Predators modify biogeographic constraints on species distributions in an insect metacommunity

Tess Nahanni Grainger,[1] Rachel M. Germain, Natalie T. Jones, and Benjamin Gilbert

Department of Ecology and Evolutionary Biology, University of Toronto, 25 Willcocks Street, Toronto, Ontario M5S 3B2 Canada

Abstract. Theory describing the positive effects of patch size and connectivity on diversity in fragmented systems has stimulated a large body of empirical work, yet predicting when and how local species interactions mediate these responses remains challenging. We used insects that specialize on milkweed plants as a model metacommunity to investigate how local predation alters the effects of biogeographic constraints on species distributions. Species-specific dispersal ability and susceptibility to predation were used to predict when patch size and connectivity should shape species distributions, and when these should be modified by local predator densities. We surveyed specialist herbivores and their predators in milkweed patches in two matrix types, a forest and an old field. Predator-resistant species showed the predicted direct positive effects of patch size and connectivity on occupancy rates. For predator-susceptible species, predators consistently altered the impact of biogeographic constraints, rather than acting independently. Finally, differences between matrix types in species' responses and overall occupancy rates indicate a potential role of the inter-patch environment in mediating the joint effects of predators and spatial drivers. Together, these results highlight the importance of local top-down pressure in mediating classic biogeographic relationships, and demonstrate how species-specific responses to local and regional constraints can be used to predict these effects.

Key words: Asclepias syriaca; *biotic interactions; dispersal; Island Biogeography; matrix; metacommunity; metapopulation; milkweed; predation; species distributions; top-down.*

INTRODUCTION

In heterogeneous landscapes, the size and spatial isolation of habitat patches shape the populations and communities that inhabit them (MacArthur and Wilson 1967, Hanski 1994*a*, Jones et al. 2015). Island Biogeography and metapopulation theories predict that species are most likely to occur in large, well-connected habitat patches that receive new colonists at high frequencies and support large populations that are resistant to extinction (MacArthur and Wilson 1967, Levins 1969, Hanski 1994*a*). Although these classic predictions have explained species distributions in a range of taxa (Hanski 1994*a*, van Noordwijk et al. 2015), in other cases their explanatory power has been limited or absent (Gilbert 1980, Prugh et al. 2008). Identifying when and why the biogeographical constraints of patch size and connectivity drive species distributions would bring us closer to understanding the mechanisms that underlie broad diversity patterns.

One explanation for why species distributions diverge from classic biogeographical predictions is that local biotic interactions can overshadow or modify the impact of regional processes (Gripenberg and Roslin 2007, Gravel et al. 2011). For example, predators can obscure relationships between connectivity and diversity by inhibiting species that are able to reach a patch from establishing or persisting (Shurin 2001, Kneitel and Miller 2003). Top-down pressure from predators may even reverse predicted spatial relationships if small or isolated patches act as refugia from predator-induced extinctions (Holyoak and Lawler 1996). While the links between resource heterogeneity and species distributions are well explored in the metacommunity literature, the effects of top-down constraints are less understood (Logue et al. 2011, Grainger and Gilbert 2016). In particular, predictions for when and how local trophic interactions will alter regional patterns of diversity have remained elusive (Resetarits et al. 2005, Grainger and Gilbert 2016).

A key to understanding the interplay between local trophic drivers and regional spatial drivers of species distributions are the characteristics of a species' biology that govern its local persistence and inter-patch movements (Harvey and MacDougall 2014, van Noordwijk et al. 2015). Dispersal ability determines the rate at which species move between patches, and has been used to predict species' responses to spatial patch characteristics (De Bie et al. 2012, Jones et al. 2015, van Noordwijk et al. 2015). While weak or passive dispersers are only likely to reach patches that are well-connected or of a large target size, strong, active dispersers may reach and select among a broader range of habitat patches (Kennedy and Gray 1993, Resetarits et al. 2005). An integration of biotic

constraints, along with dispersal constraints, could provide a more mechanistic understanding of the forces that structure metacommunity diversity. For example, inedible or well-defended species should show little effect of top-down pressure, while readily consumed prey species are expected to have higher extinction rates or altered dispersal choices when predators are abundant (Shurin 2001, Resetarits et al. 2005). For such species, lower occupancy rates resulting from predator-induced mortality may dampen spatial relationships (Shurin 2001), or change relationships between spatial drivers and occupancy for species capable of actively dispersing away from predators (Kennedy and Gray 1993, Resetarits et al. 2005). The combined use of dispersal ability and susceptibility to predation could enable predictions of how local and regional factors independently and interactively shape species distributions.

In addition to the intrinsic characteristics of species, the inter-patch matrix can also structure species distributions by altering both dispersal rates among patches and the persistence of populations within patches (Ricketts 2001, Prevedello and Vieira 2010). For example, the physical characteristics of the matrix can aid or impede a species' movement among patches, depending on the degree of physical barriers to dispersal and the fitness costs of traversing the matrix (Ricketts 2001). Likewise, patches within matrices preferred by predators could suffer higher predation rates due to spillover into local patches (Bayne and Hobson 1997).

We developed and tested predictions for when patch size, connectivity and predators constrain the distributions of nine specialist herbivores that live in milkweed

patches. Common milkweed (*Asclepias syriaca*) is a perennial forb that produces toxic cardenolides and sticky latex to defend against herbivores. The small suite of insect herbivores that are adapted to eat milkweed have served as a model system in studies of dispersal and plant-herbivore interactions. As such, there is a wealth of natural history information for these species, including published data on dispersal distances and susceptibility to predation (Table 1; Zalucki and Kitching 1982a, Matter 1996, Smith et al. 2008). We used these data to position the nine specialists into a framework that predicts whether the distribution of each species should be constrained by predators, patch spatial characteristics, or some combination thereof (Fig. 1). In this framework, the seven species with average dispersal distances of <100 m are predicted to show positive relationships with patch size and connectivity (right half of Fig. 1). In contrast, the two lepidopterans (tussock moth and monarch butterfly), which frequently disperse over 1 km, are predicted to be unconstrained by patch size and connectivity (left half of Fig. 1). Similarly, early instar monarch caterpillars and three aphid species are consumed by predators and should be negatively impacted by their presence (top half of Fig. 1), while the defensive coloring or hard bodies of the remaining five species result in their having few known invertebrate predators (bottom half of Fig. 1).

