



Patterns of phylogenetic diversity are linked to invasion impacts, not invasion resistance, in a native grassland

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Abundance; Alien species; Biodiversity; Community phylogenetics; Darwin's naturalization hypothesis; Diffuse competition; Dominance; Facilitation; Over-dispersion; Pair-wise competition; Rarity; Smooth brome

Nomenclature

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Abstract

Question: There are often more invasive species in communities that are less phylogenetically diverse or distantly related to the invaders. This is thought to indicate reduced biotic resistance, but recent theory predicts that phylogenetic relationships have more influence on competitive outcomes when interactions are more pair-wise than diffuse. Therefore, phylogenetic relationships should change when the invader becomes dominant and interactions are more pair-wise, rather than alter biotic resistance, which is the outcome of diffuse interactions with the resident community; however both processes can produce similar phylogenetic structures within communities. We ask whether phylogenetic structure is more associated with biotic resistance or invasion impacts following *Bromus inermis* (brome) invasion and identify the mechanisms behind changes to phylogenetic structure.

Location: Native grassland in Alberta, Canada.

Methods: We tested whether phylogenetic structure affected biotic resistance by transplanting brome seedlings into intact vegetation and quantified invasion impacts on community structure by surveying across multiple invasion edges. Additionally, we tested whether relatedness, rarity, average patch size, evolutionary distinctiveness or environmental tolerances determined species' response to brome invasion.

Results: Neither phylogenetic diversity, nor relatedness to brome, influenced the strength of biotic resistance; resource availability was the strongest determinant of resistance. However, communities did become less diverse and phylogenetically over-dispersed following brome invasion, but not because of the loss of related species. Brome invasion was associated with declines in common species from common lineages and increases in shade-tolerant species and rare species from species-poor lineages.

Conclusions: Our results suggest that invasion is more likely to affect the phylogenetic structure of the community than the phylogenetic structure of the community will affect invasion. However, they also suggest that the degree of relatedness between the invader and the resident community is unlikely to drive these effects on phylogenetic community structure. Consistent with previous studies, invasion effects were stronger for common species as they have reduced shade tolerance and cannot persist in a subordinate role. This suggests that invasion effects on phylogenetic community structure will depend on which species exhibit traits that enable persistence with the invader and how these traits are distributed across the phylogeny.

Introduction

The phylogenetic relationships between invasive species and the resident community have been identified as key features affecting invasion resistance; resident species closely related to the invader and communities with high phylogenetic diversity are thought to increase invasion resistance (Strauss et al. 2006; Diez et al. 2008; Gerhold et al. 2011). However, many characteristics proposed to increase invasion resistance within communities also change as a consequence of invasion; invasive species can be passengers or drivers of community change (MacDougall & Turkington 2005; White et al. 2012). For example, higher species diversity often reduces the likelihood of successful invasion (Levine et al. 2004), but successful invasion also reduces species diversity (Levine et al. 2003; Vilà et al. 2011). Therefore, the relationships found between invasion and phylogenetic diversity or invasion and relatedness could represent the impact of invasion, rather than invasion resistance. Further, recent theory suggests that relatedness may only influence the outcome of species interactions if competition is pair-wise or if one species is dominant (Thorpe et al. 2011; Bennett et al. 2013) due to indirect interactions among species when competition is diffuse (Moen 1989; Levine 1999). This suggests that relatedness and phylogenetic diversity are more likely to be important in determining the impacts of a dominant invader on the resident community than in determining initial invasion resistance, when the invader is competing with many members of the resident community in a diffuse fashion. Here, we use both experimental and observational approaches to differentiate the effects of phylogenetic relationships on invasion resistance from the effect of invasion on phylogenetic relationships.

The impact of an invader on the native community is thought to depend on the fitness of the invader relative to the resident community (MacDougall et al. 2009). If an invader is a better competitor or is less affected by predators than the resident community, then it has higher fitness and it should have higher impacts. However, which of the species within the resident community are most affected by the invader can depend on many factors. If niches are conserved and the invader is a strong competitor, then close relatives should be most affected and the community should become phylogenetically over-dispersed (Webb et al. 2002; Mayfield & Levine 2010). Conversely, if competitive abilities are conserved, then we expect distant relatives to be most affected and the community to become phylogenetically clustered (Mayfield & Levine 2010). Alternatively, if competition is non-transitive (Frean & Abraham 2001), we may expect the invader to exclude some lineages, but not others. Many of these

hypotheses rely on the idea that some aspect of a species' ecology is conserved, although there is considerable doubt about the degree of ecological conservatism (Silvertown et al. 2006; Cahill et al. 2008; Bennett & Cahill 2013). Further, they assume that the invader is best able to compete with certain groups of species and is therefore a 'competitive specialist'. However, any species able to achieve dominance is more likely to affect most of the species within a community and be a 'competitive generalist'.

If the invader is a competitive generalist, many species should be affected and species richness should decline, as often happens following invasion (Levine et al. 2003; Vilà et al. 2011). However, any changes to phylogenetic structure will depend on which species can co-exist with the invader. Co-existence with the invader is likely to depend on the ability to tolerate low resource conditions, which is more likely in less common or rare species as they already exist in a subordinate role (Powell et al. 2013). However, the effects of species exclusion on phylogenetic structure would depend on the evolutionary distinctiveness (Redding & Mooers 2006) of the co-existing species. Evolutionary distinctiveness is a measure of the amount of unique evolutionary history contained within a species. If co-existing species have high evolutionary distinctiveness, then phylogenetic dispersion should increase, whereas if they have low evolutionary distinctiveness, phylogenetic dispersion should decline.

