

1 **Using ecological niche theory to avoid uninformative biodiversity surrogates**

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17

18 **Abstract**

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

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39 **Keywords:** Conservation; Indicator; Environmental Change; Proxy; Causal Relationship;
40 Ecological Theory; Biodiversity Management; Biotic Surrogacy Paradox

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43 **Surrogates provide a way to monitor the state and dynamics of biodiversity**

44 Biodiversity surrogates are used widely to make inferences about the status or trend of a
45 biodiversity target of interest that cannot be measured easily or directly (Hunter Jr et al. 2016;
46 Lindenmayer et al. 2015b; O'Loughlin et al. 2018). Here, we define a biodiversity surrogate
47 as an ecosystem attribute (the surrogate) that is intended to provide useful and reliable
48 information about some aspect of biodiversity of interest (the target), but which is too costly
49 or difficult to measure directly (Hunter et al. 2016; Lindenmayer & Likens 2011). Strong
50 demand exists for surrogates to inform decisions about the management of species of
51 conservation concern (Caro 2010), to design reserve networks that efficiently protect
52 biodiversity (Rodrigues & Brooks 2007), or to track biotic responses to anthropogenic
53 disturbances (Hunter et al. 2016). Consequently, the use of biodiversity surrogates has
54 increased rapidly in recent years (Caro 2010; Lindenmayer et al. 2015b; Mellin et al. 2011;
55 Niemi & McDonald 2004; Westgate et al. 2014). In response to this growth, many
56 frameworks have been developed to assist in selecting biodiversity surrogates and indicators
57 while considering practical constraints, different surrogate applications, or taxon-specific
58 requirements (e.g. Lindenmayer et al. 2015a; McGeoch 1998; Noss 1990; van Oudenhoven et
59 al. 2012). Yet there have been very few studies that have explicitly examined ecological
60 theory and how it might be used to inform or prioritise the selection of surrogates
61 (Lindenmayer & Likens 2011; Muller & Lenz 2006; Sætersdal & Gjerde 2011). Closing this
62 knowledge gap is critical because there is insufficient time to test the utility or validity of the
63 vast array of potential surrogates identified using these existing frameworks. We suggest there
64 are important opportunities to explore the ways in which ecological theory can provide
65 conceptual guidance to the selection of biodiversity surrogates.

66

67 **Ecological theory and biodiversity surrogates**

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

83 One way that theory could be useful is by identifying quickly what surrogates are
84 likely to be ineffective. Rather than searching for theoretical support for proposed surrogates,
85 theory could be used to rule out surrogates and to narrow down a potential pool of candidate
86 variables, thus helping to focus effort and further examination. A starting point for theory and
87 surrogates is to give greater attention to the causal mechanisms that might influence surrogate
88 effectiveness and identify the contexts in which associations between a surrogate and its
89 target are likely to be strong (Barton et al. 2015; Sætersdal & Gjerde 2011). In contrast,
90 surrogates chosen only because of empirical correlations with a target, even if easier to
91 measure, may not provide useful information about the target in all circumstances (Barton et

92 al. 2019). This is a problem because surrogates that perform well in changing environments,
93 or in multiple spatial or temporal contexts (e.g. following ecological disturbance), are critical
94 for effective management and conservation. Surrogacy built from purely correlative
95 associations, such as cross-taxonomic surrogates (Heino 2010; Lovell et al. 2007; Westgate et
96 al. 2014; Yong et al. 2018) or focal indicator species (Lambeck 1997; Lindenmayer et al.
97 2014b) has an important role in prioritising some taxa over others, and this might lead to
98 reduced cost or effort in biodiversity management. Surrogates based on correlative
99 associations in one context, however, may be weak or ineffective at another location or
100 different time, resulting in poor decision making about surrogates or where to allocate scarce
101 resources (Westgate et al. 2017).

102 Ecological constraints or limits to species abundances and distributions are often
103 found to be causal, and represent a kind of relationship that has received little attention in the
104 literature on biodiversity surrogates. Despite the plethora of studies of limits on ecological
105 phenomena, like population growth rates, carrying capacity and species distributions (e.g.
106 Abrams 1983; Austin 2007; Danger et al. 2008; Scheiner & Willig 2011; Tilman 1990), very
107 few have explicitly examined ecological constraints to guide the selection of biodiversity
108 surrogates. We suggest that niche theory is useful for establishing clearer expectations and
109 boundaries concerning when and where ecological relationships hold. Niche theory therefore
110 provides an *a priori* set of principles to guide the selection of robust surrogates. Theory
111 concerning ecological constraints provides valuable shortcuts for improved effectiveness of
112 biodiversity monitoring and conservation. This is because a constraining relationship between
113 a surrogate and its target can, for example, be identified intuitively (such as a limiting
114 resource or habitat requirement), and then examined critically (in a range of contexts) to fully
115 understand and develop a predictive relationship. The niche concept encapsulates the idea of

116 limits and constraints to species, and we argue this might be an effective way to begin linking
117 ecological theory with biodiversity surrogates.

118

119 **Niche theory as an integrative framework for surrogates**

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

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

140 selection of biodiversity surrogates, and identify situations where they are likely to be
141 ineffective.

142

143 **Limits to species distributions**

144 Despite the ubiquity of bioclimatic modelling as an approach for estimating species
145 distributions (Araujo & Peterson 2012), climatic characteristics are not the only dimensions of
146 niche space, which may include many other abiotic and biotic dimensions (Godsoe et al.
147 2017; Mackey & Lindenmayer 2001; Pulliam 2000; Scheele et al. 2017). The most important
148 of these dimensions will have the strongest and most pervasive limiting effect on a species
149 distribution, and might therefore be a suitable surrogate. For example, abiotic variables like
150 water chemistry (e.g. McArthur et al. 2010) or rainfall (e.g. Manzoni et al. 2012), can be
151 constraining mechanisms for a target species or community. When such characteristics attain
152 values beyond a certain limit or range, the conditions for reproduction, growth, or occupancy
153 become less optimal, and ultimately constrain the abundance or distribution of a species.

