

Beyond metacommunity paradigms: habitat configuration, life history, and movement shape an herbivore community on oak

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Abstract. Many empirical studies of metacommunities have focused on the classification of observational patterns into four contrasting paradigms characterized by different levels of movement and habitat heterogeneity. However, deeper insight into the underlying local and regional processes may be derived from a combination of long-term observational data and experimental studies. With the aim of exploring forces structuring the insect metacommunity on oak, we fit a hierarchical Bayesian state-space model to data from observations and experiments. The fitted model reveals large variation in species-specific dispersal abilities and basic reproduction numbers, R_0 . The residuals from the model show only weak correlations among species, suggesting a lack of strong interspecific interactions. Simulations with model-derived parameter estimates indicate that habitat configuration and species attributes both contribute substantially to structuring insect communities. Overall, our findings demonstrate that community-level variation in movement and life history are key drivers of metacommunity dynamics.

Key words: Bayesian community model; dispersal ability; habitat configuration; metacommunity; movement; oak herbivore communities; plant–insect interactions; *Quercus robur*; southern Finland.

INTRODUCTION

For at least half a century, community ecologists have emphasized that local communities are structured by both local and regional processes (Elton 1949, Huffaker 1958, MacArthur and Wilson 1967, Holt 1993, Holyoak et al. 2005). This view has been formalized in the context of metacommunity theory (Leibold et al. 2004, Logue et al. 2011). Much of this theory is centered around four conceptual “metacommunity paradigms,” as originally outlined and contrasted with each other in a seminal paper by Leibold et al. (2004). The differences among these four paradigms derive from differences in relative dispersal rates among their component species, and in the level of heterogeneity among habitat units. The *species-sorting* and *mass-effects* paradigms envisage heterogeneous habitat, where the dispersal of the species (relative to the grain size of environmental variation) is either “intermediate” (allowing species to aggregate in their optimal environment) or “high” (allowing species to establish in sink habitats due to continuing immigration), respectively (Shmida and Wilson 1985, Holt 1993, Leibold 1998, Mouquet and Loreau 2002, Cottenie et al. 2003). By contrast, the *patch dynamics* paradigm focuses

on a homogeneous landscape with species differing in local dominance and dispersal. Such systems have been explored from a variety of perspectives, e.g., by models that allow for regional coexistence by a trade-off between competitive ability and colonization (Skellam 1951, Levins and Culver 1971, Hastings 1980, Tilman 1994, Calcagno et al. 2006). Refuting the other paradigms, the *neutral* paradigm assumes that species do not differ in fitness, competitive ability, or movement (Hubbell 2001), and states that communities are structured by ecological drift rather than by species-specific differences. Importantly, the paradigms are not mutually exclusive, and several theoretical studies have explored cross-paradigm scenarios (Horn and MacArthur 1972, Amarasekare 2003, Mouquet and Loreau 2003, Amarasekare et al. 2004).

The metacommunity framework, and the explicit identification of contrasting paradigms within it, has been of clear heuristic value. It has stimulated both theoretical advancements (e.g., Mouquet and Loreau 2003) and empirical tests (cf. Logue et al. 2011, the present study) regarding the influence of dispersal rates, habitat heterogeneity, and population stochasticity on local and regional dynamics. Nonetheless, more mechanistic integration of theory and empirical studies is needed, as argued by the recent synthesis of the status quo by Logue et al. (2011), who identified two key problems hampering progress toward an eventual synthesis between theory and empirical patterns. First, we lack robust statistical tools to distinguish among the

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four different metacommunity paradigms. This shortage partly reflects the scarcity of direct assessments of species' dispersal abilities (Logue et al. 2011). Second, theoretical and experimental studies of metacommunity dynamics tend to focus on highly simplified habitat networks, at odds with the strikingly complex spatial network configurations found in nature. Because habitat configuration may have a major impact on local and regional population dynamics (Cottenie et al. 2003, Cadotte 2006, Moritz et al. 2013), this discrepancy in complexity may restrict the scope for generalizations between theory, experiments, and natural community dynamics.

Logue et al. (2011) identified several problems with the statistical approaches widely used to assign individual study systems to specific theoretical paradigms. In particular, the three methods most commonly applied to date (zero-sum multinomial distribution, site-by-species incidence matrix, and variance partitioning) focus on assessing patterns rather than processes, and thus lack actual power for separating between different metacommunity paradigms (Logue et al. 2011). For example, the popular framework of variance partitioning is based on the idea of comparing the relative effects of environmental and spatial variation on observed spatial patterns of species distributions (e.g., Cottenie 2005). However, such an approach does not allow for direct interpretation of spatial covariance, because spatial autocorrelation can stem from spatial structure in environmental variables left unmeasured equally well as from actual dispersal limitation, or from any combination of the two (Jacobson and Peres-Neto 2010, Smith and Lundholm 2010). As a way forward, Winegardner et al. (2012) argued that metacommunity ecologists should return to basic principles. Instead of attempting to fit metacommunities into four simple, nonexclusive, and perhaps partly artificial paradigms, one should focus more on estimating the actual processes behind the distributional patterns observed in real metacommunities. Furthermore, because community dynamics may be highly stochastic (Hubbell 2001), metacommunity models should explicitly account for ecological drift, i.e., chance variation in births and deaths.

