

1 Detection of eco-evolutionary dynamics in metacommunities using
2 Joint Species Distribution Models

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1 Title

Detection of eco-evolutionary dynamics in metacommunities using Joint Species Distribution Models

2 Abstract

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3 Introduction

Analysis of biodiversity at large spatial scales can be complex, because numerous environmental properties, spatial structure and connectivity, interactions between species, as well as stochastic processes such as drift and priority effects operate and determine observed patterns. Statistical models in ecology have made tremendous progress in reflecting these numerous ecological processes at multiple scales. There are now a diversity of joint species distribution models [JSDMs; Pollock et al. (2014)] (Pichler and Hartig 2021) or multi-species occupancy models (Devarajan et al. 2020) (Poggiato et al. 2021), which can incorporate these diverse components that structure variance in biological data. Many of these models increasingly have implementations in R packages (e.g. spOccupancy, (Doser et al. 2022)), and have been used to measure the relative importance of different ecological drivers in fungi, birds, mammals, phytoplankton, fish, and other taxa, from local to continental scales (e.g. (Abrego et al. 2020) (Antão et al. 2022) (Keppeler et al. 2022)). There are some remaining drivers of community composition that aren't currently reflected in these models. The dynamics of populations and communities, and resulting biodiversity patterns, are also influenced by the genotypic and phenotypic properties of organisms as well. Although traits can be considered in some JSDMs, they typically require fixed values for species' traits ((Ovaskainen et al. 2017) (Tikhonov et al. 2020); but see Abrego et al. (2024)). However, ecological dynamic processes can impact selection on genes and phenotypes, potentially resulting in interactions or feedback loops between ecological and evolutionary processes (Lion 2018) (Barbour et al. 2022). Although an increasing number of theoretical and empirical

studies have evaluated the impact of evolutionary dynamics for community assembly and metacommunity dynamics (Loeuille and Leibold 2008) (Osmond and Mazancourt 2013) (Pantel et al. 2015) (Toju et al. 2017), analytical methods to consider this additional complexity lag behind the scope of data collected in eco-evolutionary studies. Some methods exist that ultimately apply an ANOVA framework to partition variance in traits or growth rates across contributions of ecological and evolutionary components ((Hairston Jr et al. 2005) (Ellner et al. 2011) (Govaert et al. 2016)). These methods tend to be cited more frequently for their potential than for their actual application to empirical data (but see (terHorst et al. 2014) (Hiltunen and Becks 2014)), because this approach is ultimately limited by the same requirements that can limit application of ANOVA - data should follow a normal distribution, the processes that structure the target response variable must be linear and additive, and complicated structuring mechanisms must be reduced into one or a few target categories labeled as ‘ecology’ or ‘evolution’. Flexible models, which can vary depending on the mechanisms and structure of the diverse kinds of data that most studies of eco-evolutionary dynamics will collect, are needed for rigorous inference about eco-evolutionary processes (Pantel and Becks 2023).

Two existing statistical models are potentially well suited for analysis of eco-evolutionary data at the microevolutionary and metacommunity scale but also have some considerations before their application to complex community data. Lasky et al. (2020) (Lasky et al. 2020) developed an integrated reaction norm model, linking genetic, phenotypic, and demographic processes, and Benito Garzón et al. (2019) (Benito Garzón et al. 2019) presented a species distribution model with local adaptation and phenotypic plasticity (Δ SDMs). The model of Lasky et al. is an excellent candidate for spatially complex population dynamics, and awaits an extension to the multispecies level. The Δ SDM models described by Benito Garzón et al. truly disentangle the role that plastic and evolutionary trait divergence can play in species distributions, but they also require common garden experimental data across sites to estimate these effects. Observational data collected in metacommunity surveys may only have observational data across sites or time points, as large-scale experimental measures of reaction norms required by the Δ SDM model may be difficult to obtain.

One particular metacommunity statistical model, the Hierarchical Modelling of Species Communities (HMSC) framework (Ovaskainen et al. 2017) (Tikhonov et al. 2020), explicitly considers the multitude of processes that can structure community composition across time and space (Leibold et al. 2022) and is

thus well suited to consider analysis of metacommunity eco-evolutionary data. This model of environmental filtering via variation and covariation in how species respond to their environment considers the impacts of (fixed) trait values and phylogenetic relationships, and uses latent variables to account for the numerous unobserved environmental and spatial features that are difficult to exhaustively measure in community surveys. The associated R package has immense flexibility, and has been applied to study environmental and abiotic drivers of diverse assemblages of organisms (e.g. (Sandal et al. 2022) (Weigel et al. 2023)). HMSC is potentially useful for studying eco-evolutionary drivers of community structure, but the model has not previously been applied to include heritable changes in trait values over time.