154 Bioclimatic constraints on biodiversity often work in concert with other biotic factors
155 to determine a species distribution (Mackey and Lindenmayer, 2001). For example,
156 bioclimatic surrogates are sometimes used to identify the potential spread or impact of
157 invasive species (McGeoch et al. 2010), with species distribution models developed for a
158 native range applied to an area of introduction to assist management or facilitate prediction of
159 invasion risk. However, niche theory predicts that the environmental space that a species
160 occupies in its native range (its *realized* or *contemporary* niche) may poorly represent the
161 environmental range that species could potentially occupy (its *fundamental* niche) (Shea &
162 Chesson 2002). This may arise because of biotic constraints operating in its native range, and
163 release from such constraints in its area of introduction. For example, an analysis of invasive
164 fish in the Mediterranean Basin found almost no conservatism of climatic niche from its

165 native range (Parravicini et al. 2015). For these invasive fish, a climatic niche surrogate
166 significantly under-estimated invasion risk as it did not consider release from the biotic
167 interactions (predation or competition) that restricted its native range.

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

176

177 **Limits to species abundance**

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

188 Soil nutrients (e.g. N- or P-limitation) provide a clear example of how limiting
189 resources can shape plant species distributions (Tilman 1990) or soil organisms (Mulder &

190 Elser 2009), and therefore may represent an effective mechanistic surrogate for plant
191 abundances in some circumstances. From the perspective of biodiversity surrogacy, the
192 identification of an easily measured but limiting soil nutrient could provide a useful shortcut
193 for inferring something about a biodiversity target such as the occurrence of plant species or
194 composition of a plant community. The concept of limiting resources can be relevant to many
195 other taxa, such as suitable plant hosts for insects or mammalian hosts for parasitic lice, for
196 example. Critical to many forms of resource limitation, therefore, is knowledge of the
197 particular part of a life cycle of an organism that is dependent on the resource (e.g. plant host
198 required for larvae of a butterfly). Limiting environmental or habitat-based resources also
199 might be suitable surrogates of biodiversity. For example, cavity-bearing trees are a popular
200 surrogate for cavity-nesting vertebrates, as they are more easily measured than the cryptic
201 animals that inhabit them (Gibbons & Lindenmayer 2002; Lindenmayer et al. 2014a). Tree
202 cavities are also an essential limiting resource for many species, and extending Liebig's Law,
203 a clear mechanism exists for using cavities as a surrogate as they are a limiting resource for
204 nesting and shelter that constrain population growth and persistence (Lindenmayer et al.
205 2014a). Yet, the strength of that association can differ significantly among different
206 ecosystems, and in some cases, cavity-bearing trees will not accurately represent the status of
207 these vertebrates at all (Pierson et al. 2015). This limitation could be due to different
208 interspecific competitive dynamics or a different hierarchy of limiting food or habitat
209 resources in different regions.

210

211 **Limits to species coexistence**

212 Niche and coexistence theory (Abrams 1983; Amarasekare 2003) suggest that ecologically
213 similar species are more likely to share resources or occupy a similar site. Yet competition
214 will also limit spatial co-occurrence and shared site occupancy by species that are

215 ecologically similar (Carmel et al. 2017; der Boer 1986). Awareness of these concepts can
216 help identify what species might, or might not, be useful surrogates. One way that
217 competition and exclusion are mediated is via other interspecific interactions, which form part
218 of a species' realized or biotic niche space. Interactions also generally occur between species
219 at a particular location (e.g. a bee visiting a flower, a shark eating a fish), and so interactions
220 require spatial co-existence by definition. Various kinds of competitive, enemy-victim, or
221 mutualistic interactions can constrain a species distribution and its co-existence with other
222 species, and could be used to predict the abundance or site occupancy of a species. The
223 coexistence concept is important for surrogacy because it is common to use the occurrence or
224 abundance of one species (the surrogate) to infer the occurrence or abundance of another
225 species or suite of species (the target) (e.g. Lane et al. 2014; Neeson & Mandelik 2014). This
226 kind of surrogate rests on the assumption that the indicator (species A) and target (species B)
227 occur among a set of sites in a consistent way, perhaps due to a shared habitat or food
228 resources. Species-based surrogates, such as focal species (Lambeck 1997), are nearly always
229 sought within a single taxonomic group, often within the same order or family (Azeria et al.
230 2009; Lane et al. 2014). This approach is based on practicality – members of the same taxon
231 can often be sampled using a single methodology – but also on the idea of niche conservatism
232 in which phylogenetic relatedness is a useful proxy for ecological and functional similarity
233 (Caro 2010).

234 When taken to extremes, however, this approach contradicts niche theory and the
235 competitive exclusion principle (der Boer 1986; Hardin 1960). This contradiction occurs
236 because an ideal surrogate is functionally identical to the target species and thus overlaps
237 perfectly with its' niche. We term this problem the “*biotic surrogacy paradox*”. Even if very
238 similar species do not always exclude each another (Carmel et al. 2017), this does not avoid
239 the biotic surrogacy paradox because the likelihood that two co-occurring species will be

240 identical in all attributes except observability is extremely low (Figure 1). A solution is to
241 seek surrogates that reflect functional associations between species that are independent of
242 their relatedness. Useful candidates include strong mutualisms, such as between butterflies
243 and their host plants, or even parasite-host relationships. Weaker forms of ecological
244 association might include shared use of habitat, such as cavity-dependent fauna at their host
245 trees (Pierson et al. 2015).

246

247 **Maximising information about niche constraints**

248 So far, we have focused on examples of how ecological constraints might reduce the number
249 of potential biodiversity surrogates, but this does not tell us which of the remaining surrogates
250 is ‘best’ for a given situation. Maximizing the information about niche constraints, and
251 assessment of their suitability as surrogates requires consideration of the variability of
252 different niche characteristics that are thought to constrain the biodiversity target of interest.
253 Too little or too much variability can give rise to problems with statistical analyses and
254 interpretations of the data. Put differently, a niche characteristic may not be a useful surrogate
255 for the distribution of a species if it shows no variation across that species’ range. This means
256 that the degree of variation in a limiting variable should be considered when determining how
257 useful a surrogate might be for providing information about a target.

258 For both statistical and ecological reasons, any mismatch in spatial or temporal
259 associations between a surrogate and the target of interest increases the likelihood of a
260 surrogate not providing useful information. From a temporal perspective, for example,
261 monitoring commercial fish populations might require frequent intra-annual measures of
262 numbers of individuals relative to a benchmark sustainability target (Johansen et al. 2018). By
263 contrast, tracking the recovery of taxa after a disturbance (e.g. wildfire) might require less
264 frequent measures over longer timeframes to identify the long-term trajectory (Barton et al.