In response to this plea, we here apply a Bayesian state-space approach to a spatially complex metacommunity of herbivores specializing on the oak *Quercus robur*. Our aims are to directly evaluate the impacts of movement, life history, habitat configuration, and interspecific interactions on the dynamics of this metacommunity. We base our approach on the following steps. (1) To estimate the community-wide distribution of movement and life-history parameters, we develop a spatially explicit metacommunity model, where individual species display spatially structured population dynamics without interspecific interactions. We parameterize this model with data from a long-term metacommunity survey within a landscape of 5 km² and two independent dispersal experiments, and we validate

the structural assumptions of the model by examining whether patterns simulated from the model match those of the data. (2) To look for imprints of biological processes not included in our model (e.g., interspecific competition or similar responses to plant quality), we assess negative and positive correlations in residual variation between species. (3) To address how variation in habitat configuration as well as variation among species in life history and movement affect metacommunity dynamics (occupancy, extinction, and colonization), we simulate metacommunities in a diverse set of artificial landscapes.

MATERIALS AND METHODS

Study system

As our model metacommunity system, we use a set of herbivorous species associated with the pedunculate oak *Quercus robur*. This tree species is patchily distributed in southern Finland, and sustains a wide range of herbivore species. Overall, the leaf-feeding metacommunity of *Q. robur* includes 24 species of leaf miners, galls, and leaf-folders (see Appendix A: Table A1 for the species list).

Long-term observational data

To analyze the dynamics of the herbivore community through space and time, we monitored local species assemblages on 88 small (1–4 m) trees growing naturally in different locations on the island of Wattkast (Fig. 1). These trees are a subset of a total of 1875 live oak trees (>0.5 m tall) occurring on the island, for all of which we have measured the location and diameter. For a period of six years (2003–2008), we assessed the occurrence (0/1) of the focal species on the full foliage of 88 trees, and their local abundance on 20 haphazardly selected shoots of the same trees. We searched the trees in early September, by which time each species can reliably be detected. Because the trees were relatively small, all foliage could be searched from the ground.

Extinction experiment

To explore the potential of each insect species to colonize unoccupied trees, we created targets for colonization by experimentally removing all focal herbivores on 63 small (1–4 m tall) trees in the northwestern corner of Wattkast (Fig. 1B). All leaves with leaf mines and/or galls were manually picked off in early September in 2005, 2006, and 2007. Because the average number of miners and galls is generally low (Tack et al. 2009, 2010), this procedure is not likely to induce any systemic responses in the target trees (Tack et al. 2009). In the three years following the experimental extinctions (2006–2008), we revisited the trees and recorded the abundances of the insect species. For a few species that exit the leaves before completing development, the procedure of removing mined or galled leaves is not likely to be efficient. Hence, this treatment was

