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1 **Community diversity outweighs effect of warming on species colonization**

2 Jane A. Catford¹, John M. Dwyer², Estibaliz Palma³, Jane M. Cowles⁴ & David
3 Tilman⁵

4
5 ¹Department of Geography, King's College London, Strand, WC2B 4BG, UK; School
6 of BioSciences, University of Melbourne, Vic 3010, Australia;
7 jane.catford@kcl.ac.uk

8 ²School of Biological Sciences, The University of Queensland, QLD 4072, Australia;
9 j.dwyer2@uq.edu.au

10 ³School of BioSciences, University of Melbourne, Vic 3010, Australia;
11 estibaliz.palma@gmail.com

12 ⁴Department of Ecology, Evolution & Behavior, University of Minnesota, St Paul,
13 MN 55108, USA; jcowles@umn.edu

14 ⁵Department of Ecology, Evolution & Behavior, University of Minnesota, St Paul,
15 MN 55108, USA; Bren School of Environmental Science and Management,
16 University of California, Santa Barbara, 2400 Bren Hall, Santa Barbara, CA 93106,
17 USA; tilman@umn.edu

18
19 **Corresponding author:** Jane A. Catford, Department of Geography, King's College
20 London, Strand, London, WC2B 4BG, UK; jane.catford@kcl.ac.uk

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Data accessibility statement: Should the manuscript be accepted, the data supporting the results will be archived in a public repository (Figshare) and the data DOI will be included at the end of the article.

Current data availability: Data sets are archived as experiment ‘e249’ and can be obtained from: <https://www.cedarcreek.umn.edu/research/data>. Trait data, and detailed methods about their collection, are available through TRY (Dataset ID 354, owned by the authors): <https://www.try-db.org>.

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44 **Abstract**

45 Abiotic environmental change, local species extinctions and colonization of new
46 species often co-occur. Whether species colonization is driven by changes in abiotic
47 conditions or reduced biotic resistance will affect community functional composition
48 and ecosystem management. We use a grassland experiment to disentangle effects of
49 climate warming and community diversity on colonization. Three times as many
50 species colonized monocultures than 17-species plots (~30 vs 10 species) and
51 collectively produced 10-times as much biomass. Colonists with resource-acquisitive
52 strategies (high SLA, light seeds, short heights) accrued more biomass in low
53 diversity communities, whereas species with conservative strategies accrued most
54 biomass in high diversity communities. Compared with diversity effects, six years of
55 3°C-above-ambient temperatures had little impact on plant colonization. Warmed
56 subplots, with ~3 fewer colonist species than ambient subplots, selected for heavier-
57 seeded colonists and showed diversity-dependent changes in biomass of C3 grass
58 colonists. Our findings suggest that species colonization is more strongly affected by
59 biotic resistance from residents than 3°C of climate warming.

60 **Introduction**

61 A key prediction and observation of abiotic environmental change, including global
62 warming, is increased levels of species incursion, including invasion by exotic species
63 (Sorte et al. 2013, Hulme 2017, Liu et al. 2017, Auffret and Thomas 2019, Catford
64 and Jones 2019) and colonization of previously absent natives (Inderjit et al. 2017,
65 Essl et al. 2019). However, abiotic change can reduce the diversity of historical
66 communities (Harrison et al. 2015) and low diversity can facilitate species
67 colonization (Fargione and Tilman 2005). This prompts a series of questions: Does
68 abiotic environmental change strongly and directly facilitate colonization of new
69 species? Does colonization usually occur in the wake of abiotic-driven reductions in
70 the diversity of resident communities? Or is it a combination of the two, where abiotic
71 change alters the competitive environment, enabling new species to colonize and
72 outcompete resident species?

73 Abiotic environmental change could facilitate the colonization of new species in three
74 ways. First, it may shift the abiotic conditions of a site such that a new suite of
75 species, previously intolerant of the site's abiotic conditions, can colonize and
76 establish (Pathway A, Fig. 1). Second, established resident species intolerant of the
77 modified abiotic conditions may be filtered out, leading to a decline in resource
78 uptake and biotic resistance, increasing opportunities for colonization of new species
79 (Pathway B, Catford et al. 2011). Third, abiotic change may affect the relative fitness
80 of resident and colonizing species in that site, altering biotic interactions and giving
81 newcomers a competitive advantage over residents that had not occurred previously
82 (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 (Gedan and Bertness 2009, Bansal and Sheley 2016), including in experiments (Harpole et al. 2016, Haeuser et al. 2017). 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- and away from C3-photosynthetic pathways under climate warming, Bremond et al. 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 et al. 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 non-resident species. Using a unique experiment that isolates abiotic

effects of warming from indirect biotic effects, we focus on relationships (i), (ii) and (iii) in Fig. 1, which contribute to Pathways A and B, to specifically ask how diversity and warming affect: the extent of colonization by non-resident 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 non-legume forb) and functional traits (seed mass, specific leaf area, leaf dry matter content and plant height). The grassland experiment allows us to examine effects of varying levels of diversity (spanning 1 to 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 Fig. 1 because colonists were regularly removed in the study experiment, minimising effects of colonists on resident species (purple arrow in Fig. 1), and because sown community membership (i.e. species identity but not relative abundances, Cowles et al. 2016) remained unchanged, minimising the potential for warming-induced changes in biotic interactions. However, it is important to consider implications of nullifying Pathway C when interpreting our results.

