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Host–parasitoid evolution in a metacommunity

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Patch size and isolation are predicted to alter both species diversity and evolution; yet, there are few empirical examples of eco-evolutionary feedback in metacommunities. We tested three hypotheses about eco-evolutionary feedback in a gall-forming fly, *Eurosta solidaginis* and two of its natural enemies that select for opposite traits: (i) specialization and poor dispersal ability constrain a subset of natural enemies from occupying small and isolated patches, (ii) this constraint alters selection on the gall fly, causing phenotypic shifts towards traits resistant to generalist and dispersive enemies in small and isolated patches, and (iii) reduced dispersal evolves in small, isolated populations. We sampled patches in a natural metacommunity and found support for all hypotheses; *Eurosta*'s specialist wasp parasitoid attacked fewer galls in small and isolated patches, generating a selection gradient that favoured small galls resistant to predation by a dispersive and generalist bird predator. Phenotype distributions matched this selection gradient, and these phenotypic differences were maintained in a common garden experiment. Finally, we found lower dispersal abilities in small and isolated patches, a phenotypic shift that aids in the maintenance of local adaptation. We suggest that the trophic rank and the species traits of consumers are central to evolution in metacommunities.

1. Introduction

Ecological communities are commonly believed to reflect ongoing feedback between evolutionary dynamics and ecological interactions, yet empirical examples of these types of feedback have only been established for a handful of ecosystems [1,2]. Metacommunities and island-mainland systems describe distinct communities linked by dispersal that may be particularly prone to eco-evolutionary dynamics, owing to the potential for local adaptation, limited dispersal across ecologically distinct patches, and clear effects of species traits on their spatial distributions in these systems [3–5]. The recent focus on eco-evolutionary dynamics in metacommunities raises the challenge of testing relationships among species interactions, selection and phenotypic variation over complex landscapes.

Despite extensive testing of metacommunity theory, we still do not have a thorough understanding of when particular species should be present or absent in a patch, or the evolutionary consequences of these differences. For example, we have only recently begun to understand why trophic groups respond differently to patch size and isolation [4,6]. Predators and parasitoids are usually more sensitive to habitat size and isolation than their prey [3]. While both predators and parasitoids consume prey species, parasitoids reproduce within their host and tend to be specialized [7]. The increased sensitivity of predators and parasitoids to habitat size and isolation is caused by a number of mechanisms including sampling effects, increased detection of large patches by consumers, high metabolic demands necessitating a greater resource base, difficulty finding rare prey [8] and trophic dependencies [4]. Trophic dependency, the reliance of a consumer on its resource, may be particularly important in restricting the distribution of specialist consumers including many parasitoids [3,6,7,9]. Together, these mechanisms reduce colonization and increase extinction rates of consumers, decreasing consumer species richness. Nonetheless, the specific consumers that will be lost from small and

isolated patches, and the evolutionary consequences of such losses, have only been superficially explored and only at large spatial scales [10].

Loss of consumers and top predators on islands has been implicated as the cause of several macro-evolutionary patterns. Charles Darwin first noted that finches and marine iguanas on the Galapagos Islands were more docile than their mainland equivalents [11,12], and attributed these differences to the lack of predators on remote islands. Island gigantism, a common trend where island populations of insects and small mammals and lizards evolve increased body size, is similarly thought to result from selection on optimal body size following predator release [13,14]. These evolutionary patterns are extreme examples of the evolutionary consequences of predator loss on island which occur over long timescales when virtually all predators are absent.

A more typical scenario for metacommunities is that consumer species should be found less frequently and be lost at different rates as patch size and connectivity decrease, creating spatial gradients in selection [6,9,15]. Consumer species often select for specific prey phenotypes [16–18]; when different consumer species have distinct responses to patch size and isolation, patches differing in these biogeographic factors should produce alternative selection regimes. One way species may differ in their sensitivity to patch size and isolation is by their degree of specialization. In food webs composed of specialist and generalist consumers, specialists will be more sensitive to patch size owing to stronger trophic dependencies [6], and an inability to occupy the matrix. In the most extreme cases, specialists can attack only one species precluding the possibility of resource switching where generalists can consume alternative prey should one resource become extirpated. For example, island populations of the Glanville fritillary butterfly exhibit a classic metapopulation structure, occurring less frequently in small and isolated patches [19]. Its local abundance or absence also determines the landscape structure of its specialist parasitoids, causing a scaling through trophic levels [20]. However, the Glanville fritillary butterfly also hosts generalist hyperparasitoids that are expected to have broader spatial distributions [21]. These types of patterns are likely common to a wide range of specialist herbivores and parasitoids that are restricted to patchy distributions of their host plants [22]. Differences in the sensitivity of consumers to patch size and the resulting changes in community composition can equally be mediated by differences in consumer behaviour or dispersal ability. For example, more dispersive consumers are usually more common in small and isolated communities [23]. Regardless of the underlying mechanism, spatial shifts in community assemblage are not simply ecological patterns of trophic richness—they commonly alter natural selection and thus the evolution of resource populations [16,17].

