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RESEARCH PAPER

Anthropogenic-based regional-scale factors most consistently explain plot-level exotic diversity in grasslands

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ABSTRACT

Aim Evidence linking the accumulation of exotic species to the suppression of native diversity is equivocal, often relying on data from studies that have used different methods. Plot-level studies often attribute inverse relationships between native and exotic diversity to competition, but regional abiotic filters, including anthropogenic influences, can produce similar patterns. We seek to test these alternatives using identical scale-dependent sampling protocols in multiple grasslands on two continents.

Location Thirty-two grassland sites in North America and Australia.

Methods We use multiscale observational data, collected identically in grain and extent at each site, to test the association of local and regional factors with the plot-level richness and abundance of native and exotic plants. Sites captured environmental and anthropogenic gradients including land-use intensity, human population density, light and soil resources, climate and elevation. Site selection occurred independently of exotic diversity, meaning that the numbers of exotic species varied randomly thereby reducing potential biases if only highly invaded sites were chosen.

Results Regional factors associated directly or indirectly with human activity had the strongest associations with plot-level diversity. These regional drivers had divergent effects: urban-based economic activity was associated with high exotic : native diversity ratios; climate- and landscape-based indicators of lower human population density were associated with low exotic : native ratios. Negative correlations between plot-level native and exotic diversity, a potential signature of competitive interactions, were not prevalent; this result did not change along gradients of productivity or heterogeneity.

Main conclusion We show that plot-level diversity of native and exotic plants are more consistently associated with regional-scale factors relating to urbanization and climate suitability than measures indicative of competition. These findings clarify the long-standing difficulty in resolving drivers of exotic diversity using single-factor mechanisms, suggesting that multiple interacting anthropogenic-based processes best explain the accumulation of exotic diversity in modern landscapes.

Keywords

Anthropogenic disturbance, environmental heterogeneity, exotic plant species, Nutnet (Nutrient Network), productivity, scale dependency, species diversity.

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INTRODUCTION

Two uncertainties in plant invasion ecology are whether native diversity consistently regulates the establishment of exotic species (e.g. competitive-based biotic resistance in species-rich communities; Kennedy *et al*., 2002) and, conversely, the degree to which exotic species cause direct reductions in native biodiversity (Sax *et al*., 2005; Davis *et al*., 2011). A key to evaluating these factors is determining the strength of negative interactions between the two species groups [i.e. whether or not they strongly interact during (establishment) and after (impact) the invasion process]. Models emphasizing the importance of species interactions for diversity and function in plant communities predict that competition will strongly influence the establishment and performance of exotic flora (e.g. Keane & Crawley, 2002), which is consistent with evidence from numerous invasions (Levine *et al*., 2003; Heard & Sax, 2013). Models emphasizing regional filtering based on trait differences suggest that the evolutionary association of exotic species with anthropogenic environments can favour their abundance, with competitive interactions being potentially important, but not a necessity, for exotic dominance or diversity (Firn *et al*., 2011; Leifso *et al*., 2012). This latter model is consistent with the anthropogenic-based biotic homogenization of regional species pools across the planet, where human disturbance can select the same subsets of species within and among sites (McKinney, 2006; Olden *et al*., 2006; Firn *et al*., 2011). While the traits and environmental contexts associated with the establishment of exotic species are increasingly well understood (Sax *et al*., 2005; Richardson & Pyšek, 2006; Seastedt & Pyšek, 2011), uncertainty persists with regard to how local and regional factors alone and interactively affect diversity in invaded systems (Daehler, 2003).

The relative influence of local and regional processes can be difficult to test due to a number of methodological challenges, especially because such tests require sites, scales and gradients to be spanned simultaneously (Stohlgren *et al*., 1999). Studies spanning multiple sites and scales can be sensitive to differences in sampling grain and extent, a common challenge, especially for meta-analyses (Chase & Knight, 2013; Powell *et al*., 2013). Local and regional processes can produce identical signatures of plot-level plant diversity in invaded systems, meaning that their relative effects on diversity are difficult to test in isolation (Chytrý *et al*., 2008). High ratios of exotic-to-native diversity at fine scales, for example, can reflect competitive displacement of native species (Levine *et al*., 2003), regional-scale disturbances that open establishment windows for exotics (MacDougall & Turkington, 2005) or unsaturation prior to invasion due to biogeographical constraints (Sax *et al*., 2005).