In addition to informing our understanding of the ecology of invasions, identifying how invasion affects rare (Pärtel et al. 2005) and evolutionarily distinct (Redding & Mooers 2006; Isaac et al. 2007) species is important for developing conservation priorities and potentially for predicting future impacts in novel environments (Mouquet et al. 2012). Further, conserving areas with high phylogenetic diversity has become increasingly identified as a priority for biodiversity conservation efforts (Faith 1992; Rolland et al. 2012). High phylogenetic diversity areas represent a disproportionate amount of evolutionary history and preserving such areas can potentially increase both the diversity and stability of ecosystem functions (Cadotte et al. 2008, 2012; Srivastava et al. 2012). However, the application of phylogenetic information to conservation efforts is somewhat controversial (Rosauer & Mooers 2013; Winter et al. 2013) and the utility of applying these measures requires further evaluation.

In this study, we use a competition experiment and surveys across the edge of multiple invasion points to separate the effects of community characteristics on invasion resistance from how invasion affects these community characteristics. Focusing on smooth brome (*Bromus inermis* Leyss.) invasion into a native grassland in Alberta, Canada,

we tested three questions: (i) do relatedness, species diversity or phylogenetic diversity alter biotic resistance or is the association between these community characteristics and invasion an effect of invasion; (ii) which species characteristics (resource responses, relation to the invader, evolutionary distinctiveness, phylogenetic lineage, commonness or average patch size) best predict a species response to invasion; and (iii) can we use changes in phylogenetic diversity or the abundance of high evolutionary distinctiveness species to identify conservation concerns resulting from invasion?

Methods

Study site and species

This study occurred at the University of Alberta Ranch in Kinsella, Alberta, Canada, within the Aspen Parkland ecoregion. The fields used encompass a 50-ha section of native grassland within a savanna-type habitat consisting of a mixture of rough fescue (*Festuca hallii* (Vasey) Piper) grassland and patches of aspen (*Populus tremuloides* Michx.). Herbaceous biomass is primarily graminoid although the majority of species are forbs (Appendix S1).

There are few invasive, or even non-native, species at the site (see Appendix S1). Of the invasive species, smooth brome is among the most abundant. Brome is a long-lived perennial grass that was intentionally introduced to North America in the late 1800s to be used as a forage crop. It is also among the most serious invasive plants in Canada (Catling & Mitrow 2005). Brome continues to spread across Canada and the United States (Sinkins & Otfinowski 2012; Ellis-Felege et al. 2013) and is often associated with reduced native plant diversity (Otfinowski et al. 2007; Fink & Wilson 2011). Similarly, brome is increasing in extent at the study site, with brome patches advancing by over 30 cm on average (± 17 cm SE) between 2012 and 2013 alone (G.C. Stotz, unpubl. data). Thus, brome invasion is a serious on-going problem at the site with high potential for increased future impacts.

Phylogeny construction

We used the molecular community phylogeny outlined in Bennett et al. (2013), which sampled 146 species across 35 families found at the study site. The phylogeny was based on a 1400 bp section of the ribulose-bisphosphate carboxylase gene (*rbcL*) and showed high concordance with other published phylogenies (Bennett et al. 2013). For all analyses, we substituted congeners otherwise absent from the data set for species for which we had no phylogenetic information (four species in total). One species, *Danthonia intermedia* Vasey, had no congeners, but was only present in 2/200 plots, so we excluded it from all analyses.

Relatedness, diversity and biotic resistance

We define biotic resistance as the reduction in survival and growth of the invasive species by the resident community. To test for biotic resistance, we transplanted brome seedlings into 20 pairs of 4-m² plots, one plot of intact native prairie and one where the resident community was removed. The intact resident community within the plots varied in species richness from seven to 20 species per 0.25 m² (Fig. 2a,d) and exhibited a range of phylogenetic structures from clustered to over-dispersed (see Appendix S2). None of the plots had previously been invaded by brome, but all plots were within 50 m of a brome invasion site. Further, the communities present in the experimental plots showed nearly complete overlap with communities directly adjacent to brome invasion sites (see Appendix S3 for methods and Appendix S4 for results). Given the high rate of brome advance into such adjacent communities, we see no reason to expect that these communities are inherently more invasion resistant than those communities that are already being invaded. Initial removal of the resident community was accomplished by applying glyphosate (Roundup[®]) in August 2008 and again in early May 2009. In late May 2009, a total of 120 brome seedlings (three seedlings per plot) were transplanted into the 20 plot pairs. After transplanting, the removal treatments were primarily maintained through hand weeding. A 0.5 m buffer was maintained around each removal plot by applying glyphosate every 6 wk; extreme care was taken to avoid contacting target plants. To further reduce interaction with the surrounding community, roots were cut to 10-cm depth around the outside of the buffer every 6 wk. Further details of the experimental set-up are published elsewhere (Bennett & Cahill 2012).

