

Hierarchical Metapopulation Dynamics of Two Aphid Species on a Shared Host Plant

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ABSTRACT: We modeled hierarchical multiscale colonization-extinction dynamics of two aphid species living in a shared host plant. We parameterized the model with data collected at the level of individual ramets of the host plant, with the plants being organized as groups within islands. As expected, the extinction rates and per capita colonization rates decreased with increasing spatial scale. The per capita colonization rates were greater for winged than for unwinged individuals, but as the unwinged individuals were much more abundant, they actually performed most of the colonizations. Colonizations and extinctions were negatively correlated, so that when the colonization rate in a given island was high, the extinction rate in the same island was low. There was a clear indication of interspecific interaction, with the presence of one species increasing the extinction rate and decreasing the colonization rate of the other species. Further simulation results based on the parameterized model show a contrasting pattern between the two species, with *Metopeurum fuscoviride* (with relatively stable dynamics) being favored by a highly aggregated distribution of the ramets, whereas for *Macrosiphoniella tanacetaria* (with a high turnover rate), an equally high persistence time follows if the plants are distributed in a segregated manner over several islands.

Keywords: multiscale metapopulation, *Metopeurum fuscoviride*, *Macrosiphoniella tanacetaria*, Bayesian modeling.

Introduction

Spatial scale is a central concept in ecology (Levin 1992, 2000). Intra- and interspecific interactions across multiple scales shape the dynamics and diversity of metacommunities (Cadotte and Fukami 2005; Rahbek 2005). To understand how patterns observed in the field result from biological processes operating at various spatial scales, it is necessary to make simultaneous observations in a hierarchy of scales (Noda 2004; Heikkinen et al. 2007). Examples of observational and experimental multiscale ap-

proaches include research on dendritic networks formed by rivers with their tributaries (Lowe et al. 2006; Grant et al. 2007) and nested hierarchical patch networks in both terrestrial and freshwater systems (Lancaster and Belyea 1997; Fagan et al. 2005).

Despite the steadily increasing number of empirical multiscale studies, very few studies have explicitly accounted for the hierarchical structure of the data in the analysis phase. For example, most of the published approaches ignore correlations across scales (Benedetti-Cecchi 2001; Borcard et al. 2004; Keitt and Urban 2005). One approach to model hierarchically structured data is the use of hierarchical linear models (Gelman and Pardoe 2006). These models provide a flexible framework for making inferences about ecological processes across scales of organizations (Berk and de Keeuw 2006; McMahon and Diez 2007) and can account for correlation structures caused by environmental factors operating at different scales.

In the context of metapopulation dynamics, the spatial distribution of a species results from a combination of extinctions of local populations and colonizations of previously unoccupied habitat. Colonizations are the result of dispersal, so an aggregated occupancy pattern can result simply from distance-dependent dispersal. On the other hand, synchronous colonizations can also be triggered by favorable environmental conditions that may simultaneously affect a scale smaller or larger than that of typical dispersal distances (Liebhold et al. 2004; Weisser and Härrä 2005). In the case of extinctions, a local population occupying a given spatial unit may become extinct because of an extinction mechanism operating at the scale of the population or at any scale larger than that of the population. The population may also become extinct if several events leading to local extinctions take place simultaneously at scales smaller than that of the population. Since extinction and colonization patterns in observational data can be affected simultaneously by a number of processes, a particular challenge for the analysis is to disentangle the

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extinction and colonization rates that operate intrinsically at different spatial scales. Most analyses have simply described the observed total rates at a given level because of the difficulties in distinguishing the contributions of each spatial scale (Hartley and Kunin 2003; Fagan et al. 2005; Weisser and Härrä 2005).

In this article, we study the colonization-extinction dynamics of two specialist aphid species at four spatial scales: the aphid populations occupy individual ramets of the host plant, the host plants form well-defined groups, and such groups are found on several islands (fig. 1; Weisser and Härrä 2005). We analyze data on within-season dynamics with a spatially nested hierarchical metapopulation model, defined in terms of colonization and extinction rates operating specifically at each spatial level. These scale-specific rates sum to total colonization and extinction rates, enabling us to link the model to data using Bayesian inference.

Because both colonizations and extinctions are ultimately driven by births, deaths, and movements of individuals, these two processes are likely to be correlated with each other. One possibility is that there would be variation in the general suitability among different sites, with high-quality sites having higher colonization rates and lower extinction rates than low-quality sites. Such a mechanism would produce a negative correlation between extinction and colonization rates. The correlation could be either of permanent nature (e.g., due to a permanent difference in habitat quality) or of temporary nature (e.g., due to temporal variation in host plant quality driven by weather conditions). A positive correlation between extinctions and colonizations could follow if the individuals would move between the habitat patches so that an apparent extinction would be followed by a colonization in a nearby location. To tease these possibilities apart, we combined extinction and colonization models through random effects representing permanent and temporary variation among the islands. Based on the above reasoning, we hypothesized that there could be negative permanent, negative temporary, or positive temporary correlation between colonizations and extinctions.

