

# Exploring the dimensions of metapopulation persistence: a comparison of structural and temporal measures

Tad A Dallas<sup>a,b,\*</sup>, Marjo Saastamoinen<sup>b,c</sup> and Otso Ovaskainen<sup>b,d</sup>

<sup>a</sup>*Department of Biological Science, Louisiana State University, Baton Rouge, LA, USA*

<sup>b</sup>*Organismal and Evolutionary Biology Research Programme, P.O. Box 65, 00014 University of Helsinki, Finland*

<sup>c</sup>*Helsinki Institute of Life Science, University of Helsinki, Finland*

<sup>d</sup>*Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and Technology.  
N-7491 Trondheim, Norway*

\*Corresponding author: [tad.a.dallas@gmail.com](mailto:tad.a.dallas@gmail.com); ORCID: 0000-0003-3328-9958

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**Authors' information:** Tad Dallas; [tad.a.dallas@gmail.com](mailto:tad.a.dallas@gmail.com); ORCID: 0000-0003-3328-9958

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## *Abstract*

1  
2 The spatial arrangement of habitat patches in a metapopulation, and the dispersal connections  
3 among them, influence metapopulation persistence. Metapopulation persistence emerges from  
4 a dynamic process, namely the serial extinctions and recolonizations of local habitat patches,  
5 while measures of persistence are typically based solely on structural properties of the spatial  
6 network (e.g., spatial distance between sites). Persistence estimators based on static properties  
7 may be unable to capture the dynamic nature of persistence. Understanding the shape of the  
8 distribution of extinction times is a central goal in population ecology. Here, we examine  
9 the goodness of fit of the power law to patch persistence time distributions using data on a  
10 foundational metapopulation system – the Glanville fritillary butterfly in the Åland islands.  
11 Further, we address the relationship between structural measures of metapopulation persistence  
12 (i.e., metapopulation capacity) and our temporal distributional fits to patch persistence times  
13 based on a power law. Patch persistence time distributions were well fit by a power law for the  
14 majority of semi-independent networks. Power law fits to persistence time distributions were  
15 related to metapopulation capacity, linking structural and temporal measures of metapopulation  
16 persistence. Several environmental variables and measures of network topology were correlated  
17 with both measures of metapopulation persistence, though correlations tended to be stronger for  
18 the structural measure of metapopulation persistence (i.e., metapopulation capacity). Together,  
19 our findings suggest that persistence time distributions are useful dynamic properties of metapopulations,  
20 and provide evidence of a relationship between metapopulation structure and metapopulation  
21 dynamics.

## Introduction

Habitat fragmentation reduces patch size leading to smaller local populations that are at greater risk of stochastic extinction. Dispersal between fragmented suitable habitat patches is therefore essential to maintain the network of small populations i.e., the metapopulation (Hanski, 1999; Hanski and Gilpin, 1991). A body of theory has been developed to describe threshold conditions for metapopulation persistence (Keymer et al., 2000), the influence of dispersal on metapopulation dynamics (Doebeli, 1995; Holland and Hastings, 2008; Vuilleumier et al., 2010), and the dependence of persistence on the spatial distribution of habitat patches (Ovaskainen and Hanski, 2003). Metapopulation persistence estimators attempt to quantify the threshold after which colonization and dispersal are unable to maintain patch occupancy, leading to metapopulation collapse. The initial development of metapopulation theory drew heavily on the Levin's model, which tracks species occurrences among patches regardless of spatial location or size of habitat patches (Levins, 1969). Building on this, Hanski (1994) developed a spatially-explicit metapopulation model which incorporated variation in habitat patch size and explicitly considered the role of space. Through this work, the development of a persistence measure called *metapopulation capacity* was developed (Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001).

. We use *metapopulation capacity* to measure metapopulation persistence based on the spatial distribution of habitat patches and dispersal links between them (Hanski and Ovaskainen, 2000; Ovaskainen and Hanski, 2001). This information is contained within the landscape matrix ( $M$ ), which describes the putative dispersal links between all habitat patches (Hanski, 1999; Ovaskainen and Hanski, 2001). While the landscape matrix is often constructed in the absence of a dynamic model, the original formulation of metapopulation capacity ( $\lambda$ ) was based on a metapopulation model (Hanski and Ovaskainen, 2000). Previous work has suggested that metapopulation capacity ( $\lambda$ ) is associated with equilibrium patch occupancy when habitat patches are of good quality and are aggregated in space (Hanski and Ovaskainen, 2000; Visconti and Elkin, 2009), suggesting a role for both environmental quality and spatial network structure on metapopulation capacity (Hanski et al., 2017). Conservation and management decisions have

49 been informed by metapopulation capacity (Hanski, 2011; Hanski and Thomas, 1994; McCullough,  
50 1996), as it is used to estimate long term metapopulation persistence (Hanski and Ovaskainen,  
51 2000). Similar eigenvalue-decompositions have been used to estimate *a*) epidemic thresholds in  
52 social contact networks (Saha et al., 2015), *b*) nestedness in bipartite networks (Staniczenko et al.,  
53 2013), *c*) the basic reproductive number ( $R_0$ ) of infectious disease given infection time series  
54 (Diekmann et al., 2010), and *d*) early warning signals of spatial population collapse (Chen et al.,  
55 2019).

56 . Previous efforts to link metapopulation persistence measures derived from the spatial distribution  
57 of patches to the resulting dynamics have largely focused on metapopulation persistence in an  
58 absolute sense, quantifying the number of times in model simulations the metapopulation goes  
59 extinct (Kleinhans and Jonsson, 2011). Other efforts have defined persistence using measures  
60 related to extinction-colonization ratios or mean species occupancy (i.e., fraction of patches where  
61 the species is found). These measures often define metapopulation persistence as either the  
62 probability that the entire metapopulation goes extinct, or the mean species occupancy over  
63 some time window (Johst et al., 2002; Molofsky and Ferdy, 2005). The first is a coarse measure,  
64 and is difficult to empirically test, given the need for a metapopulation extinction event, which  
65 tend to be rare and not easily replicated. The second measure may fail to capture rescue effects  
66 or transient patch occupancy followed by local extinction, that may serve as an early warning  
67 signal of metapopulation collapse (but see Holmes et al. (2020)). Ideally, a measure of persistence  
68 at the metapopulation scale would incorporate information on each habitat patch explicitly, both  
69 in terms of mean and variation in climatic conditions. For instance, Increasing climatic variability  
70 may drive metapopulation dynamics near extinction thresholds, even those as established as the  
71 Glanville fritillary metapopulation in the Åland islands (van Bergen et al., 2020).

72 . In population ecology, a body of theory related to the distribution of extinction times for  
73 single populations has been developed (Drake, 2006, 2014). That is, without immigration or  
74 emigration, what does the distribution of extinction times look like for a set of populations?  
75 A common observation is that this distribution has a heavy tail, where most populations go

76 extinct in a relatively short time, but few populations exist for far longer (Drake, 2014). In  
77 the context of metapopulations, the distributional fit to patch extinction times – which are  
78 equivalent to *persistence times* – may provide information on the metapopulation as a whole while  
79 directly incorporating patch level dynamics (Bertuzzo et al., 2011). This approach requires either  
80 simulated or empirical data on patch persistence times to generate the persistence estimate. That  
81 is, estimating the distribution of persistence times for each patch in the network could provide  
82 insight into the presence of long-persisting nodes, and those which go extinct but recolonize  
83 quickly. One such distributional fit proposed recently is the power law (Bertuzzo et al., 2011),  
84 where some quantity  $x$  is drawn from a probability distribution  $p(x) \propto x^{-\alpha}$ . The interpretation  
85 of  $\alpha$  then becomes important, as this scaling parameter starts to address the heavy-tailed nature  
86 of the distribution of empirical values of  $x$ . Power law relationships are commonly found in  
87 natural systems, such as the bivariate scaling of the number of species with increasing geographic  
88 area (the species-area relationship; Martín and Goldenfeld (2006)). Power law relationships  
89 in frequency distributions, as examined here, are equally common in ecological studies of the  
90 distribution of species body sizes (Morse et al., 1985), abundance estimates (Keitt and Stanley,  
91 1998), and vegetation patch size (Kéfi et al., 2007), as reviewed in White et al. (2008).

92 . Here, the parameter  $\alpha$  estimates the shape of the long tail of persistence times, with smaller  
93  $\alpha$  values corresponding to heavier tails. This means that large  $\alpha$  values correspond to more  
94 extreme decay rates in persistence times ( $x$ ), with very few long persistent patches, indicative of  
95 high extinction and rapid recolonization of habitat patches. That is, the probability density of  
96 persistence times ( $x$ ) are proportional to  $x^{-\alpha}$ . As such, there are two clear possible relationships  
97 between metapopulation capacity ( $\lambda$ ) and persistence time distributions ( $\alpha$ ). First, a positive  
98 relationship may emerge between persistence time distributional fits ( $\alpha$ ) and metapopulation  
99 capacity ( $\lambda$ ) if long-term persistent habitat patches drive metapopulation persistence. These  
100 long-term persistent patches would lead to a heavier-tailed distribution of persistence times,  
101 reducing the  $\alpha$  value. On the other hand, metapopulations are characterized by rapid extinction  
102 and re-colonization dynamics, and these dynamics may be indicative of a persistent metapopulation.  
103 Thus, a second possibility is that we may expect a negative relationship between metapopulation

104 capacity ( $\lambda$ ) and persistence time fits ( $\alpha$ ). This would suggest that short-lived, but quickly  
105 recolonized habitat patches, are a signature of a persistent metapopulation.

106 . Apart from implications to metapopulation persistence, the  $\alpha$  parameter may also be useful  
107 in differentiating different *types* of metapopulations (as identified in Harrison and Taylor (1997)).  
108 This is because the balance between ephemeral and persistent habitat patches can inform metapopulation  
109 structure. For instance, *mainland-island* metapopulations would be expected to have a smaller  $\alpha$   
110 value, driven by the long-persisting source patches, while *classic* metapopulations would have  
111 larger  $\alpha$  values due to the common extinction and colonization events reducing the probability  
112 of long-persisting patches. Finally, understanding the differences in power law relationships for  
113 unconnected populations (Drake, 2006, 2014) – corresponding to *non-equilibrium metapopulations*  
114 as defined in Harrison and Taylor (1997) – and connected metapopulations can provide insight  
115 into the role of dispersal and rescue effects on persistence.

