Letter

Assessing the ecological resilience of communities to environmental changes

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Abstract

Here we propose two metrics to assess the ecological resilience of communities based on how changes in the overall abundance of individuals affect the number of species. The *community sensitivity* expresses the rate of change in the log expected number of species with respect to the log expected total number of individuals, whereas the *community resistance* is the proportional reduction in community size that will reduce the expected number of species by one. Estimates of these metrics in four bird communities in European deciduous forests using a stochastic model for the community dynamics revealed large differences in the resilience to permanent changes of the environment. In particular, stochastic influences from environmental fluctuations strongly affected the sensitivity and the resistance caused by area loss or increased environmental stochasticity. This shows that ecological resilience is closely related to which processes that most strongly affect the temporal dynamics of communities.

INTRODUCTION

An important feature of any ecological system is its resilience to external disturbances, which Pimm (1991) defined as the time to return to conditions before the disturbance. This also determines the magnitude of disturbances that can be absorbed before structures and processes affecting basic characteristics of the system are altered (Holling 1973), which Pimm termed the system's resistance to environmental changes. During a time when Earth's ecosystems change at an alarmingly high rate (Diaz *et al.* 2019), precise and easily interpretable measures of the capacity to withstand external disturbances become important to quantify and predict ecological changes. Still, quantification of ecological resilience remains challenging, mainly due to the complexity of the processes involved in structuring ecosystems both in time and space (Baho *et al.* 2017; Ross *et al.* 2021). Here we propose two measures that can be used assess the resilience of communities to permanent changes in the environment based on characteristics of the community dynamics.

An important characteristic of communities is the form of the distribution of species abundances (Preston 1948; Williams 1964; Tokeshi 1993). Their shape is dependent on the patterns in the population dynamics of the species constituting the community. For example, the neutral theory of community dynamics (Hubbell 2001) assumes that the dynamics is only affected by demographic stochasticity and generates Fisher's famous logarithmic series species abundance distribution (Fisher *et al.* 1943). Another, more ecologically realistic model for the population dynamics is to assume a loglinear model of density regulation and to include environmental stochasticity, which results in a lognormal species abundance model (Engen & Lande 1996b). Thus, specific assumptions about the underlying dynamics of the species affect temporal turnover rates of species, which influence the relationship between number species and total abundance of individuals in the community (McGill *et al.* 2007;

Sæther *et al.* 2013; Engen *et al.* 2017) and may generate stability as a consequence of long-term evolution of competing species (Engen *et al.* 2021) .

Modelling community dynamics have shown that the temporal variance in the log abundances of species can be partitioned into different components with an ecological meaningful interpretation (Engen & Lande 1996b, a; Engen 2007a; Engen *et al.* 2017). Empirical analyses of communities from several taxa have shown that in most cases the permanent heterogeneity among species in the dynamics, generated by species-specific differences in the stochastic population growth rates also giving variation in carrying capacities K, is the component explaining the largest proportion of the variance in the species abundance distribution (Engen *et al.* 2002; Lande *et al.* 2003; Grøtan *et al.* 2012; Grøtan *et al.* 2014; Solbu *et al.* 2018). This component can be interpreted as representing the effect of niche differentiation among the species (Chase & Leibold 2003; Engen *et al.* 2021). Additional important components affecting the dynamics are fluctuations in the environment influencing all species similarly over time as well as species-specific environmental stochasticity (Bowler *et al.* 2018). Thus, the temporal relationship between species number and abundance is determined by specific assumptions about how different ecological processes contribute to the community dynamics (Gotelli *et al.* 2017). We suggest that this can provide a quantitative framework to assess the impact of environmental changes on community structure.

Many changes of the environment affecting the species composition of communities do not only have a temporal component, but also influence the spatial distribution of abundances (Chase *et al.* 2019; Antao *et al.* 2021). For example, climate change and loss or fragmentation of important habitat types, which are considered as two of the major threats to the diversity of species on the Earth (Diaz *et al.* 2019). Variation in climate primarily affects the dynamics at a given locality either through the magnitude of environmental stochasticity

105 or by inducing permanent changes in the environment affecting resource abundances and
106 population sizes in the average environment, whereas habitat loss primarily influences the
107 spatial configuration of landscape. However, these two threats are not independent of each
108 other because the stochastic influences on the population dynamics as well as community
109 structure such as the total number of species tend to depend on area size (Rosenzweig 1995;
110 Hanski & Gaggiotti 2004). As a consequence, the effects on the extinction risk of a species
111 caused by an increase in the environmental stochasticity or by deterioration of the
112 environment will be stronger in small than in large areas (Lande *et al.* 2003). Thus,
113 decreasing area sizes combined with increased environmental stochasticity may have
114 dramatic consequences for species diversity in a larger area. This illustrates that assessment
115 of the resilience of communities should include a temporal as well as a spatial dimension
116 (Allen *et al.* 2016; Jones *et al.* 2020).

117 One of the most general relationships in ecology is the increase in the number of
118 species with increasing area (Rosenzweig 1995). In principle, such a relationship can also be
119 used to estimate the number of species expected to be found when randomly sampling a sub-
120 area or a random fraction of the individuals in the community. This approach was pioneered
121 by Fisher et al. (1943), who found, using the well-known limiting form of the gamma
122 distribution, that the number of species was approximately proportional to the log number of
123 individuals in the sample. However, Preston (1962), Engen (1974) and May (1975) rather
124 suggested a linear relationship on a double-logarithmic plot, which has received wide
125 empirical support although the slopes show large variability (Rosenzweig 1995). Engen
126 (2007b) showed, assuming a lognormal species abundance distribution, that these linear
127 relationships at logarithmic scales were strongly influenced by the factors affecting the
128 community dynamics. Thus, this indicates that species area curves can be used to characterize
129 the impact of a permanent environmental change on the resilience of communities.

