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Multi-scale responses to warming in an experimental insect metacommunity

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Abstract

In metacommunities, diversity is the product of species interactions at the local scale and dispersal between habitat patches at the regional scale. Although warming can alter both species interactions and dispersal, the combined effects of warming on these two processes remains uncertain. To determine the independent and interactive effects of warming-induced changes to local species interactions and dispersal, we constructed experimental metacommunities consisting of enclosed milkweed patches seeded with five herbivorous milkweed specialist insect species. We treated metacommunities with two levels of warming (unwarmed and warmed) and three levels of connectivity (isolated, low connectivity, high connectivity). Based on metabolic theory, we predicted that if plant resources were limited, warming would accelerate resource drawdown, causing local insect declines and increasing both insect dispersal and the importance of connectivity to neighboring patches for insect persistence. Conversely, given abundant resources, warming could have positive local effects on insects, and the risk of traversing a corridor to reach a neighboring patch could outweigh the benefits of additional resources. We found support for the latter scenario. Neither resource drawdown nor the weak insect-insect associations in our system were affected by warming, and most insect species did better locally in warmed conditions and had dispersal responses that were unchanged or indirectly affected by warming. Dispersal across the matrix posed a species-specific risk that led to declines in two species in connected metacommunities. Combined, this scaled up to cause an interactive effect of warming and connectivity on diversity, with unwarmed metacommunities with low connectivity incurring the most rapid declines in diversity. Overall, this study demonstrates the importance of integrating the complex outcomes of species interactions and spatial structure in understanding community response to climate change.

KEYWORDS
climate change, connectivity, dispersal, herbivory, milkweed, species interactions, warming

1 | INTRODUCTION

The ongoing rise in global temperatures is precipitating dramatic changes in the earth's biota at a range of spatial scales (Walther et al., 2002). Locally, warming can accelerate species' physiological processes and biological rates (Brown, Gillooly, Allen, Savage, & West, 2004; Rall et al., 2012), with cascading impacts on population dynamics and species interactions (Dell, Pawar, & Savage, 2014; O'Connor, Gilbert, & Brown, 2011; Savage, Gillooly, Brown, West, & Charnov, 2004). Globally, widespread range shifts and extinctions are being projected and documented through mapping and observational approaches (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011;

Thomas, Franco, & Hill, 2006). However, there is a scarcity of climate change research focused at intermediate scales; despite the recognition that many species occupy networks of habitat patches, or metacommunities, only recently have ecologists begun investigating the effects of warming on the processes that govern the persistence and diversity of species living in patchy habitats (Thompson, Beisner, & Gonzalez, 2015; Yvon-Durocher et al., 2015). Metacommunity diversity is a product of species' interactions with their abiotic and biotic environments at the local scale, and movement between habitat patches at the regional scale (Leibold et al., 2004). Both of these processes have been shown to be sensitive to changes in temperature (O'Connor et al., 2011; Travis et al., 2013). Despite this, the combined impact of warming-induced changes to local community dynamics and inter-patch movement remains unknown. Integrating predictions for how warming alters local and regional metacommunity processes, and testing how these effects scale up to shape diversity in metacommunities, would provide a more complete understanding of the varied impacts of climate change on biological systems (Gilbert & O'Connor, 2013).

Metabolic theory predicts that the vital rates of herbivores should be more strongly temperature-dependent than those of primary producers, causing warming to strengthen plant-herbivore interactions at the local scale (Allen, Brown, & Gillooly, 2002; O'Connor, 2009; Savage et al., 2004). This increased top-down pressure can hasten resource depletion (Jiang & Morin, 2004; O'Connor et al., 2011), which for a single species of herbivore, can produce a large impact on host plants that precipitates herbivore population declines (Jiang & Morin, 2004; O'Connor et al., 2011). In multi-species communities, rapid resource depletion induced by warming can strengthen competitive interactions between consumers that may manifest as declines in abundances of a poorer competitor (Jiang & Morin, 2004) or reduced co-occurrence rates if species attempt to avoid or are excluded by one another (Gilbert & O'Connor, 2013; Gilpin & Diamond, 1982). In the absence of resource limitation to primary producers, however, there may be little cost of warming to herbivores if temperatures remain below thermal thresholds (O'Connor et al., 2011). In this case, resource depletion and competitive interactions will be weak and unaffected by warming, and warming-induced increases in physiological rates should translate into shorter development times, higher population growth rates and larger population sizes (Gilbert et al., 2014; Ritchie, 2000). The ultimate cost or benefit of warming for herbivore species is therefore likely to be context-dependent, and should rely critically on resource availability and competitive interactions.

The impact of warming on dispersal, and how this translates to a metacommunity-level response, also depends on a species' physiological responses and interactions with its abiotic and biotic environments within habitat patches and the inter-patch matrix (Travis et al., 2013). Temperature can alter dispersal rates directly by changing body size and behavior, or indirectly by prompting dispersal away from low-quality resources or antagonistic species interactions (Altermatt, Pajunen, & Ebert, 2008; Fronhofer, Klecka, Melián, & Altermatt, 2015; Travis et al., 2013). The ability for species to

successfully move between patches, or functional connectivity, could therefore be altered by temperature changes that affect a species' propensity or ability to move (Altermatt et al., 2008). Connectivity between patches allows poor dispersers to reach alternate habitat, allows species to reach patches containing their preferred habitat (species sorting), and allows individuals from high quality patches to supplement populations in poor quality patches (mass effects) (Leibold et al., 2004; Tilman, 1994). As a result, temperature-induced increases in functional connectivity could increase diversity at both local and regional scales within metacommunities (Cadotte & Fukami, 2005; Verreydt et al., 2012). Although previous experiments investigating the effect of warming on metacommunity dynamics have maintained tractability by warming local patches while manipulating dispersal rates (Limberger, Low-Décarie, & Fussmann, 2014; Thompson et al., 2015), allowing warming to simultaneously alter both local species interactions and species' movement between patches would provide a critical next step toward understanding the full impact of warming in spatially structured environments (Salt, Bulit, Zhang, Qi, & Montagnes, 2016).

In contrast to the positive effects of dispersal, moving across an inhospitable matrix with less food and more predators often carries a substantial risk of mortality (Lucas, Waser, & Creel, 1994). When increasing temperature causes individuals to be exposed to greater risk by increasing within-generation dispersal propensity, for example, a positive effect of warming on dispersal could decrease metapopulation sizes of constituent species. Temperature could therefore lower the persistence of species in a metacommunity even when it increases dispersal rates. However, typical experimental manipulations of dispersal that manually transfer individuals between patches involve either no, very low, or uniform risk of movement, making it impossible to distinguish the positive and negative impacts of changing dispersal rates (Grainger & Gilbert, 2016). Incorporating dispersal risk into experimental work could reveal a more realistic cost-benefit trade-off associated inter-patch movement, and a more accurate picture of how this will be impacted by warming.

The overall effect of warming on metacommunities is the product of costs and benefits of warming at the local scale, and how these feed back to dampen or amplify the costs and benefits associated with dispersal between patches (Gilbert & O'Connor, 2013). For example, if warming induces local declines in limited resources and intensifies competition; connectivity to neighboring patches that contain additional resources could become more important for maintaining species diversity. Conversely, the risk of dispersing across the matrix could outweigh any benefits of additional food resources and competitor avoidance achieved by leaving a local patch, especially if resources are not limited locally.