116 . How well do structural (metapopulation capacity) or temporal (persistence time distributions)  
117 measures of metapopulation persistence describe metapopulation dynamics, given that they both  
118 putatively quantify metapopulation persistence? A common assumption of many metapopulation  
119 studies is that structural properties of the metapopulation (e.g., metapopulation capacity) capture  
120 dynamic processes (Hanski and Ovaskainen, 2000). That is, a positive relationship between  
121 structural (metapopulation capacity) and temporal (persistence time distributional fit) measures  
122 of metapopulation persistence should exist. Further, the relationships between environmental  
123 and topological aspects of the metapopulation should correlate well with both measures of  
124 metapopulation persistence, though perhaps with different strength. We would expect that  
125 measures of spatial network topology (e.g., connectance) should strongly correlate with metapopulation  
126 capacity ( $\lambda$ ), as the both measures are based on the same data (i.e., the landscape matrix  $\mathbf{M}$ ).  
127 However, factors influencing distributional fits to persistence times should correspond more to  
128 local environmental conditions and resource availability, as measures of metapopulation persistence  
129 that are based on local dynamics are likely to be more sensitive to local environmental conditions  
130 than measures based on metapopulation structure alone.

131 . Here, we examine the relationship between structural (metapopulation capacity) and temporal  
132 (persistence time distributions) measures of metapopulation persistence, providing a link between  
133 the geographic distribution of habitat patches and the resulting temporal metapopulation dynamics.  
134 Further, we explore power law scaling relationships in patch persistence times, providing evidence  
135 that interconnected populations have similarly heavy-tailed persistence (or extinction) time distributions  
136 compared to isolated replicated populations (Drake, 2014). Using a long-term sampling effort of  
137 *Melitaea cinxia* populations distributed across meadow habitats in the Åland islands sampled over  
138 20 years, we demonstrate a positive relationship our measures of metapopulation persistence for  
139 a set of 88 semi-independent spatial networks (also referred to as *network components*). Further, we  
140 investigate how environmental and topological aspects of the spatial network are related to both  
141 measures of metapopulation persistence. Environmental characteristics, such as mean resource  
142 availability and grazing pressure, were largely unrelated to either measure of metapopulation  
143 persistence, while topological properties – such as modularity and the number of patches in the  
144 network – were strongly correlated to both measures of metapopulation persistence. Together,  
145 this provides a link between structural and temporal measures of metapopulation persistence,  
146 and demonstrates clear relationships between aspects of the landscape matrix and the resulting  
147 measures of metapopulation persistence, either measured using putative dispersal connections,  
148 or through a power law scaling relationship in patch persistence times.

149

## Methods

150

### *Glanville fritillary metapopulation data*

151 In the Åland islands, a set of approximately 4500 habitat patches have been monitored since 1993.  
152 Here, we use data from the Fall surveys of the Glanville fritillary butterfly (*Melitaea cinxia*) nests  
153 sampled annually between 1993 and 2016 (Ojanen et al., 2013). Each habitat patch was occupied  
154 by at least one of two host plant species – either *Plantago lanceolata* or *Veronica spicata* – which  
155 serves as a food and oviposition resource for *M. cinxia*. Habitat patches exist in a mosaic of  
156 inhospitable habitat, and links between habitat patches represent potential dispersal pathways.



157 We examined a subset of 2249 habitat patches which contained sufficient data, leading to the  
158 creation of 88 semi-independent networks (SINs). Each SIN has been identified to be a cluster of  
159 patches where most of the dispersal dynamics are assumed to take place within the SIN (Hanski  
160 et al., 2017). This allows for a certain degree of replication of metapopulations in a natural setting.

161 . Each of these 88 SINs is treated as a metapopulation, and represent a wide range of metapopulation  
162 structures. The number of habitat patches in the SINs ranges from 2 to 147, and patch sizes  
163 ranged from 0.001 to 10.2 hectares. Patch size within SINs tends to be quite variable, with  
164 coefficient of variation (mean divided by standard deviation) varying between 0.03 and 0.34.  
165 This range of metapopulation structures provides both challenge and opportunity to examine  
166 the relationship between metapopulation capacity and persistence time distributions.

167 . R code and data to reproduce the analyses is provided at  
168 <https://doi.org/10.6084/m9.figshare.12576038>.

### 169 *Metapopulation capacity: the structural persistence measure*

170 Metapopulation capacity estimates the ability of a metapopulation to support long-term persistence  
171 of a given species (Hanski and Ovaskainen, 2000) based on the distances among habitat patches  
172 in the spatial network. Specifically, metapopulation capacity ( $\lambda$ ) is the dominant eigenvalue  
173 of the landscape matrix  $\mathbf{M}$ , which is a square matrix describing dispersal connections among  
174 habitat patches. Concretely, the diagonal elements of the landscape matrix  $\mathbf{M}$  are zero, and  
175 off-diagonal elements estimate dispersal probabilities between two habitat patches  $i$  and  $j$  that  
176 are some distance  $d_{ij}$  away from one another. The landscape matrix  $\mathbf{M}$  is estimated for each SIN,  
177 assuming that an exponential decay function as the basis for dispersal (Equation 1), based on  
178 previous research in this system (Hanski et al., 2017).

$$\mathbf{M} = A_i^{x+\gamma} e^{-\epsilon d_{ij}} A_j^\psi \quad (1)$$

179 . In the original formulation, entries of the landscape matrix ( $\mathbf{M}$ ) were defined by including  
 180 patch area ( $A_i$  and  $A_j$ ) as a surrogate measure of carrying capacity. However, non-linear relationships  
 181 and density-dependent dispersal probabilities may influence the relationship between patch area  
 182 and population size (and subsequent dispersal probabilities). To address this, we formulate the  
 183  $\mathbf{M}$  matrix with the inclusion of patch area, assuming that immigration ( $\gamma$ ), extinction ( $x$ ), and  
 184 emigration ( $\psi$ ) are functions of patch area and collectively balance (i.e.,  $x + \gamma = \psi = 0.25$ ;  
 185 Hanski et al. (2017)). We examine the influence of excluding patch area in the calculation of the  
 186  $\mathbf{M}$  matrix in the Supplemental Materials.

### 187 *Persistence time distributions: the temporal persistence measure*

188 We examine power law scaling relationships in persistence time distributions obtained for each  
 189 semi-independent network (SIN). For a given SIN, we calculated persistence times for each patch  
 190 over the course of the study period (1993-2016). Persistence was defined as any consecutive  
 191 period that a given patch was occupied, taking values between 1 to 24. While previous studies  
 192 have developed approaches to address the potential left and right censoring of the time series  
 193 data (i.e., patches may persist for longer than 24 years. Due to the extremely dynamic nature of  
 194 the SINs examined – mean patch persistence time across SINs ranged from 1 to 4.8 – we do not  
 195 attempt to extrapolate to unsampled periods. No patch was occupied for every sampling period,  
 196 and only 4 out of the 2249 habitat patches in the 88 SINs examined persisted for 23 years.

197 . Because of the dynamic nature of these metapopulations, patches could contribute multiple  
 198 persistence times to the distribution. This means that patches that go extinct and are recolonized  
 199 contribute more data to the distribution. However, it is the persistent patches that drive the  
 200 heavy tail of the persistence time distribution, as well as the corresponding value of  $\alpha$ . This  $\alpha$  is  
 201 estimated using maximum likelihood, following the equation

$$\hat{\alpha} = 1 + n \left[ \sum_{i=1}^n \log \left( \frac{x_i}{x_{min} - 0.5} \right) \right]^{-1} \quad (2)$$

202 . Here, we use the hatted symbol ( $\hat{\alpha}$ ) to denote  $\alpha$  as estimated from data. The parameter  $x_{min}$   
203 is the lower bound of persistence times  $x$  where the power law can be fit to the data. Each  
204 SIN has a fit  $x_{min}$  and  $\alpha$  value. In the Supplemental Materials, we explore the distribution  
205 and relationship between  $x_{min}$  and  $\alpha$  values fit for each SIN. Power law distributions were fit  
206 using the `powerLaw` package in R, following the bootstrapping procedure to account for parameter  
207 uncertainty (Gillespie, 2015). Further, goodness of fit to the power law distribution was determined  
208 via bootstrapping following Clauset et al. (2009).

### 209 *Relating metapopulation persistence measures*

210 We related metapopulation capacity ( $\lambda$ ) to the power law fit parameter ( $\alpha$ ) characterizing the tail  
211 of the persistence time distribution for each SIN using a Spearman's rank correlation to account  
212 for a potentially non-linear relationship. Larger values of metapopulation capacity are indicative  
213 of a greater chance of species persistence in the metapopulation. Larger values of persistence  
214 time fits ( $\alpha$ ) correspond to a faster decay in persistence times, and an increased number of  
215 short-lived but quickly recolonized patches. Assuming that consistently colonized patches are a  
216 sign of network-level persistence, a negative relationship between metapopulation capacity ( $\lambda$ )  
217 and persistence time fits ( $\alpha$ ) is expected. However, if we interpret the rapid recolonization and  
218 extinction of patches as a signature of a dynamic, but persistent, metapopulation, a positive  
219 relationship may emerge.

### 220 *Correlates of metapopulation persistence measures*

221 Numerous environmental covariates may influence habitat patch quality, which affects subsequent  
222 colonization and extinction dynamics (Fleishman et al., 2002; Thomas, 1994). Given that metapopulation  
223 capacity does not directly incorporate information on variation in patch quality, but that the  
224 persistence time distributional fit does likely reflect patch quality, we would expect that environmental  
225 conditions would most strongly correlate with the persistence time distributional fits ( $\alpha$ ).

