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

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Title

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Abstract

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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 (e.g. (Ovaskainen et al. 2017) (Tikhonov et al. 2020); but see Abrego et al. (2024)). However, ecological dynamics 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

27 studies have evaluated the impact of evolutionary dynamics for community assembly and metacommunity

28 dynamics (Loeuille and Leibold 2008) (Osmond and Mazancourt 2013) (Pantel et al. 2015) (Toju et al.

29 2017), analytical methods to consider this additional complexity lag behind the scope of data collected in

30 eco-evolutionary studies. Some methods exist that ultimately apply ANOVA to partition variance in traits

31 or growth rates across contributions of ecological and evolutionary components ((Hairston Jr et al. 2005)

32 (Ellner et al. 2011) (Govaert et al. 2016); additional methods for continuous data are also described in

33 Ellner et al. (2011)). These methods are more frequently cited for their potential rather than for their

34 actual application to empirical data (but see (terHorst et al. 2014) (Hiltunen and Becks 2014)), because this

35 approach is ultimately limited by the same requirements that can limit application of ANOVA - data should

36 follow a normal distribution, the processes that structure the target response variable must be linear and

37 additive, and complicated structuring mechanisms must be reduced into one or a few target categories labeled

38 as 'ecology' or 'evolution'. Flexible models, which can vary depending on the mechanisms and structure of

39 the diverse kinds of data that most studies of eco-evolutionary dynamics will collect, are needed for rigorous

40 inference about eco-evolutionary processes (Pantel and Becks 2023).

41 Two existing statistical models are potentially well suited for analysis of eco-evolutionary data at the mi-

42 croevolutionary and metacommunity scale but also have some considerations before their application to

43 complex community data. Lasky et al. (2020) (Lasky et al. 2020) developed an integrated reaction norm

44 model, linking genetic, phenotypic, and demographic processes, and Benito Garzón et al. (2019) (Benito

45 Garzón et al. 2019) presented a species distribution model with local adaptation and phenotypic plasticity

46 (Δ SDMs). The model of Lasky et al. is an excellent candidate for spatially complex population dynamics,

47 and awaits an extension to the multispecies level. The Δ SDM models described by Benito Garzón et al. truly

48 disentangle the role that plastic and evolutionary trait divergence can play in species distributions, but they

49 also require common garden experimental data across sites to estimate these effects. Observational data

50 collected in metacommunity surveys may only have survey data across sites or time points, as large-scale

51 experimental measures of reaction norms required by the Δ SDM model may be difficult to obtain.

52 One particular metacommunity statistical model, the Hierarchical Modelling of Species Communities

53 (HMSC) framework (Ovaskainen et al. 2017) (Tikhonov et al. 2020), explicitly considers the multitude of

54 processes that can structure community composition across time and space (Leibold et al. 2022) and is

55 potentially well suited to consider analysis of metacommunity eco-evolutionary processes. This model of

56 environmental filtering via variation and covariation in how species respond to their environment considers

57 the impacts of (fixed) trait values and phylogenetic relationships, and uses latent variables to account for

58 the numerous unobserved environmental and spatial features that are difficult to exhaustively measure

59 in community surveys. It has been demonstrated that this statistical model reflects the diverse array of

60 community assembly and metacommunity processes that structure species abundances (i.e. species sorting,

61 environmental filtering, priority effects; (Little and Altermatt 2018) (Ovaskainen and Abrego 2020) (Leibold

62 et al. 2022)). The associated R package has been applied to study environmental and abiotic drivers of

63 diverse assemblages of organisms (e.g. (Sandal et al. 2022) (Weigel et al. 2023)). HMSC is potentially

64 useful for studying eco-evolutionary drivers of community structure, but the model has not previously been

65 applied to include heritable changes in trait values over time.