Methods

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 non-leguminous forbs, Table S1). All plots received 10 g/m² 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 seedbank, and was ploughed. Further details can be found in Tilman et al. (2001).

From 2009, 32 plots were used in a diversity-and-warming experiment (Cowles et al. 2016). The 32 plots included 12 monoculture plots, 2 2-species plots, 3 3-species plots, 5 4-species plots, 1 5-species plot, 4 15-species plots, 4 16-species plots and 1 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 (1200 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 h/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°C 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 Results for effects of warming on the sown communities).

To quantify colonization by non-sown species into the experimental plots, in 2014, we sorted the aboveground biomass of all plants removed through weeding to species-level, dried the sorted samples at 60°C for at least 48 hours and weighed them. The composition and aboveground 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 aboveground 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 (Fig. S1, Table S2).

Plant traits

We used the literature (Tilman 1997, USDA-NRCS 2018) 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, non-leguminous 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) (Pérez-Harguindeguy et al. 2013, Catford et al. 2019). We measured leaf dry matter content (LDMC, mg/g) and specific leaf area (SLA, mm²/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 (3 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 $\geq 93\%$ 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 characterise traits of the regional species pool of all non-woody grassland species (155 grassland species in total including 16 sown species, 70 non-sown colonists and 69 non-sown non-colonists; we did not have complete trait data for 6 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, grasses had consistently higher LDMC, legumes had consistently larger seeds and, on average, were slightly taller, and annuals had consistently high SLA than other groups (Figs S2 & 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.

Statistical analysis

We examined colonization into experimental plots and subplots using response variables that describe i) the richness and biomass of groups of non-sown colonist

species, and ii) the biomass of individual colonist species. We considered warming-induced changes in the sown communities in so far 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, non-sown colonists, 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.

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 i) the number of colonist species, ii) the summed biomass of all colonist species (log-transformed), iii) the summed biomass of colonist species in each of four functional groups, and iv) 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 $\times$ diversity interaction using Type III Analysis of Variance (Satterthwaite's method, Giesbrecht and Burns 1985) implemented in lmerTest (Kuznetsova et al. 2017). Non-significant interaction terms and main terms were dropped when plotting key results from these models.

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 i) the summed biomass of sown species in each of four functional groups, and ii) 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 $\times$ warming interaction to allow warming effects to vary with sown diversity.

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 standardised (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 to 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 >0.2 ; 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 multi-level 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 absolute 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 AICc.

Results

The trait space of the regional species pool was larger than the trait space of the sown (resident) community (Fig. 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 (Fig. S5). The only detected difference 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 (Fig. S5a).

Effects of warming on species colonization (Relationship i, Pathway A in Fig. 1)

Subplots gained fewer colonist species when exposed to warming; subplots warmed by 3°C had on average 3 fewer species than ambient plots (Fig. 2a). But total biomass of colonists did not vary with warming (Table S4, Fig. 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 (Table S4, Fig. 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 (Fig. 4a, c & d). However, once the non-significant diversity × warming interaction was removed from the seed mass model, there was evidence that colonist CWM seed mass increased under

warming (Fig. 4b, Table S4; the colonist CWM seed mass relationships remained significant even when invading legumes, which had high seed mass (Fig. S2b), were excluded from the CWM calculation). As noted in the methods, warming was not associated with the biomass of individual colonist species (Table S3).

Effects of warming on sown communities (Relationship ii, Pathway B in Fig. 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 (Fig. 5a & c), as were CWM height and seed mass (Fig. 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.

Effects of sown community diversity on species colonization (Relationship iii, Pathway B in Fig. 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 (Fig. 2). Three times as many species colonized the monocultures than the highest diversity plots (~30 vs 10 species, Fig. 2a), and colonist biomass dropped 10-fold from the monocultures to the highest diversity communities (~30 to 3 g/m², Fig. 2b). Absolute biomass of colonists in all four functional groups declined with increasing community diversity (Fig. 3). The biomass of groups of colonizing c3 grasses, non-leguminous forbs and legumes all declined

with increasing biomass of sown C4 grasses (Fig. S7b-d). Biomass of C4 grass and forb colonists declined with increasing biomass of sown legumes and C3 grasses respectively (Fig. S7a & c). As a group, colonist CWM SLA decreased and colonist seed mass increased with increasing diversity of the sown community (Table S4, Fig. 4a-b). These group-level trait-based trends matched the responses of individual colonist species (Fig. 6a-b).

Colonists with low SLA accumulated more biomass in higher diversity plots than their high SLA counterparts (Fig. 6a), as did colonists with heavier vs lighter seeds (Fig. 6b). Tall colonist species also produced more biomass in high diversity plots than shorter colonists (Fig. 6c). Models built using relative trait differences between colonists and the CWM of sown communities showed the same trends, albeit with slightly higher performance ($\Delta AICc = 4.921$) 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 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 (<0.1) indicating large amounts of variation in colonist biomass not explained by species traits and community diversity.