226 . Patch area was estimated during sampling, with the median patch area being approximately  
227 0.6 ha, and the majority of habitat patches smaller than 2 ha. The two common host plants of *M.*  
228 *cinxia* are *Plantago lanceolata* and *Veronica spicata*. We quantified resource availability as the sum  
229 of abundance of these two host plants based on an ordinal scale between 0 and 3 for each species,  
230 with larger values corresponding to a greater plant abundance (Ojanen et al., 2013). Previously,  
231 the summed abundance of these two host plants has been predictive of colonization, extinction,  
232 and occupancy in the Åland islands (Dallas et al., 2019). For each SIN, we calculated the mean  
233 resource abundance and the variance in resource abundance. Grazing pressure was estimated  
234 as the estimated fraction of the habitat patch subjected to grazing based on observations of  
235 damaged plants. *Plantago lanceolata*, which serves as the dominant host plant through much of  
236 the Åland island system, is infected by a powdery mildew pathogen (*Podosphaera plantaginis*;  
237 Tollenaere et al. (2014)), which reduces plant resource quality and subsequent overwintering  
238 survival and emergence of larvae in the spring (van Nouhuys and Laine, 2008). Mildew infection  
239 was estimated as the mean fraction of patches within each SIN where the mildew pathogen was  
240 present across each sampling period.

241 . Aspects of the structure of each SIN may be related to metapopulation persistence. These  
242 include the number of habitat patches in the SIN, as well as several measures of spatial network  
243 structure. For instance, the tendency of patches to cluster into small groups, forming smaller  
244 communities in which dispersal is expected to be stronger, is likely related to spatial network  
245 persistence (Fletcher Jr et al., 2013). To quantify this, we used a series of measures which  
246 capture different aspects of community formation. All measures were performed on the weighted  
247 landscape matrix  $M$  for each SIN, where weights were the dispersal probabilities generated from  
248 the negative exponential dispersal kernel described above.

249 . First, we estimated modularity of the network by first identifying clusters within each SIN  
250 using the random walk approach of Pons and Latapy (2005), and then quantifying the tendency  
251 of these identified communities to result in a modular network, estimated using the *igraph* R  
252 package (Csardi and Nepusz, 2006). Second, we calculated the hub score of the landscape matrix

253  $M$  (Kleinberg, 1999), which is nearly identical to calculation as metapopulation capacity, and is  
254 the dominant eigenvalue corresponding to the principal eigenvector of  $M \times t(M)$  (the landscape  
255 matrix  $M$  multiplied by its transpose). Lastly, we measured a weighted form of transitivity –  
256 also referred to as the ‘clustering coefficient’ – which quantifies the degree of spatial aggregation  
257 in habitat patches within a given SIN (Barrat et al., 2007). All of these measures attempt to  
258 address the distribution of patches in each SIN with respect to their estimated dispersal links  
259 estimated in Equation 1. Consequently, it is important to note that estimates of network structure  
260 described above will be sensitive to the formation of the landscape matrix ( $M$ ). Given that only  
261 metapopulation capacity ( $\lambda$ ) uses information contained in the landscape matrix ( $M$ ), we would  
262 expect metapopulation capacity to be more strongly related to these aspects of dispersal network  
263 structure than persistence time distributional fits.

## 264 Results

265 Some SINs ( $n = 27$ ) did not have enough data to compute distributional fits to the persistence  
266 times ( $\alpha$ ). For the SINs that did have enough data, the best fit values of  $x_{min}$  and  $\alpha$  were quite  
267 variable (see Supplemental Material, Figures A2 - A4). The majority of  $\alpha$  values were between  
268 2 and 3, supporting previous observations (Clauset et al., 2009). Based on bootstrap tests, there  
269 is evidence that the power law is the best fit distribution for 87% ( $n = 53$  of the 61 SINs) of the  
270 persistence time distributions, based on a significance level of 0.05 following the procedure of  
271 Clauset et al. (2009). The  $p$ -value generated from this test can be used as a measure of plausibility  
272 of the fit between empirical data and power law fit. It is not a test of the goodness-of-fit of the  
273 power law directly, as  $p > 0.05$  cannot be interpreted as support of the power law fit, while  $p <$   
274  $0.05$  would suggest that the power law is not the best fit.

275 . There was no apparent spatial pattern in power law fit parameter ( $\alpha$ ) to the persistence  
276 time distribution (Figure 1d) or metapopulation capacity (Figure 1b) of each SIN, though clear  
277 variation was observed in both fit persistence time distributions ( $\alpha \in [1.86 - 5.04]$ ) and metapopulation  
278 capacities ( $\lambda \in [0.003 - 1.56]$ ). Further, there was no significant relationships observed between

279 either metapopulation persistence measure – metapopulation capacity ( $\lambda$ ) or persistence time  
280 distributional fits ( $\alpha$ ) – to either mean patch persistence times or mean fraction of occupied  
281 patches (Figure 2). However, the two measures of metapopulation persistence were strongly  
282 related to one another (Figure 3), suggesting a clear link between the two measures of metapopulation  
283 persistence.

### 284 *Correlates of metapopulation persistence measures*

285 We then related a set of environmental (e.g., mean resource availability) and network (e.g.,  
286 number of habitat patches) to both persistence time distributions ( $\alpha$ ) and metapopulation capacities  
287 ( $\lambda$ ) for each of the studied SINs. We hypothesized that variables not captured in the landscape  
288 matrix may be better described by persistence time distributions, while structural properties  
289 of the landscape matrix ( $M$ ) may be more strongly related to metapopulation capacity. We  
290 found that environmental variables and measures of spatial network structure tended to be more  
291 strongly related to metapopulation capacity (Figure 4). The exception to this was the mean  
292 fraction of patches infected by a mildew pathogen, which was negatively related to persistence  
293 time distributional fits, while we failed to detect any relationship with metapopulation capacity  
294 (Figure 4). Together, we found strong relationships between the metapopulation capacity and  
295 both measures of dispersal network structure and local environmental covariates (Figure 4), but  
296 generally slightly weaker relationships for the distributional fits to patch persistence times.

## 297 **Discussion**

298 The majority of patch persistence time distributions were best fit by the power law, clarifying a  
299 link between extinction time distributions from population ecology – as well as other power law  
300 relationships (Marquet et al., 2005) – and patch-scale persistence time distributions of interconnected  
301 populations. Weak correlations between composite measures of each SIN (mean persistence time  
302 and mean occupancy) and metapopulation capacity belie the significant positive relationship  
303 between structural (metapopulation capacity) and temporal (persistence time distributional fit)

304 measures. This provides evidence for a clear relationship between the two measures of metapopulation  
305 persistence, despite the two measures using information on *either* static network topology (as  
306 estimated in the landscape matrix  $M$ ) *or* temporal data on patch persistence times, effectively  
307 linking two approaches to the estimation of metapopulation persistence. Further, several environmental  
308 and network structural variables were correlated with both metapopulation persistence measures.  
309 However, we found little support for the hypothesis that persistence time distributional fits would  
310 be more closely related to aspects of patch quality which are not considered in the calculation of  
311 metapopulation capacity. This suggests that – at least in the Åland island system – persistence  
312 time distributions for each SIN are largely unrelated to habitat variables at the scale of the entire  
313 metapopulation. Taken together, this suggests a strong link between spatial network topology  
314 and the resulting dynamics, provides evidence for the use of persistence time distributions to  
315 understand metapopulation persistence, and extends theory related to heavy-tailed population  
316 extinction time distributions to understanding interconnected populations and metapopulations.

317 . Patch persistence time distributions characterized by high values – corresponding to dynamic  
318 metapopulations where rapid colonization and extinction events shorten the tail of the persistence  
319 time distribution – were associated with high metapopulation capacity ( $\alpha$ ). This suggests that  
320 the existence of long-term persistent patches may not be a signature of overall metapopulation  
321 persistence. The opposite appears to be the case, where metapopulations composed of patches  
322 which rapidly become extinct and are rapidly recolonized tend to be the most structurally  
323 persistent (based on metapopulation capacity). This finding may be influenced by species traits  
324 such as dispersal ability and survival. However, a species which colonizes a set of habitat  
325 patches and persists in each patch is not a *true* metapopulation (Harrison and Taylor, 1997).  
326 However, the persistence time distribution may be useful outside of these *true* metapopulations,  
327 as understanding the distribution of extinction times is central to population ecology (Drake,  
328 2006, 2014). Further, the persistence time distribution may signal metapopulation "type" (as  
329 defined in Harrison and Taylor (1997)), as mainland-island metapopulations would have a longer  
330 tailed persistence time distribution relative to the classical metapopulation or patchy population.

331 . We failed to detect strong relationships between persistence time distributional fits and local-scale  
332 environmental variation in the Åland island metapopulation. The lack of relationship between  
333 persistence time distributional fits and patch quality variables might simply be a function of the  
334 inherent variation in persistence time distributions and the subsequent power law distributional  
335 fits. This is because habitat patch persistence may largely be a stochastic process, in which  
336 patches go extinct and are recolonized often. This, in turn, strongly influences the distribution  
337 of persistence times and resulting distributional fits. Despite the weak relationships between  
338 patch quality and persistence time distributions, we found strong relationships between network  
339 structure (e.g., modularity) and both measures of metapopulation persistence, suggesting a signal  
340 of the effect of landscape matrix structure on resulting metapopulation persistence. Lastly,  
341 metapopulation capacity was found to be positively related to local-scale habitat covariates  
342 (e.g., mean patch area), even when patch area was not used to quantify dispersal links in the  
343 metapopulation (Figure A8). These correlations could not be explained by the associations  
344 between patch area, resource abundance, and grazing pressure (Figure A9) alone (see Supplemental  
345 Materials for further discussion). Spatial autocorrelation in local environmental conditions which  
346 scale up to the network level might result in correlations between environmental covariates and  
347 metapopulation capacity as well. Examining other metapopulation systems may provide insight  
348 into the relative strength of relationships between environmental and topological covariates and  
349 measures of metapopulation persistence.