We used an experimental approach to test how warming affects local dynamics, dispersal and feedbacks between these two responses. We manipulated the temperature and connectivity of experimental two-patch metacommunities housing milkweed plants and the specialist herbivores that eat them to determine how warming affects (i) the strength of local species interactions (plant-insect and insect-insect), (ii) insect species' performance within a patch, (iii)

insect movement within and between milkweed patches, and (iv) the impact of connectivity on individual insect species performance and metacommunity diversity.

2 | MATERIALS AND METHODS

2.1 | Natural history

Common milkweed (*Asclepias syriaca*) is a perennial forb found in old fields across eastern North America. Milkweed is chemically defended with toxic cardenolides, and physically defended with trichomes covering the leaf surface and sticky latex expelled when leaves are damaged. Milkweed defenses (trichomes and latex) occur constitutively, and can be induced by herbivory (Ali & Agrawal, 2014; Van Zandt & Agrawal, 2004b; Woods, Hastings, Turley, Heard, & Agrawal, 2012). Milkweed grows primarily in old fields, in patches ranging from a few to thousands of plants (Grainger, Germain, Jones, & Gilbert, 2017).

As a result of its defenses, common milkweed hosts only eleven specialist insects capable of consuming it, five of which were included in this experiment: two species of aphid (*Aphis nerii* and *Aphis asclepiadis*), the long-horned milkweed beetle (*Tetraopes tetrophthalmus*; hereafter milkweed beetle), the small milkweed bug (*Lygaeus kalmii*; hereafter milkweed bug) and the monarch butterfly (*Danaus plexippus*). *A. nerii* and *A. asclepiadis* feed on milkweed phloem and can disperse short distances by crawling, or longer distances by producing winged morphs (Antolin & Addicott, 1991). While *A. asclepiadis* is almost always tended by mutualistic ants offering protection from predators, *A. nerii* is only sometimes anttended (Mooney, Jones, & Agrawal, 2008). The milkweed beetle consumes leaves, while the milkweed bug feeds primarily on milkweed seeds, and both species can fly short to moderate distances, up to tens of meters in a single flight (Caldwell, 1974; Matter, 1996; McCauley, Ott, Stine, & McGrath, 1981). Monarch caterpillars feed on milkweed leaves and crawl short distances between plants. All five species co-occur in our study area during the time period that our experiment was conducted (early July to late August), with some variation in the timing of their peak abundances: monarch caterpillars and *A. asclepiadis* abundances peak around late July, *A. nerii* abundances peak toward the end of August, while milkweed bugs and beetles have relatively low but stable abundances between June and September (Grainger, 2014). We selected these five species for their range of dispersal abilities (Grainger et al., 2017) and feeding guilds.

2.2 | Experimental set-up

In the summer of 2014, we built an array of experimental metacommunities at Koffler Scientific Reserve, in Southern Ontario (44°03′N, 79°53′W). We selected a flat, grassy site with no naturally growing milkweed and built metacommunities consisting of a cleared circular 1 m² plot covered with a cylindrical insect-proof cage (1.3 m high X 1.1 m diameter), and either connected to another cage by a mesh corridor (1 m high X 0.5 m wide and one of two lengths, described below) or left isolated (Fig. S1). Cages were made of wire garden fencing lined with aluminum insect screen (C.R. Lawrence, Vaughn, ON, USA) and topped with a fiberglass insect screen lid (Barton & Schmitz, 2009; Fig. S1). Each metacommunity was randomly assigned one of three levels of connectivity: totally isolated (not connected to another cage), low connectivity (connected to neighboring cage with a long, 6 m long corridor) or high connectivity (connected to neighboring cage with a short, 2 m long corridor; Fig. S1) and one of two levels of warming (unwarmed or warmed, described below) in a fully crossed design. We also had additional isolated unwarmed and warmed cages with plants only (no insects) as controls. This resulted in a total of eight treatments, each of which was replicated seven times in a blocked design. Two milkweed plants (see Methods below) were planted into each cage in July 2014 (hereafter, 1-year old plants), and an additional plant (approximately 15 cm tall with eight mature leaves) was planted in June 2015. This resulted in a total of three milkweed plants per cage, arranged in an equilateral triangle and spaced 30 cm apart.

Our warming treatment consisted of plastic sheeting (Home Hardware 3.3 mm polyethylene plastic film) stapled to the sides of cages and corridors with the tops left open to allow rain to enter (Barton & Schmitz, 2009). We selected the plastic type for its high transmittance of ultraviolet and visible light (Fig. S2). We monitored the temperature and humidity in cages and corridors daily using Hobo data loggers (Onset, Bourne, MA, USA) attached to sticks and set to log every half hour. We measured cage temperature at three heights (30 cm, 60 cm and 90 cm from the ground) and cage humidity at 60 cm. We rotated loggers between cages (alternating between unwarmed and warmed cages) every 24 hr, for a total of 72 cages logged over the course of the experiment. We measured corridor temperatures in the center of the corridor, at 30 cm high. In cages, warming raised average cage temperatures by 2.7°C during the daytime (9 a.m. to 9 p.m.), and 1.1°C overall (Fig. S3a,b). Our warming treatment also increased the average temperature variability observed daily (mean of the standard deviation of temperature measured from 9 a.m. to 9 p.m.) by 1.0°C (Fig. S3c). Our warming treatment had no effect on humidity (Fig. S3f). In corridors, the warming treatment raised temperatures by 0.8°C on average (Fig. S3d,e).

2.3 | Experimental plants and insects

Milkweed plants were grown from seed obtained from a commercial nursery, and were planted into experimental metacommunities at 8-week old (Supporting Information; Prairie Moon Nursery, Winona, MN, USA). *Aphis nerii*, *A. asclepiadis*, milkweed beetles, and milkweed bugs were collected from milkweed plants growing on the reserve, while monarch caterpillars were reared from eggs imported from International Butterfly Breeders Association breeders. Insects were kept in indoor cages with potted milkweed (*A. nerii*, *A. asclepiadis*, monarch caterpillars) or milkweed leaves and seeds (milkweed bugs),

or in outdoor cages with naturally growing milkweed plants (milkweed beetles) prior to being released into the experiment (Supporting Information).

In early July, we placed one monarch caterpillar, two milkweed beetles, two milkweed bugs, and 15 each of *A. nerii* and *A. asclepiadis* on the largest 1-year old plant in one plot per metacommunity (hereafter the plant that was "seeded" with insects). Each two-plot metacommunity connected by a corridor (ie, metacommunities in the low and high connectivity treatments) therefore had one plot into which all species were added, and one plot that had no insects at the beginning of the experiment. Monarchs and aphid populations that died within an initial 5-day acclimation period were replaced. To track dispersing individuals, we marked milkweed beetles (on elytra) and milkweed bugs (on pronotum) with unique identifiers (one or two small dots) using liquid correction fluid (Bic Quick-Dry Correctional Fluid). Marking did not interfere with wing expansion or flying.