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 (Stachowicz et al. 2002, Catford et al. 2011, Moles et al. 2012, Seabloom et al. 2015, Essl et al. 2019). Using a unique experiment that allowed us to isolate direct abiotic effects of environmental change (Pathway A, Fig. 1) from indirect biotic effects (Pathway B), here 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 (Catford et al. 2014, Alexander et al. 2015, Kraft et al. 2015, Bansal and Sheley 2016, 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 et al. 2017). However, our work, plus that of

others (Suttle et al. 2007, Catford et al. 2014, Alexander et al. 2015, Bansal and Sheley 2016, Carboni et al. 2016, Catford et al. 2019), suggests that most small-scale (<1 ha) impacts of abiotic environmental change on plant community composition may come 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 m²) – 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 Fig. 1).

Effects of diversity

Consistent with previous studies (Levine et al. 2004, Fargione and Tilman 2005), 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 and 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, Fig. 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, non-legume forbs and C3 grasses, but not by C4 grasses (Fig. S7), consistent with previous findings (Fargione et al. 2003).

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 Fig. 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, Fig. 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, 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, Fig. 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 (Fig. 5a; biomass of sown C4 grasses did not affect biomass of C4 grass colonists, Fig. S7a, Fargione et al. 2003). The optimal temperature range of C4 grasses is 20-45°C, whereas C3 grasses have optima of 10-30°C (Bremond et al. 2012), so abundance of C4 grasses is expected to increase under warming (Catford and 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 (Fig. 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 et al. 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 et al. 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 and LaForgia 2019).

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, Fig. 1, Alexander et al. 2016).

Second, because warming was restricted to 2.5 m x 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 et al. 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 and Thomas 2019). Introduction of exotic species that are not yet naturalised 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), six years of warming may have been of insufficient duration to witness local extinctions 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.

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 and 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 (Fig. 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 and Watson 2016), maintaining community diversity seems a viable approach to help limit species turnover and invasion under abiotic environmental change.

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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 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 minimised in the experiment through regular removal of non-sown colonists, which maintained species membership and richness of the sown (resident) communities.

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726 **Figure 2** Fitted relationships between sown species richness and **(a)** the richness of
 727 colonist species assemblages and **(b)** the biomass of colonist assemblages in subplots.

728 Fitted lines are from linear mixed-effects models. In **(a)** separate lines are fitted for
 729 each warming treatment to illustrate the small but significant warming effect (Table
 730 S4). In **(b)** a single line is fitted because warming was not significant. Note the log-
 731 scale of the x-axis in both panels, and the y-axis in **(b)**.

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Figure 3 Fitted relationships between sown (resident) species richness and biomass of colonist species categorised as **(a)** C4 grasses, **(b)** C3 grasses, **(c)** legumes, and **(d)** non-legume 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 visualising the data. In **(b)** separate lines are fitted for each warming treatment to illustrate the significant richness $\times$ 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.

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 non-significant 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.

Figure 5 Fitted relationships between sown (resident) community diversity and, where present, biomass of sown species categorised as **(a)** C4 grasses, **(b)** C3 grasses, **(c)** legumes, and **(d)** non-legume 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 still present). Solid lines indicate significant relationships with diversity **(a, d)**; dashed lines indicate non-significant relationships with diversity **(b, c)**; multiple lines in each panels are used where effects of warming were significant **(a, c)**, whereas single lines are used when they are not **(b, d)**.

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768 **Figure 6** Fitted relationships from the species-level regression within the multi-level
 769 model examining effects of sown richness and colonist species' traits on biomass
 770 accrual. In all panels each point is a single colonist species and y-values are the
 771 estimated slopes of species' relationships between $\log(\text{biomass})$ and $\log(\text{sown}$
 772 $\text{richness})$, and the bars indicate standard errors associated with these species-level
 773 slopes. Fitted lines and associated 95% CIs are from the fitted multi-level model; *
 774 $P < 0.05$, N.S. $P \geq 0.05$. Slopes of the fitted lines correspond to the coefficient estimates
 775 for interactions between $\log(\text{sown richness})$ and (a) $\log(\text{SLA})$, (b) $\log(\text{Seed Mass})$, (c)
 776 $\sqrt{\text{Maximum Height}}$ and (d) $\log(\text{LDMC})$. Species labels and colours indicate
 777 selected species with negative (blue) and positive biomass-richness slopes (orange)
 778 (species selected for illustrative purposes only). Species with asterisks are non-native.

Table S1 List of sown (resident) and colonist species in our analyses. Sown species are indicated in bold, but these species also served as colonists in plots where they were not sown. Details are provided for family, origin, duration, functional group and values for four functional traits. In four cases, mean of co-occurring †congeneric or ‡confamilial taxa at Cedar Creek were used. Authority: USDA Plants 2019.