350 . To date, metapopulation persistence in a dynamic sense has largely been determined through  
351 model simulations, which quantify metapopulation persistence as the fraction of simulations  
352 in which the metapopulation avoids extinction (Molofsky and Ferdy, 2005) or the mean time  
353 until metapopulation extinction (Johst et al., 2002). While models may be parameterized with  
354 observational data, there remains a disconnect between the theory of metapopulation persistence  
355 and metapopulation dynamics in natural systems (Moilanen, 2002). By quantifying metapopulation  
356 persistence using the distribution of persistence times, it is possible to characterize metapopulation  
357 persistence without the necessity of metapopulation extinction. However, the fit power law  
358 parameter ( $\alpha$ ) to the distribution of persistence times has some limitations. For instance, imperfect



359 detection could cause gaps that strongly influence the tail of the persistence time distribution (i.e.,  
360 those long persisting patches), which can alter the  $\alpha$  parameter of the power law. Further, the  
361 habitat patches which go extinct and are recolonized differentially contribute to the distribution  
362 of persistence times, as they can contribute many small values, whereas persistent patches  
363 contribute fewer values. The ideal measure of metapopulation persistence would incorporate  
364 both information on the spatial arrangement of habitat patches and the persistence times of  
365 patches. Currently, the measures of metapopulation persistence examined here rely on *either*  
366 spatial patch arrangement (metapopulation capacity) or patch persistence times (power law fits).  
367 Future work should attempt to bridge this gap to capture a complete view of metapopulation  
368 persistence, as well as incorporating the role of self-connections of habitat patches (Zamborain-Mason  
369 et al., 2017). Lastly, it is noteworthy that these measures of metapopulation persistence may be  
370 independent of metapopulation stability in some situations. That is, the measures of metapopulation  
371 persistence used here may not capture the ability of the metapopulation to recover from a  
372 perturbation (Gilarranz et al., 2017) (but see Ovaskainen and Hanski (2002)) or targeted attack  
373 (Albert et al., 2000).

374 . The relationship between spatial dispersal network structure and resulting metapopulation  
375 dynamics is not only of theoretical interest. Designing reserves capable of sustaining persistent  
376 populations is a high priority in conservation biology and management of endangered species  
377 (McCarthy et al., 2004; Nicholson and Ovaskainen, 2009). For the majority of these systems, the  
378 data necessary to calculate persistence time distributions are not available. Thus, the finding  
379 of a positive relationship between structural measures of metapopulation persistence and their  
380 temporal counterparts suggests that the use of spatial habitat patch arrangement in reserve  
381 design is justified as a means to enhance metapopulation persistence. Beyond reserve design,  
382 the arrangement of nodes in spatial networks in a fashion that maximizes persistence is of great  
383 importance to the design of many different types of networks (Ebel et al., 2002; Kamra et al., 2006;  
384 Rothenberg, 2001; Wu et al., 2017), including those related to transportation (e.g., highways),  
385 communication (e.g., telephone service centers), disease transmission, and sensor arrays (e.g., air  
386 quality towers). Providing demonstrations of the relationships between topological properties of

387 networks and their corresponding dynamics will further aid the creation of persistent networks.  
388 Identifying these topological properties in ecological networks provides evidence for self-organization  
389 to promote persistence, providing insight into the structure and stability of ecological systems.

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## *Figure legends*

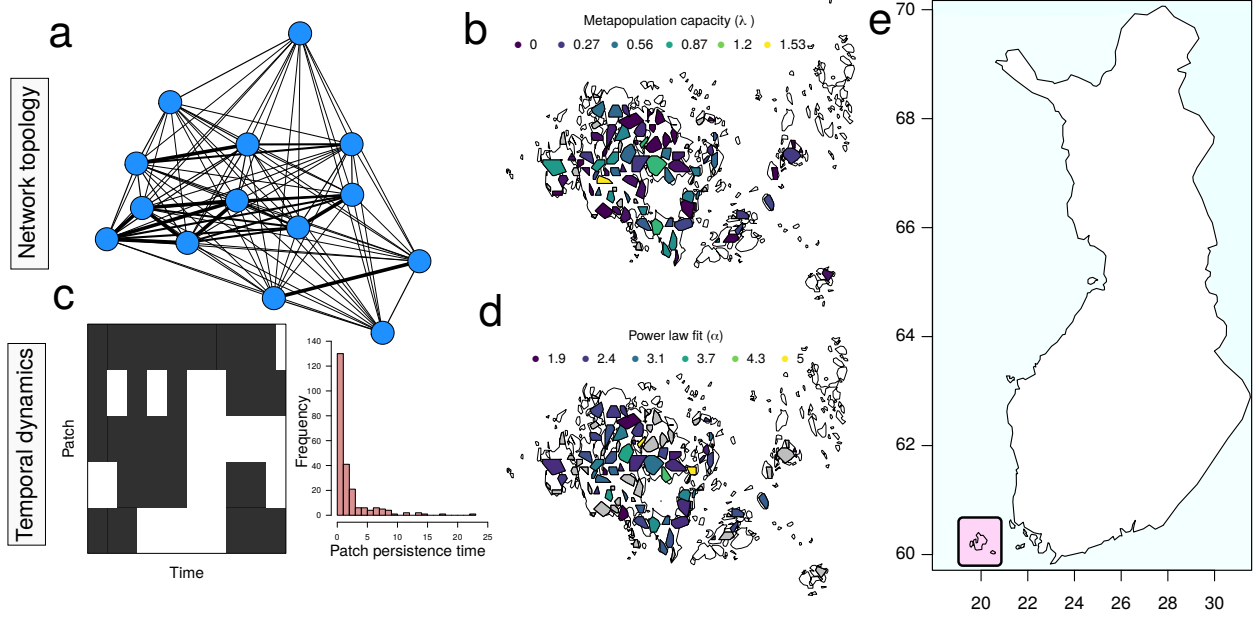
Figure 1: Estimates of metapopulation persistence were based on either the structure of the interaction network (**a**) or the distribution of patch persistence times (**c**), where measures exclusively consider either landscape matrix structure or patch persistence times, respectively. Estimates of metapopulation persistence are mapped onto the set of 88 semi-independent networks in the Åland islands (**b** and **d**), illustrating the variation in metapopulation capacity in **b** and the power law fit ( $\alpha$ ) to the persistence time distribution (**d**). Grey shaded polygons correspond to networks where network statistics could not be calculated.

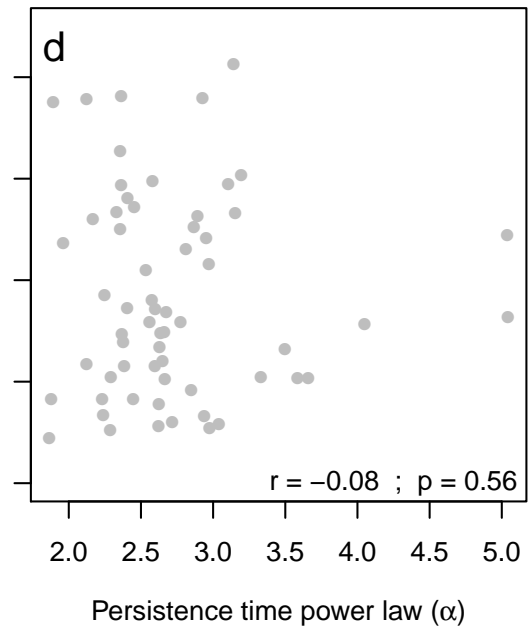
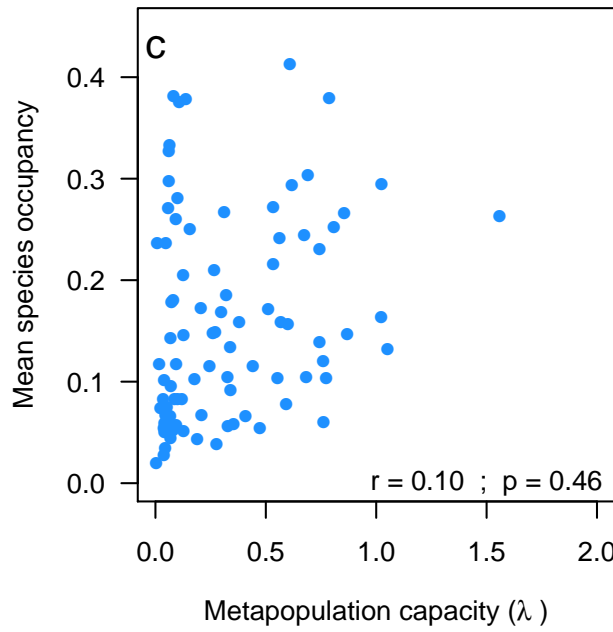
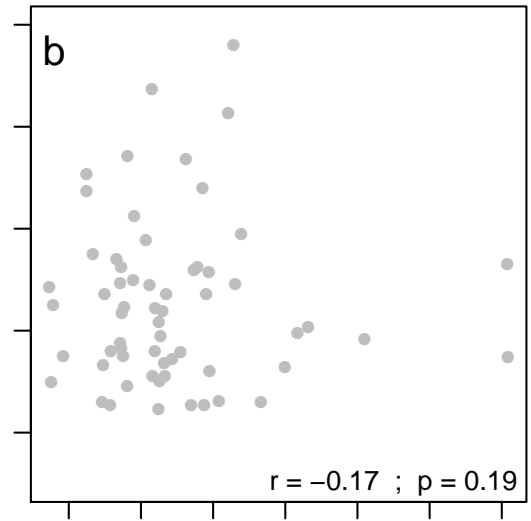
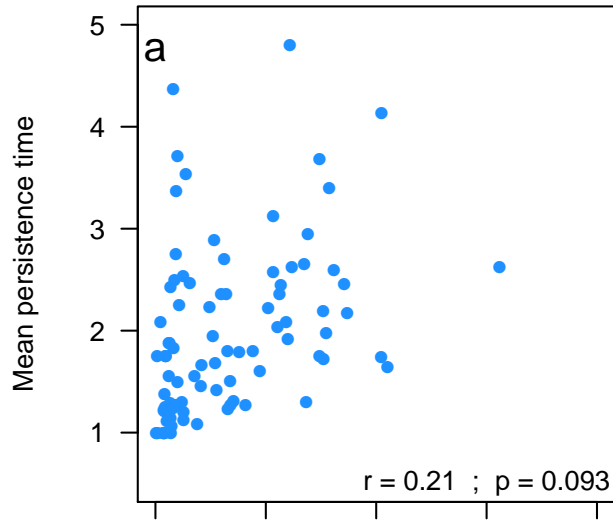
Figure 2: Relationships between metapopulation persistence measures – metapopulation capacity ( $\lambda$ ) and persistence time distributions (power law fits;  $\alpha$ ) – and the mean persistence time of patches (**a** and **b**) and the mean fraction of occupied patches (**c** and **d**) for each semi-independent network (SIN). Reported statistics correspond to Spearman's partial rank correlation coefficient and associated p-value.