Generalist arthropod predators (mainly spiders, but also ladybugs and stink bugs) were found throughout our study site. Because some milkweed specialists avoid or are vulnerable to predators, but were unable to disperse out of our isolated cages, we removed predators from cages at the beginning of the experiment. As removal of predators is rarely perfect, we consider this a predator reduction, and counted all predators in each cage halfway through the experiment to determine baseline predator abundances and to test for differences among treatments.

The experimental corridors contained plants and insects typical of old-field 'matrix' that occurs between milkweed patches at our field site. Corridor communities were primarily dominated by the grass *Bromus inermis*, which typically contains a diversity of herbivores and some predators, mainly spiders (Genua, Start, & Gilbert, 2017).

2.4 | Insect and plant surveys

We ran the experiment for 6 weeks, from early July to late August, 2015. We measured plant height, trichomes and latex 5 days before the start of the experiment and 1 day after the end of the experiment in order to quantitate plant growth, change in trichome density and change in latex exudation rate over the course of the experiment (see Supporting Information for detailed methods for trichomes and latex measurements). We considered plants to be dead when more than half the leaves had senesced.

We recorded the location of milkweed beetles and bugs and the location and body length of monarch caterpillars every day for the first 5 days of the experiment, and then three times a week thereafter, for a total of 22 insect surveys. We counted the number of aphids on each plant every 3 days starting after the initial replacement period, for a total of 17 aphid surveys. We also recorded the presence or absence of ants on each plant at each survey. All monarch caterpillars either died or pupated during the experiment, and we recorded the time to pupation and measured wing lengths of butterflies (a proxy for adult fitness) within 1 day of emergence from chrysalises.

2.5 | Statistical analysis

All statistical analyses were performed in R (version 3.2.4). We included block as a random factor in all analyses, and used the package 'lme4' to run linear mixed effects models (LMEs) and generalized linear mixed effects models (GLMEs), except when noted. For all analyses, we started with the most complex model, tested for interactions using a likelihood ratio test ('drop1' function), dropped all non-significant high-order interactions, and re-tested the simplified model. We present the highest order significant interaction or significant main effects from each model. Except where noted (two analyses for which connectivity treatments were grouped), there were $N = 7$ independent replicates (cages) of each treatment in all analyses.

We analyzed the effects of warming and the presence of insects on plants by comparing plants seeded with insects (the tallest plant in each isolated insect plot) to comparable plants never exposed to milkweed specialists (the tallest plant in each isolated control plot). We focused on four plant responses: growth (change in height), death, change in trichome density and change in latex exudation. We used LMEs for continuous responses (growth, trichomes, latex) and a binomial GLME for the binary responses (death), with warming and insects (presence or absence) as predictors, one of the four plant responses as the response, and the 'weights' function (nlme library) to account for heteroscedasticity of variance among treatments in the LMEs.

We analyzed the effect of warming on two types of insect-insect interactions: the probability of each species pair co-occurring on the same plant (a measure general competitive exclusion or avoidance) and the relationship between abundances of our two aphid species (a measure of competitive interactions between our two most closely related species). To determine whether warming affected the likelihood of two species occurring on the same plant within isolated plots seeded with insects, we summed the total number of surveys on which two species were found on the same plant and divided this by the total number of surveys on which both species were observed on milkweed (ie, we removed surveys for which one species was found on the ground, the cage wall, or not located). This gave us the rate of plant-level co-occurrence for each species pair. We compared this to a null expected co-occurrence rate, calculated as the likelihood of any two individuals of different species occurring on the same plant within a cage. The null expected co-occurrence took into account the observed plant mortality throughout the experiment and the frequency at which each aphid species, milkweed bugs and milkweed beetles occupied one, two or three plants within a cage at each time step (calculations in Supporting Information). The null expectation was 0.41 for species pairs that did not include aphids, 0.6 for species pairs that included *A. nerii* and 0.47 for species pairs that included *A. asclepiadis* (Supporting Information).

To determine whether warming affected the relative abundances of our two aphid species on shared plants, we ran an LME with *A. nerii* maximum population size and warming as predictors and *A. asclepiadis* maximum population size as the response. Because *A. nerii*

and *A. asclepiadis* population sizes were unexpectedly positively correlated (see Results), and we suspected an underlying effect of ant mutualists, we also analyzed the effect of ants on aphids by running separate LMEs for each aphid species with ant occurrence (number of surveys in which ants occurred on a plant, of a total of 17 aphid surveys) and warming as predictors, and maximum aphid population size as the response. Given the sedentary and colony-forming habit of aphids, for these analyses we only included data from plants in isolated plots that had aphids introduced. Ant occurrence and aphid population sizes were strongly positively correlated (see Results), so we included the number of ants observed in plots as a covariate to account for the variation across our replicates in all tests of warming effects on aphids (local-scale performance, metacommunity-scale performance and dispersal) (see Methods below).

We analyzed the impact of warming on the local-scale performance of each of our five insect species in isolated plots, with performance quantified according to the life history and demography of each species. For monarchs, we used survival rate as our primary metric of local performance, as all monarchs either died as caterpillars or survived to become butterflies. We also analyzed the effect of warming on monarch caterpillar growth rates, time to pupation, and butterfly wing length. For milkweed beetles and bugs, 80 of 84 individuals died before the experiment ended, and so we defined local performance for these two species as the number of days that an individual survived. Each individual was considered alive until the last day it was observed, and for each experimental replicate we took the average number of days surviving for the two milkweed beetles and two milkweed bugs. For aphids, we defined local performance as the maximum population size reached by each aphid species in each isolated treatment replicate. To account for the effects of ants on aphid abundances, we first ran a separate LME with ant occurrence as the predictor and the maximum population size reached by each species as the response. We then ran LMEs with warming as the predictor and residuals from this model as the response. To visualize species' responses on a common scale, we used model results to calculate standardized effect sizes (Cohen's *d*) with the package 'compute.es.'

We analyzed the effect of warming on dispersal, with dispersal quantified using species-specific measures that best represent each species. Because monarchs and aphids moved across corridors too infrequently to allow statistical analysis of cross-corridor dispersal (Table S1), we analyzed within-cage movements between plants (0.3 m) for these species. For each monarch caterpillar, we counted the total number of movements recorded from one survey to the next (off of a plant, onto a plant, or from one plant to another) and divided this by the number of days that caterpillar was alive to obtain a standardized dispersal metric. Because this analysis focused on within-cage movement, we grouped all connectivity treatments together (*N* = 21 for each of unwarmed and warmed treatments), and for the six caterpillars that moved across corridors (Table S1), we truncated the data at the date at which they left the seeded cage. We ran an LME with warming as the predictor and standardized dispersal as the response. Because we noticed a much higher

variance within the unwarmed cages that was driven by differences in dispersal rate between caterpillars that died and those that survived to pupation, we ran an additional LME with warming and survival (died or survived to become a butterfly) as the predictors, and standardized dispersal as the response.

Milkweed beetles and bugs moved between plants too frequently to capture within-cage movements in our thrice-weekly surveys, so we focused on cross-corridor dispersal for these two species. For each species, we counted the total number of moves across a corridor (total moves for both individuals) and standardized this by the average number of days that the two individuals survived. We ran LMEs with warming and connectivity (low and high connectivity only, as isolated plots did not permit cross-corridor dispersal) as predictors, and standardized dispersal as the response.