Predators may also cause phenotypic differentiation among local prey communities, permitting the development of ecological interactions that differ among patches in a metacommunity. Phenotypic shifts in local populations can be driven by local selection regimes if populations have sufficient reproductive isolation to allow for strong assortative mating [24]. Classic research has shown that islands isolated by only tens of metres, and as small as a few metres across, were colonized by arthropods in ways consistent with predictions made by island biogeography [15], suggesting that the conditions necessary for isolation-based assortative mating may be commonly met for insects. However, dispersal among patches,

and thus the importance of assortative mating, may also be subject to evolution in metacommunities. For example, highly dispersive phenotypes of the Glanville butterfly are associated with smaller patches that are prone to extinction [25], a pattern that should decrease local adaptation to small patches. By contrast, many populations evolve reduced dispersal on islands, which is adaptive when populations are locally adapted or dispersal is very costly due to the low success in finding other suitable habitat patches (islands; [26,27]). Although both selective forces may be present in metacommunities, increases in host population sizes in the absence of predators, and local adaptation to predator-free conditions, seem more likely to select for lower dispersal in isolated populations of a resource species.

In this paper, we test how trophic rank, differences among top predators, and the spatial structure of a natural metacommunity impact evolutionary processes and the ecological distributions of species and anti-predator traits. We use patches of tall goldenrod (*Solidago altissima*) plants that support a specialist, gall-forming fly parasite (*Eurosta solidaginis*) and the fly's specialist parasitoid, *Eurytoma gigantea* [28]. Research in this well-studied system has shown that gall size of *Eurosta* is under stabilizing selection when *Eurytoma* and generalist bird consumers are present (woodpeckers and chickadees), with *Eurytoma* selecting for larger gall sizes and bird predators selecting for smaller galls [16,29]. We quantified attack rates and selection imposed by *Eurytoma* and bird predators in patches of goldenrod that varied in size (less than 10 to more than 250 stems) and distance (3–88 m) from a large 'mainland' field of goldenrod. Our study tested the above ideas by hypothesizing that (i) *Eurosta* will be less abundant in small and isolated goldenrod patches, (ii) *Eurosta* attack by *Eurytoma*, the specialist parasitoid, will decline in small and isolated goldenrod patches but attack by birds will be unchanged, (iii) the decline in *Eurytoma* attack frequency will shift selection gradients to favour galls that are more susceptible to parasitoid attack but less susceptible to attack by downy woodpeckers, (iv) changes in selection gradients will cause morphological shifts towards *Eurosta* phenotypes with decreased susceptibility to downy woodpecker attack in small and isolated patches, and (v) *Eurosta* from isolated goldenrod patches will have reduced dispersal ability.

2. Material and methods

(a) Study system

Solidago altissima (hereafter referred to as goldenrod) is a common old-field plant in much of eastern North America [30] and can be patchily distributed, often in forest clearings [31]. Goldenrod tends to occur in large clonal patches, almost never occurring singly [31]. Goldenrod is attacked by *E. solidaginis* (hereafter referred to as *Eurosta*), a univoltine fly (Diptera: Tephitidae) whose larvae cause goldenrod to develop a spherical, tumour-like stem gall [28,32]. Adult females emerge from galls, mate and oviposit in late May in Southern Ontario. The gall appears roughly three weeks later and continues to grow for another month [16]. Galls are attacked by birds (downy woodpeckers and chickadees), and two species of *Eurytoma* wasp, and *Mordellistena* beetles, but only downy woodpeckers and *E. gigantea* preferentially attack galls of a particular size [28]. *Eurytoma* is a true specialist, attacking only *E. solidaginis* galls, whereas woodpeckers and chickadees are generalists, both consuming dozens of arthropod species [33].