Material and Methods

Study Species

The common tansy (*Tanacetum vulgare* L., Asteraceae) is a perennial composite native to Europe and Asia that occurs mainly along rivers and on wastelands. Tansy propagates by both sexual and asexual reproduction. Plants grow up to a length of 1.70 m, and a single genet plant may consist of up to several hundred ramets (shoots). In most cases, genets can be clearly delineated in the field. *Metopeurum fuscoviride* Stroyan (henceforth MF) is a

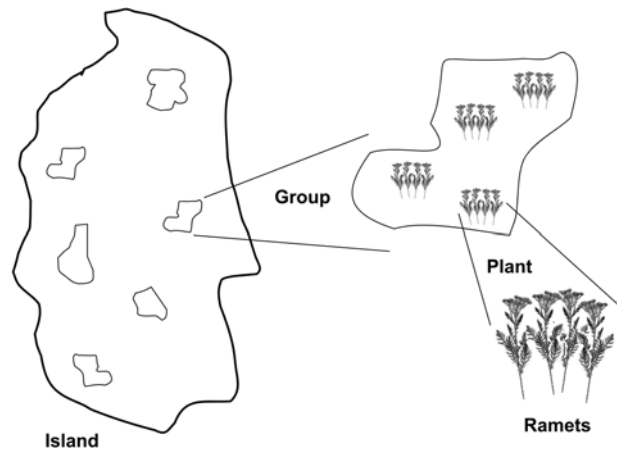


Figure 1: An illustration of the hierarchical structure of the study design. The Tvärminne study area consists of eight real islands, whereas the Basel study area consists of two study sites (called islands for notational simplicity).

monophagous aphid species that feeds exclusively on tansy and is obligatorily ant-tended (Flatt and Weisser 2000). *Macrosiphoniella tanacetaria* Kaltenbach (henceforth MT) is an oligophagous aphid species feeding mainly on tansy but also on some relatives of tansy, such as *Chrysanthemum* spp. and *Matricaria* spp., which were not common in the study areas. Both species are cyclical parthenogens in which several asexual generations are followed by a single sexual generation in autumn. Females of the sexual generation lay eggs near the host plants. First-generation females hatch the following spring and colonize the newly sprouting ramets of the same genet where they originated. In both species, there is no host alternation; that is, the entire life cycle takes place on tansy. Aggregations (colonies) of both aphid species form below the inflorescence of a ramet. At the level of a genet, there may be as many aphid colonies as there are ramets.

During the parthenogenetic phase, most females of both species are unwinged. Dispersal by unwinged females occurs mainly within a genet because the chance of colonizing adjacent genets is very low given the high risk of predation off the plant. Winged females occur in early summer and can colonize other genets. Both males and females of the sexual generation are unwinged in MF, whereas sexual females are unwinged and males are winged in MT.

Study Areas

Our main study area is located in the Tvärminne archipelago (59°50'N, 23°14'E), in the immediate vicinity of Tvärminne Zoological Station of the University of Hel-

sinki. In addition to appearing on the mainland, tansy occurs on islands in the archipelago, allowing the study of aphid metapopulation dynamics not only at the level of ramets and genets but also at the level of plant groups and entire islands. Two genets growing at most 5 m apart were considered to belong to the same group, with the criteria based on the assumption that unwinged aphids are unlikely to disperse farther than this distance. In June 2001, eight islands were chosen as the study sites (Weisser and Härrä 2005). All ramets on these islands (7,032 ramets in 679 genets) were numbered and inspected weekly from June 20 (week 1) until September 13 (week 13), 2001, after which most aphid colonies disappeared. If a ramet was colonized by aphids, it was marked uniquely and the size of the colony and the fraction of winged aphids were estimated, the latter of which we averaged over each island to obtain more reliable estimates. Because our aim was to determine the fate of undisturbed aphid colonies, no samples were taken in the field. Full details on the sampling procedures and a general description of the aphid population dynamics are given by Weisser (2000), Massonnet et al. (2002), and Weisser and Härrä (2005).

To examine the robustness of our results, we repeated the analysis for an independent data set acquired near Basel, Switzerland, in 1997. In the Basel study area (47°34'N, 7°36'E), two sites (which we will call islands for notational consistency with the Tvärminne data) were chosen along the Rhine River (Weisser 2000), and 107 genets with 2,651 ramets were marked and inspected every week for the occurrence of *M. fuscoviride* and *M. tanacetaria*. The study continued for the entire season, from the hatching of the first aphid eggs in spring on May 8 (week 1) until the last aphid colony became extinct on November 26 (week 29). Due to a relatively uniform distribution of host plants, the Basel data lack the group level.

