

1 Extinction rate has a complex and non-linear relationship with area

2

3 **Authors:** Petr Keil^{1,2}, Juliano S. Cabral^{1,2,3}, Jonathan Chase^{1,4}, Ines S. Martins¹, Felix May^{1,5},
4 Henrique M. Pereira^{1,4,6} & Marten Winter^{1,4}

5

6 **Author affiliations:**

7 1. German Centre for Integrative Biodiversity Research (iDiv), Halle-Jena-Leipzig, Deutscher
8 Platz 5e, 04103 Leipzig, Germany

9 2. Institute of Biology, Leipzig University, Johannisallee 21, 04103 Leipzig, Germany

10 3. Ecosystem Modeling, Center for Computational and Theoretical Biology (CCTB), University
11 of Würzburg, Germany

12 4. Institute of Biology, Martin Luther University Halle-Wittenberg, Am Kirchtor 1, 06108 Halle
13 (Saale), Germany

14 5. Institute of Computer Science, Martin-Luther University Halle-Wittenberg, 06099 Halle
15 (Saale), Germany

16 6. Cátedra Infraestruturas de Portugal-Biodiversidade, CIBIO/InBIO, Universidade do Porto,
17 Campus Agrário de Vairão, 4485-661 Vairão, Portugal

18

19 **Key words:** Anthropocene, continental, grain, habitat loss, island biogeography, local, mass
20 extinction, MAUP, metapopulation, occupancy, patch, resolution.

21

22 **Manuscript type:** Concepts

23 **Running title:** Spatial scaling of extinction rates

24 **Correspondence:** Petr Keil, pkeil@seznam.cz

25 # of words in Abstract: 299

26 # of words in the Main text: 4871

27 # of references: 54

28 ABSTRACT

29 **Aim.** Biodiversity loss, measured as count of extinction events, is a key component of biodiversity
30 change, and can significantly impact ecosystem services. However, estimation of the loss has
31 focused mostly on per-species extinction rates measured over limited numbers of spatial scales,
32 with no theory linking small-scale extirpations with global extinctions. Here we provide such link
33 by introducing the relationship between area and per-species probability of extinction (PxAR) and
34 between area and count of realized extinction events in that area (NxAR). We show theoretical
35 and empirical forms of these relationships, and we discuss their role in perception and estimation
36 of the current extinction crisis.

37 **Location.** USA, Europe, Czech Republic, Barro Colorado Island

38 **Methods.** We derived the expected forms of PxAR and NxAR from a range of theoretical
39 frameworks based on theory of island biogeography, neutral models, and species-area
40 relationships. We constructed PxAR and NxAR in five empirical datasets on butterflies, plants,
41 trees and birds, collected over range of spatial scales.

42 **Results.** Both the theoretical arguments and empirical data support monotonically decreasing
43 PxAR, i.e. per-species extinction probability decreasing with increasing area; however, we also
44 report a rare theoretical possibility of locally increasing PxAR. In contrast, both theory and data
45 revealed complex NxAR, i.e. counts of extinction events follow variety of relationships with area,
46 including nonlinear unimodal, multimodal and U-shaped relationships, depending on region and
47 taxon.

48 **Main conclusions.** The uncovered wealth of forms of NxAR can explain why biodiversity change
49 (the net outcome of losses and gains) also appears scale-dependent. Furthermore, the complex
50 scale dependence of PxAR and NxAR means that global extinctions indicate little about local
51 extirpations, and vice versa. Hence, effort should be made to understand and report extinction
52 crisis as a scale-dependent problem. In this effort, estimation of scaling relationships such as PxAR
53 and NxAR should be central.

54 INTRODUCTION

55 Biodiversity loss as a result of species extinctions is potentially one of the most serious
56 environmental problems we face, and estimates of its rate and magnitude are needed for
57 informed decisions and conservation policy. The Aichi target 12 under the Strategic Plan for
58 Biodiversity 2011-2020 (www.cbd.int/sp/targets/) aims at preventing extinctions of known
59 threatened species, and all regional and the upcoming global IPBES assessments
60 (<http://www.ipbes.net/>) are committed to report past, present, and future trends of biodiversity.
61 Given the importance of assessing extinction rates, it is striking that there are major unresolved
62 issues related to its spatial scaling and metrics.

63 So far, large-scale extinction science has focused on estimation of per-species extinction
64 rates, measured as number of extinctions per million species-years (E/MSY) (Barnosky *et al.*, 2011;
65 Proenca & Pereira, 2013; Pimm *et al.*, 2014). Similar metrics have been used in island
66 biogeography (Wu & Vankat, 1995) and metapopulation biology (Hanski, 1991), where they are
67 termed per-species extinction rate or per-species extinction probability. All these metrics are
68 independent on absolute number of species (S), which makes them comparable across epochs,
69 regions, and taxa.

70 However, apart from the per-species rates, absolute counts of extinction events per unit of
71 time (hereafter N_X) should also be of major interest, since they affect species richness S – a
72 quantity that is at the core of basic biodiversity science (Gaston, 2000) and which has been
73 associated with ecosystem services (Hooper *et al.*, 2005; Cardinale *et al.*, 2012). Recently, a
74 number of authors have been particularly interested in understanding how S changes through
75 time (hereafter ΔS), with debate as to whether it is declining at all scales, or instead has more
76 variable outcomes (Vellend *et al.*, 2013; Dornelas *et al.*, 2014; McGill *et al.*, 2015). However,
77 compared to the per-species extinction rates, N_X has rarely been calculated [but see Tedesco *et al.*
78 (2013)].

79 The role of spatial scale is a fundamental, but often overlooked, aspect of understanding
80 patterns of extinct rates. Current extinction rates have been estimated at global and continental
81 extents (Barnosky *et al.*, 2011; Alroy, 2015), and global extinctions are indeed crucial since they

82 are irreversible. Yet, any global extinction is preceded by a series of local and regional extinctions
83 (a.k.a. *extirpations*), which often have ecological or iconic significance, or both.

84 For example, although Danube Clouded Yellow (*Colias myrmidone*, Esper 1780) still
85 survives in some parts of Europe, the butterfly was extirpated from the Czech Republic in 2006,
86 and this local extinction event triggered considerable attention for its implications for landscape
87 management across the whole continent (Konvicka *et al.*, 2007). More prominent examples
88 include extirpations of the bison (Isenberg, 2001) or lion (*Panthera leo*, Linnaeus 1758) (Riggio *et*
89 *al.*, 2012) – local loss of such keystone species has direct impact on local ecosystem services, while
90 country-wide extirpations matter because countries are obliged to protect their species either
91 through international treaties (e.g. Aichi targets) or through national legislations. Clearly, focusing
92 solely at the global extinctions can underestimate extirpations at smaller scales, and vice versa,
93 and hence there is a need to assess the current extinction crisis at multiple spatial scales
94 simultaneously.

95 In this Concept paper we propose a new way of looking at extinction rates to address the
96 issues of metric and scale of extinction. Specifically, we propose to jointly consider how both the
97 per-species extinction rates P_X and the counts of extinctions N_X scale with area over which they
98 are observed. We first provide several theoretical expectations for the scaling of P_X and N_X
99 derived from the theory of island biogeography, from neutral theory of biodiversity, and from a
100 simple model based on species-area relationship. We then demonstrate the scaling using five
101 empirical datasets, covering local, regional and continental scales. We show that while P_X mostly
102 decreases with area, N_X follows complex relationships with area; the key finding is that N_X in small
103 areas can be lower, but also higher, than N_X in large areas, making it impossible to get the
104 complete picture of the current extinction crisis from looking at the global extinctions only.

105

106 **TERMS AND DEFINITIONS**

107 We classify an event as *extinction* when a species disappears in the focal area (present at time 1,
108 but absent at time 2), regardless to whether it still survives outside of the area. When the focal
109 area is the entire world, an extinction event becomes a *global extinction*. Thus, a local or regional

110 extinction event may also be called local or regional *extirpation*, if the species still prevails outside
111 of that locality or region.

112 We use P_X for *mean per-species probability of extinction* in a given area A , and N_X for
113 *mean number of extinctions* in A during a specified time period. We use *mean* because we
114 consider P_X and N_X as means of probability distributions over multiple species that occur in a
115 given area. Thus, our N_X is similar to E/t metric described by Proenca & Pereira (2013), and our
116 P_X is similar to their $(E/S)/t$ metric. We use PxAR to describe the relationship between P_X and A ,
117 and we use NxAR to describe the relationship between N_X and A . We shall note here that PxAR
118 has been referred to as an *extinction-area relationship* in Hugueny et al. (2011). This term is also
119 used by Kitzes & Harte (2014) for a different concept: the probability of extinction conditional on
120 the area of lost habitat (instead of the size of the sampled area). To prevent confusion, we avoid
121 the term extinction-area relationship altogether.

