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Community diversity outweighs effect of warming on plant colonization

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Abstract

Abiotic environmental change, local species extinctions and colonization of new species often co-occur. Whether species colonization is driven by changes in abiotic conditions or reduced biotic resistance will affect community functional composition and ecosystem management. We use a grassland experiment to disentangle effects of climate warming and community diversity on plant species colonization. Community diversity had dramatic impacts on the biomass, richness and traits of plant colonists. Three times as many species colonized the monocultures than the high diversity 17 species communities (~30 vs. 10 species), and colonists collectively produced 10 times as much biomass in the monocultures than the high diversity communities (~30 vs. 3 g/m^2). Colonists with resource-acquisitive strategies (high specific leaf area, light seeds, short heights) accrued more biomass in low diversity communities, whereas species with conservative strategies accrued most biomass in high diversity communities. Communities with higher biomass of resident C4 grasses were more resistant to colonization by legume, nonlegume forb and C3 grass colonists, but not by C4 grass colonists. Compared with effects of diversity, 6 years of 3°C-above-ambient temperatures had little impact on plant colonization. Warmed subplots had ~3 fewer colonist species than ambient subplots and selected for heavier seeded colonists. They also showed diversity-dependent changes in biomass of C3 grass colonists, which decreased under low diversity and increased under high diversity. Our findings suggest that species colonization is more strongly affected by biotic resistance from residents than 3°C of climate warming. If these results were extended to invasive species management, preserving community diversity should help limit plant invasion, even under climate warming.

KEYWORDS

biotic resistance, Cedar Creek Ecosystem Science Reserve, climate change, community diversity, experimental warming, functional traits, global environmental change, long-term grassland experiment, plant species colonization, species invasion

1 | INTRODUCTION

A key prediction and observation of abiotic environmental change, including global warming, is increased levels of species incursion, including invasion by exotic species (Auffret & Thomas, 2019; Catford & Jones, 2019; Hulme, 2017; Liu et al., 2017; Sorte et al., 2013) and colonization of previously absent natives (Essl et al., 2019; Inderjit, Catford, Kalisz, Simberloff, & Wardle, 2017). However, abiotic change can reduce the diversity of historical communities (Harrison, Gornish, & Copeland, 2015) and low diversity

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can facilitate species colonization (Fargione & Tilman, 2005). This prompts a series of questions: Does abiotic environmental change strongly and directly facilitate colonization of new species? Does colonization usually occur in the wake of abiotic-driven reductions in the diversity of resident communities? Or is it a combination of the two, where abiotic change alters the competitive environment, enabling new species to colonize and outcompete resident species?

Abiotic environmental change could facilitate the colonization of new species in three ways. First, it may shift the abiotic conditions of a site such that a new suite of species, previously intolerant of the site's abiotic conditions, can colonize and establish (Pathway A, Figure 1). Second, established resident species intolerant of the modified abiotic conditions may be filtered out, leading to a decline in resource uptake and biotic resistance, increasing opportunities for colonization of new species (Pathway B; Catford, Downes, Gippel, & Vesk, 2011).

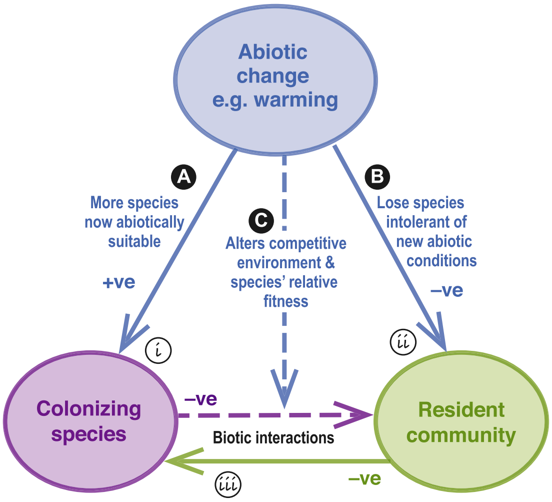

FIGURE 1 Conceptual figure showing how changes in abiotic conditions and established resident communities can facilitate colonization of new species via environmental filtering (Pathway A, blue arrow and white letter), environmental filtering and associated reductions in biotic resistance (Pathway B) and through changed competitive environments (Pathway C). Pathways A and B capture the process of environmental filtering, which—when strictly applied—relates to species' abiotic tolerances only (Kraft et al., 2015). Pathways B and C are affected by biotic interactions and hence biotic resistance of resident communities. Resident species and colonizing species could both be excluded via Pathways A and B, but Pathway A may enable colonization of 'new' species that are present in the regional species pool, potentially facilitating increased turnover. The green and purple horizontal arrows represent competition among residents and colonists. Pathway C captures the way in which environmental conditions modulate biotic interactions, changing the relative fitness of competing species. The positive (+ve) and negative (−ve) signs indicate facilitative or inhibitive effects respectively. In this study, we examine relationships (i), (ii) and (iii) (solid arrows), which contribute to Pathways A and B. We do not interrogate Pathway C or effects of colonists on resident communities (dashed arrows) because their effects are minimized in the experiment through regular removal of non-sown colonists [Colour figure can be viewed at wileyonlinelibrary.com]

Third, abiotic change may affect the relative fitness of resident and colonizing species in that site, altering biotic interactions and giving newcomers a competitive advantage over residents that had not occurred previously (Pathway C; Kraft et al., 2015; Liu et al., 2017).