The Hierarchical Metapopulation Model

We model the data using a hierarchical approach with four spatial levels: islands, plant groups (to be called simply groups), plants (i.e., genets), and ramets (fig. 1). We use I_i to denote island i , G_{ij} to denote group j on this island, P_{ijk} to denote plant k in this group, and R_{ijkl} to denote ramet l in this plant. The occupancy state of a given unit X (we use X as a generic variable standing for a particular island, group, plant, or ramet) by species s is denoted by $y_X(t; s) \in \{0, 1\}$, with value 1 indicating that species $s \in \{\text{MT}, \text{MF}\}$ was present in unit X at time t and value 0 indicating that this was not the case. We abbreviate $y_X(t; s)$ to $y_X(t)$ if there is no ambiguousness of the species s . The data consist of a time series of the presence-absence of each species on each ramet with a weekly resolution. We next detail the submodels for extinction and coloni-

zation dynamics, after which we describe how the two models are coupled with each other.

Extinction Dynamics

Extinctions can be caused by a number of processes operating at different spatial scales. A ramet-level extinction might be caused by a predator finding the local population, whereas a group-level extinction might be caused by the host plants becoming unsuitable, for example, due to drought. Rather than attempting to identify the underlying causal mechanisms, we assume that processes leading to local extinction can operate at all four spatial levels, and we quantify the relative roles of these processes.

We use $e_X(t)$ to denote the probability that an event operating intrinsically at the scale of the unit X wipes out the local population from that unit during the time interval $(t-1, t]$. The unit X may also become extinct because there is an extinction event at the larger unit to which it belongs or because there are simultaneous extinction events operating at all occupied subunits of the unit X . Using $\hat{e}_X(t)$ to denote the probability by which unit X becomes extinct due to events operating at the scale of X or at smaller scales, we have the following relationships:

$$\begin{aligned}\hat{e}_{R_{ijkl}}(t) &= e_{R_{ijkl}}(t), \\ \hat{e}_{P_{ijk}}(t) &= e_{P_{ijk}}(t) + (1 - e_{P_{ijk}}(t)) \prod_{l|y_{R_{ijkl}}(t-1)=1} \hat{e}_{R_{ijkl}}(t), \\ \hat{e}_{G_{ij}}(t) &= e_{G_{ij}}(t) + (1 - e_{G_{ij}}(t)) \prod_{k|y_{P_{ijk}}(t-1)=1} \hat{e}_{P_{ijk}}(t), \\ \hat{e}_{I_i}(t) &= e_{I_i}(t) + (1 - e_{I_i}(t)) \prod_{j|y_{G_{ij}}(t-1)=1} \hat{e}_{G_{ij}}(t).\end{aligned}\quad (1)$$

Field observations and the data considered here suggest that extinction rates do not remain constants but may vary in both space and time. We model spatiotemporal variation in the ramet-level extinction rates among the islands as

$$\text{logit}[e_{R_{ijkl}}(t)] = \mu_R^E + \beta_{s_1 \leftarrow s_2}^E y_{R_{ijkl}}(t-1; s_2) + \varepsilon_i^E(t), \quad (2)$$

where $\text{logit}(x) = \ln[x/(1-x)]$, μ_R^E is the mean value, $\varepsilon_i^E(t)$ is the island-level random effect, and $\beta_{s_1 \leftarrow s_2}^E$ measures the effect of species s_2 on the extinction probability of the focal species s_1 . We note that spatiotemporal variation may be present also at other hierarchical levels, but we limit the complexity of the model by assuming that the intrinsic extinction probabilities at the levels of island, group, and plant are constants, that is, that $e_{I_i}(t) = e_I$, $e_{G_{ij}}(t) = e_G$, and $e_{P_{ijk}}(t) = e_P$.

Colonization Dynamics

We model three distinct types of colonizations: primary colonizations by winged (indicated by superscript W) or unwinged (superscript U) aphids and secondary colonizations by offspring of the primary colonizer (superscript O).

Primary colonizations are the result of aphids dispersing from existing populations to empty ramets. We use $N_{R_{ijkl}}^A(t)$ (with $A \in \{U, W\}$) to denote the numbers of such unwinged and winged aphids that arrive at the focal ramet R_{ijkl} during the time interval $(t - 1, t]$ and would be successful in colonizing it if the ramet was still unoccupied. These random variables depend on the sizes of the source populations, the per capita emigration probability, the probability of successful migration, and the probability of population establishment. We take the patch-occupancy approach by assuming that population size (including winged and unwinged individuals) in occupied ramets is constant, but we allow the per capita emigration probabilities to be different between winged and unwinged aphids.

We denote the expected numbers of unwinged and winged aphids that emigrate from the occupied ramet R_{ijkl} and move successfully (i.e., will colonize the ramet if still unoccupied) to another ramet in the same plant with $(1 - \nu_i(t))\phi_R^U(t)$ and $\nu_i(t)\phi_R^W(t)$, where the ϕ_R^A (with $A \in \{U, W\}$) are model parameters and $\nu_i(t)$ is the estimated fraction of winged aphids in the source population. We assume that unwinged and winged aphids can also colonize ramets of other plants in the same group (with parameters ϕ_p^A , $A \in \{U, W\}$) and that winged aphids can additionally colonize ramets in different groups (ϕ_g^W) or in different islands (ϕ_I^W). We assume that a dispersing aphid randomly selects the target island among all islands (if dispersing to a different island) first, then the target group within that island (if dispersing to a different group), then the target plant within that group (if dispersing to a different plant), and finally the target ramet within the plant.

