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Detection of Eco-Evolutionary Dynamics in Communities Using Joint Species Distribution Models

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ABSTRACT

Biodiversity at the metacommunity scale is typically influenced by numerous environmental, spatial, biotic, and stochastic factors. These factors can simultaneously impact evolution in individual species, due to site-varying local selection pressures and the impact of connectivity for gene flow and genetic drift. Joint species distribution models (JSDMs) can estimate the relative impacts of environmental, spatial, biotic, and other drivers on community composition, but these models do not currently consider the impact of contemporary evolutionary change. We applied a JSDM to analyse simulated and experimental populations and communities that experience contemporary trait evolution. We found that it successfully partitioned variance contributed by environmental, spatial, and evolving phenotypic drivers, and also estimated site- and time-specific covariance. We further demonstrated how the model-estimated effect sizes of trait evolution for community composition can be used to test predictions about the underlying mechanistic drivers of eco-evolutionary dynamics in communities.

1 | 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 substantial progress in reflecting these numerous ecological processes at multiple scales. Joint species distribution models (JSDMs; Pollock et al. 2014; Pichler and Hartig 2021) and multi-species occupancy models (Devarajan et al. 2020; Poggiato et al. 2021) can incorporate these diverse components that structure variance in biological data. They have been used to measure the relative importance of different ecological drivers in communities of 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).

Despite this variety of components, there are additional drivers of community composition which are not currently reflected. The dynamics of populations and communities are also influenced by the genotypic and phenotypic properties of organisms (Barbour et al. 2022; Hermann et al. 2024). Traits can be considered in some JSDMs, but they typically require fixed values for species' traits (e.g., Ovaskainen et al. 2017; Tikhonov et al. 2020; but see Abrego et al. 2025). However, ecological dynamics (e.g., shifts in population growth rates or species turnover in communities), can impact selection on genes and phenotypes, potentially resulting in interactions or feedback loops between ecological and evolutionary processes

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(Lion 2018; Barbour et al. 2022). 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 de Mazancourt 2013; Pantel et al. 2015; Toju et al. 2017), but analytical methods to consider this additional complexity do not reflect the distinct mechanisms structuring data in eco-evolutionary studies. Some methods exist that apply ANOVA to partition variance in traits or growth rates across contributions of ecological and evolutionary components (Hairston Jr et al. 2005; Govaert et al. 2016; but see Ellner et al. 2011 for discrete and continuous analyses). These methods are more frequently cited for their potential rather than application to empirical data (but see terHorst et al. 2014; Hiltunen and Becks 2014), because this approach is limited by the same requirements that limit 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 and grouped into 'ecology' or 'evolution' categories. Flexible models, which can better reflect 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 require more consideration before their application to study community processes. Lasky et al. (2020) developed an integrated reaction norm model, linking genetic, phenotypic, and demographic processes, and Benito Garzón et al. (2019) presented a species distribution model with local adaptation and phenotypic plasticity (ΔSDMs). The model of Lasky et al. is an excellent candidate for spatially complex population dynamics and the ΔSDM models described by Benito Garzón et al. truly disentangle the role that plastic and evolutionary trait divergence can play in species distributions. However, the ΔSDM model requires common garden experimental data across sites to estimate these effects, while the observational data collected in metacommunity surveys may instead only have survey data across sites or time points. Currently, both models await an extension to the multispecies level.

Hierarchical Modelling of Species Communities (HMSC) (Ovaskainen et al. 2017; Tikhonov et al. 2020) is a JSDM, that explicitly considers a multitude of ecological processes that can structure community composition across time and space (Leibold et al. 2022) and is potentially well suited to analyze metacommunity eco-evolutionary processes. This model infers the role 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 measure in community surveys. Previous studies have demonstrated that this statistical model can reflect the diverse array of community assembly and metacommunity processes structuring species abundances (i.e., species sorting, environmental filtering, priority effects; Little and Altermatt 2018; Ovaskainen and Abrego 2020; Leibold et al. 2022). HMSC 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 therefore potentially useful for studying eco-evolutionary drivers of community composition, but it 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 and communities, at the local and metacommunity scale, to study eco-evolutionary dynamics (Figure 1). After generating simulated time series of population sizes and mean trait values, we then use HMSC to analyse the resulting data, to determine whether HMSC can estimate the impacts of trait evolution on community composition, and to generate relative contributions of fixed environmental and trait evolution drivers as well as random effects of spatial and temporal covariance among species. We asked three main questions: (i) can linear statistical models (like HMSC) 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 in community dynamics in experimental systems using HMSC?

2 | Methods

2.1 | Linear Statistical Models for One- and Two-Species Models of Growth, Competition, and Trait Evolution

We first evaluated how linear regression models reflect the nonlinear dynamics that can drive species abundances in relatively simple ecological systems. We fit data generated from simulation models with increasing complexity (Table 1) 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, (D) that was expanded to consider a randomly fluctuating environmental property, and (E) further expanded to consider evolution in a trait x that is under selection by the environmental property. Model (F) applied the two-species growth, competition, environmental change, and evolution model to a spatially structured (10-patch) habitat.

To fit linear regression models to the simulated data (natural logarithm of population size over time N_t), we began with models using population size (model A) and environment (model B) as fixed effects ($\log(N_t) \sim \log(N_{t-1}) + E_t + E_t^2$), and progressed to evaluate data from two-species simulations with a mixed model using environment and trait evolution as fixed effects ($\log(N_t) \sim E_t + E_t^2 + |\Delta x_t|$; for simulation model E) and time (models C, D, E, and F) and spatial distance (model F) as random effects. For consistency, all linear regression models were implemented as hierarchical Bayesian models using HMSC. HMSC uses a latent variable approach as an alternative to directly modelling species interaction coefficients, estimating a reduced number of linear combinations