Most studies investigating impacts of abiotic environmental change on the colonization and invasion of new species do not isolate effects of these three pathways (Catford et al., 2011; Kraft et al., 2015; Seabloom et al., 2015). This is largely because abiotic change and reductions in biodiversity often co-occur (Bansal & Sheley, 2016; Gedan & Bertness, 2009), including in experiments (Haeuser, Dawson, & van Kleunen, 2017; Harpole et al., 2016). The pathways are not mutually exclusive, but it is important to determine their relative influence because they will likely affect the functional composition of communities in different ways, will indicate the inevitability of species turnover following abiotic change and will influence optimal management responses. For example, if abiotic change drives species colonization directly (Pathway A), the functional traits of colonists would reflect environmental filtering and therefore be biased towards certain trait values, skewing the community in that direction (e.g. towards C4-photosynthetic and away from C3-photosynthetic pathways under climate warming, Bremond, Boom, & Favier, 2012). Conversely, if colonization occurs in the wake of local extinctions and associated reductions in resource use (Pathway B), successful colonists may be poor competitors and have traits associated with high resource acquisition (Reich, 2014). On a practical level, if colonization is driven or facilitated by reductions in the diversity or competitive abilities of resident species (Pathways B or C), then management that maintains or augments resident diversity could help limit biotic change (Funk, Cleland, Suding, & Zavaleta, 2008), even under modified abiotic conditions.

Here we use a full factorial grassland experiment where plant species richness and membership of sown communities were maintained under experimental warming to examine how community diversity and warming, together and in isolation, affect colonization of nonresident species. Using a unique experiment that isolates abiotic effects of warming from indirect biotic effects, we focus on relationships (i), (ii) and (iii) in Figure 1, which contribute to Pathways A and B, to specifically ask how diversity and warming affect: the extent of colonization by nonresident species—as indicated by the biomass and number of non-sown species that colonized the plots without human intervention; and the type of species that were successful—as indicated by colonists' functional group (C4 grass, C3 grass, legume or nonlegume forb) and functional traits (seed mass, specific leaf area [SLA], leaf dry matter content [LDMC] and plant height). The grassland experiment allows us to examine effects of varying levels of diversity (spanning 1–17 species, in communities that have been established for 21 years) and three levels of warming (ambient, +1.5°C and +3°C, maintained for 6 years) on the colonization of non-sown species over one growing season. We do not test Pathway C in Figure 1 because colonists were regularly removed in the study experiment, minimizing effects of colonists on resident species (purple arrow in Figure 1), and because sown community membership (i.e. species identity but not relative abundances, Cowles, Wragg, Wright, Powers, & Tilman, 2016) remained unchanged, minimizing the potential for warming-induced changes in biotic interactions. However, it is important to consider implications of nullifying Pathway C when interpreting our results.

2 | MATERIALS AND METHODS

2.1 | Warming and diversity experiment

Our diversity-and-warming grassland experiment was nested within an existing biodiversity experiment at Cedar Creek Ecosystem Science Reserve, Minnesota, USA (45.4°N, 93.2°W). The biodiversity experiment was established in 1994 by sowing 168 9 m × 9 m plots with perennial grassland species randomly selected from a pool of 17 locally occurring native species (three species of C3 grasses, four species of C4 grasses, five species of legumes and five species of nonleguminous forbs, Table S1). All plots received 10 g/m^2 of pure live seed in May 1994. Species were hand-sown at equal densities. Before seeds were sown, the experimental site was treated with herbicide and burned in August 1993, had the top 6–8 cm of soil removed to reduce the soil seed bank and was ploughed. Further details can be found in Tilman et al. (2001).

From 2009, 32 plots were used in the diversity and warming experiment (Cowles et al., 2016). The 32 plots included 12 monoculture plots, two 2 species plots, three 3 species plots, five 4 species plots, one 5 species plot, four 15 species plots, four 16 species plots and one 17 species plot; the plots only contained herbaceous species. Within each of the 32 plots, 2.5 m × 3 m subplots were warmed with infrared heaters to give ambient (0 W), low (600 W) or high (1,200 W) warming treatments (Cowles et al., 2016). The heaters (or metal shades for the control subplots) were suspended from metal frames at a height of 1.8 m above the ground. Heaters were on 24 hr/day through the duration of the growing season (March through November). In situ soil temperature measurements indicated that the warming treatments increased bare ground soil temperature at 1 cm depth by approximately 1.5 and 3°C above ambient in the low and high warming treatments, though the actual warming would depend on wind, time of day, plot productivity, soil moisture and soil depth (Cowles et al., 2016 and references therein). Sown communities were maintained by removing all non-sown species by hand from all plots in early June and July of each growing season (seeds were only sown at the start of the experiment in 1994; none of the sown species were subsequently re-sown). We call the sown assemblages the ‘sown communities’ throughout the manuscript (see Section 3 for effects of warming on the sown communities).

To quantify colonization by non-sown species (hereon colonist species) into the experimental plots, in 2014, we sorted the above-ground biomass of all plants removed through weeding to species-level, dried the sorted samples at 60°C for at least 48 hr and weighed them. The composition and above-ground biomass of each subplot was estimated by clipping a 0.1 m × 2.5 m long strip in each subplot in late summer, which was then sorted to species, dried and weighed; the clip strips included some biomass of colonist species that had been missed through weeding. The biomass of all sown and colonist species in the subplots was converted to g/m^2. Plots were burned each spring before plant growth had begun. As such, the harvested biomass indicates annual above-ground net primary productivity, minus any biomass removed by small mammal or insect herbivores.

The climatic conditions in 2014 were similar to recent (2009–2014, i.e. the period of this experiment) and long-term (1963–2018) averages for the region based on daily temperature and rainfall measurements taken at Cedar Creek (Figure S1, Table S2).

2.2 | Plant traits

We used the literature (Tilman, 1997; USDA, NRCS, 2019) and field observations to classify all 92 taxa observed in the study based on their lifespan (annual and biennial OR perennial), functional group (C3 grass, C4 grass, legume, nonleguminous forb) and biogeographic origin (native OR non-native to Minnesota; seven taxa were of unknown origin; Table S1).