In addition, there is often a positive connection between regional-scale human activity and exotic diversity, but this does not clarify mechanism. Humans could be vectors of dispersal for exotic taxa including those with superior competitive traits (Reichard & White, 2001), or play a more direct role in the establishment of exotics through the perturbation of native communities that might otherwise be resistant (MacDougall & Turkington, 2005). Native diversity can also be positively associated with human activity, albeit by different mechanisms such as the concentration of human populations in diversity hotspots (Cincotta *et al*., 2000). Finally, the relationship between native and exotic diversity can vary along environmental gradients (Melbourne *et al*., 2007), with fine-scale negative species interactions predicted to be more prevalent when production is high or heterogeneity low (Davies *et al*., 2005, 2007; Melbourne *et al*., 2007). Given these various challenges, it is not surprising that a wide array of outcomes from a range of systems have been reported for the relationship between plot-level native and exotic diversity (Stohlgren *et al*., 1999; Cleland *et al*., 2004; Sax *et al*., 2005; Fridley *et al*., 2007; Powell *et al*., 2013), suggesting there may not be a consistent global relationship or that it might be obscured by sampling biases or site contingencies (Chase & Knight, 2013).

In this paper, we explore these issues using a multiscale observational dataset from 32 grassland sites on two continents, testing the association of local and regional factors with the plot-level diversity of native and exotic plants. Our data were sampled identically in grain and extent at each site (Borer *et al*., 2014), with sites capturing a range of environmental and anthropogenic gradients including land-use intensity, nearby human population density, variation in light and soil resources, climate and elevation. Because site selection and the layout of the sampling design occurred independently of exotic diversity, the numbers of exotic species varied randomly within and among sites, thereby reducing potential analytical biases that could occur if we explicitly targeted only highly invaded sites.

Our primary analysis uses mixed-effects models to examine the direction and magnitude of influence on plot-level (1 m^2) diversity. Direction refers to the possibility that regional-scale anthropogenic and environmental factors may be similarly associated with both species pools (e.g. potential shared positive associations of native and exotic diversity) or divergently associated (factors positively associated with exotic diversity are negatively associated with native diversity). We also test for the prevalence of several pattern-based signatures associated with local negative species interactions, quantifying the frequency of plot-level negative relationships between the two species groups, whether these negative relationships intensify by environmental heterogeneity and productivity, and evidence for species displacement (i.e. native species *x* is absent or rare where exotic species *y* is present). These tests are motivated by the assumption that if competition is highly prevalent, then one or more of these patterns should be consistently detectable at one or more spatial scales (plots, sites).

METHODS

We uniformly collected data from 32 sites from North American and Australian grasslands (Table S1 in Supporting Information), part of the global Nutrient Network (Nutnet, http://www.nutnet.org/). All sites in the network are herbaceous-dominated plant communities, with site selection occurring independently of levels of native or exotic diversity. We selected the subset of NutNet sites from across the planet with one or

more exotic species (which excluded our sites from Europe, Asia and Africa, most of which are uninvaded). All data are in non-manipulated plots, placed within a *c.* 1000 m^2 area, and are uniform in vegetation type at each site (i.e. avoiding transitional boundaries). Sites were restricted to natural grasslands (no planted pastures) and included several where native–exotic diversity relationships had been previously examined (e.g. Kennedy *et al.*, 2002; Davies *et al.*, 2005, 2007). Pooled together, the sites capture gradients of exotic diversity, environmental conditions and anthropogenic disturbance (Table S2).

The data at each site were sampled at an identical spatial extent (total area covered) and with the same sampling units, and were nested at four scales: plots (1 m^2), blocks (10 m^2), sites (30 m^2) and regions. There were four regions on the two continents – central North American grasslands, intermountain grasslands of North America, Pacific coast grasslands of North America and coastal grasslands of Australia – with the regions defined based on floral affinities. Our primary response variable was the ratio of exotic and native species diversity per 1 m^2 plot (i.e. we are not directly testing diversity levels among sites, regions or continents, or using species accumulation curves). We also examined the relative abundance of native and exotic species (Table S3), given that richness may not fully reflect effects of exotic species. 'Local' processes are those environmental factors sampled in 1 m^2 plots, the resolution where species interactions are mostly likely to unfold (Davies *et al.*, 2005). 'Regional' processes are those measured at the site level or higher. In total, there were 706 native species and 179 exotic species among the 32 sites. Specific details on the measurement of plot-level diversity, cover and abiotic factors (light, biomass, nutrients) are found in the Appendix S1 and Borer *et al.* (2014).