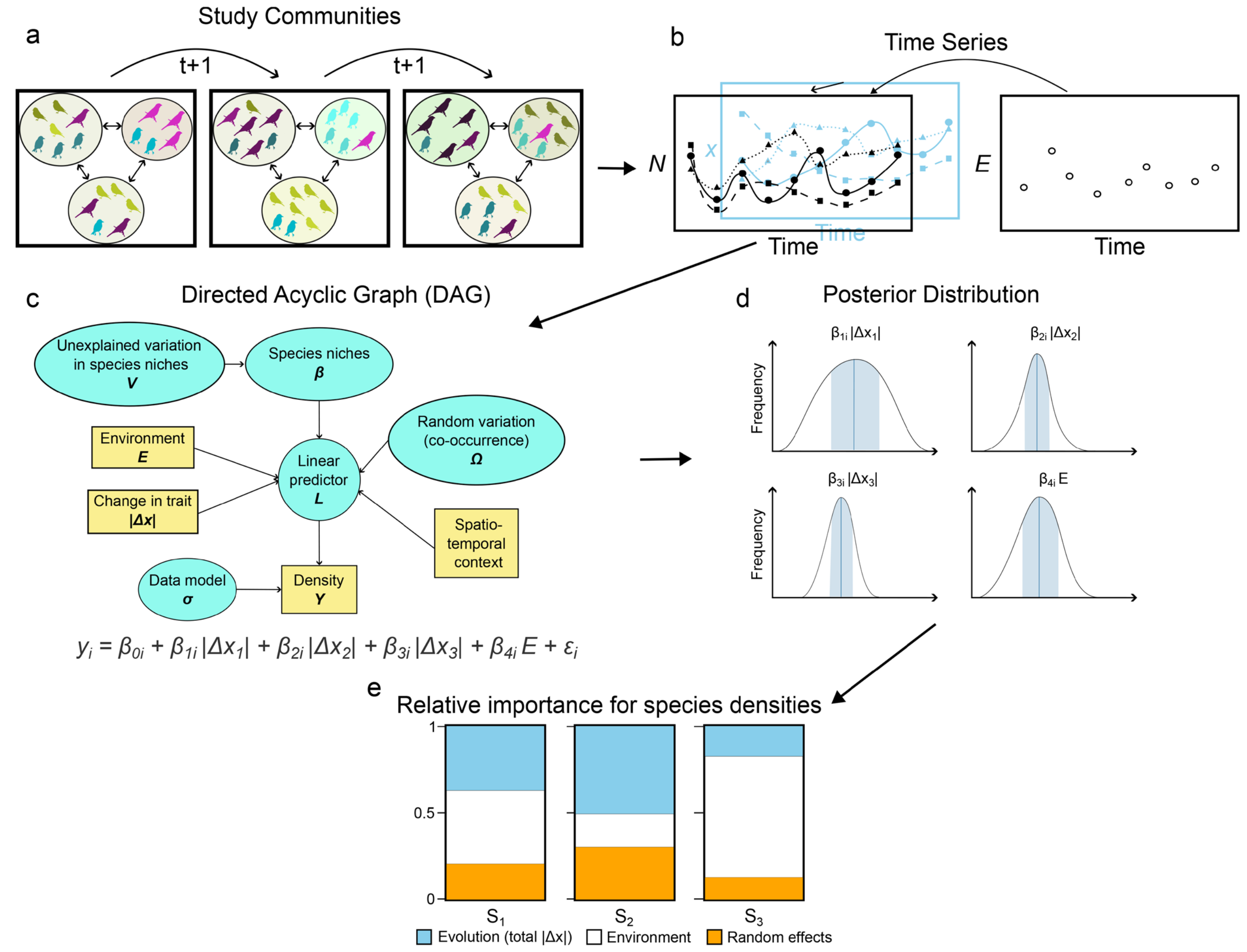

FIGURE 1 | Workflow to study the impact of evolving traits, as well as environmental, biotic, and spatial drivers, for community dynamics. (a) Metacommunity dynamics of interacting bird species can be monitored at different patches over time. Densities, trait data (i.e., beak size, wing length; colour of individual birds), and environmental properties (i.e., patch colour) should be measured. (b) Dynamics for covariates and densities can be visualised as time series. The purpose of the investigation is to understand how these different covariates impact species dynamics in the metacommunity over time. (c) All measured data are implemented into a particular joint species distribution model, HMSC. The DAG is a visualisation of how the measured data (yellow boxes) is applied by HMSC to estimate different model parameters (blue ellipses; figure 1c after Ovaskainen et al. 2017). Each model predictor (i.e., environmental values E, change in the trait $|\Delta x|$) has a corresponding β term which indicates how species density responds to that predictor (these are referred to as the species niches). Data observations may not be independent samples, and may have spatio-temporal structure. HMSC estimates spatial and temporal covariance (Ω) as a species-to-species association matrix, which takes into account numerous factors such as the impacts of dispersal, landscape connectivity, as well as species interactions. The resulting linear predictors L inform the deterministic part of species densities Y. An example of the linear predictors for fixed effects is shown in the statistical formula in black text. The data model σ represents variance that is not explained by the model linear predictors. (d) In the hierarchical Bayesian model, all model parameters are estimated as posterior distributions. The species niche coefficients β estimate the impact of measured covariates on species densities. Bayesian posteriors can indicate uncertainty in parameter estimates (the width of the distribution). (e) The relative importance of different model factors for species densities can be summarised by variance partitioning (VP). Covariates (fixed effects) and random effects can be evaluated individually or divided into groups. The graphs thus display the relative impact of each covariate (E) or group of covariates (total effect of $|\Delta x|$) and spatial or temporal random effects driven by factors such as dispersal or species interactions for species densities in the metacommunity. This can be calculated for individual species (as shown in this example, S_1, S_2, and S_3), or averaged across all species. This approach can be used to answer interesting questions in community eco-evolutionary dynamics, e.g., what is the relative importance of trait evolution for species densities or occurrences in a community or metacommunity, and how might this relative importance change as a function of, e.g., organismal or landscape properties.

of species abundances that best predict future population size. For linear models fit to data generated in simulations C, D, E, and F, the time random effect was implemented to capture species interactions (producing a temporal species association matrix), and the spatial random effect was implemented in model F to capture spatial covariance in abundances as a function of distance between sites. Simulations were run in R (R Core Team 2025; v4.5.1) using the ecoevoR package (Pantel and Becks 2023) and HMSC models were implemented using the Hmsc package (Tikhonov et al. 2022) (Appendix S1).

TABLE 1 | Models for population growth.

	Model	Formula
A	1 species, logistic	$N_{i,t+1} = \frac{r_i N_{it}}{1+\alpha_{ii}N_{it}}$
B	1 species, logistic, env	$\text{A}, r_i = \widehat{W}e^{-(E_t - x_{it})^2}$
C	2 species, logistic, competition	$N_{i,t+1} = \frac{r_i N_{it}}{1+\alpha_{ii}N_{it}+\alpha_{ij}N_{jt}}$
D	2 species, logistic, competition, env	$\text{C}, r_i = \widehat{W}e^{-(E_t - x_{it})^2}$
E	2 species, logistic, competition, env, trait evolution	$\text{C}, r_i = \widehat{W}e^{\frac{-\left[\left(\frac{w+\left(1-h^2\right)P}{P+w}\right)(E_t - x_{it})\right]^2}{2(P+w)}}$
F	2 species, logistic, competition, env, trait evolution, spatial structure	$\text{E}, N_{ik,t+1} = N_{ikt} + \sigma_k + \sigma_{kl}$

Note: See Appendix S1 for parameter values used in simulation. i, j = species, t = time, k, l = site.

