Opposite relationships between invasibility and native species richness at patch versus landscape scales

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Using a nested plot design in oak forests in Minnesota, USA we measured the percent cover of young individuals of an exotic invading shrub, *Rhamnus cathartica* (common buckthorn), to assess the relationships at two scales between invasibility, propagule and light availability, and richness and cover of native species. Comparing patches (1 m^2) within 17 *Quercus*-dominated stands (each 1 ha, within a 100 km by 150 km area), cover of young *R. cathartica* was negatively related to both species richness and cover of native species. In 1 m^2 patches, native cover was positively associated with native richness and thus cover-related competition was a likely mechanism by which richness influenced *R. cathartica*. At the landscape scale (comparing the aggregate stand-scale metrics among the 17 stands), native cover and richness were still positively related, but had opposite relationships with *R. cathartica* cover. *R. cathartica* cover was positively related to species richness and negatively related to native species cover. The observed switch at different scales from a positive to a negative relationship between *R. cathartica* cover and native richness supported the hypothesized scale dependence of these relations. Propagule pressure, which we estimated by measuring the size of nearby mature *R. cathartica* shrubs, had a large positive effect on *R. cathartica* seedling cover at the landscape scale. These results suggest that landscape patterns of invasion may be best understood in light of the combination of many factors including native diversity, native cover, and propagule pressure.

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Biological invasions present the single greatest threat to North American eastern deciduous forests (Vitousek et al. 1996) and the second leading threat to biodiversity across all ecosystems in the United States (Wilcove et al. 1998). Understanding factors that control invasion patterns has been a central focus for ecologists, but the relative importance of different factors and even the direction of relationships between factors are not clear. To elucidate their contributions to invasion patterns, we examined the roles of species richness, plant resources, and propagule pressure (estimated by abundance of mature individuals) at two scales.

The observed landscape patterns of invasion are the product of the propagule pressure of non-native organ-

isms and the invasibility, or susceptibility to invasion, of the ecosystem into which the propagules are dispersed (Lonsdale 1999). The influence of competition from the native plant community is mediated by invader propagule pressure (Lord and Lee 2001). Therefore, it is difficult to study large-scale patterns of invasibility without some knowledge of propagule pressure. There have been several approaches to understanding invasibility, including small scale experiments in which propagule pressure is controlled, large scale surveys in which propagule pressure is not controlled, and theoretical studies in which propagule pressure is held constant.

Small scale experiments, where propagule pressure is directly controlled (Tilman 1997, Naeem et al. 2000,

Dukes 2001, Foster et al. 2002) or assumed to be similar in all plots (Knops et al. 1999, Stachowicz et al. 1999, Hector et al. 2001, Kennedy et al. 2002, Troumbis et al. 2002, Pfisterer et al. 2004), have demonstrated negative relationships between diversity and invasibility (but see Foster et al. 2002). Invasibility has been measured as the number of species that successfully invade (Tilman 1997, Knops et al. 1999, Hector et al. 2001, Foster et al. 2002, Kennedy et al. 2002, Troumbis et al. 2002, Pfisterer et al. 2004), the biomass of these invaders (Knops et al. 1999, Hector et al. 2001, Kennedy et al. 2002, Troumbis et al. 2002), or the presence or abundance of a particular successful invader (Levine 2000, Naeem et al. 2000, Dukes 2001). This effect of diversity on invasion has been attributed to greater spatial and temporal use of resources, including nutrients (Knops et al. 1999, Naeem et al. 2000, Hector et al. 2001), water (Dukes 2001), light (Naeem et al. 2000, Knops et al. 1999), and physical space (Stachowicz et al. 1999, Hector et al. 2001) by more diverse resident communities. Small scale experiments that affect resources through direct additions or disturbance have shown that invasibility increases with gross resource supply (Burke and Grime 1996, Davis and Pelsor 2001).