For regional factors, we quantified precipitation and temperature data using the WorldClim global climate database (version 1.4; http://www.worldclim.org/), focusing on five factors: mean annual temperature (°C), standard deviation in temperature, mean annual range in temperature (°C), mean temperature during the wettest 4 months, mean annual precipitation (mm) and coefficient of variation of precipitation (an estimate of seasonality). We determined distance to coast or major river system, given the known importance of this to human population density (Small & Cohen, 2004); distance to the closest settlement (e.g. village, town, city); mean housing prices and mean family income in those settlements; closest permanent road and closest cultivated area including pasture and oldfield given that both can serve as vectors of establishment for exotic species. Economic data came from online municipal databases (e.g. http://www.city-data.com/).

Statistical analyses

We developed linear mixed effect models (hereafter LMEMs) to test the explanatory power of anthropogenic, climatic, soil and biomass factors on native and exotic species richness at the plot level. The LMEMs treated exotic or native richness, climatic conditions, landscape and human influences, primary productivity and non-climatic environmental variability as fixed effects, with random intercepts due to site (σ^2_{site}). We used Wald *F*-tests to test the significance of the fixed effects in each model. These analyses were performed using the nlme library (R version 3.1; R Development Core Team, 2012) in R 2.13.1. Using JMP 8.0 (SAS, 2009), we developed generalized linear mixed models with Poisson distributions to describe the relationship between the counts of native and exotic species (i.e. diversity) at the various scales within each of the four regions, including whether the slopes become increasingly positive at broader spatial scales. We used a nested random effects design, analysing diversity within plot, block, site and region to determine the slope between native and exotic diversity for each spatial scale. We analysed the influence of productivity and environmental heterogeneity on these relationship slopes, testing whether slope angles were contingent on environmental context.

Statistical analyses: species associations

We tested whether observed plot-level percentage cover relationships among species pairs are more negative (competition or divergent habitat preferences) or positive (facilitation or shared habitat preferences) than expected by chance (see Ricklefs, 2011). Testing against random expectations is necessary given the potential for neutral processes to produce negative slopes between native and exotic diversity at fine scales (Fridley *et al.*, 2004). We tested this possibility at two levels: the regional level and the site level. The regional level tests for species associations among plots within regions, and the site level tests for species associations among plots within individual sites.

To diminish the possibility of spurious correlations among the multiple comparisons at the regional level, only species with 10 or more occurrences in plots per region were used, for a total of 16,187 pairings among the 32 sites. We decreased this number to a minimum of three occurrences per site, testing whether the inclusion of greater numbers of rarer species altered the outcome of the analysis, but the results of the analysis did not change.

While tests of individual correlation coefficients are not interpretable due to potential Type I error inflation from multiple tests, the general trends themselves are testable, and comparable with random expectations. Under a predominant influence of competition, negative associations would be greater than either positive associations or the random expectation. If shared environmental affiliations or facilitation were predominant, positive associations would be greater than the random expectation. Under a neutral pattern, where species identity would be unimportant, no difference from the random expectation would be expected.

Our analysis occurred in two stages. First, for each region (plots within regions) or site (plots within sites) we determined the proportion of correlations in a Pearson correlation matrix of species pairs that were significantly positive or negative. The significant positive and negative correlations (using critical values of *r* for each sample size) were identified for exotic versus exotic (e.g. EE in Fig. 3), native versus native (NN) and native versus exotic species pairs (NE). Next, the occurrences of each species were randomized among the samples in the region (i.e.