2.2 | Evolution in Metacommunities and HMSC

2.2.1 | 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 that selects on an evolving trait. Population growth for species in the metacommunity followed a Leslie–Gower model (a discrete-time version of a Lotka–Volterra model, Beverton and Holt 1957; Leslie and Gower 1958). We considered 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 was:

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

where N_{it} is the population size of species i at time t, $\widehat{W}$ is calculated as $\widehat{W} = W_{max}\sqrt{\left(\frac{w}{P+w}\right)}$, 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), 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_{opt}), x_{it} is the mean 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 stochastic extinction at a probability of p (Gomulkiewicz and Holt 1995).

This model was used in 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 $E = x_{opt}$ 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 dispersal rate d.

We used the evolving metacommunity model to test whether landscape connectivity (varying d) and the speed of evolution (varying h^2) influenced the relative importance of trait evolution ($|\Delta x|$) for metacommunity composition N_{ikt} (measured as $V_{|\Delta x|}$, the proportion of variation in species abundances explained by $|\Delta x|$ as estimated by HMSC). We hypothesized that the overall importance of trait evolution ($V_{|\Delta x|}$) would decrease with increasing dispersal rate—at low dispersal rates, locally maladapted species are less likely to emigrate to more optimal patches and will experience strong local selection, resulting in more trait evolution. Population sizes for initial, maladapted 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 trait evolution—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 maladapted populations persist. Therefore, simulations with 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 ($\alpha_{ii} = 0.00125$; $\alpha_{ij} \sim U(0, 0.0015)$), and initial conditions (initial richness $s_{0k} \sim Pois$ (0.75); initial population size $N_{0i} \sim Pois$ (10); initial degree of maladaptation $B_{i0} \sim Gamma$ (0.75, 1), initial distance to the local patch's optimum phenotype $dm_{i0} = \sqrt{B_{i0}(w+P)}$, initial trait value $x_{i0} = E_k - dm_{i0}$; simulating for example colonisation of small vernal pools from a source lake with a very different environment). 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}. Code for all simulations and model fits is available at https://github.com/jhpantel/ecoevo-hmsc.

2.2.2 | Statistical Model

To determine the relative influence of environmental and spatial properties, intra- and interspecific population dynamics, and evolutionary dynamics for community composition, we applied HMSC to model the log-abundance at each site and time step for each species. The log-abundance values were modelled as $log\left(N_{ikt}\right) \sim N\left(L_{ikt}, \sigma_2\right)$, where the linear predictors $\mathbf{L}$ are the sum of fixed and random effects $\mathbf{L}^{\mathbf{F}} + \mathbf{L}^{\mathbf{R}}$ (Tikhonov et al. 2020). The fixed effects were E_k and the absolute value of the change in each species' trait value from the previous time step to the next $\left|\Delta x_{ik,t-1\rightarrow t}\right|$. Random effects included time 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.

2.2.3 | Applying HMSC to Empirical Data

To test the applicability of HMSC for ecological and evolutionary effects in empirical studies, we applied HMSC to the experimental data of Jewell and Bell (2023). The authors conducted a community selection experiment in which they grew four floating and short-lived aquatic plants (the angiosperms *Lemna minor* [Lm], *Spirodela polyrhiza* [Sp] and *Wolffia columbiana* [Wc], and the liverwort *Ricciocarpos natans* [Rn]) under different environmental treatments (levels of shading and nutrients) for 12 weeks. The shade and nutrient levels for the experimental pools were a factorial combination of 3%, 12% and 50% shade, and low (dissolved nitrogen (DN) = 200 μg L^{-1}, dissolved phosphorous (DP) = 10 μg L^{-1}), medium (DN = 800 μg L^{-1}, DP = 40 μg L^{-1}), and high (DN = 3200 μg L^{-1}, DP = 160 μg L^{-1}) concentrations of nutrients. The frond size of 10 individuals from each species and the density of each species were measured every 2 weeks during the 12-week experiment. To estimate the importance of trait change in the HMSC model, we calculated the average trait change as $\Delta x = \bar{x}_{ijt} - \bar{x}_{ij,t-1}$, where $\bar{x}_{ijt}$ is the mean trait of species i in environment j and week t. To estimate the genetic (as opposed to plastic) component of trait change, we used data from an accompanying reciprocal transplant experiment of Jewell and Bell (2023) to create a reaction norm for frond area across the nine experimental environments (Falconer 1989; Stearns 1992). We then used a linear mixed model (van Rossum 2025) and variance decomposition (Piepho and Möhring 2007) to estimate broad-sense heritability (h^2) for all species (Appendix S5).

To determine the relative importance of genetic trait change for community composition, we fit three HMSC models: An ‘evolution model’ in which $|\Delta x| h^2$ of each species and environmental treatment (using the first and second order polynomial term for both light and nutrients) were used as covariates, a ‘no-evolution model’ that included only the environmental conditions (first and second order polynomial terms), and a ‘null-model’ with no covariates. Species density was log-transformed, and we included replicate ($n = 2$) and time as random effects. For each model we ran four MCMC chains to generate 1000 samples of the posterior distribution for all model parameters, and we compared the explanatory power of all three models. We then used the ‘evolution model’ to estimate the predicted conditional effects of trait evolution in species Lm and Sp for density in species Sp (i.e., predicted value when other covariates are held to their mean value; Appendix S4).

3 | Results

3.1 | Linear Statistical Models for One- and Two-Species Models of Growth, Competition, and Trait Evolution

We evaluated the performance of linear models in simple cases (1–2 species, 1-few sites), to validate that effect size estimates and predicted densities accurately reflected mechanisms. When only one species was present (models A, B), the regression coefficients (A: $N_t \sim \beta_0 + \beta_1 N_{t\text{-}1} + \epsilon$; B: $N_t \sim \beta_0 + \beta_1 N_{t\text{-}1} + \beta_2 E_t + \beta_3 E_t^2 + \epsilon$) reflected the direction and magnitude of the mechanistic drivers of population size. β_1 correctly captured the positive relationship between $N_{t\text{-}1}$ and N_t under our simulation conditions (posterior mean and 90% Highest Density Interval [HDI]: A: $\beta_1 = 0.847$ (0.830, 0.865); B: $\beta_1 = 0.852$ (0.834, 0.871)), and β_2 (*B*: 2.55 (−0.036, 5.108)) and β_3 (−1.492 (−2.784, −0.220)) correctly captured the quadratic unimodal relationship between E_t and N_t (A: $R^2 = 0.997$, B: $R^2 = 0.997$).

When a second species was added (models C, D), the regression coefficients predicted density values at all time points (C: $R^2_{sp1} = 0.997$, $R^2_{sp2} = 0.999$; D: $R^2_{sp1} = 0.999$, $R^2_{sp2} = 0.999$), but their direction and magnitude did not reflect the intra- and interspecific competition strengths included in the mechanistic model (Appendix S1.3, Figures S1.16 and S1.17). We instead used a latent variable approach (implemented in HMSC) to consider these species interactions as part of the temporal random effects included in the model. This approach produced effect size estimates that both predicted the population dynamics well (95% HDI of model-predicted values, Figure 2a) and captured the conditional effects of environment for species densities (Figure 2b). The variation partition also captured the relative importance of the environmental predictor and the temporal random effects for model D (which in this case were driven by intra- and interspecific species interactions; Figure 2c; Appendices S1.3 and S1.4).