The expectation of $N_{R_{ijkl}}^A(t)$ (with $A \in \{U, W\}$), denoted by $\bar{N}_{R_{ijkl}}^A(t)$, is obtained by summing the number of aphids that are expected to move to the focal ramet R_{ijkl} over all source populations. The number of aphids arriving at a given ramet is a sum of many Bernoulli-distributed random variables, each having a small mean so it can be approximated to follow the Poisson distribution (Grimmett and Stirzaker 2001). Summing over the Poisson distribution for the number of immigrating aphids shows that the probability by which the ramet R_{ijkl} will be colonized by a primary colonizer is $C_{R_{ijkl}} = 1 - \exp(-M_{ijkl}(t))$, where $M_{ijkl}(t)$ is the expected number of primary colonizers arriving to ramet R_{ijkl} . We incorporate the effects of environmental variation and interspecific interaction as

$$\log(M_{ijkl}(t)) = \log(\bar{N}_{R_{ijkl}}^U(t) + \bar{N}_{R_{ijkl}}^W(t)) + \beta_{s_1 \leftarrow s_2}^C y_{R_{ijkl}}(t - 1; s_2) + \varepsilon_i^C(t), \quad (3)$$

where $\varepsilon_i^C(t)$ is the island-level random effect and $\beta_{s_1 \leftarrow s_2}^C$ measures the effect of species s_2 on the colonization probability of the focal species s_1 . We note that while we used the logit-link function for the extinction probability (eq. [2]), $M_{ijkl}(t)$ can take any positive value, so here we used the log-link function.

The generation time of aphids is of the order of 10 days, and it is possible that an aphid that colonizes a ramet may produce offspring that generate secondary colonizations within one time step of the model (1 week). Without such secondary colonizations, it would be very unlikely that many ramets of a plant would become simultaneously colonized if the plant was originally located in an empty group or an empty island. Analogously to our model of primary colonization, we use $N_{R_{ijkl}}^O(t)$ to denote the number of secondary colonizers that move to the focal ramet R_{ijkl} during the time interval $(t - 1, t]$. Since these individuals are young and there is limited time for dispersal within one time step, we assume that secondary colonizations occur only within the ramets of the same plant. We denote the expected number of successful offspring colonizers (per primary colonizer) with ϕ_R^O and assume that these individuals randomly select the target ramet. The expectation of $N_{R_{ijkl}}^O(t)$, denoted by $\bar{N}_{R_{ijkl}}^O(t)$, is obtained as a sum over the newly established source colonies in the plant k , and the probability of the ramet R_{ijkl} being colonized by the offspring of the primary colonizer is $C_{R_{ijkl}}^O = 1 - \exp[-\bar{N}_{R_{ijkl}}^O(t)]$. For simplicity here, we ignore the potential effects of spatiotemporally varying environmental conditions and interspecific interactions.

Coupling the Extinction and Colonization Dynamics

In the two submodels described above, the random effects $\varepsilon_i^E(t)$ and $\varepsilon_i^C(t)$ represent island-level environmental variation affecting the ramet-level extinction and colonization processes. We model these random effects as a sum of three variance components, so that

$$\varepsilon_i^E(t) = T^E(t) + S_i^E + (S \times T)_i^E(t),$$

$$\varepsilon_i^C(t) = T^C(t) + S_i^C + (S \times T)_i^C(t).$$

Here the terms T , S , and $S \times T$ represent temporal, spatial, and spatiotemporal variation. We assume that all of the three variance components follow normal distributions with zero means and denote the standard deviations with σ_Z^Y , where $Z \in \{T, S, S \times T\}$ and $Y \in \{C, E\}$. We couple the extinction and colonization submodels by assuming that the spatial and spatiotemporal random effects have a