66 In this study, we use simulations of population dynamics, environmental drivers, species interactions, and

67 trait evolution in populations, communities, at the local and metacommunity scale, to study eco-evolutionary

68 dynamics. After generating simulated time series of population sizes and mean trait values, we then use

69 HMSC to analyze the resulting data, to determine whether HMSC can successfully estimate the impacts of

70 trait evolution for community composition, and to generate relative contributions of fixed environmental,

71 spatial, and trait evolution drivers as well as random effects of spatial and temporal covariance among

72 species. We asked three main questions: (i) can linear statistical models (like HMSC) accurately capture the

73 impact of non-linear population, community, and evolutionary dynamic processes?, (ii) can HMSC be used

74 to evaluate hypothesized drivers of the relative importance of evolution for community composition at the

75 metacommunity scale?, and (iii) can we better understand the role of evolution for community dynamics in

76 experimental systems using HMSC?

Table 1: Models for population growth

	model	formula
A	1 species, logistic	$N_{i,t+1} = \frac{r_i N_{i,t}}{1+\alpha_{ii} N_{i,t}}$
B	1 species, logistic, env	A, $r_i = \hat{W} e^{-(E_t - x_{i,t})^2}$
C	2 species, logistic, competition	$N_{i,t+1} = \frac{r_i N_{i,t}}{1+\alpha_{ii} N_{i,t}+\alpha_{ij} N_{j,t}}$
D	2 species, logistic, competition, env	C, $r_i = \hat{W} e^{-(E_t - x_{i,t})^2}$
E	2 species, logistic, competition, env, trait evolution	C, $r_i = \hat{W} e^{\frac{-[(\frac{w+(1-h^2)P}{P+w})(E_t - x_{i,t})]^2}{2(P+w)}}$
F	2 species, logistic, competition, env, trait evolution, spatial structure	E, $N_{i,k,t+1} = N_{i,k,t} + \sigma_k + \sigma_{kl}$

Note: i, j = species, t = time, k, l = site

[1] See Appendix S1 for parameter values used in simulation

Methods

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 (@ref(tab:tab1)) to Bayesian linear regression models. These simulation models were (A) a single-species model of discrete-time logistic population growth, (B) expanded to include a randomly fluctuating environmental property E that impacts the species' population growth rate, (C) a two-species model of logistic growth and competition that was then (D) expanded to consider a randomly fluctuating environmental property, (E) and further expanded to consider evolution in a trait x that is selected by the environmental property, and finally (F) the model of two-species growth, competition, environmental change, and evolution in a spatially structured (10-patch) habitat.

To fit linear regression models to the simulated population size data, we began with models using population size and environment (including the second-order term, to better reflect species optimum values) as fixed effects ($N_t \sim N_{t+1} + E_t + E_t^2$; for simulation models *A* and *B*), and progressed to a mixed model using environment and trait evolution as fixed effects ($N_t \sim E_t + E_t^2 + |\Delta x|$; for simulation models *C*, *D*, and *E*) and time (models *C*, *D*, and *E*) and spatial distance (model *F*) as random effects. For consistency, all linear

94   regression models were implemented as heirarchical Bayesian models using HMSC (Hierarchical Modelling

95   of Species Communities (Ovaskainen et al. 2017) (Tikhonov et al. 2020)). HMSC uses a latent variable

96   approach as an alternative to directly modelling species interaction coefficients, estimating a reduced number

97   of linear combinations of species abundances that best predict future population size values. For linear models

98   fit to data generated in simulations C, D, E, and F above, the time random effect was implemented to capture

99   species interactions (as part of the temporal species association matrix estimated by the model), and the

100 spatial random effect was implemented in model F to capture spatial covariance in abundances as a function

101 of distance between sites. Full methodological details are given in Appendix S1. All simulations were run

102 in R (R Core Team (2024)) and HMSC models were implemented using the `Hmsc` package (Tikhonov et al.

103 (2022)).

