of contexts) to fully understand and develop a predictive relationship. The niche concept encapsulates the idea of limits and constraints to species, and we argue this might be an effective way to begin linking ecological theory with biodiversity surrogates.

3. Niche theory as an integrative framework for surrogates

The niche concept, in its broadest sense, describes the set of abiotic and biotic conditions that constrain a species distribution, abundance and coexistence with other species (Chase and Leibold, 2003; Hutchinson, 1957). Knowledge of the mechanisms constraining species can contribute to the establishment of *a priori* expectations for when surrogate-target relationships are plausible. We focus on three kinds of ecological constraints that fall under the niche concept. These are: (1) limits to species distributions, (2) limits to species abundance, and (3) limits to species coexistence (Table 1). Species' distributions can be considered a special case of abundance in the sense that when abundance = 0 a species is not present. However, we have made the deliberate point of treating distribution and abundance separately, as they are often quite different goals in the application of biodiversity surrogates. Whereas knowledge of species distributions and their ranges might be the goal from a reserve-selection perspective, knowledge of species abundances is often the goal for conservation practitioners tasked with managing populations of rare species (Caro, 2010).

Constraints to species distribution, abundance, and coexistence operate at a range of scales (depending on the species), and interact with each other (and many other factors) to form a complex niche space or 'n-dimensional hypervolume' (Blonder et al., 2014; Hutchinson, 1957). Yet biodiversity surrogates must focus on what is practical and useful to solve applied ecological and conservation problems (Caro, 2010; Lindenmayer et al., 2015b). By focusing on three key constraints we do not attempt to be comprehensive, but rather provide a clear point of departure for thinking about how limits to species might inform the selection of biodiversity surrogates, and identify situations where they are likely to be ineffective.

4. Limits to species distributions

Despite the ubiquity of bioclimatic modelling as an approach for estimating species distributions (Araujo and Peterson, 2012), climatic characteristics are not the only dimensions of niche space, which may include many other abiotic and biotic dimensions (Godsoe et al., 2017; Mackey and Lindenmayer, 2001; Pulliam, 2000; Scheele et al., 2017). The most important of these dimensions will have the strongest and most pervasive limiting effect on a species distribution, and might

therefore be a suitable surrogate. For example, abiotic variables like water chemistry (e.g. McArthur et al., 2010) or rainfall (e.g. Manzoni et al., 2012), can be constraining mechanisms for a target species or community. When such characteristics attain values beyond a certain limit or range, the conditions for reproduction, growth, or occupancy become less optimal, and ultimately constrain the abundance or distribution of a species.

Bioclimatic constraints on biodiversity often work in concert with other biotic factors to determine a species distribution (Mackey and Lindenmayer, 2001). For example, bioclimatic surrogates are sometimes used to identify the potential spread or impact of invasive species (McGeoch et al., 2010), with species distribution models developed for a native range applied to an area of introduction to assist management or facilitate prediction of invasion risk. However, niche theory predicts that the environmental space that a species occupies in its native range (its *realized* or *contemporary* niche) may poorly represent the environmental range that species could potentially occupy (its *fundamental* niche) (Shea and Chesson, 2002). This may arise because of biotic constraints operating in its native range, and release from such constraints in its area of introduction. For example, an analysis of invasive fish in the Mediterranean Basin found almost no conservatism of climatic niche from its native range (Parravicini et al., 2015). For these invasive fish, a climatic niche surrogate significantly under-estimated invasion risk as it did not consider release from the biotic interactions (predation or competition) that restricted its native range.

In addition, the “invasional meltdown hypothesis” (Simberloff and Von Holle, 1999) posits that ecosystem impacts from one invasion might facilitate further invasion (e.g. invader-facilitated invasion, O’Loughlin and Green, 2017). For example, invasion of the giant African land snail (*Achatina fulica*) in rainforest on Christmas Island (Australia) occurred only after an abundant native predator was extirpated by other invaders, despite the snail being a prolific invader of tropical rainforest elsewhere (Green et al., 2011). Thus, surrogates developed in one spatial context are unlikely to transfer to a different context due to differences in the abiotic or biotic limitations defining the original niche space.

