Submitted to Ecological Modelling, August 2018

Heterogeneity among species and community dynamics – Norwegian bird communities as a case study.

Erik B. Solbu[1], Ola H. Diserud[2*], John A. Kålås[2] and Steinar Engen[3]

[*] Corresponding author. OHD: orcid.org/0000-0002-7331-3230. ola.diserud@nina.no

[1] Dept. of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway.

[2] Norwegian Institute for Nature Research, P.O. Box 5685 Torgard, NO-7485 Trondheim, Norway

[3] Dept. of Mathematical Sciences, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway.

EBS: orcid.org/0000-0002-6023-3100. erikbsolbu@protonmail.com

JAK: john.kalas@nina.no

SE: steinar.engen@math.ntnu.no

Solbu, Erik Blystad; Diserud, Ola Håvard; Kålås, John Atle; Engen, Steinar.
Heterogeneity among species and community dynamics – Norwegian bird communities as a case study. Ecological Modelling 2018 ;Volum 388. s. 13-23
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Abstract

We have in this study analysed bird communities across Norway with a heterogeneous species abundance model, where dynamical parameters can vary among species. Similarity in community composition over time, used as a measure of temporal β-diversity or the turnover rate, was then estimated. When we account for heterogeneity in dynamical parameters among species it will affect how we estimate environmental stochasticity, and, subsequently, how the temporal dynamics is modelled. In addition, spatial variation in species abundance within a sampling area can obscure the temporal dynamics of communities. By inadvertently including small-scale spatial variation within sampling areas in the sample noise term, it will be difficult to correctly detect changes in community structure, or species abundance similarity, in time. Using Norwegian bird communities as a case study, we have shown how to interpret the sample correlation of the bivariate Poisson lognormal distribution, fitted to pairs of transects, and why separation of the transects into spatially similar subgroups can be beneficial. This approach also makes us able to account for sampling error and over-dispersion relative to Poisson sampling. The partitioning of the variance of the species abundance distributions showed that heterogeneity among species in temporal dynamics accounted for roughly 75% of the variation, close to estimates for other taxa. High temporal similarity can be interpreted as a low baseline turnover rate, which is important when studying changes to ecosystems due to e.g. anthropogenic effects. Furthermore, the environmental stochasticity was more realistically estimated in this heterogeneous model. This is essential for predicting the dynamics of species abundances forward in time.

Keywords: β-diversity, environmental stochasticity, heterogeneous species abundance models, over-dispersion, temporal community dynamics.

1. Introduction

Understanding how human activities affect biodiversity is a key issue in community ecology. However, even without human interference, fluctuations in species abundance, extinctions and speciations change biodiversity naturally, and this baseline turnover rate needs to be accounted for when analysing species communities and how they change (Magurran 2016). One measure for the turnover rate in communities is the similarity in species' abundances over time. Communities where species change considerably in relative abundance from one year to the next will have a high turnover rate, while if the species have almost the same relative abundance over time the turnover rate will be low. This difference in community dynamics can be described by introducing the concept of community heterogeneity. If species in a community have different temporal dynamics, this heterogeneity can be modelled by letting population dynamical parameters vary among species (Engen and Lande 1996; Solbu et al. 2016). Conversely, in a homogeneous community, the parameters describing the dynamics are assumed to be equal for all species. Here, community heterogeneity is defined as the variation in carrying capacity among species (Engen et al. 2002), introduced in the model by assuming that the species' growth rates are a sample from some distribution. The proportion of the total variation in the observed species abundance distribution that can be attributed to heterogeneity will then be a measure of the community's temporal turnover rate. If heterogeneity accounts for a large part of the variation in species abundances, the turnover rate will be low, whereas a community with low levels of heterogeneity will have a high turnover rate.

In addition to a baseline turnover rate, the plethora of different measures of biodiversity and different spatial resolutions breed conflicting results in terms of consequences of human-induced changes (McGill et al. 2015). Several considerations regarding sampling design should be made before samples to analyse species diversity and abundance are collected (Bonar et al. 2011). One important issue to consider, when conducting biodiversity analysis, is the choice of sampling unit. A common sampling unit is counting individuals along line transects. Ideally, these transects should be randomly distributed within the area where the community of interest is analysed. However, it is often not physically possible to randomly distribute transects due to the topography of the area, e.g. steep hills, thick vegetation or rivers, and instead the transects follow trails already in the landscape. Or the sampling may have been designed to study spatial structures in species diversity as well as temporal dynamics, thereby distributing sampling units along gradients. The analysis presented here illustrates how spatial variation between sampling units, intentional or not, can affect the estimation of temporal heterogeneity in bird communities.

The proportion of variation in the species abundance distribution that can be attributed to community heterogeneity is estimated by the correlation between sampling units over time. If species abundances from sampling units within an area the same year are dissimilar, i.e. a species having high abundance in one transect can have low abundance in the other transect, this spatial dissimilarity will obscure analyses of temporal dynamics. It is then crucial to know how to separate the effect of spatial variation from temporal heterogeneity in spatiotemporal species abundance data sets. We show how within-year comparison of

correlation between transects can be used to estimate spatial variation that needs to be under control when studying temporal dynamics and community heterogeneity.

The choice of species to include in the samples, i.e. our prior definition of the community, will affect a similarity analysis, although some species may not have a large influence on the estimated community dynamics. Individuals could, for instance, belong to species that are not endemic to the area and can, therefore, introduce variation in the species abundance distribution that is not necessarily true for the assessment of the local community dynamics, thereby also affecting the estimated turnover rate. As an illustration, we will compare the analysis of a community including all registered bird species with a community including only passerine birds and discuss how the difference in community limitation may affect the estimated spatial variation and temporal heterogeneity of the community.

Our approach is to fit a bivariate Poisson lognormal species abundance distribution to all pairs of transects within an area and estimate the correlation among transects within the same year, and then study how the correlation changes with increasing time difference between transects. The use of the lognormal distribution has a long history in community ecology (Preston 1948) and the Poisson sampling of this distribution is well known (Bulmer 1974). A species abundance distribution described by a Poisson lognormal distribution can be modelled by a continuous time dynamic population model with a Gompertz type of density regulation, which can also account for different temporal dynamics among species (Engen and Lande 1996). The difference in temporal dynamics in this model, i.e. the degree of community heterogeneity, can be attributed to variation in the carrying capacity among

species; some species fluctuate at high abundances while others remain at low abundances over time. Species having different carrying capacities can be generated by niche segregation (Hutchinson 1957; MacArthur 1960), but we do not attempt to test this theory formally here. However, heterogeneity among species does deviate from the assumptions in the neutral theory of community dynamics where species are assumed to have the same dynamics, and population fluctuations are caused by demographic stochasticity only (Hubbell 2001).

2. Material and Methods

2.1 Sampling design

The data we analyse have been collected since the early 1990s to document long-term changes in Norwegian wildlife. Seven different areas were selected across Norway to cover a wide range of climatic variation (Fig. 1A). Areas in the southern part of Norway have historically been more exposed to pollution and while there is farming in some of the areas, they are otherwise considered undisturbed habitats. Although data have been collected for a wide range of plant and mammal species, we will here limit the community to consist of bird species only. Within each area, several sampling points along transects have been used to count the abundance of each species by listening for bird song. There are ten transects within each area, except for Møsvatn which has eight. Each transect has usually 20 observation points with 200-300 m distance, but this number can vary in some areas due to landscape constraints, for example in Solhomfjell (Fig. 1C). We use the transect as sampling unit because the observer conducting the census along a transect corrected for observations of the same individuals made at adjacent points, and we illustrate the applicability of the

method to data where the researcher only has information at the transect level. An alternative design is to aggregate the points with respect to some covariate such as elevation or vegetation, but we show that even with such potential underlying differences in spatial composition, informative results can be obtained.