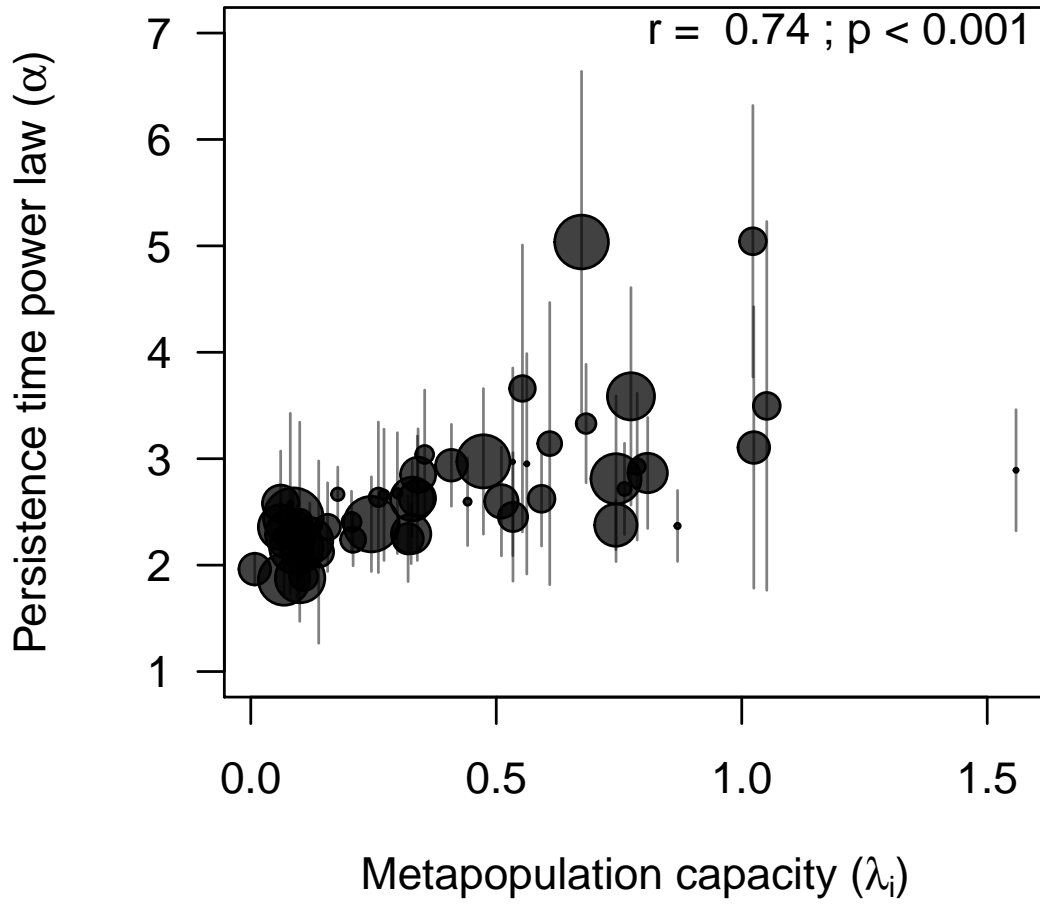
Figure 3: The relationship between metapopulation capacity ( $\lambda$ ) and persistence time distributions (power law fits;  $\alpha$ ) for each semi-independent network (SIN). Error bars represent the estimated standard deviation in the  $\alpha$  parameter, and point size is proportional to the  $p$ -value of the goodness of fit test for the power law fit to the persistence time distribution. Reported statistics correspond to Spearman's rank correlation coefficient and associated  $p$ -value.

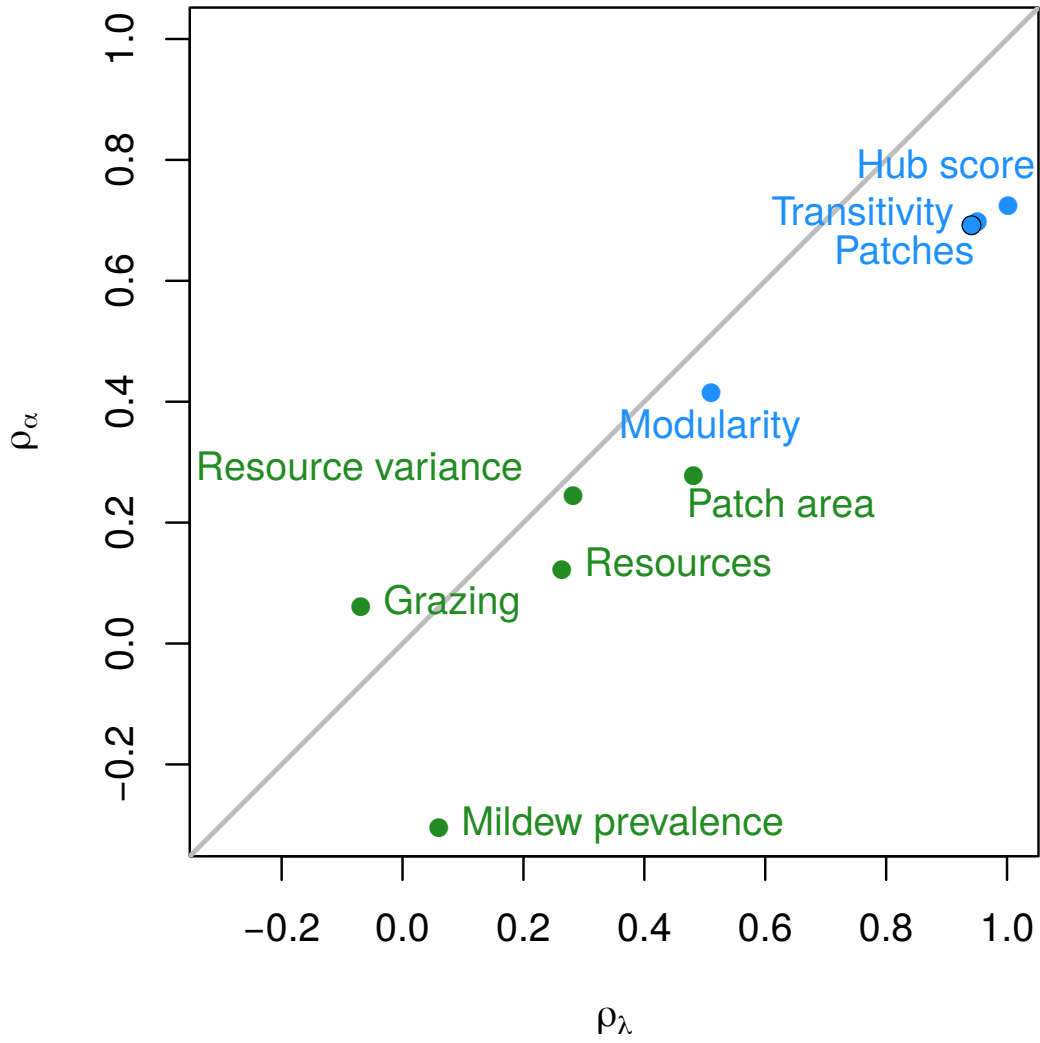
Figure 4: Spearman's correlation coefficients between network (in blue) and environmental (in green) covariates, and both measures of metapopulation persistence ((metapopulation capacity  $\lambda$  and persistence time distribution fits  $\alpha$ ). The grey line corresponds to an equally strong correlation with both measures of metapopulation persistence. The majority of covariates are close to this line, signaling a similar relationship between each covariate and the two persistence measures.

# Figures









527

## Appendix A: Supplementary Materials

528

529 Tad Dallas<sup>a,b,\*</sup>, Marjo Saastamoinen<sup>b,c</sup>, Otso Ovaskainen<sup>b,d</sup>

530

531 <sup>a</sup> Department of Biological Sciences, Louisiana State University, Baton Rouge, LA, USA

532 <sup>b</sup> Organismal and Evolutionary Biology Research Programme, P.O. Box 65, 00014 University of  
533 Helsinki, Finland

534 <sup>c</sup> Helsinki Institute of Life Science, University of Helsinki, Finland

535 <sup>d</sup> Centre for Biodiversity Dynamics, Department of Biology, Norwegian University of Science and  
536 Technology. N-7491 Trondheim, Norway

537 \* tad.a.dallas@gmail.com

538

### *Properties of semi-independent networks*

539

540 The semi-independent networks (SINs) examined in this manuscript were made up of a wide  
541 range of habitat patches in terms of overall number of patches per SIN (Figure A1) and area of  
542 each patch (Figure A6). We view this as an overall strength, as this likely increases the chances  
543 that our findings are robust to other metapopulation systems.