Species	Family	Origin	Duration	Functional Group	SLA (mg mm ⁻²)	Seed mass (g)	Maximum height (cm)	LDMC (mg g ⁻¹)
<i>Achillea millefolium</i>	Asteraceae	Native	Perennial	Non-legume forb	15.81	0.015	56	192.31
<i>Agrostis scabra</i>	Poaceae	Native	Perennial	C3 Grass	9.08	0.009	27	280†
<i>Ambrosia artemisiifolia</i>	Asteraceae	Native	Annual	Non-legume forb	26.19	0.17	23	200
<i>Amorpha canescens</i>	Fabaceae	Native	Perennial	Legume	18.71	0.145	16	338.17
<i>Andropogon gerardii</i>	Poaceae	Native	Perennial	C4 Grass	17.82	0.139	143	327.75
<i>Anemone cylindrica</i>	Ranunculaceae	Native	Perennial	Non-legume forb	15.99	0.036	31	341.46
<i>Antennaria howellii</i>	Asteraceae	Native	Perennial	Non-legume forb	17.92	0.011	3	220.62
<i>Aristida basiramea</i>	Poaceae	Native	Annual	C4 Grass	32.89	0.064	13	413.05
<i>Artemisia campestris</i>	Asteraceae	Native	Biennial	Non-legume forb	12.4	0.006	77	231.77
<i>Artemisia ludoviciana</i>	Asteraceae	Native	Perennial	Non-legume forb	18.52	0.011	60	272.73
<i>Asclepias syriaca</i>	Asclepiaceae	Native	Perennial	Non-legume forb	21.14	0.331	89	119.4
<i>Asclepias tuberosa</i>	Asclepiaceae	Native	Perennial	Non-legume forb	22.96	0.636	46	181.82
<i>Baptisia alba</i>	Fabaceae	Native	Perennial	Legume	10.46	1.664	57	317.06
<i>Berteroa incana</i>	Brassicaceae	Introduced	Biennial	Non-legume forb	52.79	0.049	56	214.61
<i>Bouteloua curtipendula</i>	Poaceae	Native	Perennial	C4 Grass	10.43	0.06	27	416.67
<i>Bouteloua gracilis</i>	Poaceae	Native	Perennial	C4 Grass	16.24	0.043	8	422.67
<i>Bromus sp.</i>	Poaceae	Introduced	Perennial	C3 Grass	20.34	0.267	81	500
<i>Carex sp.</i>	Cyperaceae	Native	Perennial	Sedge	22.97	NA	27	348.7
<i>Chamaesyce glyptosperma</i>	Euphorbiaceae	Native	Annual	Non-legume forb	23.48	0.014	1	228.36
<i>Chenopodium album</i>	Chenopodiaceae	Introduced	Annual	Non-legume forb	27.23	0.037	40	172.59
<i>Chenopodium leptophyllum</i>	Chenopodiaceae	Native	Annual	Non-legume forb	27.6	0.04	50	NA

<i>Conyza canadensis</i>	Asteraceae	Introduced	Annual	Non-legume forb	25.5	0.003	68	231.21
<i>Coreopsis palmata</i>	Asteraceae	Native	Perennial	Non-legume forb	12.74	0.118	61	250
<i>Crepis tectorum</i>	Asteraceae	Introduced	Annual	Non-legume forb	32.95	0.022	15	333.33
<i>Cyperus sp.</i>	Cyperaceae	Native	Perennial	Sedge	16.97	0.037	22	256.96
<i>Dalea candida</i>	Fabaceae	Native	Perennial	Legume	11.09	0.088	54	200
<i>Dalea purpurea</i>	Fabaceae	Native	Perennial	Legume	9.68	0.116	69	500
<i>Dalea villosa</i>	Fabaceae	Native	Perennial	Legume	10.38	0.127	51	350
<i>Delphinium carolinianum</i>	Ranunculaceae	Native	Perennial	Non-legume forb	21.02	0.062	48	160.54
<i>Desmodium canadense</i>	Fabaceae	Native	Perennial	Legume	21.56	0.445	80	269.23
<i>Dichanthelium linearifolium</i>	Poaceae	Native	Perennial	C3 Grass	15.2	NA	19	272.73
<i>Dichanthelium oligosanthes</i>	Poaceae	Native	Perennial	C3 Grass	26.34	0.09	38	400
<i>Dichanthelium villosissimum</i> <i>var. praecocius</i>	Poaceae	Native	Perennial	C3 Grass	25.01	0.022	25	200
<i>Digitaria cognatum</i>	Poaceae	Native	Perennial	C4 Grass	34.15	0.032	24	250
<i>Digitaria sp.</i>	Poaceae	Unknown	Annual	C4 Grass	37.02	0.028	27	220.93
<i>Elymus canadensis</i>	Poaceae	Native	Perennial	C3 Grass	10.38	0.001	51	350
<i>Elymus repens</i>	Poaceae	Introduced	Perennial	C3 Grass	20.43	0.153	77	408.67
<i>Equisetum laevigatum</i>	Equisetaceae	Native	Perennial	Horsetail	4.84	0.007	75	137.5
<i>Eragrostis spectabilis</i>	Poaceae	Native	Perennial	C4 Grass	20.78	0.007	23	294.34
<i>Erigeron strigosus</i>	Asteraceae	Native	Annual	Non-legume forb	20.86	0.002	57	500
<i>Euphorbia corollata</i>	Euphorbiaceae	Native	Perennial	Non-legume forb	19.21	0.33	38	400
<i>Festuca sp.</i>	Poaceae	Unknown	Perennial	C3 Grass	22.49	NA	NA	322.58
<i>Fragaria virginiana</i>	Rosaceae	Native	Perennial	Non-legume forb	16.99	0.028	17	310.34
<i>Hedeoma hispida</i>	Lamiaceae	Native	Annual	Non-legume forb	20.96	0.025	19	375
<i>Hieracium sp.</i>	Asteraceae	Unknown	Biennial	Non-legume forb	16.02	0.023	16	208.47
<i>Koeleria macrantha</i>	Poaceae	Native	Perennial	C3 Grass	10.19	0.013	12	399.42
<i>Lathyrus venosus</i>	Fabaceae	Native	Perennial	Legume	22.3	2.728	35	277.78
<i>Lepidium densiflorum</i>	Brassicaceae	Native	Annual	Non-legume forb	25.68	0.024	32	173.55