Individual brome plants were monitored for 4 yrs, with surviving plants harvested at peak biomass in late July 2012. From these measurements we calculated the effects of biotic resistance on brome survival and growth. For survival, we calculated biotic resistance as the difference in the number of survivors between the intact community and the removal plots (control – removal) for each pair of plots ($N = 20$). For biomass, we calculated biotic resistance as the log response ratio (Cahill 1999) of the average size of survivors between removal and control plots ($\ln(\text{control}/\text{removal})$). However, for biomass, we only included paired plots if both contained at least one brome seedling ($N = 10$).

To determine which characteristics were associated with biotic resistance, we measured aspects of both the biotic and abiotic environment. We estimated the composition of the resident community (Bennett & Cahill 2012) within a central 0.25-m² subplot within the

control plot, a common method in plant ecology (e.g. Fargione & Tilman 2005; Lamb 2008). Using this approach, the maximum distance between any brome seedling and the central plot was 1.12 m; community composition was relatively consistent across this distance (J.A. Bennett, pers. obs.). Invasion success is often dependent on resource availability (Suding et al. 2004); to control for this, we measured nitrogen, phosphorus, water and light availability within each control plot in 2012 (see Appendix S3 for further details).

From the community composition data, we calculated multiple community metrics potentially associated with biotic resistance, including species richness, species evenness and a number of phylogenetic indices. We calculated phylogenetic diversity (PD; Faith 1992) and a standardized version of the same index following Procheş et al. (2006). Here, PD is a measure of the total amount of evolutionary history within the plot not including the root (Cadotte et al. 2008) and varies with richness, while standardizing PD shows the amount of evolutionary history independent of richness and allows for comparison among plots varying in richness; we included only standardized PD in the analysis of biotic resistance to avoid collinearity. Additionally, we calculated an abundance-weighted metric of phylogenetic diversity related to species evenness, phylogenetic species evenness (PSE; Helmus et al. 2007). Both PD and PSE were calculated using the picante package (Kembel et al. 2010) in R (v.2.13.2, R Foundation for Statistical Computing, Vienna, AT). To test the importance of relatedness, we calculated the mean phylogenetic distance from brome as the branch length between brome and each species found within each plot; an abundance-weighted index of phylogenetic distance was calculated using the proportional abundance of species rather than presence-absence data.

We used best-subsets linear regression in SPSS (v.20.0, IBM Corp., Armonk, NY, USA) to identify which factors influenced biotic resistance and used separate models for survival and size. There was substantial collinearity between occurrence- and abundance-weighted community characteristics, so we ran all possible combinations of models from two subsets of the predictors: one with community characteristics based on species occurrence (richness, standardized PD and phylogenetic distance) and one based on abundance data (evenness, PSE and abundance-weighted phylogenetic distance). Both sets of potential predictors included all four environmental covariates. From these candidate models, we identified the ten best models and calculated the weighting for each factor based on the Akaike weights of these models (Burnham & Anderson 2002). Similar analyses were conducted using survival ($N = 20$) and growth ($N = 12$) of brome in the

intact resident community, rather than relative to brome without competition, with similar results (see Appendix S5).

Invasion impacts on diversity

To determine whether invasion changes taxonomic or phylogenetic diversity in the resident community, pre-invasion data are crucial, but detailed and spatially referenced records are hard to find, if they exist at all. However, brome forms dense stands within the field site, which abruptly drop in brome cover leaving a clear visual edge between the invaded and non-invaded areas (Fig. 1a). By measuring community changes across this transition, we can develop a spatial representation of the chronosequence of invasion. Space-for-time substitutions are commonly used in invasion studies (Hejda & Pyšek 2006; Powell et al. 2013) and are of immense value to the understanding of long-term dynamics of invasive species (Strayer et al. 2006). Although space-for-time substitutions have limitations, brome invasion offers a good system for its implementation. There is on-going spread of the invader as evidenced by the high rate of spread, with native areas transitioning into invaded areas as evidenced by the edges of brome invasion showing an intermediate state between native and fully invaded areas (Hejda & Pyšek 2006; Fig. 1).

In the summer of 2012, we laid belt transects perpendicular to the edge of 20 unconnected brome patches separated by at least 5 m. Each transect was centred at the invasion edge and included nine 0.2×0.5 -m plots for a total area of 0.2×4.5 m. For analysis, plots were grouped based upon their positions along the transect, which represent areas dominated by brome, edge areas and adjacent native community (Fig. 1a). In each plot, we estimated community composition as percentage cover and from these estimates we calculated richness, evenness, phylogenetic diversity, standardized phylogenetic diversity and PSE. We tested for brome invasion effects on diversity by comparing each diversity metric among the three community types (brome, edge and native) using separate linear mixed models in SPSS (v 20.0, IBM). For each model, community type was a fixed effect, with transect number as a random effect. We treated individual plots as repeated measures of community type within each transect using an autoregressive covariance structure to account for the spatial structure of the plots within the community type.