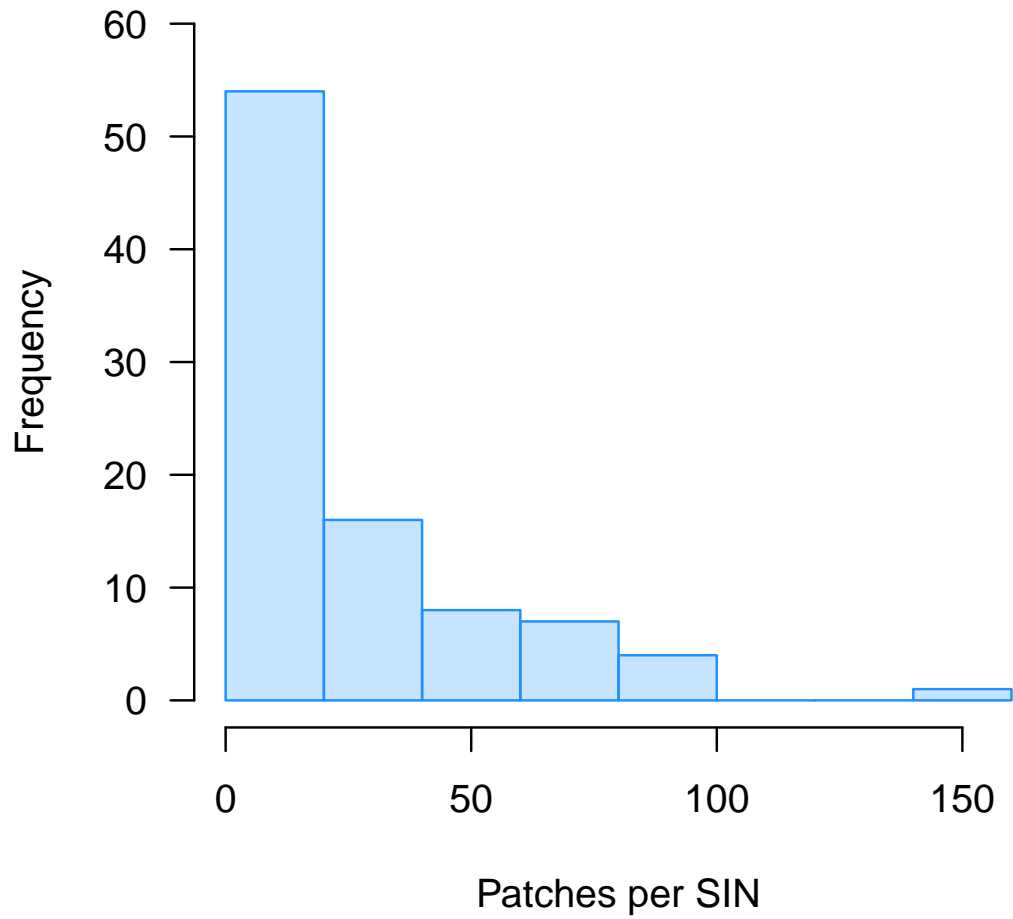


Figure A1: The distribution of the number of habitat patches for each semi-independent network (SIN) in the Åland islands system.



544 *Power law fits to patch persistence times*

545 Best fit power law distributions to the empirical data different greatly in their best fit parameterizations  
546 of  $x_{min}$  – corresponding to the lower threshold persistence time in the power law fit (Figure A2)–  
547 and  $\alpha$  – corresponding to the scaling or shape parameter of the power law (Figure A3). Further,  
548 the standard deviation in the best fit parameter for each semi-independent network tended to be  
549 fairly large as  $x_{min}$  and  $\alpha$  became larger (Figure A4), demonstrating a clear relationship between  
550 the two fit parameters. Finally, the result of the best fit power laws to the persistence time  
551 distribution for a sample of the semi-independent networks demonstrates both the difficulty in  
552 fitting some distributions (e.g., SIN 107 in Figure A5) and the qualitative goodness of fit to other  
553 persistence time distributions (e.g., SIN 17,22,and 3 in Figure A5).

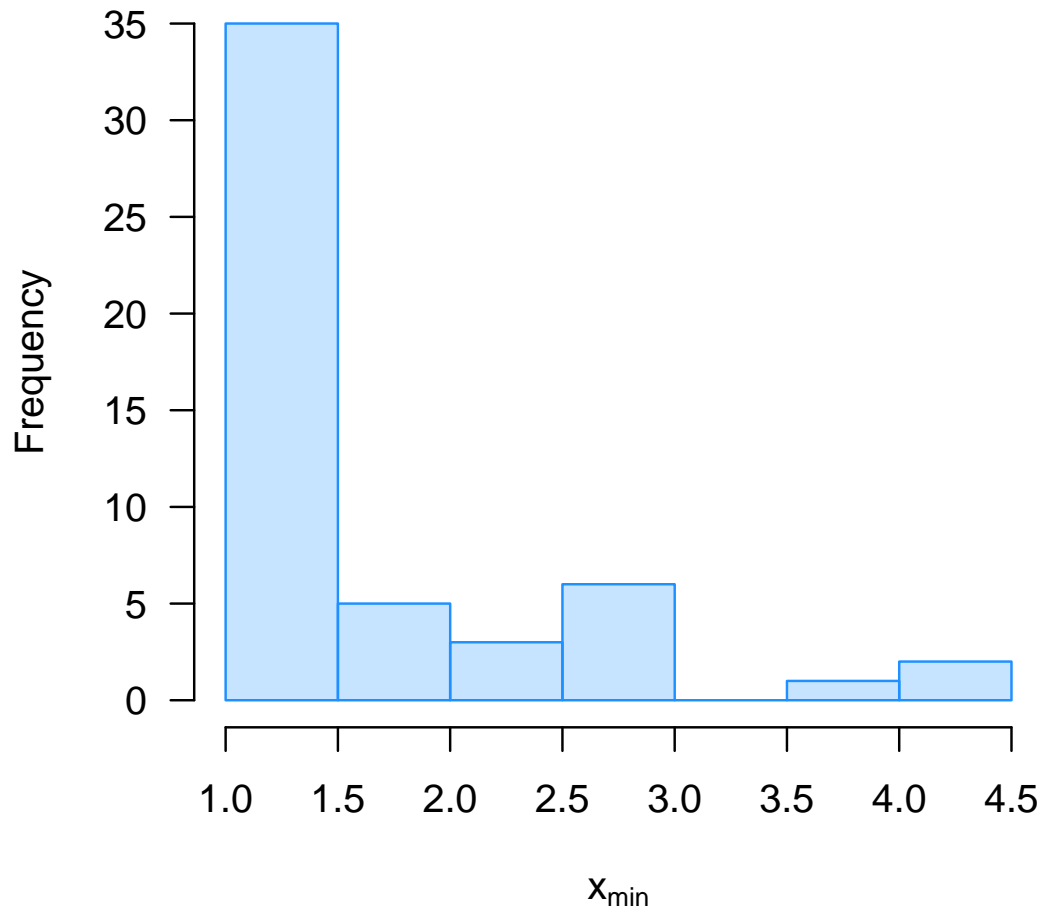


Figure A2: The distribution of  $x_{\min}$  values for the set of semi-independent networks, corresponding to the lower threshold for the power law fitting procedure, optimized using the Kolmogorov-Smirnoff statistic.

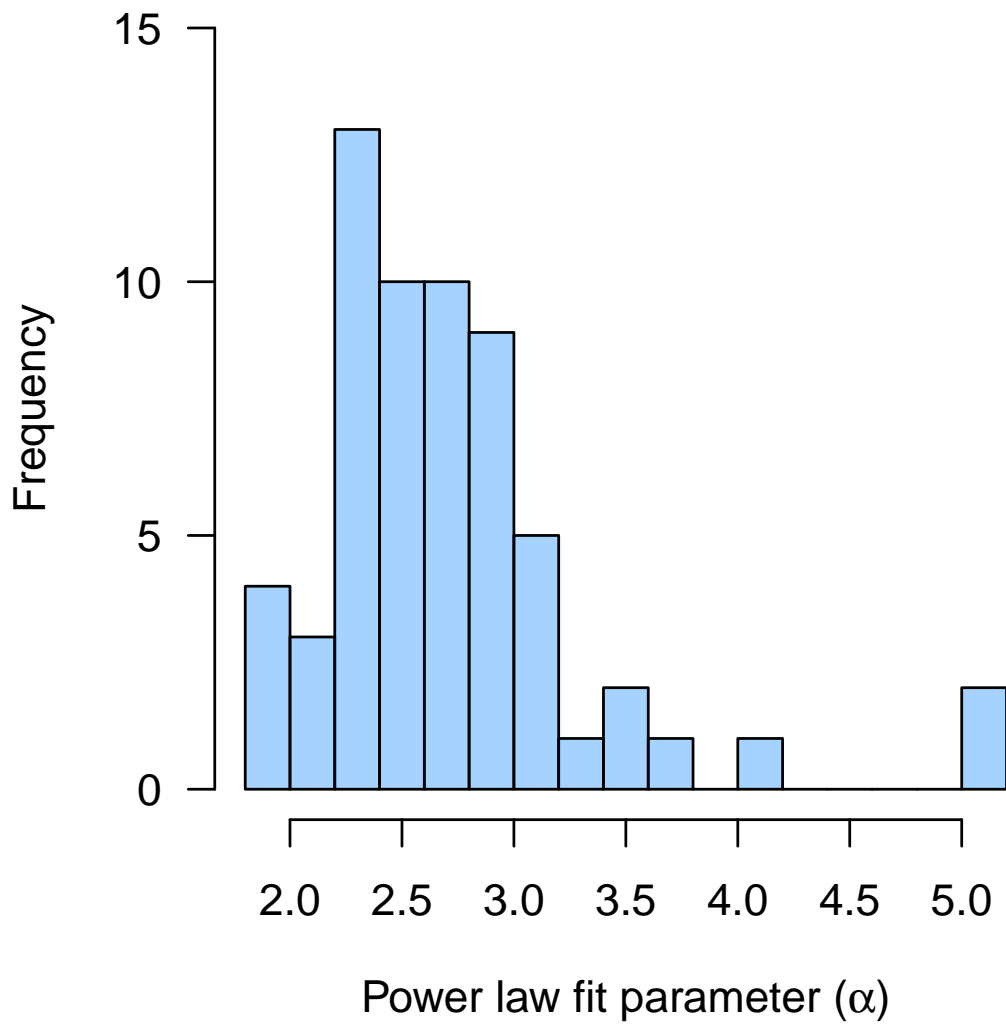


Figure A3: The distribution of power law fit scaling parameter ( $\alpha$ ) for the set of semi-independent networks. The majority of values fall between 2 and 3, as suggested in other empirical systems (Clauset et al., 2009).