In the summers of 2014 and 2015, we measured maximum vegetative height of taxa growing naturally at Cedar Creek (≥5 individuals/taxa; Catford et al., 2019; Pérez-Harguindeguy et al., 2013). We measured LDMC (mg/g) and SLA (mm^2/mg; ≥5 leaves/taxon) using ImageJ (rsb.info.nih.gov/ij/). Seeds from ≥5 plants growing at Cedar Creek or sourced from local suppliers (Prairie Moon Pty Ltd, Prairie Restorations Pty Ltd) were dried and weighed (three replicates/taxon, ≥20 seeds/replicate). Traits were measured from plants growing in polyculture under ambient conditions within 1 km of the study site. Across the four traits analysed, we had trait data for ≥93% of the 92 species recorded in the survey in 2014 (98% for SLA, 93% for LDMC, 93% for height, 97% for seed mass; Table S1). This included complete trait coverage for 16 of the 17 sown species. We also collected trait data for grassland species that were not observed in the experimental plots as either colonists or sown species (i.e. non-sown non-colonist species). Combined with the species found in our experiment, these species help characterize traits of the regional species pool of all non-woody grassland species (155 grassland species in total including 16 sown species, 70 colonists and 69 non-sown non-colonists; we did not have complete trait data for six species observed in the experiment).

The four measured continuous functional traits described many of the important differences among species’ lifespans and functional groups. For example, compared with other groups: grasses had consistently higher LDMC; legumes had consistently larger seeds and, on average, were slightly taller; and annuals had consistently high SLA (Figures S2 and S3). Given the greater statistical flexibility that comes with using continuous predictors, we only used the four continuous traits (and not functional groups) in some of our analyses.

2.3 | Statistical analysis

We examined colonization into experimental plots and subplots using response variables that describe (a) the richness and biomass of groups of colonist species, and (b) the biomass of individual colonist species. We considered warming-induced changes in the sown communities insofar as they would affect colonization of non-sown species; see Cowles et al. (2016) for detailed examination of warming effects on the sown communities in this experiment.

We undertook a principal component analysis based on four continuous traits (sqrt-transformed plant height, ln-transformed seed mass, ln-transformed SLA and ln-transformed LDMC) of 155 herbaceous taxa that occur in grasslands at Cedar Creek Ecosystem Science Reserve. We used the PCA to visually assess trait space of the regional species pool, and the relative positions of sown species, colonist species and non-sown non-colonist species within that pool. We also conducted ANOVAs with post hoc Tukey tests to assess differences in trait values among these species pool groups. We separated the colonists and non-colonists into native and non-native groups for this analysis.

2.3.1 | Analysis 1: Warming and diversity effects on biomass, richness and functional characteristics of non-sown species that colonized subplots

This first set of analyses was undertaken at the subplot scale. The response variables were (a) the number of colonist species, (b) the summed biomass of all colonist species (log-transformed), (c) the summed biomass of colonist species in each of four functional groups and (d) the community-weighted trait means of all colonist species as a group. We used linear mixed-effects models with warming treatment, diversity treatment (log-transformed sown species richness) and their interaction as fixed effects. We also included log-transformed biomass of the sown community as an additional fixed effect as a proxy for available space and resources. Plot was included as a random effect (varying intercepts) to account for spatial nesting of subplot observations within plots. For all models, we tested the significance of the warming × diversity interaction using Type III Analysis of Variance (Satterthwaite's method, Giesbrecht & Burns, 1985) implemented in lmerTest (Kuznetsova, Brockhoff, & Christensen, 2017). Nonsignificant interaction terms and main terms were dropped when plotting key results from these models.

2.3.2 | Analysis 2: Warming effects on the functional characteristics of sown communities

The second set of analyses was also undertaken at the subplot scale using linear mixed-effects models with the same fixed and random effects as Analysis 1. The response variables were (a) the summed biomass of sown species in each of four functional groups, and (b) the community-weighted trait means of sown species. Our focus in these analyses were on warming effects, but we included sown diversity and the diversity × warming interaction to allow warming effects to vary with sown diversity.

2.3.3 | Analysis 3: Warming and diversity effects on the traits of non-sown species that colonized plots

The third set of analyses was initially undertaken at the species-in-subplot scale (i.e. observations were species' log-transformed biomass values in each subplot). We fitted a linear mixed-effects model that included the warming and diversity treatments, species functional traits (SLA, seed mass, maximum height and LDMC) and two-way interactions between the treatments and each trait. To facilitate convergence of this more complex model, all continuous explanatory variables were first standardized (mean = 0; *SD* = 1). Plot and subplot were included as nested spatial random effects (varying intercepts) and species was included as a crossed random effect, because a colonist species could be present in multiple plots and subplots. In addition to including random intercepts for each species, we let the effects of log-transformed sown richness and warming also vary by species. This initial model indicated that warming, both as a main effect and interacting with species traits, was not an important predictor of biomass accrual by colonists (*p*-values for all fixed-effect terms >.2; Table S3). Even after removing all fixed-effect terms involving warming, the random effect variance estimate for subplot (within plot) was effectively zero, indicating that there was no colonist biomass variation among subplots that could be explained by warming. As such, we chose to undertake all further analyses at the species-in-plot scale (i.e. we summed the biomass of each colonist species over the three subplots in each plot).

Using the species-in-plot data, we fitted a linear mixed-effects model that included the diversity treatment (log-transformed sown richness), functional traits of colonists and two-way interactions between diversity and each trait. In this model, significant interactions between traits and log-transformed sown richness indicate that the trait values of colonist species influence their ability to colonize and accrue biomass in plots of varying sown diversity. Plot was included as a random effect (varying intercepts only). We also allowed species' intercepts and slopes to vary with log-transformed sown richness, resulting in species-level regressions within the multilevel model structure.

Finally, we compared the model above that included colonist species' mean trait values as predictors of their biomass in plots to a model where colonists' traits were expressed as relative distances from sown CWMs (i.e. colonist trait value minus the CWM of sown species). Comparing fits of these two models tests if colonization is more strongly related to the actual trait values of colonist species (regardless of traits of the sown communities) or to the relative difference between traits of the colonist species and those of the sown community (Catford et al., 2019). We assessed support for these different trait expressions using Akaike information criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002).

3 | RESULTS

The trait space of the regional species pool was larger than the trait space of the sown (resident) community (Figure S4), as would be expected based on species numbers alone (155 vs. 16). Among the non-sown species, there were no significant differences between colonists and non-colonists for any of the traits (Figure S5). The only detected difference is related to the origin of species in the pool. Non-native pool members had significantly higher SLA than native pool members, and this was the case for both colonists and non-colonists (Figure S5a).