For each aphid species, we quantified dispersal as a binary response (whether or not aphids from seeded plants colonized any other plants within the same cage). For each aphid species, we considered whether warming or the population size on the seeded plant influenced dispersal. Warming and population sizes were correlated (see Results), so we tested these two effects separately using GLMEs with either warming and ants or the number of aphids (of that species) on the seeded plant as the predictors, and binary colonization as the response. We selected the best model (lowest AIC value) for each species. Because this analysis was focused on within-cage movement, we grouped all connectivity treatments together (*N* = 21 for each of unwarmed and warmed treatments).

We analyzed the combined effects of connectivity and warming on each species' performance at the metacommunity scale. We used the same metrics of performance for each species as in the local analysis (survival rates for monarchs, days surviving for milkweed beetles and bugs, and maximum population sizes for aphids), but included data from entire metacommunities (eg, maximum number of aphids totalled across cages seeded with insects and cages initially without insects) and included all three levels of connectivity in the analysis. We ran separate LMEs with warming and connectivity as predictors and the performance metric as the response. As with the local analysis, to account for the effects of ants on aphid abundances, we first ran separate LMEs with ant occurrence as the predictor and the maximum population size reached by each aphid species as the response. We then used the residuals from these models to run our final LMEs that had connectivity and warming as predictors, and the residuals of the initial ant model as the response.

To determine the effect of warming and connectivity on diversity, we calculated species richness (of a maximum of five species) within each metacommunity at each of the 19 thrice-weekly insect surveys. We first performed a linear regression for each metacommunity (experimental replicate) with intercepts forced through five (the initial richness of all metacommunities) to calculate the slope of the decline in richness over time and the standard error of that slope. We then ran a weighted LME that had warming and connectivity as the predictors, the slopes from the above model as the response, and that weighted the slopes by the inverse of their standard errors.

Finally, to ensure that our results were not impacted by inadvertent differences in predators among treatments, we tested the effect of our treatments on predator abundances using an LME with warming and connectivity as predictors and predator abundance as the response.

3 | RESULTS

The presence of insects had a negative effect on milkweed growth ($\chi^2 = 4.4$, $p = .036$; Figure 1a), while warming had a positive effect ($\chi^2 = 4.3$, $p = .039$). Insects increased milkweed mortality ($\chi^2 = 6.60$, $p = .01$; Figure 1b) and limited the increase in trichome density observed in control plants over the course of the experiment ($\chi^2 = 5.9$, $p = .01$; Figure 1c), whereas warming had no effect on either measure (both $p > .1$). Neither warming nor insects impacted latex exudation (both $p > .4$; Figure 1d). There were no interactions between insects and warming for any plant response (all $p > .2$), indicating that warming did not alter the impact of insects on any of these four milkweed responses (Figure 1).

Species co-occurrence rates were higher than expected by chance for all species pairs except for the milkweed bug-milkweed beetle pair (Figure 2a–c), and warming did not affect co-occurrence rates for any species pair (all $p > .05$). Likewise, there was a positive relationship between the maximum population sizes reached by *A. nerii* and *A. asclepiadis* ($\chi^2 = 28.6$, $p < .001$; Figure 2d), both aphid species were also positively associated with ants (both

$p < .001$, Fig. S4), and neither relationship was affected by warming ($p > .7$).

Warming improved the local-scale performance of three focal species and negatively impacted one species (Figure 3). For monarchs, warming increased survival rates ($\chi^2 = 4.5$, $p = .03$; Figure 3), increased growth rates ($\chi^2 = 8.13$, $p = .004$), decreased the time it took to pupate ($\chi^2 = 6.1$, $p = .01$) and had no effect on butterfly wing length ($\chi^2 = .005$, $p = .95$). Warming decreased the number of days that milkweed bugs survived ($\chi^2 = 4.7$, $p = .03$; Figure 3), and did not affect the number of days that milkweed beetles survived ($\chi^2 = 1.7$, $p = .19$; Figure 3). Warming increased the maximum population sizes reached by both *A. nerii* (warming $\chi^2 = 10.9$, $p < .001$; Figure 3) and *A. asclepiadis* (warming $\chi^2 = 6.5$, $p = .01$; Figure 3).

There was no effect of warming on monarch caterpillar within-cage movement ($p > .3$). Monarchs did however show an interactive effect of warming and survival status (whether or not an individual died during experiment or survived to pupation) on movement ($\chi^2 = 6.04$, $p = .014$); in unwarmed conditions, monarchs that died dispersed less (per day) than those that survived (Fig. S5). Neither warming nor connectivity affected daily cross-corridor movement by milkweed bugs or milkweed beetles (all $p > .1$). For *A. nerii*, the best dispersal model included warming and ants, and there was a positive effect of both on dispersal (AIC = 40.9; warming $\chi^2 = 4.5$, $p = .03$, ants $\chi^2 = 18.8$, $p < .001$). Population size was also a significant predictor of dispersal for this species (AIC = 46.0, $\chi^2 = 13.5$, $p < .001$), indicating that for *A. nerii*, warming effects on dispersal likely occurred via increased population size (Figure 4a). For *A. asclepiadis*
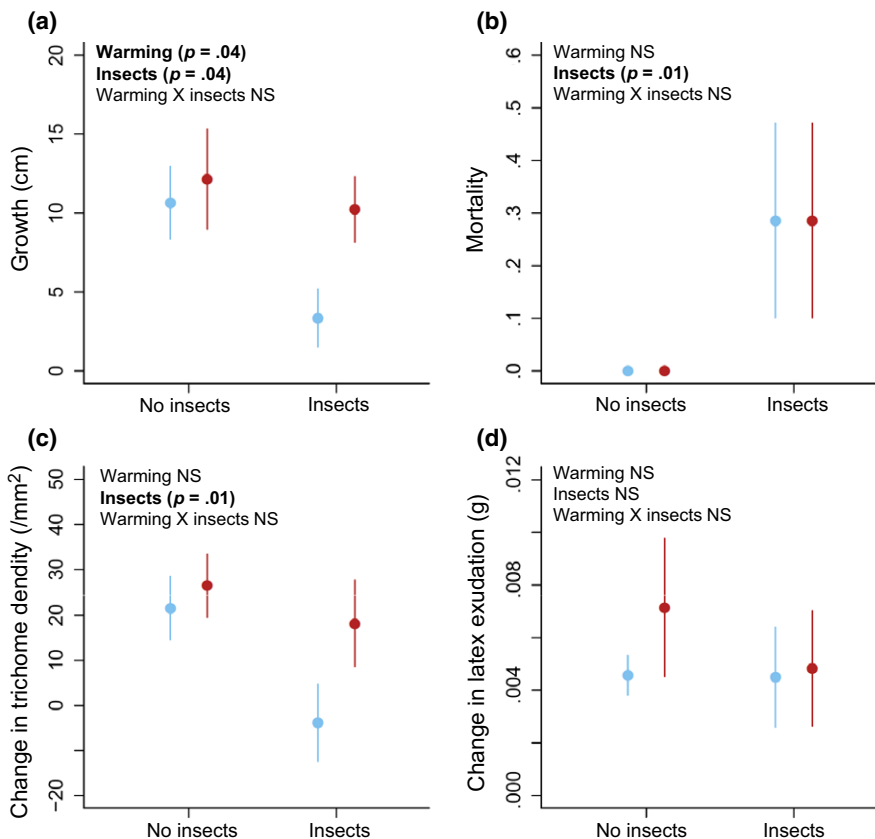