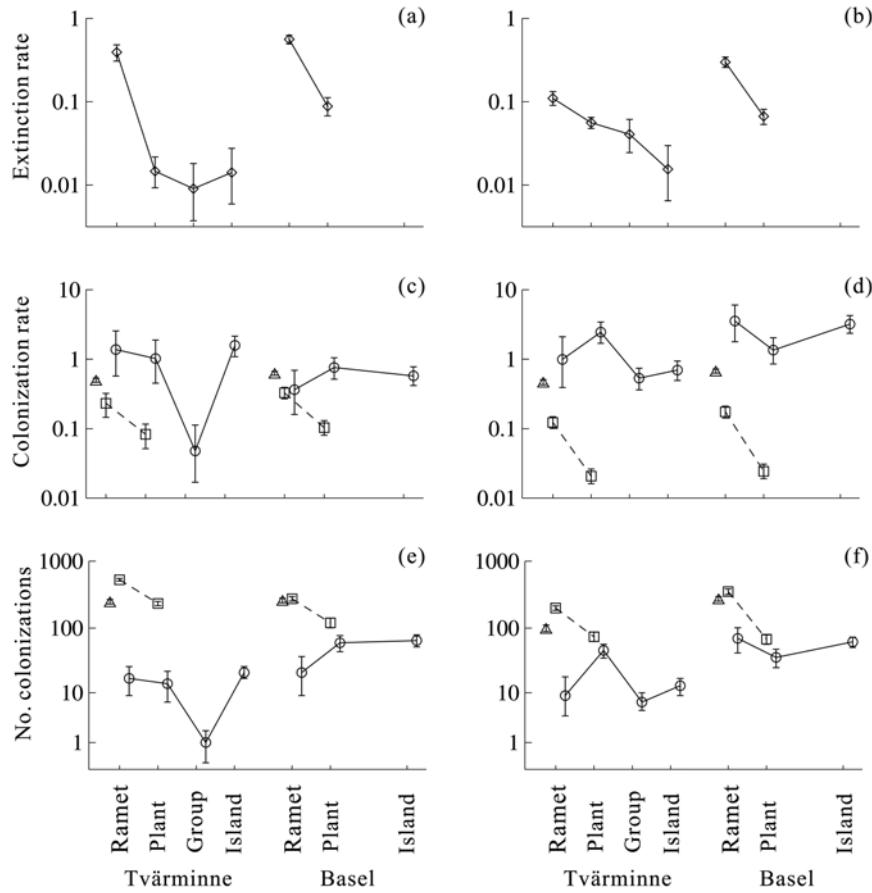


Figure 2: Posterior distributions of extinction and colonization parameters. *a, b*, Extinction rate parameters (μ_R^E , e_p , e_G , and e_I); *c, d*, colonization rate parameters (ϕ_R^O , ϕ_R^U , ϕ_P^U , ϕ_P^W , ϕ_P^W , ϕ_G^W , and ϕ_I^W). *e, f*, For the two study areas, the number of ramets colonized by individuals originating from another ramet in the same plant, another plant in the same group, another group in the same island, or another island. *c–f*, Boxes correspond to unwinged aphids, circles to winged aphids, and triangles to secondary colonizations by the offspring of the primary colonizer. *a, c, and e* correspond to MT (*Macrosiphoniella tanacetaria*); *b, d, and f* correspond to MF (*Metopeurum fuscoviride*). The symbols represent the median estimates, and the bars span the 50% central posterior intervals.

joint covariance structure, $\text{Cov}[S_i^E, S_i^C] = \rho_S \sigma_S^E \sigma_S^C$ and $\text{Cov}[(S \times T)_i^E(t), (S \times T)_i^C(t)] = \rho_{(S \times T)} \sigma_{(S \times T)}^E \sigma_{(S \times T)}^C$, where ρ_S and $\rho_{(S \times T)}$ denote the correlation coefficients.

Parameter Estimation and Model Fit

We estimated the parameters of the model using a Bayesian approach. To do so, we derive expressions for the likelihood of the data (app. A in the online edition of the *American Naturalist*). We used uniform distributions in $[0, 1]$ for the extinction probabilities (e_p , e_G , e_I); exponential distribution with mean = 100 for colonization parameters (ϕ_R^O , ϕ_R^U , ϕ_P^U , ϕ_P^W , ϕ_P^W , ϕ_G^W , ϕ_I^W); uniform distribution in $[-1, 1]$ for the correlation coefficients (ρ_S , $\rho_{(S \times T)}$); normal distribution $N(0, 100)$ for μ_R^E , β^E , and β^C ; and a half-Cauchy distribution with scale parameter 0.5 for the stan-

dard deviations (σ_Z^Y , where $Z \in \{T, S, S \times T\}$ and $Y \in \{C, E\}$). Because the prior used for the variance components is likely to influence the results (Gelman 2006), we tested the sensitivity of our results to this choice of the prior by setting the scale parameter of the half-Cauchy distribution to 0.25 or to 1.0.

We computed the posterior distribution separately for each of the four data sets. The posteriors were sampled using a Markov chain Monte Carlo (MCMC) approach implemented with Mathematica 6.0 (Wolfram, Champaign, IL) as described in detail in appendix B in the online edition of the *American Naturalist*.