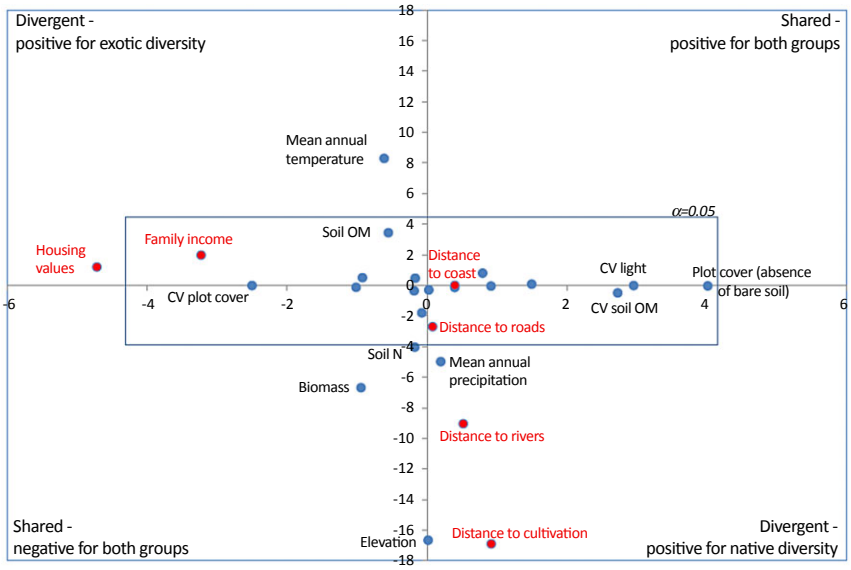

Figure 1 Shared and divergent drivers of plot-level species diversity, based on *F*-values derived from separate linear missed-effect models (LMEM) for exotic and native species (Table S6). *F*-values are reported as positive numbers if the relationship between the explanatory variable and the response was positive, and negative numbers if the relationship was negative. Data are for 32 sites on two continents, relating to landscape and human influences (red) or to non-human environmental factors (blue). The internal box indicates significance level for one or both *F*-values from the separate LMEM analyses for exotic and native species ($\alpha = 0.05$). OM, organic matter; CV, coefficient of variation.

we shuffled the rows in each column, where the samples are rows and species are columns) 1000 times, and the correlations were recalculated each time. *Z*-tests were used to determine whether the true proportions of significant positive and negative correlations were greater or smaller than the mean proportions using randomized data, for the NN, EE and NE species pairs. This stage allowed us to determine whether positive associations (shared environmental affiliation or facilitation) and negative associations (competition or divergent environmental affiliation) were greater than expected by chance.

For the second stage of the analysis, we corrected the proportions of significant positive and negative correlations by their random expectations ($X_{corrected} = X_{true} - X_{randomized}$). We then used *Z*-tests to test for differences between the proportions of significant positive and negative correlations among the three types of species pairs (NN, EE, NE). This stage allowed us to determine whether the proportion of positive associations (e.g. shared habitat affiliations, facilitation) was greater or less than the proportion of negative associations (e.g. competition, divergent habitat affiliations).

We used an identical approach to test whether dominant exotic species (i.e. the most abundant species in percentage cover at each site) had a disproportionate number of negative associations with other species, either at the regional or site levels. We tested for proportions of significant positive or negative associations between the most abundant exotic species compared with native and other exotic species, versus the null expectation for each group based on randomization, as described above. Due to sample size restrictions, we could only conduct this analysis with species that met the minimum frequency criterion of three occurrences per site for a total of 725 pairings among the 32 sites.

RESULTS

The strongest associations of local versus regional factors with plot-level diversity were regional factors associated directly or indirectly with human activity (Fig. 1, Table S4). Further, the direction of association was almost entirely divergent (favouring or selecting against one species pool but not the other), indicating that exotic and native diversity were being influenced by different drivers. We did not detect any reciprocal association between the two species groups, with no significant negative relationship between native diversity and the number of exotic species, and vice versa.

There was one significant positive association with exotic diversity – higher mean annual temperature (Fig. 1, Table S4). Exotic diversity was negatively associated with factors related to remoteness from urban centres and intensive land management (high elevation, distance from rivers, distance from cultivation), and with mean annual precipitation and standing biomass. In our study, sites with higher mean temperatures and less precipitation are mostly in lower-elevation coastal areas associated with relatively moderate climates, including milder winter temperatures averaging > 0 °C (e.g. California, south-eastern Australia). For standing biomass, we could not distinguish statistically whether this negative association was a function of high native diversity (i.e. over-yielding, resulting in resistance to establishment by exotics) or dominance by one or a few exotic species (preventing any further accumulation of exotic diversity).

For native species, there was also only one significant factor – a negative association with higher housing values. There were trends toward lower native diversity in areas with higher average family incomes (e.g. California) and higher native diversity in sites with greater total percentage cover in plots, but neither were significant (Fig. 1).