The size preferences of bird predators and *E. gigantea* (hereafter referred to as *Eurytoma*) have been shown to drive selection on gall size. *Eurytoma* females probe galls of all sizes but can only insert an egg when the width of the gall wall is less than the length of the ovipositor. This parasitoid is therefore limited to smaller galls, causing selection for increased gall size [16,34]. During winter months, downy woodpeckers (*Picoides pubescens*) and black-capped chickadees (*Poecile atricapillus*) attack *Eurosta* galls, preferentially consuming large galls, and imposing selection for small gall size [29,35]. The preferences of bird predators and *Eurytoma* cause stabilizing selection [16] with the optimum gall size dependent on the attack rate of each [28,34].

(b) Field methods

In Early May 2015, we collected *Eurosta* galls from 28 goldenrod patches surrounded by a forest matrix at Koffler Scientific Reserve, King Township, Ontario, Canada. We surveyed all goldenrod patches within 150 m of a large 'mainland' field which bordered the forest. The goldenrod patches varied in the number of stems (7–266 ramets; hereafter referred to as patch size) and distance from the mainland field (3–88 m, hereafter referred to as isolation). Patch size and isolation were not related to one another (electronic supplementary material figure S1; $R^2 = 0.002$, $p = 0.8$), and no other large populations of goldenrod were nearby. We collected every gall from each patch, measured the maximum gall diameter then dissected each gall to determine its content. We scored galls containing *Eurosta* larvae as survivors, and reared the *Eurosta* larvae for further tests (below). We marked galls with large holes as having been killed by birds, those containing wasp larvae as having been attacked by *Eurytoma*, and empty galls showing no signs of habitation as early larval death (ELD).

To ensure that any among-patch differences in gall size were driven by underlying differences of *Eurosta* rather than differences in goldenrod quality or genotype that is related to patch characteristics, we reared populations of *Eurosta* in a common garden. We reared out all *Eurosta* from each patch less those used in dispersal trials (below) in centrifuge tubes, then introduced them to cages (diameter = 1.13 m, height = 1.5 m) placed over *S. altissima* ramets. Each population was housed in a different cage, but all cages were close to each other in a continuous patch of goldenrod. In August, after galls had stopped growing [16], we harvested all galls, measuring diameter then comparing mean gall diameter in the common garden with mean gall diameter in the original population.

To test for differences in dispersal ability among *Eurosta* from different patches, we used a subset of the collected pupae from each patch as well as from the mainland field, and reared these pupae in 50 ml Falcon tubes until emergence in early June. After emergence, we conducted dispersal assays on up to three individuals per population. We tested individuals within 2 days of emergence after marking them on the wing with a fine point marker. We released focal individuals in equal sex ratios, from the same point in a 9 m² patch of goldenrod surrounded by forest. This set-up was to assess dispersal among forest patches (i.e. dispersal that would occur in this metacommunity). We started each trial at 9.00 and searched for flies every 2 h for the first 6 h, then once the following day at 9.00. At each time step, we marked the position of each individual using a flag, then measured the distance moved since the previous capture. To standardize the environment between trials, we only released flies on days that were rainless with little wind (i.e. less than 10 km h⁻¹). Dispersal estimates may be biased when long-distance dispersal goes undetected, which may occur when distances are not recorded for individuals that disappear from a trial. To ensure that this was not influencing

dispersal estimates from our study, we quantified the number of *Eurosta* we failed to re-sight.

(c) Statistical analyses

We used a series of linear models (LMs) to test for the effects of patch size and isolation on the attack rate of natural enemies, selection gradients caused by differences in attack rate and phenotypic shifts in anti-predator traits. We first standardized all independent variables by subtracting the mean and dividing by the standard deviation. We then used a generalized linear mixed model (GLMM) with a binomial distribution and logit link function to test for differences in the rate of goldenrod parasitism by *Eurosta* among patches differing in size and isolation. To avoid trends caused by correlations among individuals in a patch, we included patch as a random effect. We included patch size, isolation and their interaction as independent variables, and removed the interaction term and reanalysed the model if the interaction term was not significant. We used the same model to test for differences in attack rate of bird predators and the parasitoid *Eurytoma*. We used log-likelihood ratios to test for significance of all models, with likelihoods determined from the maximum-likelihood solution.