130 The purpose of the present paper is to show, following Engen (2007b, a), how
131 changes in overall resource availability or area affect the expected number of species in a
132 community, using a stochastic model for the community dynamics that includes permanent
133 species-specific differences in the population dynamics. This relationship will be used to
134 propose two metrics that can be used to characterize the *sensitivity* and *resistance* of the
135 community to permanent changes in the environment. We will then illustrate the application
136 of this approach by comparing the resilience of four European bird communities with very
137 different dynamical characteristics. Finally, we will analyse the sensitivity and resilience of
138 these communities to two specific forms of environmental change: a reduction in area size
139 and increased environmental stochasticity. This will enable us to evaluate which types of
140 communities that are most resilient against environmental change.
141

142 **MODEL FOR THE COMMUNITY DYNAMICS**

143 To illustrate the basic concepts, temporal variation in community structure is described based
144 on results obtained by Engen and Lande (1996b) using a Gompertz model of density
145 regulation (May 1981) with permanent differences among species in their dynamics. If the
146 vector of log abundances in a community with S species is $\mathbf{X} = (X_1, X_2 .....X_s)$, the
147 dynamics of the i'th species can be described by a Ornstein-Uhlenbeck diffusion process
148 (Karlin & Taylor 1981)

149 $$dX_i(t) = [r_i - \gamma X_i(t)]dt + \sigma_e dB_i(t), \qquad (1)$$

150 where r_i is the growth rate of species i at small densities, γ is the strength of density
151 regulation and σ_e^2 denotes the variance of the process, caused by environmental stochasticity.
152 The mean change in log abundance $r_i - \gamma X_i$, is linear at the logarithmic scale by the
153 Gompertz form of density regulation (Royama 1992). This loglinear diffusion process

produces a lognormal species abundance distribution (Engen & Lande 1996b), assuming independent population dynamics among the species. Comparative analyses suggest that the distribution of abundances of species in many communities fits this distribution quite well (Ulrich *et al.* 2010). Furthermore, patterns of temporal variation in a large number of communities from several taxa indicate evidence for stationarity of the dynamical process (Dornelas *et al.* 2013; Gotelli *et al.* 2017).

We introduce heterogeneity among species in the population dynamics following Engen and Lande (1996b) by assuming the growth rate r is normally distributed among species with mean r_0 and variance σ_r^2. Based on the characteristics of the stationary distribution of the Ornstein-Uhlenbeck diffusion process (Karlin & Taylor 1981), the log abundances are normally distributed with mean r/γ and variance $\sigma_e^2/2\gamma$. The heterogeneity among species in their dynamics is introduced as variation in r/γ, which is equivalent to variation in the carrying capacity K at a logarithmic scale. This gives the stationary distribution with mean r_0/γ and variance $\sigma_e^2/2\gamma+\sigma_r^2/\gamma^2$.

The environmental variance in the population dynamics can be partitioned as $\sigma_e^2=\sigma_c^2+\sigma_s^2$, where σ_c^2 denotes the common stochasticity in the environment affecting all species similarly. The second term is the species-specific stochastic effects that yields a temporal autocorrelation in log abundances, $\mathrm{cov}[X_i(t),X_i(t+u)]=\sigma_e^2e^{-\gamma u}/2\gamma$, with exponential decay at rate γ. The variance of log abundances among species, including species-specific heterogeneity in the dynamics, becomes

$$\mathrm{var}[X_i(t)]=\frac{\sigma_s^2}{2\gamma}+\frac{\sigma_c^2}{2\gamma}+\frac{\sigma_r^2}{\gamma^2}. \qquad (2)$$

For this dynamic community model Engen (2007b) showed that the expected number of species in the community is

177 $$\mathrm{E}[S] = \frac{2\beta}{\sigma_e^2} e^{s_0/(\omega\sigma_e^2)} \sqrt{\pi\sigma_e^2/\omega}\,\Phi(\eta/\rho), \quad (3)$$

178 where β is the rate at which new species enter the community through speciation or
179 immigration, s_0 is the mean stochastic growth rate (and $r_0 = s_0 + \sigma_e^2/2$), $\omega = \gamma - 2\sigma_r^2/\sigma_e^2$,
180 $\eta = s_0/\omega$, $\rho^2 = \sigma_e^2/(2\omega)$ and Φ is the standard normal integral. Similarly, the expected
181 number of individuals in the community is

182 $$\mathrm{E}[N] = \frac{2\beta}{\sigma_e^2} e^{s_0^2/(\omega\sigma_e^2)} \sqrt{\pi\sigma_e^2/\omega}\, e^{(s_0+\sigma_e^2/4)/\omega}\,\Phi(\eta/\rho + \rho). \quad (4)$$

183 The advantage of this approach is that it provides links between parameters
184 describing the dynamics of the single species, the form of the distribution of abundances of
185 species constituting the community and the community dynamics described by the
186 temporal turnover of species (Sæther *et al.* 2013; Engen *et al.* 2017). This enables us to
187 assess how different processes affecting fluctuations in abundance of single species affect
188 the temporal changes in species composition of the community. Here we focus on the
189 lognormal species abundance distributions (Sæther *et al.* 2013). Other assumptions about
190 the underlying dynamics will produce different species abundance distributions (Engen &
191 Lande 1996a; Hubbell 2001) and differences in turnover of species over time (Engen
192 2007a). Still, our basic concepts for evaluating ecological resilience will apply, irrespective
193 of assumptions regarding factors affecting the dynamics of single species.
194
195 **MEASURES OF ECOLOGICAL RESILIENCE**
196 Species composition and the total abundance of individuals in a community at a single
197 locality often shows large variability over time (Preston 1960; Williams 1964; Pimm
198 1991). Here we propose that an important impact of environmental changes on the species
199 diversity is how changes in total abundance (eq. 4) affect species numbers (eq. 3). The

200 *community sensitivity* can be expressed according to Engen (2007b) as the rate of change in
201 the log expected number of species with variation in the log expected total number of
202 individuals determined by varying area size or amount of resources, which is

203 $$z = \frac{d \ln \mathrm{E}[S]}{d \ln \mathrm{E}[N]} = \frac{1 + \eta^2 / \rho^2 + G(\eta / \rho)}{1 + \eta^2 / \rho^2 + G(\eta / \rho + \rho) + 2\eta + \rho^2}, \quad (5)$$

204 where $G(y) = y\phi(y) / \Phi(y)$. Accordingly, a large value of z indicates a community in
205 which the number of species is strongly affected by a change in available resources.