There was no general prevalence of negative slopes between plot-level native and exotic diversity within the 32 sites or among the four regions (grey and coloured trend lines; Figs 2 & S1). Although the global pooled relationship was significantly negative (black trend line in Fig. 2), the trend derived from combinations of non-significant, negative and positive associations among sites and regions on the two continents (inset panel in Fig. 2). There were pronounced regional differences in ratios

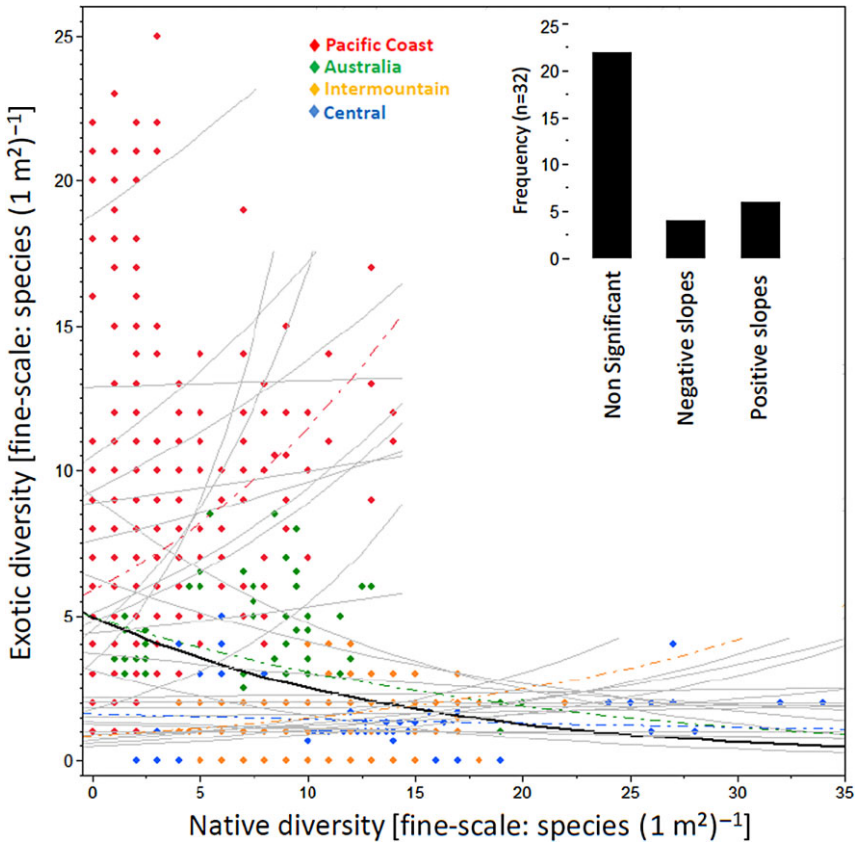

Figure 2 Slopes of plot-level native–exotic diversity relationships in 32 grassland sites in four regions of Australia and North America. The bold line is the significant net negative trend among all sites, consistent with theoretical predictions of diversity-mediated invasion resistance. The grey slopes indicate this trend is actually a composite of relationships that are mostly non-significant (see inset graph). The coloured dashed lines indicate the net trends within each region.

of exotic and native diversity in plots, with central North American sites, and to a lesser extent Australian sites, typically having lower exotic : native ratios while sites on the Pacific Coast of North America tended to have positive plot-level relationships. Significant plot-level negative slopes were evident at only 5 of 32 sites.

These results did not change when accounting for productivity or heterogeneity, where negative slopes might be more evident at higher above-ground biomass or with lower within-site environmental heterogeneity (Figs S1 & S2A,B). For productivity, we tested if the slope of the relationship between native and exotic richness became more negative as levels of several within-site factors associated with production increased (biomass, cover, soil P and soil N; Fig. S1). Only soil P influenced plot-level diversity, but the trend varied regionally, with a negative relationship in central North America but a positive slope for Pacific Coast sites (Fig. S2A). For heterogeneity, only one factor affected diversity levels with increasing spatial scale – the coefficient of variation (CV) of total biomass (Fig. S2B). However, the direction of this relationship was opposite for native and exotic species (Fig. S2B). Native diversity generally increased with variation in biomass, although only significantly so in Australia. Exotic diversity declined with plot-level heterogeneity in biomass cover, a trend consistent across regions.