We examined the validity and performance of the estimation scheme by generating simulated data with hypothetical parameter values and by estimating the model parameters back from the simulated data (for details, see

Table 1: Statistical support for scale dependency in extinction and colonization rates, colonizer type dependency in colonization rates, and extinction and colonization rates being modified by the presence of the other species

| | Tvärminne | | Basel | |
|---|-----------|------|-------|------|
| | MT | MF | MT | MF |
| Scale dependency in extinction rates: | | | | |
| $\text{logit}(e_p) < \mu_R^E$ | >.99 | .95 | >.99 | .99 |
| $e_G < e_p$ | .65 | .67 | ... | ... |
| $e_I < e_G$ | .39 | .78 | ... | ... |
| Scale dependency in colonization rates: | | | | |
| $\phi_P^U < \phi_R^U$ | >.99 | >.99 | >.99 | >.99 |
| $\phi_P^W < \phi_R^W$ | .62 | .15 | .22 | .89 |
| $\phi_G^W < \phi_P^W$ | .98 | >.99 | ... | ... |
| $\phi_I^W < \phi_G^W$ | <.01 | .36 | ... | ... |
| Colonizer type dependency in colonization rates: | | | | |
| $\phi_R^U < \phi_R^O$ | .97 | >.99 | .96 | >.99 |
| $\phi_R^O < \phi_R^W$ | .78 | .71 | .29 | .93 |
| $\phi_R^U < \phi_R^W$ | .94 | .91 | .54 | .99 |
| $\phi_P^U < \phi_P^W$ | .98 | >.99 | .99 | >.99 |
| Effect of interspecific interactions on extinction and colonization rates: | | | | |
| MT : $\beta_{MT \leftrightarrow MF}^E > 0$; MF : $\beta_{MF \leftrightarrow MT}^E > 0$ | .97 | .98 | .61 | >.99 |
| MT : $\beta_{MT \leftrightarrow MF}^C < 0$; MF : $\beta_{MF \leftrightarrow MT}^C < 0$ | >.99 | .85 | >.99 | .96 |

Note: The values show the posterior probabilities of the statements being true. See text for definition of terms.

app. B). To focus on a biologically plausible parameter range, we used the data structure corresponding to real data on the species MF at the Tvärminne study area and generated the simulated data using parameter values similar to the ones estimated from the real data. The resolution in these data allow one to identify all fixed effects and the variance parameters of the random effects in a relatively accurate and unbiased manner.

We tested the model fit by examining whether and how the posterior predictive data differed from the real data (app. B). Summing over all four data sets, 354 out of 364 (97.3%) of the real data points (ramet-level colonization or extinction events) fell within their 95% posterior predictive central intervals, indicating that the structural assumptions of the model were in line with the data.

Results

As expected, the extinction rates operating specifically at a given spatial scale generally decreased with increasing scale (fig. 2*a*, 2*b*; table 1). Most clearly, for both species and both study sites, extinction events operating at the scale of ramets were much more frequent than those operating at the scale of plants. Scale mattered also for colonizations, with unwinged aphids being much more likely to colonize ramets of their natal plant than ramets of other plants (fig. 2*c*, 2*d*; table 1). For winged aphids, there was

no consistent difference between colonizations at the ramet and plant levels, but for the species MT, the probability of colonizing ramets in another group was much lower than the probability of colonizing ramets within the same group. Somewhat surprisingly, for the species MT, the

Table 2: Statistical support for differences between the two species in the extinction and colonization rates and for asymmetry in interspecific interactions

| | Tvärminne | Basel |
|---|-----------|-------|
| Extinction rates: | | |
| $\mu_R^E(\text{MT}) < \mu_R^E(\text{MF})$ | .02 | .06 |
| $e_p(\text{MT}) < e_p(\text{MF})$ | >.99 | .28 |
| $e_G(\text{MT}) < e_G(\text{MF})$ | .88 | ... |
| $e_I(\text{MT}) < e_I(\text{MF})$ | .52 | ... |
| Colonization rates: | | |
| $\phi_R^O(\text{MT}) < \phi_R^O(\text{MF})$ | .34 | .71 |
| $\phi_R^U(\text{MT}) < \phi_R^U(\text{MF})$ | .21 | .10 |
| $\phi_R^W(\text{MT}) < \phi_R^W(\text{MF})$ | .43 | .94 |
| $\phi_P^U(\text{MT}) < \phi_P^U(\text{MF})$ | .07 | .02 |
| $\phi_P^W(\text{MT}) < \phi_P^W(\text{MF})$ | .80 | .75 |
| $\phi_G^W(\text{MT}) < \phi_G^W(\text{MF})$ | .97 | ... |
| $\phi_I^W(\text{MT}) < \phi_I^W(\text{MF})$ | .15 | .98 |
| Interspecific interactions: | | |
| $\beta_{MT \leftrightarrow MF}^E < \beta_{MF \leftrightarrow MT}^E$ | .25 | >.99 |
| $\beta_{MT \leftrightarrow MF}^C < \beta_{MF \leftrightarrow MT}^C$ | .60 | >.99 |

Note: The values show the posterior probabilities of the statements being true. See text for definition of terms.