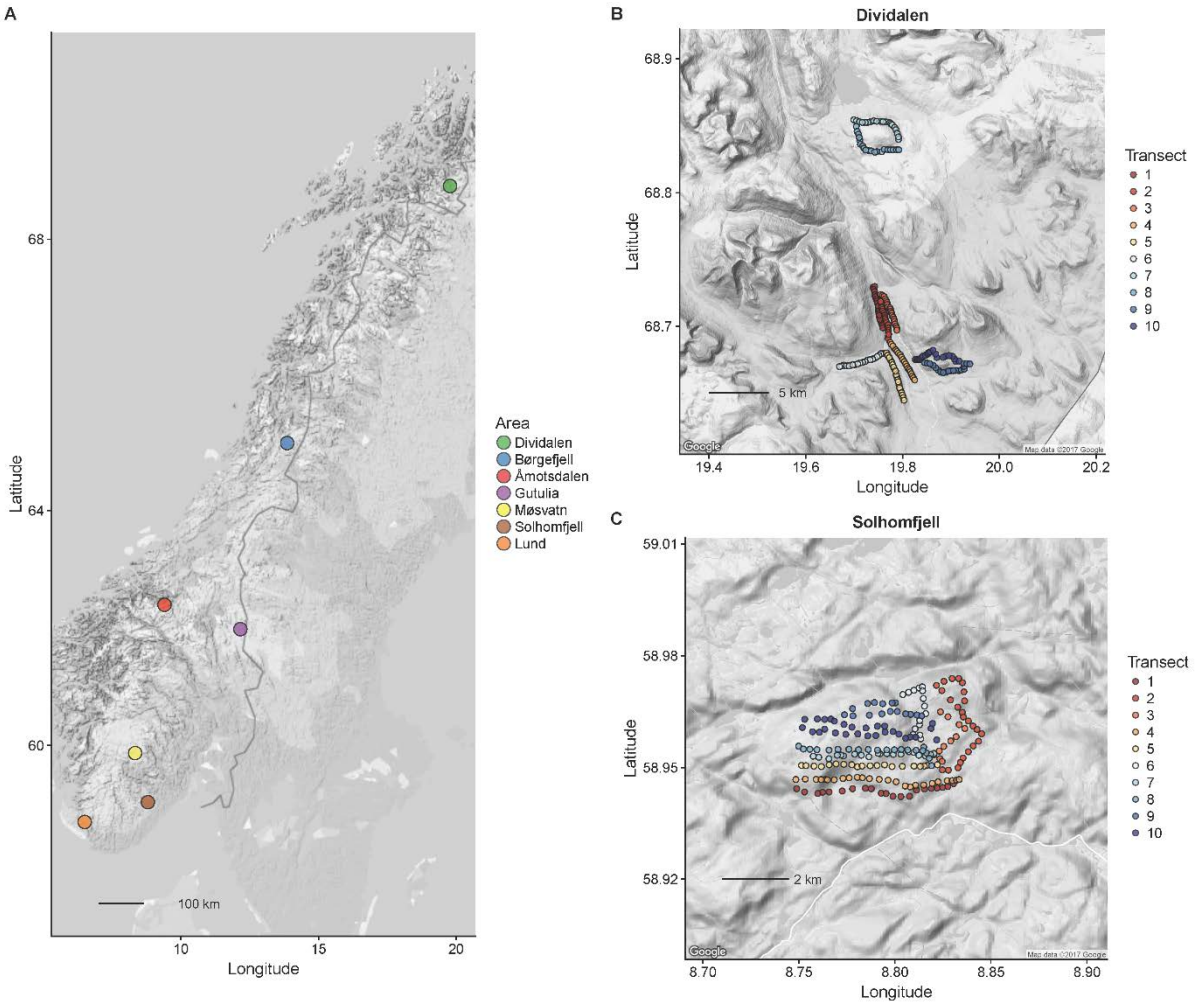

Figure 1. (A) Location of the seven areas where sampling has been conducted. (B) Location of the sampling points for each transect in Dividalen. (C) Location of the sampling points for each transect in Solhomfjell. The transects have been ordered according to mean elevation from low (1) to high (10). Note that there is a considerable difference between the spatial scales in the maps of Dividalen and Solhomfjell.

2.2 Spatial variation

As the locations of the areas cover the entire span of Norway, there is considerable spatial variation both within and between areas in terms of sampling area size (Fig. 1B and 1C), elevation (Fig. 2) and vegetation (Fig. 3). The transects in Dividalen cover an area of roughly 250 square kilometres (Fig. 1B), while the area covered in Solhomfjell is roughly 20 square kilometres (Fig. 1C). The difference in the area covered by the transects in Dividalen and Solhomfjell could indicate a greater variation in the species found among the transects in Dividalen compared to those found in Solhomfjell. The elevation of each sampling point varies both within and between areas (Fig. 2). While the overall mean elevation in Dividalen and Solhomfjell is roughly the same, circa 500 meters, the difference between the lowest and highest points (the range) within the areas is twice as large in Dividalen compared to Solhomfjell. Lund has an overall mean elevation and range similar to Solhomfjell. Børgefjell and Gutulia differ in their overall mean elevation, but have the same range, while Åmotsdalen and Møsvatn have the same overall mean, but differ in range.

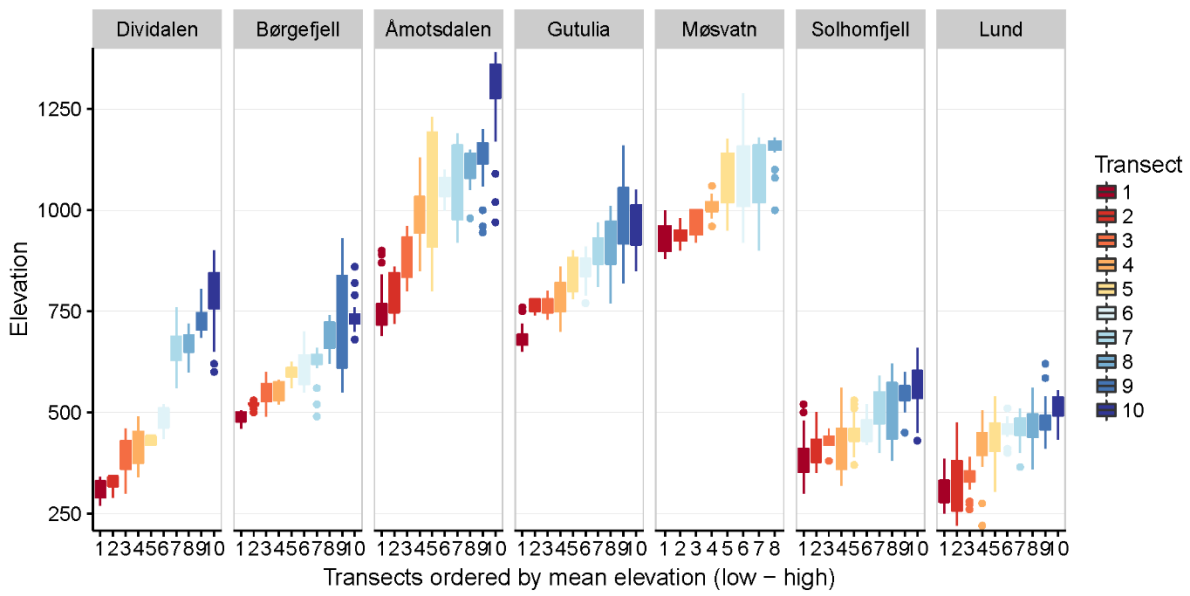

Figure 2. Elevation distribution of the sampling points within each area, where the transects are ordered by their mean elevation from low (1) to high (10).

Each sampling point has been classified to a vegetation category, so aggregating the proportion of each vegetation class within transects can illustrate the spatial variation within a sampling area. Comparing the distribution of vegetation classes between Dividalen and Solhomfjell reveals some interesting features of the sampling areas (Fig. 3). First, the individual transects in Dividalen have little variation, they have roughly five classes each, while the transects in Solhomfjell have around ten classes each. Part of the reason for the greater variation within transects in Solhomfjell is the number of observation points, but the number of classes is almost constant for each transect, even though the number of points varies. Second, the difference between the measured characteristics is greater in Dividalen than Solhomfjell. For instance, transects one to six in Dividalen have more forest vegetation in common, such as conifers, lichens and birches, while the four other transects have more open vegetation consisting of graminoid ridges, heather and grasses. In Solhomfjell on the other hand, all transects consist of some type of coniferous or birch forest in addition to some areas of bryophyte.

Knowing the spatial variation in each area is essential when we estimate the temporal autocorrelation of the community, which in turn gives us an estimate of the heterogeneity among species in dynamical parameters. When there is spatial variation among sampling units, either due to suboptimal sampling designs or if sampling is designed with an intention to study spatial diversity, it will obscure temporal autocorrelation among samples over time if not handled appropriately. The available spatial information will be used as guidance when

determining how to analyse the transects to minimize the effect of spatial variation on temporal estimates and predictions.