As we broadened our sampling resolution to examine native versus exotic diversity at the site and regional levels, the slope of the relationship between native and exotic diversity sometimes became more positive (Fig. S1), as expected given that environmental heterogeneity and diversity both tend to increase with scale. However, these increases in slope angle were rarely significant and did not occur consistently within or among regions (Fig. S1).

When testing for possible species displacement, we found that significant species associations (negative or positive) in plots were uncommon among the 16,187 species pairs that were examined (Fig. 3, Tables S5 & S6), with significantly negative native–exotic pairings no more frequent than significant negative native–native pairings. At the regional level, only Australia demonstrated more negative plot-level associations between native and exotic species (Table S5), consistent with the species diversity relationships modelled for this region in Fig. 2. Among the four regions, significant negative native–exotic associations averaged only 3.1% of all tested pairings (range 1.6–4.7%; Fig. 3).

Similarly inconsistent results were observed when testing if negative associations were more prevalent for the most dominant exotic at each site (given that many exotic species could be naturalized but with low impacts; Fig. S3, Table S3). In total, negative associations specific to exotic dominants were detected in only 42 of 725 total pairings in 1184 plots (i.e. 5.8% of all pairings with exotic dominants across the 32 sites). Testing for changes in abundance of native species in the presence of the most dominant exotic, we detected significant cover reductions at some sites that suggest that some exotics do have competitive impacts on native flora, but 20 of the 32 sites showed no relationship (Table S3, Fig. S3).

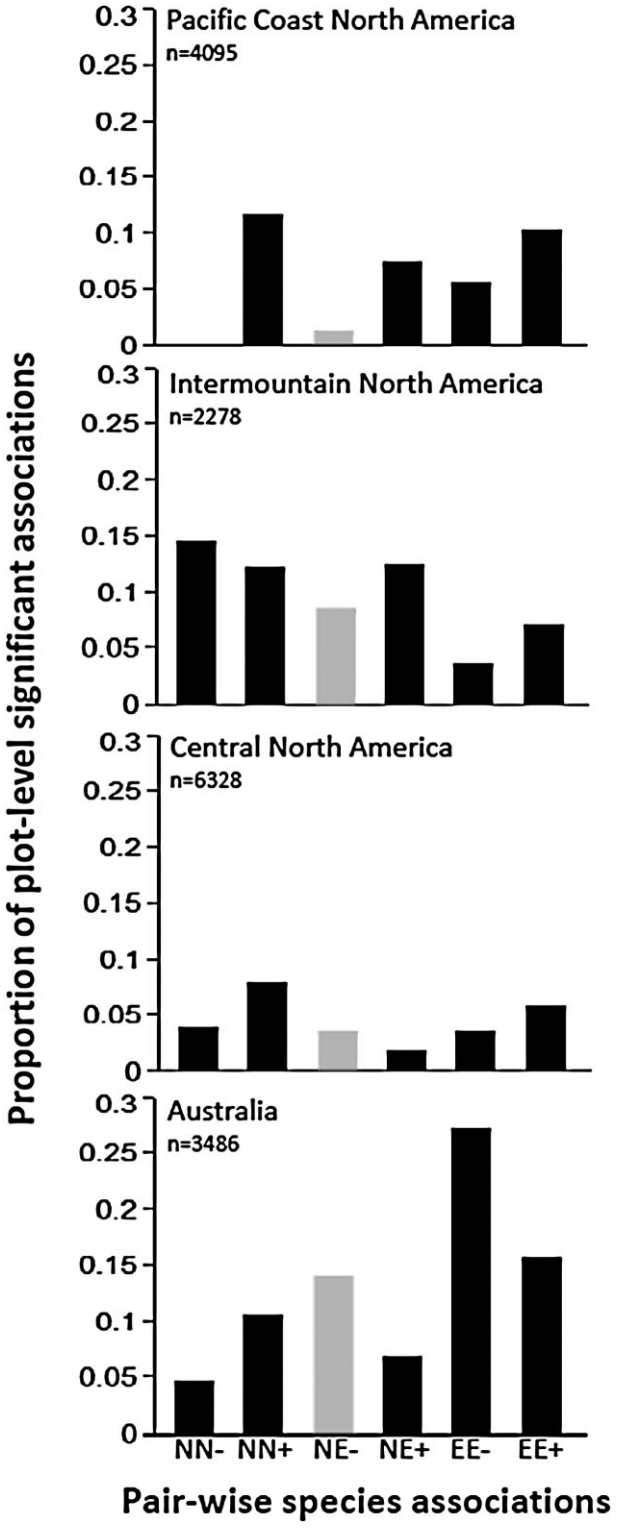

Figure 3 Proportions of significant null-corrected plot-level pairwise species associations within the four study regions, for species occurring in 10 or more 1 m^2 plots. Sample sizes (n) indicate the total number of pairwise species comparisons by region. N indicates native species and E exotic species, with the grey bar indicating the frequency of negative native–exotic species associations.