Surveys of existing invasion patterns, which do not take propagule pressure into account, occasionally show positive relationships between diversity and invasibility at large scales within a vegetation type, and often show this pattern when different vegetation types are included in the same analysis (Stohlgren et al. 1998, 1999, Lonsdale 1999, Levine 2000, Brown and Peet 2003). At smaller scales, surveys of the same areas sometimes show negative relationships between diversity and invasibility, suggesting that this relationship may depend on the size of the area observed (Stohlgren et al. 1999, Brown and Peet 2003). The relationship between invasion and native plant cover depends on vegetation type and the scale of observation, but is most often negative (Stohlgren et al. 1998). Surveys that have also measured abiotic resources usually show a positive correlation between invasion and these resources at large scales, suggesting that both native and exotic species respond positively to resource increases (Stohlgren et al. 1998, 1999, Brown and Peet 2003).

The differences between the large scale survey and small scale experimental results may be due to propagule pressure (Lonsdale 1999, Levine 2000) or other extrinsic factors that vary with native diversity (Shea and Chesson 2002, Byers and Noonburg 2003). Differences in propagule pressure could cause positive large scale correlations between native and exotic diversity if human activity causes preferential release of propagules in areas of high native diversity (Rejmanek 2003). In the absence of variation in propagule pressure, extrinsic factors such as resource availability or heterogeneity that covary with native diversity at large scales could theoretically cause

positive large scale and negative small scale correlations (Shea and Chesson 2002, Byers and Noonburg 2003).

At large scales, for example, gross resource levels differ greatly between sites, and sites with high gross resource levels are expected to support a high diversity of native plants and yet be highly invasible. Therefore, a positive relationship between invasibility and native species richness may exist (Shea and Chesson 2002). Within a small area, however, gross resource levels are less variable, and the demand by resident species determines the resource availability (Shea and Chesson 2002). Therefore, at smaller scales, a negative relationship between invasibility and native species richness is expected. Supporting this hypothesis, resource levels in small scale experiments were lower in higher diversity plots where invasion was decreased (Knops et al. 1999, Dukes 2001).

The heterogeneity of resources within a site could also be an "extrinsic factor" that causes these large-scale patterns. A completely homogeneous site would in theory have only type of one microsite. Any one species would either be extremely abundant or nonexistent at this site, depending on whether it grows well in that microsite type. In contrast, a heterogeneous site would have a larger variety of microsites and could support a larger variety of plant species. Therefore, as heterogeneity increases, species richness of both native and exotic plants would be expected to increase (Huston and DeAngelis 1994). As heterogeneity and species richness increase, the maximum number of individuals of any one species would decrease.

In this study, we examined the invasion patterns of a single invader, *Rhamnus cathartica* L., in response to native diversity, light, and propagule pressure. *R. cathartica* (common buckthorn), a native of many areas in Europe, is a shrub or tree 3–9 m in height (Godwin 1943). It was introduced to North America through planting near houses and in urban areas as an ornamental shrub beginning in the mid 1800s (Possessky et al. 2000). *R. cathartica* became naturalized, invading forests and becoming the dominant understory vegetation in some cases, creating a major threat to native biodiversity (Catling 1997). Given the importance of this invader in Midwestern woodlands, the abundance of *R. cathartica* is a more meaningful measurement of invasibility than invader richness (which in our study was unimportant because *R. cathartica* made up >99% of all invading individuals). Limiting our study to *R. cathartica* allowed us to estimate propagule pressure using the summed size of nearby mature *R. cathartica*. Although *R. cathartica* is dispersed by birds, the majority of the seeds fall beneath the parent shrub, and the density of germinants is 40 times greater within 5 m of mature plants than in areas >15 m away (K. S. Knight, unpubl.).

We studied *R. cathartica* invasion in stands varying in light availability and understory diversity and cover, but having some degree of *R. cathartica* propagule availability and comparable overstory woody dominants. We examined the spatial dependence of *R. cathartica* seedling abundance on understory species richness and percent cover, and light availability, using 20 plots nested within each of 17 forest stands in southeastern Minnesota, USA. In this study, we tested the hypotheses that *R. cathartica* percent cover would be negatively related to understory species richness ("small scale species richness") and percent cover ("small scale cover") at the small patch scale, positively related to understory species richness ("large scale species richness") and negatively related to percent cover ("large scale cover") at the landscape scale (Fig. 1), and positively related to light availability and propagule

pressure at both scales ("small scale light", "large scale light", "small scale propagule", and "large scale propagule").