Trait evolution was included as a predictor in model E. The resulting linear regression coefficients could predict species dynamics (95% HDI, Figure 2d) and reflected the impact and magnitude of environmental and trait evolution predictors (Figure 2e). The variation partition also showed that trait evolution in species 1 ($|\Delta x_1|$) was a strong driver of variation in abundance (blue portion of bar plot, Figure 2f), primarily for species 1 but also for species 2 (Appendix S1.5; Appendix S2).

For the spatially complex model F, we included a spatial random effect to capture species covariances as a function of distance between sites. By considering species interactions as a temporal random effect and including spatial random effects, the HMSC model could estimate regression coefficients for the impacts of the environment E and trait evolution $|\Delta x_1|$ and $|\Delta x_2|$ for both species that fit to the simulated data points (observed points within 95% HDI in Figure 2g; Appendix S1.6) and capture conditional effects of environment and trait evolution for both species (Figure 2h). Spatial random effects explained a large proportion of variation in abundance for both species, but trait evolution remained a strong driver for species 1.

3.2 | 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 3a). Resulting biodiversity dynamics depended on the dispersal level and heritability values (Figure 3b). For dispersal, results mirrored some expectations from existing metacommunity models, i.e., that regional γ diversity decreases with increasing dispersal level d (Mouquet and Loreau 2003; Figure 3b). 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

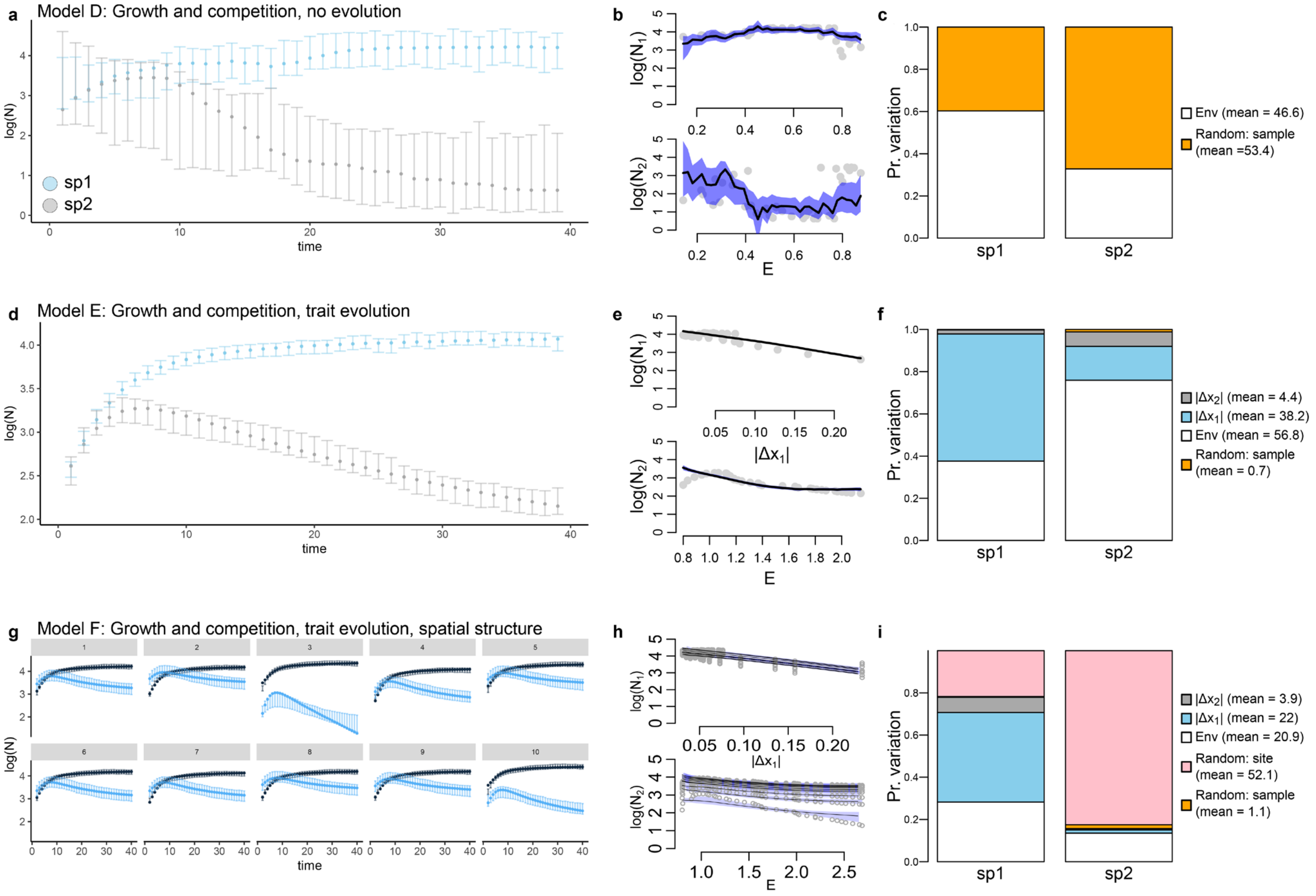

FIGURE 2 | Simulation models for 2-species ecological and eco-evolutionary dynamics. Panels a, d, and g show log-population size (y-axis) over time (x-axis) for species 1 and 2 when they grow and compete for resources with random environmental fluctuations over time. Error bars give the 95% highest density interval (HDI) for posterior predictions from the HMSC model fit. 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 observed (points) and model-predicted (black line with blue shading) log-population size ($log(N)$) 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 environment, trait evolution ($|\Delta x_1|$ and $|\Delta x_2|$), and temporal and spatial random effects for $log(N)$ for species 1 and 2.

metacommunity scale. Regional species diversity (γ) increased with increasing h^2 levels (Figure 3b).

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 3c; see Box 1 for inference about the impacts of trait evolution from effect size estimates). The importance of spatial random effects increased with dispersal rate, and the importance of evolution decreased with increasing h^2 (see Appendix S3, analysis of 1-species-1-site models of evolutionary rescue to better understand these effects).

3.3 | Empirical Data

We fit the empirical data (community dynamics and frond size of four aquatic plant species under different environmental treatments) to an HMSC model, and estimated the effect size of shade cover, nutrient level, and trait change (in all four species) for changes in species densities. The variation partition produced by the HMSC model fit shows the estimated relative importance of evolutionary (genetic component of change in the frond size trait) and ecological (shading and nutrient treatments) effects on species densities. 14.3% of the variation in species density could be explained by $|\Delta x|$ (Figure 5a; dLm, dRn, dSp, dWc). Including trait change in the statistical model led to reductions for the estimated importance of ecological effects by a total of 24.3% (from 48.7% to 38.8% for shading and from 24.4% to 20% for nutrients), while the random effects remained similar (Figure 5a,b). Including evolution resulted in a higher explanatory power (56%) compared to the 'no-evolution-model' (51%) and especially compared to the 'null-model' (8%).