5. Limits to species abundance

The abundance of a species observed within its distributional range is driven by the energy surplus gained after meeting the costs of biotic interactions such as competition or predation (Hall et al., 1992). Resource availability is key to meeting energy costs, as well as for fundamental growth or behavioural needs. One of the best-known theories describing constraining resources is Liebig’s Law of the Minimum (Danger et al., 2008; Thomas, 1929), which states that the scarcest resource will constrain the growth rate of a population. If this constraint is removed, then the next most limiting resource will take its place as the key constraint on growth, and so on (e.g. Hedwall et al., 2017; Thomas, 1929). Identification of a limiting resource, or knowledge that a resource is not limiting, might quickly rule in or out a potential surrogate for further investigation.

Soil nutrients (e.g. N- or P-limitation) provide a clear example of how limiting resources can shape plant species distributions (Tilman, 1990) or soil organisms (Mulder and Elser, 2009), and therefore may represent an effective mechanistic surrogate for plant abundances in some circumstances. From the perspective of biodiversity surrogacy, the identification of an easily measured but limiting soil nutrient could provide a useful shortcut for inferring something about a biodiversity target such as the occurrence of plant species or composition of a plant community. The concept of limiting resources can be relevant to many other taxa, such as suitable plant hosts for insects or mammalian hosts for parasitic lice, for example. Critical to many forms of resource limitation, therefore, is knowledge of the particular part of a life cycle of an organism that is dependent on the resource (e.g. plant host required for larvae of a butterfly). Limiting environmental or habitat-based

resources also might be suitable surrogates of biodiversity. For example, cavity-bearing trees are a popular surrogate for cavity-nesting vertebrates, as they are more easily measured than the cryptic animals that inhabit them (Gibbons and Lindenmayer, 2002; Lindenmayer et al., 2014a). Tree cavities are also an essential limiting resource for many species, and extending Liebig’s Law, a clear mechanism exists for using cavities as a surrogate as they are a limiting resource for nesting and shelter that constrain population growth and persistence (Lindenmayer et al., 2014a). Yet, the strength of that association can differ significantly among different ecosystems, and in some cases, cavity-bearing trees will not accurately represent the status of these vertebrates at all (Pierson et al., 2015). This limitation could be due to different interspecific competitive dynamics or a different hierarchy of limiting food or habitat resources in different regions.

6. Limits to species coexistence

Niche and coexistence theory (Abrams, 1983; Amarasekare, 2003) suggest that ecologically similar species are more likely to share resources or occupy a similar site. Yet competition will also limit spatial co-occurrence and shared site occupancy by species that are ecologically similar (Carmel et al., 2017; der Boer, 1986). Awareness of these concepts can help identify what species might, or might not, be useful surrogates. One way that competition and exclusion are mediated is via other interspecific interactions, which form part of a species’ realized or biotic niche space. Interactions also generally occur between species at a particular location (e.g. a bee visiting a flower, a shark eating a fish), and so interactions require spatial co-existence by definition. Various kinds of competitive, enemy-victim, or mutualistic interactions can constrain a species distribution and its co-existence with other species, and could be used to predict the abundance or site occupancy of a species. The coexistence concept is important for surrogacy because it is common to use the occurrence or abundance of one species (the surrogate) to infer the occurrence or abundance of another species or suite of species (the target) (e.g. Lane et al., 2014; Neeson and Mandelik, 2014). This kind of surrogate rests on the assumption that the indicator (species A) and target (species B) occur among a set of sites in a consistent way, perhaps due to a shared habitat or food resources. Species-based surrogates, such as focal species (Lambeck, 1997), are nearly always sought within a single taxonomic group, often within the same order or family (Azeria et al., 2009; Lane et al., 2014). This approach is based on practicality – members of the same taxon can often be sampled using a single methodology – but also on the idea of niche conservatism in which phylogenetic relatedness is a useful proxy for ecological and functional similarity (Caro, 2010).