265 2014). These two objectives of surrogacy are quite different and present a problem for
266 choosing a surrogate that is either sensitive to fine-scale changes or insensitive to short-term
267 changes, but capable of revealing long-term trends. Another key decision involves the choice
268 of surrogate that best represents variation in an objective through both space and time. For
269 example, spatial variation in plant richness of some grasslands is linked strongly to soil
270 nitrogen (Soons et al. 2017), but temporal variation is most strongly linked with other drivers
271 such as multi-year trends in rainfall (Adler & Levine 2007). Because spatial variability in
272 richness *among* sites is often much greater than temporal variability in richness *within* a site,
273 this means that nitrogen might be a poor surrogate for temporal change in grassland species
274 richness, and climate might be a poor surrogate for spatial variation in richness (Figure 2). In
275 this example, considering niche theory can help match the temporal and spatial scales of
276 interest with the surrogates that are constraining at the scales of interest.

277

278 **Putting niche theory into surrogate practice**

279 We describe two case studies where different variables might be considered as potential
280 suitable surrogates of biodiversity. We step through each case study to explain how niche
281 theory might shape thinking about the suitability of potential surrogates, depending on how
282 they are intended to be used and the target they are representing.

283

284 **Case study 1 – surrogates for native plant diversity**

285 Maintaining or improving ground-layer plant diversity is a common goal for land
286 management in grazing landscapes in south-eastern Australia (Lunt et al. 2007; McIntyre &
287 Lavorel 1994). In this region a large number of plant species have been introduced via
288 agricultural activities, and these introduced species can outperform native species, particularly
289 when high phosphorus fertilizers are added to the soil. Measuring trends in native plant

290 diversity is the direct approach to inform management effectiveness, but is often difficult to
291 quantify if botanical expertise is not available, or costly if there are many sites to survey.
292 Alternative surrogate variables might include (i) native plant cover, (ii) exotic plant cover,
293 (iii) exotic dominance, or (iv) soil phosphorus (Driscoll & Strong 2018; McIntyre & Lavorel
294 1994), yet each of these variables relate to the niche of the target in different ways.

295 (i) Native plant cover describes the distribution of native plants, tautologically, yet plant
296 cover is likely to be constrained by factors different from those constraining plant
297 species richness, and so the two may only be loosely correlated in space and time
298 (Lundholm & Larson 2004; McIntyre & Lavorel 1994).

299 (ii) Exotic cover constrains the distribution of native plants via competitive exclusion and
300 co-occurrence mechanisms, and can therefore reduce native plant species diversity
301 (Lundholm & Larson 2004; McIntyre & Lavorel 1994). However, the niche of both
302 exotic and native species in this ecosystem are also strongly constrained by factors
303 such as rainfall, which may drive temporal “noise” to this potential surrogate.

304 (iii) Exotic dominance (exotic cover / total cover) is a measure of the extent to which
305 exotics may be constraining native plants via competitive exclusion, while absorbing
306 variation from niche constraints that drive fluctuations in growth and abundance.
307 Dominance may therefore be less temporally noisy than pure cover measures. .

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

313 Given the limited constraints of native cover on native species diversity, and the likelihood
314 they are constrained by different extrinsic factors, this potential surrogate should be excluded

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

327

328 **Case study 2 – surrogates for threatened woodland bird species richness**

329 Restoration of vegetation cover has been undertaken in south-eastern Australia through the
330 planting of large areas of trees to provide shelter for livestock, reduce erosion and salinity, as
331 well as for biodiversity benefits (Belder et al. 2018; Gibb & Cunningham 2010). A key target
332 for restoration plantings is woodland bird diversity, with several species declining and of
333 conservation concern (Ikin et al. 2016; Lindenmayer et al. 2016). Yet, woodland birds of
334 conservation concern can be small, cryptic, and rare, and therefore difficult to observe.

335 Potential surrogates for woodland bird diversity include (i) vegetation cover (Cunningham et
336 al. 2014), (ii) the occurrence of the aggressive noisy miner (Lane et al. 2014), or (iii) the
337 occurrence of a particular, functionally similar bird species (Lindenmayer et al. 2014b), yet
338 each of these variables relate to the target niche in different ways.

339 (i) Many studies have demonstrated the positive relationship between vegetation structure
340 and bird diversity (Cunningham et al. 2014; Recher 1969). Woody vegetation cover is
341 often correlated with woodland bird diversity, but the constraining factor is thought to
342 be structural complexity (MacArthur & MacArthur 1961), which increases habitat
343 availability and resources, and facilitates species co-occurrence.

344 (ii) Noisy miner birds are aggressive native species that harass smaller species present in
345 their territory (Mortelliti et al. 2016). This behaviour suppresses native bird diversity
346 in woodland patches where they occur (Lindenmayer et al. 2018). The constraining
347 mechanism here is competitive exclusion reducing co-occurrence (Lane et al. 2014;
348 Montague-Drake et al. 2011). Noisy miner effects on small birds tend to be stronger in
349 habitats with low structural complexity.

350 (iii) Individual bird species might also be used as predictors for the occurrence of other
351 species, including woodland birds of conservation concern (Lindenmayer et al.
352 2014b). The constraining mechanism here is hypothesised to be increasing co-
353 occurrence due to similarity in resource or habitat requirement traits, i.e. similarity in
354 niche constraints (Lambeck 1997; Nicholson et al. 2013).