DISCUSSION

We tested the relative influence of regional and local factors on the plot-level diversity of native and exotic species, using standardized methods in 32 grasslands on two continents. We were especially interested in the prevalence of pattern-based signatures associated with local competition, given uncertainties about whether relationships between native plant diversity and resistance to exotic establishment are consistent among sites (low exotic : native ratios), and whether native taxa are commonly displaced at fine scales by exotic species (high exotic : native ratios) (e.g. Gurevitch & Padilla, 2004; Pimentel *et al.*, 2005; Powell *et al.*, 2013).

We did not consistently observe either pattern. Instead, we found that only regional-scale factors were significantly associated with plot-level diversity for both species groups, both directly via factors relating to human land use and population density and indirectly via climatic conditions that may influence the accumulation of exotic species but also affect human settlement. Specifically, exotic diversity declined with remoteness (high elevation, distance from river valleys and cultivation), in cooler and wetter climates and at sites with higher biomass, while native diversity was inversely correlated with economic measures. There were no significant drivers shared between the two groups, nor did the pool sizes significantly affect one another. Several sites showed consistent pattern-based signatures of competition, including study areas where these relationships had been previously described (e.g. Kennedy *et al.*, 2002; Davies *et al.*, 2005), but this was not a generalizable trend. There has been considerable debate over the influences of regional versus local factors on the accumulation of exotic diversity (Daehler, 2003). Our data suggest that the establishment of exotic species most consistently accelerates when co-occurring with various forms of human disturbance.

The connection between humans and high exotic diversity is almost axiomatic (Rejmanek, 2003; Taylor & Irwin, 2004; Williams *et al.*, 2005; McKinney, 2006; Olden *et al.*, 2006; Mikkelson *et al.*, 2007), but the mechanisms are not always clear. Humans could be vectors of dispersal for exotic taxa with superior competitive ability, sometimes in association with factors such as enemy escape or novel weapons (Keane & Crawley, 2002; Callaway, 2007). Alternatively, exotic establishment could more often derive from regional-scale perturbations that displace the native community (e.g. cultivation, overgrazing) without competition necessarily playing a strong role. This can unfold, for example, if exotics disperse *en masse* (intentionally or inadvertently) into perturbed habitat, with no mechanism for re-establishment by native taxa if they do not differ substantially in competitive ability (Daleo *et al.*, 2009). More likely, however, is that competitive superiority is context dependent, with regional filtering favouring traits for tolerating anthropogenic perturbation thereby leading to superior resource acquisition (Seabloom *et al.*, 2003). While either scenario is possible, our data most strongly point towards regional trait-based filtering as the more prevalent influence on the accumulation of exotic plant taxa, with no consistent signal of local

displacement. This result did not change when we examined patterns of exotic and native abundance (see also Seabloom *et al.*, 2013). Our data also indicate that this filtering is divergent, with strong inverse relationships detected between native and exotic diversity versus the intensity and type of human activity. All 32 sites have been influenced by some form of anthropogenic activity and support varying levels of exotic diversity, but sites nearer to densely populated settlements had the highest ratios of exotic : native diversity. The diversity of plot-level native and exotic species pools has the potential to respond similarly to environmental drivers – with shared negative responses to factors such as soil N or biomass, or positive shared responses to factors such as heterogeneity in soil resources – but we detected neither relationship.

There has been considerable debate on how competition affects the establishment and impact of exotic species (Sax *et al.*, 2005; Davis *et al.*, 2011). Although competition is clearly important for the establishment of many exotic species, including those that become invasive (Levine *et al.*, 2003; Heard & Sax, 2013), our analyses suggest that its influence can vary by location and environmental context, a finding consistent with previous studies that have examined competition and invasion more directly (e.g. Vilà & Weiner, 2004; Stachowicz & Byrnes, 2006). There was no consistent signal of exotics associated with low native diversity, nor was high native diversity always correlated with resistance to the accumulation of exotic species. Negative slopes have commonly been interpreted as a signal of competition at fine scales (Shea & Chesson, 2002), but we only observed significant negative slopes at 15% of our sites and the slopes were not related with higher productivity or lower heterogeneity. Past work has highlighted how direct connections between the accumulation of exotic diversity and the extinction of native species are not readily observed (Davis *et al.*, 2011). We similarly see no consistent trends of negative associations in the occurrence or abundance of native and exotic diversity within plots, the spatial scale where signatures of competition should be most evident.