When taken to extremes, however, this approach contradicts niche theory and the competitive exclusion principle (der Boer, 1986; Hardin, 1960). This contradiction occurs because an ideal surrogate is functionally identical to the target species and thus overlaps perfectly with its’ niche. We term this problem the “*biotic surrogacy paradox*”. Even if very similar species do not always exclude each other (Carmel et al., 2017), this does not avoid the biotic surrogacy paradox because the likelihood that two co-occurring species will be identical in all attributes except observability is extremely low (Fig. 1). A solution is to seek surrogates that reflect functional associations between species that are independent of their relatedness. Useful candidates include strong mutualisms, such as between butterflies and their host plants, or even parasite-host relationships. Weaker forms of ecological association might include shared use of habitat, such as cavity-dependent fauna at their host trees (Pierson et al., 2015).

7. Maximising information about niche constraints

So far, we have focused on examples of how ecological constraints might reduce the number of potential biodiversity surrogates, but this does not tell us which of the remaining surrogates is ‘best’ for a given

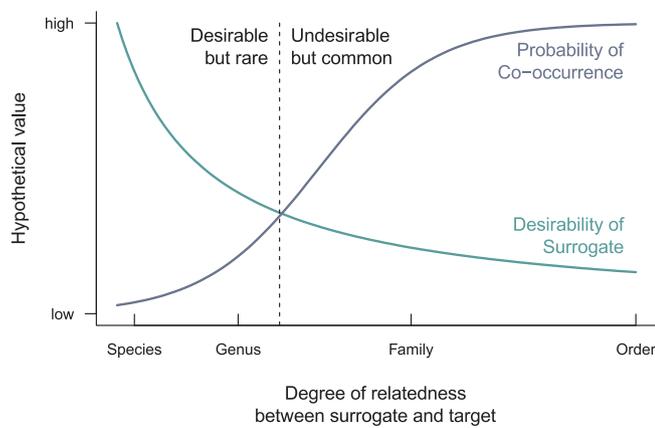


Fig. 1. The trade-off between surrogate desirability and probability of co-occurrence with the target species. A theoretically desirable species-based surrogate is identical to the target species in all ways, except with regard to observability, and this is likely to be more true the closer their relatedness. Yet such species are unlikely to exist, and are contrary to predictions of the competitive exclusion principle. Thus, a tradeoff between surrogate desirability and probability of co-occurrence lead to the prediction of intermediate levels of relatedness between effective targets and surrogates. We term this problem the “biotic surrogacy paradox” because the likelihood that two co-occurring species will be identical in all attributes except observability is relatively low.

situation. Maximizing the information about niche constraints, and assessment of their suitability as surrogates requires consideration of the variability of different niche characteristics that are thought to constrain the biodiversity target of interest. Too little or too much variability can give rise to problems with statistical analyses and interpretations of the data. Put differently, a niche characteristic may not be a useful surrogate for the distribution of a species if it shows no variation across that species’ range. This means that the degree of variation in a limiting variable should be considered when determining how useful a surrogate might be for providing information about a target.

For both statistical and ecological reasons, any mismatch in spatial or temporal associations between a surrogate and the target of interest increases the likelihood of a surrogate not providing useful information. From a temporal perspective, for example, monitoring commercial fish populations might require frequent intra-annual measures of numbers of individuals relative to a benchmark sustainability target (Johansen et al., 2018). By contrast, tracking the recovery of taxa after a disturbance (e.g. wildfire) might require less frequent measures over longer timeframes to identify the long-term trajectory (Barton et al., 2014). These two objectives of surrogacy are quite different and present a problem for choosing a surrogate that is either sensitive to fine-scale changes or insensitive to short-term changes, but capable of revealing long-term trends. Another key decision involves the choice of surrogate that best represents variation in an objective through both space and time. For example, spatial variation in plant richness of some grasslands is linked strongly to soil nitrogen (Soons et al., 2017), but temporal variation is most strongly linked with other drivers such as multi-year trends in rainfall (Adler and Levine, 2007). Because spatial variability in richness among sites is often much greater than temporal variability in richness within a site, this means that nitrogen might be a poor surrogate for temporal change in grassland species richness, and climate might be a poor surrogate for spatial variation in richness (Fig. 2). In this example, considering niche theory can help match the temporal and spatial scales of interest with the surrogates that are constraining at the scales of interest.