122 We use *spatial scale* as a synonym for *sampling area, resolution, and/or grain*; that is, the
123 area (A) of an observation window (grid cell, country) in which extinction events are counted. We
124 focus exclusively on spatial scaling, disregarding the role of *temporal scale* (i.e., the length of
125 temporal window over which extinctions are counted (Barnosky *et al.*, 2011). We circumvent the
126 problem by assuming the temporal window approximately or exactly constant in each individual
127 dataset or in a particular theoretical argument. However, the temporal scaling of extinction rates
128 is a critical issue that should be addressed in future research.

129 Some existing work on spatial scaling of extinction rates is rooted in island biogeography
130 and metapopulation theory, where extinction rates are calculated over non-nested islands or
131 habitat patches of varying size (Scheiner, 2003). We call these *island systems*. In contrast, almost
132 no attention has been focused on spatial scaling of extinction rates in continuous regions, in which
133 a region is overlaid by a system of nested grids of increasing resolution (Storch *et al.*, 2012; Keil *et*
134 *al.*, 2015), and P_X and N_X are calculated at each resolution. Grid cells in the grid can be either
135 regular rectangles, or irregular administrative divisions, but are always aggregated (up-scaled) in a
136 strictly nested way, and hence we call them *nested systems* – as such they are similar to the Type I
137 species-area curves of (Scheiner, 2003).

138 To avoid confusion, we note that our treatment of spatial scaling of extinction rates is
139 fundamentally different from approaches using the *Endemics-Area Relationship* (EAR) and
140 backward *Species-Area Relationship* (SAR) to predict extinction rates due to habitable area loss (He

141 & Hubbell, 2011; Pimm *et al.*, 2014; Keil *et al.*, 2015) (Fig. 1). The EAR- describes a hypothetical
142 impact one specific driver of extinction; loss of habitable area. In contrast, PxAR and NxAR provide
143 spatial scaling of a *dynamic* process of the actual realized extinctions in a given area of
144 observational window A and over given temporal window, without regard to the causes of
145 extinction (habitat loss, global warming, pathogens, hunting, or invasions; see Fig. 1 for details).

146

147 THEORETICAL EXPECTATIONS

148 We offer several complementary ways of reasoning, showing that N_X and P_X should be expected
149 to follow a wealth of functional responses to A . These are not meant as theories to be tested per
150 se; rather, they are different ways to think about spatial scaling of extinctions in different systems
151 and over different spatial grains and extents.

152 *Scaling of per-species extinction probability P_X*

153 Here we show that, theoretically, the relationship between P_X and A should mostly be negative,
154 with some exceptions.

155 *Island systems.* – There is a general expectation that per-species probability of extinction
156 (P_X) decreases with area of an island. This is supported both empirically (Diamond, 1984; Quinn &
157 Hastings, 1987; Hugueny *et al.*, 2011) and theoretically (Hanski & Ovaskainen, 2000). The
158 paradigm is that larger areas can host larger populations, which are less likely to perish due to
159 environmental and demographic stochasticity (Lande, 1993). The latter mechanism is implicitly
160 assumed in the equilibrium theory of island biogeography (ETIB) (MacArthur & Wilson, 1967) and
161 in spatially realistic models in metapopulation ecology (Hanski & Ovaskainen, 2000; Hanski, 2001).
162 An example of a specific scaling function assumed in metapopulation ecology is a hyperbola $P_X =$
163 e/A , where A is a patch area and e is a constant reflecting both population density in a unit of
164 area and rate of reproduction per unit of time (Hanski & Ovaskainen, 2000), with the assumption
165 that extinction risk scales as an inverse of population size in taxa affected by moderate
166 environmental stochasticity (Lande, 1993), and population size is proportional to area of habitat
167 patch or island.

168 *Neutral models.* – The mentioned hyperbolically decreasing PxAR has also been described
169 in neutral models (Ricklefs, 2006; Halley & Iwasa, 2011). However, Ricklefs (2006) only examined
170 extinction rates at the scale of the entire metacommunity, while Halley & Iwasa (2011)

171 disregarded the potentially important role of immigration, and they generated their abundance
172 distributions by ad-hoc mechanisms, not by the neutral model itself. To get a hint of possible
173 forms of P_X in neutrally modeled local communities with immigration, we simulated from a
174 neutral model presented by Hubbell (2001), which we parametrized using the classical
175 combination of parameters used in Hubbell (2001) (page 135): $\theta = 50$, $J = 5 \times 10^5$, local
176 mortality rate $D = 0.1$ and immigration rate $m = 0.1$. We simulated 50 local communities, each
177 with 10, 100, 1,000 and 10,000 individuals, which we converted to area [ha] assuming the density
178 of 24,341 individuals per 50 ha (Hubbell, 2001). We initialized the local community with a single
179 species, discarded the first 1,000 simulation steps as burn-in, and looked at P_X after 5 generations
180 and also after 50 generations (Fig. 2).

181 We found that P_X decreased with area of the local community after 50 generations, but
182 the decrease was initially shallower than expected in a hyperbolic decay proposed by Ricklefs
183 (2006) and Halley & Iwasa (2011) (Fig. 2a). This suggest the role of immigration in reducing local
184 P_X , since immigration is what is missing in the neutral drift models of Ricklefs (2006) and Halley &
185 Iwasa (2011). Surprisingly, the P_X was hump-shaped when P_X was measured over only 5
186 generations (Fig. 2a), highlighting the crucial role of temporal scale, which we otherwise ignore in
187 this paper.

188 *Heterogeneous nested non-equilibrium systems.* – The mentioned assumption of
189 proportional relationship between population size and area is reasonable when focusing solely on
190 area of homogeneous patches of habitats with randomly or regularly distributed populations
191 within habitats. However, the assumption falls short in nested systems, where observation
192 windows contain multiple habitats, where populations are spatially aggregated, and where the
193 magnitude of the aggregation varies with scale. In such situation we can express P_X at a given
194 scale as the proportional loss of occupied grid cells of area A (Fig. 3a) – an idea that builds on the
195 framework outlined by Kunin (1998) and later applied to temporal dynamics of species
196 distributions by Wilson et al. (2004). Our novel point here is that P_X calculated in nested systems

197 can decrease, but also *increase* with A , depending on the range of A values that is examined, and
198 depending on where exactly are populations lost (see Fig. 3a for full exposition).

199 **Scaling of counts of extinctions N_X**

200 Here we show that the relationship between N_X and A can follow wealth of functional forms,
201 including negative, positive, or non-linear.

202 *Island systems.* – The equilibrium theory of island biogeography (MacArthur & Wilson,
203 1967) can be used to derive the NxAR. The ETIB-based model considers equilibrium extinction
204 rate, i.e. extinctions are in balance with species gains. According to ETIB, the equilibrium rate N_X
205 is:

$$206 \quad N_X = \frac{P_X P_I S_{pool}}{P_X + P_E} \quad (1)$$

207 Where S_{pool} is number of species in species pool, P_I is per-species probability of
208 immigration, and P_E is per-species probability of extinction (Wu & Vankat, 1995). We assume that
209 $P_X = 0.01/A$ (the hyperbola mentioned above). Critical is the relationship between P_I and A ,
210 which we present in two forms: (1) P_I is *constant* (Fig. 4a) and independent on A . In the simplest
211 formulation of ETIB, there is no relationship between P_I and A . The resulting NxAR in this case is
212 always monotonically decreasing (Fig. 4a). (2) P_I *increases with area*. In this scenario, increasing
213 area means lower P_I as before, but also higher immigration rates because larger areas are larger
214 targets (Lomolino *et al.*, 2010); hence, we introduce a positive linear proportional relationship
215 between P_I and A . This generates a hump-shaped NxAR (Fig. 4b).

216 Other NxAR shapes are likely to emerge from different relationships between A and P_X , P_I
217 and S_{pool} . Additionally, limiting the range of areas that are being observed (x-axis of the NxAR
218 plot) can also lead to a monotonically increasing or decreasing NxAR. Therefore, in the ETIB model,
219 various shapes of NxAR are produced by the interplay between per-species extinction probability
220 with per-species immigration and the size of the species pool.