In this study, we use simulations of population dynamics, environmental drivers, species interactions, and trait evolution in populations, communities, at the local and metacommunity scale, to generate simulated time series of population sizes and mean trait values. We then use HMSC to analyze the resulting data, to determine whether HMSC can successfully estimate the impacts of trait evolution for community composition, and to generate relative contributions of fixed environmental, spatial, and trait evolution drivers as well as random effects of spatial and temporal covariance among species. We asked three main questions: (i) do linear statistical models (like HMSC) accurately capture the impact of non-linear population, community, and evolutionary dynamic processes?, (ii) can HMSC be used to evaluate hypothesized drivers of the relative importance of evolution for community composition at the metacommunity scale?, and (iii) can we better understand the role of evolution for community dynamics in experimental systems using HMSC?

4 Methods

4.1 Linear statistical models for one- and two-species models of growth, competition, and trait evolution

We evaluated whether linear regression models can appropriately capture the dynamics that drive species abundances in relatively simple populations and communities. We fit data generated from simulation models with increasing complexity to Bayesian linear regression models. These simulation models were (i) a single-

species model of discrete-time logistic population growth, (ii) expanded to include a randomly fluctuating environmental property E that impacts the species' population growth rate, (iii) a two-species model of logistic growth and competition that was then (iv) expanded to consider a randomly fluctuating environmental property, (v) and further expanded to consider evolution in a trait x that is selected by the environmental property, and finally (vi) the model of two-species growth, competition, environmental change, and evolution in a spatially structured (10-patch) habitat.

For linear regression models to fit to the simulated population size data, we began with models using population size and environment as fixed effects ($N_t \sim N_{t+1} + E_t + E_t^2$), and progressed to a mixed model using environment and trait evolution as fixed effects ($N_t \sim E_t + E_t^2 + |\Delta x|$) and time and spatial distance as random effects. For consistency, all linear regression models were implemented as hierarchical Bayesian models using HMSC (Hierarchical Modelling of Species Communities (Ovaskainen et al. 2017) (Tikhonov et al. 2020)). HMSC uses a latent variable approach as an alternative to directly modelling species interaction coefficients, estimating a reduced number of linear combinations of species abundances that best predict future population size values. For linear models fit to data generated in simulations *iii*, *iv*, *v*, and *vi* above, the time random effect was implemented to capture species interactions (as part of the temporal species association matrix estimated by the model), and the spatial random effect was implemented in model *vi* to capture spatial covariance in abundances as a function of distance between sites. Full methodological details are given in Appendix S1. All simulations were run in R (R Core Team (2024)) and HMSC models were implemented using the `Hmsc` package (Tikhonov et al. (2022)).

4.2 Evolution in metacommunities and HMSC

Simulation model

We also simulated growth and competition dynamics for a multi-species assemblage in a patchy landscape, with site variation in one environmental property, and with evolution in a trait that is selected on by the environment. Population growth for species in the metacommunity simulation follows a Leslie-Gower model (a discrete-time version of a Lotka-Volterra model (Beverton and Holt 1957) (Leslie and Gower 1958)).

We consider the impact of trait evolution for growth using a discrete time quantitative genetic model of evolutionary rescue (Gomulkiewicz and Holt 1995). The model for population size is as follows:

$$N_{i,t+1} = \frac{\hat{W} e^{-\frac{[(\frac{w+(1-h^2)P}{P+w})(E-x_{i,t})]^2}{2(P+w)}}}{1 + \alpha_{ii}N_{i,t} + \sum_{j \neq i}^S \alpha_{ij}N_{j,t}} N_{i,t}$$

where $N_{i,t}$ is the population size of species i at time t , \hat{W} is calculated as $\hat{W} = W_{max} \sqrt{(\frac{w}{P+w})}$, W_{max} is the species' maximum per-capita growth rate, w is the width of the Gaussian fitness function (which determines the strength of selection, as increasing values indicate a weaker reduction in fitness with distance from optimum trait value), P is the width of the distribution of the phenotype x , h^2 is the heritability of the trait x , E is the local environmental optimum trait value, $x_{i,t}$ is the trait value of species i at time t , α_{ii} is the intraspecific competition coefficient (the per capita impact of species i on itself) and α_{ij} is the interspecific competition coefficient. Populations have a critical density N_c , below which the population is subject to extinction due to demographic stochasticity at a probability of p (Gomulkiewicz and Holt 1995).