355 Vegetation cover broadly constrains the distribution of bird assemblages by limiting habitat
356 availability, thus making vegetation cover a clear surrogate worthy of further investigation
357 (Ikin et al. 2016), particularly for spatial surrogacy applications. However, temporal changes
358 in vegetation extent occur over decadal timescales (particularly positive changes), thus
359 making it unsuitable for short-term surrogacy requirements. Patch-scale occurrence of noisy
360 miner birds is a good predictor of bird assemblage composition, with competitive exclusion
361 and aggressive behaviour constraining the presence of key woodland bird species of
362 conservation concern (Beggs et al. 2019; Montague-Drake et al. 2011). Noisy miners are
363 easily observed, and so are a potential surrogate for woodland bird diversity. However, patch-

364 scale colonisation and extinction dynamics of noisy miners, as well as context-dependence in
365 the impacts on smaller birds, make this bird suitable only for intra- or inter-annual scale
366 dynamics, and within-landscape scales (Beggs et al. 2019; Montague-Drake et al. 2011;
367 Mortelliti et al. 2016). Individual bird species that are functionally similar to woodland birds
368 of conservation concern (e.g. small, canopy-dwelling insectivores), should be constrained by
369 similar habitat or resource requirements – i.e. share similar niche characteristics. Yet the
370 biodiversity surrogacy paradox (Figure 1) challenges this idea. Similarly, hypothesis such as
371 the focal species approach (FSA) which proposes that management of the most range-
372 restricted or dispersal-limited species should, by default, cater to most other species, is also
373 flawed or no better than choosing species at random (Lindenmayer et al. 2014b). This
374 suggests one individual species is unlikely to be an appropriate surrogate for a suite of species
375 of conservation concern, unless that species strongly constrains the niche of many species
376 through biotic interactions (as per the noisy miner).

377

378 **Implications and future challenges**

379 We have described how aspects of the niche concept might be applied to the selection of
380 biodiversity surrogates. The use theory to predict which surrogates are likely to be effective in
381 a range of instances is difficult due to the variety of contexts and specific applications.
382 Nevertheless, the likelihood of success will improve if effort is directed towards surrogate
383 variables with clear constraining effects on the biodiversity target. Importantly, the absence of
384 ecological constraints will help to identify situations where surrogates are likely to be
385 *ineffective*. We suggest that a surrogate should be selected when there is a clear constraining
386 influence on a target species' distribution, abundance, or interactions. An approach to the
387 selection of surrogates that incorporates ecological constraints should provide a useful and
388 efficient shortcut to more robust surrogacy relationships. Given the amount of time and effort

389 needed to properly validate surrogates (Lindenmayer et al. 2015a), any conceptual or heuristic
390 tool that can help rule-out possible options *a priori* has the potential to reduce the cost of
391 establishing or updating biodiversity monitoring programs. By allowing those programs to
392 identify informative surrogates more quickly, this approach should reduce the probability of
393 poor biodiversity outcomes, such as failure to detect declines in threatened species.

394 A key challenge for broadly applying niche theory to surrogates is the issue of moving
395 from qualitative to quantitative investigation of constraints. We have discussed the role of
396 variability and scale in affecting surrogate selection, which represents a first step towards
397 these goals. Research on species distribution modelling has made substantial advances by
398 developing methods to estimate biotic and abiotic constraints on species distributions (e.g.
399 Booth et al. 2014; D'Amen et al. 2018; Elith et al. 2006). The methods used to generate
400 species distribution models are derived from regression (Renner & Warton 2013), so the
401 extent to which they represent mechanistic or correlative insights is open to debate (Kearney
402 et al. 2010). In contrast, theoretically derived methods for modelling constraints – such as the
403 maximum entropy theory of ecology (Harte 2011) – have yet to receive widespread
404 acceptance, or be tested for their predictive capacity (Xiao et al. 2015). A key problem with
405 investigating constraints is that different resources may be limiting in different environmental
406 contexts, restricting our capacity to transfer learning to new ecosystems (e.g. Pierson et al.
407 2015). Therefore, quantitatively characterizing the mechanisms that determine how species
408 respond to environmental variation is a major challenge for future research.

409 Conservation and management would benefit from future research that seeks to
410 understand which aspect of a niche are most fluid or context-dependent, particularly in
411 response to global change (e.g. Scheele et al. 2017). Integration of niche concepts and its
412 theoretical underpinnings with applied surrogacy problems will provide guidance to scientists
413 tasked with establishing surrogacy by showing how key theories might contradict

414 hypothesized surrogacy relationships and inflate the risk of failure. Theory concerning
415 ecological constraints has the potential to provide valuable shortcuts for improved
416 effectiveness of biodiversity monitoring and conservation.

417

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

428

429 **References**

- 430 Abrams, P. 1983. The theory of limiting similarity. *Annual Review of Ecology and*
431 *Systematics* **14**:359-376.
- 432 Adler, P. B., and J. M. Levine. 2007. Contrasting relationships between precipitation and
433 species richness in space and time. *Oikos* **116**:221-232.
- 434 Amarasekare, P. 2003. Competitive coexistence in spatially structured environments: a
435 synthesis. *Ecology Letters* **6**:1109-1122.
- 436 Araujo, M. B., and A. T. Peterson. 2012. Uses and misuses of bioclimatic envelope modeling.
437 *Ecology* **93**:1527-1539.
- 438 Austin, M. 2007. Species distribution models and ecological theory: A critical assessment and
439 some possible new approaches. *Ecological Modelling* **200**:1-19.

- 440 Azeria, E. T., D. Fortin, C. Hebert, P. Peres-Neto, D. Pothier, and J. C. Ruel. 2009. Using null
441 model analysis of species co-occurrences to deconstruct biodiversity patterns and
442 select indicator species. *Diversity and Distributions* **15**:958-971.
- 443 Barton, P., M. Evans, C. Sato, L. O'Loughlin, C. Foster, D. Florance, and D. Lindenmayer.
444 2019. Effects of livestock grazing on higher taxon and functional groupings of ants
445 and bird assemblages: a test of an explicit surrogate concept. *Ecological Indicators* **96**:
446 458-465.
- 447 Barton, P. S., J. C. Pierson, M. J. Westgate, P. W. Lane, and D. B. Lindenmayer. 2015.
448 Learning from clinical medicine to improve the use of surrogates in ecology. *Oikos*
449 **124**:391-398.
- 450 Barton, P. S., M. J. Westgate, P. W. Lane, C. MacGregor, and D. B. Lindenmayer. 2014.
451 Robustness of habitat-based surrogates of animal diversity: a multi-taxa comparison
452 over time. *Journal of Applied Ecology* **51**:1434–1443.
- 453 Beggs, R., A. Tulloch, J. Pierson, W. Blanchard, M. Crane, and D. B. Lindenmayer. 2019.
454 Patch-scale culls of an overabundant bird defeated by immediate recolonization.
455 *Ecological Applications*: e01846.
- 456 Belder, D. J., J. C. Pierson, K. Ikin, and D. B. Lindenmayer. 2018. Beyond pattern to process:
457 current themes and future directions for the conservation of woodland birds through
458 restoration plantings. *Wildlife Research* **45**:473-489.
- 459 Blonder, B., C. Lamanna, C. Violle, and B. J. Enquist. 2014. The n-dimensional
460 hypervolume. *Global Ecology and Biogeography* **23**:595-609.
- 461 Booth, T. H., H. A. Nix, J. R. Busby, and M. F. Hutchinson. 2014. BIOCLIM: the first
462 species distribution modelling package, its early applications and relevance to most
463 current MAXENT studies. *Diversity and Distributions* **20**:1-9.
- 464 Carmel, Y., Y. F. Suprunenko, W. E. Kunin, R. Kent, J. Belmaker, A. Bar-Massada, and S. J.
465 Cornell. 2017. Using exclusion rate to unify niche and neutral perspectives on
466 coexistence. *Oikos* **126**:1451-1458.
- 467 Caro, T. 2010. *Conservation by Proxy: Indicator, Umbrella, Keystone, Flagship, and Other*
468 *Surrogate Species*. . Island Press, Washington, DC.
- 469 Chase, J. M., & Leibold, M. A. 2003. *Ecological niches: linking classical and contemporary*
470 *approaches*. University of Chicago Press, Chicago.
- 471 Cunningham, R. B., D. B. Lindenmayer, P. S. Barton, K. Ikin, M. Crane, D. Michael, S.
472 Okada, P. Gibbons, and J. Stein. 2014. Cross-sectional and temporal relationships