221 *Neutral models.* – We are not aware of any literature examining NxAR in neutral models.
222 Our parametrization of the spatially implicit neutral model [see Hubbell (2001) and the previous

223 section] predicts positive relationship between N_x and area of local community, measured over
224 the limited range of spatial and temporal scales that we examined (Fig. 2b).

225 *Heterogeneous nested non-equilibrium systems.* – Here we show two lines of reasoning,
226 both leading to a wealth of NxAR shapes.

227 First, let us consider a nested system and a simple verbal qualitative model. Imagine two
228 scenarios that lead to different NxARs (Fig. 3b): (1) A continent loses several geographically
229 extremely restricted species, and nothing happens to the widespread species. The localized
230 extinctions will have almost no effect on N_x at small scale, but will increase N_x at the continental
231 scale. In this scenario, N_x increases with A . (2) There are range contractions in several widespread
232 species, but no species goes completely lost from the continent. This results in high N_x at small
233 scale, but no extinctions at the continental scale. Here, N_x decreases with A (Fig. 3b).

234 In the second line of reasoning, we can assume that mean species richness S at each grain
235 follows the *species-area relationship* (SAR), for example a power law (Fig. 5a). We then invoke a
236 one-time ad-hoc stress event during which each species at each location either goes extinct or
237 survives. We assume that, on average, the per-species extinction probability (P_E) monotonically
238 decreases with A , but that monotonic decreases can have various forms (Fig. 5b). In such system,
239 NxAR is obtained by multiplication of SAR with PxAR, or formally: If $S = f(A)$ and $P_x = g(A)$, then
240 number of extinctions (N_x) per area of observation window (A) is $N_x = f(A)g(A)$. As a result, the
241 emerging shapes of NxAR can vary from increasing to hump-shaped (Fig. 5c), with the possibility of
242 observing monotonically decreasing NxAR over limited extents of A (Fig. 5c).

243

244 **EMPIRICAL EVALUATION**

245 We calculated empirical NxAR and PxAR using five datasets, with the aim to cover wide range of
246 geographic extents and types of temporal dynamics. We focus on terrestrial mainland nested
247 systems, mostly due to our own research background, and because there already is some
248 literature on empirical extinction rates in island-like systems (Diamond, 1984; Quinn & Hastings,
249 1987; Hugueny *et al.*, 2011; Tedesco *et al.*, 2013), although the literature does not cover NxAR.
250 Hence, an assessment of empirical PxAR and NxAR on islands is an important future task.

251 **Data**

252 *European butterflies.* – We extracted data on extinction events and on the extant species of
253 *butterflies* (Lepidoptera: Rhopalocera) in European administrative areas during the last ~ 100 years
254 from Red data book of European butterflies (Van Swaay & Warren, 1999); specifically, we
255 considered species extinct in a given country if its status in Van Swaay & Warren (1999) Appendix
256 6 table was “Ex”.

257 *European plants.* – We extracted the same kind of data on extinctions (between AD 1500
258 and 2009) and extant species of European *vascular plants* from Winter et al. (2009), available
259 upon request from MW. Note that the plant data cover different extent and administrative units
260 than the butterfly data (Fig. 6).

261 *United States plants.* – We used data on the extant native species of *Plantae* (ferns,
262 conifers and flowering plants) in 47 states of the USA (i.e. excluding Hawaii, Alaska, and
263 Washington DC) provided in the BONAP’s North American Plant Atlas (Kartesz, 1999); for an
264 example use of these data in a quantitative analysis see Winter et al. (2010). We used data on
265 contemporary (AD 1500 - 2009) extinction events also at the level of individual states. This
266 information is provided by NatureServe (www.natureserve.org) and its network of Natural
267 Heritage member programs, a leading source of information about rare and endangered species,
268 and threatened ecosystems (NatureServe, 2016). The data provided by NatureServe are for
269 informational purposes, and should not be considered a definitive statement on the presence or
270 absence of biological elements at any given location. Site-specific projects or activities should be
271 reviewed for potential environmental impacts with appropriate regulatory agencies.

272 *Czech birds.* – We used digitized presences and absences of breeding birds recorded in a
273 regular grid of 11.7 x 11.7 km grid cells in the Czech Republic, and covering two temporal periods:
274 1985-1989 (Šťastný *et al.*, 1997) with 56,780 species-per-cell incidences, and 2001-2003 (Šťastný
275 *et al.*, 2006) with 59,354 species-per-cell incidences.

276 *Barro Colorado 50ha plot.* – We used tree data from 50-ha forest plot from Barro Colorado
277 Island (BCI), Panama (Condit, 1998; Hubbell *et al.*, 1999, 2005). We only included trees with ≥ 10
278 cm DBH, and we compared two temporal snapshots that are 25 years apart. The results were

279 qualitatively similar when the temporal lag between the two snapshots was 5, 10, 15 and 20 years,
280 and also when we considered all trees with ≥ 1 cm DBH.

281 ***PxAR and NxAR calculation***

282 In the European, US and Czech datasets, we constructed PxAR and NxAR curves by placing a small
283 circle at a random location within the geographic extent of the data, then gradually increasing the
284 circle size. For each circle size, we aggregated spatial units (EU countries, US states, CZ grid cells)
285 overlapped by the circle. In the resulting aggregated units we noted A , P_x , N_x and S , where A is
286 the area of the aggregated unit, N_x the number of extinction events, S the number of all species
287 found in the aggregated unit in the first temporal window, and $P_x = \frac{N_x}{S}$. This whole procedure was
288 repeated 200 times, each time starting at a different random location of the smallest circle. We
289 obtained a set of curves for each starting position, which we summarized using LOESS regression
290 with smoothing span of 0.3.

291 In the BCI forest plot, we overlaid the entire plot area with rectangular grids of increasing
292 resolution, from $20\text{ m} \times 20\text{ m}$ up to the entire 50 ha plot. In each grid cell we counted the
293 number of species (S_0) in the 1985 census and checked which of these species were present in the
294 2010 census (S_1). We then calculated $P_x = (S_0 - S_1)/S_0$ and $N_x = S_0 - S_1$. We calculated
295 average (\pm standard deviation) P_x and N_x over all grid cells at a particular grid resolution.

296 ***Results***

297 In the five empirical datasets, P_x decreases with area A of observation window (Figs. 6a, c, e, 7a,
298 c). This contrasts with N_x , which scales with A in a variety of ways. The two datasets from Europe,
299 plants and butterflies, produced highly divergent NxARs (Fig. 6): European butterflies (Fig. 6b) had
300 a hump-shaped NxAR, with only a single pan-continental extinction, but with pronounced losses at
301 intermediate scales. In contrast, European vascular plants (Fig. 6d) have an upward-accelerating
302 NxAR, with highest rates of extinction at the largest scale. NxAR of the US plants is similar to the
303 NxAR of the European plants (Fig. 6f), with clear upward-acceleration at large areas.

304 A decreasing NxAR is found in Czech birds (Fig. 7b). Here we note that the high values of N_x
305 at small scales can be a result of under-sampled grid cells. On the even smaller scale of the 50 ha

306 BCI forest plot (Fig. 7d), the N_xAR first sharply increases at the finest scale, with humps at larger
307 scales, unveiling the possibility of multi-modal empirical ExARs.

308

309 **DISCUSSION**

310 We have demonstrated both theoretically and empirically that extinction rates do not follow a
311 simple monotonic relationship with area. Instead, both local and regional extinction rates can be
312 low, with high rates at intermediate regional scales – or the situation can be completely the
313 opposite. Moreover, even curved relationships can be expected.

314 The observations of negative PxAR and positive NxAR at the local scale of BCI plot are in
315 line with predictions of the neutral model. In both cases N_x approaches 0 as A approaches 0,
316 which stems from the trivial fact that limited number of individuals at small areas can only be
317 divided in a limited number of species. Interestingly, as A increases and approaches the size of the
318 BCI plot, both the neutral model and the empirical BCI data reveal a flat phase of the NxAR; we
319 suggest that this is because the strong limiting effect of small number of individuals no longer
320 applies above a certain A . Future research should focus on more realistic versions of the neutral
321 model, perhaps in a spatially explicit setting (Rosindell & Cornell, 2007), and over larger spatial
322 extents.