Evolution in metacommunities and HMSC

Simulation model

106 We also simulated growth and competition dynamics for a multi-species assemblage in a patchy landscape,

107 with site variation in one environmental property, and with evolution in a trait that is selected on by the

108 environment. Population growth for species in the metacommunity simulation followed a Leslie-Gower model

109 (a discrete-time version of a Lotka-Volterra model (Beverton and Holt 1957) (Leslie and Gower 1958)). We

110 considered the impact of trait evolution for growth using a discrete time quantitative genetic model of

111 evolutionary rescue (Gomulkiewicz and Holt 1995). The model for population size was:

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

112 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

113 species' maximum per-capita growth rate, w is the width of the Gaussian fitness function (which determines

114 the strength of selection), P is the width of the distribution of the phenotype x, h^2 is the heritability of

115 the trait x, E is the local environmental optimum trait value, $x_{i,t}$ is the trait value of species i at time t,

116   α_{ii} is the intraspecific competition coefficient (the per capita impact of species i on itself) and α_{ij} is the

117   interspecific competition coefficient. Populations have a critical density N_c, below which the population is

118   subject to extinction due to demographic stochasticity at a probability of p (Gomulkiewicz and Holt 1995).

119   This model was used in Pantel & Becks (Pantel and Becks 2023) to evaluate the consequences of adaptive

120   evolution for coexistence in a three-species system. To expand this model to a metacommunity, we consider

121   the evolution of multiple species ($S = 15$) in a landscape of patches ($k = 50$). The patches have values of

122   an environmental property $E \sim U(0, 1)$ that determines the local optimum phenotype $E = x_{opt}$, i.e. where

123   species experience their absolute fitness W_{max}, and patches also have spatial locations X and Y (both drawn

124   from $U(0, 1)$). The patches thus have a connectivity matrix $\mathbf{D}$ (here given by their Euclidean distance), as

125   well as a connectivity matrix $\mathbf{C}$ that is a Gaussian function of $\mathbf{D}$ and species dispersal rate d_i.

126   We used the evolving metacommunity model to test whether landscape connectivity (the overall dispersal

127   rate d) and the speed of evolution (evaluated by varying h^2) influenced the relative importance of trait

128   evolution ($|\Delta x|$) for metacommunity composition $N_{i,t,k}$ (evaluated as $V_{|\Delta x|}$, the proportion of variation in

129   species abundances explained by $|\Delta x|$ as estimated by the HMSC model fit to the simulated data across d

130   and h^2 levels). We hypothesized that the overall importance of trait evolution ($V_{|\Delta x|}$) would decrease with

131   increasing dispersal rate - at low dispersal rates, locally mal-adapted species are less likely to emigrate to

132   more optimal patches and will experience strong local selection, leading to a large amount of trait evolution.

133   Population sizes for these initially mal-adapted populations will also likely be lower, leading to reduced

134   relative importance of density-dependent intra- and interspecific competition. We also hypothesized that

135   heritability (h^2) would mediate the relative importance of dispersal rate - at higher h^2, species will evolve

136   quickly and we expected the importance of trait evolution $V_{|\Delta x|}$ to depend on the amount of time that

137   mal-adapted populations persist. Therefore simulations with higher h^2 would have decreased importance

138   of evolution $V_{|\Delta x|}$ for community composition. For the same reason, we hypothesized generally that, for a

139   given dispersal rate d, the importance of evolution $V_{|\Delta x|}$ would decrease with increasing h^2.

140   All simulations used the same parameter values ($W_{max} = 2$, $P = 1$, $w = 2$, $N_c = 100$, $p = 0.001$), species in-

141   teraction matrix ($\alpha_{ii} = 0.00125$; $\alpha_{ij} \sim U(0.0015, 1)$), and initial conditions (initial richness $s_{0k} \sim Pois(0.75)$;

142   initial population size $N_{0i} \sim Pois(10)$; initial degree of maladaptation $\beta_{i0} \sim Gamma(0.75, 1)$, initial dis-

tance 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 log-abundance values were modeled as $ln(N_{ikt}) \sim N(L_{ikt}, \sigma_2)$, 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 $|\Delta x_{ik,t-1 \to t}|$. 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). When there was no dispersal in the system ($d = 0$), spatial random effects were not included in the model.