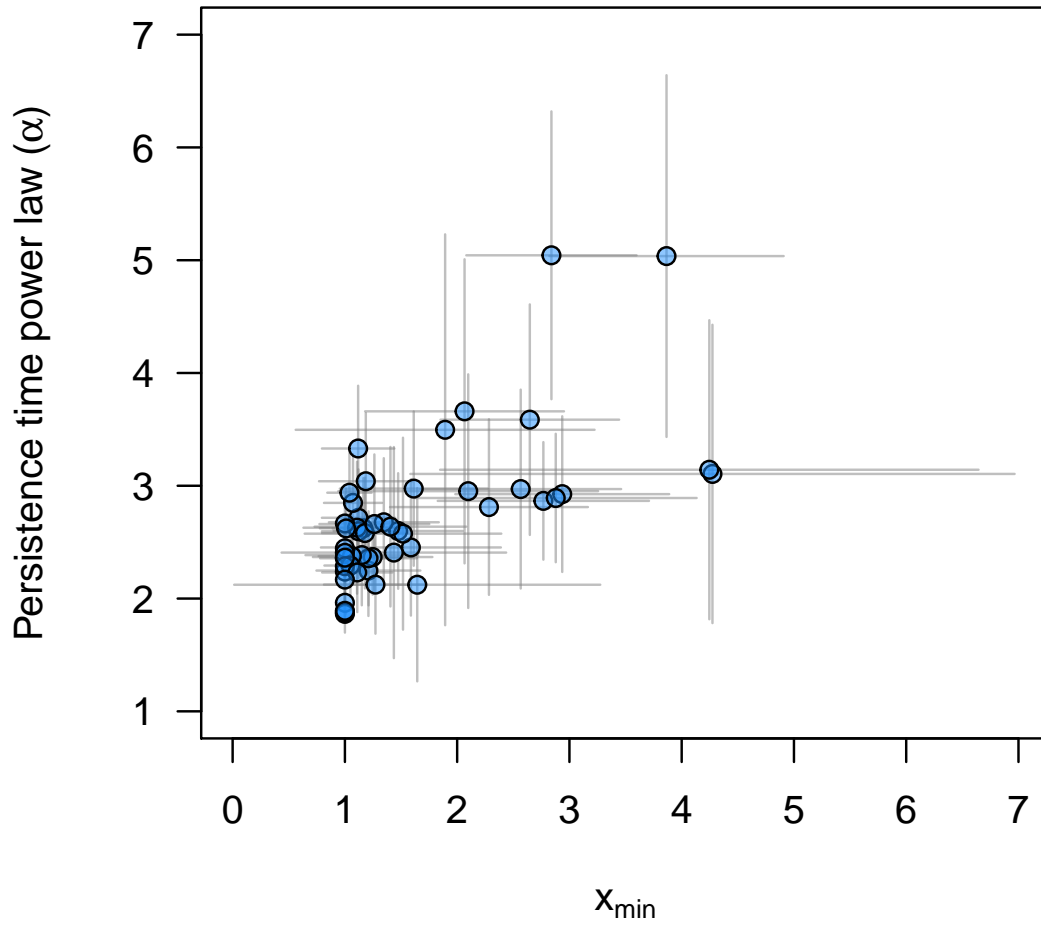


Figure A4: The relationship between the power law fit  $x_{\min}$  and scaling parameter ( $\alpha$ ). Points are best fit values, and error bars correspond to standard deviations in parameter estimates.

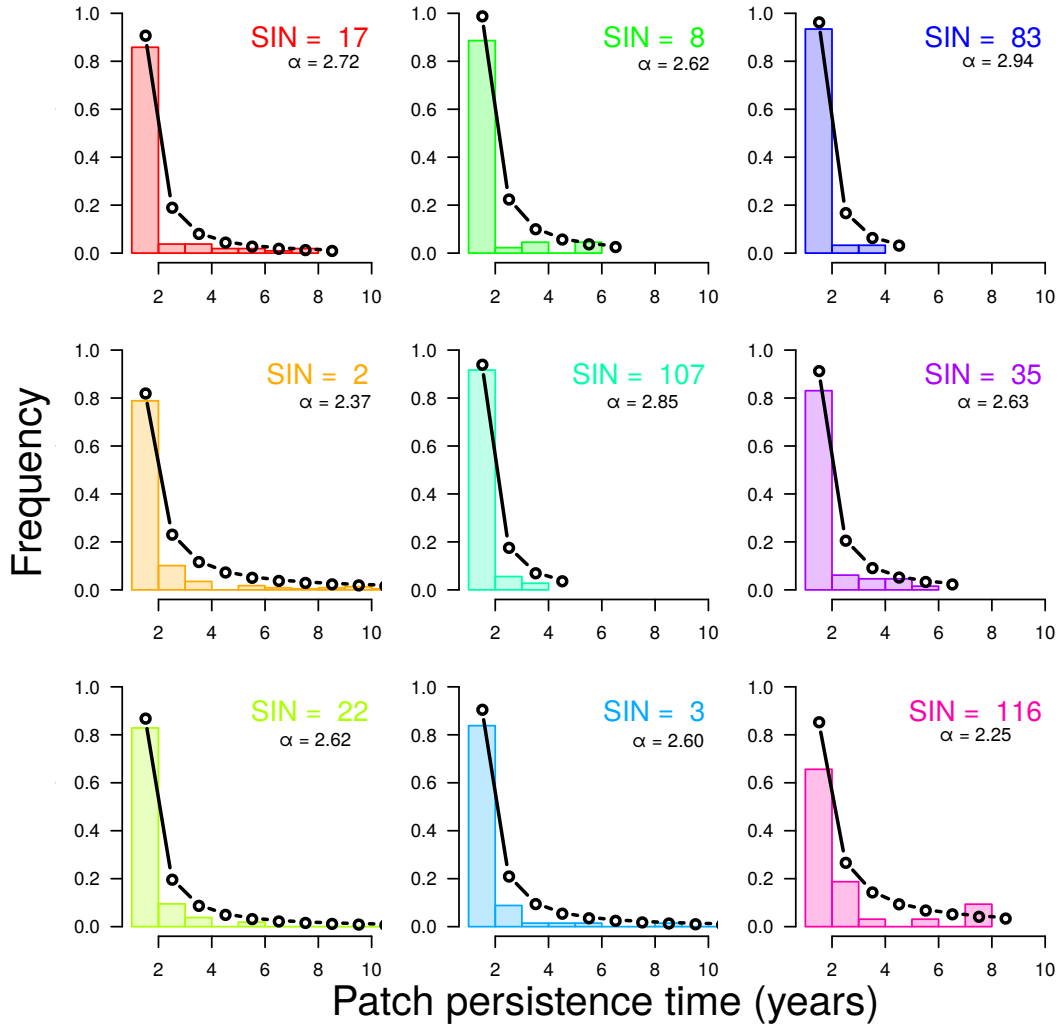


Figure A5: A set of nine of the patch persistence time distributions (bars) and power law fits (black lines, values of power law  $\alpha$  parameter in black), where each panel corresponds to a single SIN (SIN identifier in color).

554

*Without considering patch area in the landscape matrix*

555 Patch area was included in quantification of links between habitat patches. This assumes that  
556 larger habitat patches are more strongly connected than smaller habitat patches. The putative  
557 mechanism underlying this is that larger habitat patches support larger populations, and dispersal  
558 is density-dependent, resulting in a larger number of emigrants from large habitat patches. Patch  
559 area was quite variable in the set of habitat patches and SInS examined (Figure A6), suggesting  
560 that patch area may play a large role in estimating entries of the landscape matrix  $M$ . Here,  
561 we quantify metapopulation capacity based on a landscape matrix ( $M$ ) without the influence of  
562 patch area, finding strikingly similar results compared to when patch area was included (Figure  
563 A7 and A8).

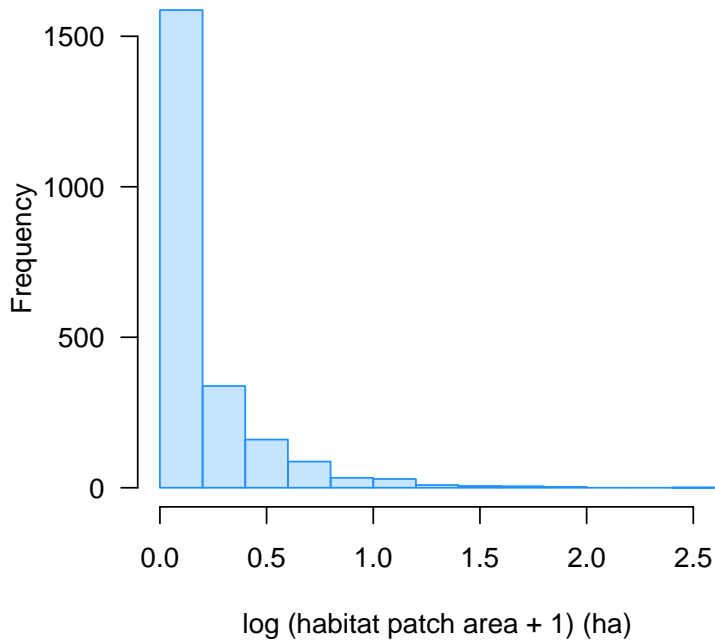


Figure A6: The distribution of habitat patch areas (log+1 transformed) in the Åland islands.