323 In contrast with the BCI plot, it is unreasonable to assume equilibrium or neutral dynamics
324 at the extent of the entire countries and continents, especially when considering contemporary
325 human-induced extinctions and extirpations. In such situations it is more instrumental to explain
326 the observed extinction scaling with range contractions of rare and widespread species (see the
327 Theoretical expectations section): The observed *decrease* of N_x with A at large scales in European
328 butterflies likely reflects range contractions, but not complete extinctions, of widespread species.
329 This is the opposite of the observed *increase* of N_x with A at large scales in European and US
330 plants, which reflects complete losses of small-ranged species. Importantly, these disparate
331 directions of NxAR are perfectly reconcilable with the decreasing PxAR in all of these datasets, as
332 we have described in the SAR-based model (see the Theoretical expectations section and Figure
333 5).

334 For the first time, we have shown that in theory, *per-species probability of extinction* can
335 increase with area. Seemingly, this goes against the classical views (MacArthur & Wilson, 1967;

336 Diamond, 1984; Quinn & Hastings, 1987; Hanski, 2001) – how can a species be more likely to go
337 extinct in a large area than in small one? One key is a potential existence of remote populations
338 occupying a small fraction of an entire region (i.e., a country). Loss of such small population can
339 mean a complete extinction in the entire country, but may not contribute to the small-scale P_X ,
340 since the species still retains numerous small-scale populations outside of the country. Is this an
341 artifact of the specific position of the observation windows? Probably not, since some
342 parametrizations of the neutral model can also give a higher P_X , and since the model is spatially
343 implicit (the observation window has size, but no position). Note: In our empirical data, we
344 detected only negative PxAR, suggesting that it is still the prevalent form in real-world nested
345 systems.

346 The uncovered wealth of possible relationships of *counts of extinctions* with area has
347 several crucial implications. First, it can reconcile the reported lack of biodiversity change, on
348 average, at local scales (Vellend *et al.*, 2013; Dornelas *et al.*, 2014) with reported losses at global
349 scales (Barnosky *et al.*, 2011; Alroy, 2015). We are aware that, for a complete reconciliation, one
350 may also need to know the spatial scaling of species gains (Jackson & Sax, 2010), which we see as
351 an important future research avenue. However, the important lesson here is that even when
352 species gains are ignored, or when they are scale-invariant, NxAR alone is sufficient to cause scale-
353 dependent biodiversity dynamics. Furthermore, our results on extinctions indicate that
354 biodiversity change at intermediate regional scales can be completely different from both local
355 and global patterns. Therefore, simple *interpolation* between scales should be done with caution,
356 if at all.

357 This leads to implications of our results for *extrapolation* of extinction rates at grains for
358 which we have limited data (He & Hubbell, 2011; Pimm *et al.*, 2014). Given the richness of possible
359 NxAR shapes, we warn that estimating magnitude of global extinction crisis from local species loss
360 can be challenging. Similarly, numbers of local extinctions will be tricky to predict from global or
361 continental extinction numbers. We suggest that, in both cases, extra information is necessary on
362 spatial scaling of the drivers of extinction (e.g. on spatial scaling of habitat dynamics or spatial
363 scaling of intensity of extinction debts), on the specific distributions of species within the studied
364 area, and on their theoretical links to NxAR.

365 An alternative, and perhaps more promising approach could be to extrapolate PxAR, since
366 in our five datasets it was always decreasing and hence more predictable than NxAR. If in the
367 future there is a broader empirical support for an exact form of PxAR, then it should be possible to

368 combine it with SAR (Fig. 4) derived from the current global distributional information on some
369 taxa (i.e. the IUCN range maps) to reliably extrapolate extinction counts to grains that are coarser
370 or finer than the grain of the extinction data. This can be a viable alternative to the recent
371 approaches that predict extinction numbers solely from habitat loss (Pimm & Raven, 2000; Pereira
372 & Daily, 2006; He & Hubbell, 2011; Keil *et al.*, 2015). Further, a predictable PxAR can be
373 instrumental in statistical models that link patterns of biodiversity with environmental drivers at
374 multiple spatial scales (McInerney & Purves, 2011; Keil *et al.*, 2013; Keil & Jetz, 2013).

375 Although we have focused exclusively on extinction, we suggest that a complementary
376 approach can be used to study species gains, which includes immigration and speciation. This
377 could be an exciting new opportunity especially for invasion biology. Another fruitful research can
378 involve a more detailed comparison of the nested and island systems. It is well known that island
379 and nested (mainland) systems differ in their static scaling patterns of biodiversity, but the causes
380 of such discrepancy remain controversial (Whittaker *et al.*, 2001; Triantis *et al.*, 2012). In this
381 paper, we suggested that nested observation windows that contain multiple habitat types can
382 potentially differ in their PxAR from island systems of homogeneous habitat patches. However, the
383 differences may potentially be elsewhere, and may be related to the same mechanisms that cause
384 the differences, e.g. between the island and mainland SARs (Pereira & Borda-de-Água, 2013).

385 To conclude, our results underscore the need to treat species loss as a scale-dependent
386 problem, or more precisely, a grain-dependent problem. By focusing at global extinctions only, we
387 can miss that either not much is happening at small grains, or that there are drastic losses at the
388 small grains. To provide a complete picture, local, regional and global losses should be reported at
389 the same time, simultaneously. Here the PxAR and NxAR curves offer a straightforward way to
390 summarize and report such multi-scale species loss, and we argue that estimation of these
391 relationships can benefit assessments of the past and current state of biodiversity, as well as in
392 forecasts of biodiversity's future.

393

394 **ACKNOWLEDGEMENTS**

395 We are grateful to A. Berger and C. Meyer for helpful comments. The BCI forest dynamics research
396 project was founded by S.P. Hubbell and R.B. Foster and is now managed by R. Condit, S. Lao, and
397 R. Perez under the Center for Tropical Forest Science and the Smithsonian tropical Research in

398 Panama. Numerous organizations have provided funding, principally the U.S. National Science
399 Foundation, and hundreds of field workers have contributed.

400

401 **DATA ACCESSIBILITY**

402 Digitized form of the European butterfly data is available on Figshare at
403 <https://dx.doi.org/10.6084/m9.figshare.4036236.v1> . An electronic form of the Czech bird dataset
404 is not publicly available; contact PK for details. Data on extant species of plants in US states and
405 European countries, and on plant extinctions of European countries are also not publicly available;
406 contact MW for details. Data on US plant extinctions were purchased from NatureServe. The BCI
407 data are available from CTFS through a request form (<http://ctfs.si.edu/webatlas/datasets/bci/>).

408

409 **BIOSKETCH**

410 **Petr Keil** is a postdoc at iDiv. His main interest is spatial scaling of multiple facets of biodiversity
411 and its change. His hobby is statistics.

412 **German Centre for Integrative Biodiversity Research (iDiv)** is a research institute run by Martin
413 Luther University Halle-Wittenberg (MLU), Friedrich Schiller University Jena (FSU) and Leipzig
414 University (UL) – and in cooperation with the Helmholtz Centre for Environmental Research (UFZ).
415 The goals of the institute, which was set up back in 2012, are to record biological diversity in its
416 complexity, to make available and use scientific data on a global level, and to develop strategies,
417 solutions and utilization concepts for decision-makers in order to prevent any further loss of
418 biodiversity. iDiv promotes theory-driven synthesis, experiments and data-driven theory in
419 biodiversity sciences, and provides scientific foundation for sustainable management of Earth's
420 biodiversity.