206 Another measure of the effects of permanent changes in the environment is the
207 *community resistance*, defined as the rate of change in log number of individuals N with
208 respect to the expected number of species

209 $$I = \frac{d \ln \mathrm{E}[N]}{d\mathrm{E}[S]} = \frac{d \ln \mathrm{E}[N]}{\mathrm{E}[S] d \ln \mathrm{E}[S]} = 1 / (z \mathrm{E}[S]), \quad (6)$$

210 which is the reduction in log community size that will result in a reduction of the expected
211 number of species equal to one (Engen 2007b).

212 To estimate community resistance I, we need an estimate of the expected number of
213 species. We estimate the expected number of species by

214 $$\widehat{\mathrm{E}[S]} = S_{observed} / (1 - p(0)), \quad (7)$$

215 where $S_{observed}$ is the total number of unique species observed across all time points, and
216 $p(0)$ is the probability that a species is not observed over the same number of time points,
217 estimated by fitting the Poisson lognormal species abundance distribution (Bulmer 1974;
218 Sæther *et al.* 2013). Although this estimate often becomes uncertain (O'Hara 2005), we
219 propose that it still can be used to analyse overall trends in species numbers (Figure 1).
220
221
222

ANALYSES OF RESILIENCE OF TEMPERATE BIRD COMMUNITIES

To illustrate the application of this approach to quantify the effects of environmental change on the characteristics of communities, we use four long-term studies ($\geq$37 years) of temporal variation in species abundances in four bird communities, located in European deciduous forests. All population estimates were based on nest search or mapping of territorial individuals within a specific area (Enemar 1959; Anonymous 1969). The two most northern study areas, Ammarnäs and Budal, were located in subalpine birch forests in northern Sweden (65ºN) at 540 to 720 m a.s.l. (Enemar *et al.* 2004) and in Central Norway (62ºN) at 750 to 920 m a.s.l. (Hogstad 2005), respectively. The other Swedish study area was located in the Birdsong Valley in southern Sweden (55º N) containing a mixture of deciduous tree species (see maps in Enemar et al. (1994)). The British study site was Eastern Wood, which is an oak woodland located in the southern English county of Surrey (51º N). Here the temporal variation in the composition of the avifauna was studied in a macro-ecological perspective by Gaston and Blackburn (2000).

Estimation procedures

We model the species abundance distributions by a Poisson GLMM with the log link function

$$\ln \lambda_i(t) = \mu + k_i + s_i(t) + c(t). \qquad (8)$$

Here $\mu = r_0 / \gamma$ is the mean log abundance or the carrying capacity of species in the community, which is the intercept in a GLMM. There are three random effects in this model: k_i is the species heterogeneity, describing variation among species in the carrying capacity, $k_i \sim N(0, \sigma_k^2 / 2\gamma^2)$. Following Engen and Lande (a, b), we can also describe species heterogeneity as variation among species in the growth rate *r* since $\mathrm{var}[k_i] = \sigma_k^2 = \sigma_r^2 / \gamma^2$. Environmental stochasticity is described by two components, a species-specific and a

common response to fluctuations in the environment. The species-specific contribution to the environmental variance is $s_i(t) \sim N(0, \sigma_s^2 / 2\gamma)$, which is temporally correlated at time steps t and u so that $\text{cov}[s_i(t), s_i(t+u)] = \sigma_s^2 e^{-\gamma u} / 2\gamma$. The common environmental variance is $c(t) \sim N(0, \sigma_c^2/2\gamma)$ and generates interspecific correlation in the noise (Loreau & de Mazancourt 2008). The environmental variance then becomes $\sigma_e^2 = \sigma_s^2 + \sigma_c^2$, which gives (eqn. 2) that the total variance of the species abundance distribution is $\sigma^2 = \sigma_s^2 / 2\gamma + \sigma_r^2 / \gamma^2 + \sigma_c^2 / 2\gamma$. To estimate community sustainability, we need the estimated mean log abundance, $\eta = \mu$, and variation due to species specific responses to environmental fluctuations, $\rho^2 = \sigma_s^2/2\gamma$.

We estimate the parameters of the Poisson GLMM above using the package `jqpWPE` in R (Brooks et al. 2017, R Core Team 2021). When fitting a Poisson GLMM to community data, the optimisation algorithm will in some cases find the among-species variation to be close to zero. Although this might be the optimal value for the algorithm, it does not necessarily make ecological sense. In these cases, we keep the value of among-species variation fixed for a range of values and estimate the other parameters. This will generate parameter estimates as a function of the fixed value for among-species variation. For within-species variation, this function is convex, and therefore we select the value of among-species variation that minimises the within-species variation. In many cases this value also maximises the strength of density regulation or is close to the maximum.

RESULTS

In none of the communities a significant trend in the expected number of species recorded was apparent (Figure 1). This indicates that the underlying assumption of a stationary community dynamics is not violated. However, both species richness (Figure 1, Table 1) and the relative contribution of different processes to the dynamics (Table 1) showed large

differences among the communities. The dynamics of the bird community in Budal was characterized by the largest species-specific response to environmental fluctuations, indicating large within-species differences in fluctuations over time. The strong density regulation in Budal also contributed to the largest ecological heterogeneity among species, described as variation in long-run growth rate (σ_r^2). The two Swedish communities had similar strength of density regulation, but the species-specific response to environmental variation (σ_s^2) was 50% larger, whereas the proportion of variation due to common environmental noise ($\sigma_c^2 / 2\gamma$) was almost nine times higher in Ammarnäs than in the Birdsong Valley.

The community sensitivity was quite similar among two pairs of communities (Table 2), with Ammarnäs and the Eastern Wood having the highest sensitivity, roughly 30% higher than in Budal and Birdsong Valley. Note that the difference in mean log abundance was substantial among communities (Table 1), however this does not affect the sensitivity as much as the variance components do.