<i>Lespedeza capitata</i>	Fabaceae	Native	Perennial	Legume	13.53	0.258	84	250
<i>Liatris aspera</i>	Asteraceae	Native	Perennial	Non-legume forb	12.38	0.047	68	250
<i>Linaria vulgaris</i>	Scrophulariaceae	Introduced	Perennial	Non-legume forb	19.35	0.02	32	194.29
<i>Lupinus perennis</i>	Fabaceae	Native	Perennial	Legume	18.44	2.363	17	139.27
<i>Mirabilis hirsuta</i>	Nyctaginaceae	Native	Perennial	Non-legume forb	17.43	1.57	38	126.92
<i>Mollugo verticillata</i>	Molluginaceae	Introduced	Annual	Non-legume forb	27.12	0.006	1	119.08
<i>Monarda fistulosa</i>	Lamiaceae	Native	Perennial	Non-legume forb	19.13	0.041	66	285.71
<i>Monarda punctata</i>	Lamiaceae	Native	Perennial	Non-legume forb	NA	0.027	NA	NA
<i>Oenothera biennis</i>	Onagraceae	Native	Biennial	Non-legume forb	13.17	0.034	31	187.50
<i>Oenothera sp.</i>	Onagraceae	Unknown	Biennial	Non-legume forb	13.17	0.035	31	187.50
<i>Oligoneuron rigidum</i>	Asteraceae	Native	Perennial	Non-legume forb	11.69†	0.058	60	300.68†
<i>Oxalis sp.</i>	Oxalidaceae	Unknown	Perennial	Non-legume forb	44.25	NA	32	170.15
<i>Panicum virgatum</i>	Poaceae	Native	Perennial	C4 Grass	15.96	0.101	36	337.96
<i>Penstemon gracilis</i>	Scrophulariaceae	Native	Perennial	Non-legume forb	NA	0.005	NA	NA
<i>Penstemon grandiflorus</i>	Scrophulariaceae	Native	Perennial	Non-legume forb	9.37	0.159	64	253.52
<i>Physalis hispida</i>	Solanaceae	Native	Perennial	Non-legume forb	25.33	0.153	22	200.00
<i>Poa pratensis</i>	Poaceae	Native and/or Introduced	Perennial	C3 Grass	19.11	0.019	25	222.22
<i>Polygonum convolvulus</i>	Polygonaceae	Introduced	Annual	Non-legume forb	49.69	0.46	20	200.00
<i>Polygonum tenue</i>	Polygonaceae	Native	Annual	Non-legume forb	6.77	0.147	23	410.02
<i>Potentilla argentea</i>	Rosaceae	Introduced	Perennial	Non-legume forb	17.17	0.009	31	325.95
<i>Prunus sp.</i>	Rosaceae	Unknown	Perennial	Woody	29.79	NA	NA	268.29
<i>Pseudognaphalium helleri</i>	Asteraceae	Native	Biennial	Non-legume forb	25.99	0.003	38	251.61
<i>Quercus ellipsoidalis</i>	Fagaceae	Native	Perennial	Woody	14.59	NA	NA	450.00
<i>Rosa arkansana</i>	Rosaceae	Native	Perennial	Woody	22.96	0.934	29	578.95
<i>Rudbeckia hirta</i>	Asteraceae	Native	Biennial	Non-legume forb	21.75	0.03	19	165.32
<i>Rumex acetosella</i>	Polygonaceae	Introduced	Perennial	Non-legume forb	38.51	0.001	24	260.60