We surveyed nine specialist milkweed herbivores and their general predators in milkweed patches imbedded in an old field and a deciduous forest to test two predictions: (1) the impact of local predators and biogeographical constraints (patch size and connectivity) on each species can be predicted by its dispersal ability and susceptibility

TABLE 1. References for dispersal estimates and predation susceptibility for specialist milkweed herbivores used to derive the predictions presented in Fig. 1.

Species	Average dispersal (m)	Species used for dispersal reference	Susceptible to predation
Aphis asclepiadis†	100[1–7]	Various aphid species (*Aphis* and other genera)	Yes[17,18]
Aphis nerii†	100[1–7]	As above	Yes[17,18]
Myzocallis asclepiadis†	100[1–7]	As above	Yes[17,18]
Milkweed weevil	15[8]	Milkweed weevil	No‡
Milkweed leaf miner	20[9]	Congener of the milkweed miner	No‡
Small milkweed bug	30[10,11]	Small milkweed bug	No[19,20]
Long-horned milkweed beetle	37[12–14]	Long-horned milkweed beetle	No[20]
Monarch butterfly	>1,000[15]	Monarch butterfly	Yes[21–23]
Milkweed tussock moth	>1,000[16]	Confamiliar of the milkweed tussock moth	No[24,25]

Notes: [1]Dickson (1959); [2]Taylor et al. (1979); [3]Nault et al. (2004); [4]Zhang et al. (2008); [5]Underwood et al. (2011); [6]Harrington and Taylor (1990); [7]Grainger, T. N. and B. Gilbert (*unpublished data*); [8]St Pierre and Hendrix (2003); [9]Jones and Parella (1986); [10]Evans (1983); [11]Caldwell (1974); [12]McCauley et al. (1981); [13]Lawrence (1988); [14]Matter (1996); [15]Urquhart and Urquhart (1978); [16]Guichard et al. (2012); [17]Smith et al. (2008); [18]Malcolm (1991); [19]Berenbaum and Miliczky (1984); [20]Duffey and Scudder (1972); [21]Prysby (2004); [22]Zalucki and Kitching (1982b); [23]McCoshum et al. (2016); [24]Torgersen et al. (1983); [25]Barber and Conner (2007). †Aphids are weak flyers capable of active dispersal on the scale of metres to tens of metres, but they can also be passively dispersed by wind currents for kilometers. In our system, where all patches are <2,000 m apart and many patches are less than 100 m apart, active short-distance dispersal and short to medium distance blowing are likely to be more relevant than rare long-distance wind dispersal events for moving aphids between patches. We therefore estimated average aphid dispersal to be between the literature estimates for these two dispersal modes (100 m), but with more weight given to short-distance dispersal. ‡No references were available for weevils and miner predator susceptibility, so we classified these species as unsusceptible due to the cryptic lifestyle of leaf miners and the hard protected body form of weevils.

Constrained by
predators

(a)

Predict: negative
effect of predators

Butterfly

(b)

Predict: effects of predators
and spatial drivers

Aphids

Unconstrained by
spatial drivers

Constrained by
spatial drivers

Moth

Bug   Beetle   Weevil   Miner

Predict: no
significant effects

Predict: positive effects of
patch size and connectivity

(c)

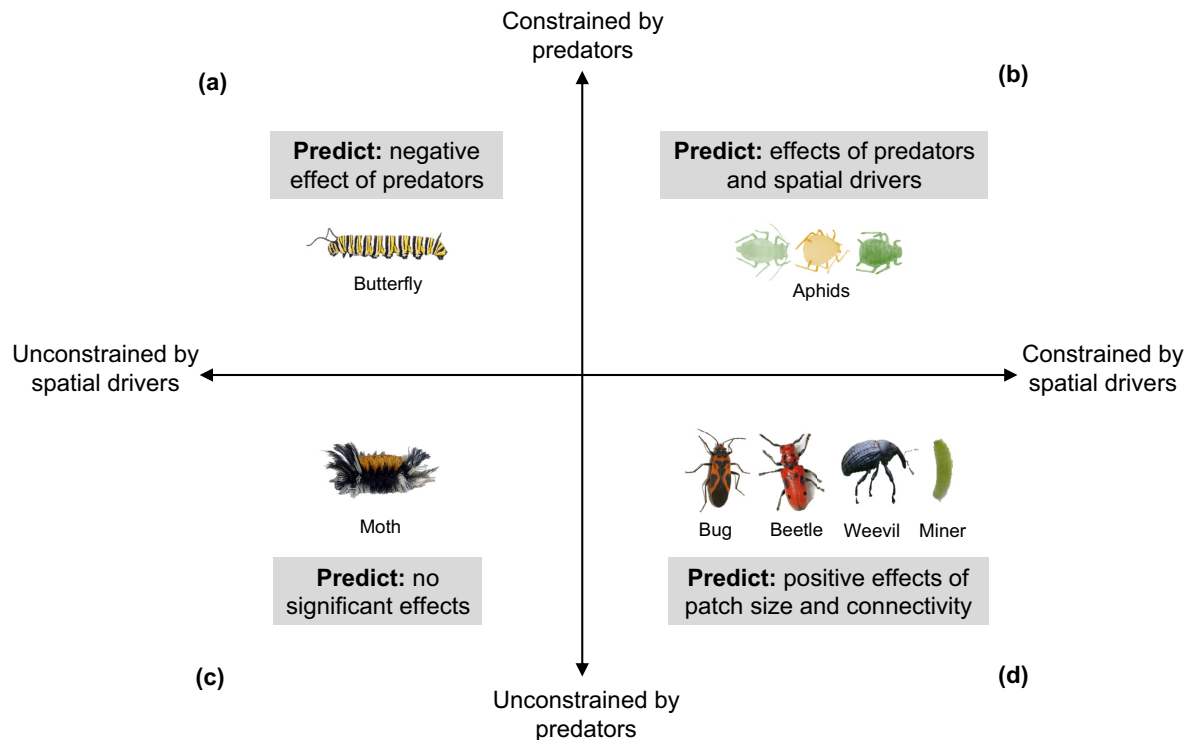Unconstrained by
predators

(d)

Fig. 1. Predictions for constraints caused by local predators and spatial drivers (patch size and connectivity) for nine focal specialist milkweed herbivores. See Table 1 for references used to derive predictions, and Appendix S1 for insect image sources. [Color figure can be viewed at wileyonlinelibrary.com]

to predation, and (2) local predators will modify the impacts of biogeographical constraints on the distributions of species susceptible to predation.