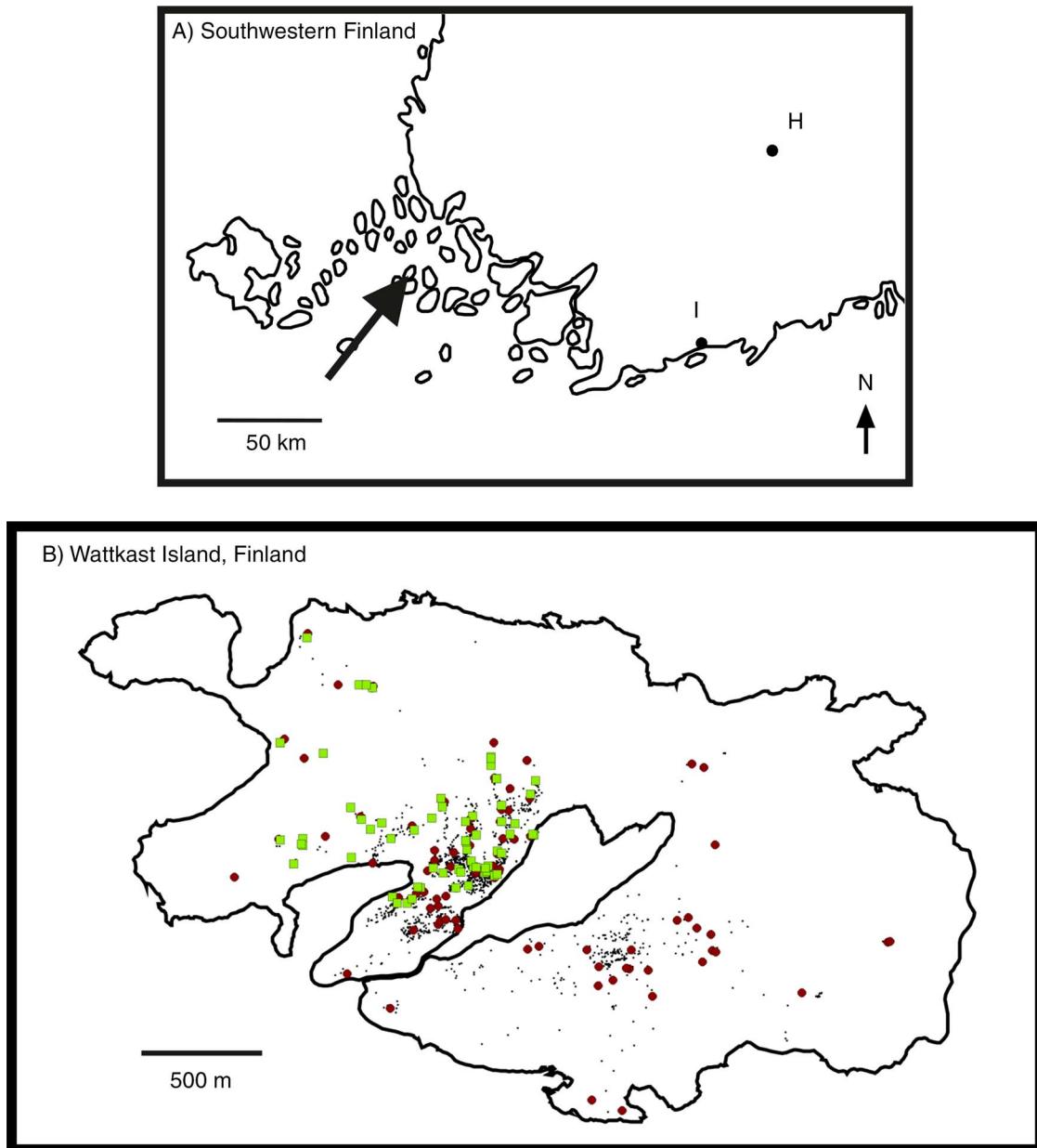


FIG. 1. Field sites for experimental and observational data sets in southwestern Finland. In panel (A), letters indicate the location of the two dispersal experiments: I, Inkoo; H, Hakoinen. The arrow indicates the location of the island of Wattkast. Panel (B) shows an enlargement of this island, where the small black dots indicate the location of each oak tree (>0.5 m tall). Red circles identify the 88 trees that were surveyed from 2003 to 2008, and green squares represent the trees included in the extinction experiment, from which the insect herbivore community was manually removed during years 2005–2007.

considered to have an effect only for a subset of species ($n = 15$ species; see Appendix A: Table A1).

Dispersal experiments

To estimate species-specific dispersal abilities, we conducted two independent experiments in vegetation similar to that of Wattkast. In the early spring of 2004, well before the flight period of the focal insect species, 32 potted treelets were arranged in clusters of four trees

each at different directions and distances from an isolated oak stand in Inkoo, southwestern Finland ($60^{\circ}0'13''$ N, $23^{\circ}45'54''$ E; Fig. 1A). Two clusters were placed at each of the distances 37.5 m, 75 m, and 150 m, and single clusters at distances of 300 m and 350 m. In autumn 2004, we recorded the abundance of insect herbivores on the full foliage of each treelet.

In 2006, we conducted a similar, independent dispersal experiment in Hakoinen, south-central Finland

(60°52'29" N, 24°33'15" E; Fig. 1A). Here we placed individual potted oak treelets ($n = 57$) at four different distances from an isolated oak stand (37.5 m, 75 m, 150 m, and 300 m). In autumn of 2006, we searched through the full foliage of the trees to assess the abundance of the focal herbivores.

Metacommunity model

As a community-level extension of a previous single-species metapopulation model of the leaf mining moth *Tischeria ekebladella* (Gripengren et al. 2008), we built a spatially explicit Bayesian state-space model that allowed us to integrate the empirical data of the herbivore community with the dispersal experiment data. The state-space model consists of two parts: the process model describing the dispersal of herbivores between oaks and local population dynamics, and the observation model accounting for the study designs and the sampling processes. Based on the shared lifestyle of galling and leaf-mining species, we used the same model structure for each species, but assumed species-specific parameter values. The community structure was modeled through a joint prior distribution of the species-specific parameters. For clarity, we will always refer to species by index $i = 1, \dots, n_S = 24$, to trees by j and l , and to year by $t = 1, \dots, n_T$, with $t = 1$ corresponding to the initial year 2003. The model structure and the notation are summarized in a graphical description in Appendix B: Fig. B1.

Dispersal model.—We assumed that each species disperses by active flight of adults, and thus we ignored the passive drifting of larvae inside of leaves abscised in the autumn (empirically shown to be of minor effect for the sole species explicitly studied in this respect, *T. ekebladella*; Gripengren et al. 2008). We modeled the adult flight by a heterogeneous space diffusion model with edge-mediated behavior (Ovaskainen 2004), thus assuming that the individuals leave the oak trees less frequently than would be predicted by a pure random walk process. We denote the dispersal ability of species i by $1/\alpha_i$ (mean dispersal distance, derived from the diffusion coefficient; see Appendix B for details), its preference for habitat patches (relative to the matrix) by k_i , and its adult mortality (assumed to be the same in patches and in the matrix) by m_i . We simplified the landscape structure by assuming that oak crowns are circular. For computational ease, we followed Zheng et al. (2009) and merged oak crowns with a center-to-center distance less than five times the average crown diameter, setting the area of the merged patch equal to the sum of the component crowns, and its location to the center of mass of the resultant compound crown. We measured the trunk diameters and estimated the crown diameters by the relationship $d_C = 2.25 + 15d_T$, where d_C and d_T are the diameters (in meters) for the crown and the trunk, respectively. This relationship is based on data for another oak species, *Q. suber* (Paulo et al. 2002).

Population dynamic model.—Based on the life cycle of the focal herbivores, we constructed a population dynamical model that proceeds from first-instar larvae in the previous year through adults to new eggs and new larvae in the current year, and so on for further years. For simplicity, we focus our model on females only, assuming no male limitation. For bivoltine species (cf. Appendix A: Table A1), the parameters should be interpreted as effective parameters that integrate population dynamic processes over the full season.

We denote by $a_{ij}(t - 1)$ the number of first-instar larvae of species i in tree j at the previous year $t - 1$ before the extinction experiment. Assuming that all individuals of a species subjected to targeted removal on a given tree were removed, we denote by $a_{ij}^*(t - 1)$ the number of first-instar larvae after the extinction experiment. Each first-instar larva of species i in tree l in year $t - 1$ was assumed to be a female, to survive over the larval stage, to successfully emerge as an adult in the current year t , and to become mated with probability $p_{il}(t - 1)$. The expected number $n_{ij}(t)$ of mated females that visit tree j at year t was then modeled as $a_{ij}^*(t - 1)p_{il}(t - 1)\mathfrak{R}_{ij}^{(i)}$, where $\mathfrak{R}_{ij}^{(i)}$ is the probability (predicted by the diffusion model) that a mated female emerged in tree l visits tree j before it dies (see Appendix B).