FIGURE 1 Plant responses. The effect of warming and the presence of insects on (a) plant growth, (b) plant mortality (the proportion of plants that died before the end of the experiment), (c) change in trichome density and (d) change in latex exudation. Panels a, c and d show the change in height, trichome density or latex exudation over the course of the 6-week experiment. Data are from the largest plant in each isolated plot; these plots were either kept free of milkweed specialists ("no insects") or were seeded with five milkweed specialists ("insects"). Unwarmed treatments are in light blue, and warmed treatments are in dark red. Data points are mean values ± one standard error [Colour figure can be viewed at wileyonlinelibrary.com]

FIGURE 2 Associations between species pairs. Rates of co-occurrence on the same plant for (a) species pairs that do not include aphids, (b) species pairs that include *A. asclepiadis* and (c) species pairs that include *A. nerii*. Panel (d) shows the positive correlations between the maximum population sizes of the two aphid species (*A. nerii* and *A. asclepiadis*). Horizontal dashed lines in panels a-c show the null expectation for each group, calculated to account for plant death over the course of the experiment, and for aphids occupying multiple plants at a single time point (see Methods). Error bars are 95% confidence intervals, so error bars not crossing the horizontal dashed line represent co-occurrence rates that are significantly different from the null expectation. Data for all panels are from plants in isolated plots that were seeded with five milkweed specialists. In all panels, warmed and unwarmed treatments are grouped because warming had no effect on associations between any species pair [Colour figure can be viewed at wileyonlinelibrary.com]
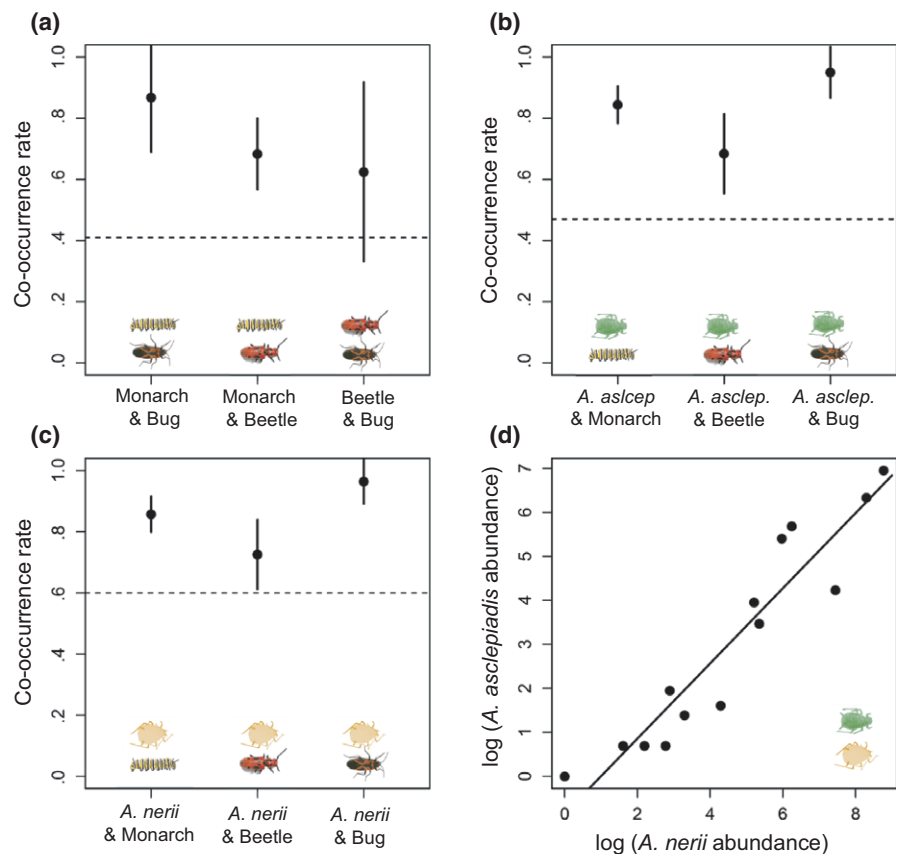
dispersal, the model with population size (AIC = 46.2, χ^2 = 15.7, $p < .001$) performed equally well as the model with warming and ants, although in the latter, only ants affected dispersal (AIC = 49.5; warming χ^2 = 0.6, $p = .43$, ants χ^2 = 14.3, $p < .001$). This indicates that for *A. asclepiadis*, population size but not warming impacted dispersal (Figure 4b).

At the scale of the entire metacommunity, the performance of three out of five insect species was affected by warming, connectivity or both (Figure 5). For monarchs, survival was higher in warmed conditions (χ^2 = 6.45, $p = .01$), and lowest in low connectivity metacommunities (χ^2 = 10.13, $p = .006$; Figure 5a). For milkweed bugs, there was an interactive effect of warming and connectivity on the number of days surviving (χ^2 = 11.4, $p = .0034$; Figure 5b); in isolated plots, milkweed bugs survived for longer in unwarmed conditions, while in low and high connectivity plots, they survived for longer in warmed conditions. For milkweed beetles, there was no effect of warming or connectivity on the number of days surviving (both $p > .6$, Figure 5c). For aphid maximum population size, *A. nerii* showed a positive effect of warming (χ^2 = 3.9, $p = .048$; Figure 5d) and no effect of connectivity (χ^2 = 3.5, $p = .17$), while *A. asclepiadis* showed no effect of either warming or connectivity (both $p > .2$; Figure 5e).

Species richness at the metacommunity scale declined from the initial five species as species died off throughout the experiment (Figure 6a,b). There was an interactive effect of warming and connectivity on the rate of this decline; in unwarmed conditions, richness declined most rapidly in low connectivity

metacommunities (ie, those connected by 6 m corridors), whereas connectivity did not alter rates of decline in warmed treatments (Warming × Connectivity interaction, χ^2 = 5.3, $p = .02$; Figure 6c). Predator abundances were unaffected by warming or connectivity (both $p > .2$).