Applying HMSC on empirical data

To test the applicability of HMSC on ecological and evolutionary effects in empirical data, we applied HMSC on the experimental data of Jewel & Bell (2023) (Jewell and Bell 2023). The authors conducted a community selection experiments in which they grew four floating and short-lived aquatic plants (the angiosperms *Lemna minor* here designated as Lm, *Spirodela polyrhiza* designated as Sp and *Wolffia columbiana* designated as Wc, and the liverwort *Ricciocarpos natans* designated as Rn) under different environmental conditions for twelve weeks. The environmental conditions were defined by three differed amount of shadings of the water pool, 3%, 12% and 50%, and different nutrient concentrations, with low (dissolved nitrogen (DN) = 200 $\mu g L^{-1}$, dissolved phosphorous (DP) = 10 $\mu g L^{-1}$, medium (DN = 800 $\mu g L^{-1}$, DP = 40 $\mu g L^{-1}$), and high

168 concentration (DN = 3200 $\mu g L^{-1}$, DP = 160 $\mu g L^{-1}$) of nutrients. They combined each shading with

169 each nutrient level, resulting in nine different environmental conditions. Throughout the experiment they

170 measured biweekly, from week one to week eleven, the frond size of ten individuals from each species, as body

171 size trait, in each environmental condition alongside their corresponding species density. We calculated the

172 average trait change as $\Delta x = x_{ijt} - x_{ijt-1}$, where x_{ij} described the mean trait of species i in environment j

173 and week t. As no $\Delta \hat{x}$ value could be calculated for week one of the experiments, it was omitted from the

174 analysis.

175 We fitted two HMSC models to the data: An 'evolution model' in which $\Delta \hat{x}$ of each species and environmental

176 conditions were applied as explanatory variable, and a 'no-evolution model', in which only the environmental

177 conditions were included. Species density was log-transformed species before applying it to the model,

178 therefore we could use normal distribution in the model. Additionally, we applied replicates ($n = 2$) and

179 time as random effects. For each model we ran four Markov chain Monte-Carlos' for 1,875,000 iterations

180 from which the first 625,000 were cut off as the transient phase and with a thinning factor of 5,000 250

181 samples were taken from each chain.

182 To test the impact of evolution by the model, we extracted the posterior distributions of the estimated beta

183 effects. These were multiplied with the $\Delta \hat{x}$ of the corresponding species and summed up together with the

184 intercept.

Results

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

188 Linear regression models can estimate the impacts of intra- and interspecific competition, environmental

189 variation, and trait evolution for population size in simple one- and two-species models of population growth.

190 In simple cases (one-species models, linear and quadratic relationships between environment and population

191 size; models A and B), the regression coefficients can successfully reflect the direction and magnitude of the

₁₉₂ relationships included in the non-linear simulation model (the impact of N_t and E_t for N_{t+1}). However, as

₁₉₃ the processes included in the simulation models become slightly more complex (competition with a second

₁₉₄ species, spatial structure; models C, D, E, F), regression coefficients were useful for prediction but not for

₁₉₅ recreating the underlying processes driving changes in population size (Appendix S1).

₁₉₆ To consider species interactions and environmental fluctuations (model D; Figure 1a @ref(fig:fig1)), we used

₁₉₇ the latent variable modelling approach implemented in HMSC. The linear model successfully estimated

₁₉₈ coefficients for fixed environmental effects that captured the impacts of environment for population size in

₁₉₉ both species (Figure 1b) and partitioned the relative importance of the environment and species interactions

₂₀₀ for species abundances (Figure 1c). The model coefficients could also predict the population size values over

₂₀₁ time (Figure 1a), though the quality of this prediction varied depending on the level of environmental noise

₂₀₂ (Appendix S1).