473 between bird occupancy and vegetation cover at multiple spatial scales. *Ecological*
474 *Applications* **24**:1275-1288.

475 D'Amen, M., H. K. Mod, N. J. Gotelli, and A. Guisan. 2018. Disentangling biotic interactions,
476 environmental filters, and dispersal limitation as drivers of species co-occurrence.
477 *Ecography* **41**:1233-1244.

478 Danger, M., T. Daufresne, F. Lucas, S. Pissard, and G. Lacroix. 2008. Does Liebig's law of
479 the minimum scale up from species to communities? *Oikos* **117**:1741-1751.

480 der Boer, P. 1986. The present status of the competitive exclusion principle. *Trends in*
481 *Ecology & Evolution* **1**:25-28.

482 Driscoll, D. A., and C. Strong. 2018. Covariation of soil nutrients drives occurrence of exotic
483 and native plant species. *Journal of Applied Ecology* **55**:777-785.

484 Elith, J., C. H. Graham, R. P. Anderson, M. Dudik, S. Ferrier, A. Guisan, R. J. Hijmans, F.
485 Huettmann, J. R. Leathwick, A. Lehmann, J. Li, L. G. Lohmann, B. A. Loiselle, G.
486 Manion, C. Moritz, M. Nakamura, Y. Nakazawa, J. M. Overton, A. T. Peterson, S. J.
487 Phillips, K. Richardson, R. Scachetti-Pereira, R. E. Schapire, J. Soberon, S. Williams,
488 M. S. Wisz, and N. E. Zimmermann. 2006. Novel methods improve prediction of
489 species' distributions from occurrence data. *Ecography* **29**:129-151.

490 Fleishman, E., J. R. Thomson, R. Mac Nally, D. D. Murphy, and J. P. Fay. 2005. Using
491 indicator species to predict species richness of multiple taxonomic groups.
492 *Conservation Biology* **19**:1125-1137.

493 Gibb, H., and S. A. Cunningham. 2010. Revegetation of farmland restores function and
494 composition of epigaeic beetle assemblages. *Biological Conservation* **143**:677-687.

495 Gibbons, P., and D. B. Lindenmayer 2002. *Tree Hollows and Wildlife Conservation in*
496 *Australia*. CSIRO Publishing, Melbourne.

497 Godsoe, W., J. Jankowski, R. D. Holt, and D. Gravel. 2017. Integrating Biogeography with
498 Contemporary Niche Theory. *Trends in Ecology & Evolution* **32**:488-499.

499 Green, P. T., D. J. O'Dowd, K. L. Abbott, M. Jeffery, K. Retallick, and R. Mac Nally. 2011.
500 Invasional meltdown: Invader-invader mutualism facilitates a secondary invasion.
501 *Ecology* **92**:1758-1768.

502 Hall, C. A. S., J. A. Stanford, and F. R. Hauer. 1992. The distribution and abundance of
503 organisms as a consequence of energy balances along multiple environmental
504 gradients. *Oikos* **65**:377-390.

505 Hardin, G. 1960. The competitive exclusion principle. *Science* **131**:1292-1297.

506 Harte, J. 2011. Maximum Entropy and Ecology: A Theory of Abundance, Distribution, and
507 Energetics. . Oxford University Press, Oxford.

508 Hedwall, P. O., J. Bergh, and J. Brunet. 2017. Phosphorus and nitrogen co-limitation of forest
509 ground vegetation under elevated anthropogenic nitrogen deposition. *Oecologia*
510 **185**:317-326.

511 Heino, J. 2010. Are indicator groups and cross-taxon congruence useful for predicting
512 biodiversity in aquatic ecosystems? *Ecological Indicators* **10**:112-117.

513 Hunter Jr, M., M. Westgate, P. Barton, A. Calhoun, J. Pierson, A. Tulloch, M. Beger, C.
514 Branquinho, T. Caro, J. Gross, J. Heino, P. Lane, C. Longo, K. Martin, W. H.
515 McDowell, C. Mellin, H. Salo, and D. Lindenmayer. 2016. Two roles for ecological
516 surrogacy: Indicator surrogates and management surrogates. *Ecological Indicators*
517 **63**:121-125.

518 Hunter, M., M. Westgate, P. Barton, A. Calhoun, J. Pierson, A. Tulloch, M. Beger, C.
519 Branquinho, T. Caro, J. Gross, J. Heino, P. Lane, C. Longo, K. Martin, W. H.
520 McDowell, C. Mellin, H. Salo, and D. Lindenmayer. 2016. Two roles for ecological
521 surrogacy: Indicator surrogates and management surrogates. *Ecological Indicators*
522 **63**:121-125.

523 Hutchinson, G. E. 1957. Concluding remarks. . Cold Spring Harbour Symposium on
524 Quantitative Biology **22**:415–427.