We calculated selection coefficients both across all patches (globally) and for each patch individually (locally). Before analysing selection coefficients, we calculated relative fitness by dividing an individual's survival by the mean survival measured in the population [36]. Fitness was relativized across all patches for the global selection analysis, but within each patch when calculating local selection gradients. Relativizing fitness globally assumes that populations are panmictic, whereas local fitness assumes that individuals interact only within their patch.

We used separate models to estimate significance values and regression coefficients because coefficients from GLMMs cannot be directly related to selection, and LMs of transformed binary data cannot be assessed for statistical significance, because distribution and variance assumptions are violated. We tested for significant selection coefficients by regressing survival against standardized gall size using a GLMM with a logit link function for all data together (global selection), and for each patch separately (local selection). We included patch as a random effect in the global selection analysis. We then used an LM with relative fitness as the response variable to estimate the selection coefficient and standard error of each coefficient. To estimate nonlinear selection coefficients, we included the squared standardized gall size in the models [36], and then doubled the coefficients from LMs to calculate the actual magnitude of nonlinear selection [37]. We then re-ran LMs without the quadratic term to estimate the coefficient of directional selection.

We tested for systematic differences in selection among patches by regressing isolation and patch size against local selection coefficients using an LM, again removing the isolation by patch size interaction if it was non-significant. To prevent significant patterns being driven by non-significant selection coefficients, we weighted each coefficient by the inverse of its standard error. We independently tested for differences in nonlinear and linear selection by separately modelling quadratic and linear selection coefficients.

After testing for differences in selection coefficients, we investigated phenotypic differences across patch sizes and isolation. We tested for an effect of patch size and isolation on standardized gall size while including patch as a random effect in an LME. To ensure that any difference in gall size resulted from underlying differences among *Eurosta* populations (rather than goldenrod populations), we used a LM to regress the mean gall size of each *Eurosta* population measured in the spring against the mean gall size of the corresponding population in the common garden. We also tested for differences in distance dispersed by individual flies using an LME with patch size and isolation as main effects, and time nested in individual after release as a random effect.
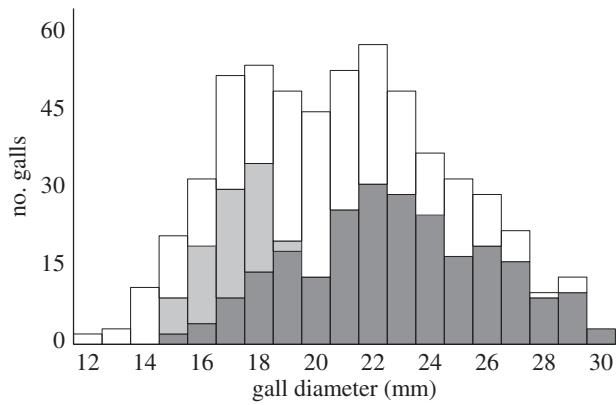
Figure 1. The number of galls attacked by *Eurytoma* (light grey), downy woodpeckers (dark grey) and surviving (white). *Eurytoma* preferentially parasitized small galls, downy woodpeckers attacked large galls, and most survivors had an intermediate gall size. The smallest galls were not attacked, but had high rates of ELD (not shown here).

To explore the likely contribution of gene flow from nearby patches (versus from the mainland), we used a metapopulation model that calculates the proportion of immigrants that come from nearby patches versus the 'mainland' patch. We calculated connectivity as the negative exponent of distance between two patches divided by α, the mean dispersal distance of an individual. We then weighted those connectivity values by multiplying by the number of stems in a given patch (following [38]). We generated connectivity calculations for several values of α (2, 10 and 100 m), with the lowest value reflecting mean observed dispersal distances over a 1-day period. Although these estimates do not give an absolute estimate of immigration or gene flow, they quantify the relative importance of different sources (patches and the mainland) to the immigrant pool. Statistical analyses were conducted in R (v. 3.1.1, 2014) using the base package and the 'lme4' package [39].

3. Results

A large proportion of *Eurosta* galls were attacked by *Eurytoma* and downy woodpeckers, with attack rates depending on gall size and patch isolation and size (figures 1 and 2). *Eurosta* was more common in large patches that were near to the large 'mainland' patch (figure 2; both $p < 0.001$). *Eurytoma* preferentially attacked small galls (figure 1; $p < 0.001$) and were rarer in small and isolated patches (figure 2; electronic supplementary material, figure S2; both $p < 0.003$). Downy woodpeckers attacked large galls (figure 1; $p < 0.001$) but attack rates did not differ with patch size or isolation (electronic supplementary material, figure S2, both $p > 0.6$). All bird predation recorded was from downy woodpeckers.