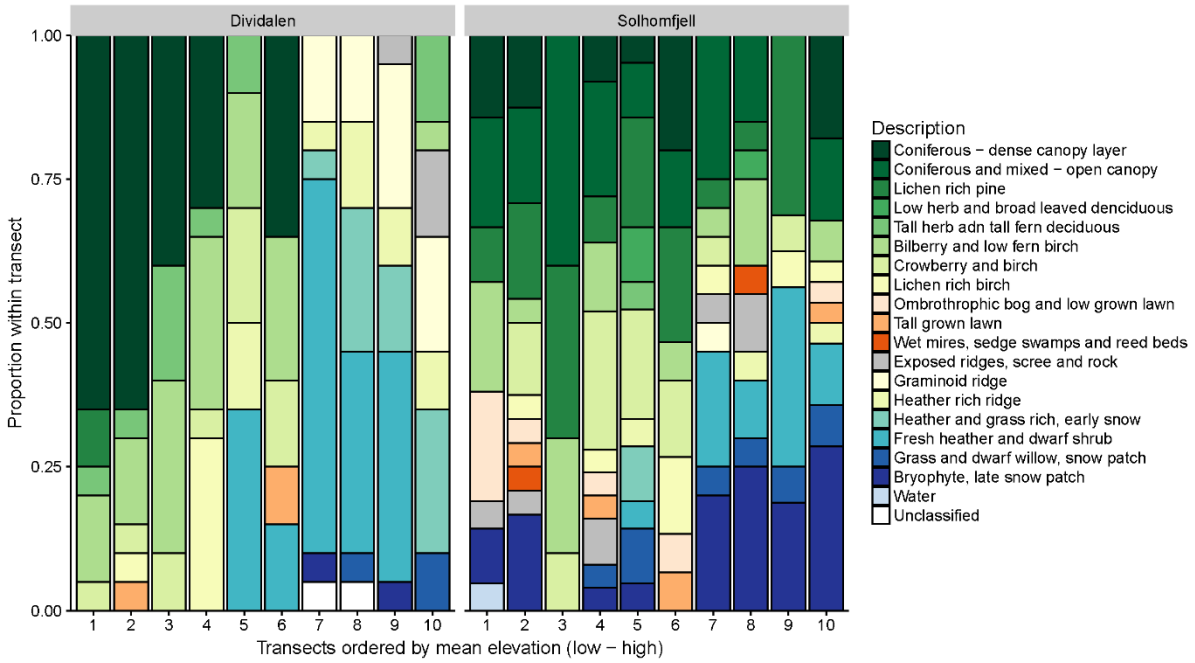

Figure 3. Vegetation description and distribution within transects in Dividalen and Solhomfjell.

We first look at the spatial variation in species abundances for the censuses from the areas Dividalen and Solhomfjell, before doing the temporal analyses in the next section. The species abundance distribution in the first census year in Dividalen (Fig. 4A) is characterized by a variation like that found in the elevation and vegetation descriptions. Starting from the transect with the lowest mean elevation (300 m), there are five species that are most abundant (*Carduelis flammea*, *Fringilla montifringilla*, *Phoenicurus phoenicurus*, *Phylloscopus trochilus* and *Turdus illacus*), but as the mean elevation increases, their presence, in addition to many of the less abundant species, decreases or ceases completely (from 650 m and up), except one species (*Carduelis flammea*). Instead, two other species become more abundant

(*Anthus pratensis* and *Pluvialis apricaria*) in addition to several other less abundant species not found at the lower altitudes. The species abundances in the first census year in Solhomfjell (Fig. 4B) have a different development among transects. The abundances in each transect are more similar, with three species (*Anthus trivalis*, *Fringilla coelebs* and *Phylloscopus trochilus*) dominating across all transects, and the less abundant species do not vary much in their presence between transects.

The community of study can be defined in many ways, both with respect to spatial and taxonomic limitations, and this may affect the results of the analyses. For example, will a community limited to bird species from one taxonomic order give different dynamic models than if all bird species are studied simultaneously? When different community definitions severely change relative abundances in the sample, model results will, of course, be affected, but limiting the community to closely related species competing for the same resources may give a more focused analysis of the degree of heterogeneity. The more abundant species in both study areas are all from the Passeriformes order, so analysing a community where low abundance non-passerine species are removed (names marked with a star (*), Fig. 4) can serve as an illustration of the sensitivity of this modelling approach to community limitation and handling of species that are rare in the sample.

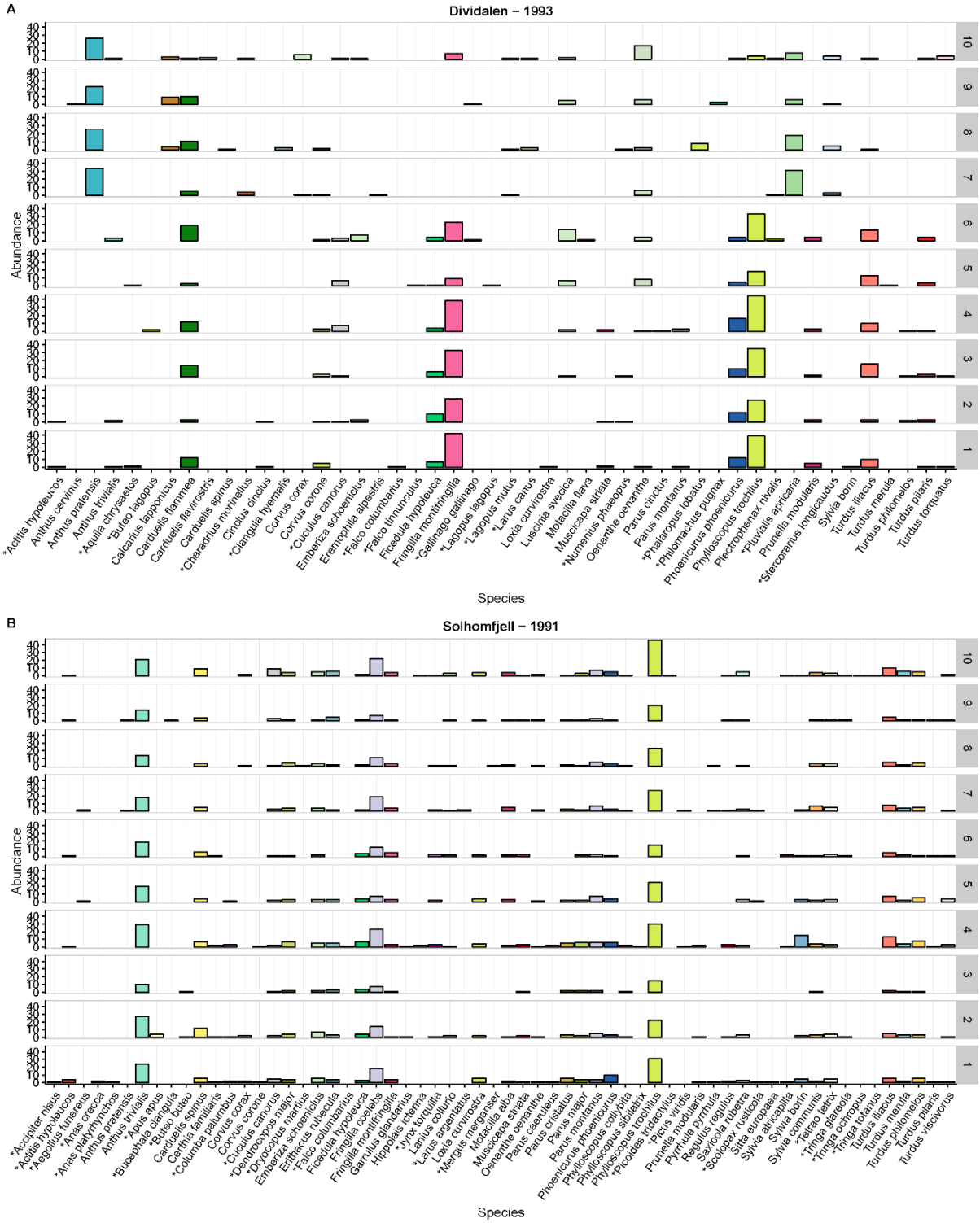

Figure 4. Species abundance observed in Dividalen in 1993 (A) and Solhomfjell in 1991 (B), i.e. at the first available census year, aggregated at transect level. The transects have been ordered by their mean elevation from low (1) to high (10). Species marked with a star (*) are the non-passerine species.

2.3 Temporal analyses

Since one goal is to identify the temporal covariation of species abundance, the spatial variation in species abundance, like the one observed in Dividalen, will be an issue if the pattern persists over time. If all the transects within an area are compared, a large habitat variation among transects will decrease the estimated temporal correlation if species occupy specific habitats. Time series of the species abundances within each transect over all census years up to 2013 in Dividalen (Fig. 5A) and Solhomfjell (Fig. 5B), show that the species that were the most abundant in the first years of the census continue their dominance over time. The total abundance is higher among the transects at low altitudes in Dividalen (transects 1 - 6, Fig. 5A), compared to those at higher elevations. The temporal heterogeneity in species abundance dynamics in Solhomfjell is slightly more obscured, but the most abundant species persist over time and there is no variation among the transects in terms of which species are most dominant, but there is considerable variation in total abundance. The difference in total abundance among transects in Solhomfjell can be explained by the number of observation points within each transect, for example, transect 3 has 10 points, compared to transect 10 which has 28 points.