METHODS

Natural history

The nine specialist milkweed herbivores observed in this study include three aphid species, one seed bug, two beetles, two lepidopterans, and one leaf-mining fly. The aphids are *Aphis nerii*, *Aphis asclepiadis* and *Myzocallis asclepiadis;* all three aphid species feed on milkweed phloem and are eaten by generalist invertebrate predators (Table 1). Monarch caterpillars consume milkweed leaves and, despite chemical defenses, are also readily consumed by generalist invertebrates, particularly at the early instar stages (Prysby 2004; Table 1). In contrast, the long-horned milkweed beetle (*Tetraopes tetrophthalmus*), milkweed stem weevil (*Rhyssomatus lineaticollis*), milkweed-leaf miner (*Liriomyza asclepiadis*), small milkweed bug (*Lygaeus kalmii*) and milkweed tussock moth (*Euchaetes egle*) are not vulnerable to predators due to their size, hard exoskeletons, aposematic coloration, cryptic lifestyle or toxicity (Table 1). The dispersal abilities of our focal species range from 15 m to over 1,000 km (Table 1). Because the mean distance between patches within a matrix type at our field site was <1,000 m in both

the old field and forest, we predicted that species with low dispersal distances (≤100 m) would be associated with large, well-connected patches, while the long-distance dispersers (≫1 km; monarchs and tussock moths) would be unconstrained by these spatial drivers (Fig. 1). While specialist milkweed herbivores are largely confined to milkweed patches, generalist predators including spiders, assassin bugs and ladybugs inhabit both milkweed patches and the surrounding matrix.

Study site and surveys

We conducted this study at the Koffler Scientific Reserve in Southern Ontario, Canada (44°03′ N, 79°53′ W). At this site, milkweed grows in old fields and in forest clearings, in patches ranging from a few to thousands of plants. For our study, we selected one old field area and one forested area (Appendix S1: Fig. S1) in order to assess whether our results were consistent across different habitats; however, the lack of replication of matrix types precludes us from drawing conclusions about the effect of the matrix on species distributions. The old field area is bounded by trees (forest or forest fragments) and cultivated land, while the forest area is bounded by residential areas and roads. Within each of these areas, we selected 30 focal milkweed patches (out of 103 old field and 36 forest patches) for insect surveys. We selected patches to maximize the range of patch sizes and inter-patch distances. We calculated the

area (hereafter patch size) and connectivity of all sampled and unsampled patches by mapping the perimeter of each patch using a high precision GPS unit (GeoXH Geoexplorer, Trimble, Sunnyvale, California, USA) and calculating the area of polygons in ArcGIS v. 10.3 (Esri, Redlands, CA, USA). We calculated the edge-to-edge distances between each patch and all other patches within the same matrix type (forest or old field) for use in our connectivity function (Statistical methods). Patches had an average area of 131 m² (±345 m² SD) in the old field and 93 m² (±345 m² SD) in the forest, and a mean distance between pairs of patches (within the same matrix type) of 271 m (±160 m SD) in the old field and 835 m (±584 m SD) in the forest (Appendix S1: Fig. S2).

For surveys, we randomly selected 30 plants that were at least 30 cm tall within each milkweed patch, and in patches with fewer than 30 individuals, we sampled all plants (Appendix S1: Tables S2 and S3). We surveyed focal plants for insects and arachnids every 2 weeks between early July and early September 2014, for a total of five surveys. Specialist milkweed herbivores were identified to species, while predators were identified to family; individuals that were difficult to identify were photographed or collected and keyed out at a later date. Twenty-five insect and arachnid families were classified as predatory, based on feeding guild classifications in published studies (Voigt et al. 2003, Harvey and MacDougall 2014; Appendix S1: Table S1). Ants (Hymenoptera, Formicidae) are a major predator of monarch caterpillars, and were included as predators in the monarch analysis (Zalucki and Kitching 1982b, Prysby 2004). As milkweed weevils and leaf miners occur primarily in the spring (May and June), before our surveys, their presence was determined post-hoc by counting leaf scars (miners) and stem scars (weevil) in late July (Van Zandt and Agrawal 2004a).

Statistical analysis

We analyzed the effect of patch size, patch connectivity and predator abundances (all predators summed) on the plant-level occupancy of each specialist milkweed herbivore in each matrix type. We used plant-level occupancy for two reasons: first, this measure allowed us to keep search effort constant across patches of different sizes that correspondingly had different numbers of plants surveyed (see *Methods*). Second, this measure allowed us to test the basic Island Biogeography hypothesis that higher colonization rates and lower extinction rates in large and connected patches should result in a greater number of individuals per species per unit area (Holt et al. 1995, Jones et al. 2015). Thus, we used plant-level occupancy to test whether insect densities, at the level of individual patches, differed.

To calculate inter-patch connectivity, we used the following metapopulation model (Hanski 1994b):

$$C_i = \sum_{j \neq i}^{n} A_j e^{-d_{ij}/\alpha}$$

where C_i is the connectivity of patch i, d is the Euclidean distance between any two patches, α is the mean dispersal distance of the species or group of interest, and A is the area of all source (non i) patches (the summation incorporates distances from all other sites). This connectivity metric uses the standard assumption of an exponential dispersal curve with a mean dispersal distance of α. As a result, connectivity between site i and j decreases at greater distances (d_{ij}) and increases with greater dispersal ability (α) and greater area (A) of source patches. This model has a similar functional form as Hanski's incidence function (eq. 4 in Hanski 1994b). We obtained estimates for the mean dispersal distance (α) for each specialist species from published studies, where possible (Table 1). For monarchs and tussock moths, which are capable of dispersing long distances (many kilometres), we used an α value of 1000 m, which represents a case of low or no dispersal limitation in this system.

For all species except leaf miners and weevils, we ran binomial generalized linear mixed models with patch size, patch connectivity and predator abundance as predictor variables, presence-absence of the species on each plant as the response variable, and patch, survey date and plant as random factors. Including patch as a random factor in the analysis ensured that patch was the unit of measure for linking insect distributions to our patch-level explanatory variables. For weevils and miners, whose occupancy was estimated at a single time point, models did not include time or predators, as many predators emerge after these two species, and predator abundances were quantified later in the season. Three species with fewer than 10 observations in either the forest or the old field could not be analyzed in that matrix type (Table 2). We also tested for effects of matrix type on predator abundances and the occurrence of each focal species using glms with matrix type as the predictor and patch as a random factor.