<i>Schizachyrium scoparium</i>	Poaceae	Native	Perennial	C4 Grass	17.97	0.081	61	285.71
<i>Setaria sp.</i>	Poaceae	Unknown	Annual	C4 Grass	28.23	0.187	55	304.27
<i>Silene antirrhina</i>	Caryophyllaceae	Native	Annual	Non-legume forb	18.11	0.008	26	220.98
<i>Silene latifolia</i>	Caryophyllaceae	Introduced	Perennial	Non-legume forb	24.18	0.072	55	230.77
<i>Sisyrinchium campestre</i>	Iridaceae	Native	Perennial	Non-legume forb	9.68	0.095	23	250.00
<i>Solidago nemoralis</i>	Asteraceae	Native	Perennial	Non-legume forb	9.72	0.006	57	291.67
<i>Solidago sp.</i>	Asteraceae	Native	Perennial	Non-legume forb	13.14	0.019	67	320.73
<i>Sorghastrum nutans</i>	Poaceae	Native	Perennial	C4 Grass	16.31	0.129	104	323.53
<i>Sporobolus cryptandrus</i>	Poaceae	Native	Perennial	C4 Grass	18.02	0.012	35	356.35
<i>Stachys palustris</i>	Lamiaceae	Native	Perennial	Non-legume forb	15.35	0.088	46	192.31
<i>Symphyotrichum oolentangiense</i>	Asteraceae	Native	Perennial	Non-legume forb	16.24	0.028	56	210.53
<i>Taraxicum officinale</i>	Asteraceae	Introduced	Perennial	Non-legume forb	52.79	0.047	4	164.18
<i>Tragopogon dubius</i>	Asteraceae	Introduced	Biennial	Non-legume forb	36.2	0.942	40	138.64
<i>Trifolium pratense</i>	Fabaceae	Introduced	Perennial	Legume	38.15	0.13	NA	250.00
<i>Trifolium repens</i>	Fabaceae	Introduced	Perennial	Legume	23.67	0.081	4	207.16
<i>Trifolium sp.</i>	Fabaceae	Introduced	Perennial	Legume	23.67	0.08	5	207.16
<i>Verbascum thapsus</i>	Scrophulariaceae	Introduced	Biennial	Non-legume forb	18.47	0.004	85	176.45
<i>Vicia villosa</i>	Fabaceae	Introduced	Annual	Legume	26.52	3.768	45	195.24‡
<i>Viola pedatifida</i>	Violaceae	Native	Perennial	Non-legume forb	18.89	0.1	16	166.46

Table S2 Summary of daily climate data for Cedar Creek study site. Temperature and rainfall for the study year (2014) falls within the 95% confidence intervals of recent and long-term time periods; means followed by standard deviations are shown in the table. Growing season included months of May, June and July, corresponding with the timing of weed removal in the experimental plots (June and July). Data were collected by an automated on-site weather station at Cedar Creek Ecosystem Science Reserve (<https://www.cedarcreek.umn.edu/research/weather>).

Time period	Mean daily maximum temperature in growing season (°C)	Highest daily maximum temperature in growing season (°C)	Mean daily minimum temperature in growing season (°C)	Highest daily minimum temperature in growing season (°C)	Total precipitation in growing season (mm)	Mean daily maximum temperature over calendar year (°C)	Mean daily minimum temperature over calendar year (°C)	Total precipitation across the calendar year (mm)
2014	23.3 ± 5.3	31.8	11.9 ± 5.0	23.0	345	10.1 ± 14.1	-0.6 ± 14.0	791
2009-2014	24.3 ± 1.2	35.4 ± 2.0	11.9 ± 1.2	23.0 ± 1.3	352 ± 139	12.5 ± 1.7	1.0 ± 1.3	725 ± 95
1994-2014	24.6 ± 1.2	35.4 ± 1.6	11.7 ± 1.0	22.7 ± 2.0	311 ± 99	12.7 ± 1.3	1.0 ± 1.2	753 ± 117
1963-2018	25.0 ± 1.4	35.4 ± 2.0	11.7 ± 1.0	22.6 ± 1.8	302 ± 92	12.7 ± 1.3	0.6 ± 1.2	769 ± 160

Table S3 Summary table of fixed effects from the species-in-subplot scale model examining effects of warming, sown community species richness and colonist species' traits on colonist biomass accrual. All explanatory variables were standardised to allow comparison of coefficient estimates and to facilitate model convergence. The reference warming level was the control (ambient). No main or interaction terms involving Low and High warming treatments were significant.

	Estimate	SE	df	t-value	p-value
(Intercept)	-2.529	0.209	91.593	-12.076	<0.001
log(SLA)	0.099	0.18	71.679	0.551	0.583
log(Seed Mass)	0.091	0.185	79.642	0.492	0.624
sqrt(Maximum Height)	0.114	0.173	67.639	0.66	0.512
log(LDMC)	0.009	0.182	76.603	0.052	0.959
<i>Terms involving the <u>Diversity</u> treatment</i>					
log(Sown Richness)	-0.062	0.13	67.231	-0.477	0.635
log(SLA) × log(Sown Richness)	-0.278	0.093	56.84	-2.989	0.004
log(Seed Mass) × log(Sown Richness)	0.245	0.099	65.655	2.479	0.016
sqrt(Max. Height) × log(Sown Richness)	0.17	0.097	56.955	1.76	0.084
log(LDMC) × log(Sown Richness)	0.204	0.095	59.226	2.15	0.036
<i>Terms involving the <u>Warming</u> treatment</i>					
Warming Treatment (High)	-0.054	0.115	1235.774	-0.474	0.635
Warming Treatment (Low)	0.049	0.113	450.237	0.433	0.666
log(SLA) × Warming (High)	0.067	0.118	1219.518	0.572	0.567
log(SLA) × Warming (Low)	-0.118	0.115	457.272	-1.02	0.308
log(Seed Mass) × Warming (High)	0.069	0.13	1250.707	0.527	0.599
log(Seed Mass) × Warming (Low)	-0.13	0.124	496.521	-1.049	0.295
sqrt(Max. Height) × Warming (High)	0.117	0.107	1149.677	1.093	0.274
sqrt(Max. Height) × Warming (Low)	0.111	0.106	389.523	1.045	0.297
log(LDMC) × Warming (High)	0.002	0.119	1120.968	0.015	0.988
log(LDMC) × Warming (Low)	-0.058	0.117	459.159	-0.495	0.621