Methods

We chose a 100×150 km area in southeastern Minnesota as our study region because it was dominated by *Quercus* woodlands and forests in the pre-settlement era (MNDNR 1993), and *R. cathartica* is now common throughout the region. Among sites recommended by area naturalists, park managers, and prior experience, we selected the first 20 forested sites we encountered that met the following criteria. To be selected as a site, average canopy cover had to exceed 75% (a forest rather than a savannah), and 50% of the overstory tree basal area had to be *Quercus* sp. We also required *R. cathartica* presence, and no recent logging, burning, or *R. cathartica* removal. All sites were located in a landscape mosaic of oak woodlands, wetlands, and agricultural fields, and the contiguous oak woodland stands used ranged in size from 2 ha to 400 ha. Within each of the 20 forested sites, a square 1 ha area was selected based on accessibility and minimization of edge effects (the area was >10 m from edges bordering open fields, lakes, or roads). In each 1 ha area, a 1 m² plot was placed at each of 20 locations, based on pairs of coordinates generated from a random number table. Plots were moved if they contained any woody species taller than 1.5 m rooted in the plot because understory plants and young buckthorn seedlings were the focus of this study.

We recorded the canopy openness which ranged from 0 to 44% open sky, with an average of 9%, 1 m above each plot with a densiometer. We recorded the percent cover (integer values) and the name of each species rooted in each plot and the stem diameter at 1.4 m height of all woody species within five meters of the center of the plot. Percent cover was measured as the horizontal area (in all layers) each species took up independent of the amount of space occupied by other species. Therefore, the total percent cover of the plot or any one species was not constrained to 100%. This design provided two spatial scales – the 20 1 m² plots within each site and an aggregated value of the 20 plots for each site – to test the scale-dependence of relationships involving buckthorn cover.

In analyses, we used the natural log transformation for *R. cathartica* percent cover in order to approximate a normal distribution. General linear model analyses using JMP4(2) (SAS Institute) were used at both scales to examine the conditional relationship between *R. cathartica* seedling abundance and understory plant diversity. For the landscape-scale analyses, testing the "large scale species richness" and "large scale cover" hypo-
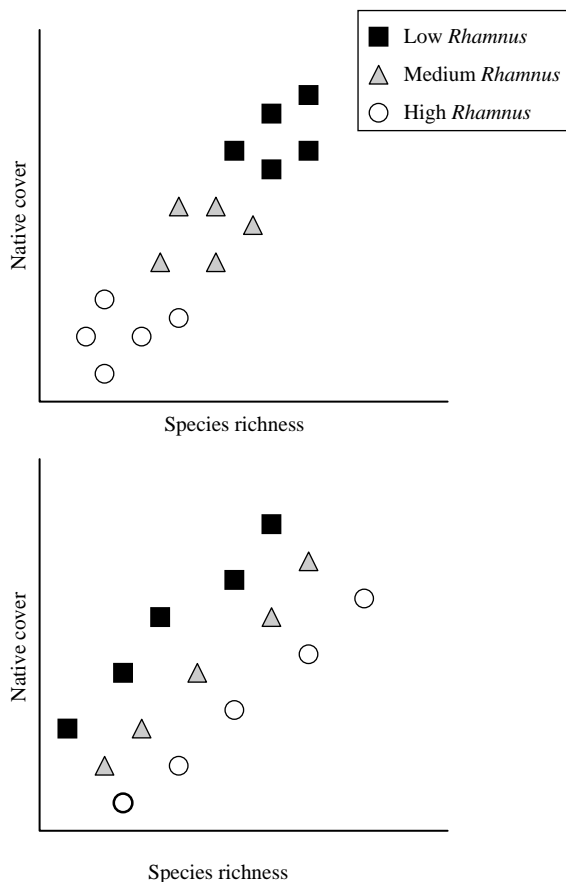

Fig. 1. The top figure represents our hypothesis for patch–scale relationships, where native cover and diversity are positively related to each other and both are negatively related to the abundance of *R. cathartica* seedlings. The bottom figure represents our hypothesis for the landscape–scale relationship, where native cover and diversity are positively related to each other, native cover is negatively related to *R. cathartica* seedling abundance, and native diversity is positively related to *R. cathartica* seedling abundance.

theses, the average percent cover of *R. cathartica* in the 20 1 m^2 plots in each site was the response. Three of the 20 sites were excluded because they had very low estimated propagule pressure and no *R. cathartica* in any of the 1 m^2 plots, which left 17 sites for the analysis. The full model including all 2nd degree interaction terms had only a marginally higher R^2 value than the best submodel, so only the submodels will be discussed.