$|\Delta x|$ of species Sp and Wc showed a low impact (2.2%, 2% respectively), while $|\Delta x|$ of Lm and Rn was higher (4.3% and 5.8%, respectively). Changes in $|\Delta x|$ impacted densities in distinct ways for intra- and interspecific comparisons (Figure 5c). For example, change in frond size of species Lm (dLm) had a negative impact on Wc and Sp, and this was reflected in the HMSC conditional predictions where higher dLm values had lower predicted

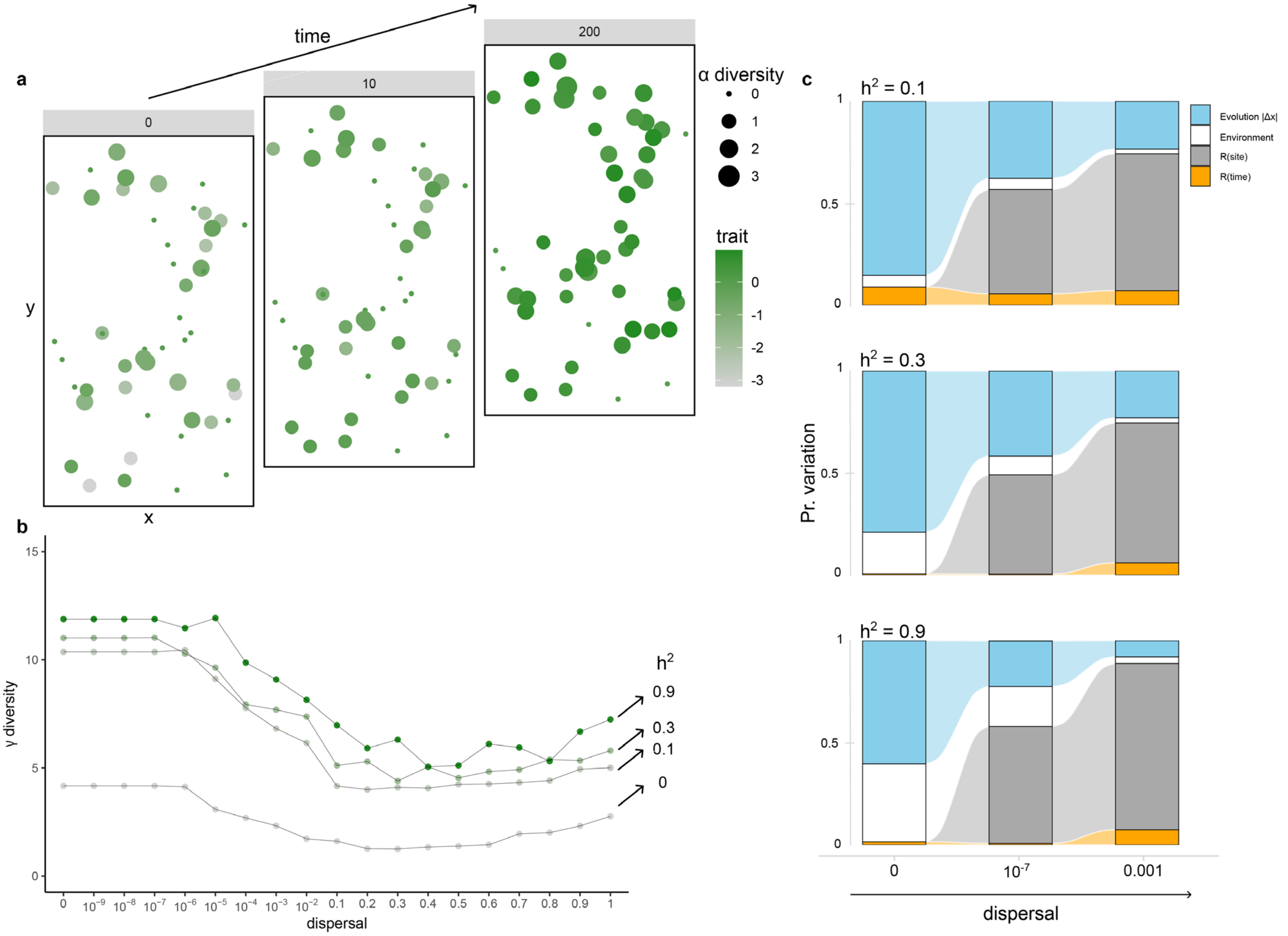

FIGURE 3 | Importance of trait evolution for change in community composition at the metacommunity scale. (a) We developed a simulation model for population growth, competition, and trait evolution in 15 species that inhabit a patchy landscape. The landscape has 50 sites (coloured points in the XY space), with distinct local environments that select for different patterns of local species diversity (size of points) and average trait values (colour 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 decreased with increasing disperal level and increased with increasing heritability (h^2). (c) Variation partition plots after fitting metacommunity time series of species abundances, $\log(N_{ikt})$, to HMSC models with environment, trait evolution, and random effects (space and time) as predictors. These variation partition results are averaged across all species in the metacommunity. The top panel is for $h^2 = 0.1$, the middle panel is for $h^2 = 0.3$, and the bottom panel is for $h^2 = 0.9$. The alluvial plots show the change in relative importance of different predictors for increasing dispersal levels.

species Sp density (Figure 5d). Trait change of species Sp had a positive effect on its own density (Figure 5d).

4 | Discussion

The analysis of community composition often requires statistical models that can consider the combined influences of environmental drivers and spatial connectivity. A more difficult, yet critical, element to incorporate is species interactions. Although the causal role of species interactions is difficult to interpret from statistical models (but see Dubart et al. 2022, Luo et al. 2022 in systems with few species), joint species distribution models (JSDMs) have implemented spatial and temporal random effects that can effectively capture these species interactions using a latent variable approach. However the resulting species covariance matrices can also reflect other processes besides species interactions, including unmeasured environmental effects (Poggiato et al. 2021). One element that has not been fully implemented into JSDMs is dynamic trait evolution (but see Benito Garzón et al. 2019 for genetic variation). We used HMSC (an existing JSDM), and developed simulation models of evolving populations in increasingly complex scenarios to determine whether the signal of trait evolution could be estimated and compared to other drivers of community composition. We also applied this statistical model to an existing empirical dataset (Jewell and Bell 2023) to show how HMSC can be used to model and predict the changes in species composition over time as a function of environmental drivers, trait change, and random effects. Dynamic trait change can be included as a fixed effect in HMSC, and the resulting effect size coefficient estimates can be used to (i) estimate the relative importance of trait evolution for community composition and (ii) predict the impacts of future trait change in the system.