4 | DISCUSSION

Our experiment integrated warming effects across multiple metacommunity scales by allowing both local processes and dispersal to be simultaneously impacted by warming. We hypothesized that the effects of warming on metacommunities would depend on the interplay between the local costs and benefits of warming and the large-scale risks and advantages of inter-patch movement. In our plant-insect system, competition for resources appeared to be weak, and warming mostly benefited insects locally. When local communities were connected into a larger metacommunity, inter-patch movement posed a species-specific mortality risk that increased mortality for two species when connectivity was low. These species-specific responses to warming at the local and metacommunity scales were shaped by life history and dispersal traits, and drove an interactive effect of warming and connectivity on metacommunity diversity. The net effect was a more rapid decline in diversity within this specialist insect guild in unwarmed, low connectivity metacommunities. Overall, this study illustrates how the impact of warming on species living in patchy habitats reflects complex responses at the species,
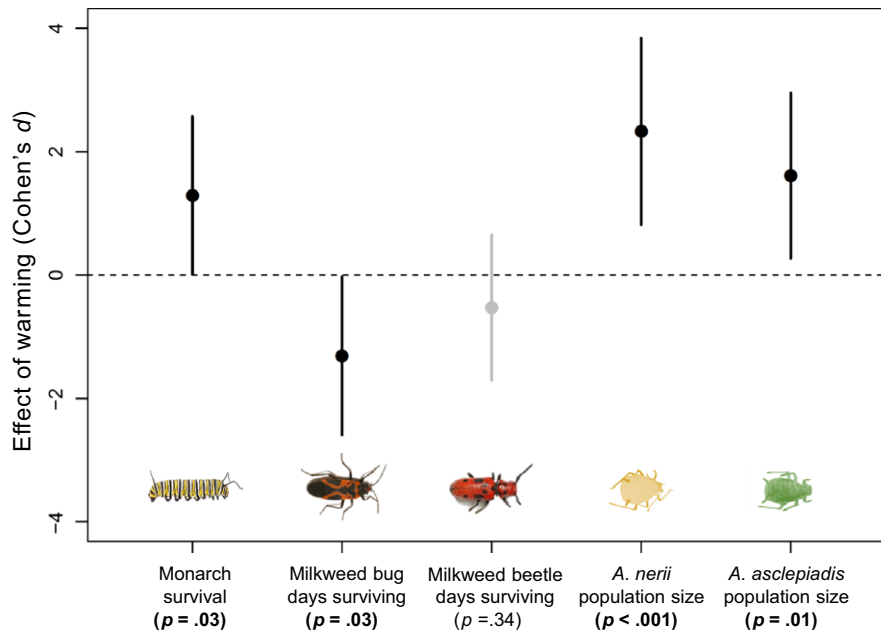
FIGURE 3 Local-scale performance of each species. Standardized effect of warming on the local-scale performance of each insect species. Positive values of Cohen's d represent positive effects of warming, and negative Cohen's d represent negative effect of warming. Performance is quantified according to each species' life history: survival rate for monarchs, the number of days that milkweed bugs and beetles survived (averaged over two individuals per plot) and the maximum population size reached by *A. nerii* and *A. asclepiadis* (the total number of aphids on all three plants in a plot) after accounting for the effect as ants as a covariate. Data are from isolated plots that were seeded with five milkweed specialists. Error bars are 95% confidence intervals, so black error bars not crossing zero (horizontal dashed line) are significant effects, while the gray bar crossing zero is a non-significant effects. *p* values are from LMEs and GLMEs [Colour figure can be viewed at wileyonlinelibrary.com]
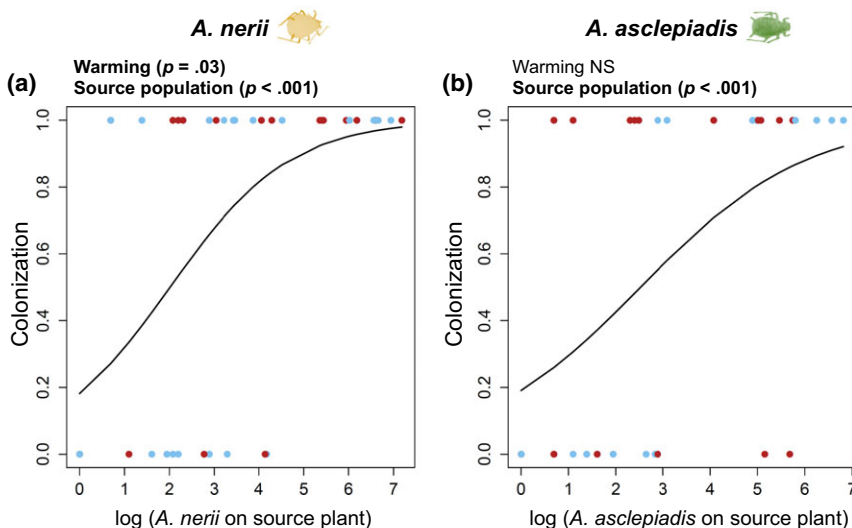

FIGURE 4 Aphid dispersal. (a) *A. nerii* and (b) *A. asclepiadis* dispersal as a function of the population size (of that species) on plants seeded with insects at the start of the experiment. Dispersal was quantified according to whether aphids colonized an unseeded plant within each cage (score = 1), or did not colonize any neighboring plants (score = 0). Unwarmed plots are as light blue dots, and warmed treatments are dark red dots [Colour figure can be viewed at wileyonlinelibrary.com]

community and metacommunity scales that can only be understood by integrating responses to warming across spatial scales.

We predicted that our focal insect species would respond negatively to warming if higher temperatures accelerated resource drawdown or intensified competitive interactions, but that they could benefit from warming if increased temperatures did not induce declines in the quantity or quality of the plant resource (Gilbert et al., 2014; O'Connor et al., 2011; Ritchie, 2000). We found support for