8. Putting niche theory into surrogate practice

We describe two case studies where different variables might be

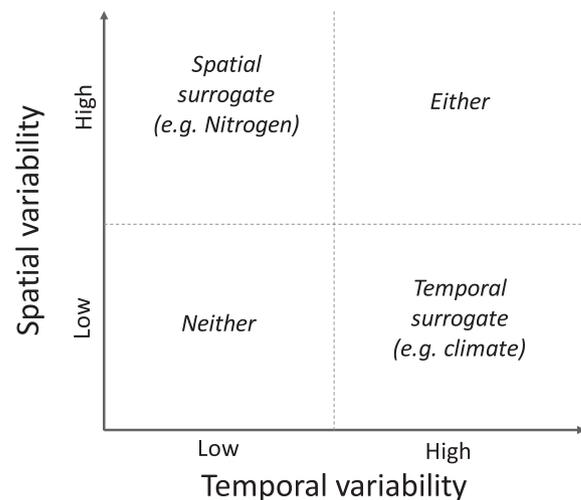


Fig. 2. Surrogates will differ in variability through space and time. The degree of variability along each axis may affect the usefulness of a surrogate for capturing variability in a biodiversity target through space or time. For example, soil characteristics (e.g., nitrogen or phosphorus concentrations) should be better surrogates for plant species richness through space, whereas climatic characteristics (e.g., average precipitation or average temperature) should be better surrogates for plant richness through time.

considered as potential suitable surrogates of biodiversity. We step through each case study to explain how niche theory might shape thinking about the suitability of potential surrogates, depending on how they are intended to be used and the target they are representing.

9. Case study 1 – surrogates for native plant diversity

Maintaining or improving ground-layer plant diversity is a common goal for land management in grazing landscapes in south-eastern Australia (Lunt et al., 2007; McIntyre and Lavorel, 1994). In this region a large number of plant species have been introduced via agricultural activities, and these introduced species can outperform native species, particularly when high phosphorus fertilizers are added to the soil. Measuring trends in native plant diversity is the direct approach to inform management effectiveness, but is often difficult to quantify if botanical expertise is not available, or costly if there are many sites to survey. Alternative surrogate variables might include (i) native plant cover, (ii) exotic plant cover, (iii) exotic dominance, or (iv) soil phosphorus (Driscoll and Strong, 2018; McIntyre and Lavorel, 1994), yet each of these variables relate to the niche of the target in different ways.

- (i) Native plant cover describes the distribution of native plants, tautologically, yet plant cover is likely to be constrained by factors different from those constraining plant species richness, and so the two may only be loosely correlated in space and time (Lundholm and Larson, 2004; McIntyre and Lavorel, 1994).
- (ii) Exotic cover constrains the distribution of native plants via competitive exclusion and co-occurrence mechanisms, and can therefore reduce native plant species diversity (Lundholm and Larson, 2004; McIntyre and Lavorel, 1994). However, the niche of both exotic and native species in this ecosystem are also strongly constrained by factors such as rainfall, which may drive temporal “noise” to this potential surrogate.
- (iii) Exotic dominance (exotic cover/total cover) is a measure of the extent to which exotics may be constraining native plants via competitive exclusion, while absorbing variation from niche constraints that drive fluctuations in growth and abundance. Dominance may therefore be less temporally noisy than pure cover measures.
- (iv) Soil phosphorus constrains the abundance, distribution, and co-

occurrence of both native and exotic species (Driscoll and Strong, 2018; McIntyre and Lavorel, 1994). High soil phosphorus is often a result of previous agricultural practices, and promotes growth of exotic species but can be toxic to many native species. High soil phosphorus also alters co-occurrence by increasing the ability of exotics to exclude native species.