3.1 | Effects of warming on species colonization (Relationship i, Pathway A in Figure 1)

Subplots gained fewer colonist species when exposed to warming (subplots warmed by 3°C had on average three fewer species than ambient subplots, Figure 2a), but total biomass of colonists did not vary with warming (Table S4; Figure 2b).

The functional composition of colonists was not strongly affected by warming, suggesting at best only minimal shifts in the relative abundances of colonist species. Based on colonist biomass, the only functional group to vary with warming was C3 grasses

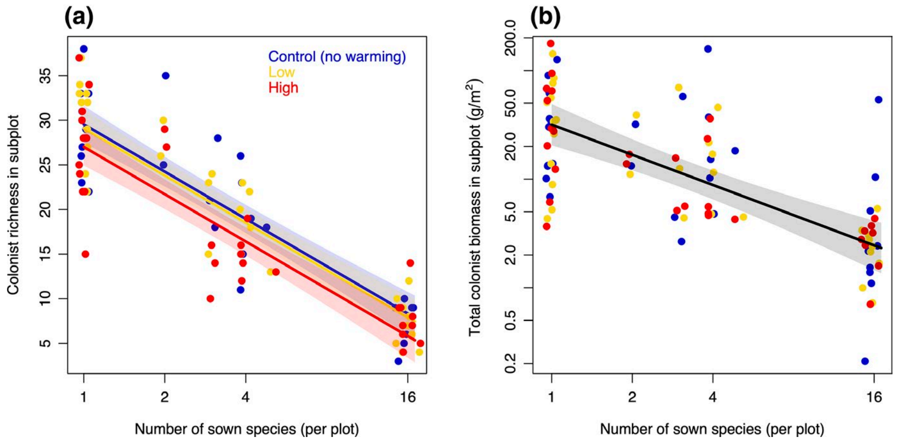

FIGURE 2 Fitted relationships between sown species richness and (a) the richness of colonist species assemblages and (b) the biomass of colonist assemblages in subplots. Fitted lines are from linear mixed-effects models. In (a) separate lines are fitted for each warming treatment to illustrate the small but significant warming effect (Table S4). In (b) a single line is fitted because warming was not significant. Note the log-scale of the *x*-axis in both panels, and the *y*-axis in (b) [Colour figure can be viewed at wileyonlinelibrary.com]

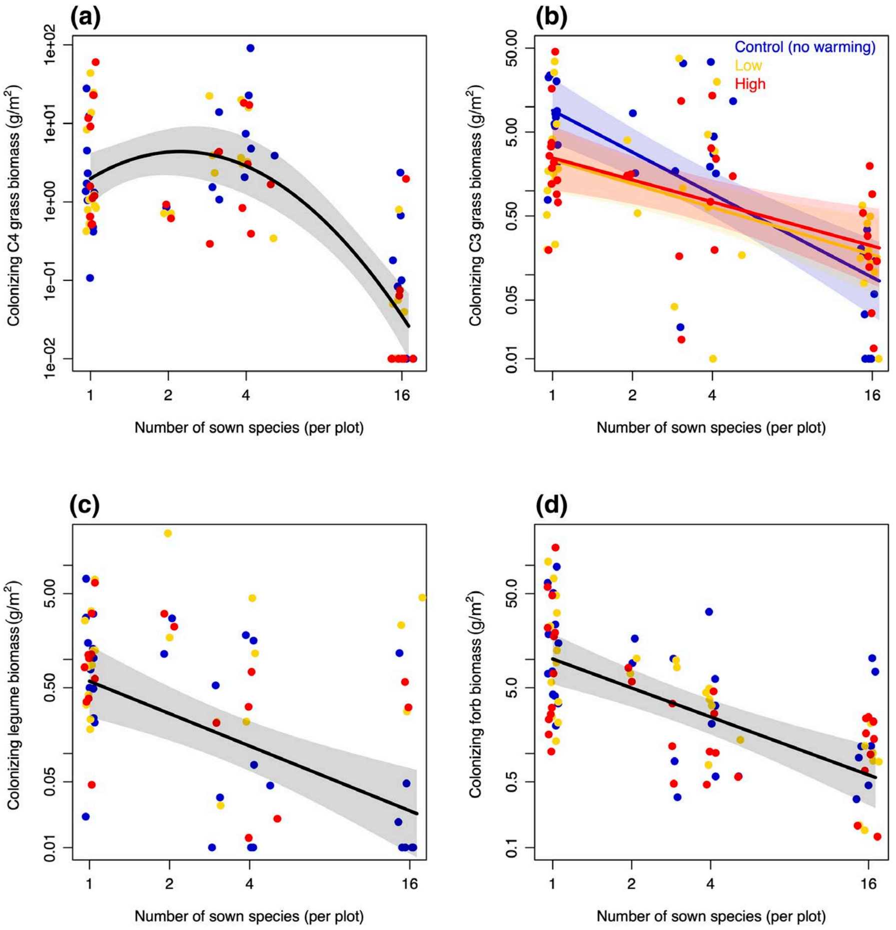

FIGURE 3 Fitted relationships between sown (resident) species richness and biomass of colonist species categorized as (a) C4 grasses, (b) C3 grasses, (c) legumes and (d) nonlegume forbs in subplots depending on warming and diversity treatment. Fitted lines are from linear mixed-effects models. A quadratic richness term was included in the model for C4 grasses (a) after visualizing the data. In (b) separate lines are fitted for each warming treatment to illustrate the significant richness × warming interaction (Table S4). In (a), (c) and (d) a single line is fitted because warming was not significant. Note the log-scale of both axes in all panels [Colour figure can be viewed at wileyonlinelibrary.com]