the latter scenario: while insects caused ~30% plant mortality and decreased plant growth, warming did not intensify these negative effects. Rather, warming increased plant growth, which appeared to offset any indirect negative impacts on plants that could have resulted from warming-induced changes in insect survival and population sizes (Figure 1a,b). Likewise, despite relying on a common resource, we found no indication that any of our focal insect species were actively avoiding competition, nor that our two aphid species
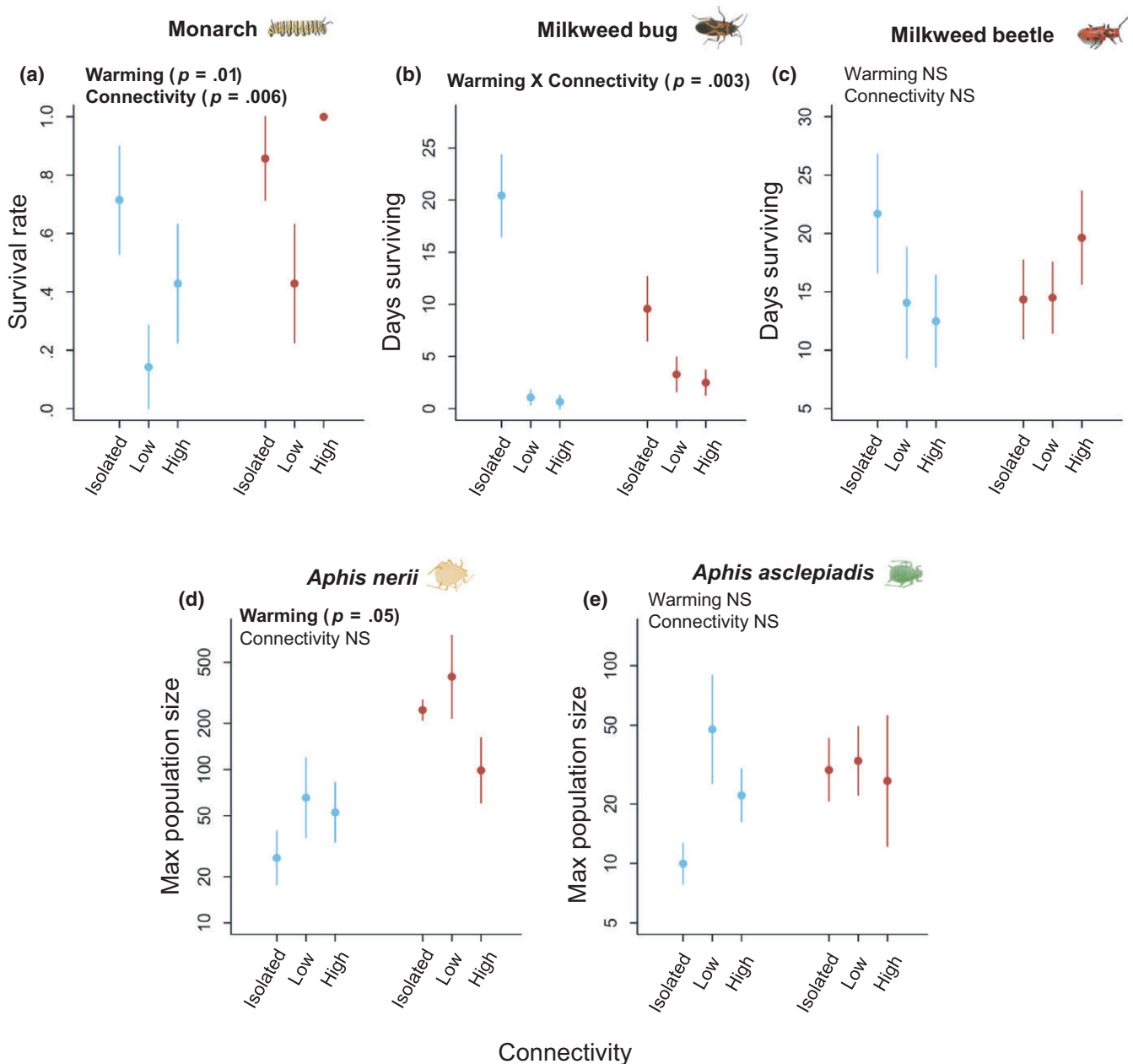
FIGURE 5 Metacommunity-scale performance of each species. The effect of warming and connectivity on the metacommunity-scale performance of each insect species. Performance is quantified according to each species' life history: (a) survival rate for monarchs, the number of days that (b) milkweed bugs and (c) milkweed beetles survived (averaged over two individuals per plot), and the maximum population size (the total number of aphids on all plants in a metacommunity) reached by (d) *A. nerii* and (e) *A. asclepiadis*. Connectivity levels are: "isolated" (cages not connected to another cage by a corridor), "low" connectivity (cages connected by a 6 m corridor) and "high" (cages connected by a 2 m corridor). Unwarmed treatments are in light blue and warmed treatments are in dark red. Data points are mean values ± one standard error. Panel d and e show back-transformed aphid population sizes after accounting for the effect of ant occurrence rates, and reported aphid results account for the effect of ants (see Methods)

were negatively affecting one another (Figure 2). On the contrary, almost all species pairs were more likely to co-occur on the same plant than expected by chance, and abundances of our two aphid species were positively correlated (Figure 2). While the insect-induced plant mortality we observed is indicative of some degree of resource limitation in this system, the patterns of insect co-occurrence and correlated abundances suggest that here, competition for

resources was not a major driver of insect behavior or population growth (Figure 2). Indeed, this lack of resource competition occurred although the size and number of experimental plants within each of our plots created smaller patches than what is often found in the wild, and our patches were stocked with relatively high densities of milkweed specialists (Grainger et al., 2017; Van Zandt & Agrawal, 2004a). Explicitly testing the role of resource availability and
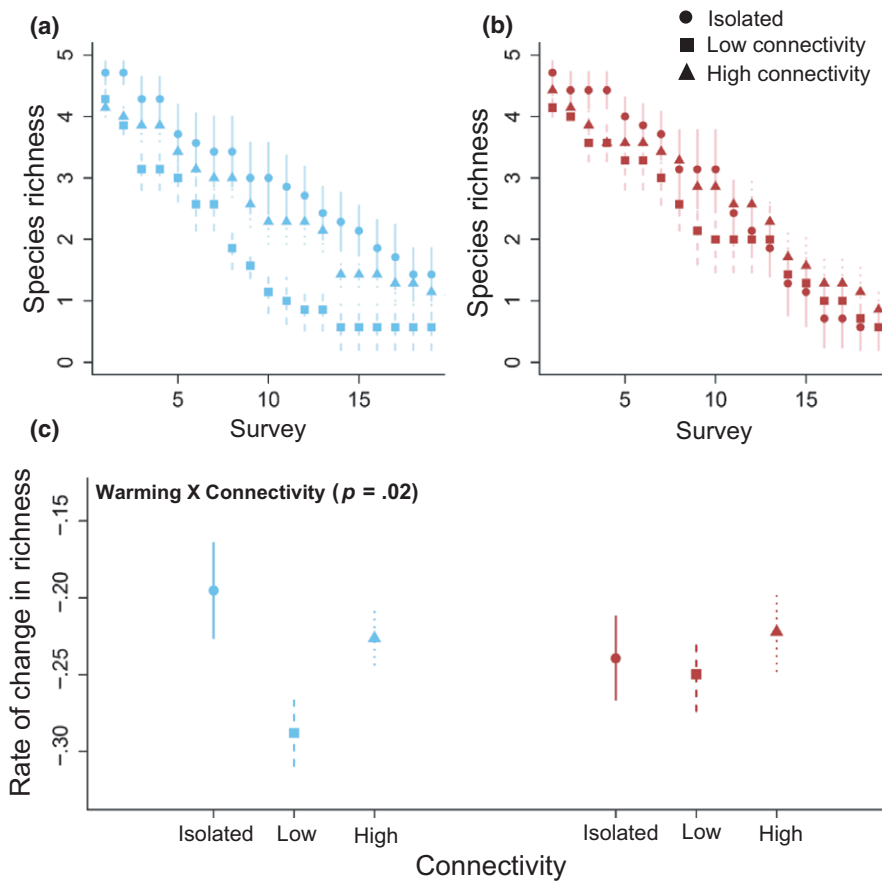
FIGURE 6 Metacommunity diversity. The effect of warming and connectivity on the decline in metacommunity-scale species richness over the course of the experiment (19 surveys) in metacommunities initially seeded with five milkweed specialists. Panel (a) shows unwarmed treatments and panel (b) shows warmed treatments. Panel (c) shows the slopes of the lines in panels a and b (with intercepts forced through five, which was the initial richness of all metacommunities). Connectivity levels are: "isolated" (cages not connected to another cage by a corridor), "low" connectivity (cages connected by a 6 m corridor) and "high" connectivity (cages connected by a 2 m corridor). Unwarmed treatments are in light blue and warmed treatments are in dark red. Error bars show ± one standard error [Colour figure can be viewed at wileyonlinelibrary.com]

resulting strength of competitive interaction strength in driving warming responses would require comparisons across multiple resource levels, which would be a worthwhile avenue for future research (O'Connor, Piehler, Leech, Anton, & Bruno, 2009). In this study, other factors may have been more important determinants of insect location than the presence of competitors; for example, bottom-up differences in microhabitat quantity and quality, such as plant size and genotype, are known to be important drivers of preference and performance of milkweed specialists (Mooney & Agrawal, 2008; Van Zandt & Agrawal, 2004a). Likewise, for aphids that engage in mutualistic interactions with ants by providing a honeydew reward, the benefits of protection against predators can be substantial, and may be a stronger driver of aphid abundances than negative aphid-aphid interactions (Fig. S4; Mooney and Agrawal (2008), Smith, Mooney, and Agrawal (2008)).