All statistical analyses were conducted in R (v. 3.2.4, R Core Team, Vienna, Austria) using the glmmadmb function in the glmmADMB package. For all analyses, we started with the most complex model and dropped all non-significant higher order interactions (see Appendix S1 for additional statistical methods). We present the highest order significant interaction(s) or main effects from each model. In all models, all predictors were standardized prior to analysis (centered on zero with a standard deviation of one) to account for differences in scale between our predictor variables, and predator abundance and patch size were log transformed to meet model assumptions. Figures were created using the visreg package, and show back-transformed predictions from models that include only fixed effects, due to issues with estimating confidence intervals in complex models when random effects are included (Bates et al. 2014).

RESULTS

Occupancy rates varied across our focal species; while some species were widespread, with occupancy rates of

TABLE 2. Details of model results.

Species	Matrix	Total occurrences	Occupancy (%)	Effect	Sig.	Fig.
Aphis asclepiadis	F	46	4.6 ± 1.9	S × P, C × P	***, **	3a, b
	OF	82	15.0 ± 4.0	C	**	2i
Aphis nerii	F	15	3.3 ± 1.4	None		
	OF	10	1.5 ± 0.6	S × P	*	3c
Myzocallis asclepiadis	F	546	43.4 ± 7.3	C × S	*	2g
	OF	381	41.6 ± 5.6	S	**	2e
Weevil	F	70	8.9 ± 3.8	S	**	2a
	OF	175	31.8 ± 5.6	None	*	
Miner	F	199	36.6 ± 5.0	C	*	2f
	OF	410	81.0 ± 3.2	None		
Small milkweed bug	F	0	0	Not analyzed		
	OF	27	3.3 ± 0.8	S, C	*, **	2b, c
Long-horned beetle	F	6	1.4 ± 0.8	Not analyzed		
	OF	13	1.6 ± 0.6	S	*	2d
Monarch	F	33	6.7 ± 2.2	S	*	2h
	OF	37	5.9 ± 1.5	C × P	**	3d
Tussock moth	F	103	25.6 ± 5.1	None		
	OF	4	0.5 ± 0.3	Not analyzed		

Notes: S, patch size; C, patch connectivity; P, predator abundance; F, forest; OF, old field. Effect indicates the highest order interaction(s), or significant main effects. 'Total occurrences' indicates total number of times each species was observed (presence, not abundance), while 'occupancy' indicates the mean percentage of plants per patch occupied by each species (±SE). For both total occurrences and occupancy rates, observations from five surveys were summed (except in the case of weevils and miners, which were surveyed at a single time point). "Not analyzed" indicates the three models that could not be run because a species' occupancy in that matrix type was too low. See Appendix S1: Tables S2 and S3 for summary data for each patch.

$*P < 0.05$; $**P < 0.01$; $***P < 0.001$.

over 30% in both matrix types (e.g., *Myzocallis*, leaf miner), others were more rare overall, occupying fewer than 5% of plants per patch (e.g., *A. nerii*, long-horned milkweed beetle) (Table 2; Appendix S1: Tables S2 and S3, Fig. S3). Occupancy rates of seven of our focal species were driven directly by patch size and/or connectivity in at least one matrix type (see Fig. 2 for direct effects of spatial drivers). Specifically, occupancy rates of five species were positively associated with patch size (*Myzocallis*, weevil, long-horned milkweed beetle), connectivity (leaf miner), or both (small milkweed bug) in one or both matrix types (Fig. 2a–f, Table 2). The positive effect of patch size on *Myzocallis* occupancy in the forest was only apparent when patches were poorly connected (area × connectivity interaction; $P = 0.03$; Fig. 2g). In contrast, monarch occupancy was negatively associated with patch size in the forest ($P = 0.009$; Fig. 2h), and *Aphis asclepiadis* occupancy was negatively associated with patch connectivity in the old field ($P = 0.003$, Fig. 2i). Tussock moth occupancy was not related to any predictor in the forest, the only habitat where this species occurred (Table 2).

Predators altered the effect of patch size and/or connectivity for three of four species that are susceptible to predation: *A. asclepiadis*, *A. nerii* and monarchs (see Fig. 3 for interactions between predators and spatial drivers). In the forest, *A. asclepiadis* had a positive relationship with patch size when predators were at low abundance that was diminished when predators were abundant (two-way interaction; $P = 0.001$; Fig. 3a). Likewise, *A. nerii* had a positive relationship with patch size in the old field that was reversed at high predator abundance (two-way interaction; $P = 0.01$; Fig. 3c). Finally, the negative relationships between connectivity and monarch (old field) and *A. asclepiadis* (forest) occupancy were only apparent when predators were abundant (two-way interaction; $P = 0.006$; Fig. 3b, d).

Occupancy rates of five out of nine species differed between the old field and forest site: whereas four species had significantly higher occurrence rates in the old field (miners, weevils, small milkweed bug and *A. asclepiadis*), only the tussock moth had significantly higher occupancy in the forest (all $P < 0.05$; Appendix S1: Fig. S3). The impact of predators, patch size and patch connectivity also varied between the old field and forest sites for most species (Table 2).