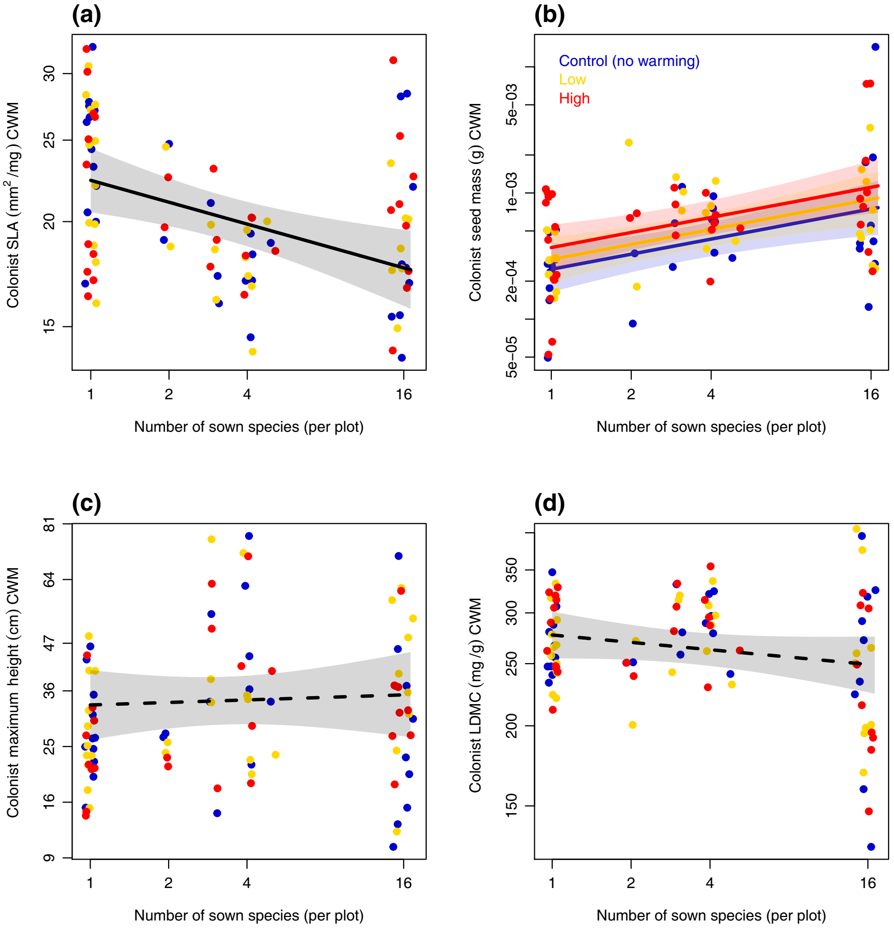

FIGURE 4 Fitted relationships between sown (resident) species richness and the community-weighted mean (CWM) of colonist species assemblages for (a) log(SLA), (b) log(seed mass), (c) sqrt(maximum height) and (d) log(LDMC). In (b) separate lines are fitted for each warming treatment to illustrate the small but significant warming effect (Table S4). Solid lines indicate significant relationships (a, b); dashed lines indicate nonsignificant relationships (c, d); single lines are used where effects of warming were not significant (a, c, d). Note the log-scale of the *x*-axis in all panels and the *y*-axis in panels (a), (b) and (d). The *y*-axis in (c) is on the sqrt scale [Colour figure can be viewed at wileyonlinelibrary.com]

(Table S4; Figure 3); their biomass decreased with warming in the low diversity plots, but increased with warming in the highest diversity plots. The colonist CWM for SLA, LDMC and height did not vary with warming (Figure 4a,c,d). However, once the nonsignificant diversity × warming interaction was removed from the seed mass model, there was evidence that colonist CWM seed mass increased under warming (Figure 4b; Table S4; the colonist CWM seed mass relationships remained significant even when invading legumes, which had high seed mass [Figure S2b], were excluded from the CWM calculation). As noted in Section 2, warming was not associated with the biomass of individual colonist species (Table S3).

3.2 | Effects of warming on sown communities (Relationship ii, Pathway B in Figure 1)

No sown species were lost from communities subject to warming, and their total biomass either increased or did not vary with warming (Cowles et al., 2016). Although community membership (species identity) and richness were unchanged, the relative abundances of species did vary with warming, altering community functional composition. Sown C4 grass and legume biomass were higher under warming (Figure 5a,c), as were CWM height and seed mass (Figure S6b,c). In the growing season of 2014 (our study year), the biomass of C3 grasses and forbs—in contrast to other years (Cowles et al., 2016)—and CWM SLA and LDMC did not vary with warming.

3.3 | Effects of sown community diversity on species colonization (Relationship iii, Pathway B in Figure 1)

The biomass of sown communities was not a significant predictor of species colonization in any model. In contrast, the extent of colonization declined significantly as sown community diversity increased, a trend that was consistent across all levels of warming (Figure 2). Three times as many species colonized the monocultures than the highest diversity plots (~30 vs. 10 species, Figure 2a), and colonist biomass dropped 10-fold from the monocultures to the highest diversity communities (~30 to 3 g/m^2, Figure 2b). The biomass of colonists in all four functional groups declined with increasing community diversity (Figure 3). The biomass of groups of colonizing c3 grasses, nonleguminous forbs and legumes all declined with increasing biomass of sown C4 grasses (Figure S7b–d). Biomass of C4 grass and forb colonists declined with increasing biomass of sown legumes and C3 grasses respectively (Figure S7a,c). As a group, colonist CWM SLA decreased and colonist seed mass increased with increasing diversity of the sown community (Table S4; Figure 4a,b). These group-level trait-based trends matched the responses of individual colonist species (Figure 6a,b).