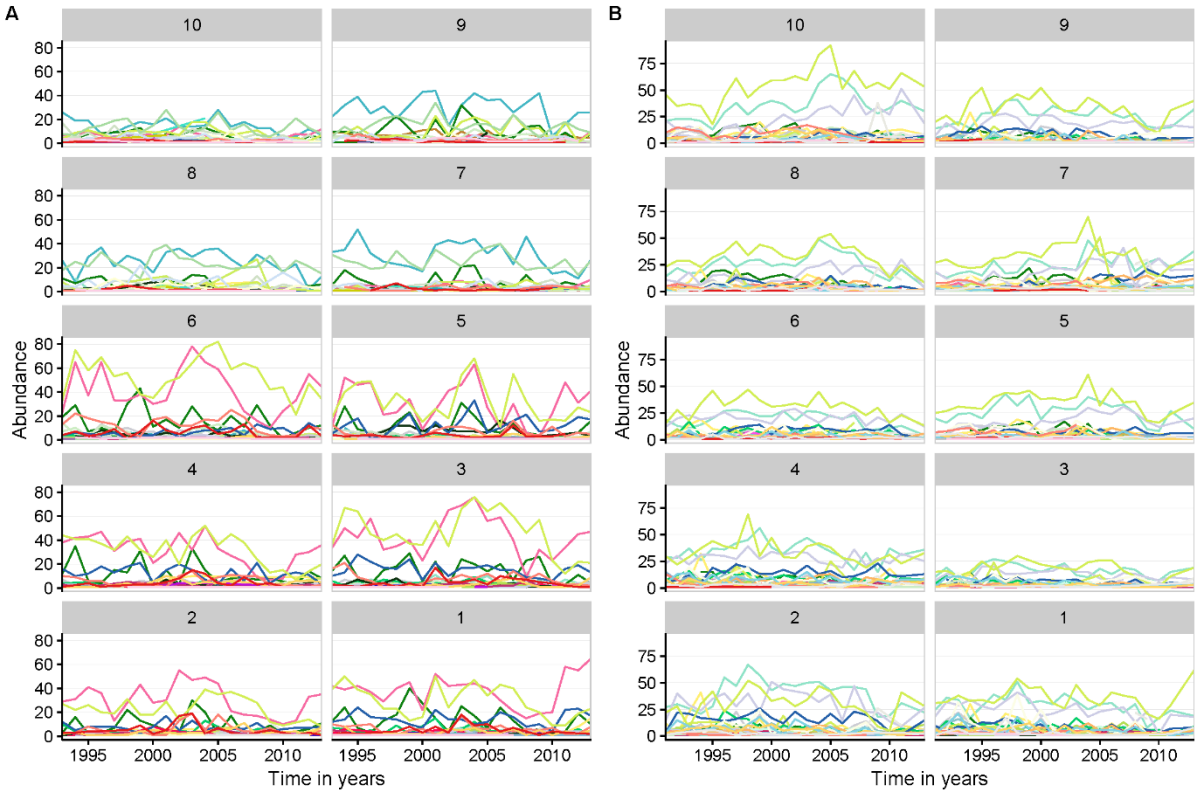

Figure 5. Species abundance for each species (coloured lines) observed in Dividalen (A) and Solhomfjell (B) over the whole census period, aggregated at transect level. The transects have been ordered by their mean elevation from low (1) to high (10). Note that the colours represent the same species as in Figure 4.

2.4 Model

Here, we apply the dynamic model of Engen and Lande (1996), assuming that the log abundance of species i follows an Ornstein-Uhlenbeck process (Karlin and Taylor 1981)

$$dX_i = \left(r_i - \delta X_i\right)dt + \sigma_s dB_i\left(t\right) + \sigma_c dB_c\left(t\right) \tag{1}$$

where $dB_i\left(t\right)$ and $dB_c\left(t\right)$ are independent increments of standard Brownian motions with zero means and variances dt. The total environmental variance is accordingly $\sigma_e^2 = \sigma_s^2 + \sigma_c^2$,

where σ_s^2 and σ_c^2 express the species-specific and common environmental noise, respectively. The intrinsic growth rates r_i are assumed to be a sample from a normal distribution with mean r_0 and variance σ_r^2, and δ describes the strength of the density regulation. The log of the carrying capacity of species i is then r_i / δ so that the log carrying capacity among species has mean $\mathrm{E}[\ln K] = r_0 / \delta$ and variance σ_r^2 / δ^2. The log abundances of species at time zero and $t > 0$ will then follow a bivariate normal distribution among species. Under Poisson sampling, the corresponding counts of individuals will then follow a bivariate Poisson-lognormal distribution (Engen et al. 2011a). A simple way of accounting for possible over-dispersion relative to the Poisson is then to assume that the sampling is described by a Poisson-lognormal distribution rather than a Poisson, with an over-dispersion parameter θ^2 which is zero under Poisson sampling. Engen et al. (2011a) showed that the counts still follow a bivariate Poisson-lognormal distribution with variance parameter

$$\sigma_{total}^2 = \sigma_s^2 / 2\delta + \sigma_r^2 / \delta^2 + \theta^2 \tag{2}$$

This is then the variance parameter in the observed species abundance distribution, which we write on the form $\sigma_{total}^2 = \sigma_{stoch}^2 + \sigma_{heter}^2 + \theta^2$, thus decomposing the variance into three terms expressing the effect of species-specific environmental noise, the heterogeneity among species and the over-dispersion in the sampling, respectively. The common environmental noise σ_c^2 only affects the sample sizes with no effect on the parameters of the distribution (Engen and Lande 1996). The bivariate Poisson-lognormal also has a correlation parameter which is the correlation between two actual abundances (not the observed ones) of the same species at time difference t, which can be expressed on the form

$$\rho_t = (\rho_0 - \rho_\infty) e^{-\delta t} + \rho_\infty \tag{3}$$

where $\rho_0 = \left(\sigma_s^2 / 2\delta + \sigma_r^2 / \delta^2\right) / \sigma_{total}^2$ and $\rho_\infty = \left(\sigma_r^2 / \delta^2\right) / \sigma_{total}^2$. By fitting the bivariate Poisson lognormal distribution to all pairs of samples at different time intervals using the *poilog* package in R (Grøtan and Engen 2008, R Core Team), the common total variance as well as the ρ_t for a large number of time differences can be estimated by maximising the likelihood function. The estimates of the ρ_t can finally be smoothed to obtain estimates of ρ_0, ρ_∞ and δ. Finally, these estimates yield estimates of the three additive components of the total variance by the relations $\sigma_{heter}^2 = \rho_\infty \sigma_{total}^2$, $\theta^2 = \left(1 - \rho_0\right)\sigma_{total}^2$ and $\sigma_{stoch}^2 = \left(\rho_0 - \rho_\infty\right)\sigma_{total}^2$.

2.5 Estimation

Within each area, we estimated the temporal autocorrelation by fitting the bivariate Poisson lognormal distribution to each possible combination of pairs of samples, for all time differences. From all the estimated correlations from transects taken at the same time, we estimated ρ_0 as the mean $\hat{\rho}_0 = \sum_{\forall t=0} \rho_t / n_{t=0}$ and the standard error as the sample standard deviation $\mathrm{SE}\left(\hat{\rho}_0\right) = \sqrt{\sum_{\forall t=0} \left(\rho_t - \hat{\rho}_0\right) / \left(n_{t=0} - 1\right)}$. The strength of density regulation δ can be estimated by fitting the autocorrelation function (Eq. 3) to the estimated sample correlations, by minimizing the sum of squares between each sample correlations and ρ_t, assuming that $\hat{\rho}_0$ is known. We imposed the boundary condition that $\rho_0 \geq \rho_\infty \geq 0$. For a density-regulated population, the return time to equilibrium is defined as the expected time required for a deviation from equilibrium to reach a fraction 1/*e* of its original value in the corresponding deterministic model (Solbu et al. 2013), and depends on life history

characteristics like survival rates, age at maturity and clutch sizes. From the estimated strength of density-regulation $\hat{\delta}$ we can obtain an estimate of the mean return time to equilibrium $\hat{T}_R = 1/\hat{\delta}$ that can be used to set the threshold for time differences used to estimate ρ_∞. Specifically, we took the smallest integer strictly greater than twice the mean return time to equilibrium. For all sample correlations with a time difference greater or equal to this threshold, we estimated the correlation in the limit as the sample mean $\hat{\rho}_\infty = \sum_{\forall t \geq 2\hat{T}_R} \rho_t / n_{t \geq 2\hat{T}_R}$ and the standard error $\mathrm{SE}\left(\hat{\rho}_\infty\right) = \sqrt{\sum_{\forall t \geq 2\hat{T}_R} \left(\rho_t - \hat{\rho}_\infty\right) / \left(n_{t \geq 2\hat{T}_R} - 1\right)}$. This method of estimating ρ_∞ can give estimates of δ that are very small, which in turn yield unrealistically long return times to equilibrium. Low estimates of δ can be due to the observed correlations decreasing very slowly (if at all) with increasing time difference, meaning that the species abundance distribution and the ranking of species abundances are almost identical over long time differences. An alternative approach to estimating ρ_∞ is then to determine a lower bound of δ or, conversely, an upper bound of T_R that is reasonable based on other studies of the temporal dynamics of the species (see e.g. Table 2 in Sæther and Engen (2002) for sample estimates of strength of density regulation in different bird species, giving estimates of return time to equilibrium of 3 years or less). If the estimated δ is less than 0.2, we will set the mean return time to equilibrium to five years and use sample correlations with a time difference of ten or more years for calculating ρ_∞. If we set the threshold for δ too high, we may end up with an unrealistically large proportion of variance attributed to heterogeneity, and consequently a too low turnover rate. At the same time, we need large enough samples to estimate ρ_∞, by not having the threshold too low.