Selection analysis revealed significant patterns of directional selection with patch size and isolation. Globally, there was selection for small galls (selection coefficient $= -0.08683$, $p < 0.001$), but nonlinear selection was non-significant (selection coefficient $= -0.0659$, $p = 0.577$). Locally, nonlinear selection did not differ across an isolation gradient ($\beta = 0.0062$, $p = 0.3223$), but there was a marginal trend for stabilizing selection to be stronger in larger patches ($\beta = -0.0876$, $p = 0.0967$). Selection for small galls was the strongest in small and isolated patches (figure 3; both $p < 0.015$), with mean selection coefficients ranging from 0 (neutral) in large, connected patches to -0.1 in small, isolated patches.

Observed phenotypic shifts were consistent with both theoretical expectations and the results of the selection analysis; *Eurosta* galls were smaller in both small and isolated patches (figure 3; both $p < 0.04$). Moreover, there was a significant correlation between gall sizes in the field and the common garden (figure 5; electronic supplementary material, figure S3; $p < 0.001$, $R^2 = 0.716$) indicating that among population differences in gall size have an underlying heritable component.

Dispersal distances of *Eurosta* from different natal populations were consistent with expected selection on dispersal ability. *Eurosta* from isolated patches dispersed shorter distances (figure 4; $p < 0.001$), but the size of the natal patch had no effect on dispersal ($p = 0.2125$). There were no patch level differences in the number of *Eurosta* we failed to re-sight (electronic supplementary material, table S1). Our metapopulation model of patch connectivity showed that the vast majority of immigrants to distant patches would be from surrounding patches rather than the mainland (figure 4b). This result was clear at the observed mean dispersal distance (2 m) and larger (10 m), but disappeared at very high mean dispersal distances of 100 m (figure 4b). In other words, the low dispersal from patches in the forest that we documented appears to be sufficient to cause spatially assortative mating.

4. Discussion

Our study demonstrates how the spatial distribution of patches in a metacommunity structures species occurrence patterns, shaping species interactions, selection and phenotypic variation. Although it is well understood that trophic dependencies, sampling effects, dispersal limitation and foraging behaviour can limit the occurrence of natural enemies in small and isolated patches, the evolutionary consequences of these differences in natural enemy presence have, until now, been unexplored. Our study shows that natural enemies are less likely to occupy small and isolated habitats, and that reduced enemy abundance can alter selection. However only the distribution of *Eurytoma*, a *Eurosta* specialist, was affected by habitat size and isolation, while attack by dispersive and generalist downy woodpeckers was unchanged. The predictable loss of a subset of consumers created gradients of selection that depended on habitat size and isolation. The adaptive phenotypic shifts that we observed were consistent with these selection gradients, and can feedback to affect ecological dynamics by influencing an individual's propensity for dispersal and susceptibility to attack.