The time that a female of species i visiting tree j spends in that tree was assumed to be exponentially distributed, with mean $T_j^{(i)}$ predicted by the diffusion model (see Appendix B). Thus, the total amount of time $q_{ij}(t)$ spent in tree j by all females visiting the tree is gamma distributed with shape $n_{ij}(t)$ and scale $T_j^{(i)}$. When the female was within a tree, she was assumed to lay eggs at a rate $1/\tau_i$, where τ_i is the mean amount of time required to oviposit one egg. Each egg was assumed to survive and develop into a first-instar larva with probability s_i . Thus, if a mated female of species i spent no time in the matrix, it would lay an average number of $1/(\tau_i m_i)$ eggs, resulting in an average number of $f_i = s_i/(\tau_i m_i)$ first-instar larvae, which combined parameter (f_i) we call the fecundity of the species i .

We used the same process model for the two dispersal experiments, for which we denote by $\tilde{a}_{ij}^{(X)}$ the number of first-instar larvae of species i . Here X denotes the study site of the dispersal experiment, $X = I$ corresponding to Inkoo and $X = H$ to Hakoinen. We denote by $h_{ij}^{(X)}$ the unknown number of mated females of species i that emigrated from the respective, isolated oak stand j located in the center of the experimental field, a parameter that we estimated along with the other model parameters.

Observation model.—For the census information collected from the island of Wattkast, we assumed that the presence-absence data are accurate, as confirmed by field validation trials where different fieldworkers scored the community on the same set of trees. We denote the abundance of first-instar larvae of species i measured in tree j at year t by $y_{ij}(t)$. Given the sampling design just described, $y_{ij}(t)$ refers to either a count from 20 randomly chosen shoots or from the full foliage. We assumed that

$$y_{ij}(t) \sim \text{Binomial}[a_{ij}(t), L_j^S/L_j]$$

where L_j is the total number of leaves of tree j , and L_j^S is the number of leaves surveyed. Thus, for the cases when all leaves were surveyed, we assumed that all occurrences were detected, $y_{ij}(t) = a_{ij}(t)$.

Because we did not count the number of leaves, we modeled them with the log-normal distribution $\ln(L_j) \sim N[\mu_j^L, (\sigma_j^L)^2]$, where $\mu_j^L = 12.68 + 2.55 \ln \text{GBH}_j$ and $\sigma_j^L = 1.94$, estimated from an independent data set of *Quercus robur* (Schönrogge et al. 2000, Gripenberg et al. 2008: Appendix S3). Here GBH denotes the girth measured at breast height, i.e., the circumference of the tree trunk. If a modeled tree resulted from merging of many nearby trees, we approximated the sum of log-normal random variables by a log-normal distribution, the mean and the variance of which were estimated by the Fenton-Wilkinson method (Fenton 1960).

In the dispersal experiment, first-instar larvae on each target tree were surveyed completely for the full foliage, and the detection probability was thus assumed to be 1.

Assumptions on community structure.—To model variation in the demographic processes among species and years, we assumed that

$$\text{logit}(p_{ij}(t)) = \mu_i^p + \varepsilon_{i,t}^p$$

where $\text{logit}(x) = \ln(x/(1-x))$ and the μ_i^p are species-specific mean values. The residuals were assumed to be distributed as $\varepsilon_{i,t}^p \sim N[0, \sigma_p^2]$ independently for $t = 1, \dots, n_T - 1$ and $i = 1, \dots, n_S$. To allow community-level inference, we followed Ovaskainen and Soininen (2011) by assuming that the species-specific parameters follow a multivariate normal distribution

$$\left(\ln k_i, \ln \frac{1}{\alpha_i}, \ln f_i, \mu_i^p \right)^\top \sim N[\boldsymbol{\mu}, \boldsymbol{\Sigma}]$$

where $N[\boldsymbol{\mu}, \boldsymbol{\Sigma}]$ denotes the multivariate normal distribution with mean $\boldsymbol{\mu}$ (a vector of length 4) and variance-covariance $\boldsymbol{\Sigma}$ (a symmetric positive-definite matrix of dimension 4×4).

To aid the interpretation of the results, we combined the life-history parameters into a single parameter representing the basic reproduction number, $R_0^{(i)}$. This entity refers to the average number of first-instar larvae of species i produced by a parental first-instar larva under average environmental conditions, assuming that the individuals are initially uniformly distributed among the total crown area within the landscape. In this case, the probability q_l of a random parental first-instar larva being in tree l is given by a fraction of the crown area of tree l over the total crown area in the landscape. Thus, $R_0^{(i)}$ was calculated as

$$R_0^{(i)} = \sum_j \sum_l q_l \text{logit}^{-1}(\mu_i^p) \mathfrak{R}_{lj}^{(i)} \mathcal{T}_j^{(i)} f_i$$

where $\mathcal{T}_j^{(i)} = T_j^{(i)} m_i$ and the product term $\mathfrak{R}_{lj}^{(i)} \mathcal{T}_j^{(i)}$ denotes the fraction of the lifetime that a mated female born in

tree l spends in tree j , which quantity can be predicted by the movement model (Appendix B) as a function of k_i and $1/\alpha_i$.

Model parameterization.—We parameterized the model with a standard Bayesian approach. We sampled the posterior distribution with a Markov chain Monte Carlo (MCMC) algorithm implemented with Mathematica 9 (code available in the Supplement). The sampling algorithm and prior distributions are described in sections 3 and 4 of Appendix B, respectively. We verified the correct implementation of the MCMC algorithm by back-estimating parameters from simulated data and validated the structural assumptions of the model by comparing posterior predictive data to the original data (section 5 of Appendix B).