₂₀₃ The HMSC model successfully modelled changes in species abundances when trait evolution was introduced

₂₀₄ (model E; Figure 1d @ref(fig:fig1)). Trait evolution played a strong role for population size, especially

₂₀₅ the effect of $|\Delta x_1|$ for $ln(N_1)$ and $ln(N_2)$ (gradient plots in Figure 1e). The model estimated the relative

₂₀₆ importance of the environmental driver, trait evolution in both species, and species interactions (Figure 1f),

₂₀₇ and predicted the observed species abundances well (Figure 1d). Spatial structure was also reproduced in

₂₀₈ the coefficients of the linear HMSC model by using spatial random effects to capture covariance in species

₂₀₉ abundances as a function of spatial distance between sites in the 10-patch simulation model (model F; Figure

₂₁₀ 1g,h,i @ref(fig:fig1)). The variation partition successfully reflected separation of environmental drivers from

₂₁₁ trait evolution, species interactions, and spatial random effects (Figure 1i), and we show in Appendix S1

₂₁₂ that the relative importance of trait evolution increases when we use a simulation model with less spatial

₂₁₃ and environmental variation and weak species interactions.

Evolution in metacommunities and HMSC

₂₁₅ The simulation model followed population size and trait value dynamics for species in the landscape across

₂₁₆ 200 time steps (Figure 2a @ref(fig:fig2)). Resulting biodiversity dynamics depended on the dispersal level and
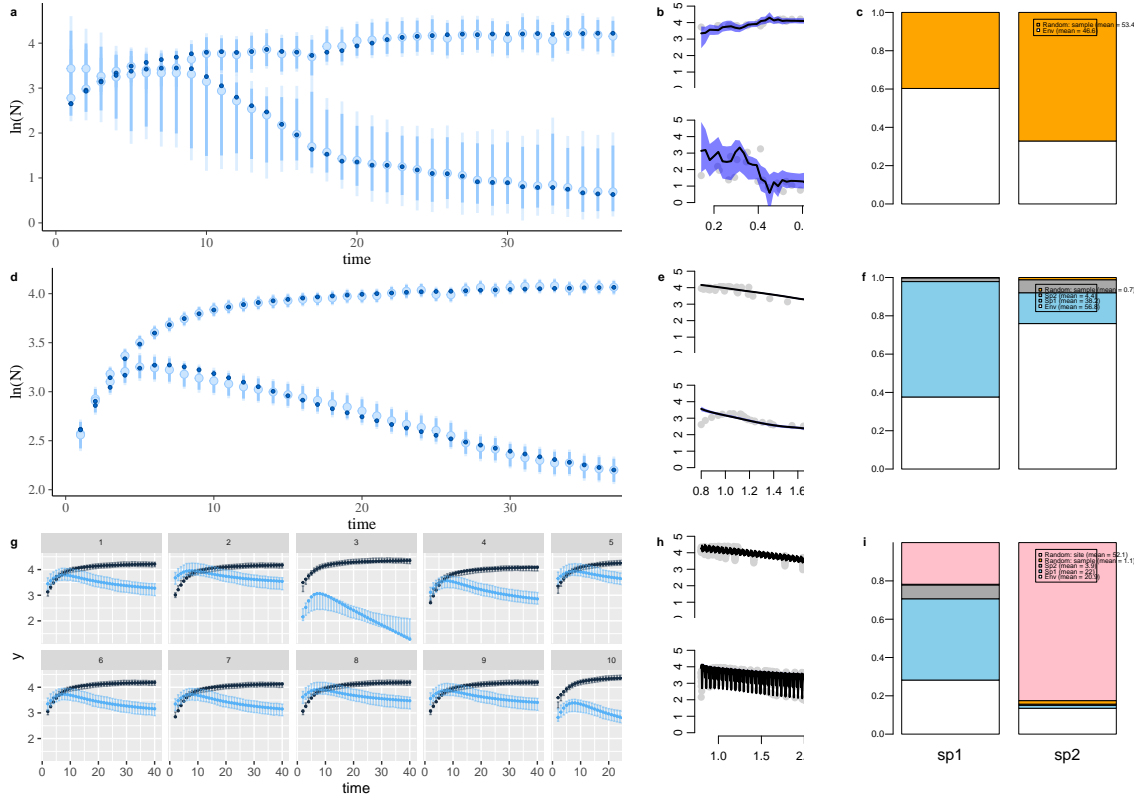
Figure 1: Simulated and model-estimated values for population dynamics in two-species systems. Panels a, d, and g show log-population size (y-axis) over time (x-axis) for species i and j when they grow and compete for resources in sites with random environmental fluctuations over time. Species either have fixed (panel a) or evolving trait values (panels d, g) and are present in either 1 (panels a, d; simulation models D and E) or multiple sites (panel g; model F). Graphs in panels b, e, and h show predicted log-population size ($ln(N)$) for species 1 and 2 across gradients of the environment ($E + E^2$) and the change in trait values of species 1 ($|\Delta x_1|$). Graphs in panels c, f, and i show the results of a variation partition after fitting data to the HMSC statistical model. The variation partition plot shows the proportion of variation explained by environmental, trait evolution ($|\Delta x_1|$ and $|\Delta x_2|$), time random, and spatial random predictors for $ln(N)$ for species 1 and 2. Error bars and shading represent the 95% highest probability density interval for posterior predictions.