This model was used in Pantel & Becks (Pantel and Becks 2023) to evaluate the consequences of adaptive evolution for coexistence in a three-species system. To expand this model to a metacommunity, we consider the evolution of multiple species ($S = 15$) in a landscape of patches ($k = 50$). The patches have values of an environmental property $E \sim U(0,1)$ that determines the local optimum phenotype $E = x_{opt}$, i.e. where species experience their absolute fitness W_{max} , and patches also have spatial locations X and Y (both drawn from $U(0,1)$). The patches thus have a connectivity matrix \mathbf{D} (here given by their Euclidean distance), as well as a connectivity matrix \mathbf{C} that is a Gaussian function of \mathbf{D} and species dispersal rate d_i .

We used the evolving metacommunity model to test whether landscape connectivity (the overall dispersal rate d) and the speed of evolution (evaluated as h^2) influenced the relative importance of trait evolution ($|\Delta x|$) for metacommunity composition (evaluated as $V_{|\Delta x|}$, the proportion of variation in species abundances explained by $|\Delta x|$ as estimated by the HMSC model fit to the simulated data across d and h^2 levels). We hypothesized that the overall importance of trait evolution ($V_{|\Delta x|}$) would decrease with increasing dispersal rate - at low dispersal, locally mal-adapted species are less likely to emigrate to more optimal patches and will experience strong local selection. Population sizes in the mal-adapted populations will also likely be

lower, leading to reduced relative importance of density-dependent intra- and interspecific competition. We also hypothesized that heritability (h^2) would mediate the relative importance of dispersal rate - at higher h^2 , species will evolve quickly and we expected the importance of trait evolution $V_{|\Delta x|}$ to depend on the amount of time that mal-adapted populations persist. Therefore simulations run using higher h^2 would have decreased importance of evolution $V_{|\Delta x|}$ for community composition. For the same reason, we hypothesized generally that, for a given dispersal rate d , the importance of evolution $V_{|\Delta x|}$ would decrease with increasing h^2 .

All simulations used the same parameter values ($W_{max} = 2$, $P = 1$, $w = 2$, $N_c = 100$, $p = 0.001$), species interaction matrix ($\alpha_{ii} = 0.00125$; $\alpha_{ij} \sim U(0.0015, 1)$), and initial conditions (initial richness $s_{0k} \sim Pois(0.75)$; initial population size $N_{0i} \sim Pois(10)$; initial degree of maladaptation $\beta_{i0} \sim Gamma(0.75, 1)$, initial distance to the local patch's optimum phenotype $d_{i0} = \sqrt{B_{i0}(w + P)}$, initial trait value $x_{i0} = E_k - d_{i0}$; Appendix S4). Simulations were run across a range of dispersal values (identical for all species; $d = 0$, 10^{-9} , 10^{-8} , 10^{-7} , 10^{-6} , 10^{-5} , 10^{-4} , 10^{-3} , 10^{-2} , 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1) and heritability values (identical for all species: $h^2 = 0$, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9, 1) for 200 time steps, producing records of N_{ikt} and x_{ikt} .

###Statistical model

To determine the relative influence of environmental and spatial properties, intra- and interspecific population dynamics, and evolutionary dynamics for community structure, we applied hierarchical modelling of species communities (HMSC, (Ovaskainen et al. 2017) (Tikhonov et al. 2020)) to model the log abundance at each site and year for each species $\ln(N_{ikt})$. The abundance values were modeled as $N_{ikt} \sim N(L_{ikt}, \sigma_2)$, where the linear predictors \mathbf{L} are the sum of fixed and random effects $\mathbf{L}^F + \mathbf{L}^R$ (Tikhonov et al. 2020). The fixed effects were E_k , E_k^2 , and the absolute value of the change in each species' trait value from the previous time step to the next $|\Delta x_{ik,t-1 \rightarrow t}|$. Random effects included time (the day of the sample) and space. The spatial latent variables represent a spatial model, where species respond to some latent spatial predictor associated with the xy coordinates of the sites (Tikhonov et al. 2020).