421 REFERENCES

- 422 Alroy, J. (2015) Current extinction rates of reptiles and amphibians. *Proceedings of the National*
423 *Academy of Sciences*, **112**, 13003–13008.
- 424 Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C.,
425 McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011) Has the Earth's
426 sixth mass extinction already arrived? *Nature*, **471**, 51–57.
- 427 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A., Mace,
428 G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B.,
429 Larigauderie, A., Srivastava, D.S. & Naeem, S. (2012) Biodiversity loss and its impact on
430 humanity. *Nature*, **486**, 59–67.
- 431 Condit, R. (1998) *Tropical forest census plots*, Springer, Berlin.
- 432 Diamond, J.M. (1984) *Extinctions*. (ed. by M.H. Nitecki), pp. 191–196. University of Chicago Press.
- 433 Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. & Magurran, A.E. (2014)
434 Assemblage time series reveal biodiversity change but not systematic loss. *Science*, **344**,
435 296–299.
- 436 Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, **405**, 220–227.
- 437 Halley, J.M. & Iwasa, Y. (2011) Neutral theory as a predictor of avifaunal extinctions after habitat
438 loss. *Proceedings of the National Academy of Sciences*, **108**, 2316–2321.
- 439 Hanski, I. (1991) Single-species metapopulation dynamics: concepts, models and observations.
440 *Biological Journal of the Linnean Society*, **42**, 17–38.
- 441 Hanski, I. (2001) Spatially realistic theory of metapopulation ecology. *Naturwissenschaften*, **88**,
442 372–381.
- 443 Hanski, I. & Ovaskainen, O. (2000) The metapopulation capacity of a fragmented landscape.
444 *Nature*, **404**, 755–758.
- 445 He, F. & Hubbell, S.P. (2011) Species-area relationships always overestimate extinction rates from
446 habitat loss. *Nature*, **473**, 368–371.
- 447 Hooper, D.U., Chapin, F.S., Ewel, J.J., Hector, A., Inchausti, P., Lavorel, S., Lawton, J.H., Lodge, D.M.,
448 Loreau, M., Naeem, S., Schmid, B., Setälä, H., Symstad, A.J., Vandermeer, J. & Wardle,

- 449 D.A. (2005) Effects of biodiversity on ecosystem functioning: A consensus of current
450 knowledge. *Ecological Monographs*, **75**, 3–35.
- 451 Hubbell, S.P. (2001) *The unified theory of biodiversity and biogeography*, Princeton Univ. Press.
- 452 Hubbell, S.P., Condit, R. & Foster, R.B. (2005) Barro Colorado Forest Census Plot Data.
453 <http://ctfs.si.edu/webatlas/datasets/bci>.
- 454 Hubbell, S.P., Foster, R.B., O'Brien, S.T., Harms, K.E., Condit, R., Wechsler, B., Wright, S.J. & Loo de
455 Lao, S. (1999) Light gap disturbances, recruitment limitation, and tree diversity in a
456 neotropical forest. *Science*, **285**, 554–557.
- 457 Hugueny, B., Movellan, A. & Belliard, J. (2011) Habitat fragmentation and extinction rates within
458 freshwater fish communities: a faunal relaxation approach. *Global Ecology and*
459 *Biogeography*, **20**, 449–463.
- 460 Isenberg, A.C. (2001) *The destruction of the bison: an environmental history, 1750-1920*,
461 Cambridge University Press, Cambridge.
- 462 Jackson, S.T. & Sax, D.F. (2010) Balancing biodiversity in a changing environment: extinction debt,
463 immigration credit and species turnover. *Trends in Ecology & Evolution*, **25**, 153–160.
- 464 Kartesz, J.T. (1999) *A synonymized checklist and atlas with biological attributes for the vascular*
465 *flora of the United States, Canada, and Greenland*, North Carolina Botanical Garden,
466 Chapel Hill, NC.
- 467 Keil, P., Belmaker, J., Wilson, A.M., Unitt, P. & Jetz, W. (2013) Downscaling of species distribution
468 models: a hierarchical approach. *Methods in Ecology and Evolution*, **4**, 82–94.
- 469 Keil, P. & Jetz, W. (2013) Downscaling the environmental associations and spatial patterns of
470 species richness. *Ecological Applications*, **24**, 823–831.
- 471 Keil, P., Storch, D. & Jetz, W. (2015) On the decline of biodiversity due to area loss. *Nature*
472 *Communications*, **6**, 8837.
- 473 Kitzes, J. & Harte, J. (2014) Beyond the species-area relationship: improving macroecological
474 extinction estimates. *Methods in Ecology and Evolution*, **5**, 1–8.
- 475 Konvicka, M., Benes, J., Cizek, O., Kopecek, F., Konvicka, O. & Vitaz, L. (2007) How too much care
476 kills species: Grassland reserves, agri-environmental schemes and extinction of *Colias*

- 477 myrmidone (Lepidoptera: Pieridae) from its former stronghold. *Journal of Insect*
478 *Conservation*, **12**, 519–525.
- 479 Kunin, W.E. (1998) Extrapolating Species Abundance Across Spatial Scales. *Science*, **281**, 1513–
480 1515.
- 481 Lande, R. (1993) Risks of population extinction from demographic and environmental stochasticity
482 and random catastrophes. *American Naturalist*, **142**, 911–927.
- 483 Lomolino, M.V., Riddle, B.R., Whittaker, R.J. & Brown, J.H. (2010) *Biogeography*, 4th edn. Sinauer
484 Associates, Sunderland, Massachusetts.
- 485 MacArthur, R.H. & Wilson, E.O. (1967) *The theory of island biogeography*, Princeton University
486 Press, Princeton.
- 487 McGill, B.J., Dornelas, M., Gotelli, N.J. & Magurran, A.E. (2015) Fifteen forms of biodiversity trend
488 in the Anthropocene. *Trends in Ecology & Evolution*, **30**, 104–113.
- 489 McInerney, G.J. & Purves, D.W. (2011) Fine-scale environmental variation in species distribution
490 modelling: regression dilution, latent variables and neighbourly advice. *Methods in*
491 *Ecology and Evolution*, **2**, 248–257.
- 492 NatureServe (2016) *NatureServe Central Databases*, Arlington, VA.
- 493 Pereira, H.M. & Borda-de-Água, L. (2013) *Modeling biodiversity dynamics in countryside and native*
494 *habitats. Encyclopedia of Biodiversity*, pp. 321–328. Elsevier.
- 495 Pereira, H.M. & Daily, G.C. (2006) Modelling biodiversity dynamics in countryside landscapes.
496 *Ecology*, **87**, 1877–1885.
- 497 Pimm, S.L., Jenkins, C.N., Abell, R., Brooks, T.M., Gittleman, J.L., Joppa, L.N., Raven, P.H., Roberts,
498 C.M. & Sexton, J.O. (2014) The biodiversity of species and their rates of extinction,
499 distribution, and protection. *Science*, **344**, 1246752.
- 500 Pimm, S.L. & Raven, P. (2000) Biodiversity: Extinction by numbers. *Nature*, **403**, 843–845.
- 501 Proenca, V. & Pereira, H.M. (2013) *Comparing extinction rates: Past, present, and future.*
502 *Encyclopedia of Biodiversity*, pp. 167–176. Elsevier.
- 503 Quinn, J.F. & Hastings, A. (1987) Extinction in subdivided habitats. *Conservation Biology*, **1**, 198–
504 208.
- 505 Ricklefs, R.E. (2006) The unified neutral theory of biodiversity: do the numbers add up? *Ecology*,
506 **87**, 1424–1431.
- 507 Riggio, J., Jacobson, A., Dollar, L., Bauer, H., Becker, M., Dickman, A., Funston, P., Groom, R.,
508 Henschel, P., Iongh, H., Lichtenfeld, L. & Pimm, S. (2012) The size of savannah Africa: a
509 lion's (*Panthera leo*) view. *Biodiversity and Conservation*, **22**, 17–35.