In summary, we detected positive associations with patch size and connectivity for four weak dispersers (small milkweed bug, long-horned milkweed beetle, weevil, and miner), and no or negative associations with these spatial drivers for the two dispersive species (tussock moth and monarch) (Fig. 2, Table 2). Interactions between predators and spatial drivers drove the distributions of three predator-susceptible species (*A. nerii*, *A. asclepiadis* and monarchs; Fig. 3). One weak disperser, *A. asclepiadis*, showed an unexpected negative effect of patch connectivity (Fig. 2i), while one predator-susceptible species (*Myzocallis*) did not
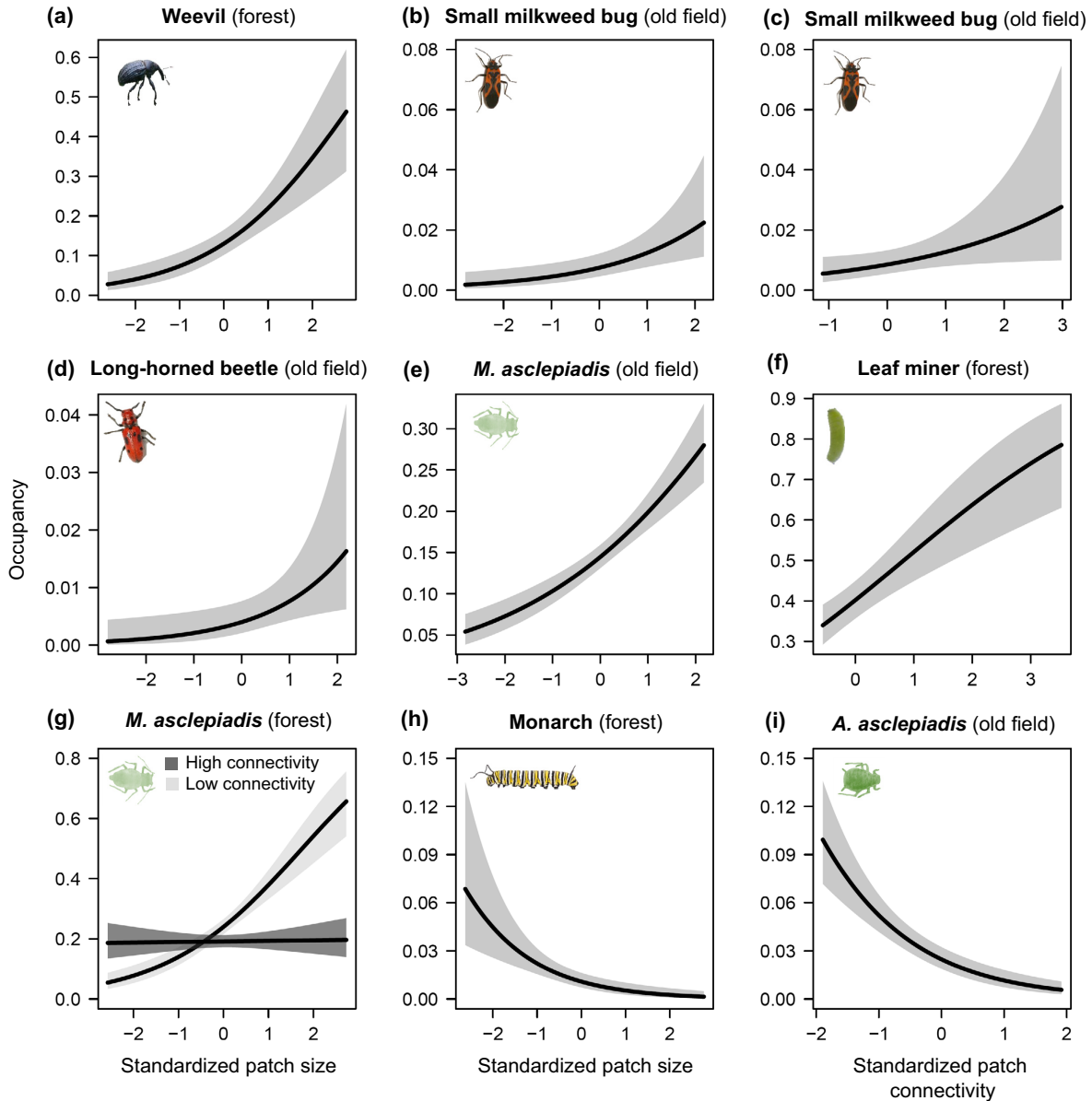
FIG. 2. Species with occupancy rates affected only by patch size (a, b, d, e, g, h) and/or connectivity (c, f, g, i), but not predators. Lines are best fits from the statistical model, and shading is a 95% confidence interval (see *Methods*). In panel g, light and dark grey bands are 95% confidence intervals around fitted lines, with connectivity set at low (10th quantile) and high (90th quantile) levels, respectively. Note the difference in *Y* axes among panels. [Color figure can be viewed at wileyonlinelibrary.com]

show the negative response to predators that we predicted (Table 2).

DISCUSSION

While many studies have examined the effects of patch size and connectivity on species distributions, the influence of local biotic processes on these relationships remains poorly understood in most natural systems. Here we found that predators altered biogeographic predictions for a third of our focal species, indicating the substantial role that local top-down pressure can play in

moderating biogeographical constraints. More generally, our study demonstrates that the independent and interactive effects of predators and spatial drivers can be well-predicted by the a priori positioning of species along axes of local and regional constraint.

Our simple framework was remarkably successful in predicting when biotic interactions or spatial drivers should impact the distributions of our focal species. The positive effect of patch size and connectivity on the distributions of the four well-defended species with limited dispersal (Figs. 1, 2) supports the emerging use of dispersal ability to predict species' responses to spatial
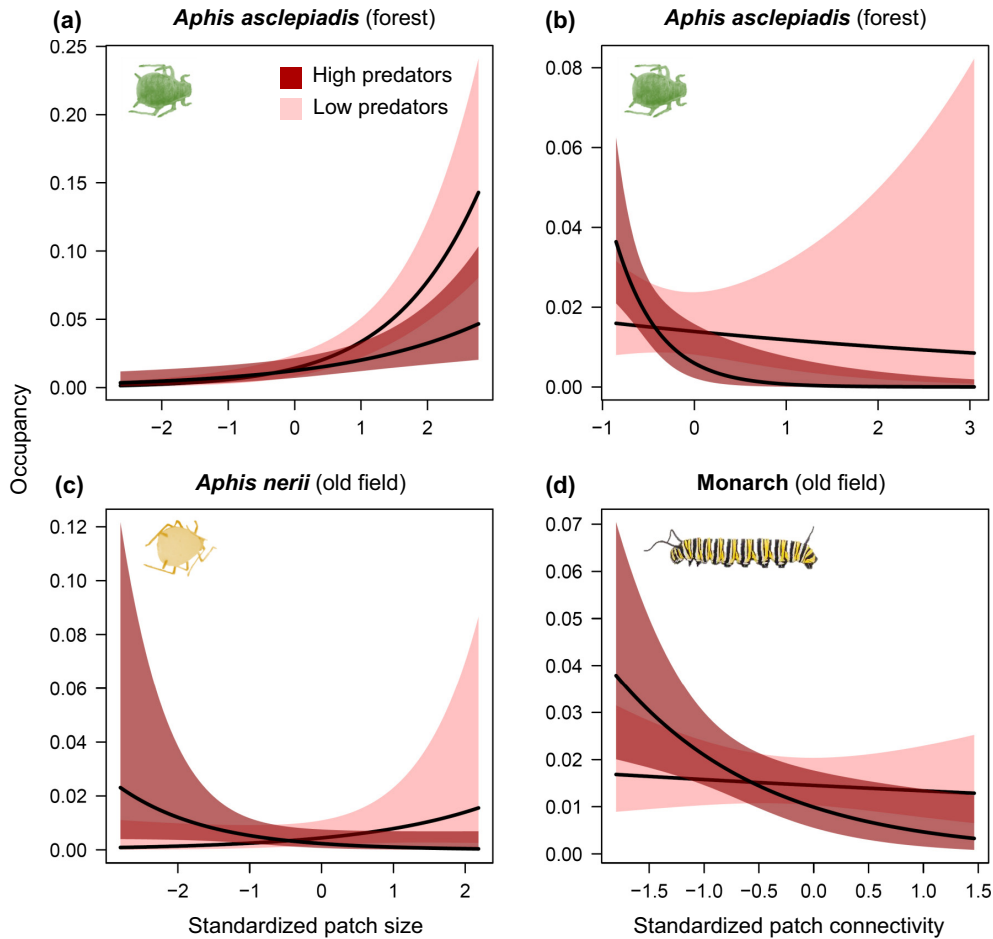
FIG. 3. Species with occupancy rates affected by both predators and spatial drivers. Lines are best fits from the statistical model and shading is a 95% confidence interval, with light pink and dark red set at low (10th quanatile) and high (90th quantile) predator abundances, respectively. Note the difference in *Y* axes among panels. [Color figure can be viewed at wileyonlinelibrary.com]