525 Ikin, K., A. Tulloch, P. Gibbons, D. Ansell, J. Seddon, and D. Lindenmayer. 2016. Evaluating
526 complementary networks of restoration plantings for landscape-scale occurrence of
527 temporally dynamic species. *Conservation Biology* **30**:1027-1037.

528 Johansen, T., J. I. Westgaard, B. B. Seliussen, K. Nedreaas, G. Dahle, K. A. Glover, R.
529 Kvalsund, and A. Aglen. 2018. "Real-time" genetic monitoring of a commercial
530 fishery on the doorstep of an MPA reveals unique insights into the interaction between
531 coastal and migratory forms of the Atlantic cod. *Ices Journal of Marine Science*
532 **75**:1093-1104.

533 Kearney, M. R., B. A. Wintle, and W. P. Porter. 2010. Correlative and mechanistic models of
534 species distribution provide congruent forecasts under climate change. *Conservation*
535 *Letters* **3**:203-213.

536 Lambeck, R. J. 1997. Focal species: A multi-species umbrella for nature conservation.
537 *Conservation Biology* **11**:849-856.

538 Lane, P. W., D. B. Lindenmayer, P. S. Barton, W. Blanchard, and M. J. Westgate. 2014.
539 Visualization of species pairwise associations: a case study of surrogacy in bird
540 assemblages. *Ecology and Evolution* **4**:3279-3289.

541 Lindenmayer, D., J. Pierson, P. Barton, M. Beger, C. Branquinho, A. Calhoun, T. Caro, H.
542 Greig, J. Gross, J. Heino, M. Hunter, P. Lane, C. Longo, K. Martin, W. H. McDowell,
543 C. Mellin, H. Salo, A. Tulloch, and M. Westgate. 2015a. A new framework for
544 selecting environmental surrogates. *Science of The Total Environment* **538**:1029-
545 1038.

546 Lindenmayer, D. B., P. S. Barton, P. W. Lane, M. J. Westgate, L. McBurney, D. Blair, P.
547 Gibbons, and G. E. Likens. 2014a. An Empirical Assessment and Comparison of
548 Species-Based and Habitat-Based Surrogates: A Case Study of Forest Vertebrates and
549 Large Old Trees. *Plos One* **9**.

550 Lindenmayer, D. B., P. S. Barton, and J. Pierson 2015b. Indicators and surrogates of
551 biodiversity and environmental change. CSIRO Publishing, Clayton South, Australia.

552 Lindenmayer, D. B., W. Blanchard, M. Crane, D. Michael, and D. Florance. 2018. Size or
553 quality. What matters in vegetation restoration for bird biodiversity in endangered
554 temperate woodlands? *Austral Ecology* **43**:798-806.

555 Lindenmayer, D. B., P. W. Lane, P. S. Barton, M. Crane, K. Ikin, D. Michael, and S. Okada.
556 2016. Long-term bird colonization and turnover in restored woodlands. *Biodiversity
557 and Conservation* **25**:1587-1603.

558 Lindenmayer, D. B., P. W. Lane, M. J. Westgate, M. Crane, D. Michael, S. Okada, and P. S.
559 Barton. 2014b. An Empirical Assessment of the Focal Species Hypothesis.
560 *Conservation Biology* **28**:1594-1603.

561 Lindenmayer, D. B., and G. E. Likens. 2011. Direct measurement versus surrogate indicator
562 species for evaluating environmental change and biodiversity loss. *Ecosystems* **14**:47-
563 59.

564 Lovell, S., M. Hamer, R. Slotow, and D. Herbert. 2007. Assessment of congruency across
565 invertebrate taxa and taxonomic levels to identify potential surrogates. *Biological
566 Conservation* **139**:113-125.

567 Lundholm, J. T., and D. W. Larson. 2004. Dominance as an overlooked measure of invader
568 success. *Biological Invasions* **6**:505–510.

569 Lunt, I. D., D. J. Eldridge, J. W. Morgan, and G. B. Witt. 2007. A framework to predict the
570 effects of livestock grazing and grazing exclusion on conservation values in natural
571 ecosystems in Australia. *Australian Journal of Botany* **55**:401-415.

572 MacArthur, R. H., and J. W. MacArthur. 1961. On bird species diversity. *Ecology* **42**:594-
573 598.

574 Mackey, B. G., and D. B. Lindenmayer. 2001. Towards a hierarchical framework for
575 modelling the spatial distribution of animals. *Journal of Biogeography* **28**:1147-1166.

576 Manzoni, S., J. P. Schimel, and A. Porporato. 2012. Responses of soil microbial communities
577 to water stress: results from a meta-analysis. *Ecology* **93**:930-938.

578 Margules, C. R., and R. L. Pressey. 2000. Systematic conservation planning. *Nature* **405**:243-
579 253.

580 McArthur, M. A., B. P. Brooke, R. Przeslawski, D. A. Ryan, V. L. Lucieer, S. Nichol, A. W.
581 McCallum, C. Mellin, I. D. Cresswell, and L. C. Radke. 2010. On the use of abiotic
582 surrogates to describe marine benthic biodiversity. *Estuarine Coastal and Shelf*
583 *Science* **88**:21-32.

584 McGeoch, M. A. 1998. The selection, testing and application of terrestrial insects as
585 bioindicators. *Biological Reviews* **73**:181-201.

586 McGeoch, M. A., S. H. M. Butchart, D. Spear, E. Marais, E. J. Kleynhans, A. Symes, J.
587 Chanson, and M. Hoffmann. 2010. Global indicators of biological invasion: species
588 numbers, biodiversity impact and policy responses. *Diversity and Distributions* **16**:95-
589 108.

590 McIntyre, S., R. Cunningham, C. Donnelly, and A. Manning. 2015. Restoration of eucalypt
591 grassy woodland: effects of experimental interventions on ground-layer vegetation.
592 *Australian Journal of Botany* **62**:570-579.

593 McIntyre, S., and S. Lavorel. 1994. Predicting richness of native, rare, and exotic plants in
594 response to habitat and disturbance variables across a variegated landscape.
595 *Conservation Biology* **8**:521-531.

596 Mellin, C., S. Delean, J. Caley, G. Edgar, M. Meekan, R. Pitcher, R. Przeslawski, A.
597 Williams, and C. Bradshaw. 2011. Effectiveness of Biological Surrogates for
598 Predicting Patterns of Marine Biodiversity: A Global Meta-Analysis. *PLoS ONE* **6**.