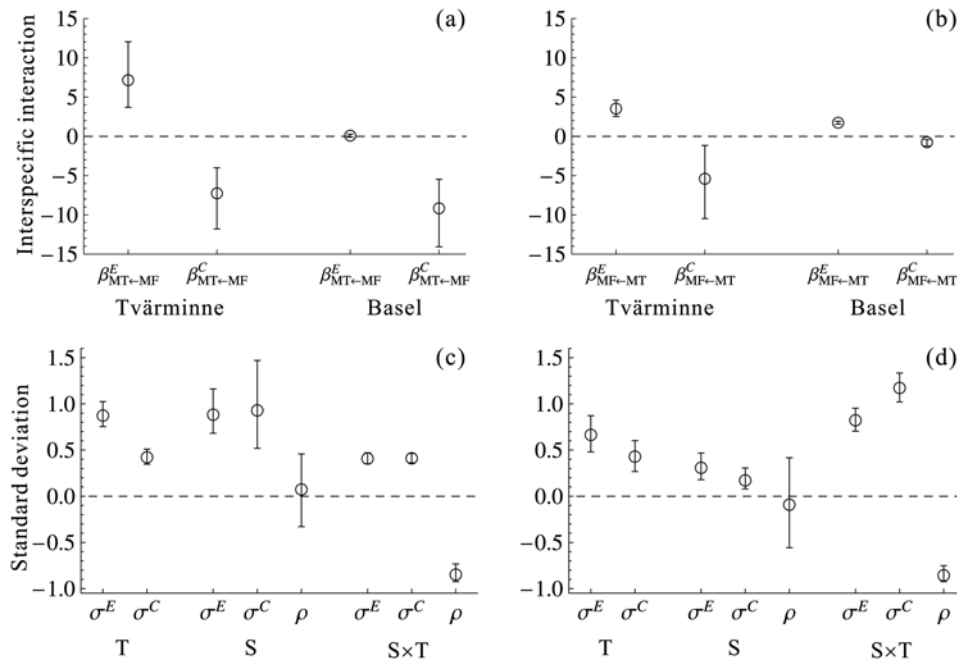


Figure 3: Parameter estimates for the effects of interspecific interactions (a, b) and the random effects (*Macrosiphoniella tanacetaria* [MT] in c and *Metopeurum fuscoviride* [MF] in d). c, d. Results from the Tvärminne study area only. The symbols represent the median estimates, and the bars span the 50% central posterior intervals.

group-level colonization rate was even lower than the island-level colonization rate. The colonization rates were generally much higher for winged aphids than for unwinged aphids. The rate of secondary colonization (per primary colonization) was higher than the primary colonization rate (per occupied ramet) for unwinged aphids but lower than the primary colonization rate for winged aphids.

The results of figure 2c, 2d refer to per capita colonization rates, but it is also interesting to ask how much a given process contributes to the total number of colonizations in the system. This question is addressed in figure 2e, 2f, which shows that for both species, winged aphids actually contributed only a minority of the colonizations, and hence, their high per capita colonization rate was over-compensated by the low number of winged individuals. For both species, a substantial fraction of all colonizations was caused by the offspring of the primary colonizers. If we classify the colonizations based on the distance from which the colonizer came from, the majorities of the colonizations took place within a plant. In the Tvärminne study area, the fraction of long-distance colonization events (the colonizer originating from a different group or a different island) was 2.1% for the species MT (95% central posterior interval 1.0%–3.6%), whereas it was 4.6% (2.2%–7.8%) for the species MF.

If we compare the two species, the ramet-level extinction rates were greater for the species MT than for the species MF, but at the scale of plants, the opposite was true (fig. 2a, 2b; table 2). In case of unwinged aphids, the species MT also had higher colonization rates than the species MF (fig. 2c, 2d; table 2). Given that our estimates for the colonization rates are per source population and that the population sizes were much lower for the species MT (median 13 in the Tvärminne study area and 5 in the Basel study area) than for the species MF (median 130 in the Tvärminne study area and 32 in the Basel study area), the per capita colonization rates of unwinged aphids were by far higher for the species MT. In contrast, the per-population colonization rates for the winged individuals tended to be higher for the species MF, though the evidence is somewhat mixed (fig. 2c, 2d; table 2).

There was a clear indication of the two species competing with each other such that the presence of one species generally increased the extinction rate and also decreased the colonization rate of the other species (table 1; fig. 3a, 3b). In the case of Tvärminne, the two species almost never co-occurred (three cases out of 5,005 occupied ramets), whereas in Basel, co-occurrence was much more common (69 out of 3,956). Thus, in Tvärminne, both species seemed able to prevent colonizations by the other species. In Basel, in contrast, there was an asymmetry between the