Table S4 Type III ANOVA tables for all linear mixed-effects models examining the effects of warming, sown diversity, and their interaction on 10 response variables describing colonist species assemblages. The biomass of sown species was included as a covariate in all models. † The main term for warming in the log(Seed Mass) CWM model was significant ($p=0.036$) once the interaction term was removed.

	SS	MS	df	F-value	p-value
<u>Extent of species colonization</u>					
Richness of colonist assemblage					
Log(sown community biomass)	10.487	10.487	1;86	1.15	0.287
log(Sown richness)	1002.71	1002.71	1;42	109.944	<0.001
Warming	111.612	55.806	2;59	6.119	0.004
log(Sown richness):Warming	22.456	11.228	2;59	1.231	0.299
log(Biomass of colonist assemblage)					
Log(sown community biomass)	0.003	0.003	1;88	0.005	0.941
log(Sown richness)	19.831	19.831	1;44	33.105	<0.001
Warming	0.035	0.018	2;60	0.029	0.971
log(Sown richness):Warming	0.848	0.424	2;60	0.708	0.497
<u>Functional groups and traits of colonists</u>					
log(Biomass of C4 grass colonists)					
Log(sown community biomass)	0.892	0.892	1;85	0.658	0.42
log(Sown richness)	9.825	9.825	1;30	7.25	0.012
Log(Sown richness) ²	28.893	28.893	1;28	21.32	<0.001
Warming	3.717	1.858	2;56	1.371	0.262
log(Sown richness):Warming	5.186	2.593	2;56	1.913	0.157
log(Sown richness) ² :Warming	3.064	1.532	2;56	1.13	0.33
log(Biomass of C3 grass colonists)					
Log(sown community biomass)	0.027	0.027	1;82	0.025	0.875
log(Sown richness)	19.251	19.251	1;42	17.552	0
Warming	17.003	8.501	2;60	7.751	0.001
log(Sown richness):Warming	14.842	7.421	2;60	6.766	0.002
log(Biomass of legume colonists)					
Log(sown community biomass)	0.051	0.051	1;82	0.035	0.851

log(Sown richness)	18.983	18.983	1;41	13.215	0.001
Warming	3.404	1.702	2;59	1.185	0.313
log(Sown richness):Warming	2.402	1.201	2;59	0.836	0.438
log(Biomass of forb colonists)					
Log(sown community biomass)	0.562	0.562	1;84	0.664	0.417
log(Sown richness)	14.92	14.92	1;41	17.633	<0.001
Warming	1.449	0.725	2;59	0.857	0.43
log(Sown richness):Warming	3.945	1.972	2;58	2.331	0.106
log(SLA) CWM of colonist assemblage					
Log(sown community biomass)	0.005	0.005	1;89	0.207	0.651
log(Sown richness)	0.223	0.223	1;44	8.544	0.005
Warming	0.014	0.007	2;59	0.266	0.767
log(Sown richness):Warming	0.073	0.036	2;59	1.393	0.256
log(Seed Mass) CWM of colonist assemblage					
Log(sown community biomass)	1.113	1.113	1;87	3.078	0.083
log(Sown richness)	5.250	5.250	1;43	14.525	<0.001
Warming†	1.717	0.859	2;60	2.375	0.102
log(Sown richness):Warming	0.245	0.123	2;60	0.339	0.714
sqrt(Max. Height) CWM of colonist assemblage					
Log(sown community biomass)	0.548	0.548	1;88	0.453	0.503
log(Sown richness)	0.005	0.005	1;44	0.004	0.95
Warming	3.236	1.618	2;60	1.338	0.27
log(Sown richness):Warming	1.783	0.892	2;60	0.737	0.483
log(LDMC) CWM of colonist assemblage					
Log(sown community biomass)	0.012	0.012	1;87	0.615	0.435
log(Sown richness)	0.053	0.053	1;44	2.665	0.11
Warming	0.028	0.014	2;60	0.704	0.498
log(Sown richness):Warming	0.052	0.026	2;60	1.311	0.277

Table S5 Summary tables of fixed effects from the species-in-plot scale models examining effects of sown species richness and colonist species' traits on colonist biomass accrual.

Summaries are provided for two models with traits expressed differently in each. All explanatory variables were standardised to allow comparison of coefficient estimates and to facilitate model convergence. Coefficient estimates for the interactions fitted in Figure 5 are also indicated. Sown CWMs refer to community weighted trait means for the sown communities.