There may be areas and sampling designs with large over-dispersion estimates that could conceal species heterogeneity within a subset of samples in an area. To see if species heterogeneity was concealed by over-dispersion, we estimated the over-dispersion for all possible partitionings of an area into two subgroups where each group had two or more transects and found the two groups that minimize the average over-dispersion, i.e. $\min\left\{\rho_0 - \left(\rho_0^{Low} + \rho_0^{High}\right)/2\right\}$. We wanted to highlight how the subsequent analysis of the temporal autocorrelation was affected by this division. The total variance σ_{total}^2 for each area was estimated by fitting a univariate Poisson lognormal distribution to all samples in each area and taking the sample mean of the estimated variances.

3. Results

We have in this study focused on the results from Dividalen and Solhomfjell, as these areas represent the extremes of difference in habitat variation within an area and are best suited for highlighting the important capabilities of our model. The other areas (Børgefjell, Åmotsdalen, Gutulia, Møsvatn and Lund) fall within the range of these two and will, therefore, not be commented on in detail, although a summary of results is provided in Table 1 and at the end of the Results section. When we analysed all the transects in Dividalen (Fig. 6A), a total of 21730 pairwise correlations, the estimated correlation between transects within the same year was $\hat{\rho}_0 = 0.471$ with a standard error 0.016 ($n_{t=0} = 936$). The estimated proportion of variance due to over-dispersion was then 0.529, generated by spatial variation (habitat differences) and demographic stochasticity (variation in individual reproduction or survival). Furthermore, the estimated strength of density dependence was $\hat{\delta} = 0.11$, giving a mean return time to equilibrium of nine years, suggesting that we should

use estimated correlations with time differences equal to or greater than 18 years to be confident that the autocorrelation function is close to ρ_∞. However, for the species we are studying, such a mean return time to equilibrium seemed unrealistic. Therefore, assuming a return time of five years, we used the sample correlations with time differences greater or equal to ten to estimate the correlation in the limit, giving $\hat{\rho}_\infty = 0.468$ $\left(\mathrm{SE} = 0.0058, n_{t\geq 10} = 6548\right)$, which equals the proportion of variance due to temporal heterogeneity among species. Using time difference greater or equal to 18 gave $\hat{\rho}_\infty = 0.459$, indicating that the assumed species' strength of density regulation does not seem to influence our estimate of heterogeneity significantly.

A small proportion $\rho_0 - \rho_\infty = 0.0032$ of the total variance $\hat{\sigma}^2_{total} = 3.42$ was due to environmental stochasticity ($\hat{\sigma}^2_{stoch} = 0.011$), compared to the variance due to heterogeneity $\hat{\sigma}^2_{heter} = 1.6$. To investigate what was causing the large over-dispersion within the Dividalen area, we looked at the two-sample correlations within the same year (Fig. 6B) and found high correlations among transects from the same group, either [1 – 6] or [7 – 10], while there was a low or negative correlation among transects from each of the groups [1 – 6] and [7 – 10]. If we estimated ρ_0 for all possible ways of grouping the transects in Dividalen in two, it transpired that by grouping [1 – 6] and [7 – 10], we obtained the largest mean estimates of ρ_0 within the two subgroups, i.e. minimized the spatial variation component of the over-dispersion the most, compared to the initial joint estimate of all transects. From our initial inspection of the data, this subdivision seemed reasonable as there were considerable

differences in elevation (Fig. 2) and vegetation characteristics (Fig. 3) between the two groups, so we called these subgroups Low and High (altitudes) respectively.

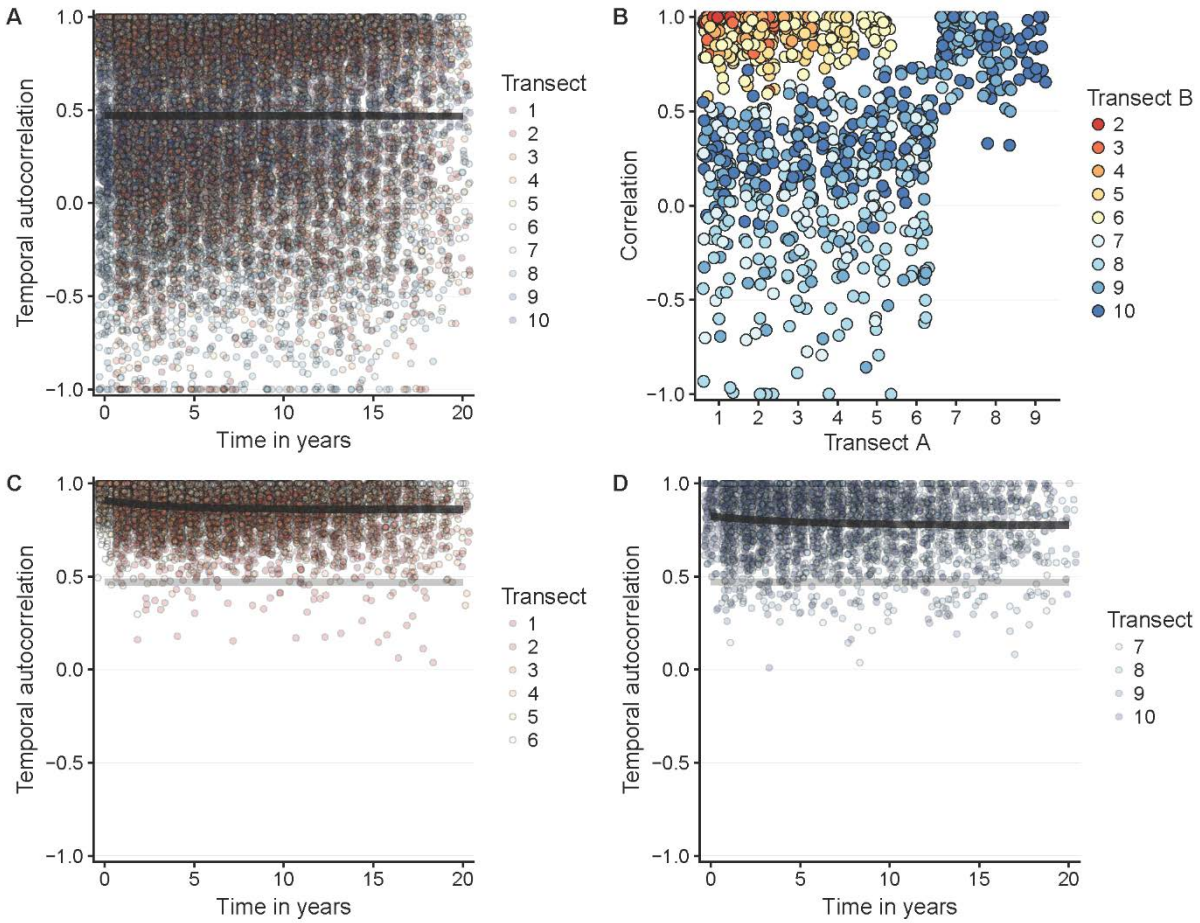

Figure 6: (**A**) Temporal autocorrelation function $\rho(t)$ (black line) estimated in Dividalen when transects are considered as a single spatial group. The points are pairwise correlations between a transect and the transect indicated by the colour, estimated from the bivariate Poisson lognormal distribution. (**B**) Estimated correlations between transect A (x-axis) and transect B (colour) in Dividalen within the same year ρ_0. (**C**) Temporal autocorrelation function $\rho(t)$ (black line) estimated in Dividalen for transects grouped as Low mean elevation [1 – 6]. The points are correlations between a transect and the transect indicated by the colour within the Low spatial group, estimated from the bivariate Poisson lognormal

distribution. The grey line is the temporal autocorrelation function fitted in **A**. (**D**) Same as **C**, but for transects grouped as High mean elevation [7 – 10].

Performing the variance partitioning within the two subgroups, we got rather different results than our initial analysis indicated (Fig. 6C and 6D). First, the estimated proportion of variance due to over-dispersion was much smaller, with $1-\hat{\rho}_0 = 0.0916$ and 0.176 for the Low and High groups respectively. Second, the Low group had a much shorter return time to equilibrium $T_R = 3.5$, while the High group had a much longer return time compared to the initial estimate $T_R = 14$. We, therefore, used sample correlations with a time difference seven years or greater to estimate ρ_∞ within the Low transects, while we used ten or more years for the High transects. The estimated proportion of variance due to heterogeneity among species was $\hat{\rho}_\infty = 0.859$ for Low ($\hat{\sigma}^2_{heter} = 3.2$) and 0.774 for High ($\hat{\sigma}^2_{heter} = 2.3$) which was a large increase compared to what the initial analysis indicated. Finally, the proportion of variance attributed to environmental stochasticity was similar in the two subgroups, with $\hat{\rho}_0 - \hat{\rho}_\infty = 0.0489$ and 0.0497, of their total variance $\hat{\sigma}^2_{total} = 3.72$ and 2.97, respectively. This gave environmental variance component estimates of $\hat{\sigma}^2_{stoch} = 0.182$ within Low and $\hat{\sigma}^2_{stoch} = 0.147$ within High transects.