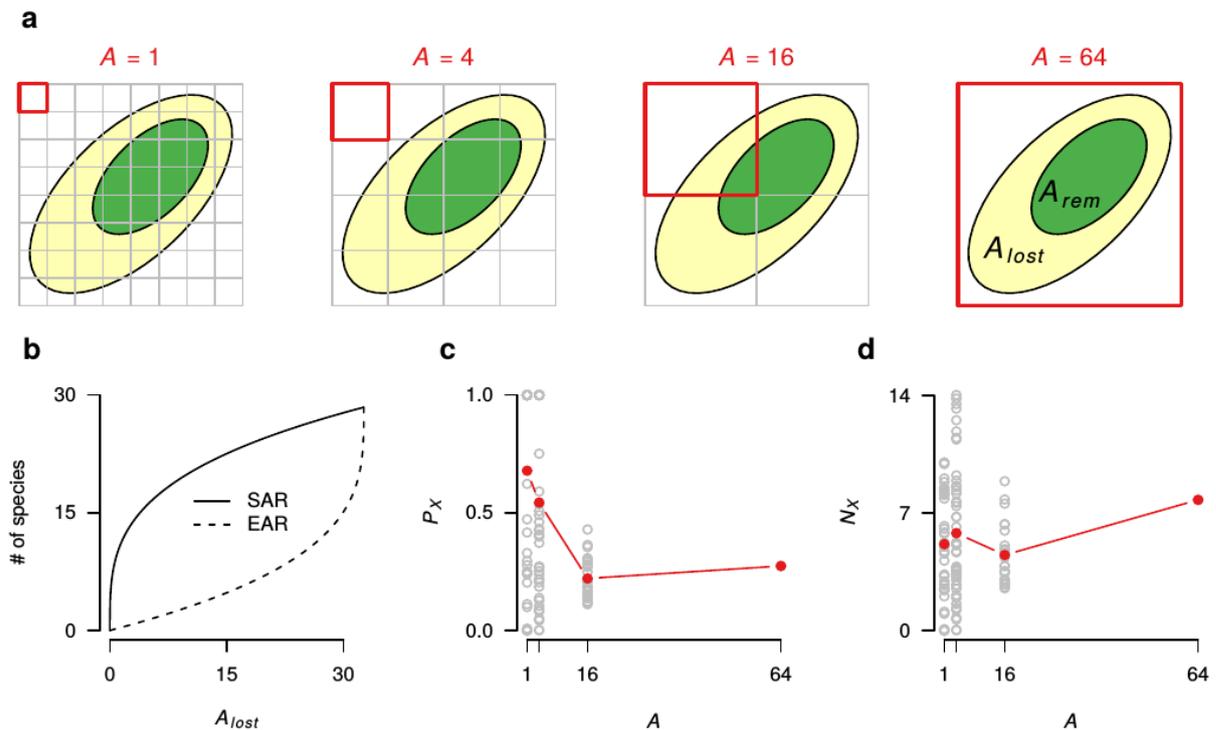
- 510 Rosindell, J. & Cornell, S.J. (2007) Species-area relationships from a spatially explicit neutral model
511 in an infinite landscape. *Ecology Letters*, **10**, 586–595.
- 512 Scheiner, S.M. (2003) Six types of species-area curves. *Global Ecology and Biogeography*, **12**, 441–
513 447.
- 514 Šťastný, K., Bejček, V. & Hudec, K. (2006) *Atlas hnízdního rozšíření ptáků v České republice, 2001–*
515 *2003*, Aventinum.
- 516 Šťastný, K., Procházka, P., Bejček, V. & Hudec, K. (1997) *Atlas hnízdního rozšíření ptáků v České*
517 *republice, 1985–1989*, H & H.
- 518 Storch, D., Keil, P. & Jetz, W. (2012) Universal species-area and endemics-area relationships at
519 continental scales. *Nature*, **488**, 78–81.
- 520 Tedesco, P.A., Oberdorff, T., Cornu, J.-F., Beauchard, O., Brosse, S., Dürr, H.H., Grenouillet, G.,
521 Leprieur, F., Tisseuil, C., Zaiss, R. & Hugueny, B. (2013) A scenario for impacts of water
522 availability loss due to climate change on riverine fish extinction rates. *Journal of Applied*
523 *Ecology*, **50**, 1105–1115.
- 524 Triantis, K.A., Guilhaumon, F. & Whittaker, R.J. (2012) The island species–area relationship: biology
525 and statistics. *Journal of Biogeography*, **39**, 215–231.
- 526 Van Swaay, C.A.M. & Warren, M.S. (1999) *Red data book of European butterflies*, Council of
527 Europe Publishing, Strasbourg.
- 528 Vellend, M., Baeten, L., Myers-Smith, I.H., Elmendorf, S.C., Beauséjour, R., Brown, C.D., Frenne,
529 P.D., Verheyen, K. & Wipf, S. (2013) Global meta-analysis reveals no net change in local-
530 scale plant biodiversity over time. *Proceedings of the National Academy of Sciences*, **110**,
531 19456–19459.
- 532 Whittaker, R.J., Willis, K.J. & Field, R. (2001) Scale and species richness: towards a general,
533 hierarchical theory of species diversity. *Journal of Biogeography*, **28**, 453–470.
- 534 Wilson, R.J., Thomas, C.D., Fox, R., Roy, D.B. & Kunin, W.E. (2004) Spatial patterns in species
535 distributions reveal biodiversity change. *Nature*, **432**, 393–396.
- 536 Winter, M., Kühn, I., La Sorte, F.A., Schweiger, O., Nentwig, W. & Klotz, S. (2010) The role of non-
537 native plants and vertebrates in defining patterns of compositional dissimilarity within
538 and across continents. *Global Ecology and Biogeography*, **19**, 332–342.
- 539 Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M., Basnou, C.,
540 Delipetrou, P., Didžiulis, V., Hejda, M., Hulme, P.E., Lambdon, P.W., Pergl, J., Pyšek, P.,
541 Roy, D.B. & Kühn, I. (2009) Plant extinctions and introductions lead to phylogenetic and

542 taxonomic homogenization of the European flora. *Proceedings of the National Academy*
543 *of Sciences*, **106**, 21721–21725.

544 Wu, J. & Vankat, J.L. (1995) *Island Biogeography: Theory and Application*. (ed. by W.A.
545 Nierenberg), pp. 371–379. Academic Press, San Diego.