5 Results

5.1 Linear statistical models for one- and two-species models of growth, competition, and trait evolution

Linear regression models can estimate the impacts of intra- and interspecific competition, environmental variation, and trait evolution for population size in simple one- and two-species models of population growth. In simple cases (one-species models, linear and quadratic relationships between environment and population size), the regression coefficients successfully reflect the direction and magnitude of the relationships included in the non-linear simulation model (the impact of N_t and E_t for N_{t+1}). However, as the processes included in the simulation models become slightly more complex (competition with a second species, spatial structure), regression coefficients were useful for prediction but not for recreating the underlying processes driving changes in population size (Appendix S1; REF?).

To consider species interactions and environmental fluctuations (model *iv*; Figure 1a ??), we used the latent variable modelling approach implemented in HMSC. The linear model successfully estimated coefficients for fixed environmental effects that captured the impacts of environment for population size in both species (Figure 1b,c) and partitioned the relative importance of the environment and species interactions for species abundances (Figure 1d). The model coefficients could also predict the population size values over time (Figure 1a), though the quality of this prediction varied depending on the level of environmental noise (Appendix S1).

The HMSC model was successfully modelled changes in species abundances when trait evolution was introduced (model *v*; Figure 1e ??). Fixed effect coefficients for the environmental driver and the total trait change from one time to the next ($|x|$) matched well with observed data (Figure 1f,g). The model estimated the relative importance of the environmental driver, trait evolution in both species, and species interactions (Figure 1h), and predicted the observed species abundances well (Figure 1e). Spatial structure was also reproduced in the coefficients of the linear HMSC model by using spatial random effects to capture covariance in species abundances as a function of spatial distance between sites in the 10-patch simulation model

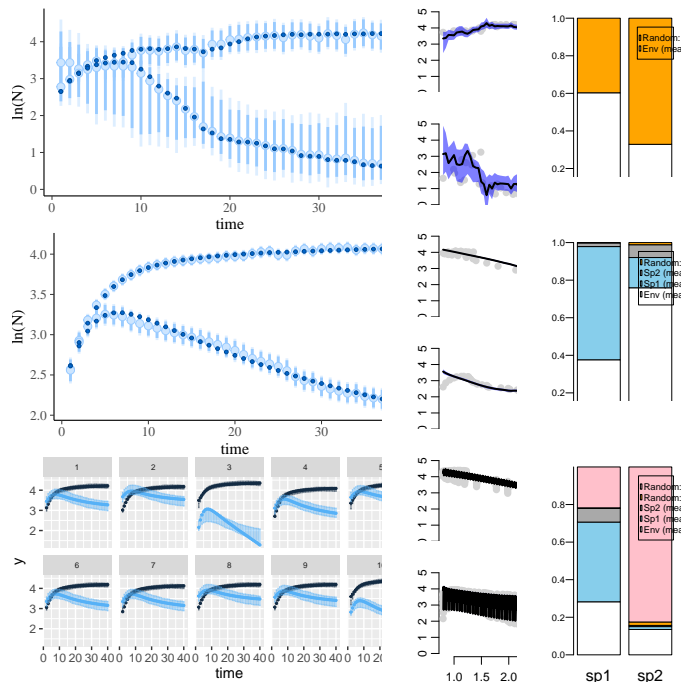


Figure 1: your caption

(model *vi*; Figure 1i,j,k ??). The variation partition successfully reflects separation of environmental drivers from trait evolution, species interactions, and spatial random effects (Figure 1l), and we show in Appendix S1 that the relative importance of trait evolution increases when we use a simulation model with less spatial and environmental variation and weak species interactions.

5.2 Evolution in metacommunities and HMSC

The simulation model followed population size and trait value dynamics for species in the landscape across 200 time steps (Figure 4a ??). Resulting biodiversity dynamics depended on the dispersal level and heritability values (Figure 4b ??). For dispersal, results mirrored some expectations from existing metacommunity models, i.e. that regional γ diversity decreases with increasing dispersal level ((Mouquet and Loreau 2003); Figure 4b ??). The inclusion of trait heritability had a very strong effect on community diversity, reflecting that local adaptation can rescue species and contribute to richness at the local and metacommunity scale.

Species diversity at the regional γ level increased with increasing h^2 levels (Figure 4b ??).

Analysis using the HMSC model for community time series across d and h^2 levels indicated that the importance of evolution for community composition ($V_{|\Delta x|}$) decreased with increasing dispersal and with increasing heritability (Figure 4c,d,e ??).