Species associations

To detect processes not accounted for by the above-described model, i.e., imprints of abiotic and biotic interactions beyond species' responses to the landscape, we explored deviations between model-predicted and observed species-specific abundances (henceforth "residuals"). In particular, we aimed to assess whether pairs of species show aggregation (or segregation), and therefore examined cross-correlations in residuals at the tree level among pairs of species. Such aggregation (or segregation) could suggest direct biotic interactions among the species, indirect interactions mediated by the larger community, or that different species respond similarly (or differently) to un-modeled variation in the environment, e.g., the quality of trees (cf. Peres-Neto et al. 2001, Ovaskainen et al. 2010). To derive tree- and year-specific residuals, we subtracted the binomial mean of the posterior latent abundances from the empirically observed abundances. For each species pair, we computed the Pearson correlation coefficient and its 95% confidence interval from the residuals.

Simulations

To examine the influence of landscape configuration on the herbivore community, we generated hypothetical landscapes differing in the numbers and sizes of habitat patches, as well as in their spatial aggregation. We then used the Bayesian process-based model to simulate the dynamics of the herbivore community for the duration of 10 years in these landscapes, using species-specific parameter estimates.

All hypothetical landscapes were created within a 1-km² square. As a baseline scenario, we selected $T = 100$ trees of identical crown area $A = 10 \text{ m}^2$ to be distributed according to complete spatial randomness (i.e., a cluster size of $C = 1$). We then varied the three parameters T , A , and C one at a time, keeping the others at their baseline values, with (1) the number of trees set to either $T = 50$ or $T = 200$, (2) the cluster size representing aggregation in the spatial distribution of the trees set to either $C = 5$ or $C = 10$, and (3) the size of the trees set to a crown area of either $A = 5$ or $A = 20 \text{ m}^2$. For the scenario denoted by

$A = 10R$, we assumed random variation in tree size, assuming that $A - 5$ follows an exponential distribution with mean 5, so that the average tree size equals that of the baseline scenario (10 m^2).

We conducted 2000 replicate simulations for each of the eight scenarios. To take into account the influences of process uncertainty and parameter uncertainty, the species-specific parameter values were resampled for each replicate from the posterior distribution. For simplicity, temporal variation in survival rates was set to zero. We examined how much of the variation in the simulated dynamics could be attributed to the species ($n = 24$), the habitat configuration ($n = 8$ scenarios), and the interaction between these two. To do so, we recorded from the simulations three aspects of population dynamics for each species i and for each habitat configuration h : (1) the logit-transformed probability of tree occupancy O_{ihr} (probability of a randomly selected tree being occupied in the 10th year of each simulation replicate r); (2) the logit-transformed per capita colonization probability C_{ihr} (probability of a first instar in the 10th year producing first-instar offspring in non-natal trees in the next year for each simulation replicate r); and (3) the logit-transformed probability of extinction E_{ih} of the species, averaged over the simulation replicates. We used the framework of generalized linear mixed models to explain variation in the three response variables (occupancy, colonization, and extinction) by species identity and habitat configuration, both treated as random effects. For occupancy and colonization (which were estimated for each replicate), we also included the interactions among species identity and habitat configuration. The models were fitted to the data using restricted maximum likelihood (REML) methods implemented in package lme4, version 1.1-7 (Bates et al. 2014) in *R* (R Core Team 2012). The resultant variance estimates were used to partition the overall variation into fractions attributable to species, habitat configuration, their interaction, and residual variation.

RESULTS

Estimated life-history parameters

In spite of being confined to the same resource, species differed substantially in their parameter values: there was large (threefold) variation among species in median posterior values of both basic reproduction number and dispersal ability, with differences in the latter being better resolved (Fig. 2). No phylogenetic or ecological imprint was evident in parameter values: we did not detect any consistency in the basic reproduction number or in estimates of movement parameters among species from the same order, family, or genus, among species from the same feeding guild, or among species with the same number of generations per year (Fig. 2; Appendix A: Table A1).

Species interactions

Residual variation in tree-specific abundances showed no or weak correlations among herbivore taxa: correlation coefficients were variably (weakly) positive or negative in sign, with only two out of the 210 correlations significantly different from those expected by chance alone (Appendix B: Fig. B5). Hence, at the tree level, species were apparently distributed independently of each other.

Simulated impact of habitat change on the herbivore community

Simulated variation in landscape structure (Fig. 3A) had a substantial influence on the herbivore communities. As expected, species richness strongly increased with an increase in the total number and crown size of trees (Fig. 3B). Species richness also increased, but less pronouncedly so, by the trees being clustered in space rather than randomly distributed. Variation in tree size (as compared to constant crown size) had a mild positive effect on species richness. Species-specific life-history parameters (dispersal, reproduction number) explained variation in species incidence, regional extinction, and per capita colonization (Fig. 3C–H). As expected, species with a high basic reproduction number had a high incidence and a low extinction risk (Fig. 3C, D). Furthermore, species characterized by a long dispersal range showed a high per capita colonization rate (Fig. 3H), whereas dispersal range had only a minor influence on incidence or extinction risk (Fig. 3F, G). These links from the life-history parameters to their population dynamical consequences were robust in the sense that the strengths and signs of the correlations were largely independent of landscape structure. However, the effect of the basic reproduction number on per capita colonization rate varied among the landscapes (Fig. 3E): in landscapes with a high density of patches, colonization rate increased with basic reproduction number, whereas in landscapes with a low density of patches, the opposite pattern was found.