Despite having similar sensitivities, the community resistance differs more considerably (Table 2). The smallest resistance was found in the community in the Eastern Wood due to the highest species richness and largest sensitivity. In contrast. Ammarnäs, with almost the same sensitivity, had twice resistance than was estimated for the community in the Eastern Wood. Budal, with low sensitivity and few species has the highest resistance, while Birdsong Valley has the second lowest resistance.

Responses to environmental changes

Another way to explore these differences among communities in their resilience is to examine the consequences of removal of a certain proportion of the available area. We simply assume that the expected number of individuals in the community is the product of the

295 expected number of individuals per unit area, $\mathrm{E}[D]$, and area size, A, so that the expected
296 number of species is

297 $$\mathrm{E}[S] = cA^z, \quad (9)$$

298 where $c = k(\mathrm{E}[D])^z$ is assumed constant . From this species-area curve (Rosenzweig 1995)
299 we can calculate following Engen (2007b) for which area size A_1 the number of species is
300 expected to be reduced by one $A_1 = [(E[S] - 1)/c]^{1/z}$. The relative change in area $\Delta \ln A = I$,
301 assuming the expected density is constant. Figure 3 shows that the structure of the bird
302 community in Budal was the one least affected by a reduction in area size. In contrast, a
303 relatively small reduction of the available area in the more diverse communities both in the
304 Birdsong Valley and in the Eastern Wood (see also Figure 2) was likely to cause a loss of one
305 species.

306 Another factor that can influence the resilience of communities is an altered pattern of
307 fluctuations in the environment, e.g. caused by climate change. When the species-specific σ_s^2
308 environmental variance increases, the community sensitivity decreases (eqn. 5). Assuming
309 the constant k and $\mathrm{E}[D]$ remains fixed, so that $c_{\mathrm{new}} = k(\mathrm{E}[D])^{z_{\mathrm{new}}}$, this implies that a larger
310 area is necessary to maintain the expected number when the environmental stochasticity is
311 increased (Figs. 4, S1) as the area required to maintain the observed number of species is
312 $A_{\mathrm{new}} = (\mathrm{E}[S]/c_{\mathrm{new}})^{1/z_{\mathrm{new}}}$. In particular, the bird community in Budal and Birdsong Valley
313 was strongly affected by a change in environmental stochasticity (Figure 4).
314

315 **DISCUSSION**

316 Here we present a simple method for assessing the resilience of communities based on the
317 effects of changes in the expected number of species as function of abundance of individuals
318 in the community, determined by the available amount of area or resources. We propose a
319 metric that describes the absolute effect on species number, the resistance I, and the relative

change *z*, the sensitivity, to a permanent alteration of the environment. A comparison across four different bird communities showed that their resilience against a permanent environmental change showed large variation, mainly related to the relative contribution of environmental stochasticity to the community dynamics. An important aspect of this approach is that it can be used to quantitively assess the impact of a permanent change in the environment, e.g. caused by loss of important habitat types or an increase of the stochastic fluctuations in the environment (Figs. 3, 4). Our approach assumes, however, an underlying lognormal species abundance distribution, which often represents a good approximation for the distribution of log abundances in many natural communities (Preston 1962; Williams 1964; Rosenzweig 1995; Ulrich *et al.* 2010; Enquist *et al.* 2019).

Here we have used a dynamical model to estimate the parameters affecting the resilience of the bird communities. With more than one year of samples available, we are able to estimate different variance components, in particular among-species variation (heterogeneity) and within-species variation. The partitioning of the variance enables us to quantify the magnitude of species-specific responses to environmental fluctuations more accurately, which is the main component determining community sensitivity. Using only a single year of sample limits our options for inference and we must assume that the variation in species abundance is due to environmental fluctuations. Comparative studies including several taxa have shown that this component strongly affects patterns in the community dynamics (Lande *et al.* 2003, p. 177; Engen *et al.* 2011; Bellier *et al.* 2014; Solbu *et al.* 2018). The consequence is likely to be an overestimate of the community sensitivity. One way to reduce this bias could be to fix several parameters based on à priori information about the magnitude of the different components, following the approach in Engen (2007b).

Another, more simple, approach would be to use properties by the Poisson-lognormal distribution to estimate the sensitivity *z* and resistance *I*. Estimation in a lognormal species

345 abundance model can then be done by appropriate specification of the sampling distribution
346 (Sæther *et al.* 2013). For instance, Bulmer (1974) assumed that a species with a given
347 abundance had a Poisson distributed number of individuals in a sample with parameter equal
348 to the product of the sampling intensity ν, i.e. the fraction of the community being sampled,
349 and its abundance in the community. This approach was extended by Engen et al. (2002),
350 who proposed to use the Poisson-lognormal distribution as sampling distribution to account
351 for over-dispersion θ relative to the Poisson distribution. Using this approach z and I can be
352 expressed as estimates of θ and ν (Engen 2007b). If the sampling intensity and
353 overdispersion are unknown, the resilience of the community must be based on estimation of
354 z and I using relevant values of these two parameters. In general, estimates of I decreases
355 whereas estimates of z increases with decreasing sampling intensity (Figure 5), illustrating
356 the importance of including estimates of sampling error or specifying underlying assumptions
357 about the sampling procedures.

358 One of the most general patterns in ecology is the approximately linear increase at a
359 logarithmic scale in species numbers with increasing area (Rosenzweig 1995). However, the
360 large variation in the slopes of these relationships is poorly understood. A general outcome of
361 the dynamical models developed by Engen (2007b, a) is that a relationship exists between the
362 form of the species-area curve, determined by the community sensitivity *z*, and characteristics
363 of the community dynamics. For instance, large species-specific effects of environmental
364 stochasticity generate small values of *z* and small increases in species numbers with
365 increasing area size. This means that the α - and β - components of species diversity
366 (Whittaker 1970, 1972) are closely interrelated, dependent on the patterns in the temporal
367 dynamics. Thus, our approach can be used to assess both spatial and temporal resilience of
368 communities to permanent changes in the environment (Allen *et al.* 2016).