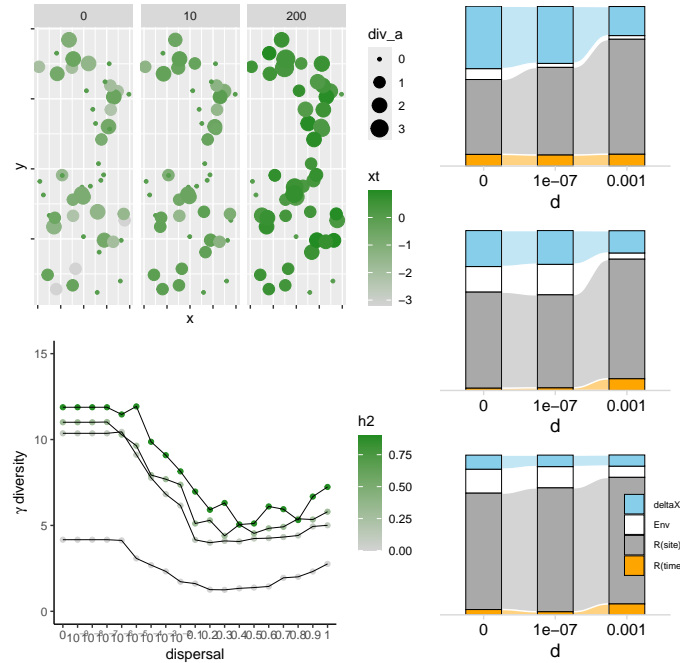


Figure 2: your caption

6 Discussion

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7 References

Abrego, N., B. Crosier, P. Somervuo, N. Ivanova, A. Abrahamyan, A. Abdi, K. Hämäläinen, et al. 2020.

[Fungal communities decline with urbanization—more in air than in soil.](#) The ISME Journal 14:2806–2815.

- Abrego, N., P. Niittynen, J. Kemppinen, and O. Ovaskainen. 2024. Disentangling the role of intraspecific trait variation in community assembly with joint species-trait distribution modelling. *Authorea Preprints*.
- Antão, L. H., B. Weigel, G. Strona, M. Hällfors, E. Kaarlejärvi, T. Dallas, Ø. H. Opedal, et al. 2022. [Climate change reshuffles northern species within their niches](#). *Nature Climate Change* 12:587–592.
- Barbour, M. A., D. J. Kliebenstein, and J. Bascompte. 2022. [A keystone gene underlies the persistence of an experimental food web](#). *Science* 376:70–73.
- Benito Garzón, M., T. M. Robson, and A. Hampe. 2019. [ΔTraitSDMs: Species distribution models that account for local adaptation and phenotypic plasticity](#). *New Phytologist* 222:1757–1765.
- Beverton, R. J., and S. J. Holt. 1957. *On the dynamics of exploited fish populations* (Vol. 11). Springer Science & Business Media.
- Devarajan, K., T. L. Morelli, and S. Tenan. 2020. [Multi-species occupancy models: Review, roadmap, and recommendations](#). *Ecography* 43:1612–1624.
- Doser, J. W., A. O. Finley, M. Kéry, and E. F. Zipkin. 2022. [spOccupancy: An r package for single-species, multi-species, and integrated spatial occupancy models](#). *Methods in Ecology and Evolution* 13:1670–1678.
- Ellner, S. P., M. A. Geber, and N. G. Hairston Jr. 2011. [Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics](#). *Ecology Letters* 14:603–614.
- Gomulkiewicz, R., and R. D. Holt. 1995. [When does evolution by natural selection prevent extinction?](#) *Evolution* 49:201–207.
- Govaert, L., J. H. Pantel, and L. De Meester. 2016. [Eco-evolutionary partitioning metrics: Assessing the importance of ecological and evolutionary contributions to population and community change](#). *Ecology Letters* 19:839–853.
- Hairston Jr, N. G., S. P. Ellner, M. A. Geber, T. Yoshida, and J. A. Fox. 2005. [Rapid evolution and the convergence of ecological and evolutionary time](#). *Ecology Letters* 8:1114–1127.
- Hiltunen, T., and L. Becks. 2014. Consumer co-evolution as an important component of the eco-evolutionary feedback. *Nature communications* 5:5226.
- Keppeler, F. W., M. C. Andrade, P. A. A. Trindade, L. M. Sousa, C. C. Arantes, K. O. Winemiller, O. P. Jensen, et al. 2022. [Early impacts of the largest amazonian hydropower project on fish communities](#).