Invasion impacts and species characteristics

To identify which species characteristics (phylogeny, abundance or resource responses) make species more

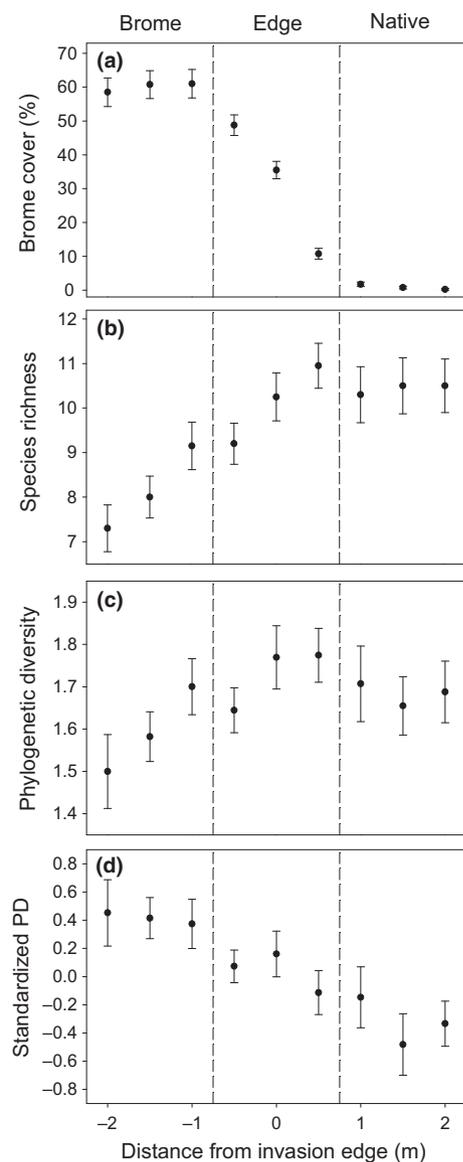


Fig. 1. Bromo abundance (a), species richness (b), phylogenetic diversity (c), and phylogenetic diversity standardized by species richness (d) across the brome invasion edge. Dashed vertical lines represent our division of plots into brome, edge and native community types. Error bars represent SE.

susceptible to the effects of invasion, we first calculated each species' response to brome invasion. Species responses were calculated from the community composition data obtained in the invasion impact survey as the log response ratio of occurrence frequency in brome invaded areas relative to the adjacent native communities ($\ln(\text{invaded}/\text{native})$), with occurrence frequency calculated as the total number of plots in which each species occurred in each community type.

Certain lineages may respond to brome invasion in a characteristic fashion. We identified whether lineages varied in their response to brome invasion by decomposing the variation in brome invasion response across the phylogenetic tree (Pavoine et al. 2010). This method provides three randomization tests that identify whether response variation is skewed towards a single node or a few nodes, and whether response variation is skewed towards the root or tips of the tree (Pavoine et al. 2010). Further, it isolates the proportion of response variation represented by individual nodes that can be used to identify the most responsive groups.

For each species, we also calculated their phylogenetic distance to brome, evolutionary distinctiveness, commonness, patch size, and responses to shading, water and nutrients. We calculated phylogenetic distance to brome in the same fashion as when measuring biotic resistance and evolutionary distinctiveness relative to all species sampled at the site over the last 11 yrs (see Appendix S1) using the fair proportions index (Isaac et al. 2007) in the picante package in R (Kembel et al. 2010). Commonness and patch size were calculated using data from 179 unrelated, unmanipulated study plots surveyed at various intervals between 2001 and 2012 across the site (see Appendix S1). Commonness was calculated as the proportion of plots occupied by a species and patch size as the average percentage cover within plots where the species was found. Plant responses to shading, nutrient addition (as NPK) and watering were measured as the log response ratio of the change in abundance following experimental manipulations at the focal site (Bennett & Cahill 2013).

Data for all characteristics were not available for all species. For four species, representing a total of five occurrences, we had no data on commonness or relative abundance across the site; these species were excluded from subsequent analyses. Further, resource response data were not available for all species, and most of the species for which these data were available were from common lineages. This biased our data, so we ran two separate models to determine which characteristics determine species responses to brome invasion. The first model included all species ($N = 50$), but only included phylogenetic distance to brome, evolutionary distinctiveness, commonness and patch size as predictor variables. The second model included a reduced species set, but also included responses to nutrients, shading and water as predictors of response to brome invasion ($N = 36$). Both models were general linear models in SPSS (v 20.0, IBM). Prior to analysis phylogenetic distance to brome was squared, evolutionary distinctiveness was natural logarithm transformed, commonness cube root transformed, and patch size square root transformed to reduce the influence of extreme values.

Results

Relatedness, diversity and biotic resistance

Biotic resistance of brome invasion was relatively high; survival was reduced 51.4% and size 99.7% by competition with the resident community, but the strength of biotic resistance was also quite variable. This variation was best explained through the abiotic environment, not the measured community characteristics (see Appendix S6, S7). Phosphorus availability increased resistance to brome survival (Fig. 2a) and was the top weighted factor (Akaike weight = 0.746). Nitrogen availability decreased resistance to brome growth (Fig. 2b) and was the most heavily weighted factor in this group of models (Akaike weight = 0.495). In fact, the model with only nitrogen availability was the only model explaining resistance to brome growth that fit better than an intercept only model