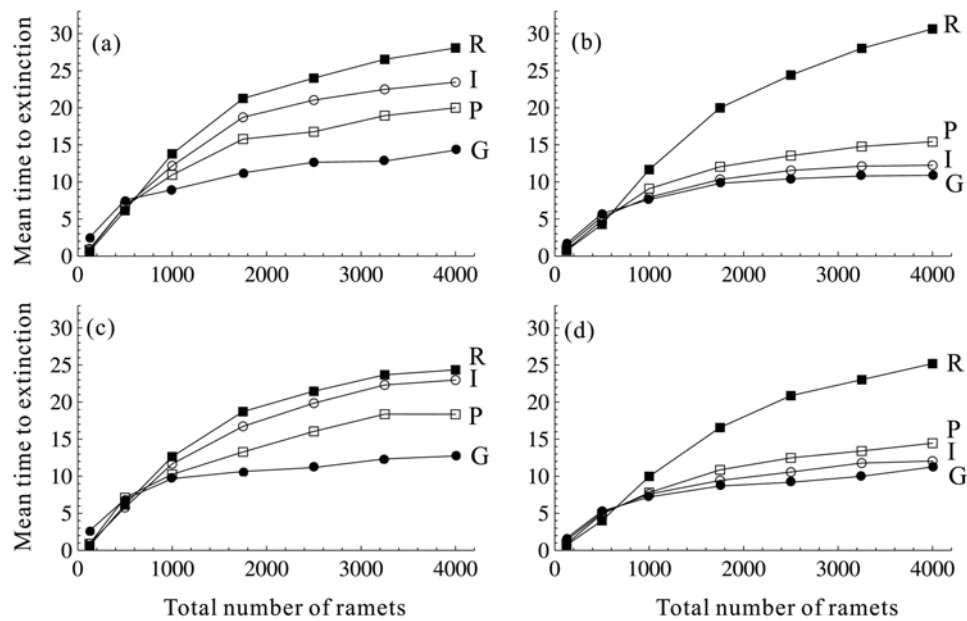


Figure 4: Mean time to metapopulation extinction as a function of the number and the distribution of ramets. *a* and *c* correspond to *Macrosiphoniella tanacetaria*, *b* and *d* to *Metopeurum fuscoviride*. *a* and *b* are based on the assumption that only the focal species is present, and *c* and *d* include the effect of interspecific interactions. Each of the lines corresponds to a different assumption on how the ramets are distributed in space. In the baseline model, there are five islands, five groups in each island, five plants in each group, and five ramets in each plant. The total number of ramets is varied by allowing one of these parameters to change, with the letter *I*, *G*, *P*, or *R* indicating which of the values is variable. Each point represents the mean value over 1,000 replicates. For a detailed description of the model, see appendix C in the online edition of the *American Naturalist*.

species (table 2), with MT unable to colonize sites occupied by MF but having only a limited impact on the colonization ability of MF. Due to the low number of co-occurrences, the Tvärminne data provide very little resolution to examine whether extinctions were triggered by interspecific competition. In the Basel data, the presence of MT increased the extinction rate of MF more than MF presence increased MT extinction rates.

As the Basel study area contains only two sites, there is not enough information to reliably quantify the spatio-temporal random effects, so we focus here on the Tvärminne data (fig. 3c, 3d). Temporal variation (variance component T), caused largely by seasonality, explained a considerable proportion of the total variation for both colonizations and extinctions. The colonizations and extinctions of the species MT were more affected by permanent variation than by temporary variation among the islands ($\Pr[\sigma_S^E > \sigma_{S \times T}^E] = 0.97$, $\Pr[\sigma_S^C > \sigma_{S \times T}^C] = 0.82$), whereas most of the variation for the species MF was classified as spatiotemporal ($\Pr[\sigma_{S \times T}^E > \sigma_S^E] = 0.93$, $\Pr[\sigma_{S \times T}^C > \sigma_S^C] > 0.99$). The spatiotemporal correlation coefficient $\rho_{S \times T}$ was negative for both species, but the posterior distribution for the permanent spatial correlation coefficient ρ_S remained largely uninformative.

The results reported here are not sensitive to the scale

parameter of the half-Cauchy distribution, except the estimates for the variance components (app. B). Changing the value of the scale parameter from 0.5 to 0.25 leads to the posterior probabilities $\Pr(\sigma_{S \times T}^E > \sigma_S^E) = 0.97$ and $\Pr(\sigma_{S \times T}^C > \sigma_S^C) > 0.99$ for species MF, while setting the scale parameter to 1.0 leads to $\Pr(\sigma_{S \times T}^E > \sigma_S^E) = 0.88$ and $\Pr(\sigma_{S \times T}^C > \sigma_S^C) = 0.99$.

Discussion

Much of the early work in metapopulation theory was based on spatially implicit models (e.g., Levins 1969, 1970; Hanski 1991), which assume that suitable habitat occurs in discrete patches, with the patches being identical in quality and equally connected to each other. These models have been extended to include a more realistic description of space using either a regular lattice (e.g., Durrett and Levin 1994; Keymer et al. 2000) or a patch-based description of the landscape (e.g., Ovaskainen 2002; Nicholson et al. 2006), both approaches making it possible to connect theoretical work to empirical data. In this work, we developed a multiscale approach by describing the distribution of the resource units (ramets) with the help of four hierarchical levels. Within each hierarchical level, we have ignored the actual spatial configuration and thus taken the