heritability values (Figure 2b @ref(fig:fig2)). 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 2b @ref(fig:fig2)). The inclusion of trait heritability had a strong effect on community diversity, reflecting that local adaptation can rescue species and contribute to richness at the local and metacommunity scale. Regional species diversity (γ) increased with increasing h^2 levels (Figure 2b @ref(fig:fig2)).

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 2c,d,e @ref(fig:fig2)). The importance of spatial random effects increased with dispersal rate, and overall the importance of evolution decreased with increasing h^2.

Empirical data

The empirical data (Jewell and Bell 2023) showed the community dynamics of four plant species under different environmental conditions, additionally the front size of each species was measured to determine its trait change over time. We calculated the mean variance partitioning (VP) over all species, to evaluate the impact of evolutionary (change of the front size trait) and ecological (light and nutrient treatments) effects on changes on species density. Almost one fifth (18.6%) of the variance in species density could be explained by the variance in $\Delta \hat{x}$ (@ref(fig:fig5)a). This is due to the reduction of the VP of the ecological effects by a total of 14.4% (from 37% to 26.6% for the amount of shading and from 31% to 27.1% for the nutrient concentrations) and the reduction of 4.2% of the random effects (from 18.7% to 15% for time and from 13.3% to 12.8% for replicates) (@ref(fig:fig5)). While $\Delta \hat{x}$ of the species Lm, Sp and Wc showed a similarly low impact, on