Variance partitioning demonstrated that species identity, and to a lesser extent habitat configuration, were important drivers of three central metacommunity descriptors: species incidence, regional extinction, and per capita colonization rate (Fig. 4). The interaction among habitat configuration and species identity had an only marginal effect on species incidence and per capita colonization probabilities (Fig. 4), meaning that differences among species prevail among different landscapes: a species rare in one landscape will remain so in another.

DISCUSSION

Although our study focused on an insect community occupying a single resource type, our results revealed substantial differences between species in life history and movement. We detected threefold variation in both basic reproduction number R_0 and in dispersal ability. Of interactions among species, we found no strong

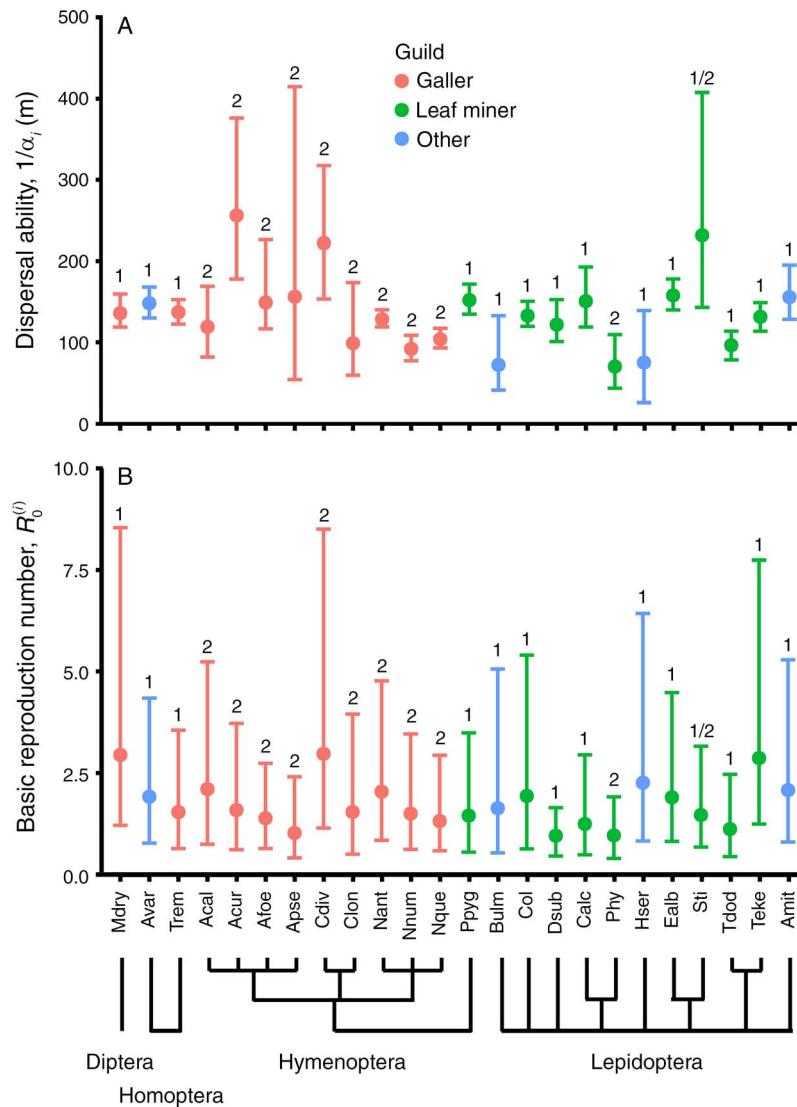


FIG. 2. Posterior distributions of (A) the species-specific dispersal ability ($1/\alpha_i$) and (B) the basic reproduction number ($R_0^{(i)}$), calculated as the average number of first-instar larvae of species i produced by a parental first-instar larva under average environmental conditions. Circles refer to median values and error bars to 95% central posterior intervals. Species abbreviations on the x -axis correspond to those identified in Appendix A: Table A1. Species are sorted according to taxonomic relationship (order, family, and genus), as illustrated by a rudimentary “phylogeny” below panel (B). Feeding guild (galler, leaf miner, other) is indicated by color, and the number of generations per year (voltinism) is shown above the error bars.

signals, because model residuals were only weakly correlated among species. When combined, these findings suggest that effects of spatial configuration may override biotic interactions in determining metacommunity structure. In model simulations, both species-specific differences and habitat configuration modified species’ incidence, risk of regional extinction, and per capita colonization rate. Overall, these findings reveal the joint imprint of life history, dispersal, and habitat configuration in structuring a metacommunity on oak, and suggest that real communities will defy classification into any of the simplified metacommunity

paradigms dominating recent literature. Next, we will discuss each of these insights in turn.

Species sharing the same resource vary strongly in life history and movement

A major impediment to matching metacommunity theory with empirical data has been the lack of reliable dispersal estimates from sets of species inhabiting a shared natural landscape. Although such estimates are available from mark–release–recapture experiments of conspicuous groups such as butterflies and macro-moths (Nieminen 1996, Baguette et al. 2000, Slade et al. 2013),