Locally, warming increased monarch survival and population sizes of both aphid species, but decreased the longevity of milkweed bugs (Figure 3). Warming experiments have reported both positive and negative effects of warming on species performance, with the direction of these effects depending on species identity, the ranges of temperatures used, the individual or population response of interest, and the nature and strength of species interactions (Bale et al., 2002; Barton & Schmitz, 2009; Gruner et al., 2017; Jiang & Morin, 2004; O'Connor, 2009; Walker et al., 2006). When resource limitation or temperature stress do not limit population growth, warming can accelerate reproductive rates and induce larger populations of

species with rapid reproduction and overlapping generations such as aphids (Barton & Ives, 2014; Ju, Zhu, Gao, Zhou, & Li, 2015). Indeed, we saw a positive effect of warming on aphid abundances (Figure 3). Likewise, the accelerated growth and development we observed for monarchs is a common response to warming that, when scaled up to the community level, can have implications for species interactions such as herbivory and predation (Gillooly, Charnov, West, Savage, & Brown, 2002; Yang & Rudolf, 2010). For example, the decreased time to monarch pupation in warmed conditions may have helped caterpillars avoid the high mortality rates incurred at early larval stages from predation and desiccation (Bale et al., 2002; Prysby, 2004). In contrast to the positive warming effects on aphids and monarchs, milkweed bugs suffered shorter longevity at higher temperatures. While it is possible that increased competitive pressure from aphids and monarchs with warming precipitated the more rapid death of milkweed bugs via indirect competitive effects, the lack of avoidance or exclusion between these species makes this unlikely (Figure 2). Rather, this negative response may reflect accelerated ectotherm development with warming that can hasten death (Amarasekare & Savage, 2012). Overall, the local effects of warming observed here support the growing recognition that predicting the impact of climate change on ecological communities will necessitate integrating responses that span multiple levels of organization, including developmental rates, population growth rates and species interactions (Amarasekare & Savage, 2012; Brown et al., 2004; Gilman, Urban, Tewksbury, Gilchrist, & Holt, 2010).

Warming altered dispersal indirectly for two species, but did not result in the large increases in dispersal predicted if warming-induced resource declines prompt species to leave the host patch en masse (Benard & McCauley, 2008; Zera & Denno, 1997). For *A. nerii*, the warming-induced increase in dispersal (Figure 4) was likely the result of larger population sizes in warmed conditions (Figure 3), as crowding is a well-documented cue for aphid dispersal (Müller, Williams, & Hardie, 2001). For monarch caterpillars, warming altered the relationship between survival and movement (Fig. S5). This could either indicate that in unwarmed conditions, higher quality individuals are more likely to both move and survive, or that moving between plants is advantageous because it facilitates the selection of superior resources or predator-free areas. While our study does not have the power to determine the directionality of this relationship or its underlying mechanism, this result raises the intriguing possibility that the benefits of movement can be temperature-dependant, and suggests an avenue of future research. On a broader spatial scale, climatic changes in wind currents or weather events could alter long-distance dispersal patterns of these species in ways not captured here, for example, by shifting the arrival times of species that overwinter further south and disperse northward to our site each spring (monarchs and *A. nerii*) (Travis et al., 2013). On a broader temporal scale, shifts in the emergence times of the species that overwinter in our region (milkweed bug, milkweed beetle and *A. asclepiadis*) could also alter the performance and competitive dynamics of these species (Williams, Henry, & Sinclair, 2015). Despite limitations inherent in the spatial and temporal scale of our study, our results support a growing body of evidence that dispersal responses to warming are often context and condition-dependent (Benard & McCauley, 2008; Fronhofer et al., 2015; McCauley & Mabry, 2011; Müller et al., 2001).

There was a substantial species-specific mortality risk in metacommunities connected by corridors, that, when combined with positive local effects of warming, scaled up to shape species-specific responses to warming and connectivity. Both monarch caterpillars and milkweed bugs had lower survival in connected metacommunities (Figure 5). For these two species, attempts to move across corridors to a neighboring milkweed patch may have been thwarted by generalist predators that occur within the grass matrix at this site, or individuals may have simply died before reaching their destination. In contrast, large aphid populations incur little cost from each departing individual that are unsuccessful in crossing the matrix, and milkweed beetles may have been better able to reach neighboring patches or return to their original patch as a result of their superior dispersal ability (Lawrence, 1988; Matter, 1996). Although connectivity is widely viewed as beneficial to metacommunity diversity because neighboring patches provide refuge from resource limitation, predators or competitors (Cadotte, 2006; Leibold et al., 2004), our results demonstrate that in cases where local conditions are favorable, the risk of dispersing can outweigh the benefits. This risk associated with moving between habitat patches is widely recognized in dispersal ecology (Bonte et al., 2012), yet methods used to manipulate dispersal in metacommunity experiments often eliminate

dispersal risk or homogenize risk across species (Grainger & Gilbert, 2016). The effects of this important feature of spatially structured environments on species and community-level responses are therefore likely to be under-reported. Continuing to incorporate dispersal risk into experimental work will provide a more complete picture of how inter-patch movement affects local and regional diversity.

The combined effects of local warming responses and inter-patch connectivity scaled up to shape diversity in our metacommunities (Figure 6). Specifically, we saw more rapid declines in species richness in unwarmed metacommunities with low connectivity, compared to isolated or well-connected communities (Figure 6). Higher temperatures offset the disadvantage of low connectivity; warming increased the survival of monarchs and milkweed bugs in metacommunities connected by corridors, while in unwarmed connected metacommunities, these species were lost early in the experiment (Figure 5). Taken separately, warming experiments that usually report declines in diversity at higher temperatures (Gruner et al., 2017), and metacommunity experiments that typically find increases in diversity at higher dispersal rates (Cadotte, 2006; Grainger & Gilbert, 2016), suggest that warming could induce declines in diversity that could be offset by connectivity. However, we found the opposite, indicating an interesting and surprising interaction between warming and connectivity at intermediate scales. Compared to isolated communities, low connectivity treatments that allow for dispersal experienced more rapid declines in diversity at ambient temperatures, and these losses were offset by warming. Recent experiments testing the combined influence of warming and connectivity on metacommunity diversity have likewise hypothesized that connectivity could mitigate negative impacts of warming, and have also failed to find support for this hypothesis; instead, these studies report declines in diversity at higher temperatures that were not mitigated by higher inter-patch dispersal rates (Limberger et al., 2014), or positive effects of dispersal at ambient but not warm temperatures (Thompson et al., 2015). Although these experiments differ from ours in their methodology and study organisms, when considered together these experiments demonstrate that responses to warming at the metacommunity scale can produce surprising outcomes. Although testing responses to warming across multiple spatial scales while capturing the range of local warming effects and the costs and benefits of dispersal remains a challenge, this study suggests a way forward for better integrating spatial structure into climate change research.

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