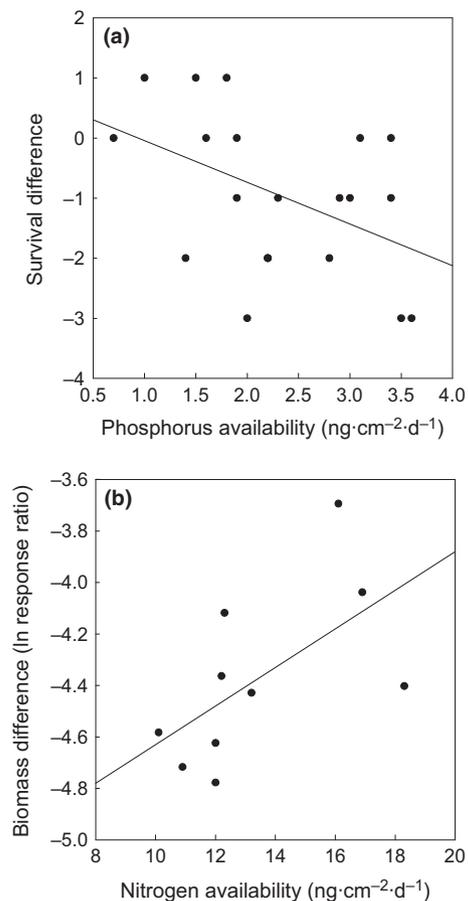


Fig. 2. Biotic resistance to brome survival as a function of phosphorus availability (a) and resistance to brome growth as a function of nitrogen availability (b). Positive values show facilitation and negative values biotic resistance by competition. Differences in survival were calculated as control – removal and biomass differences as $\ln(\text{control}/\text{removal})$.

(see Appendix S6). For growth resistance models, all plant community characteristics were non-significant and models containing these characteristics had low weights (see Appendix S6, S7). Community characteristics did a slightly better job of predicting biotic resistance to brome survival (see Appendix S6), although most were not significant (see Appendix S6). Communities with greater evenness were significantly more invasible in some models (Akaike weight = 0.334; see Appendix S6); however, evenness and phosphorus availability were negatively correlated ($r = -0.435$, $P = 0.055$) and evenness explained little variation in models where both variables were included (see Appendix S6). This correlation coupled with a factor weighting less than half that of phosphorus availability suggests a limited influence of evenness on biotic resistance.

Invasion impacts on diversity

Although we found no effect of species richness or phylogenetic diversity on resistance to brome invasion, both were highly influenced by brome invasion. Brome invasion decreased species richness (Fig. 1b; $F_{2,44} = 13.77$, $P < 0.001$), but did not significantly affect phylogenetic diversity (Fig. 1c; $F_{2,49} = 2.28$, $P = 0.113$). The lack of change in phylogenetic diversity with invasion was likely due to an increase in the average amount of evolutionary history represented by species able to co-exist with brome, as seen in the increase in standardized phylogenetic diversity (Fig. 1d; $F_{2,52} = 9.98$, $P < 0.001$). Consequently, brome-dominated communities were phylogenetically over-dispersed, while native communities were more phylogenetically clustered (Fig. 1d). Edge communities generally represented a transition zone between native and brome communities, and showed a random degree of phylogenetic dispersion (Fig. 1d). Similar patterns were found using abundance-based indices (see Appendix S8).

Invasion impacts and species characteristics

The increase in phylogenetic dispersion following brome invasion can be explained through non-random effects on specific lineages. Brome effects were skewed towards multiple nodes (single node skewness $P = 0.229$; few nodes skewness $P = 0.027$; Fig. 3) deep within the phylogeny (root skewness $P = 0.003$; Fig. 3). Specifically, the Asteraceae and Poaceae were the most negatively affected by brome invasion, with most species within both groups showing fairly consistent declines following brome invasion (Fig. 3). These results are reinforced by our findings that species closely related to brome (Fig. 4d; $F_{1,45} = 3.52$, $P = 0.067$) and common species (Fig. 4a; $F_{1,45} = 10.68$, $P = 0.002$) declined to a greater extent following brome

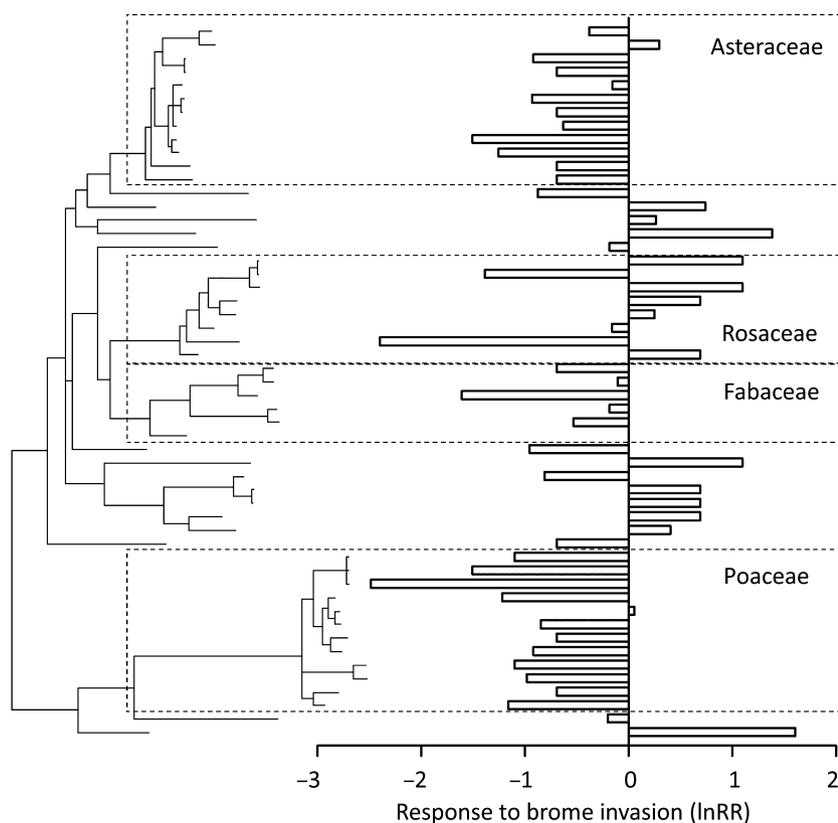


Fig. 3. Species responses to brome invasion as a function of phylogenetic position. Responses were calculated as the natural logarithm transformed response ratio (lnRR) of frequency of occurrence in brome patches relative to the adjacent native community. Each of the major grassland families is grouped within dashed boxes.