Our study suggests that metacommunity theory may be a powerful tool for understanding feedback between ecology and evolution. As predicted by trophic dependency [3,6], we found that the distribution of species was nested by trophic level, with *Eurosta* only surviving in goldenrod patches, and the specialist parasitoid *Eurytoma* only surviving in patches with *Eurosta* (figure 2). These spatial patterns of trophic dependency are likely common in a wide range of ecosystems. For example, isolated grassland fragments contained fewer predators than large or well-connected patches, and these differences were attributed to trophic dependencies [40]. Even in ecosystems where trophic dependencies do not seem to drive predator distributions, the relatively low regional abundances of consumers and biased detection of large habitats can still cause them to be absent from smaller patches [4], suggesting that multiple causal mechanisms such as sampling effects or
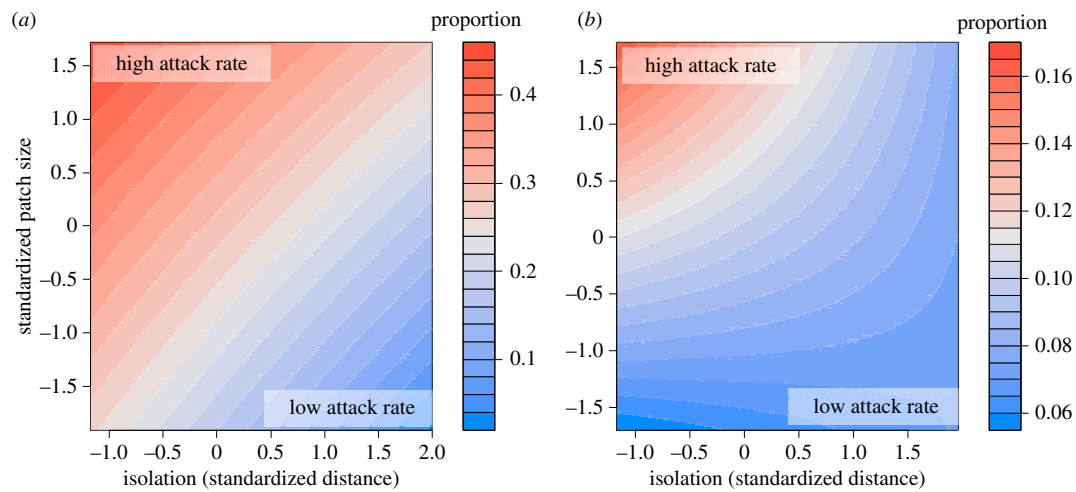
Figure 2. Predicted values of *Eurosta* and *Eurytoma* attack rate from GLMMs of patches differing in size and isolation. (*a*) Proportion of goldenrod stems galled by *Eurosta* and (*b*) proportion of *Eurosta* galls and proportion parasitized by *Eurytoma*. GLMMs used a logit link function with isolation and patch size as main effects, and patch as a random effect. High and low attack rates are depicted in red and blue, respectively, although the scales differ between plots. In both cases, attack was most frequent in large and near patches, but the attack rate of *Eurosta* was consistently higher.
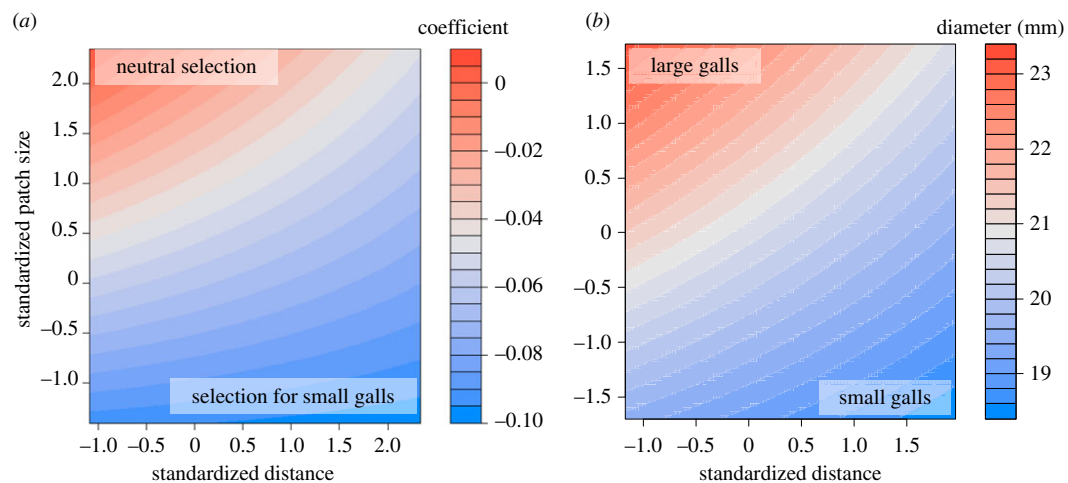

Figure 3. Predicted values of directional selection coefficients and gall sizes from an LM and LME, respectively. (*a*) Selection on gall diameter and (*b*) gall diameter (mm). Patch size and isolation were included in both models, and patch was included as a random effect when analysing gall sizes. Low selection coefficients indicate directional selection for smaller gall sizes, while the highest selection coefficients represent neutral selection. High selection coefficients and large galls are represented by red, while low selection coefficients and small galls are shown in blue. Patterns of selection and gall size were congruent, with low selection coefficients and small galls being present in small and isolated patches.

behavioural differences may lead to the pervasive pattern of fewer predators occurring in small habitats.