At the same time, fixed effects for the impacts of trait evolution on population size should be interpreted with caution (Box 1). Of course, this is not unique to including trait evolution as a

BOX 1 | Interpreting the impacts of trait evolution.

The HMSC statistical model can estimate the impact of multiple (fixed and random) effects on the measured response variable. Interpretation of these effects, as in any statistical model, requires understanding the potential mechanisms that combine to produce the observations and estimated effect coefficients. In this study, we evaluated the effects of the absolute value in trait change from one time step to the next, $|\Delta x|$, for species densities ($log(N)$). This produces a linear regression coefficient $\beta_{|\Delta x_{ij}|}$, the effect of trait change in species j for density in species i. In our metacommunity simulation models, we often observed a strong impact of $\beta_{|\Delta x_{ii}|}$, and in some instances also strong $\beta_{|\Delta x_{ij}|}$.

We highlight two examples of the metacommunity simulations to consider how to interpret effects of trait evolution: (1) $\beta_{|\Delta x_{12,15}|} = 18.384$ (influence of $|\Delta x_{15}|$ on N_{12}, posterior median) under the simulation conditions $h^2 = 0.1$ and dispersal $d = 10^{-3}$ and (2) $\beta_{|\Delta x_{4,3}|} = -1.741$ under $h^2 = 0.9$ and dispersal $d = 10^{-3}$. To interpret these effects, we first note that in the mechanistic model we used to simulate growth in a metacommunity, $|\Delta x_j|$ does not directly impact N_i. It instead impacts the growth rate and resulting density of species j, and this can have an impact for species i through the strength of interspecific competition α_{ij}. We also note that in our simulation, the greater the degree of local maladaptation (the distance between trait x_i and the local optimum x_{opt}), the greater the corresponding selection pressure and thus the greater the value of $|\Delta x|$ will be. Our simulation uses an initially maladapted assemblage of species and therefore the highest $|\Delta x|$ values occur at the beginning of the simulation. We also initiated the simulation with low densities for all species. For this reason, the high $|\Delta x|$ observed in early time steps occurs frequently with the initially low N values.

This background can help when interpreting the posterior effect size estimates for $\beta_{|\Delta x_{12,15}|}$ and $\beta_{|\Delta x_{4,3}|}$ (Figure 4a,d). Species 15 (pink points, Figure 4b), repeatedly invades patches where Species 12 (green points) was a resident (e.g., patches 4, 7). The invading Species 15 is initially at a low density, resulting once in stochastic extinction. However, compared to the resident Species 12, it is able to establish as a result of its strong interspecific competitive effect, $\alpha_{12,15} = 0.0009950$. This competitive effect is not symmetric, as competition in the other direction is weaker ($\alpha_{15,12} = 0.0005909$). Thus as species 15 adapts (Δx changes in the direction of the local environmental optimum; Figure 4c), species 12 is simultaneously declining. This mechanism explains the positive effect of $\beta_{|\Delta x_{12,15}|} = 18.384$.

In a different example, species 3 (light brown points, Figure 4e) and 4 (dark grey points) can coexist in multiple patches (i.e., patches 2 and 26). Both species have low strength of interspecific competition ($\alpha_{4,3} = 0.0004165$, $\alpha_{3,4} = 0.0005555$). Due to landscape connectivity patterns, these coexisting species often invade patches at similar time points, and thus their adaptive trait change (high values of $|\Delta x|$, decreasing as they adapt; Figure 4f) is often occurring at the same time periods. Species 4 is thus frequently increasing in density as $|\Delta x_3|$ decreases, resulting in the negative effect $\beta_{|\Delta x_{4,3}|} = -1.741$.

The examples here are a reminder that effect sizes of trait evolution for population density (or potentially for other ecological responses) should thus be interpreted carefully. Positive effects of $|\Delta x_j|$ for N_i in one instance resulted from competitive suppression, while in another instance a negative effect resulted simply from independent evolutionary and ecological dynamics occurring at the same time.

predictor of community composition. Previous research has shown that the effect size coefficients from linear and autoregressive models using $N_{i,t-1}$ to predict $N_{i,t}$ or $N_{j,t}$ are not equivalent to the intra- and interspecific interaction coefficients that determine species density dependence and should not automatically be used to interpret the direction and magnitude of species interactions (Kloppers and Greeff 2013; Certain et al. 2018; Mühlbauer et al. 2020; Olivença et al. 2021). Our findings for using HMSC to estimate the impact of trait evolution ($|\Delta x_i|$) for species abundances are similar—(i) the relative importance of trait evolution estimated by a variation partition accurately reflects the relative strength of simulated species interactions vs. magnitude of trait change and (ii) the coefficients greatly increase the predictive ability of the statistical model for simulated data (Appendix S1). HMSC is therefore a useful tool for understanding the role that evolution can play in community dynamics.

This was also observed when using HMSC to evaluate the importance of evolution for metacommunity composition using simulated data from a model of population growth, competition, dispersal, and trait evolution in a spatially structured habitat (e.g., explaining 23.4% of changes in species density in simulation $h^2 = 0.1$ and $d = 10^{-3}$; Figure 3c). The simulations themselves revealed an intriguing role of adaptive evolution for rescuing individual species from extinction (i.e., Gomulkiewicz and Holt 1995) and as a consequence greatly increasing biodiversity (i.e., community rescue, Low-Décarie et al. 2015; Bell et al. 2019; Figure 3b). The recovery of species via local adaptation had consequent effects for coexistence, as species that were initially maladapted could recover in population size and exert competitive effects. Because HMSC can accurately estimate the relative importance of trait evolution for community composition (Appendix S1), we were able to test hypotheses about some processes that drive increased or decreased impacts of trait evolution in communities. Our simulation models fit to HMSC confirmed our hypotheses that the importance of evolution would decrease with increasing landscape connectivity (modelled as species dispersal rate d) and the overall speed of adaptive evolution (modelled as heritability h^2). Previous theoretical models have shown that these two properties can have a strong influence on resulting community composition (Urban et al. 2008; Loeuille and Leibold 2008; Urban and De Meester 2009; De Meester et al. 2016). By demonstrating that HMSC can accurately estimate the proportion of variation explained by trait evolution, we show how hypotheses from theoretical models can be tested using empirical data, with effect size estimates that can be compared across different study systems.