Ecological resilience generally includes a time dimension, referring to the time needed for the system to return to the state before the disturbance (Pimm 1991; Baho *et al.* 2017). In our approach we do not measure resilience as a rate but rather consider the effects of a change in abundance on the number of species, assuming stationarity in the community dynamics after a disturbance. Consequently, the species is considered as the unit, ignoring any inter-specific differences in functional role (Roberts *et al.* 2019) which can affect species-specific influences on ecosystem characteristics (Fanin *et al.* 2018; Kardol *et al.* 2018; Feit *et al.* 2019; Engen *et al.* 2021). However, the advantage of this approach is that community resistance and sensitivity relate directly to the underlying dynamics of the species which constitute the community and therefore provide comparable estimates (Table 2) based on transparent statistical methods.

Several studies of ecological resilience relate the amount of disturbance a system can withstand (Holling 1973) to basic characteristics of ecosystems (Gunderson 2000). A central focus has been to relate the degree of resilience to the deviation from an equilibrium state; thus, indicating a direct relationship between stability over time and resilience. Our approach focuses more on the dynamical characteristics of the system in variations around such an equilibrium reached after a disturbance. We show that permanent changes in the environment caused by both area loss and environmental stochasticity affect the community dynamics in this stationary model (Figs. 3, 4). Thus, this provides applicable measures of stability expressed by the dynamical characteristics of the community (eqn. 1, 2) and resilience (eqn. 3, 4), as highlighted by Holling (1973). In our four bird communities, both the resistance and sensitivity showed large variation (Table 1), dependent on the processes contributing most to fluctuations in the total abundance in the community.

Recent evidence strongly indicates large changes in structures of communities in ecosystems all over the world (Blowes *et al.* 2019; van Klink *et al.* 2020; Eichenberg *et al.* 2021). However, quantifying the extent of these changes and future consequences is often difficult, mainly related to challenges in accounting for differences among species in their detectability (Yoccoz *et al.* 2001). Our approach provides a general approach that can be used to compare the effects permanent changes both at an absolute and relative scale, which facilitate identification of communities most at risk.

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624 **Table 1**. Estimated parameters characterizing the dynamics of four European bird
625 communties. μ is the mean log abundance and σ^2 is the total variance in the species
626 abundance distribution. The environmental variance σ_e^2 is decomposed into additive
627 components due to a common effect across species on the dynamics σ_c^2 as well as a species-
628 specific effect σ_s^2. The permanent hetereogeneity in the dynamics among species is
629 characterized by the variance in the the population growt rate σ_r^2 as well in the carrying
630 capacity σ_K^2. γ expresses the strength of density-dependence, i.e. the inverse of the return
631 time to the equlibirium population size. $S_{observed}$ is the total number of species observed
632 throughout the study period, and $\widehat{ES}$ is the estimated total number of species in the
633 community.

Locality	μ	σ^2	$\sigma_e^2/2\gamma$	$\sigma_s^2/2\gamma$	$\sigma_c^2/2\gamma$	σ_K^2	σ_s^2	σ_r^2	γ	$S_{observed}$	$\widehat{ES}$
Ammarnäs	-0.904	6.366	1.117	1.064	0.053	5.249	0.038	0.002	0.018	19	21
Budal	-0.275	8.961	1.705	1.674	0.031	7.256	0.335	0.073	0.100	20	20
Birdsong Valley	-0.618	9.544	1.776	1.770	0.006	7.768	0.057	0.002	0.016	39	45
Eastern Wood	0.250	4.694	0.852	0.823	0.029	3.842	0.019	0.001	0.012	45	47

634
635

636 **TABLE 2**. The sensivity *z* and the resistance of four bird communities to permanent changes
637 in the community calculated based on the estimated total number of species recorded in the
638 community. *z* expresses how the rate of change in the log expected number of species
639 depends on variation in the log expected total number of individuals. *I* can be interpreted as
640 the proportional reduction in community size that will give a reduction in the expected
641 number of species equal to one.

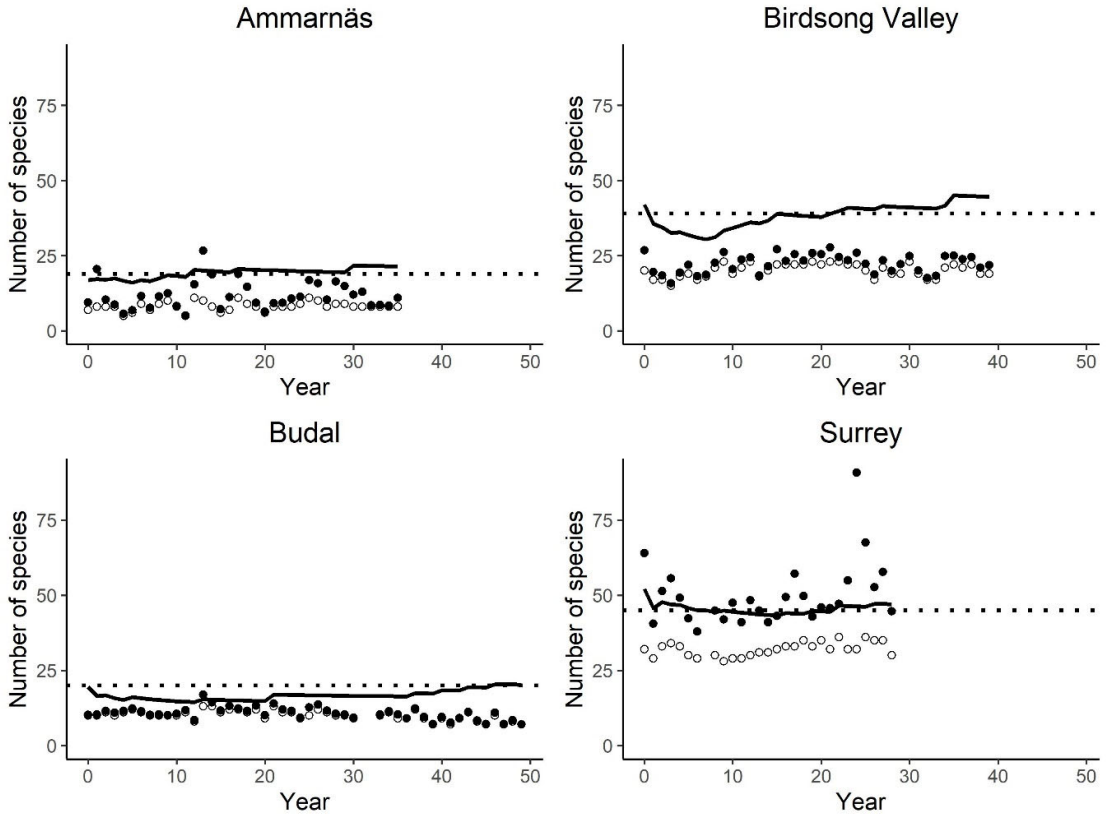
Locality	*Area (hectare)*	*z*	*I*
Ammarnäs	900	0.457	0.102
Budal	24	0.345	0.143
Birdsong Valley	13	0.341	0.066
Eastern Wood	16	0.469	0.045