Given the limited constraints of native cover on native species diversity, and the likelihood they are constrained by different extrinsic factors, this potential surrogate should be excluded from further examination. For spatial applications, both soil phosphorus and exotic species cover clearly constrain native species richness and are strong candidates for further investigation. However, for inter-annual monitoring, these surrogates may perform poorly; exotic cover, because large changes to the cover or biomass of some species can occur on an annual basis (in response to factors such as rainfall), but slow growth and recolonization rates mean that changes in native plant diversity takes many years (McIntyre et al., 2015); and soil phosphorus because soil phosphorus is likely to be very slow to respond to land management changes compared with plants (Schelfhout et al., 2015). For inter-annual monitoring, a surrogate such as exotic dominance may be worth exploring as it is closely aligned with constraints on native species richness, but resilient to fluctuations on total community biomass. Aligning the scales of variability between surrogate and target suggests that surrogates may be inappropriate for some applications yet strong candidates for others.

10. Case study 2 – surrogates for threatened woodland bird species richness

Restoration of vegetation cover has been undertaken in south-eastern Australia through the planting of large areas of trees to provide shelter for livestock, reduce erosion and salinity, as well as for biodiversity benefits (Belder et al., 2018; Gibb and Cunningham, 2010). A key target for restoration plantings is woodland bird diversity, with several species declining and of conservation concern (Ikin et al., 2016; Lindenmayer et al., 2016). Yet, woodland birds of conservation concern can be small, cryptic, and rare, and therefore difficult to observe. Potential surrogates for woodland bird diversity include (i) vegetation cover (Cunningham et al., 2014), (ii) the occurrence of the aggressive noisy miner (Lane et al., 2014), or (iii) the occurrence of a particular, functionally similar bird species (Lindenmayer et al., 2014b), yet each of these variables relate to the target niche in different ways.

- (i) Many studies have demonstrated the positive relationship between vegetation structure and bird diversity (Cunningham et al., 2014; Recher, 1969). Woody vegetation cover is often correlated with woodland bird diversity, but the constraining factor is thought to be structural complexity (MacArthur and MacArthur, 1961), which increases habitat availability and resources, and facilitates species co-occurrence.
- (ii) Noisy miner birds are aggressive native species that harass smaller species present in their territory (Mortelliti et al., 2016). This behaviour suppresses native bird diversity in woodland patches where they occur (Lindenmayer et al., 2018). The constraining mechanism here is competitive exclusion reducing co-occurrence (Lane et al., 2014; Montague-Drake et al., 2011). Noisy miner effects on small birds tend to be stronger in habitats with low structural complexity.
- (iii) Individual bird species might also be used as predictors for the occurrence of other species, including woodland birds of conservation concern (Lindenmayer et al., 2014b). The constraining mechanism here is hypothesised to be increasing co-occurrence due to similarity in resource or habitat requirement traits, i.e. similarity in niche constraints (Lambeck, 1997; Nicholson et al., 2013).