In our study system, two traits appear to determine the sensitivity of consumers to patch size and isolation: dispersal ability and diet specialization. In particular, the highly dispersive downy woodpecker, a generalist insect predator, attacked *Eurosta* at a consistent rate across patches, whereas the specialist parasitoid *Eurytoma* was more common in large and well-connected patches (figure 2*b*). These differences suggest that *Eurytoma* was either unable to immediately disperse to patches from which it was absent, that it was constrained by the low abundance of *Eurosta* in small and isolated patches (figure 2*a*), or both. In contrast to *Eurytoma*, downy woodpeckers could easily disperse over the small spatial extent of our study, and even if dispersal limited, downy woodpeckers could feed on alternate resources in the absence of *Eurosta*. Differences in both dispersal ability [23] and diet breadth [41–43] are typical in many food webs, suggesting that different predator species will commonly

have distinct responses to patch size and isolation. For example, Gravel *et al.* [6] found that across 50 Adirondack lakes, consumers with generalist diets were more likely to be found in a given lake, and that this effect was magnified in small lakes. Similarly, invertebrate diversity declined in isolated rock pools, but this pattern was caused by the absence of poorly dispersing species [23]. Differences in dispersal ability may vary by species but also be dependent upon the habitat separating patches or other conditions affecting an individual's likelihood of dispersing [7]. Together, these and other studies show that species traits can create disparate consumer communities in patches differing in size and isolation. These changes in consumer community composition may create novel patterns of species interactions and ultimately selection.

The loss of a subset of natural enemies in small and isolated patches may systematically alter selection on prey species in metacommunities. In many cases, resisting consumption has a cost, creating selection against resistance if consumers are absent. For example, Van Buskirk & Schmidt [44] found that
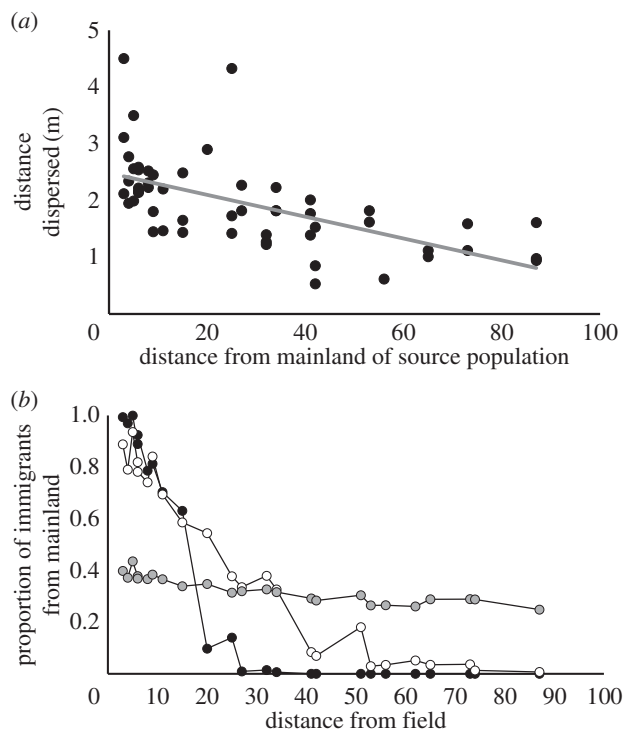
Figure 4. (a) The distance dispersed in 24 h by individual *Eurosta* from natal patches differing in distance from a mainland. The line of best fit was estimated using a linear mixed effects model with patch size and isolation as main effects, and patch as a random effect. *Eurosta* from distant patches were poorer dispersers than individuals from near patches. (b) Estimates of the proportion of immigrants originating in the mainland for each patch. Estimates were calculated with mean dispersal distances (α) of 2 (black), 10 (white) and 100 (grey) metres. The genetic contribution from the mainland is initially high but declines quickly when dispersal distances are short but is relatively constant when individuals are dispersive.
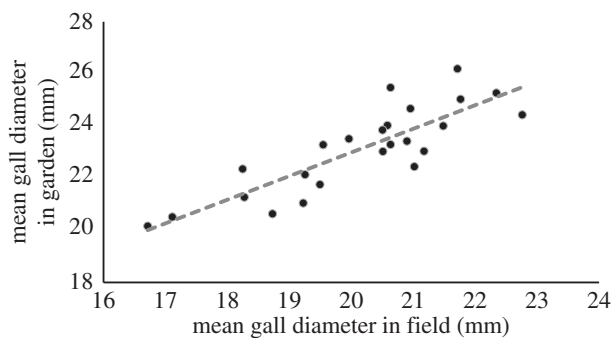
Figure 5. Mean gall diameter in the common garden was positively correlated with mean gall diameter in the field, indicating a genetic component to the observed variation in gall size. The line of best fit was estimated using an LM.