Estimating the temporal autocorrelation for the community in Solhomfjell (Fig. 7A) we found that spatial variation or demographic stochasticity only accounted for a small proportion $1-\hat{\rho}_0 = 0.0789$ of the total variation $\hat{\sigma}^2_{total} = 2.57$. The strength of density regulation was 0.12, so we used sample correlations with time difference ten years or greater when

estimating ρ_∞, as we did in Dividalen when we considered all the transects together, but in Solhomfjell heterogeneity accounted for a large proportion $\hat{\rho}_\infty = 0.816$ of the total variance, corresponding to $\hat{\sigma}^2_{heter} = 2.09$. The proportion of variance due to environmental stochasticity was then $\hat{\rho}_0 - \hat{\rho}_\infty = 0.106$, i.e. $\hat{\sigma}^2_{stoch} = 0.271$. The over-dispersion estimate did not indicate any large spatial differences among the transects, a result supported by the sample correlations within the same year (Fig. 7B), where no apparent patterns of correlation between the transects emerged. The small over-dispersion estimate was also as expected from the preliminary inspection of the spatial data of elevation (Fig. 2) and vegetation (Fig. 3), where no systematic difference between the transects was observed. When we performed the subdivision of transects, the two subgroups that minimized the mean estimated over-dispersion were transects [1 – 7, 9] (Low) and [8, 10] (High). The correlation between transects 8 and 9 (Fig. 7B) was high but slightly lower between transect 9 and 10. Therefore, the 9th transect was excluded from the High group according to our simple grouping rule. The variance decomposition for the two subgroups showed that while the over-dispersion was reduced for the High group, it did not change our conclusions regarding heterogeneity, environmental stochasticity or strength of density regulation (Fig. 7C and 7D, Table 1) compared to the joint analysis of all the transects.

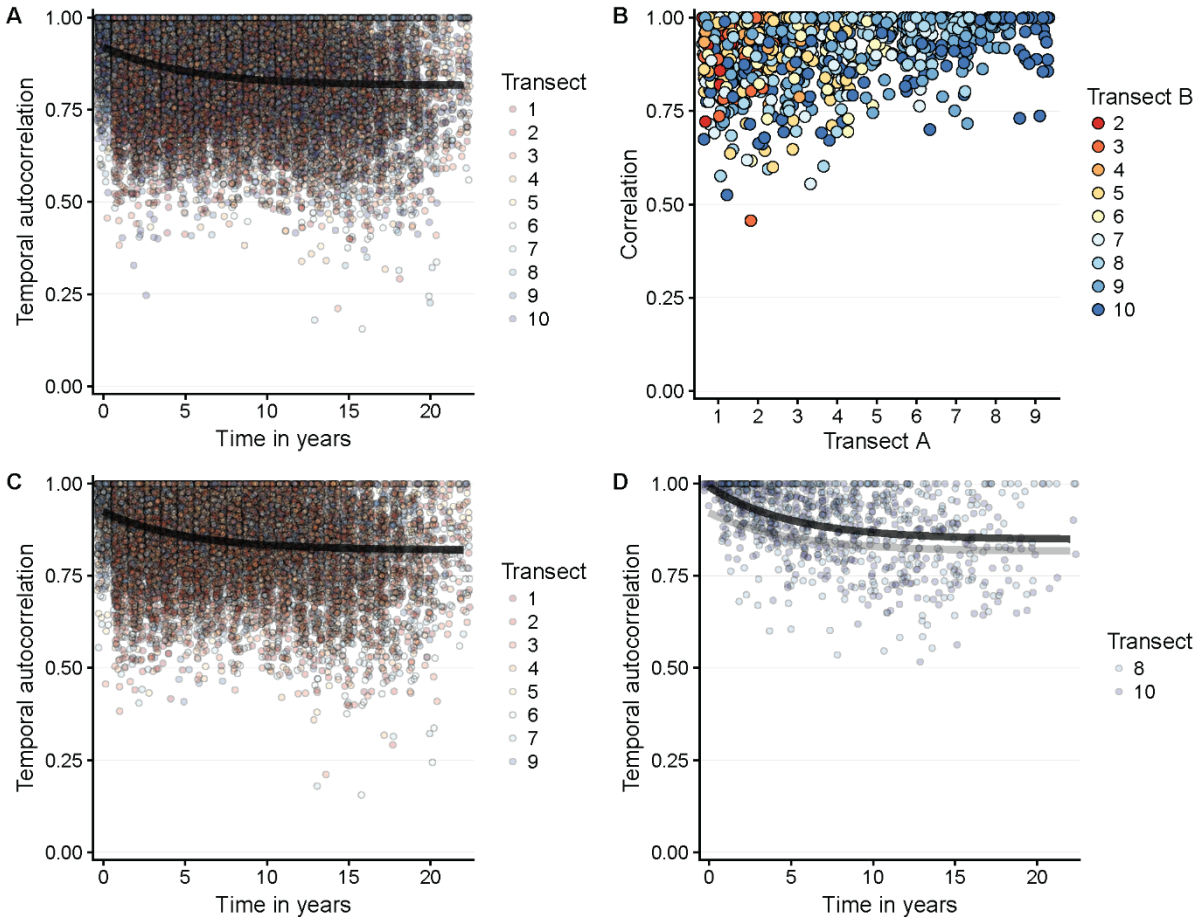

Figure 7: (**A**) Temporal autocorrelation function $\rho(t)$ (black line) estimated in Solhomfjell when transects are considered as a single spatial group. The points are correlations between a transect and the transect indicated by the colour, estimated from the bivariate Poisson lognormal distribution. (**B**) Estimated correlations between transect A (x-axis) and transect B (colour) in Solhomfjell within the same year ρ_0. (**C**) Temporal autocorrelation function $\rho(t)$ (black line) estimated in Solhomfjell for transects grouped as Low mean elevation [1 – 7, 9]. The points are correlations between a transect and the transect indicated by the colour within the Low spatial group, estimated from the bivariate Poisson lognormal distribution. The grey line is the temporal autocorrelation function fitted in **A**. (**D**) Same as **C**, but for transects grouped as High mean elevation [8, 10].

When we only used passerine species in the analysis of bird communities, the results changed slightly in Dividalen, while they were practically the same in Solhomfjell (Table 1). When analysing passerine species for all transects in Dividalen, we got a small decrease in over-dispersion and a similar increase in heterogeneity. The over-dispersion, however, was still of such a magnitude that dividing the transects into two subgroups was reasonable. While the results in the Low group in Dividalen was the same for passerine species compared to all species, there was a small decrease in heterogeneity for the High group. The non-passerine species removed from the analysis (Fig. 4) were mainly species that were only found in the High transects. The removal of species exclusive to High transects could explain the decrease in over-dispersion when analysing all transects together, since restricting the analysis to passerine species made High and Low transects more similar. When analysing High transects separately, the reduction in heterogeneity among passerine species could be due to there being fewer species at a low or intermediate abundance.

Table 1: Summary of the correlation and variance component estimates, when considering all or passerine species only, and using all transects or dividing them into Low and High subgroups. Values in parenthesis for ρ_0 and ρ_∞ gives the standard errors. Rows in bold indicate our preference for subdivision of transects to Low and High groups or considering all transects jointly.