We did not test the longer-term stability of the observed diversity patterns, specifically whether the trends will be maintained (coexistence) or whether native diversity will incrementally decrease in the presence of high exotic diversity or highly abundant exotics. We do see possible reductions in plot-level native diversity or plant abundance in 12 of the 32 sites, in association with high exotic cover. The likely outcomes of these reductions for native species – lower plot-level diversity, fewer individuals per plot, with remnant populations rare and spatially aggregated – are warning signs for increased extinction risk (Gilbert & Levine, 2013; Powell *et al.*, 2013). In the majority of sites, however, these patterns were not evident, with no detectable relationship between the abundance of dominant invaders and the diversity or abundance of native species. It is also unclear whether the concentration of exotic diversity towards heavily settled regions will persist, or whether there are invasion lags where high-impact exotics in particular will eventually reach more remote locations (Alexander *et al.*, 2011). Such lags can be associated with competition–colonization trade-offs, with slower invaders having higher impacts, but if this were true then negative slopes and negative species associations should have been more prevalent. In total, we do see evidence for biotic homogenization among our 32 sites, with sites becoming more similar than different, especially at the functional group level (e.g. dominance by Eurasian agronomic species; Firn *et al.*, 2011), but this trend is not consistently associated with evidence of negative interactions among the two species groups.

Our findings have several implications. The variability in the population density of humans globally, for example, appears to strongly predict the plot-level diversity of exotic plant species in grasslands. In turn, this suggests that these exotics are likely to be functionally different in how they respond to regional-scale anthropogenic disturbance regimes, compared with many native plant taxa. This is supported by a recent global analysis of perturbation responses at our sites for 1197 native and 201 exotic species, which demonstrates that exotics are significantly more likely to respond positively to certain anthropogenic disturbances, especially nutrient increases (E.W.S., unpublished data). Our results also clarify the difficulty in inferring general invasion principles from single-site studies (Kueffer *et al.*, 2013) – the accumulation of exotic diversity is clearly a multivariate process deriving from different environmental conditions, introductory histories of exotic taxa including propagule pressure and biogeographical contexts (e.g. Novak & Mack, 2001; Reichard & White, 2001; Sax *et al.*, 2005; Leifso *et al.*, 2012). This variability in the dynamics of exotic establishment has been observed on islands versus mainland (Sax *et al.*, 2002) and along gradients of elevation and latitude (Alexander *et al.*, 2011) – here we see the same variability with gradients of land-use intensity.

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Additional references may be found at the end of the supplementary material at [website].

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 The relationship between native and exotic diversity at three spatial scales for 32 grassland sites from four regions.
Figure S2 Scale-dependent responses of diversity to environmental gradients in 32 grassland sites from four regions on two continents.
Figure S3 A scatter diagram showing the strength of the relationship between the average cover of exotic dominants (Table S4) vs. total native plant cover at the 32 study sites.
Table S1 List of study sites.
Table S2 Summary of regional metadata from the four study regions, representing 32 grassland sites on two continents.
Table S3 The most abundant (i.e. dominant) exotic species at each site.
Table S4 Results from ANOVAs conducted to assess the significance of the fixed effects for linear mixed effect models of introduced and native species richness and fixed effects representing climatic conditions, landscape and human influences, primary productivity and non-climatic environmental variability with random intercepts due to site.
Table S5 Regional-level comparisons of significant correlations among species pairs, within 32 grassland sites on two continents.
Table S6 Comparison of significant plot-level negative vs positive pairwise associations for native and exotic species.
Appendix S1 Additional methodological and analytical details.

BIOSKETCH

Andrew MacDougall is an associate professor at the University of Guelph. The Nutrient Network is a global meta-experiment testing a range of fundamental processes including how anthropogenic changes to resources and consumers transform the composition, diversity, structure and function of grasslands (http://www.nutnet.org).

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