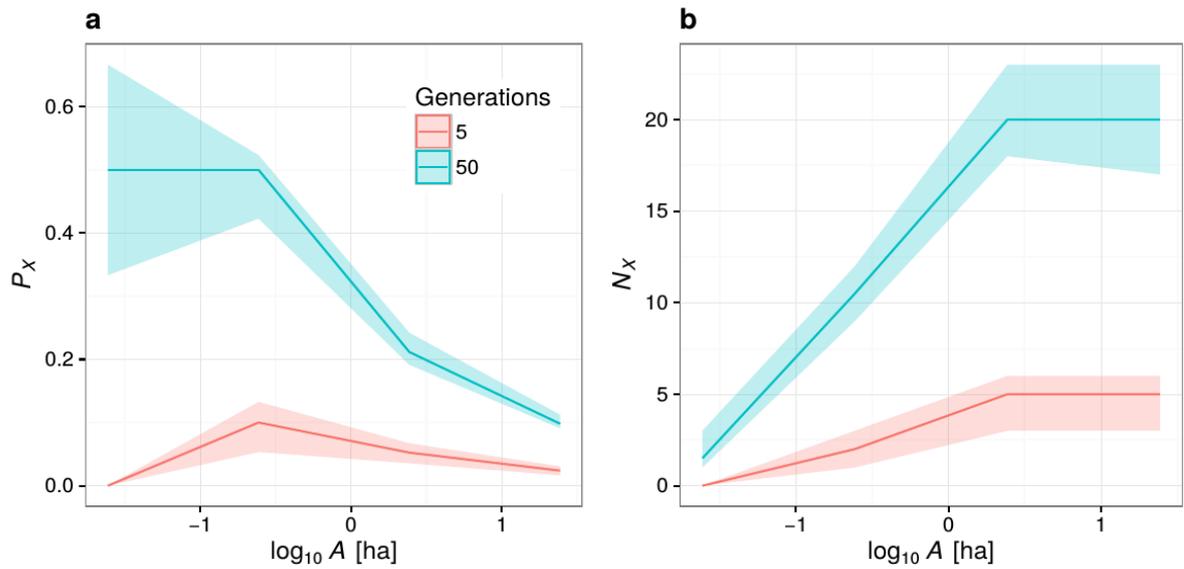
546

547 **FIGURES**



548

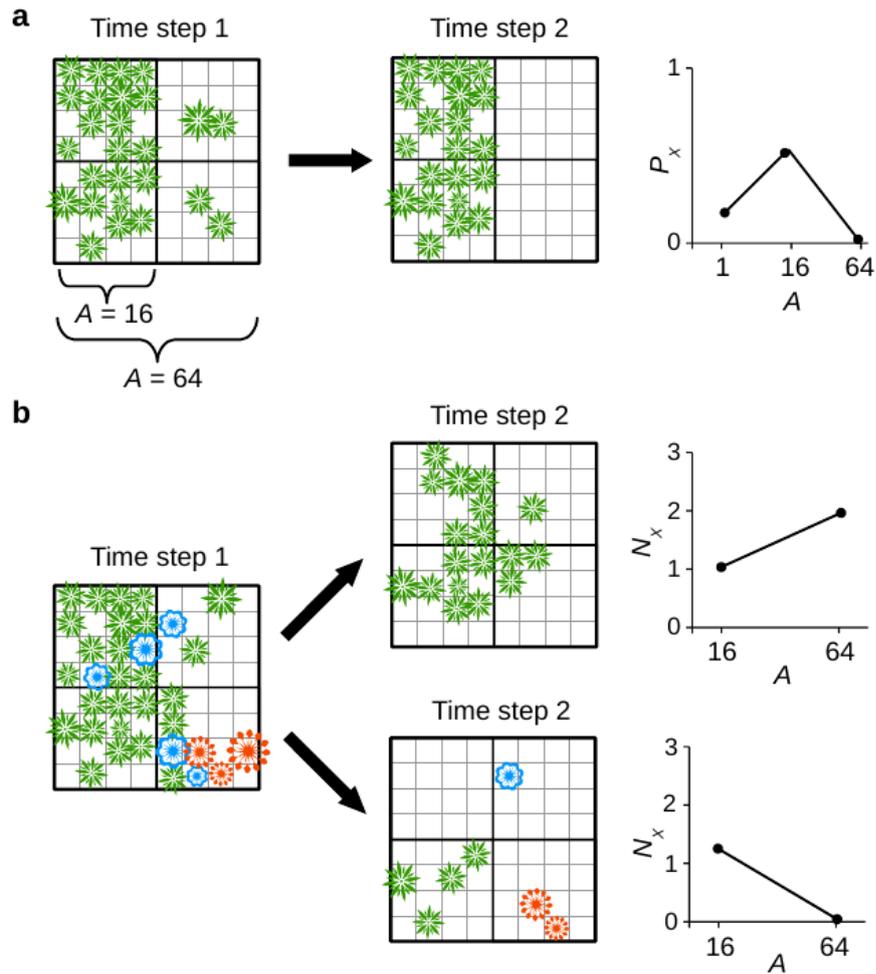
549 **Figure 1** Difference between spatial scaling of realized extinction rates (PxAR and NxAR) in nested
 550 systems and static scaling of species richness (SAR, EAR) commonly used to estimate extinction
 551 rates due to habitat loss (Pimm & Raven, 2000; He & Hubbell, 2011; Keil *et al.*, 2015). (a)
 552 Hypothetical landscape where part of the habitat area is lost (A_{lost} ; pale yellow), and part remains
 553 (A_{rem} ; green). (b) Number of species extinct in A_{lost} is described by the endemics-area
 554 relationship (EAR). Since we assume that individuals in the habitat are distributed randomly, EAR
 555 follows a point reflection symmetry with species-area relationship (SAR) (Keil *et al.*, 2015); here
 556 SAR takes the form of $S = 10A^{0.3}$. In contrast to EAR, PxAR (c) and NxAR (d) are calculated over
 557 the observation window (red) and over a given temporal period. Dots in panels c and d are values
 558 calculated directly using EAR described in panel b. Red dots correspond to the mean PxAR and
 559 mean NxAR observed across all windows of a given temporal period.



560

561

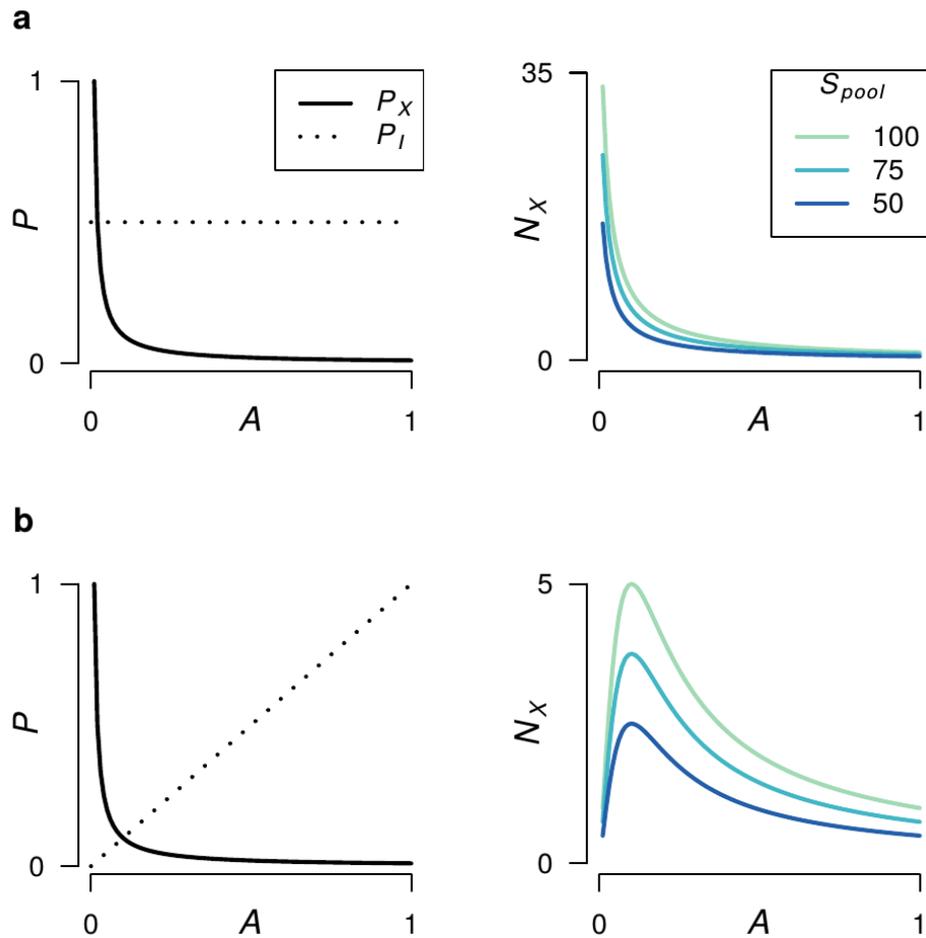
562 **Figure 2** PxAR and NxAR from simulated realizations of the classic version of the spatially implicit
563 neutral model (Hubbell, 2001). The solid lines and ribbons show medians and quartiles of the
564 simulations.



565

566

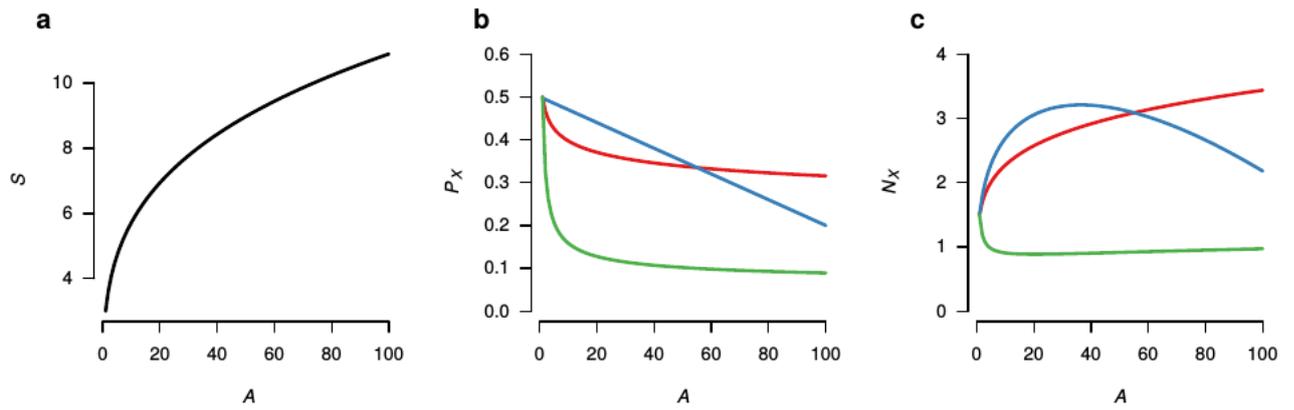
567 **Figure 3** Simple scenarios producing both increasing and decreasing shapes of P_x AR (a) and N_x AR
 568 (b) in nested systems. In panel (a) we demonstrate the theoretical possibility of P_x increasing with
 569 area A . In panel (b) we show two kinds of community dynamics producing opposite directions of
 570 N_x AR in a plant community that started with 3 species (blue, green, red) at time step 1. In the first
 571 scenario, two rare species go extinct, leading to increasing N_x AR. In the second scenario, none of
 572 the species goes completely extinct, but there are severe population declines in all species, leading
 573 to decreasing N_x AR. Values of P_x and N_x in the graphs are averages over all four areas with $A = 1$
 574 and $A = 16$.