599 Montague-Drake, R., D. B. Lindenmayer, R. B. Cunningham, and J. Stein. 2011. A reverse
600 keystone species affects the landscape distribution of woodland avifauna: a case study

601 using the Noisy Miner (*Manorina melanocephala*) and other Australian birds.
602 Landscape Ecology **26**:1383-1394.

603 Mortelliti, A., K. Ikin, A. I. T. Tulloch, R. Cunningham, J. Stein, D. Michael, and D. B.
604 Lindenmayer. 2016. Surviving with a resident despot: do revegetated patches act as
605 refuges from the effects of the noisy miner (*Manorina melanocephala*) in a highly
606 fragmented landscape? Diversity and Distributions **22**:770-782.

607 Mulder, C., and J. J. Elser. 2009. Soil acidity, ecological stoichiometry and allometric scaling
608 in grassland food webs. Global Change Biology **15**: 2730-2738.

609 Muller, F., and R. Lenz. 2006. Ecological indicators: theoretical fundamentals of consistent
610 applications in environmental management. Ecological Indicators **6**:1-5.

611 Neeson, T. M., and Y. Mandelik. 2014. Pairwise measures of species co-occurrence for
612 choosing indicator species and quantifying overlap. Ecological Indicators **45**:721-727.

613 Nicholson, E., D. B. Lindenmayer, K. Frank, and H. P. Possingham. 2013. Testing the focal
614 species approach to making conservation decisions for species persistence. Diversity
615 and Distributions **19**:530-540.

616 Niemi, G. J., and M. E. McDonald. 2004. Application of ecological indicators. Annual
617 Review of Ecology Evolution and Systematics **35**:89-111.

618 Noss, R. F. 1990. Indicators for monitoring biodiversity: A hierarchical approach.
619 Conservation Biology **4**:355-364.

620 O'Loughlin, L. S., and P. T. Green. 2017. Secondary invasion: When invasion success is
621 contingent on other invaders altering the properties of recipient ecosystems. Ecology
622 and Evolution **7**:7628-7637.

623 O'Loughlin, L. S., D. B. Lindenmayer, M. D. Smith, M. R. Willig, A. K. Knapp, K.
624 Cuddington, A. Hastings, C. N. Foster, C. F. Sato, M. J. Westgate, and P. S. Barton.
625 2018. Surrogates Underpin Ecological Understanding and Practice. Bioscience
626 **68**:640-642.

627 Parravicini, V., E. Azzurro, M. Kulbicki, and J. Belmaker. 2015. Niche shift can impair the
628 ability to predict invasion risk in the marine realm: an illustration using Mediterranean
629 fish invaders. Ecology Letters **18**:246-253.

630 Pierson, J. C., P. S. Barton, P. W. Lane, and D. B. Lindenmayer. 2015. Can habitat surrogates
631 predict the response of target species to landscape change? Biological Conservation
632 **184**:1-10.

- 633 Pulliam, H. R. 2000. On the relationship between niche and distribution. *Ecology Letters*
634 **3**:349-361.
- 635 Recher, H. F. 1969. Bird species diversity and habitat diversity in Australia and North
636 America. *American Naturalist* **103**:75-80.
- 637 Renner, I. W., and D. I. Warton. 2013. Equivalence of MAXENT and Poisson Point Process
638 Models for Species Distribution Modeling in Ecology. *Biometrics* **69**:274-281.
- 639 Rodrigues, A. S. L., and T. M. Brooks. 2007. Shortcuts for biodiversity conservation
640 planning: the effectiveness of surrogates. *Annual Review of Ecology Evolution and*
641 *Systematics* **38**:713-737.
- 642 Sætersdal, M., and I. Gjerde. 2011. Prioritising conservation areas using species surrogate
643 measures: consistent with ecological theory? *Journal of Applied Ecology* **48**:1236-
644 1240.
- 645 Scheele, B. C., C. N. Foster, S. C. Banks, and D. B. Lindenmayer. 2017. Niche Contractions
646 in Declining Species: Mechanisms and Consequences. *Trends in Ecology & Evolution*
647 **32**:346-355.
- 648 Scheiner, S. M., and M. R. Willig 2011. *The theory of ecology*. The University of Chicago
649 Press, Chicago.
- 650 Schelfhout, S., A. de Schrijver, S. de Bolle, L. de Gelder, A. Demey, T. Du Pre, and J.
651 Mertens. 2015. Phosphorus mining for ecological restoration on former agricultural
652 land. *Restoration Ecology* **23**:842–851.
- 653 Shea, K., and P. Chesson. 2002. Community ecology theory as a framework for biological
654 invasions. *Trends in Ecology & Evolution* **17**:170-176.
- 655 Simberloff, D., and B. Von Holle. 1999. Positive interactions of nonindigenous species:
656 invasional meltdown? *Biological Invasions* **1**:21–32.
- 657 Soons, M. B., M. M. Hefting, E. Dorland, L. P. M. Lamers, C. Versteeg, and R. Bobbink.
658 2017. Nitrogen effects on plant species richness in herbaceous communities are more
659 widespread and stronger than those of phosphorus. *Biological Conservation* **212**:390-
660 397.
- 661 Thomas, W. 1929. Balanced fertilizers and Liebig's law of the minimum. *Science* **70**:382-384.
- 662 Tilman, D. 1990. Constraints and tradeoffs - toward a predictive theory of competition and
663 succession. *Oikos* **58**:3-15.