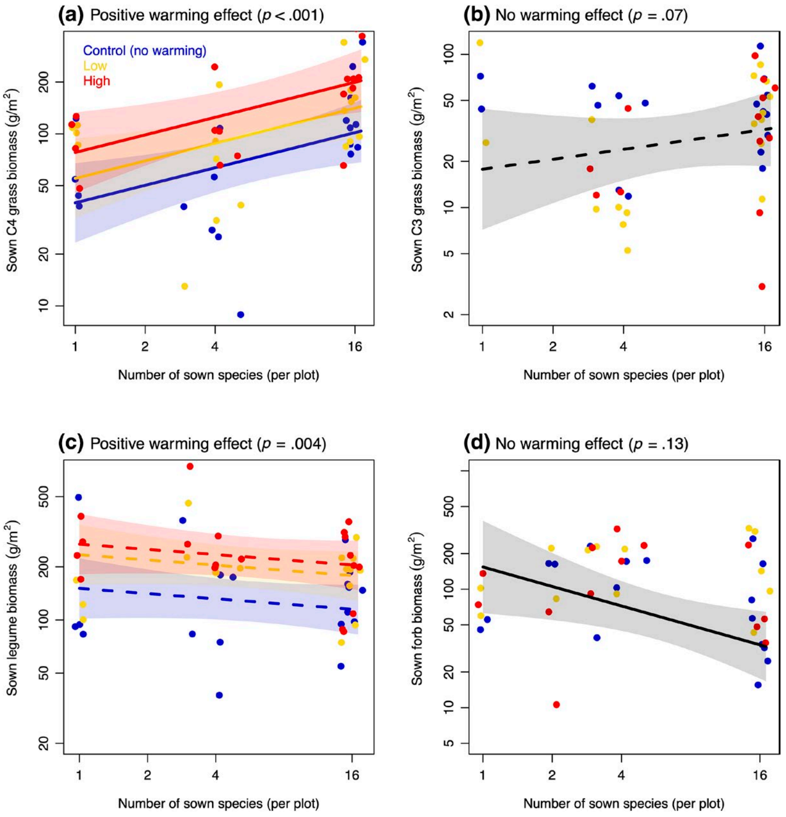

FIGURE 5 Fitted relationships between sown (resident) community diversity and, where present, biomass of sown species categorized as (a) C4 grasses, (b) C3 grasses, (c) legumes and (d) nonlegume forbs in subplots depending on warming and diversity treatment. Fitted lines are from linear mixed-effects models. Warming only affected the biomass of sown C4 grass and legume species. Subplots were only included if the relevant functional group was observed during subplot sampling (i.e. a member of the functional group was sown and recorded in the subplot). Solid lines indicate significant relationships with diversity (a, d); dashed lines indicate nonsignificant relationships with diversity (b, c); multiple lines in each panel are used where effects of warming were significant (a, c), whereas single lines are used when they are not (b, d) [Colour figure can be viewed at wileyonlinelibrary.com]

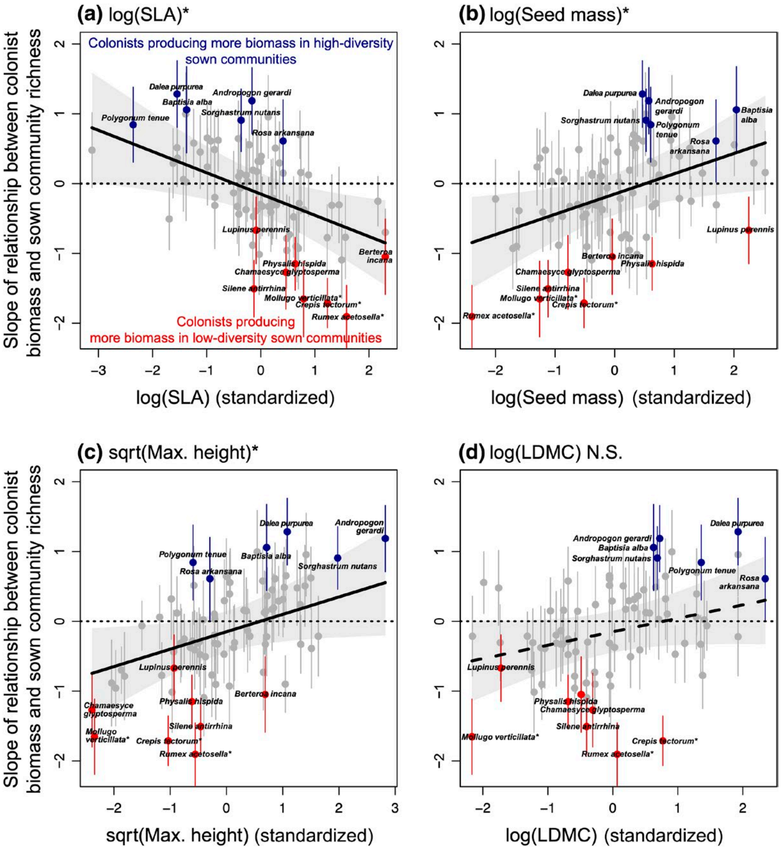

FIGURE 6 Fitted relationships from the species-level regressions within the multilevel model examining effects of sown richness and colonist species' traits on biomass accrual. In all panels each point is a single colonist species, y-values are the estimated slopes of species' relationships between log(biomass) and log(sown richness), and the bars indicate standard errors associated with these species-level slopes. Fitted lines and associated 95% CIs are from the fitted multilevel model; $^*p < .05$, N.S. $p \geq .05$. Slopes of the fitted lines correspond to the coefficient estimates for interactions between log(sown richness) and (a) log(SLA), (b) log(seed mass), (c) sqrt(maximum height) and (d) log(LDMC). Species labels and colours indicate selected species with negative (red) and positive (navy blue) biomass-richness slopes (species selected for illustrative purposes only). Species with asterisks are non-native [Colour figure can be viewed at wileyonlinelibrary.com]

Colonists with low SLA accumulated more biomass in higher diversity plots than their high SLA counterparts (Figure 6a), as did colonists with heavier versus lighter seeds (Figure 6b). Tall colonist species also produced more biomass in high diversity plots than shorter colonists (Figure 6c). Models fitted with relative trait differences between colonists and the CWM of sown communities showed the same trends, albeit with slightly higher performance (ΔAICc = 4.921) and the height-diversity trend being replaced by a height-only trend (i.e. Table S5). Because results from both models were qualitatively similar but the model using species' mean trait values (Model 1, Table S5; as opposed to trait differences to the sown community—Model 2, Table S5) allowed us to examine species-level regressions with traits as predictors, we focus on results for Model 1, the mean trait values model (Table S5). The marginal R^2 values for both models were low (<.1) indicating large amounts of variation in colonist biomass not explained by species traits and community diversity.