The HMSC model was also applied to experimental aquatic plants, to estimate the importance of heritable trait change (frond size), light, and nutrient levels for abundances of four species over 12 weeks (Jewell and Bell 2023). We additionally applied data from a reciprocal transplant experiment to estimate the genetic component of trait change (however, we use species densities as our response, not community average trait value; our results are therefore not meant to be compared directly with those of Jewell and Bell 2023). Additionally, the HMSC model does not require derivation of new categories for effect sizes (this is the case for Pantel et al. 2015; Hattich et al. 2022; Jewell

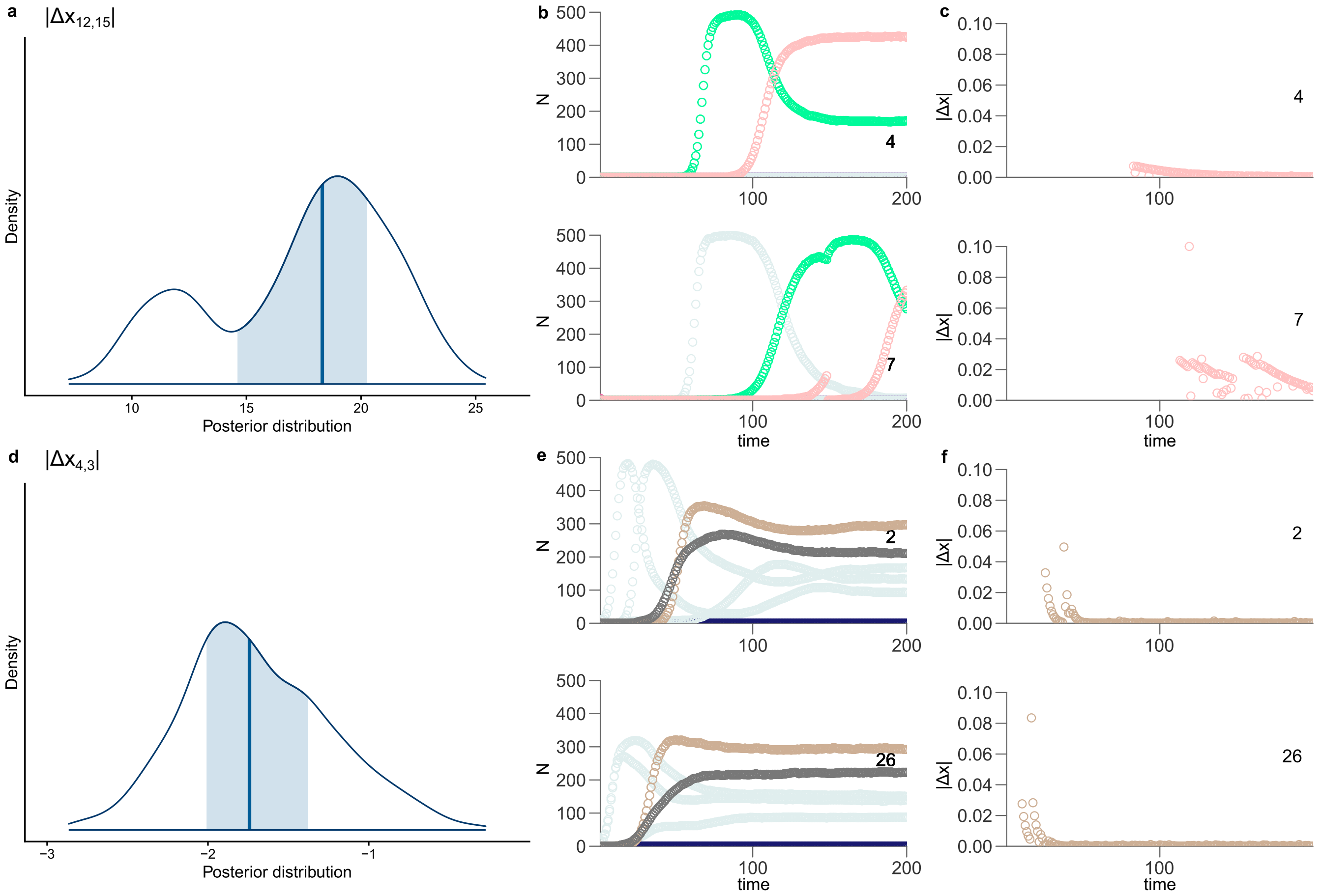

FIGURE 4 | Two effect size estimates of trait evolution for species density in a metacommunity ($\beta_{|\Delta x|}$) resulting from an HMSC analysis, with corresponding population and $|\Delta x|$ dynamics. (a) $\beta_{|\Delta x_{12,15}|}$ shows a positive effect of $|\Delta x_{15}|$ on N_{12}. In (d) $\beta_{|\Delta x_{4,3}|}$ shows a negative effect of $|\Delta x_3|$ on N_4. To explain the mechanism for these effect sizes, we evaluate population dynamics (b, e) and $|\Delta x|$ (c, f) in representative patches where the pairs of species co-occur. In (a) and (d), the blue vertical lines denote the median and the shaded area the inner 50% of the probability mass from the posterior distribution. The coloured points denote different species: 12 (green), 15 (pink), 3 (light brown), and 4 (dark grey), with all other co-occurring species shown as light blue.

and Bell 2023), nor must data be modelled as normal. HMSC has further benefits: (i) the flexible implementation of random effects according to the study design, (ii) modelling changes in population growth rate (Δr) or community mean trait values ($\bar{x}$) as response variables (Appendix S2; see also Ovaskainen and Abrego 2020) which may be more useful for mechanistic inference in some analyses, and (iii) predicting species responses to environmental gradients and trait change (i.e., Figure 5d). The Bayesian HMSC model is thus suited to understand how trait change impacts species densities under changing environmental conditions, or how the impact of trait change might depend on specific environmental conditions.

It is still important to note that this inference requires a comprehensive understanding of the study system and the need to capture the relevant environmental covariates. The potential impact of not including all covariates was investigated in detail in Ovaskainen and Abrego (2020) and Tikhonov et al. (2022). They showed that having only spatial information (e.g., using all sites, but only one time point in a temporal simulation) allows for an estimation of the different species niches (β effects), while having a time series (e.g., all time points, but using only one patch in a spatially structured simulation) is enough to estimate species associations and potential interactions and competition (Ovaskainen and Abrego 2020). The latent variables in HMSC are also shown to capture the effects of unmeasured covariates (in their example, purposefully excluding a simulated effect of a known size) in the species association matrix. The resulting model can retain its explanatory power but loses some of its predictive power (Tikhonov et al. 2022). The match of HMSC, and JSDMs generally, to a diversity of study designs is an important advantage compared to existing formulations of eco-evolutionary effect size estimates that use an ANOVA (i.e., Ellner et al. 2011; Govaert et al. 2016).