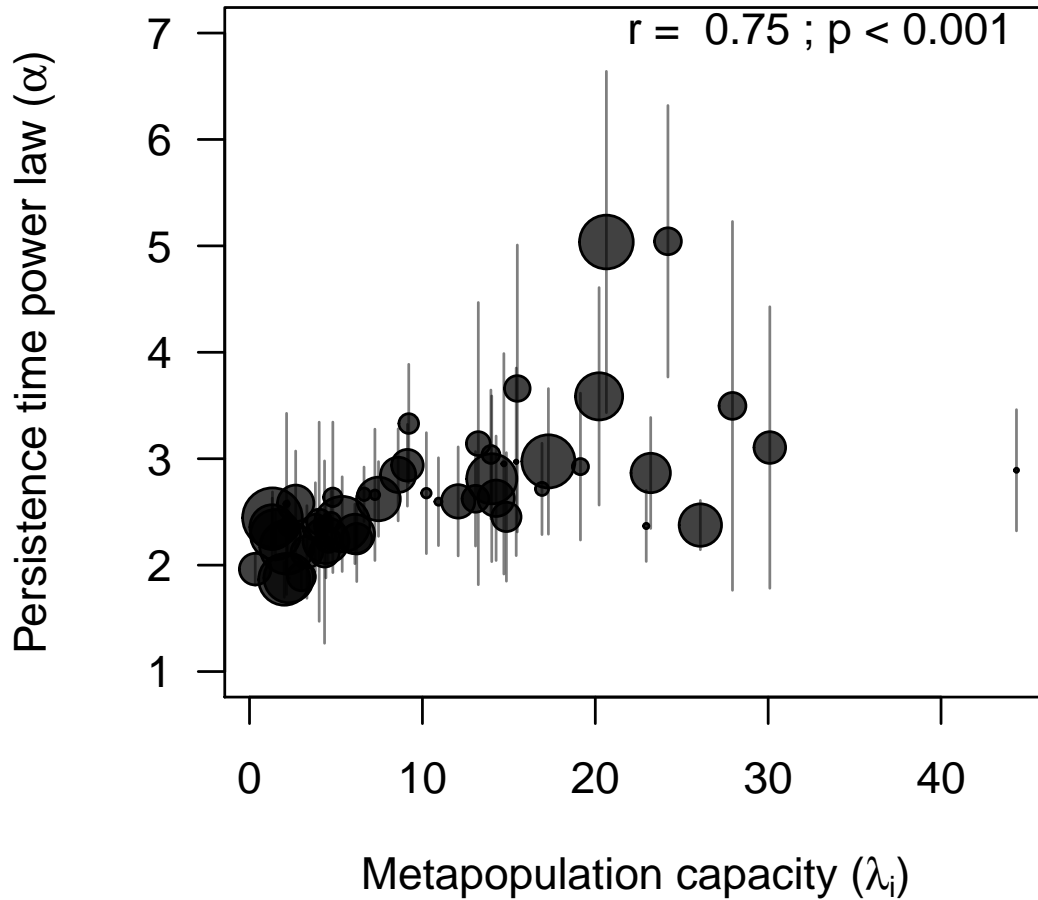


Figure A7: The relationship between metapopulation capacity ( $\lambda$ ) and persistence time distributions (power law fits;  $\alpha$ ) for each semi-independent network (SIN). Error bars represent the estimated standard deviation in the  $\alpha$  parameter, and point size is proportional to the  $p$ -value of the goodness of fit test for the power law fit to the persistence time distribution. Reported statistics correspond to Spearman's rank correlation coefficient and associated  $p$ -value.

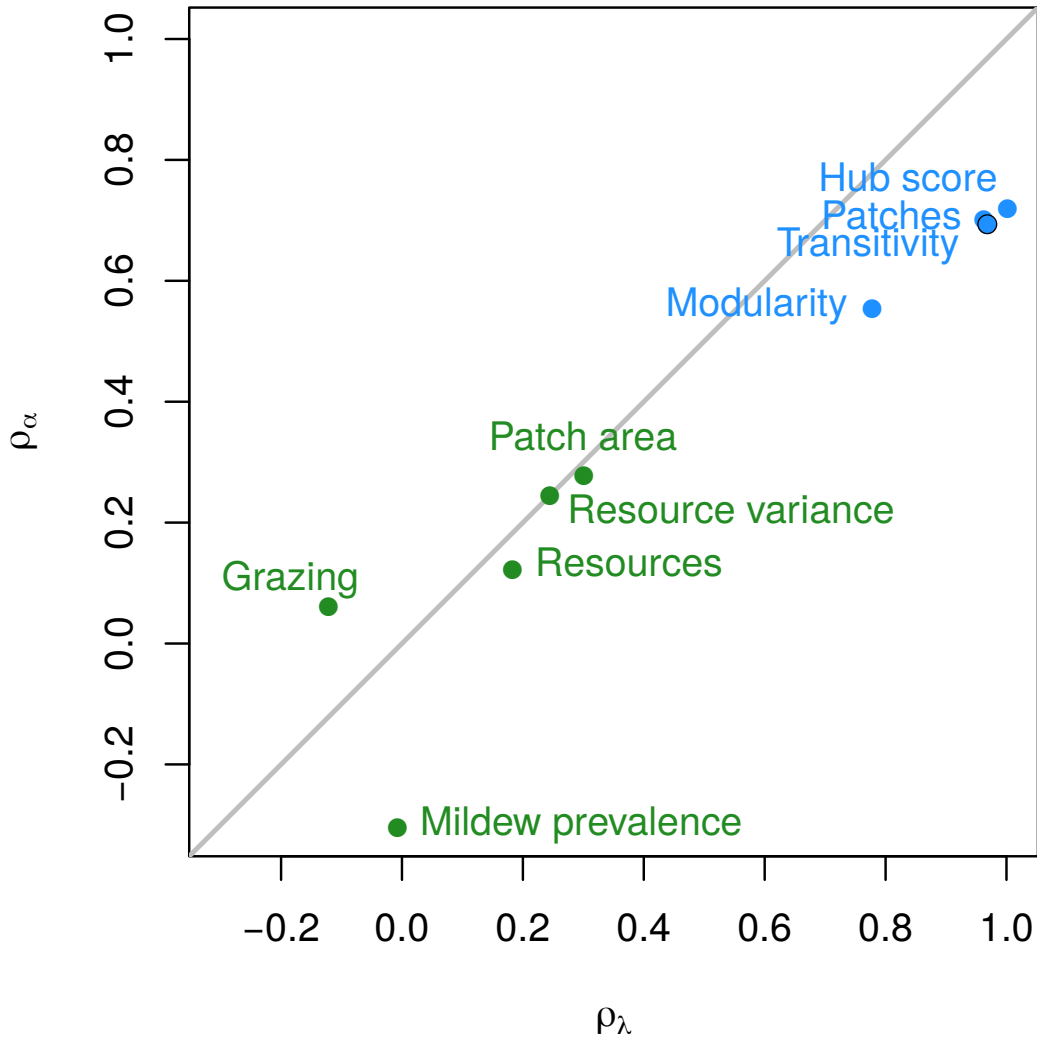


Figure A8: Spearman's correlation coefficients between network (in blue) and environmental (in green) covariates, and both measures of metapopulation persistence ((metapopulation capacity  $\lambda$  and persistence time distribution fits  $\alpha$ ). The grey line corresponds to an equally strong correlation with both measures of metapopulation persistence. The majority of covariates are close to this line, signaling a similar relationship between each covariate and the two persistence measures.



### *Resource availability and grazing pressure*

564

565 Numerous relationships existed between environmental variables and metapopulation capacity,  
566 despite metapopulation capacity being based solely on the landscape matrix (**M**). Given this, why  
567 is metapopulation capacity often related to environmental variables? One potential reason is that  
568 collinearity among patch area and environmental variables allows environmental variation to be  
569 captured by metapopulation capacity. This can be observed in the relationship between patch  
570 area and resource availability ( $r = 0.30$ ,  $p = 0.004$ ), and in the subsequent relationship between  
571 resource availability and grazing pressure ( $r = -0.37$ ,  $p = 0.0003$ ; Figure A9). However, as noted  
572 in the main text, this explanation does not account for the fact that environmental correlations to  
573 metapopulation capacity (Figure A8) were maintained when patch area was removed from the  
574 estimation of the landscape matrix (**M**).

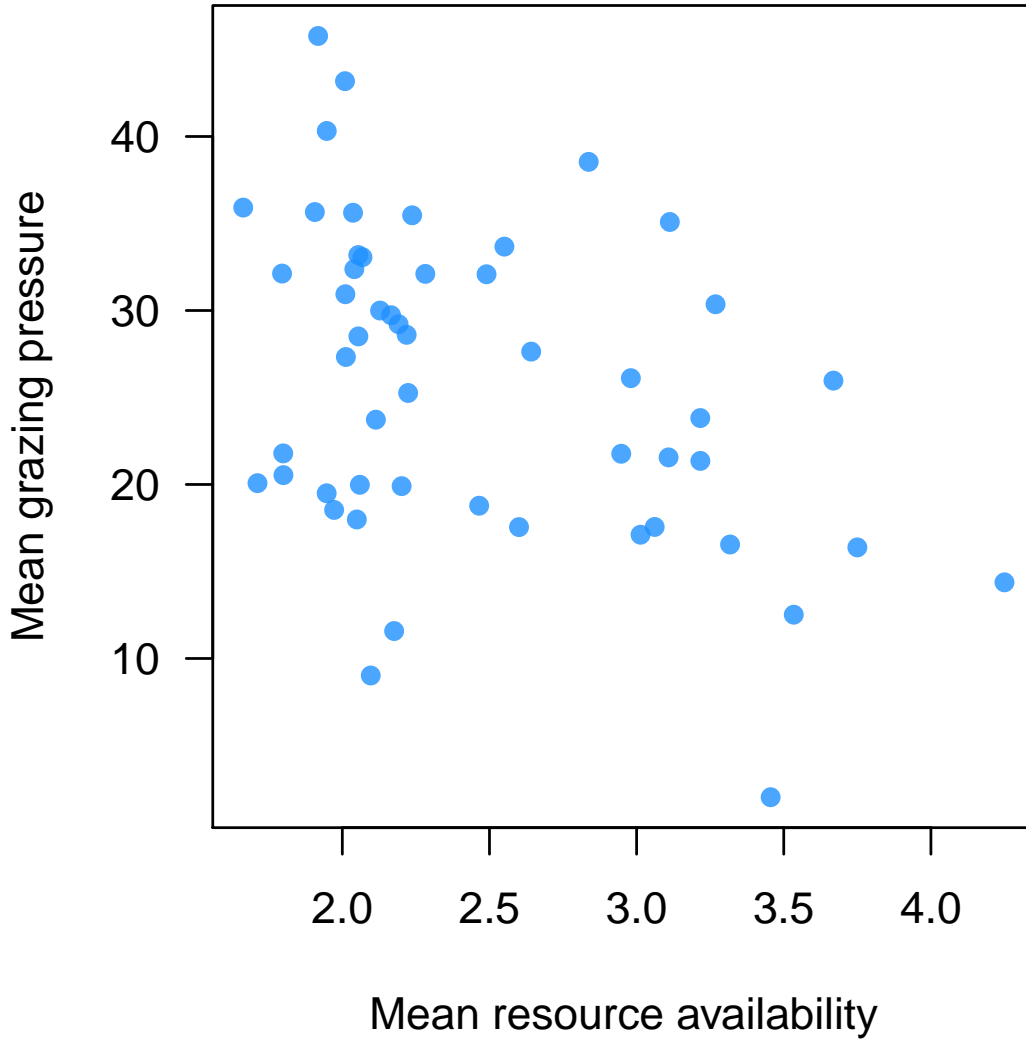


Figure A9: The relationship between mean resource availability – quantified as the mean of the sum of *V. spicata* and *P. lanceolata* abundance values across the sampling period – and mean grazing pressure over the same time period.