

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



Erik B. Solbu^a, Ola H. Diserud^{b,*}, John A. Kålås^b, Steinar Engen^c

^a Dept. of Biology, Centre for Biodiversity Dynamics, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway

^b Norwegian Institute for Nature Research, P.O. Box 5685 Torgard, NO-7485 Trondheim, Norway

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

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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.

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

* Corresponding author.

E-mail addresses: eriksolbu@protonmail.com (E.B. Solbu), ola.diserud@nina.no (O.H. Diserud), john.kalas@nina.no (J.A. Kålås), steinar.engen@math.ntnu.no (S. Engen).

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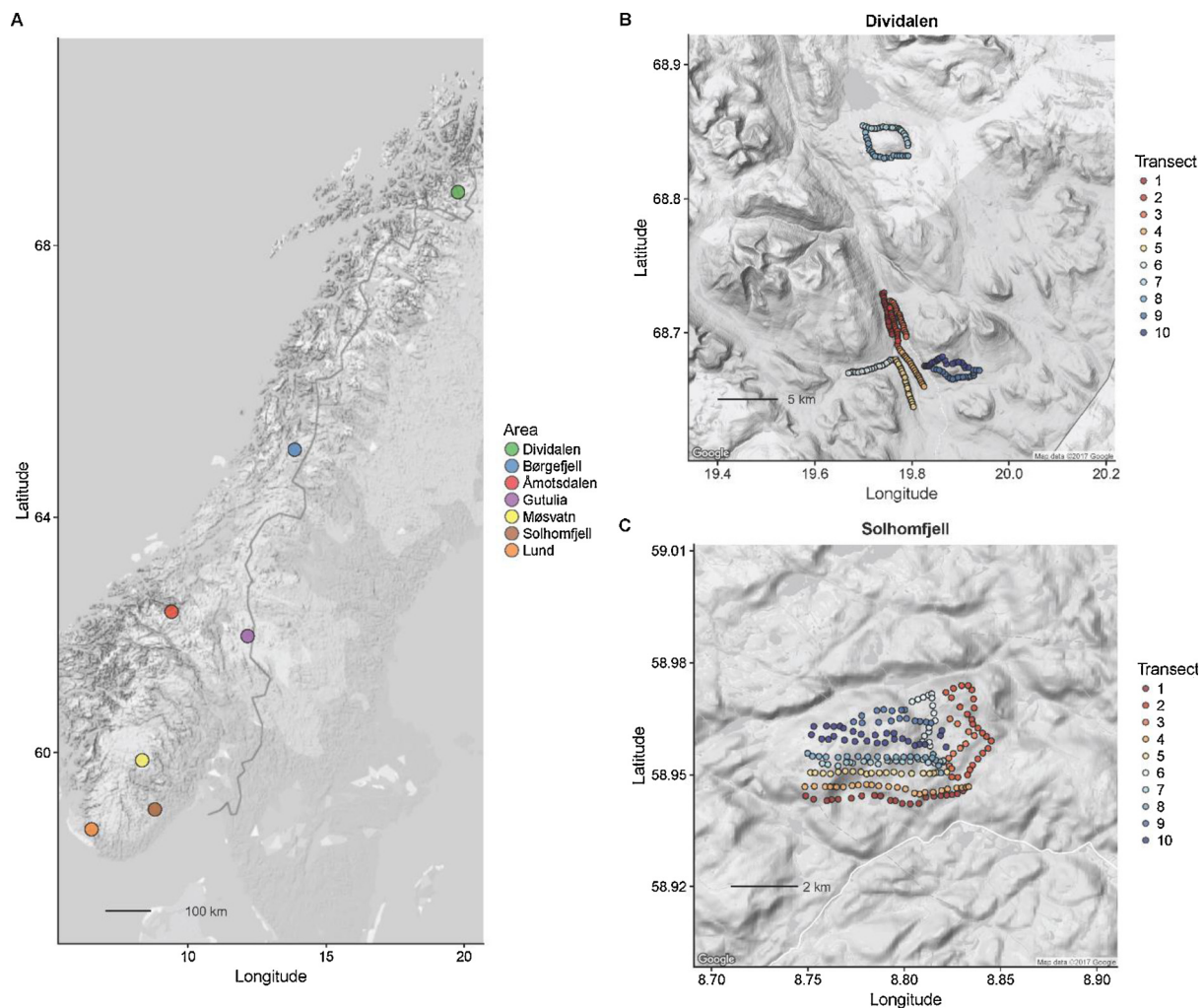


Fig. 1. (A) Location of the seven areas where sampling has been conducted. (B) Location of the sampling points for each transect in Dividalen. (C) Location of the sampling points for each transect in Solhomfjell. The transects have been ordered according to mean elevation from low (1) to high (10). Note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

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

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