Science of The Total Environment 838:155951.

Lasky, J. R., M. B. Hooten, and P. B. Adler. 2020. [What processes must we understand to forecast regional-scale population dynamics?](#) Proceedings of the Royal Society B: Biological Sciences 287:20202219.

Leibold, M. A., F. J. Rudolph, F. G. Blanchet, L. De Meester, D. Gravel, F. Hartig, P. Peres-Neto, et al. 2022. [The internal structure of metacommunities.](#) Oikos 2022.

Leslie, P. H., and J. C. Gower. 1958. [The properties of a stochastic model for two competing species.](#) Biometrika 45:316–330.

Lion, S. 2018. [Theoretical approaches in evolutionary ecology: Environmental feedback as a unifying perspective.](#) The American Naturalist 191:21–44.

Loeuille, N., and M. A. Leibold. 2008. [Evolution in metacommunities: On the relative importance of species sorting and monopolization in structuring communities.](#) The American Naturalist 171:788–799.

Mouquet, N., and M. Loreau. 2003. [Community patterns in source-sink metacommunities.](#) The American Naturalist 162:544–557.

Osmond, M. M., and C. de Mazancourt. 2013. [How competition affects evolutionary rescue.](#) Philosophical Transactions of the Royal Society B: Biological Sciences 368:20120085.

Ovaskainen, O., G. Tikhonov, A. Norberg, F. Guillaume Blanchet, L. Duan, D. Dunson, T. Roslin, et al. 2017. [How to make more out of community data? A conceptual framework and its implementation as models and software.](#) Ecology Letters 20:561–576.

Pantel, J. H., and L. Becks. 2023. [Statistical methods to identify mechanisms in studies of eco-evolutionary dynamics.](#) Trends in Ecology & Evolution 38:760–772.

Pantel, J. H., C. Duvivier, and L. D. Meester. 2015. [Rapid local adaptation mediates zooplankton community assembly in experimental mesocosms.](#) Ecology Letters 18:992–1000.

Pichler, M., and F. Hartig. 2021. [A new joint species distribution model for faster and more accurate inference of species associations from big community data.](#) Methods in Ecology and Evolution 12:2159–2173.

Poggiato, G., T. Münkemüller, D. Bystrova, J. Arbel, J. S. Clark, and W. Thuiller. 2021. On the interpretations of joint modeling in community ecology. Trends in Ecology & Evolution 36:391–401.

Pollock, L. J., R. Tingley, W. K. Morris, N. Golding, R. B. O’Hara, K. M. Parris, P. A. Vesk, et al. 2014.

- Understanding co-occurrence by modelling species simultaneously with a joint species distribution model (JSDM). *Methods in Ecology and Evolution* 5:397–406.
- R Core Team. 2024. [R: A language and environment for statistical computing](#). R Foundation for Statistical Computing, Vienna, Austria.
- Sandal, L., V. Grøtan, B.-E. Sæther, R. P. Freckleton, D. G. Noble, and O. Ovaskainen. 2022. [Effects of density, species interactions, and environmental stochasticity on the dynamics of british bird communities](#). *Ecology* 103:e3731.
- terHorst, C. P., J. T. Lennon, and J. A. Lau. 2014. [The relative importance of rapid evolution for plant-microbe interactions depends on ecological context](#). *Proceedings of the Royal Society B: Biological Sciences* 281:20140028.
- Tikhonov, G., Ø. H. Opedal, N. Abrego, A. Lehikoinen, M. M. J. de Jonge, J. Oksanen, and O. Ovaskainen. 2020. [Joint species distribution modelling with the r-package hmsc](#). *Methods in Ecology and Evolution* 11:442–447.
- Tikhonov, G., O. Ovaskainen, J. Oksanen, M. de Jonge, O. Opedal, and T. Dallas. 2022. [Hmsc: Hierarchical model of species communities](#).
- Toju, H., M. Yamamichi, P. R. Guimaraes Jr, J. M. Olesen, A. Mougi, T. Yoshida, and J. N. Thompson. 2017. Species-rich networks and eco-evolutionary synthesis at the metacommunity level. *Nature Ecology & Evolution* 1:0024.
- Weigel, B., N. Kotamäki, O. Malve, K. Vuorio, and O. Ovaskainen. 2023. [Macrosystem community change in lake phytoplankton and its implications for diversity and function](#). *Global Ecology and Biogeography* 32:295–309.

8 Figures & Tables