	Estimate	SE	df	t-value	p-value
Model 1. Colonist species' traits expressed as species' means					
<i>(849 observations; marginal $R^2 = 0.065$, AICc = 3789.803)</i>					
Intercept	-2.057	0.222	80.429	-9.277	<0.001
log(Sown Richness)	-0.15	0.151	57.68	-0.99	0.326
log(SLA)	0.111	0.197	72.186	0.562	0.576
log(Seed Mass)	0.008	0.198	80.34	0.041	0.967
sqrt(Maximum Height)	0.163	0.192	69.73	0.852	0.397
log(LDMC)	0.042	0.197	78.002	0.214	0.831
log(SLA):log(Sown Richness) (Fig. 6a)	-0.304	0.119	59.933	-2.563	0.013
log(Seed Mass):log(Sown Richness) (Fig. 6b)	0.29	0.123	69.262	2.359	0.021
sqrt(Max. Height):log(Sown Richness) (Fig. 6c)	0.249	0.125	65.148	2.002	0.049
log(LDMC):log(Sown Richness) (Fig. 6d)	0.192	0.119	62.164	1.622	0.11
Model 2. Colonist species' traits expressed as relative distances from sown CWMs					
<i>(849 observations; marginal $R^2 = 0.099$, AICc = 3784.882)</i>					
Intercept	-1.975	0.216	80.981	-9.129	<0.001
log(Sown Richness)	-0.084	0.146	53.909	-0.577	0.566
log(SLA)	0.075	0.181	97.094	0.414	0.68
log(Seed Mass)	-0.193	0.153	76.336	-1.262	0.211
sqrt(Maximum Height)	0.588	0.175	72.83	3.365	0.001
log(LDMC)	0.155	0.161	70.018	0.963	0.339
log(SLA):log(Sown Richness)	-0.305	0.118	70.849	-2.57	0.012
log(Seed Mass):log(Sown Richness)	0.306	0.118	78.793	2.601	0.011
sqrt(Max. Height):log(Sown Richness)	0.276	0.148	78.033	1.869	0.065
log(LDMC):log(Sown Richness)	0.136	0.123	75.54	1.102	0.274

Figure S1 Yearly climate data for Cedar Creek study site from 1963 to 2018 for a) total annual precipitation, b) daily maximum temperature, and c) daily minimum temperature. The study year (2014) is highlighted in each panel (deep blue, pink, light blue). Temperature records are shown with boxplots (b & c); boxes show median and interquartile range; whiskers show ranges excluding outliers (points). Data were collected daily by an automated on-site weather station at Cedar Creek Ecosystem Science Reserve (<https://www.cedarcreek.umn.edu/research/weather>).

Figure S2 Box and whisker plots for each continuous functional trait by functional group (C3 grass, C4 grass, forb and legume) for all 92 species observed in the experiment (sown residents and colonists). Boxes show median and interquartile range; whiskers show ranges excluding outliers (points).

Figure S3 Box and whisker plots for each continuous functional trait by functional group (C3 grass, C4 grass, forb and legume) and lifespan (annual, biennial and perennial) for all species observed in the experiment (sown residents and colonists) with trait data (≥ 86 taxa). Boxes show median and interquartile range; whiskers show ranges excluding outliers (points).

Figure S4 Principal component analysis of four continuous traits (square-root plant height, log seed mass, log SLA and log LDMC) for 155 herbaceous taxa found in grassland communities at Cedar Creek Ecosystem Reserve, Minnesota. Blue squares indicate species that form part of the sown communities in the experimental plots (16 species with complete trait coverage); red circles indicate species that colonized at least one of the plots in 2014 (70 taxa); grey triangles are species not observed in the experiment in 2015 but are part of the species pool for grasslands at Cedar Creek (69 taxa). Taxa inclusion in the PCA was based on the following criteria: i) occur in grasslands at Cedar Creek; ii) non-woody taxa; have locally collected trait data available for all four traits. Species with asterisks are non-native.

Figure S5 Box and whisker plots for each continuous functional trait by biogeographic origin (non-native or native to Minnesota) and species pool group (colonist, non-colonist, sown resident). Boxes show median and interquartile range; whiskers show ranges excluding outliers (points). Letters denote significantly different groups based on ANOVA and post hoc tests of pairwise differences.

Figure S6 Box and whisker plots of sown CWM trait values in each treatment combination for **(a)** SLA, **(b)** seed mass, **(c)** maximum height and **(d)** LDMC. Two-species plots were included with monocultures for this supplementary analysis. Bars and *P*-values indicate tests for warming effects on CWMs at each diversity level. (N.S. = not significant). Boxes show median and interquartile range; whiskers show ranges excluding outliers (points).

Figure S7 Relationships between the biomass of a given functional group in the sown communities (each of the four analyses, one for each functional group, represented by a distinct colour) and the biomass of colonists categorised as **(a)** C4 grasses, **(b)** C3 grasses, **(c)** non-legume forbs, and **(d)** legumes. Plots show that the biomass of forb colonists was lower in subplots with greater biomass of sown C3 and C4 grasses (panel c). C3 grass and legume colonists also had lower biomass in subplots with greater biomass of sown C4 grasses (panels b & d), whereas C4 grass colonists had lower biomass in plots with greater biomass of legumes (panel a).