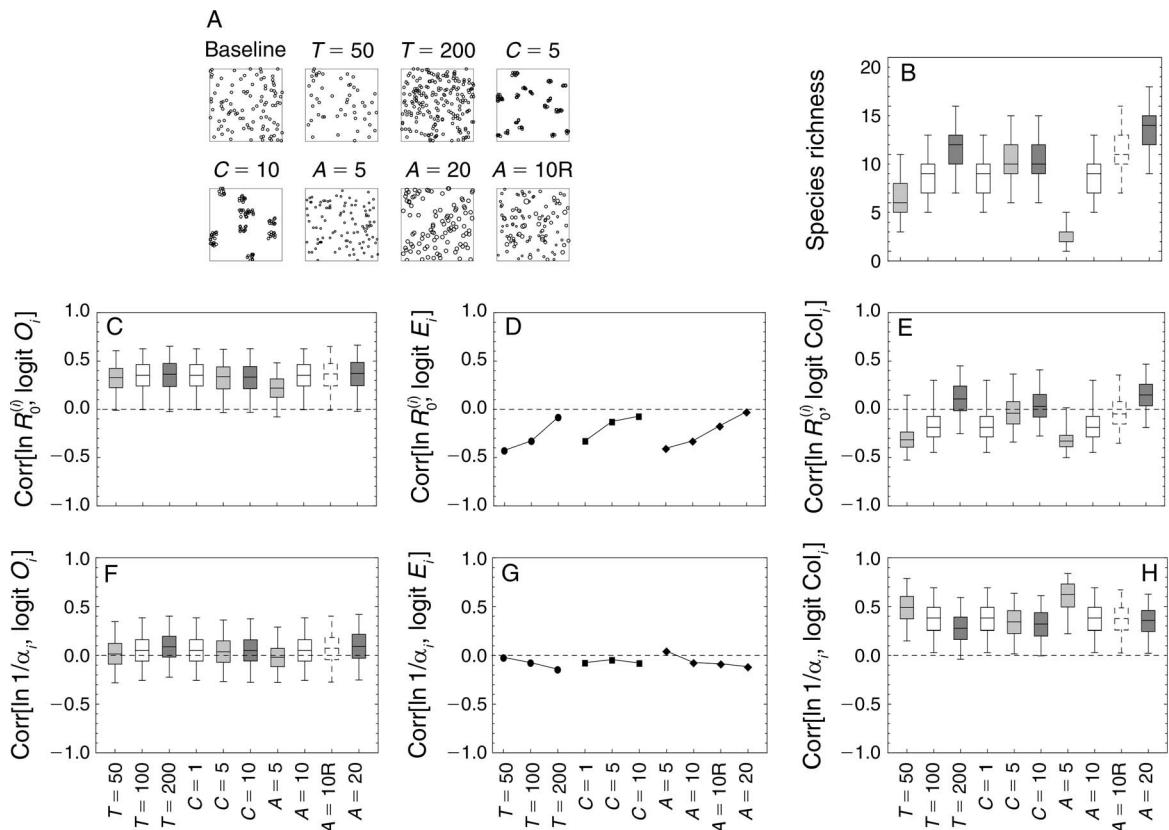


FIG. 3. Simulated impact of habitat configuration on metacommunity dynamics within a hypothetical area of 1 km². Panel (A) illustrates eight typical habitat configurations, where the tree crowns are represented as circles, and the baseline scenario is based on distributing $T=100$ trees of crown area $A=10$ m² randomly with cluster size $C=1$. Alternative scenarios are specified by varying the values of one of the three parameters, while keeping the other two parameters at their baseline values. The crown area $A=10R$ (dashed boxes in panels B, C, E, F, and H) refers to the random distribution of the crown areas with mean 10 m². In panels (B, C, E, F, and H), scenarios based on values smaller than those used in the baseline scenario are shown by lighter gray boxes, whereas scenarios based on larger values are shown by darker boxes. The baseline scenario is always indicated in white. Metacommunity dynamics were simulated for each scenario for 10 years for each of 2000 replicates. The box-whiskers in panels (B, C, E, F, and H) show the 50% and 95% central intervals, and the middle horizontal lines refer to the medians. The y-axes in panels (C–H) are the correlations $\text{Corr}[\ln X_i, \text{logit } Y_i]$ for 24 species between the properties of the species ($X_i = R_0^{(i)}$ and $1/\alpha_i$ corresponding to basic reproduction number and dispersal ability, respectively) and the properties of the observed dynamics ($Y_i = O_i, E_i$, and Col_i corresponding to tree occupancy, regional extinction probability and per capita colonization probability, respectively).

the movement data available for inconspicuous taxa such as adult galling and leaf-mining insects are mostly anecdotal (Hough 1951, Pfützenreiter and Weidner 1958; see Augustin et al. [2009] and Schönrogge et al. [2012] for estimates of long-distance dispersal of invasive leaf miners and galls, respectively). Our claim that movement behavior will vary substantially among species is also supported by results from mark–release–recapture experiments on butterflies (Baguette et al. 2000) and macro-moths (Nieminen 1996, Slade et al. 2013) and observational data on variable rates of range expansion of invasive gall wasps in Britain (Schönrogge et al. 2012). Nonetheless, neither we nor Slade et al. (2013) found any more similar movement behavior among species more closely related with each other than among taxonomically distant species. This result seems at odds with the intuitive expectation that related or

morphologically similar species would disperse in similar ways, but matches a recent review showing that phylogeny, morphology, feeding ecology, and voltinism are indeed weak predictors for dispersal ability in butterflies (Sekar 2012). When combined, the patterns uncovered by us and by previous studies thus suggest that morphological, ecological, and life-history traits alone may be uninformative for understanding the dispersal and spatial dynamics of plant-feeding insects in natural landscapes.