4 | DISCUSSION

Examining colonization of new species into experimental grassland communities with and without artificial warming, we found that resident community diversity had dramatic impacts on the biomass, richness and functional composition of colonists, whereas effects of warming were much more subtle. As community diversity increased from 1 to 17 species, total biomass and richness of colonists declined, as did the biomass of colonizing C3 and C4 grasses, legumes and non-legume forbs, and colonizing assemblages became dominated by species with low SLA and heavy seeds. At the species level, colonists with resource-acquisitive strategies (high SLA, low seed mass, short heights) accrued more biomass in low diversity communities, whereas species with conservative strategies accrued most biomass in high diversity communities. Subplots warmed by 3°C had ~3 fewer colonist species than ambient or +1.5°C subplots, and colonists in warmed subplots had higher mean seed mass than those in ambient subplots.

The arrival and establishment of new species is typically associated with some form of environmental change (Catford et al., 2011; Essl et al., 2019; Moles et al., 2012; Seabloom et al., 2015; Stachowicz, Terwin, Whitlatch, & Osman, 2002). Using a unique experiment that allowed us to isolate direct abiotic effects of environmental change (Pathway A, Figure 1) from indirect biotic effects (Pathway B), we show that direct effects of warming on species colonization are dwarfed by effects of community diversity. Combined with findings from studies that consider Pathway C (Alexander, Diez, & Levine, 2015; Bansal & Sheley, 2016; Catford, Morris, Vesk, Gippel, & Downes, 2014; Kraft et al., 2015; Wang et al., 2019), this set of results suggests that environmental change mostly facilitates species colonization indirectly, by altering biotic interactions with resident species (Pathways B or C), rather than by directly facilitating colonization based on colonists' abiotic tolerances alone (Pathway A).

The concept of environmental filtering and ideas relating to species' ecophysiological tolerances resonate strongly when considering impacts of abiotic change (Pathways A and B)—and for good reason (Merow, Bois, Allen, Xie, & Silander, 2017). However, our work, plus that of others (Alexander et al., 2015; Bansal & Sheley, 2016; Carboni et al., 2016; Catford et al., 2014, 2019; Suttle, Thomsen, & Power, 2007), suggest that most small-scale (<1 ha) impacts of abiotic environmental change on plant community composition may occur via abiotic-induced changes in competitive environments (Pathway C), rather than wholesale inclusion or exclusion of species based on their abiotic tolerances. Working across a climate gradient in the Swiss Alps, Alexander et al. (2015) found that the performance of grassland species were more strongly affected by altered competition than by altered temperatures. In California, Suttle et al. (2007) revealed that, after a few years, changes in rainfall regimes primarily affected grassland communities via impacts on species interactions, rather than via direct autecological effects. In experimental grasslands in Germany, Haeuser et al. (2017) found that native resident plant species were more negatively affected by warming than non-native species, such that warming gave non-native species a comparative advantage. Combining evidence like this with ours, it seems that—at small spatial scales (i.e. vegetation plots spanning 1–900 m^2)—colonist–community interactions overwhelmingly influence both the extent of colonization and the functional characteristics of colonists, while direct effects of abiotic environmental change are secondary (i.e. Pathway B and especially Pathway C appear more influential than Pathway A in Figure 1).

4.1 | Effects of diversity

Consistent with previous studies (Fargione & Tilman, 2005; Levine, Adler, & Yelenik, 2004), higher diversity communities were more resistant to colonization by new species. This was likely a result of reduced resource availability and stronger competition, as the trait-based trends suggest. Whether examining mean trait values of colonists or relative trait differences between colonists and CWM of sown communities (Table S5), colonists with traits associated with higher rates of resource acquisition were overrepresented in the low diversity plots (i.e. high SLA, light seeds, short heights), whereas the opposite was true in the high diversity plots. While soil moisture availability increased with sown diversity in this experiment (Cowles et al., 2016), availability of soil nitrogen (the key limiting resource at Cedar Creek) and light are lower in the more productive high diversity plots (Fargione & Tilman, 2005), favouring tall and low-SLA species, which are better able to capture light and have more conservative carbon capture strategies respectively (Reich, 2014). Though heavier seeded colonists were more abundant in the higher diversity plots, this was not driven by colonization of legumes (which tend to have heavy seeds, Figure S2b) and their ability to fix N in the low N environments. Rather, the seed mass-diversity trend may reflect greater drought tolerance and seedling survival of heavier seeded species (Moles, 2018), or simply that small-seeded species are more abundant in the more resource-rich low diversity plots, consistent with their high resource acquisition strategies.

Relationships based on the functional groups of colonists and sown communities also point to the importance of resource availability for plant colonization. Communities with higher biomass of sown C4 grasses—the dominant competitors of soil N at Cedar Creek (Tilman et al., 2001)—were more resistant to colonization by legumes, nonlegume forbs and C3 grasses, but not by C4 grasses (Figure S7), as found previously (Fargione, Brown, & Tilman, 2003).

4.2 | Effects of warming

Although impacts of warming on species colonization were dwarfed by impacts of diversity, effects were nevertheless detected. Regardless of community diversity, the number of colonist species was slightly lower under the high warming treatment. This suggested that some colonist species were unable to occupy the warmer, drier conditions of the subplots exposed to +3°C (Cowles et al., 2016), consistent with effects of abiotic exclusion (Pathway B in Figure 1, though excluding colonists rather than resident species in this case). Given that warming was applied to small subplots not landscapes, the seed pools would not have varied across the warming treatments in our experiment, and it is unlikely that species tolerant of warmed conditions but intolerant of ambient conditions would have been present in the seed pool. This may partially explain why warming did not increase the richness of colonists in this experiment (Pathway A, Figure 1). Moreover, the dominant resident (sown) species in our high diversity treatments have broad temperature tolerances and are also dominant in hotter, more southerly parts of the US Great Plains (e.g. Konza in Kansas; this may also explain why none of the sown species were excluded under warming, in contrast to other studies, Haeuser et al., 2017; Haeuser, Dawson, & van Kleunen, 2019).