	Area	Transects	ρ_0	ρ_∞	δ	σ^2_{total}	θ^2	σ^2_{heter}	σ^2_{stoch}
All species	Dividalen	All	0.471 (0.016)	0.468 (0.0058)	0.11	3.42	1.81	1.60	0.011
		Low	**0.908 (0.006)**	**0.859 (0.0012)**	**0.29**	**3.72**	**0.341**	**3.20**	**0.18**
		High (7-10)	**0.824 (0.013)**	**0.774 (0.0021)**	**0.073**	**2.97**	**0.524**	**2.30**	**0.15**
	Børgefjell	All	0.723 (0.007)	0.642 (0.0024)	0.021	2.67	0.741	1.71	0.22
		Low	**0.891 (0.005)**	**0.779 (0.0014)**	**0.060**	**3.02**	**0.331**	**2.35**	**0.34**
		High (8-10)	**0.852 (0.014)**	**0.753 (0.0017)**	**0.009**	**1.84**	**0.273**	**1.39**	**0.18**
	Åmotsdalen	All	0.629 (0.010)	0.602 (0.0035)	0.003	2.73	1.01	1.64	0.073
		Low	**0.825 (0.011)**	**0.786 (0.0015)**	**0.031**	**2.79**	**0.488**	**2.19**	**0.11**
		High (5-10)	**0.855 (0.008)**	**0.816 (0.0019)**	**0.072**	**2.68**	**0.388**	**2.19**	**0.11**
	Gutulia	All	0.728 (0.009)	0.648 (0.0036)	0.009	2.19	0.596	1.42	0.18
		Low	**0.862 (0.008)**	**0.718 (0.0026)**	**0.032**	**2.02**	**0.278**	**1.45**	**0.29**
		High (7-10)	**0.895 (0.010)**	**0.843 (0.0022)**	**0.073**	**2.46**	**0.258**	**2.07**	**0.13**
	Møsvatn	**All**	**0.794 (0.006)**	**0.757 (0.0026)**	**0.003**	**3.5**	**0.721**	**2.65**	**0.13**
		Low	0.968 (0.009)	0.903 (0.0008)	0.072	4.32	0.139	3.90	0.28
		High (3-8)	0.815 (0.008)	0.780 (0.0023)	0.002	3.23	0.597	2.52	0.11
	Solhomfjell	**All**	**0.921 (0.003)**	**0.816 (0.0014)**	**0.12**	**2.57**	**0.202**	**2.09**	**0.27**
		Low	0.924 (0.003)	0.820 (0.0014)	0.11	2.46	0.186	2.02	0.26
		High (8, 10)	0.992 (0.004)	0.848 (0.0013)	0.15	2.98	0.0242	2.53	0.43
	Lund	**All**	**0.912 (0.003)**	**0.808 (0.0015)**	**0.009**	**2.41**	**0.213**	**1.95**	**0.25**
		Low	0.900 (0.004)	0.807 (0.0016)	0.008	2.35	0.234	1.90	0.22
		High (5, 7)	0.986 (0.006)	0.834 (0.0012)	0.012	2.66	0.0363	2.21	0.41
Passerine species	Dividalen	All	0.524 (0.015)	0.511 (0.0055)	0.11	2.97	1.41	1.52	0.039
		Low	**0.915 (0.006)**	**0.854 (0.0018)**	**0.19**	**3.24**	**0.275**	**2.77**	**0.20**
		High (7-10)	**0.812 (0.017)**	**0.760 (0.0030)**	**0.005**	**2.56**	**0.48**	**1.95**	**0.13**
	Børgefjell	All	0.775 (0.007)	0.697 (0.0023)	0.015	2.48	0.557	1.73	0.20
		Low	**0.913 (0.005)**	**0.810 (0.0014)**	**0.070**	**2.77**	**0.242**	**2.24**	**0.28**
		High (8-10)	**0.880 (0.018)**	**0.771 (0.0019)**	**0.057**	**1.8**	**0.216**	**1.39**	**0.20**
	Åmotsdalen	All	0.621 (0.010)	0.588 (0.0037)	0.003	2.71	1.03	1.59	0.092
		Low	**0.810 (0.012)**	**0.758 (0.0017)**	**0.005**	**2.67**	**0.508**	**2.03**	**0.14**
		High (5-10)	**0.862 (0.009)**	**0.825 (0.0022)**	**0.004**	**2.74**	**0.377**	**2.26**	**0.10**
	Gutulia	All	0.746 (0.009)	0.667 (0.0038)	0.009	2.41	0.614	1.61	0.19
		Low	**0.870 (0.008)**	**0.714 (0.0027)**	**0.078**	**2.17**	**0.283**	**1.55**	**0.34**
		High (8-10)	**0.934 (0.009)**	**0.889 (0.0021)**	**0.110**	**2.78**	**0.183**	**2.47**	**0.13**
	Møsvatn	**All**	**0.792 (0.007)**	**0.751 (0.0027)**	**0.003**	**3.17**	**0.66**	**2.38**	**0.13**
		Low	0.973 (0.010)	0.899 (9e-04)	0.092	3.87	0.105	3.48	0.29
		High (3-8)	0.814 (0.008)	0.777 (0.0024)	0.032	2.94	0.547	2.29	0.11
	Solhomfjell	**All**	**0.923 (0.003)**	**0.825 (0.0015)**	**0.130**	**2.52**	**0.195**	**2.08**	**0.25**
		Low	0.926 (0.004)	0.831 (0.0015)	0.084	2.41	0.178	2.01	0.23
		High (8, 10)	0.992 (0.004)	0.856 (0.0012)	0.180	2.93	0.0226	2.51	0.40
	Lund	**All**	**0.912 (0.004)**	**0.807 (0.0017)**	**0.043**	**2.27**	**0.2**	**1.83**	**0.24**
		Low	0.901 (0.005)	0.806 (0.0017)	0.008	2.25	0.224	1.81	0.21
		High (5, 7)	0.987 (0.006)	0.831 (0.0012)	0.012	2.34	0.031	1.95	0.37

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For the other areas, Børgefjell, Åmotsdalen, Gutulia, Møsvatn and Lund, the estimated strength of density regulation was so small that the estimated mean return time to equilibrium $\hat{T}_R$ was greater than our observed maximum time difference. We, therefore, used the correlations with time differences of ten years or greater to estimate ρ_∞ and the variance due to heterogeneity among species, as a simple approximation in the absence of a reasonable estimate of δ. The estimated ρ_0 (Table 1) showed that there was more over-dispersion when considering all transects together in Børgefjell, Åmotsdalen and Gutulia compared to Møsvatn and Lund. Comparing the analysis for all the areas available (Fig. 8), heterogeneity among species accounted for roughly three-quarters of the variation in species abundance. For areas where over-dispersion was more than a quarter of the variance when considering all transects together (Dividalen, Børgefjell, Åmotsdalen and Gutulia), it was beneficial to partition the transects into two subgroups as this reduced the over-dispersion in both subgroups, which was not the case for the other areas (Møsvatn, Solhomfjell and Lund).

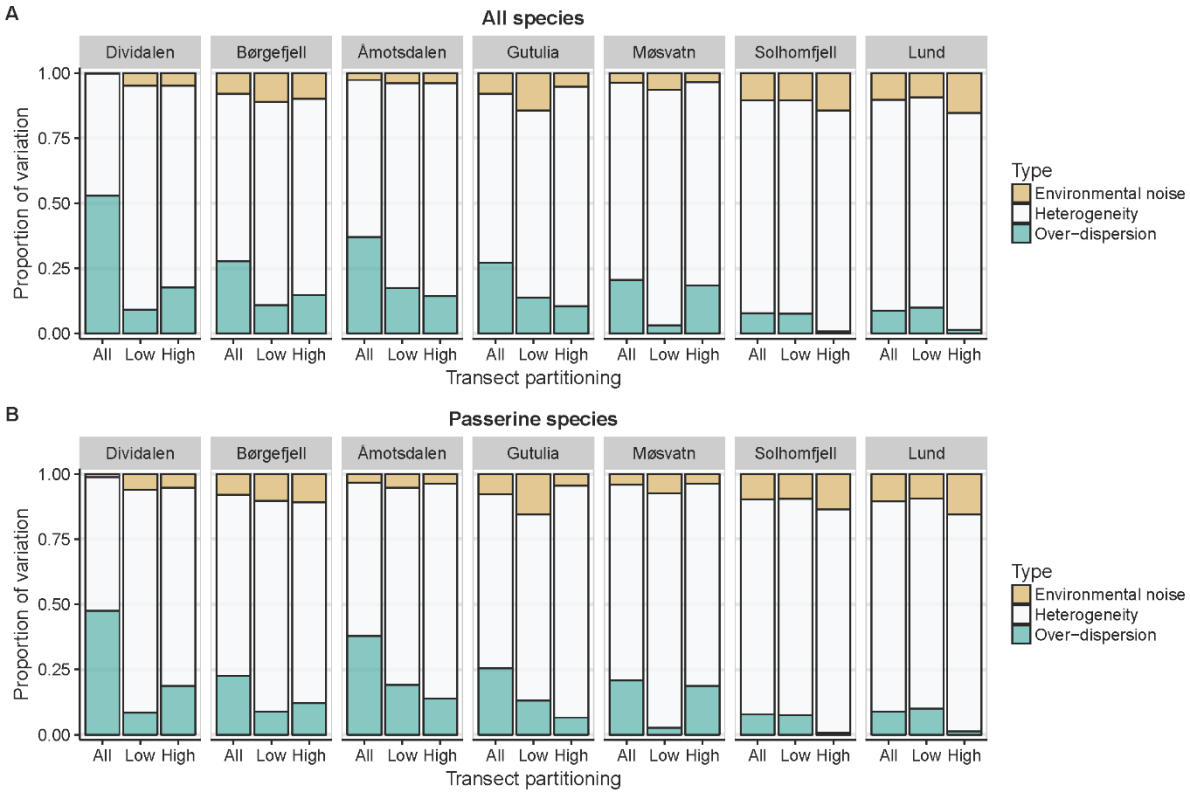

Figure 8: Partition of the total variance in species abundances into environmental noise, heterogeneity and over-dispersion components in all the areas considered.

The absolute values of the variance component estimates (Table 1) ranged from 0.11 to 0.34 for environmental noise σ^2_{stoch} if we considered High and Low subgroups in Dividalen, Børgefjell, Åmotsdalen and Gutulia, and all transects together in Møsvatn, Solhomfjell and Lund. There were no apparent trends in σ^2_{stoch} in terms of High or Low groups or the geographical location of the different areas. The optimal subdivision of the transects showed that for Dividalen, Børgefjell, Åmotsdalen, Gutulia and Møsvatn, the partitioning followed the mean elevation gradient. One of the subgroups in Møsvatn only included two transects, which seemed to reduce the over-dispersion very little in the remaining subgroup. The small reduction in over-dispersion for one of the subgroups was also the case for Solhomfjell and

Lund, where the division did not follow the mean elevation gradient, not surprising considering that the elevation range was limited compared to the other areas (Fig. 2). Due to the lack of overall reduction in over-dispersion, we would suggest keeping the analysis made with all the transects considered jointly in areas with spatial variation similar to that in Møsvatn, Solhomfjell and Lund.