There has been a strong general interest in estimating effect sizes of evolution for ecological processes (Hairston Jr et al. 2005; Ellner et al. 2011; Pantel et al. 2015; Barbour et al. 2022), but in many empirical studies these estimates focus on one or a few species where the impacts of their evolution are strong enough to play a clear and detectable role in the corresponding ecological response variable (e.g., population growth rate, community diversity, likelihood of food web collapse). There is no general knowledge of overall distributions of effect sizes for the impact of evolution on species composition in communities, nor

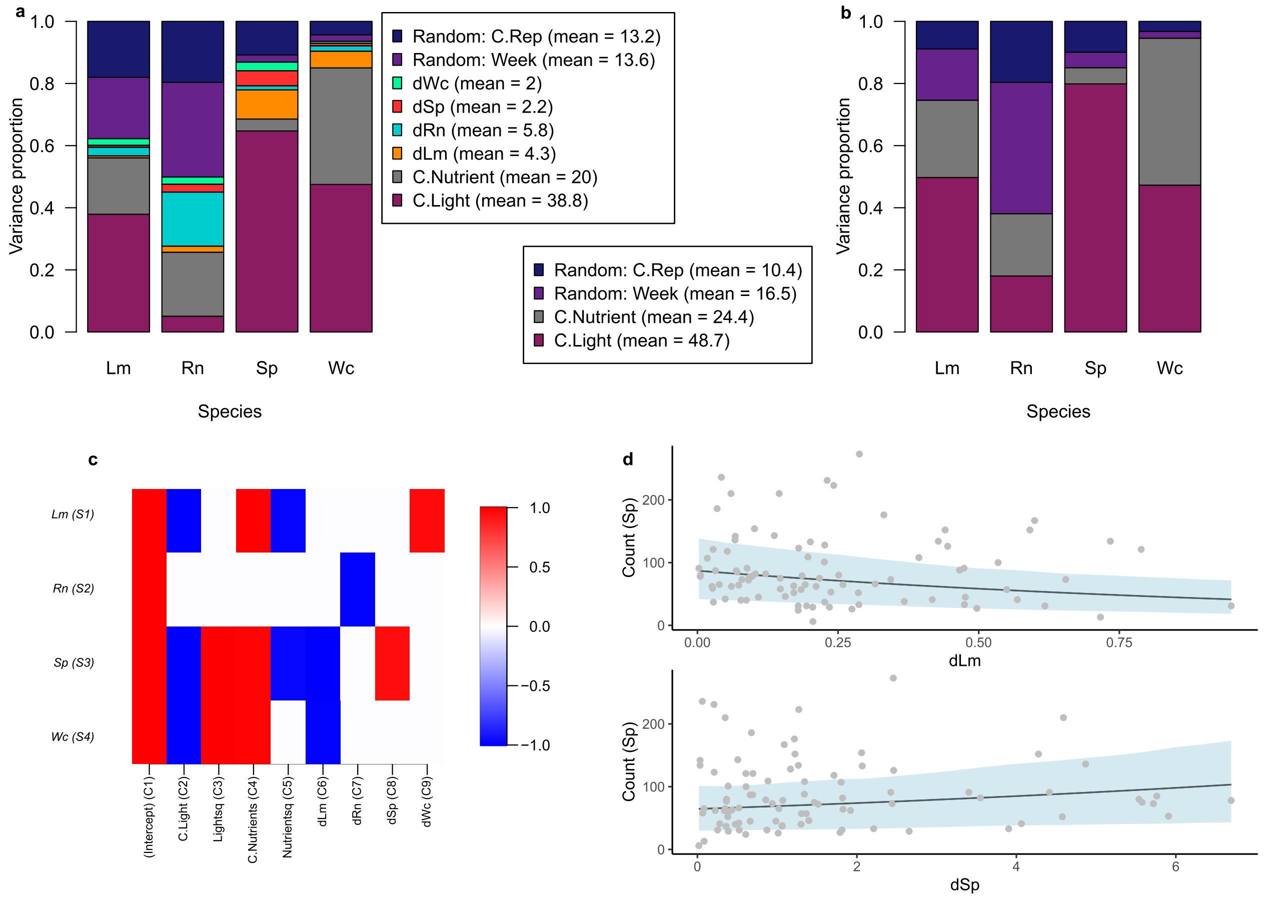

FIGURE 5 | The estimated effects of species trait changes and environmental treatments for densities of experimental aquatic plants (species Lm, Rn, Sp, and Wc). The variation partition for the HMSC model with (a) and without (b) evolved trait change $|\Delta x|$ is shown, as well as (c) the posterior estimated direction of effect (blue for negative or red for positive; effect sizes with 95% HDI that included 0 are coloured white). (d) Predicted species Sp density as a function of the magnitude of trait change in species Lm and Sp (with other model predictors held to their mean value). Mean value (of 1000 samples from the posterior distribution of predicted values) is denoted by the black line and 95% HDI by the blue shaded area. Data points from the experiments are shown as grey points.

are there studies that evaluate drivers of shifts in these distributions of effect sizes in complex communities (see Hermann et al. 2024 for estimates in a predator–prey system). We present here distributions of effect sizes of trait change and evolution for species abundances (i.e., posterior estimates of regression coefficients; Figure 4a,d; Figure 5c; Appendix S1), which allow estimation of the relative importance of evolution and trait change for community composition (i.e., Figures 2c,f,i, 3c and 5a,b) in simulated and experimental aquatic plant communities. We expect that effect size coefficients can be useful for better understanding the relative importance of evolution as a driver of community composition.

An increasing number of studies collect and analyse high-resolution time series of populations and trait values for single (Rudman et al. 2022) and multiple (Thomas et al. 2018; Gibert et al. 2023; Han et al. 2023; Shen et al. 2023) species, with an increasing number of interacting processes that can structure this data (Pantel and Becks 2023). HMSC, and JSDMs generally, can be expanded to include dynamic trait change in community ecological studies. Two critically important additions that will increase the application to field or experimental observation data will be (i) bidirectional causality and eco-evolutionary feedbacks (Granger 1969; Lion 2018; Grace 2021) and (ii) the relative contribution of plasticity and genotypic evolution for trait change (i.e., de Villemereuil and Chevin 2025; Wieczynski et al. 2025). It is also necessary to incorporate known causal processes that change the speed of evolution or the strength of species interactions (Fronhofer et al. 2023), to better model the underlying distributions of eco-evolutionary effects. While these processes represent more complexity for data analysis and interpretation, existing methods can help translate these eco-evolutionary mechanisms into flexible statistical models that more accurately estimate ecological and evolutionary drivers of community composition.

Author Contributions

J.H.P. conceptualisation, development and analysis of the models, writing – original draft and writing – review, and editing. R.J.H. analysis of empirical data, co-analysis of the full model, writing, review, and editing.

Data Availability Statement

All data and code are publicly available at https://github.com/jhpantel/ecoevo-hmsc and https://doi.org/10.5281/zenodo.17227644.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** ele70270-sup-0001-AppendixS1.pdf. **Appendix S2:** ele70270-sup-0002-AppendixS2.pdf. **Appendix S3:** ele70270-sup-0003-AppendixS3.pdf. **Appendix S4:** ele70270-sup-0004-AppendixS4.pdf. **Appendix S5:** ele70270-sup-0005-AppendixS5.pdf.