structure in patchy landscapes (e.g., De Bie et al. 2012, Jones et al. 2015). Similarly, we predicted that predators would mediate the distributions of four readily consumed species, and found supporting evidence for three of these species. In all cases, predators impacted distributions via interactions with spatial drivers, by dampening positive relationships or creating negative relationships with patch size or connectivity (Fig. 3). If not accounted for, predators could obscure the effects of spatial drivers, which might explain why biogeographic constraints do not emerge as important predictors in many taxa (Gilbert 1980, Prugh et al. 2008).

While our study cannot definitively determine the mechanisms underlying the interactive effects of predators and spatial drivers, experimental work has demonstrated that predators can alter the impact of spatial structure by changing colonization and extinction dynamics (Shurin 2001, Kneitel and Miller 2003, Resetarits et al. 2005). The negative impacts of predators can manifest both as direct consumptive effects, and as non-consumptive effects that include behavioral modifications and stress-induced

mortality and reductions in fitness (Preisser et al. 2005, McCauley et al. 2011). Through these mechanisms, predators can weaken the positive effects of patch size and connectivity on occupancy by reducing establishment of arriving species, by increasing extinction rates of species that do establish, or by causing active dispersers to avoid certain patches (Kneitel and Miller 2003, Resetarits et al. 2005, Howeth and Leibold 2010). These different predator effects are not mutually exclusive, and in this study, predators both dampened and reversed the effects of biogeographic constraints for poorly defended species (Fig. 3), suggesting that more than one of these interactive effects may play a role in shaping species distributions (Kennedy and Gray 1993, Resetarits et al. 2005).

The negative relationships with patch size and connectivity that emerged at high predator densities for three species are suggestive of active predator avoidance by these predator-sensitive species (Fig. 3b, c, d). For example, monarch butterflies are excellent dispersers and, rather than showing no association with patch size and connectivity, monarch caterpillars occurred most

often in small and isolated patches, especially when predators were present (Figs. 2h, 3d). Previous research indicates that monarch butterflies may choose to lay their eggs on small milkweed patches as a behavioral adaptation to seek refuge from predators or competitors, which could explain this result (Zalucki and Kitching 1982*a*, *b*). In addition, monarch caterpillars are negatively impacted by the latex induced by early season weevil feeding (Van Zandt and Agrawal 2004*a*), which could be why monarchs were rare in large forest patches where weevils were common (Fig. 2a, h). Although aphids have more limited dispersal than monarchs, some develop winged morphs in response to predators, indicating the potential for dynamic feedbacks between patch selection and predator abundance (Dixon and Agarwala 1999, Mehrparvar et al. 2013). The exploitation of spatial constraints by active dispersers that manifest as negative patch size and connectivity relationships is a phenomenon that is not included in many models, but could be integrated into future research.

Although the distributions of most species were well-predicted by our framework, there were two interesting departures that generate hypotheses for future study. Contrary to our predictions, there was no effect of predators on the distribution of one aphid species, *Myzocallis* (Fig. 2e, g), which contrasts with previous research suggesting that predators readily consume all three of these specialist aphid species (Smith et al. 2008). However, unlike the other two aphid species, *Myzocallis* lives on undersides of milkweed leaves and is light green in color (Smith et al. 2008), and our results raise the possibility that this cryptic habit of *Myzocallis* may be an effective strategy against invertebrate predators (Denno et al. 2003). A second departure from our expectations was the direct negative effect of connectivity on *Aphis asclepiadis* occupancy in old field patches (Fig. 2i). This species is considered more vulnerable than other aphids to competition and predation (Mooney et al. 2008, Smith et al. 2008), which it may offset by selecting more remote habitats. Both departures from our expectations provide hypotheses about divergent strategies among functionally-similar aphid species that, if tested experimentally, could help untangle the mechanisms underlying the coexistence of these close competitors (Mooney et al. 2008).

We contrasted two matrix types, forest and old field, to provide a broader scale look at how predators and spatial drivers shape the distributions of our focal species. Although our use of only one old field site and one forest site precludes general conclusions about the impact of different matrices on observed relationships, it is interesting to note that the factors driving species distributions differed between our two matrix types for most focal species (Table 2). As well, the matrix appeared to filter species at a broader scale, as five of our nine focal species were more common in one matrix type than the other (Table 2; Appendix S1: Fig. S3). These differences could have multiple underlying causes including the greater number of milkweed patches in the old field,

unmeasured differences in avian predators or micro-climate, or effects of the different landscapes surrounding each matrix. In either case, our results suggest that the inclusion of multiple replicated matrix types in future studies could reveal underappreciated landscape-scale patterns in metacommunities, and complements previous work demonstrating the importance of the matrix in shaping the distribution of species in fragmented habitats (Prevedello and Vieira 2010).

Although certain features of our study system should be considered carefully in extrapolating these results to other systems, the predictive framework used here has the potential to be applied more broadly to other types of metacommunities and local interactions. For example, local variation in bottom-up constraints such as resource quality could be used in place of, or in addition to, the top-down predator constraint we focused on here, particularly since responses to plant defenses are known to vary across herbivore species (Van Zandt and Agrawal 2004*b*, Gripenberg and Roslin 2007). The inclusion of resource quality as a local factor could be especially fruitful in systems such as ours where clonal plant growth has the potential to create substantial inter-patch differences in resource quality. Likewise, in aquatic systems in which habitat patches consist of ponds or lakes that vary in resource availability and quality, the inclusion of local bottom-up constraints could be particularly worthwhile (De Bie et al. 2012).