4. Discussion

To monitor and understand community dynamics, typically wanting to distinguish natural from human-induced changes in species assemblages, is a challenging task in community ecology. The concept of β-diversity, introduced by Whittaker (1972), described the difference in diversity between local communities and populations over larger geographical areas. This approach has also been extended to the temporal scale, defined as the metric describing changes in community composition over time, using some similarity measure to find how fast similarity changes (species turnover) (McGill et al. 2015). Here, natural temporal species turnover has been modelled by letting population model parameters vary among species, so-called community heterogeneity (Engen et al. 2011b). Describing each species' population dynamics put great demands on data sets and model parameterization, but by modelling species-specific growth rates by a distribution, leading to variation in carrying capacities among species, we do not need to specify the dynamics of each species in detail. The community can thereby be described by a parsimonious model that still captures the important properties of the dynamics. Without this assumption of heterogeneity, the estimated environmental variance would have to be extremely large to generate the variation seen in species abundance distributions and the model would still not describe the

species turnover correctly (Solbu et al. 2016). Trying to predict population dynamics with an overestimated environmental variance would also result in an unrealistic short time to extinction (Sæther et al. 2005).

With the modelling approach presented here, it is also possible to sort out potential spatial variation in species abundances among sampling units that otherwise would obscure the analysis of community dynamics. Long time series of community data are usually hard to come by, they can be designed for other purposes (even studying spatial structures), or some physical constraints may limit our freedom to design sampling optimally. The validity of this approach has been illustrated by linking the spatial variation in species abundances to elevation and vegetation, but habitat data like can often be unavailable and is not required to fit the model. Even with suboptimal sampling designs of time series data, it is possible to obtain reliable parameter estimates and predictions for the dynamics of a heterogeneous community.

Our model development was started by revisiting the theory of dynamic species abundance models (Engen and Lande 1996) to estimate the different sources of variation in species abundance distributions, which in turn can be used to quantify the community similarity over time. The method has several attractive features as it accounts for sampling error, provides approximately unbiased estimates, and enables us to decompose the total variance to variation due to species' temporal heterogeneity, species-specific environmental stochasticity and over-dispersion, which in turn can uncover spatial variation in habitat. Heterogeneity among species is the underlying assumption applied in the modelling, which

also gave us a measure of the temporal similarity. We applied this method to local communities of birds throughout Norway, which have not undergone any dramatic changes in habitat during the observation period. Other studies, such as on bird communities in North America, have shown that diversity increased for some decades pre-2000s, before starting to decline in recent years (Jarzyna and Jetz 2017). Across many taxa, communities have generally been found to decrease in similarity over time, while maintaining a stable species richness (Dornelas et al. 2014).

Our results show that a large proportion of the variation in species abundance was due to heterogeneity among species, from which we can conclude the following: First, the community composition was very similar over the whole 20-year period observed, with abundant species remaining abundant while less abundant species maintaining a low abundance. The high degree of similarity gives a small temporal β-diversity with a low turnover rate (see Fig. 1 in McGill et al. 2015). As the areas studied are rather undisturbed, the low turnover rate can be interpreted as a baseline. If the turnover rate increases, it could be an indication of species invasions or climate change that would have to be addressed by conservation managers (Magurran 2016). Second, the large proportion of variation due to heterogeneity gave estimates of environmental variance that seems reasonable compared to studies of both butterfly and aquatic insect communities (Engen et al. 2002, 2011b).

The low estimate for the strength of density regulation could be due to strong temporal correlation between transects, as indicated by the data. A small δ makes it hard to estimate the proportion of variance due to heterogeneity ρ_∞ (Eq. 3). The strategy of setting a lower

bound for the strength of density dependence, to determine the time difference used to estimate the proportion of variance due to heterogeneity ρ_∞, was based on earlier studies of temporal dynamics of bird species (Sæther and Engen 2002). An alternative, non-parametric approach for estimating the correlation in the limit ρ_∞ is to use the quantiles of the sample correlations to determine the threshold (Engen et al. 2011b). Using prior or expert knowledge about the strength of density regulation is reasonable in cases where good estimates are difficult to obtain (Solbu et al. 2015). The results from the different methods used to determine the threshold for ρ_∞ were roughly the same, as the sample correlations were high over the whole period (Fig. 6C and D, and Fig. 7A). Furthermore, the analysis is robust with respect to the assumption of a normal distributed log abundance (Engen et al. 2011a).

With the plethora of indices ecologists have available for studying biodiversity, using the bivariate Poisson lognormal distribution to estimate similarity between samples is a favourable alternative as it accounts for many modelling challenges and allows for robust analysis. Even though data may be collected within spatially varying areas, using this knowledge to separate spatial from temporal variation reveals community dynamics that to a large extent is governed by heterogeneity among species in dynamical parameters.

5. Acknowledgements

The data used are from the Norwegian Terrestrial Monitoring program financed by the Norwegian Climate and Environment Ministry and the Environment Agency. The work of EBS

and SE was supported by the Research Council of Norway (SFF-III 223257/F50). The work of OHD was financed by the NINA Strategic Institute Initiative “Integrate – effects of climate change on terrestrial biodiversity and scenarios for the future”.

The authors declare no competing interests. No permits were needed during this study.

6. References

Bonar, S. A., Fehmi, J. S. and Mercado-Silva, N. 2011. An overview of sampling issues in species diversity and abundance surveys. - In: Magurran, A. E. and McGill, B. J. (eds), Biological Diversity: Frontiers in measurement and assessment. 1st ed. Oxford University Press, pp. 11-24.

Bulmer, M. G. 1974. On fitting the Poisson Lognormal distribution to species-abundance data. - Biometrics 30: 101-110.

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. and Magurran, A. E. 2014. Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. - Science 344: 296-299.

Engen, S. and Lande, R. 1996. Population dynamic models generating the lognormal species abundance distribution. - Mathematical Biosciences 132: 169-83.

Engen, S., Lande, R., Walla, T. and DeVries, P. J. 2002. Analyzing Spatial Structure of Communities Using the Two-Dimensional Poisson Lognormal Species Abundance Model. – The American Naturalist 160: 60-73.

Engen, S., Grøtan, V. and Sæther, B.-E. 2011a. Estimating similarity of communities: A parametric approach to spatio-temporal analysis of species diversity. - Ecography 34: 220-231.

Engen, S., Aagaard, K. and Bongard, T. 2011b. Disentangling the effects of heterogeneity, stochastic dynamics and sampling in a community of aquatic insects. - Ecological Modelling 222: 1387-1393.

Grøtan, V. and Engen, S. 2008. Poilog: Poisson lognormal and bivariate Poisson lognormal distribution. P-package https://cran.r-project.org/web/packages/poilog/poilog.pdf

Hubbell, S. P. 2001. The unified neutral theory of biodiversity and biogeography. - Princeton University Press.

Hutchinson, G. E. 1957. Concluding Remarks. - Cold Spring Harbor Symposia on Quantitative Biology 22: 415-427.

Jarzyna, M. A. and Jetz, W. 2017. A near half-century of temporal change in different facets of avian diversity. - Global Change Biology 23: 2999-3011.

Karlin, S. and Taylor, H. M. 1981. A second course in stochastic processes. - Academic Press.

MacArthur, R. 1960. On the relative abundance of species. – American Naturalist 94: 25-36.

Magurran, A. E. 2016. How ecosystems change. - Science 351: 448-449.

McGill, B. J., Dornelas, M., Gotelli, N. J. and Magurran, A. E. 2015. Fifteen forms of biodiversity trend in the Anthropocene. - Trends in Ecology and Evolution 30: 104-113.

Preston, F. W. 1948. The commonness, and rarity, of species. – Ecology 29: 254-283.

R Core Team 2016. R: A language and environment for statistical computing. - R Foundation for Statistical Computing.

Sæther, B.-E. and Engen, S. 2002. Pattern of variation in avian population growth rates. - Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences 357: 1185-1195.

Sæther, B.-E. et al. 2005. Time to extinction of bird populations. - Ecology 86: 693-700.

Solbu, E. B., Engen, S. and Diserud, O. H. 2013. Changing environments causing time delays in population dynamics. - Mathematical Biosciences 244: 213-223.

Solbu, E. B., Engen, S. and Diserud, O. H. 2015. Guidelines when estimating temporal changes in density dependent populations. - Ecological Modelling 313: 355-376.

Solbu, E. B., Engen, S. and Diserud, O. H. 2016. Characteristics of temporal changes in communities where individual dynamics may vary among species. - Theoretical Population Biology 111: 65-74.

Whittaker, R. H. 1972. Evolution and measurement of species diversity. - Taxon 21: 213-251.