642

643 **LEGEND TO FIGURES**

644 **FIGURE 1**. Annual variation in the estimated number of species in the four bird
645 communities. Observer number of species a given year (open circles). Estimated number of
646 species a given year (filled circles), based on fitting a univariate Poisson lognormal
647 distribution. The estimated total number of species in the communities, $\widehat{ES}$, as the number of
648 years increases along the x-axis (solid lines). The total number of observed species in the
649 communities, S_{observed}, (dotted horisontal line).
650
651 **FIGURE 2**. The relationship between number of species and area based on estimates of the
652 sensitivity *z* to an environmental change (Table 2) and a simple species-area relationship (eq.
653 9).
654
655 **FIGURE 3**. The proprtion of species remaining as function of the proportion of area
656 removed in four bird communities. The effect of area removal was calculated from a simple
657 species-area relationship (eq. 9). The points indicate the relative decrease of area in each
658 locality to give a expected reduction in the number of species by 1 A_1.
659
660 **FIGURE 4**. Relative change in area size required to maintain the expected number of species
661 as function of variation in environmental srochasticity.
662
663 **FIGURE 5.** The estimate of sensitivity *z* (a) and resistance *I* (b) as a function of sampling
664 intensity The most intense sampling occurs close to origo.
665

666



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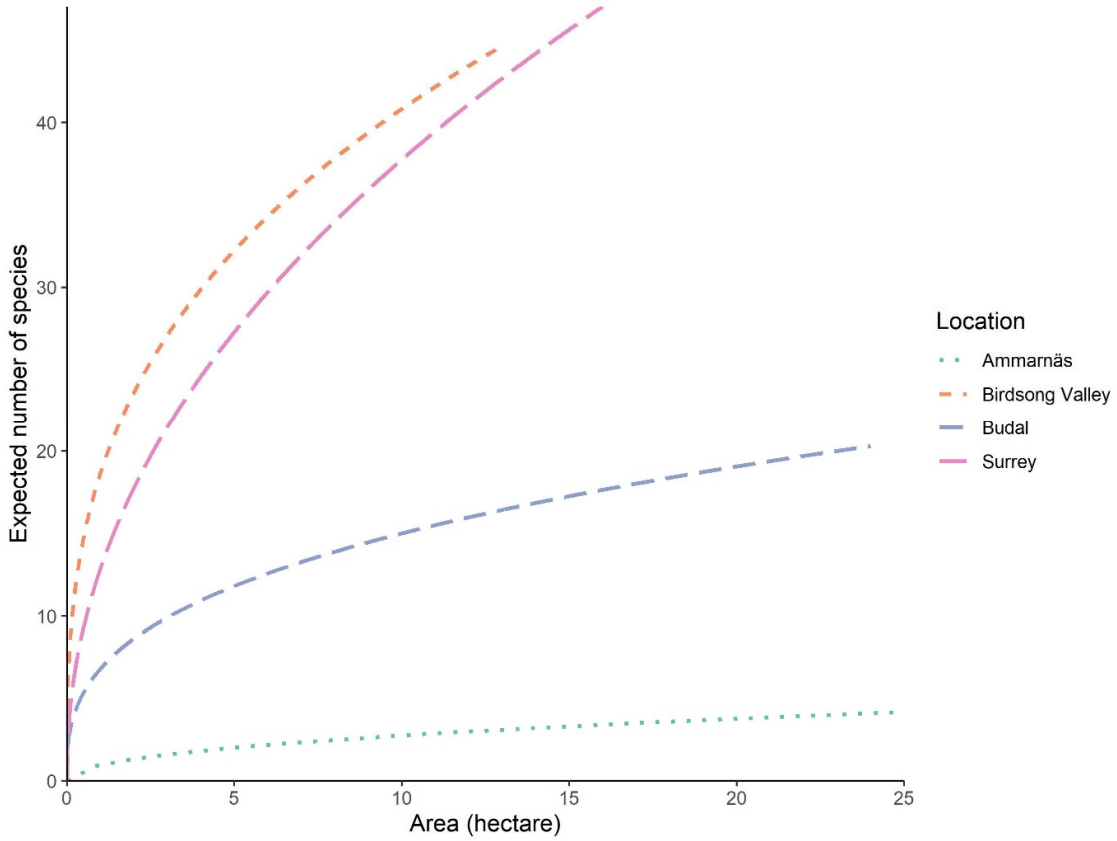
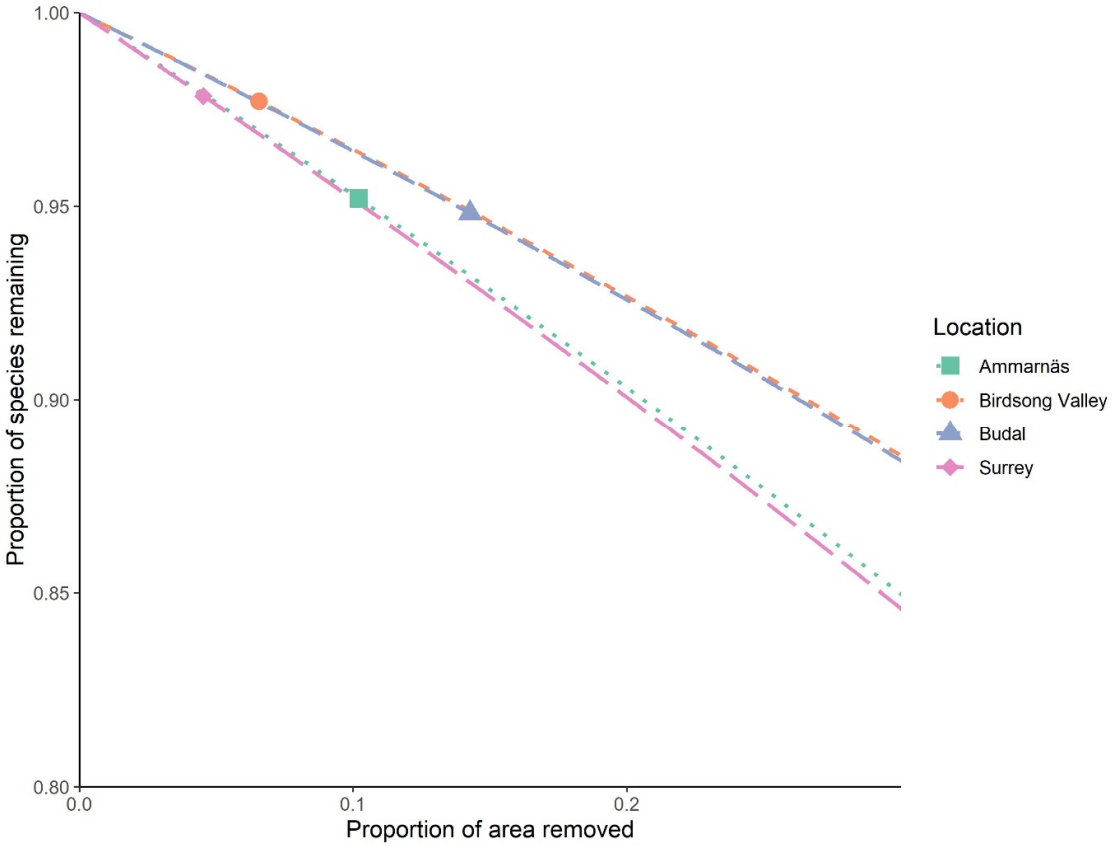
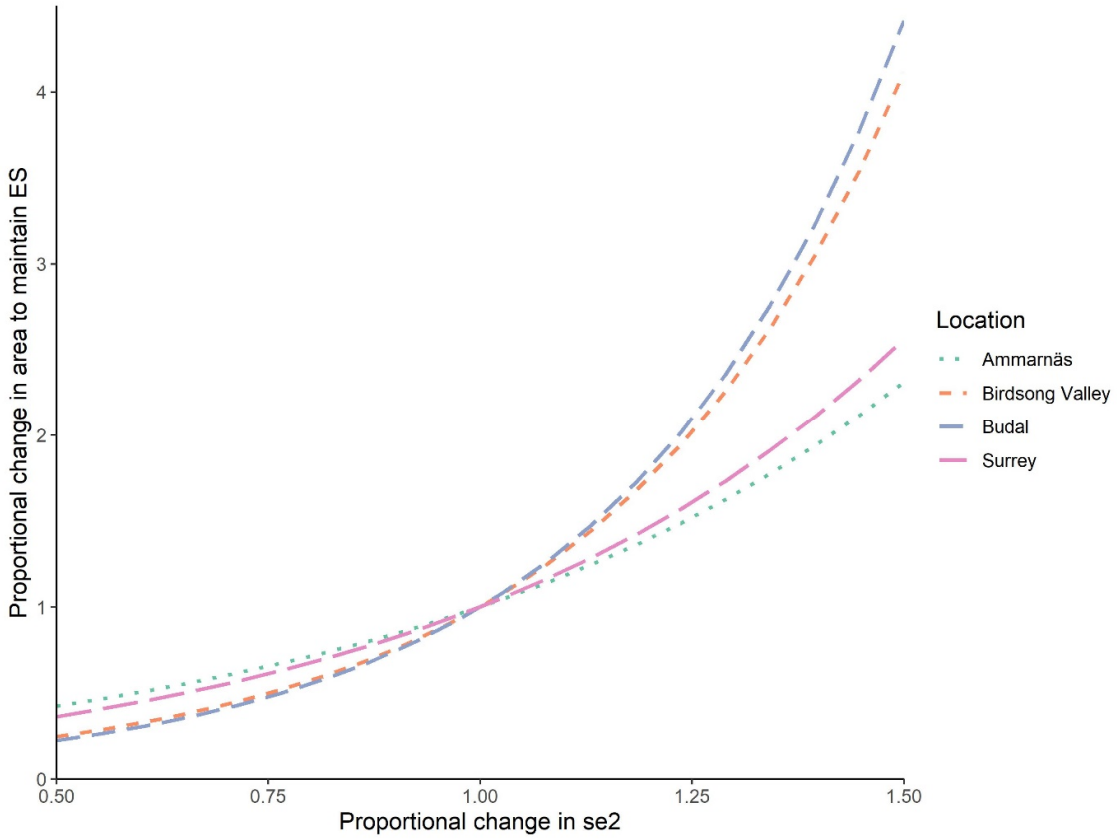

Expected number of species
0
10
20
30
40
0
5
10
15
20
25
Area (hectare)
Location
Ammarnäs
Birdsong Valley
Budal
Surrey