average 3.6%, $\Delta \hat{x}$ of species Rn showed a high impact on variance of species density, 7.8%, which can be explained by its high $\Delta \hat{x}$ changes over time (see Appendix S05). The high density intervals (HDI) of 95% estimated beta effects showed a negative correlation of Light shading with species density, while nutrient concentration correlated positively with density (@ref(fig:fig5)c). Changes in $\Delta \hat{x}$ impacted densities differently. At one hand changes of species Rn frond size correlated negatively with is density, on the other hand changes in the frond size of species Wc showed a positive correlation with the other species
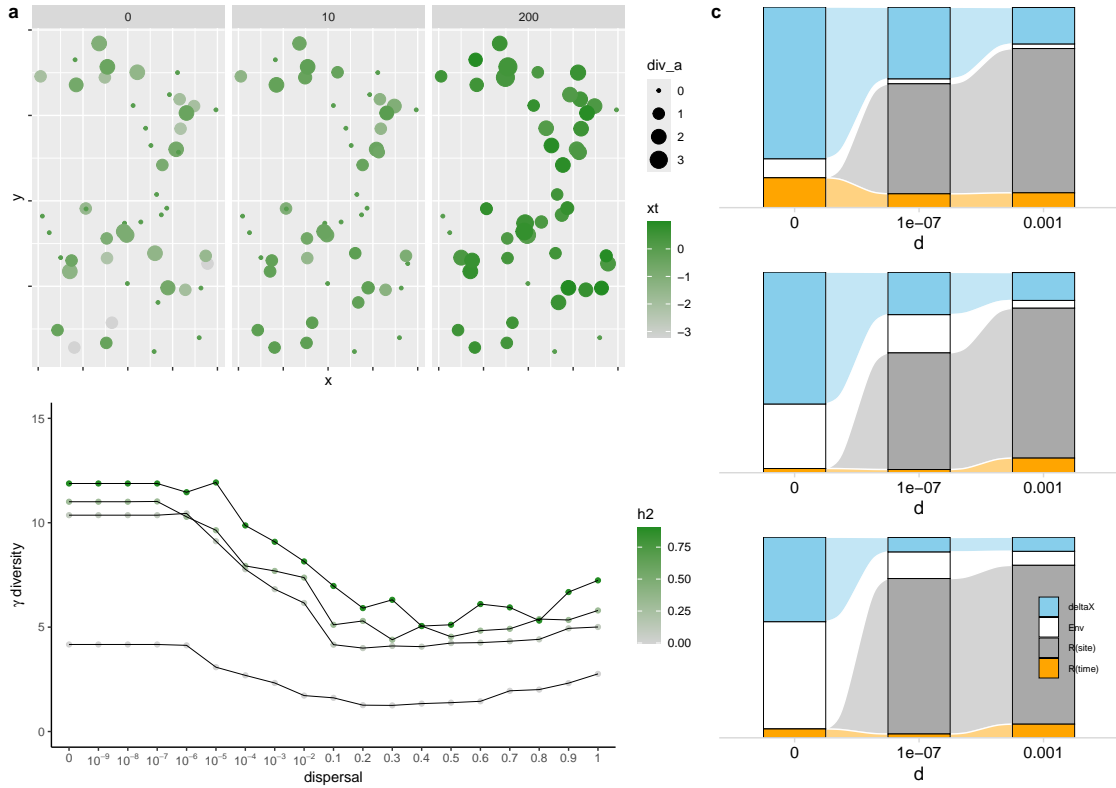
Figure 2: Importance of trait evolution for change in community composition in metacommunities. (a) We developed a simulation model for population growth, competition, and trait evolution in 15 species that inhabit a patchy landscape. The landscape has 50 sites (colored points in the XY space), with distinct local environments that select for diverse patterns of species diversity (size of points) and average trait values (color of points; results are shown at time $t = 0, 10, 200$ for a simulation with $d = 10^-3$ and $h^2 = 0.1$). (b) Regional metacommunity Γ diversity varied across levels of dispersal and heritability (h^2). (c) Variation partition plots after fitting metacommunity time series of species abundances $ln(N_{ikt})$ to HMSC models with environment, trait evolution, and random effects (space and time) as predictors. The top panel is for $h^2 = 0.1$, the middle panel is for $h^2 = 0.3$, and the bottom panel is for $h^2 = 0.9$.