The first landscape–scale regression tested whether percent cover of *R. cathartica* seedlings is negatively related to species richness. Predictors included species richness, light, and the summed size of nearby *R. cathartica* shrubs. Species richness was the total number of species other than *R. cathartica* in the 1 ha site. The average canopy openness for the site was used to approximate light availability. The summed size (diameter at 1.4 m) of *R. cathartica* shrubs within 5 m of the plots was used to estimate propagule pressure. The summed diameter is useful because it includes both the number and size of shrubs, which are both expected to contribute to propagule pressure. Understory *R. cathartica* cover was positively related to the summed size of large *R. cathartica* individuals (p = 0.002), supporting the use of this measurement to control for variation in propagule availability.

For the second landscape–scale analysis, which tested whether cover could account for the diversity effect, the summed percent cover of native (i.e. all species other than buckthorn) species in the 1 m^2 plots was added as a predictor. The third landscape–scale analysis also included the summed percent cover of native species, but eliminated the site species richness predictor. The relationships between light level, the percent cover of native species in the 1 m^2 plot, and species richness were also examined with regression analysis.

The landscape–scale relationship between cover of *R. cathartica* seedlings and light heterogeneity (the standard deviation of canopy openness for each site) was examined separately with quantile regression using Blossom Statistical Software (USGS 2001). Quantile regression allows the examination of the maximum response, rather than the mean response, of one variable to a predictor. It is useful for analyzing data with nonconstant variance because it helps to quantify nonconstant variance, which is often meaningful for ecological processes in which many unmeasured variables may affect the response (Cade and Noon 2003).

The patch–scale analyses examined the 20 1 m^2 plots within a site, addressing all 17 sites simultaneously. The full model with all 2nd degree interaction terms increased the R^2 by 20% compared to the best submodel, but none of the terms were significant at the $\alpha = 0.05$ level, so only the submodels will be discussed. The first patch–scale regression tested the "small scale species richness" hypothesis. Percent cover of *R. cathartica* seedlings in the 1 m^2 plots was the response, and species

richness of all other species in the 1 m^2 plots was used as a predictor. Only plots containing *R. cathartica* were used so the residuals would approximate a normal distribution, however, the results obtained through this analysis were generally consistent with results obtained with a logistic regression of the presence and absence of *R. cathartica* which used all plots (data not shown). Other predictors included the site, the size of large *R. cathartica* shrubs within 5 m of the plot, and the light level.

The second patch–scale analysis tested whether native percent cover could account for the species richness effect on *R. cathartica* cover. The analysis remained the same, except the total percent cover of non-*R. cathartica* species in the 1 m^2 plot was added as a predictor. The third patch–scale analysis included the percent cover of non-*R. cathartica* species and excluded the plot species richness, testing the "small scale cover" hypothesis.

Results

Within stands at the 1 m^2 patch scale, percent cover of *R. cathartica* was negatively related to species richness (p = 0.046; Table 1, Fig. 2), supporting the "small scale species richness" hypothesis. However, when native percent cover was included in the model, species richness was not a significant predictor (p = 0.27) and neither was native cover (p = 0.41). Replacing species richness with native cover did not change the overall variance explained by the model, and *R. cathartica* cover was negatively related to native cover (p = 0.062), supporting the "small scale cover" hypothesis (Fig. 2). Since species richness and percent cover of native species were positively related (R^2 = 0.43, p < 0.0001), we interpret these results to indicate that the relationship between species richness and *R. cathartica* cover was a result of higher percent cover in more diverse plots (Fig. 4). Both *R. cathartica* cover and species richness were positively related to light at the patch scale, supporting the "small scale light" hypothesis (p = 0.028 and p = 0.0004, respectively). At the patch scale, the summed size of nearby mature *R. cathartica* shrubs was not a significant predictor of *R. cathartica* seedling abundance, refuting the "small scale propagule" hypothesis (p = 0.10).