Species do not affect each other's distribution

Our model assumes no interspecific interactions, yet generated co-occurrence patterns largely consistent with those in the data: our examination of model residuals revealed no strong signs of associations beyond those generated by independent spatially structured processes

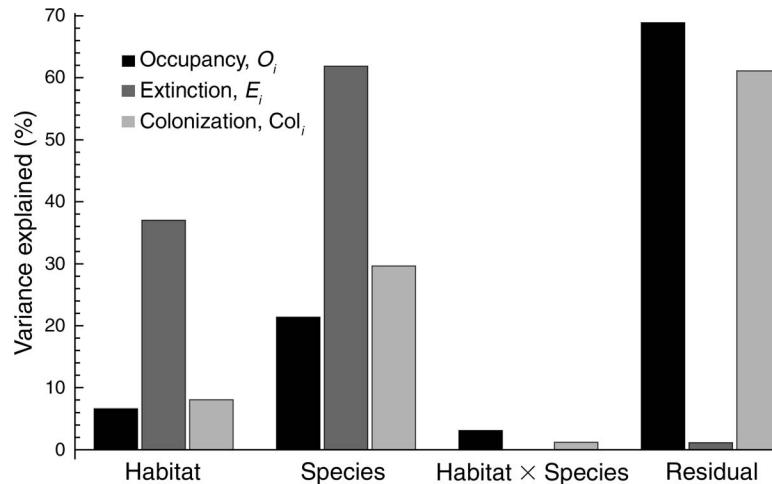


FIG. 4. Percentage of variation in simulated metacommunity patterns and processes attributable to landscape structure and species identity, respectively. Bar shades correspond to the three response variables: tree occupancy (black), regional extinction probability (dark gray), and per capita colonization probability (light gray). The heights of the bars show the percentage of variation attributed to habitat configuration, species identity and their interaction, respectively. Thus, for each shade, the columns (Habitat, Species, Habitat \times Species, and Residual) add up to 100%. The eight landscapes compared are depicted in Fig. 3A; the 24 species are described in Appendix A: Table A1.

operating within each species. This pattern offers support for the notion that species-specific spatial dynamics may go a long way toward understanding communities building up in spatially heterogeneous landscapes (Gripengberg et al. 2008). However, the approach of inferring species interactions from correlation matrices does come with a caveat, because any pattern-based approach may mix imprints of several different processes, e.g., from environmental filtering, competitive interactions among species, and indirect effects mediated by the wider community (cf. Loreau and de Mazancourt 2008). Nonetheless, in the current study system, the low correlations among taxa reported here match the outcomes of previous studies: targeting the same oak-associated taxa, we refuted with controlled experiments the importance of biotic interactions in explaining spatiotemporal community patterns. Factors relegated to a secondary role by both direct observations and experiments include direct resource competition (Tack et al. 2009), indirect competition mediated by the host plant (Tack et al. 2009), and apparent competition as mediated by parasitoids (Tack et al. 2011, Kaartinen and Roslin 2013).

From another perspective, the observed lack of interspecies correlations also indicates that species do not respond, or respond differently, to variation in quality among individual trees. Again, this observation matches previous work demonstrating that proposed correlates to tree quality (such as tree phenology, secondary chemicals, and bottom-up effects of host plant genotype) fail to stamp a coherent imprint on the distribution of our focal species (Tack et al. 2010, Tack and Roslin 2011 and references therein). Thus, what regulates the population abundances of the herbivore

species in our system (and other related plant–herbivore systems) does partly remain a conundrum. Important avenues for further research include investigating how spatial and temporal variation in climate, plant traits, and other local abiotic and biotic environmental drivers affect the dynamics and distribution of both the current and other plant-based metacommunities.

Habitat configuration and species identity explain incidence patterns, regional extinction, and per capita colonization rate

An advantage of the Bayesian state-space model is that it can be used to forecast how communities will respond to a change in the landscape. Our simulations revealed a strong impact of habitat configuration on the species richness of the insect community. As expected, increasing the number or the size of habitat patches (here, tree crowns) will result in more species thriving in the landscape, and in more species-rich local communities. Somewhat less trivially, the distribution of these patches will also affect species richness, with more species sustained by more aggregated patches, and more species in landscapes with variable, as compared to constant, patch sizes. Importantly, our results indicate that species identity and habitat configuration jointly explain a major part of the variation in species incidence, regional extinction, and per capita colonization, thereby emphasizing that species-specific variation in life history and movement plays a key role in spatial dynamics. Importantly, our finding rejects an assumption of the neutral model that is rarely challenged by ecologists: that dispersal is a neutral process without consequences at the community level (Lowe and McPeck 2014). Although changes in habitat configuration influenced

species richness, this did not result in major changes in the relative occupancy rates of individual species (i.e., there was no interaction between habitat configuration and species identity). A species rare in a given landscape is then likely to remain so even if the landscape changes, and vice versa for common species, an insight with major consequences for conservation biology.

Conclusions

Our findings have implications for metacommunity theory, conservation, and management.

In terms of metacommunity theory, we have responded to the plea of Winegardner et al. (2012), who called for the quantification of the very processes that generate empirically observable patterns across natural metacommunities. This was achieved by disentangling the relative effects of species-specific differences in life history and movement, and variation in habitat configuration.

From an applied perspective, our results imply that by changing the distribution of host trees, we may change both the persistence and dynamics of herbivores and also, consequently, their impact on the fitness of the host trees. Thus, our study suggests that the spatial structure of host plants may leave a strong imprint on local insect communities, and that changes in landscape configuration may modify the species richness and community composition of communities building up in different parts of the landscape.

Overall, we hope that our integration of empirical estimates, processes, and patterns will stimulate the development of synthetic and realistic theory. Although ecologists have spent nearly half a century debating which species interactions structure communities of plant-feeding insects (Hairston et al. 1960, Murdoch 1966, Kaplan and Denno 2007, Tack et al. 2009), our study seems to point at the easy way out: maybe, just maybe, life-history variation, dispersal limitation, and species-specific movement behavior may explain many of the patterns observed in nature?

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SUPPLEMENTAL MATERIAL

Ecological Archives

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