invasion. However, species with large patch sizes were less affected by brome invasion (Fig. 4b; $F_{1,45} = 6.60$, $P = 0.014$). In this system, the Poaceae and Asteraceae are the most common and often most abundant lineages at the site (see Appendix S1). Other members of Poaceae are obviously the most closely related to brome; however, within the Poaceae, relation to brome was not associated with response to brome (see Appendix S9), and Asteraceae are the most distantly related group within this system. Combined, we suggest that it is commonness and local patch size (Fig. 4a,b), rather than relation to brome that most strongly determined how species respond to brome invasion here. Other lineages either declined or showed mixed results, with several species-poor lineages increasing following brome invasion (Fig. 3). As such, responses to brome invasion became more positive as the evolutionary distinctiveness of species increased (Fig. 4c; $F_{1,45} = 5.29$, $P = 0.026$).

When considering only the reduced species set, more shade-tolerant species did relatively well following brome invasion (Fig. 4e; $F_{1,27} = 4.90$, $P = 0.036$). This suggests that brome excludes species through competition for light and is consistent with the reduced light availability found

inside brome patches (see Appendix S10). Neither response to water addition (Fig. 4f; $F_{1,27} = 2.66$, $P = 0.115$) nor response to nutrient addition (Fig. 4g; $F_{1,27} = 2.77$, $P = 0.108$) were significant predictors of response to brome. Commonness ($F_{1,27} = 4.72$, $P = 0.039$), patch size ($F_{1,27} = 5.74$, $P = 0.024$) and phylogenetic distance to brome ($F_{1,27} = 3.39$, $P = 0.077$) remained significant or marginally significant predictors of response to brome when reducing the number of species included from 50 to 36. However, the explanatory power of evolutionary distinctiveness ($F_{1,27} = 2.21$, $P = 0.148$) declined. These differences likely reflect a lower power to detect these effects as well as a bias against species from rare lineages when using the reduced species pool (see Appendix S11).

Discussion

Biotic resistance to brome invasion showed little evidence of an association with the community characteristics measured (Fig. 2), but brome invasion did decrease richness and increase phylogenetic dispersion in high-density areas (Fig. 1). These results challenge the idea that biotic