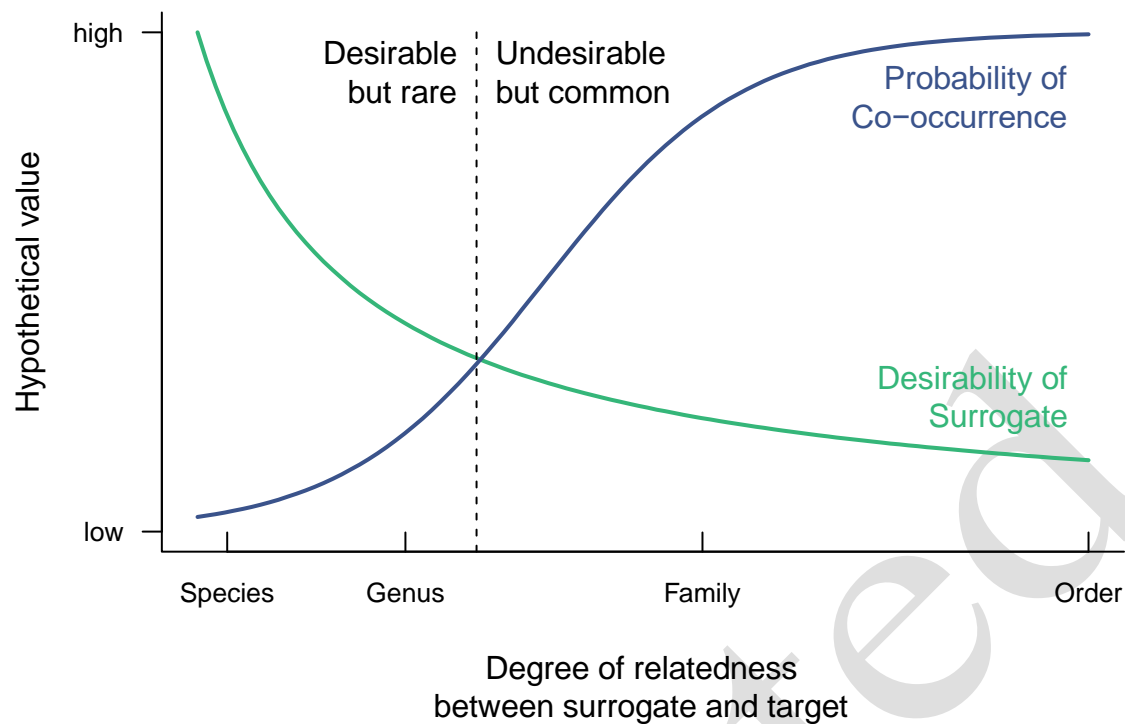
- 664 van Oudenhoven, A. P., K. Petz, R. Alkemade, L. Hein, and R. S. de Groot. 2012. Framework
665 for systematic indicator selection to assess effects of land management on ecosystem
666 services. *Ecological Indicators* **21**:110-122.
- 667 Westgate, M. J., P. S. Barton, P. W. Lane, and D. B. Lindenmayer. 2014. Global meta-
668 analysis reveals low consistency of biodiversity congruence relationships. *Nature*
669 *Communications* **5**.
- 670 Westgate, M. J., A. I. T. Tulloch, P. S. Barton, J. C. Pierson, and D. B. Lindenmayer. 2017.
671 Optimal taxonomic groups for biodiversity assessment: a meta-analytic approach.
672 *Ecography* **40**:539-548.
- 673 Xiao, X., D. J. McGlenn, and E. P. White. 2015. A Strong Test of the Maximum Entropy
674 Theory of Ecology. *American Naturalist* **185**:E70-80.
- 675 Yong, D. L., P. S. Barton, K. Ikin, M. J. Evans, M. Crane, S. Okada, S. A. Cunningham, and
676 D. B. Lindenmayer. 2018. Cross-taxonomic surrogates for biodiversity conservation in
677 human modified landscapes – a multi-taxa approach. *Biological Conservation*
678 **224**:336-346.
- 679

680 **Table 1.** Three kinds of ecological phenomena that fall under the niche concept, and could
681 contribute to the establishment of *a priori* expectations for when surrogate-target relationships
682 are plausible or not. All three phenomena and their limiting parameters will interact to define
683 a species niche via key mechanisms, thus providing a boundary around where a surrogate will
684 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

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686



687

688 **Figure 1. The trade-off between surrogate desirability and probability of co-occurrence**

689 **with the target species.** A theoretically desirable species-based surrogate is identical to the

690 target species in all ways, except with regard to observability, and this is likely to be more

691 true the closer their relatedness. Yet such species are unlikely to exist, and are contrary to

692 predictions of the competitive exclusion principle. Thus, a tradeoff between surrogate

693 desirability and probability of co-occurrence lead to the prediction of intermediate levels of

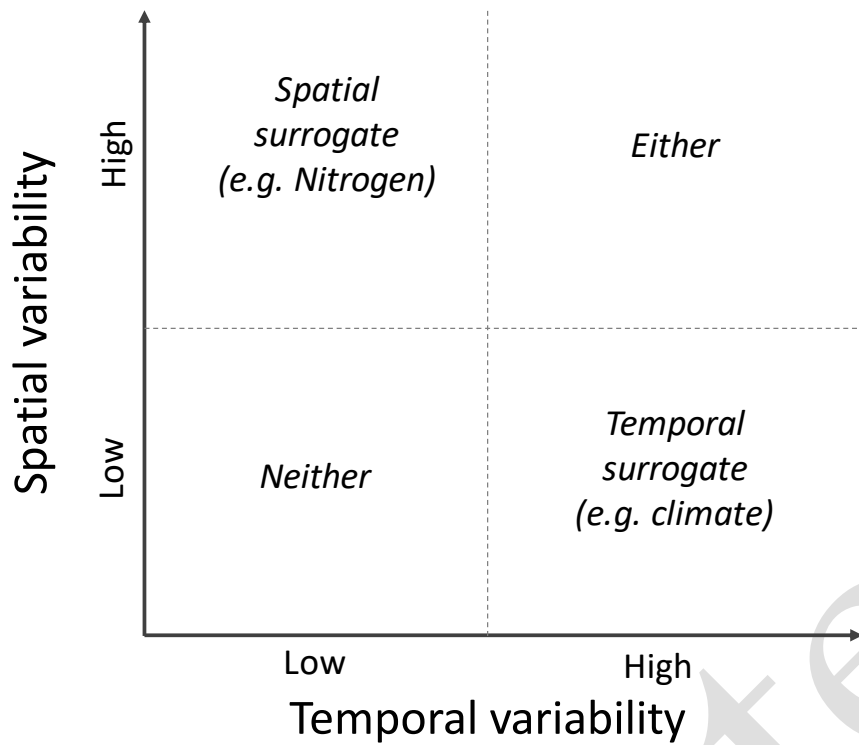
694 relatedness between effective targets and surrogates. We term this problem the “biotic

695 surrogacy paradox” because the likelihood that two co-occurring species will be identical in

696 all attributes except observability is relatively low.

697

698



699

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

706