Together with the small but significant increase in seed mass CWMs, warming seems to have filtered out some potential colonists and favoured heavier-seeded colonist species, either by acting on species' physiological tolerances or by altering competitive outcomes among species (Pathway C, Figure 1; Kraft et al., 2015). The seed mass results may reflect the greater ability of larger, heavier seeds to withstand dry periods during establishment (Moles, 2018), which would be more pronounced in the warmed plots (Cowles et al., 2016). This finding and interpretation concurs with that of Haeuser et al. (2017) based on their warming experiment in German grassland communities.

The biomass of C3 grass colonists varied with warming, but—to our surprise—the biomass of C4 grass colonists did not, despite increases in the biomass of C4 grasses in sown communities (Figure 5a; biomass of sown C4 grasses did not affect biomass of C4 grass colonists, Figure S7a; Fargione et al., 2003). The optimal temperature range of C4 grasses is 20–45°C, whereas C3 grasses have an optima of 10–30°C (Bremond et al., 2012), so abundance of C4 grasses is expected to increase under warming (Catford & Jones, 2019). The response of C3 grass colonists to warming was conditional on community diversity though: their biomass decreased with warming in the low diversity plots, but increased with warming in the high diversity plots (Figure 3b). This may have been a result of greater facilitation of C3 grasses in the high diversity plots; the high diversity plots had higher biomass and shadier and cooler soils (Cowles et al., 2016), and hence a more amenable microclimate than the lower biomass of the lower diversity plots (Wright, Schnitzer, & Reich, 2014). We expect that stronger trait-based trends in response to warming would have been detected had we measured traits under each warming treatment (Frei, Ghazoul, & Pluess, 2014; the same applies for responses to diversity, Conti et al., 2018), or had examined traits more strongly linked to warming (e.g. seedling roots, Harrison & LaForgia, 2019).

4.3 | Limitations

Our findings provide a conservative indication of likely changes in species colonization under warming. First, and even though sown species' abundances changed and soil microbial communities were not controlled, we limited warming-induced changes in the competitive environment of the sown communities by preventing non-sown species from establishing in the plots (Pathway C, Figure 1; Alexander, Diez, Hart, & Levine, 2016).

Second, because warming was restricted to 2.5 m × 3 m subplots, the experiment did not capture effects of warming on whole populations, communities and species pools, but only revealed direct effects of warming on individuals (and their interactions) occurring in the subplots. Milder winters can increase survival and extend growing seasons, enabling larger populations and greater reproductive output of species that do well under warming (Hellmann, Byers, Bierwagen, & Dukes, 2008), compounding the advantages that warming-favoured species might experience. Had warming occurred at landscape or regional scales, species migration may have changed the composition of seed pools in the different warming treatments, potentially increasing the importance of Pathway A by increasing the pool of species that could colonize (Merow et al., 2017; Wang et al., 2019)—either with range-expanding natives or exotic species with spreading populations (Auffret & Thomas, 2019). Introduction of exotic species that are not yet naturalized in the region would likely have similar effects (Haeuser et al., 2019).

Third, by removing all colonists twice each growing season, colonizing species were unable to establish populations within the experimental plots, limiting their propagule input and their competitive effects on sown resident communities (Pathway C). If the membership and richness of the sown communities had been allowed to change (i.e. allowing Pathway C, including feedback effects from colonists), it is likely that we would have observed larger changes in community composition in response to warming, perhaps even including declines in sown community diversity (Haeuser et al., 2017).

Fourth, because of lags in community responses to climate change (Alexander et al., 2018), 6 years of warming may have been of insufficient duration to witness local extinction of resident species.

Our study used randomly assembled experimental communities, which could potentially show different relationships to naturally assembled communities. Recent work by Jochum et al. (2019) showed that the diversity and functional composition of communities in Cedar Creek's biodiversity experiment (a subset of which was used in this study) encompass but show greater variance than comparable naturally assembled communities. Out of 12 biodiversity-ecosystem functioning relationships examined, 10 relationships were unchanged by the inclusion or exclusion of "unrealistic" experimental communities, however (Jochum et al., 2019). This suggests that findings from biodiversity experiments can still provide meaningful insights for natural communities.

4.4 | Implications for biological invasions and management of novel ecosystems

All colonists, regardless of their origin, undergo the same ecological processes of arrival and population establishment, and the colonization of any new species can prompt changes in the taxonomic, functional and phylogenetic composition of communities. Though the circumstances of exotic invasion differ from native species colonization (Buckley & Catford, 2016; Essl et al., 2019), studies of species colonization can nevertheless provide insights into the initial stages of species invasion. Our results highlight the influence of biotic resistance in determining the number and functional characteristics of colonizing species, both native and non-native. In the present study, 20% of colonists were non-native species, and these non-natives occupied very similar trait space as non-colonist non-natives from the broader species pool (Figure S4). Unless the functional composition of the exotic species pool changes markedly, this suggests that maintaining species-rich native communities should help to limit invasion, even under abiotic change of the magnitude examined here (+3°C for 6 years). Consistent with the maxim that intact ecosystems are the most cost-effective defence against climate change (Martin & Watson, 2016), maintaining community diversity seems a viable approach to help limit species turnover and invasion under abiotic environmental change.

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AUTHOR CONTRIBUTION

J.A.C. conceived idea; D.T. established experiment; J.A.C. and J.M.C. collected and processed data; J.D. and E.P. analysed data with input from J.A.C.; J.A.C. wrote the first draft with input from J.D.; all authors contributed to subsequent drafts.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the LTER archive (https://portal.lternet.edu/nis/mapbrowse?packagexml:id=knb-lter-cdr.386.8; https://doi.org/10.6073/pasta/214b327bc6fc0a240ec705b339e6dd83) and TRY database (https://www.try-db.org, dataset ID 354), or available from the corresponding author upon reasonable request. R script underpinning the analysis has been deposited in GitHub (https://github.com/circusdwyer/Catford_et_al_2020_GCB_R_Script).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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