The lack of herbivore diversity in the milkweed system made it feasible for us to research and classify each species along axes of spatial constraint and predator susceptibility; however, less intensive methods could also be used to classify species in more diverse or less well-studied systems. For example, if dispersal ability or responses to certain plant defenses are known to be phylogenetically conserved, then in diverse communities, higher-order taxonomic groups such as families could be placed into a predictive framework like the one presented in Fig. 1 (Blomberg et al. 2003). While our inability to control for phylogeny due to our small number of focal species presents a limitation in that dispersal ability and susceptibility to predation may not be independent of evolutionary relationships, in more speciose communities, phylogenetic constraint on traits driving local and regional responses could serve as an efficient method for predicting species' responses. Similarly, trait-based approaches could be used in speciose communities as a short-cut for generating predictions. For example, differences in dispersal can be characterized by dispersal mode and individual height for plants (Thomson et al. 2011, Jones et al. 2015), while in animals, body size has been used to predict dispersal distance, competitive hierarchies and trophic interactions (Woodward and Hildrew 2002, De Bie et al. 2012). Such traits could provide a key to predicting species' local and regional constraints a priori in a broad array of metacommunities, just as they are increasingly used for understanding communities inhabiting continuous landscapes. If used more broadly, the approach presented here could

reveal predictable impacts of local interactions on species' responses to classic biogeographic constraints, and bring us closer to untangling the combined role of local and regional drivers in shaping ecological communities.

Literature Cited

Barber, J. R., and W. E. Conner. 2007. Acoustic mimicry in a predator–prey interaction. Proceedings of the National Academy of Sciences USA 104:9331–9334.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. Fitting linear mixed-effects models using lme4. arXiv preprint arXiv:1406.5823.

Bayne, E. M., and K. A. Hobson. 1997. Comparing the effects of landscape fragmentation by forestry and agriculture on predation of artificial nests. Conservation Biology 11:1418–1429.

Berenbaum, M. R., and E. Miliczky. 1984. Mantids and milkweed bugs: efficacy of aposematic coloration against invertebrate predators. American Midland Naturalist 111:64–68.

Blomberg, S. P., T. Garland, and A. R. Ives. 2003. Testing for phylogenetic signal in comparative data: behavioral traits are more labile. Evolution 57:717–745.

Caldwell, R. 1974. A comparison of the migratory strategies of two milkweed bugs, *Oncopeltus fasciatus* and *Lygaeus kalmii*. Pages 304–316 *in* B. Brown, editor. Experimental analysis of insect behaviour. Springer, Berlin, Germany.

De Bie, T., L. Meester, L. Brendonck, K. Martens, B. Goddeeris, D. Ercken, H. Hampel, L. Denys, L. Vanhecke, and K. Gucht. 2012. Body size and dispersal mode as key traits determining metacommunity structure of aquatic organisms. Ecology Letters 15:740–747.

Denno, R. F., C. Gratton, H. Döbel, and D. L. Finke. 2003. Predation risk affects relative strength of top-down and bottom-up impacts on insect herbivores. Ecology 84:1032–1044.

Dickson, R. 1959. Aphid dispersal over southern California deserts. Annals of the Entomological Society of America 52:368–372.

Dixon, A., and B. Agarwala. 1999. Ladybird-induced life–history changes in aphids. Proceedings of the Royal Society of London B: Biological Sciences 266:1549–1553.

Duffey, S., and G. Scudder. 1972. Cardiac glycosides in North American Asclepiadaceae, a basis for unpalatability in brightly coloured Hemiptera and Coleoptera. Journal of Insect Physiology 18:63–78.

Evans, E. W. 1983. The influence of neighboring hosts on colonization of prairie milkweeds by a seed-feeding bug. Ecology 64:648–653.

Gilbert, F. 1980. The equilibrium theory of island biogeography: Fact or fiction? Journal of Biogeography 7:209–235.

Grainger, T. N., and B. Gilbert. 2016. Dispersal and diversity in experimental metacommunities: linking theory and practice. Oikos 125:1213–1223.

Gravel, D., F. Massol, E. Canard, D. Mouillot, and N. Mouquet. 2011. Trophic theory of island biogeography. Ecology Letters 14:1010–1016.

Gripenberg, S., and T. Roslin. 2007. Up or down in space? Uniting the bottom-up versus top-down paradigm and spatial ecology. Oikos 116:181–188.

Guichard, S., D. J. Kriticos, A. Leriche, J. M. Kean, and S. P. Worner. 2012. Individual-based modelling of moth dispersal to improve biosecurity incursion response. Journal of Applied Ecology 49:287–296.

Hanski, I. 1994a. Patch-occupancy dynamics in fragmented landscapes. Trends in Ecology & Evolution 9:131–135.

Hanski, I. 1994b. A practical model of metapopulation dynamics. Journal of Animal Ecology 63:151–162.

Harrington, R., and L. Taylor. 1990. Migration for survival: fine-scale population redistribution in an aphid, *Myzus persicae*. Journal of Animal Ecology 59:1177–1193.

Harvey, E., and A. S. MacDougall. 2014. Trophic island biogeography drives spatial divergence of community establishment. Ecology 95:2870–2878.

Holt, R. D., G. R. Robinson, and M. S. Gaines. 1995. Vegetation dynamics in an experimentally fragmented landscape. Ecology 76:1610–1624.

Holyoak, M., and S. P. Lawler. 1996. Persistence of an extinction-prone predator-prey interaction through metapopulation dynamics. Ecology 77:1867–1879.

Howeth, J. G., and M. A. Leibold. 2010. Species dispersal rates alter diversity and ecosystem stability in pond metacommunities. Ecology 91:2727–2741.

Jones, N. T., R. M. Germain, T. N. Grainger, A. Hall, L. Baldwin, and B. Gilbert. 2015. Dispersal mode mediates the effect of patch size and patch connectivity on metacommunity diversity. Journal of Ecology 103:935–944.

Jones, V. P., and M. P. Parella. 1986. The movement and dispersal of *Liriomyza trifola* (Díptera; Agromyzidae) in a chrysanthemum greenhouse. Annals of Applied Biology 109:33–39.

Kennedy, M., and R. D. Gray. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the ideal free distribution. Oikos 68:158–166.

Kneitel, J. M., and T. E. Miller. 2003. Dispersal rates affect species composition in metacommunities of *Sarracenia purpurea* inquilines. American Naturalist 162:165–171.

Lawrence, W. 1988. Movement ecology of the red milkweed beetle in relation to population size and structure. Journal of Animal Ecology 57:21–35.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the Entomological Society of America 15:237–240.