newts with anti-consumer defences had improved survival in the presence of dragonfly consumers but lower growth rates in their absence. In our study, woodpeckers and *Eurytoma* selected for opposite defensive traits, a pattern that is fairly general when several consumers are present—traits that confer an advantage against one consumer may be costly when defending against another [45–47]. When consumers select for alternate anti-predator traits, those traits should be under stabilizing selection when all consumers are present, but the adaptive peak will shift when one consumer is lost. Overall, the widespread observation that consumers induce selection for specific defensive traits in their prey suggests that the effects

of consumer specialization and dispersal ability observed in our study may be general to evolving metacommunities.

Differences in selection across patches can either increase standing genetic variation across all patches or mediate local adaptation. Spatial variation in selection should confer increased standing genetic variation when populations are panmictic, but increasingly promote local adaptation as populations have higher levels of assortative mating [24]. We found phenotypic shifts in *Eurosta* gall size, consistent with selection imposed by constant levels of downy woodpecker consumption but reduced *Eurytoma* attack in small and isolated patches (figure 3). These shifts in gall size suggest that local adaptation is occurring, causing the mean phenotype present in each patch to reflect the optimal gall size in that patch. In our system, local adaptation is made more likely both by the poor dispersal ability of *Eurosta* and the barrier imposed by forests to many old-field insects [48,49]. While phenotypic shifts are largely due to heritable differences in gall size (figure 5), differences in both plant genotype and plant nutritive quality can equally alter patterns of gall size among patches [17]. Among-patch differences in the environment, including differences in plant genotype or quality may themselves create differences in selection and local adaptation among patches [50]. While spatial variation in selection often causes local adaptation, the small spatial scale at which we detected phenotypic shifts consistent with local adaptation is exceptional and likely driven by poor dispersal ability through the forest matrix [17,51,52].

Just as dispersal influences patterns of genetic diversity, the spatial structure of selection gradients may alter dispersal. Selection often favours reduced dispersal ability in isolated habitats, first because the cost of dispersal is high, and later because an individual is more likely to be maladapted in other patches once local adaptation has occurred [53,54]. Increased assortative mating has been shown to result from maladaptation driving reduced immigrant fitness in a wide range of systems [55] suggesting that this mechanism may be common. Our findings are consistent with both high costs of dispersal and immigrant maladaptation—*Eurosta* from isolated natal populations were poorer dispersers than individuals from less isolated patches (figure 4), and tended to produce galls that were maladapted to patches with greater numbers of *Eurytoma* (figures 3b and 5). Widespread loss of dispersal structures in isolated populations [26,56] suggests that feedback between local adaptation and selection for reduced dispersal ability may be common in natural populations.

One question that arises from our results, is why the phenotypic distribution of gall sizes does not perfectly match the optimal gall size predicted by selection gradients. Put otherwise, why has selection not fixed the optimal phenotype in each habitat? One possibility is that ELD is more prevalent in small galls, and by excluding ELD from our analyses we biased our calculations of selection coefficients [16]. Indeed, ignoring some component of fitness is an issue for virtually all studies of selection [57–59], and in our study could not be avoided because we cannot know when small galls cause ELD and vice versa. Other reasons for imperfect phenotype–environment matching include temporally variable selection [60–62], immigration from populations differing in optimal gall size [24,63], inadequate time for populations to fully adapt to local conditions [64], or failing to account for other agents of selection. How these mechanisms interact to produce observed patterns of phenotypic variation remains a focus of

evolutionary ecology. Nonetheless, the clear trends in selection and phenotypic distributions that we observed suggest that patch size and isolation play a strong role in structuring gall sizes in this system.

By incorporating well-understood spatial and trophic processes with evolutionary dynamics, our study has begun to elucidate the intricacies of eco-evolutionary dynamics in meta-communities. We have demonstrated that accounting for trophic structure, and species-specific differences in specialization and dispersal ability, predictably alters spatial patterns of species distributions. These differences alter species interactions, selection and local phenotypes, potentially affecting ecological dynamics and generating feedback between dispersal and local adaptation. The small spatial scales over which these patterns manifest suggests that these types of dynamics are likely to be widespread in nature.

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