671

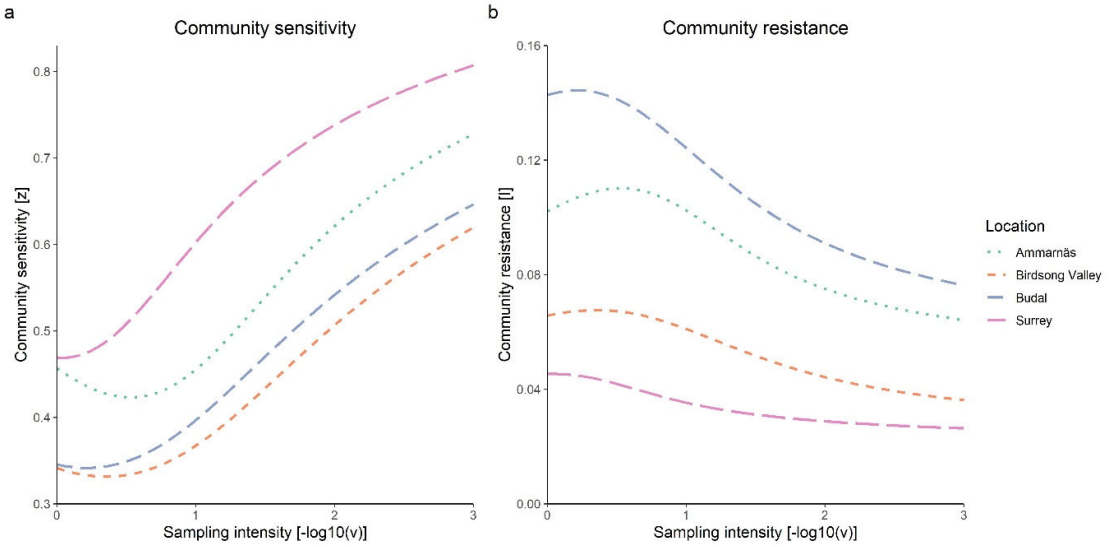
672


1.00
0.95
0.90
0.85
0.80
Proportion of species remaining
0.0
0.1
0.2
Proportion of area removed
Location
Ammarnäs
Birdsong Valley
Budal
Surrey

673


Proportional change in area to maintain ES
0
1
2
3
4
0.50
0.75
1.00
1.25
1.50
Proportional change in se2
Location
Ammarnäs
Birdsong Valley
Budal
Surrey

674

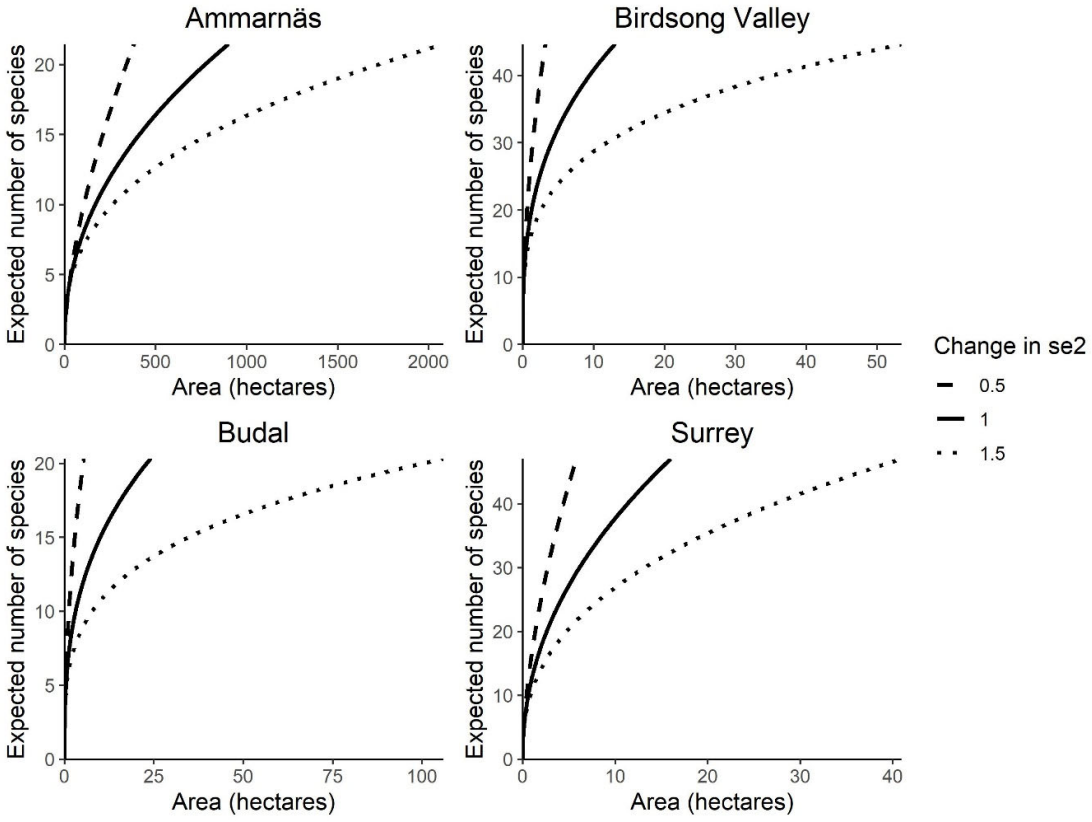

a
Community sensitivity
Community sensitivity [z]
0.8
0.7
0.6
0.5
0.4
0.3
0
1
2
3
Sampling intensity [-log10(v)]
b
Community resistance
Community resistance [l]
0.16
0.12
0.08
0.04
0.00
0
1
2
3
Sampling intensity [-log10(v)]
Location
Ammarnäs
Birdsong Valley
Budal
Surrey

675
676
677

678
679 **Appendix A**

680 Figure S1: Required area to maintain expected number of species as the community
681 sensitivity changes due to changes in species-specific response to environmental variation
682 through cA^z. That is, c is fixed, while z changes with species-specific response to
683 environmental variation and A (x-axis) determines the expected number of species (y-axis).

684



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