575

576

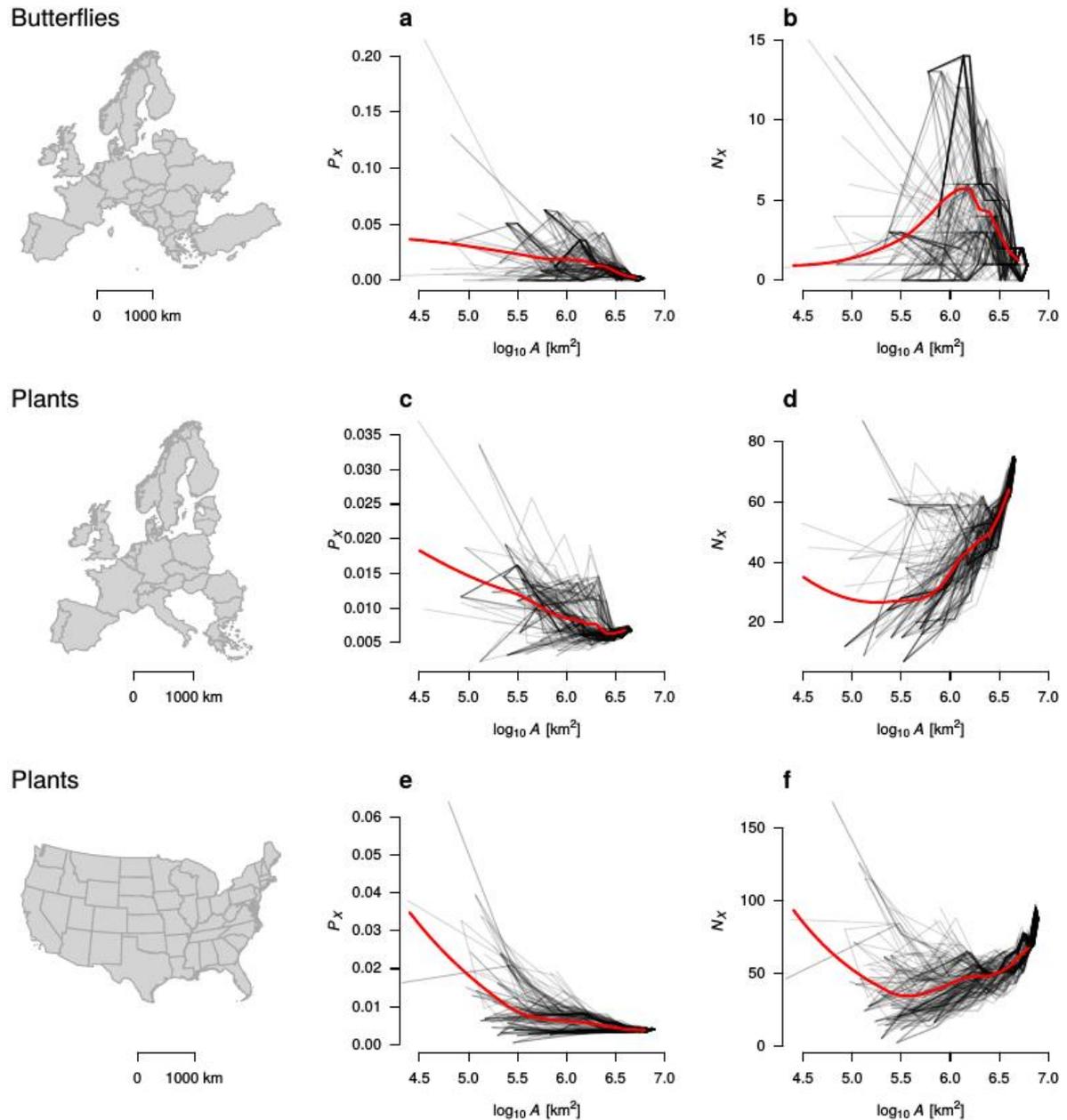
577 **Figure 4** Two scenarios describing spatial scaling of per-species extinction probability P_X , per-
578 species immigration probability P_I , and the resulting relationship (N_xAR) between area A and
579 number of extinctions N_x in island systems. (a) P_X decreases proportionally with area, P_I is
580 constant. (b) P_X decreases with area, P_I increases with area. The N_xAR curves were calculated
581 using eq. 1.



582

583

584 **Figure 5** Hypothetical examples of spatial scaling of number of extinction events (N_x) derived from
585 a simple SAR-based model. (a) Species richness S follows a power-law with area of observation
586 window A . (b) Per-species extinction probability P_x follows various monotonically decreasing
587 scaling relationships with A , which results in a rich variety of NxARs (c). Colors indicate
588 corresponding PxARs and NxARs.

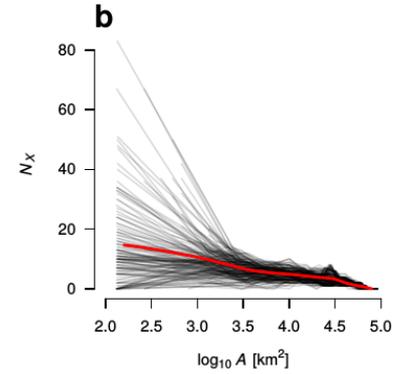
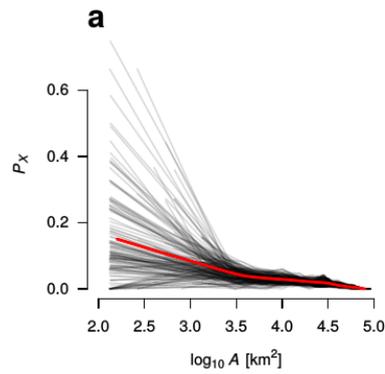
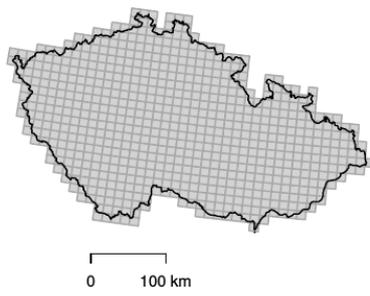


589

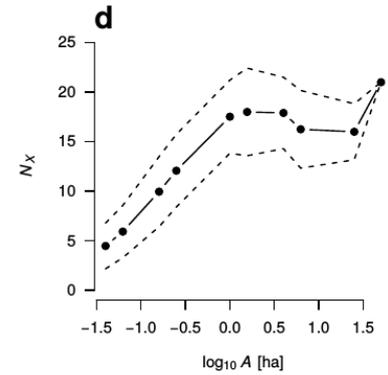
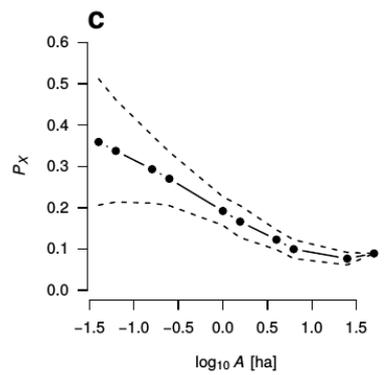
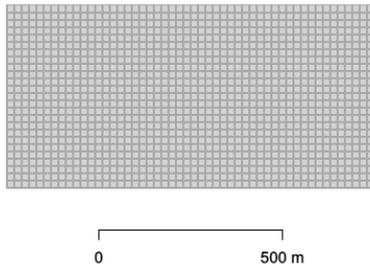
590

591 **Figure 6** Empirical spatial scaling of per-species probability of extinction P_X (a, c) and number of
592 extinctions N_X (b, d) of European butterflies (a, b) and European vascular plants (c, d) and US
593 vascular plants (e, f). Each grey line was obtained by placing (200 times) a small circle at a random
594 location within Europe, then gradually increasing the circle size up to the size of the whole
595 continent, counting number of extinction events within the countries falling in the circle. Red lines
596 are LOESS regressions with smoothing span of 0.3.

Birds



Trees



597

598

599 **Figure 7** Empirical spatial scaling of per-species probability of extinction P_x (a, c) and number of
600 extinctions N_x (b, d) in a country-wide and a local dataset. Panels a and b use atlas data on birds of
601 Czech Republic (a, b). Each grey line was obtained by placing (200 times) a small circle at a random
602 location within the Czech Republic, then gradually increasing the circle size, counting numbers of
603 extinctions in atlas cells overlapping the circle. Red lines are LOESS regressions (span = 0.3). High
604 values of P_x and N_x in some small Areas are likely caused by undersampling. Panels c and d use
605 data on trees with DBH ≥ 10 cm in the 50 ha BCI forest plot (c, d) calculated over a 25-year lag.
606 Solid circles and lines are means, dashed lines are standard deviations calculated over different
607 spatial locations of the observation window.