Sp and Lm (@ref(fig:fig5)c). The impact of evolution (of all species summed up), impacted species density

over time, yet did not show a clear direction over the course of the experiment (@ref(fig:fig5)d).
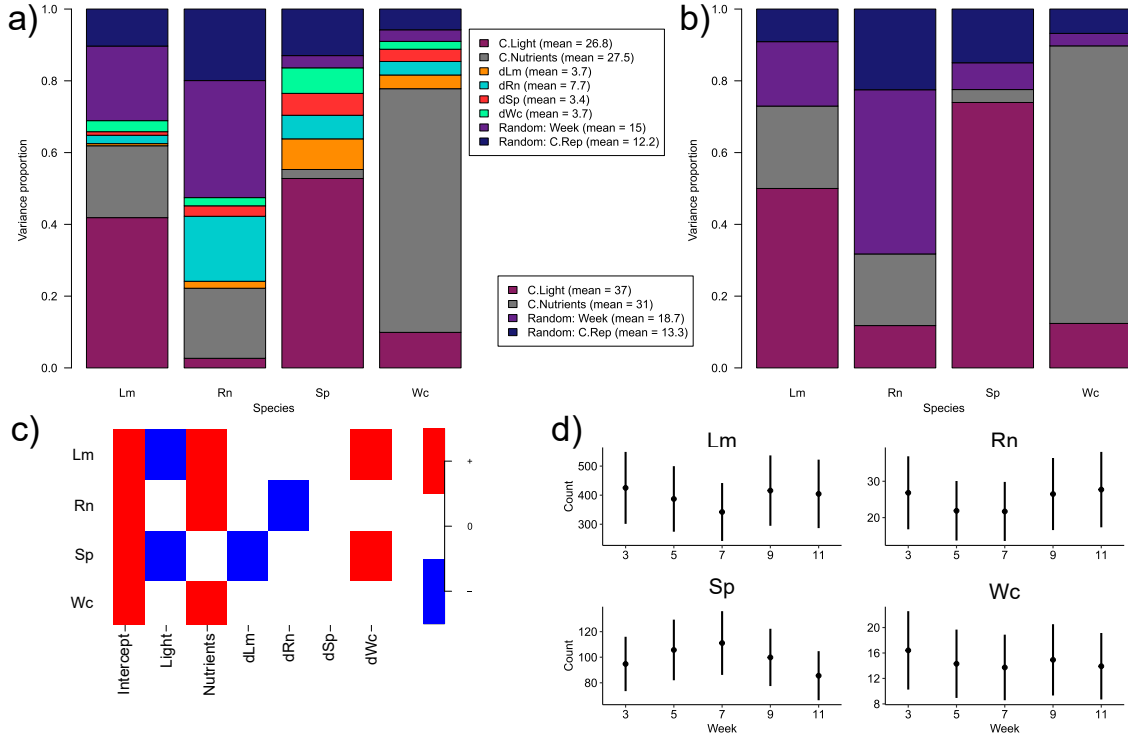

Figure 3: The estimated effects of species trait changes and environmental treatments. The variance partitioning of all fixed effects of the HMSC model (a) including trait changes with envrionmental treatments and (b) only including the environmental treamtents. The (b) high density interval of 95% showed a clear pattern for the different environmental treatments, yet differing results for trait changes and their impact on species density. This can be seen in (d) the shifting predictions of density over time due to the total trait changes of all species.

Discussion

Empirical data

By implementing the trait changes of the four different species (Lm, Rn, Sp and Wc) in the HMSC model

we were able to infer the relative impact of the trait changes on the community dynamics. This application

shows is advantages over previous methods,which estimate the impact of trait changes (thus evolution), as

it is not depended on the data structure and simplicity (Hairston Jr et al. 2005) (Ellner et al. 2011), can

be implemented on multiple species(Lasky et al. 2020) and does not require additional common garden

14

experiments (Benito Garzón et al. 2019). Therefore this allows for a straight forward implementation of HMSC on a variety of data structures as lone as a clear response variable (e.g. species density) and ecological (e.g. environmental conditions) as well as evolutionary (e.g. heritable trait change) are measured. An additional advantage of HMSC, and JSDMs in general, is the ability to use the empirical data to predict a species response to changes in the environmental variables, even beyond the measured values (Tikhonov et al. 2020) (Ovaskainen et al. 2016). With the implementation this approach can be combined with the fixed effects to answer further questions, such as: How does trait change impact the species density under changing environmental conditions? And how does the impact of trait changes depend on specific environmental conditions?

At the same time a correct interpretation of such predictions as well es the estimated posterior beta distribution require a thorough understand of the experimental system. For example we often observed a negative correlation between trait change and species density in our simulations and also in species Rn of the empirical data, yet they derived from different mechanisms. In our simulations trait changes were greater when a species trait was further away from the optimal trait value, this greater distance resulted also in lower fitness and thus lower population size, while a species with higher fitness and thus higher population size had smaller trait changes. Therefore, HMSC correlates a high trait changes with a low population size and thus estimates a negative beta effect. Such effects can be expected in empirical data of i.e. evolutionary rescue experiments, where a species has to adapt to a deleterious environment before going extinct [Gomulkiewicz and Holt (1995)](**Bell2009?**). In the empirical data this negative correlation was the result of the species Rn investing into a larger frond size (Fig. SX), this likely lead to a lower investment into reproduction, while still maintaining a similar total frond area on the water surface to capture the reduced light.

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Figures & Tables

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