Logue, J. B., N. Mouquet, H. Peter, and H. Hillebrand. 2011. Empirical approaches to metacommunities: a review and comparison with theory. Trends in Ecology & Evolution 26:482–491.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton University Press, Princeton, Connecticut, USA..

Malcolm, S. B. 1991. Cardenolide-mediated interactions between plants and herbivores. Pages 251–296 *in* G. A. Rosenthal and M. R. Berenbaum, editors. Herbivores: their interactions with secondary plant metabolites. Volume 1: The Chemical Participants. Academic Press, San Diego, USA.

Matter, S. F. 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation. Oecologia 105:447–453.

McCauley, D. E., J. R. Ott, A. Stine, and S. McGrath. 1981. Limited dispersal and its effect on population structure in the milkweed beetle *Tetraopes tetraophthalmus*. Oecologia 51:145–150.

McCauley, S. J., L. Rowe, and M.-J. Fortin. 2011. The deadly effects of "nonlethal" predators. Ecology 92:2043–2048.

McCoshum, S. M., S. L. Andreoli, C. M. Stenoien, K. S. Oberhauser, and K. A. Baum. 2016. Species distribution models for natural enemies of monarch butterfly (*Danaus plexippus*) larvae and pupae: distribution patterns and implications for conservation. Journal of Insect Conservation 20:223–237.

Mehrparvar, M., S. E. Zytynska, and W. W. Weisser. 2013. Multiple cues for winged morph production in an aphid metacommunity. PLoS One 8:e58323.

Mooney, K. A., P. Jones, and A. A. Agrawal. 2008. Coexisting congeners: demography, competition, and interactions with cardenolides for two milkweed-feeding aphids. Oikos 117: 450–458.

Nault, B. A., D. A. Shah, H. R. Dillard, and A. C. McFaul. 2004. Seasonal and spatial dynamics of alate aphid dispersal in snap bean fields in proximity to alfalfa and implications for virus management. Environmental Entomology 33:1593–1601.

Preisser, E. L., D. I. Bolnick, and M. F. Benard. 2005. Scared to death? The effects of intimidation and consumption in predator–prey interactions. Ecology 86:501–509.

Prevedello, J. A., and M. V. Vieira. 2010. Does the type of matrix matter? A quantitative review of the evidence. Biodiversity and Conservation 19:1205–1223.

Prugh, L. R., K. E. Hodges, A. R. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. Proceedings of the National Academy of Sciences USA 105:20770–20775.

Prysby, M. D. 2004. Natural enemies and survival of monarch eggs and larvae. Pages 27–38 *in* K. S. Oberhauser, and M. J. Soensky, editors. The monarch butterfly: biology and conservation. Cornell University Press, Ithaca, New York, USA.

Resetarits, W., C. A. Binckley, and D. R. Chalcraft. 2005. Habitat selection, species interactions, and processes of community assembly in complex landscapes. Pages 374–398 *in* M. Holyoak, M. Leibold, and R. D. Holt, editors. Metacommunities: spatial dynamics and ecological communities. University of Chicago Press, Chicago, Illinois, USA.

Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158:87–99.

Shurin, J. B. 2001. Interactive effects of predation and dispersal on zooplankton communities. Ecology 82:3404–3416.

Smith, R., K. Mooney, and A. Agrawal. 2008. Coexistence of three specialist aphids on common milkweed, *Asclepias syriaca*. Ecology 89:2187–2196.

St Pierre, M. J., and S. D. Hendrix. 2003. Movement patterns of *Rhyssomatus lineaticollis* Say (Coleoptera: Curculionidae) within and among *Asclepias syriaca* (Asclepiadaceae) patches in a fragmented landscape. Ecological Entomology 28:579–586.

Taylor, L., I. Woiwod, and R. Taylor. 1979. The migratory ambit of the hop aphid and its significance in aphid population dynamics. Journal of Animal Ecology 48:955–972.

Thomson, F. J., A. T. Moles, T. D. Auld, and R. T. Kingsford. 2011. Seed dispersal distance is more strongly correlated with plant height than with seed mass. Journal of Ecology 99: 1299–1307.

Torgersen, T. R., R. R. Mason, and H. G. Paul. 1983. Predation on pupae of Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunnough) (Lepidoptera: Lymantriidae). Environmental Entomology 12:1678–1682.

Underwood, N., S. Halpern, and C. Klein. 2011. Effect of host-plant genotype and neighboring plants on strawberry aphid movement in the greenhouse and field. American Midland Naturalist 165:38–49.

Urquhart, F., and N. Urquhart. 1978. Autumnal migration routes of the eastern population of the monarch butterfly (*Danaus p. plexippus* L.; Danaidae; Lepidoptera) in North America to the overwintering site in the Neovolcanic Plateau of Mexico. Canadian Journal of Zoology 56:1759–1764.

van Noordwijk, C. T., W. C. Verberk, H. Turin, T. Heijerman, K. Alders, W. Dekoninck, K. Hannig, E. Regan, S. McCormack, and M. J. Brown. 2015. Species–area relationships are modulated by trophic rank, habitat affinity, and dispersal ability. Ecology Letters 96:518–531.

Van Zandt, P. A., and A. A. Agrawal. 2004a. Community-wide impacts of herbivore-induced plant responses in milkweed (*Asclepias syriaca*). Ecology 85:2616–2629.

Van Zandt, P. A., and A. A. Agrawal. 2004b. Specificity of induced plant responses to specialist herbivores of the common milkweed *Asclepias syriaca*. Oikos 104:401–409.

Voigt, W., J. Perner, A. J. Davis, T. Eggers, J. Schumacher, R. Bährmann, B. Fabian, W. Heinrich, G. Köhler, and D. Lichter. 2003. Trophic levels are differentially sensitive to climate. Ecology 84:2444–2453.

Woodward, G., and A. G. Hildrew. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. Journal of Animal Ecology 71:1063–1074.

Zalucki, M., and R. Kitching. 1982a. Dynamics of oviposition in *Danaus plexippus* (Insecta: Lepidoptera) on milkweed, *Asclepias* spp. Journal of Zoology 198:103–116.

Zalucki, M., and R. Kitching. 1982b. Temporal and spatial variation of mortality in field populations of *Danaus plexippus* L. and *D. chrysippus* L. larvae (Lepidoptera: Nymphalidae). Oecologia 53:201–207.

Zhang, Y., L. Wang, K. Wu, K. A. Wyckhuys, and G. E. Heimpel. 2008. Flight performance of the soybean aphid, *Aphis glycines* (Hemiptera: Aphididae) under different temperature and humidity regimens. Environmental Entomology 37:301–306.

Supporting Information