Vegetation cover broadly constrains the distribution of bird assemblages by limiting habitat availability, thus making vegetation cover a clear surrogate worthy of further investigation (Ikin et al., 2016), particularly for spatial surrogacy applications. However, temporal changes in vegetation extent occur over decadal timescales (particularly positive changes), thus making it unsuitable for short-term surrogacy requirements. Patch-scale occurrence of noisy miner birds is a good predictor of bird assemblage composition, with competitive exclusion and aggressive behaviour constraining the presence of key woodland bird species of conservation concern (Beggs et al., 2019; Montague-Drake et al., 2011). Noisy miners are easily observed, and so are a potential surrogate for woodland bird diversity. However, patch-scale colonisation and extinction dynamics of noisy miners, as well as context-dependence in the impacts on smaller birds, make this bird suitable only for intra- or inter-annual scale dynamics, and within-landscape scales (Beggs et al., 2019; Montague-Drake et al., 2011; Mortelliti et al., 2016). Individual bird species that are functionally similar to woodland birds of conservation concern (e.g. small, canopy-dwelling insectivores), should be constrained by similar habitat or resource requirements – i.e. share similar niche characteristics. Yet the biodiversity surrogacy paradox (Fig. 1) challenges this idea. Similarly, hypothesis such as the focal species approach (FSA) which proposes that management of the most range-restricted or dispersal-limited species should, by default, cater to most other species, is also flawed or no better than choosing species at random (Lindenmayer et al., 2014b). This suggests one individual species is unlikely to be an appropriate surrogate for a suite of species of conservation concern, unless that species strongly constrains the niche of many species through biotic interactions (as per the noisy miner).

11. Implications and future challenges

We have described how aspects of the niche concept might be applied to the selection of biodiversity surrogates. The use theory to predict which surrogates are likely to be effective in a range of instances is difficult due to the variety of contexts and specific applications. Nevertheless, the likelihood of success will improve if effort is directed towards surrogate variables with clear constraining effects on the biodiversity target. Importantly, the absence of ecological constraints will help to identify situations where surrogates are likely to be *ineffective*. We suggest that a surrogate should be selected when there is a clear constraining influence on a target species' distribution, abundance, or interactions. An approach to the selection of surrogates that incorporates ecological constraints should provide a useful and efficient shortcut to more robust surrogacy relationships. Given the amount of time and effort needed to properly validate surrogates (Lindenmayer et al., 2015a), any conceptual or heuristic tool that can help rule-out possible options *a priori* has the potential to reduce the cost of establishing or updating biodiversity monitoring programs. By allowing those programs to identify informative surrogates more quickly, this approach should reduce the probability of poor biodiversity outcomes, such as failure to detect declines in threatened species.

A key challenge for broadly applying niche theory to surrogates is the issue of moving from qualitative to quantitative investigation of constraints. We have discussed the role of variability and scale in affecting surrogate selection, which represents a first step towards these goals. Research on species distribution modelling has made substantial advances by developing methods to estimate biotic and abiotic constraints on species distributions (e.g. Booth et al., 2014; D'Amen et al., 2018; Elith et al., 2006). The methods used to generate species distribution models are derived from regression (Renner and Warton, 2013), so the extent to which they represent mechanistic or correlative insights is open to debate (Kearney et al., 2010). In contrast, theoretically derived methods for modelling constraints – such as the maximum entropy theory of ecology (Harte, 2011) – have yet to receive widespread acceptance, or be tested for their predictive capacity (Xiao et al.,

2015). A key problem with investigating constraints is that different resources may be limiting in different environmental contexts, restricting our capacity to transfer learning to new ecosystems (e.g. Pierson et al., 2015). Therefore, quantitatively characterizing the mechanisms that determine how species respond to environmental variation is a major challenge for future research.

Conservation and management would benefit from future research that seeks to understand which aspect of a niche are most fluid or context-dependent, particularly in response to global change (e.g. Scheele et al., 2017). Integration of niche concepts and its theoretical underpinnings with applied surrogacy problems will provide guidance to scientists tasked with establishing surrogacy by showing how key theories might contradict hypothesized surrogacy relationships and inflate the risk of failure. Theory concerning ecological constraints has the potential to provide valuable shortcuts for improved effectiveness of biodiversity monitoring and conservation.

Author contributions

PSB, MJW, MRW, CFS, LSO, CNF, and DBL conceived the main ideas in this paper, with additional discussion and input from all authors. PSB led the writing of the manuscript. All authors contributed critically to drafts of the paper and gave approval for final submission.

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Appendix A. Supplementary data

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