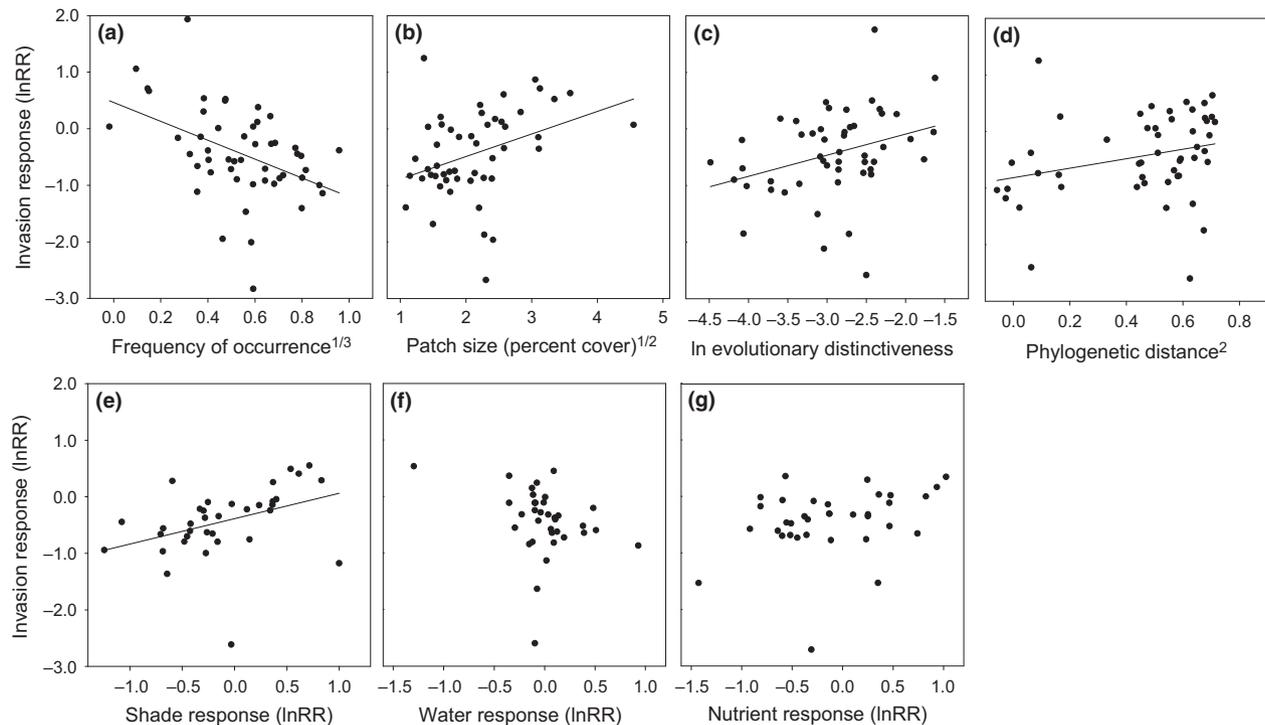


Fig. 4. Partial regression plots showing how species' characteristics affect their responses to brome invasion. Characteristics shown in the top row, (a) rarity, (b) patch size, (c) evolutionary distinctiveness and (d) relatedness to brome include all 50 species. Characteristics in the bottom row, (e) shading response, (f) watering response and (g) nutrient (NPK) response were only available for 36 of 50 species. Rarity was measured as the frequency of occurrence and cube root transformed. Patch size was measured as the average percentage cover where the species was found and was square root transformed. Evolutionary distinctiveness was measured following Isaac et al. (2007) and natural logarithm transformed. Relatedness to brome was measured as the phylogenetic distance to brome and squared. Each resource response value was taken from data in Bennett & Cahill (2013) and represents differences in abundance between control and treatment plots. Values shown represent the relationship between each variable and invasion response holding all other predictors constant.

resistance necessarily increases with relatedness between the invader and the recipient community (Strauss et al. 2006), but suggest that invasion can exclude related species from the resident community. This suggests that rather than being a 'passenger' (sensu MacDougall & Turkington 2005) of the phylogenetic structure of the community, brome invasion is the 'driver' of change in phylogenetic structure. Rather than resulting from competitive effects on close relatives, as is commonly predicted (Webb et al. 2002; Mayfield & Levine 2010), the over-dispersion within the community appears to be driven by a loss of common species and an increase in evolutionarily distinct species able to co-exist with brome (Fig. 4). These results suggest that the effects of invasion on phylogenetic structure are likely more nuanced than previously anticipated (Webb et al. 2002; Mayfield & Levine 2010), relying on how traits relating to competitive tolerance, such as shade tolerance, are distributed across the phylogenetic tree. Approaches integrating both functional traits and phylogenetic information may yield greater insight (Cadotte et al. 2013).

Biotic resistance or invasion impacts

The relationship between diversity and biotic resistance is complex, with positive and negative relationships reported for both species (Fridley et al. 2007) and phylogenetic diversity (Thuiller et al. 2010). Diversity is expected to decrease invasion success by reducing the number of empty niches (Levine et al. 2004; MacDougall et al. 2009); however, if the invader has higher fitness than the species within the recipient community, it can simply displace resident species (MacDougall et al. 2009). Brome is a better competitor than most species at the site (Wang et al. 2010), which suggests that niche availability may not limit brome invasion, thereby reducing the importance of diversity. Of the diversity metrics measured, only species evenness showed any evidence of a relationship with biotic resistance, although the effect was weak, given that most of the variation was explained by its correlation with phosphorus availability. However, rather than promoting biotic resistance, more even communities were more invasible.

This suggests that communities that have dominant species may be more resistant, especially if these communities contain species with traits that enable them to better compete with the invader (Hillebrand et al. 2008). These dominant species likely occupy a niche similar to the invader, therefore increasing resistance. However, if invasion is successful, any fitness advantage for the invader would likely lead to the exclusion of the resident dominant (MacDougall et al. 2009).

Related species are expected to reduce invader success by occupying similar niches to the invader and thus increasing competition with the invader (Strauss et al. 2006). However, competition is not always stronger among related species (Cahill et al. 2008), and related species are often ecologically dissimilar (Silvertown et al. 2006; Bennett & Cahill 2013). Even if competitive abilities are conserved, the importance of relatedness may be reduced when competition is diffuse (Thorpe et al. 2011; Bennett et al. 2013). Patterns observed in pair-wise interactions may not be as important in diverse communities due to (i) individuals interacting with multiple species at the same time, in different combinations and densities and (ii) the potential for indirect interactions (Moen 1989). For example, within the recipient community, by competing both with the invader and amongst themselves, resident species can indirectly facilitate the invader (Levine 1999). The combination of reduced interaction strength due to lower competitor density and the multitude of potential indirect interactions may explain why we rarely find invasion to be limited by similarity between the invader and resident species (Price & Pärtel 2013). Thus, for relatedness to be an important driver of biotic resistance the traits that enable the resident species to suppress the invader must be conserved and the related species must exist in sufficient abundance to have an effect.

Rather than being linked to species diversity or phylogenetic relationships, biotic resistance was associated with nutrient availability. Nutrient availability commonly dictates the outcome of competitive interactions (Wilson & Tilman 1993; Rees 2013), including for invaders (Suding et al. 2004). Brome is thought to have a competitive advantage in high nitrogen soils (Vinton & Goergen 2006). This suggests that if brome establishes, the recipient community is less able to suppress its growth when nitrogen is higher, resulting in reduced biotic resistance. However, brome is not responsive to increased phosphorus (DiAllandro et al. 2013); if the recipient community is more responsive to phosphorus, brome may be excluded at higher phosphorus levels. Alternatively, species with traits enabling them to suppress brome may be found in high phosphorus environments. A more thorough trait examination would be required to differentiate between these possibilities.

Although we found no evidence that phylogenetic relationships altered invasion resistance, we did find that invasion changed phylogenetic diversity (Fig. 1). Diffuse interactions are thought to be one of the reasons for the persistence of native species in invaded communities, which would otherwise be displaced in pair-wise interaction with the invader (Case 1991). In the case of brome invasion, brome achieves a high level of dominance, making interactions more pair-wise, resulting in the exclusion of many species and the loss of phylogenetic diversity. Similar situations are likely to result in other invasions if the invader becomes dominant, suggesting that many of the studies measuring resistance may actually measure the consequence of invasion.

Invasion impacts and species characteristics

Invasive species with higher fitness than the resident species are expected to have the strongest impacts on native communities (MacDougall et al. 2009). Brome is a superior competitor (Wang et al. 2010) and should exclude most species in the absence of other key fitness-limiting factors, such as increased herbivory (Heard & Sax 2013). We found most species to be suppressed (Fig. 3), which confirms this prediction and suggests that brome is a generalist competitor. This runs counter to the predictions that competitive effects should be strongest among a small group of species, such as the most related or most similar species (Darwin 1859; MacArthur & Levins 1967). However, it is consistent with studies that have not found a strong link between competition and relatedness (Cahill et al. 2008; Bennett et al. 2013) or similarity (Price & Pärtel 2013). Therefore, we suggest any effect on the phylogenetic structure of the community is likely to depend on which species can tolerate competition and co-exist with the invader, rather than which are more related or more similar to the invader.

Most species require the same set of resources, but some are better at tolerating low resource conditions (Silvertown 2004). Our results suggest that co-existence with the invader involves shade tolerance as brome invasion reduced light availability (see Appendix S11) and shade-tolerant species did better within brome patches (Fig. 4e). Similar requirements for growth under low-light conditions have been suggested for co-existence with other invaders in other systems (Powell et al. 2013). The increase in evolutionarily distinct and rare species is also likely related to shade tolerance. Many of the less common and more distinct species are commonly found under closed canopies (see Appendix S5). Further, rare species likely had traits that enabled existence in a subordinate role initially and allowed them to continue in that role with brome as the

dominant (Powell et al. 2013). Conversely, common species are unlikely to possess the appropriate traits to exist in a subordinate role (Dawson et al. 2012; Powell et al. 2013) and given that most common species belong to a small number of lineages, it is unsurprising that species from common lineages were also suppressed. However, common species that normally form larger patches were more likely to persist inside brome patches. Potentially, these species could possess traits that enable them to compete with brome. Given increased competition for light and the limited extent of light competition in non-invaded portions of this grassland (Lamb & Cahill 2008), it seems more likely that a high initial abundance has simply resulted in lagged exclusion for formerly abundant species following invasion (Gilbert & Levine 2013). Thus, we suggest it is a combination of competitive exclusion, environmental modification and niche differences that determine which species are affected by invasion.

Conservation implications

Preserving the evolutionary history of communities has recently become one of the goals of biodiversity conservation (Faith 1992; Rolland et al. 2012). As such, assessing the impact of invasion using the amount of evolutionary history loss adds important information to our understanding of the conservation threat. However, assessing the conservation value of an area or the impacts of global change still requires a working knowledge of the natural history of the system (Faith 1992). Our results suggest that changes in phylogenetic diversity alone are insufficient to properly understand the impact of invasion. Invasion had minimal effects on phylogenetic diversity, but primarily because it facilitated ruderal species and species from different habitats that belong to lineages uncommon at the site. Thus conservation prioritization based solely upon phylogenetic diversity, which is thought to increase potential ecological function (Cadotte et al. 2008; Rolland et al. 2012; Srivastava et al. 2012), instead of increasing functional complementarity, may only prioritize characteristics that enable co-existence with the invader. Further, the species that benefit from brome invasion may be rare locally and represent distinct lineages, but many of them are common in other habitats and others are of alien origin. This suggests that conservation prioritization based entirely upon these characteristics, without further knowledge of the ecology and origin of the species within the community, would underestimate potential impacts of invasion.

Synthesis

Differentiating between invasion resistance and invasion impacts is challenging; both are associated with similar

characteristics of the resident community. Our results suggest that reports showing the relationship between invasion and patterns of relatedness, either within the resident community or between the invader and the resident community, may be the result of invasion impacts rather than biotic resistance. More experimental evidence is needed before a relationship between phylogeny and biotic resistance can be established. Further, we echo recent findings that common species may be more at risk following invasion (Powell et al. 2013). The implications of the loss of common species and the consequent changes in community structure are unclear and could take time to manifest (Gilbert & Levine 2013), but could be drastic (MacDougall et al. 2013).

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Species occupancy and relative abundance.

Appendix S2. Phylogenetic structure of the community.

Appendix S3. Supplemental methods.

Appendix S4. Comparison of community composition between experiments.

Appendix S5. Results from best subsets regressions explaining biotic resistance in intact resident community.

Appendix S6. Full results from top ten best subsets regressions explaining biotic resistance measured as competition as in the manuscript.

Appendix S7. Relative factor Akaike weights for explaining biotic resistance.

Appendix S8. Species evenness and phylogenetic evenness across the edge of brome invasion.

Appendix S9. Effects of species characteristics on response to brome invasion within the Poaceae.

Appendix S10. Brome invasion effects on light and soil moisture.

Appendix S11. Species characteristics and their response to brome invasion.