At the landscape scale (aggregate of 20 plots per stand, n = 17 stands), in a multiple regression, species richness was not a significant predictor of *R. cathartica* cover (p = 0.21). As at the patch scale, stand species richness and average stand native percent cover were positively correlated (p = 0.004). However, when both species richness and native species cover were included in a model, species richness and native cover had significant but opposite relationships with *R. cathartica* (Fig. 3, 4). *R. cathartica* cover was positively related to species richness (R^2 = 0.43, p = 0.0011), while *R. cath-*

Table 1. Results of regression analysis with the natural log of *R. catharctica* seedling percent cover as the response. Each row shows the results of one analysis. The five columns, species richness (excluding *R. catharctica*), percent cover of native species (all species except *R. catharctica*), the summed stem diameter of *R. catharctica* within 5 m of the 1 m² plots, canopy openness, and site, are predictors in the analysis. Three regressions were performed at each scale; one included percent cover of species other than *R. catharctica*, one includes species richness and one included both. The results of each analysis are shown for each predictor, with +, −, and ns referring to positive, negative, and nonsignificant relationships, respectively. Cells not included in the analysis are labeled not included. For all three analyses performed at the 1 m² patch scale, N = 189 and p < 0.0001. For the three analyses performed at the 100 m² landscape scale, N = 17 for all analyses, and p = 0.014, p = 0.0006, and p = 0.022, respectively.

	Species richness	Native species cover	Diameter sum of nearby *R. catharctica*	Canopy openness	Site	Statistics
1 m² scale	−p =0.046	not included	ns p =0.11	+p =0.028	p <0.0001	R^2 =0.41 F =7.96
1 m² scale	ns p =0.27	ns p =0.41	ns p =0.10	+p =0.021	p <0.0001	R^2 =0.41 F =7.48
1 m² scale	not included	−p =0.062	ns p =0.09	+p =0.023	p <0.0001	R^2 =0.41 F =7.90
100 m² scale	ns p =0.20	not included	+p =0.01	ns p =0.10	not included	R^2 =0.54 F =5.18
100 m² scale	+p =0.002	−p =0.003	+p =0.002	ns p =0.89	not included	R^2 =0.78 F =10.90
100 m² scale	not included	ns p =0.39	+p =0.05	ns p =0.16	not included	R^2 =0.51 F =4.50

artica cover was negatively related to native cover (p =0.006), supporting the "large scale species richness" and "large scale cover" hypotheses.
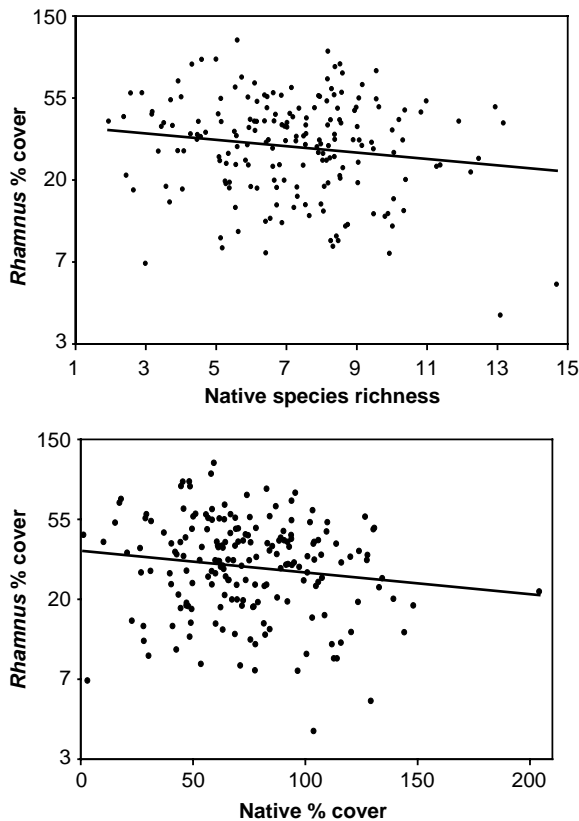

Fig. 2. The patch–scale response of percent cover of *R. catharctica* to native percent cover and native species richness was negative. These graphs are leverage plots from two multiple regression models: analysis 1 included native species richness, size of nearby *R. catharctica* trees, and light, and analysis 3 included native cover, size of nearby *R. catharctica* trees, and light.

At the landscape scale, percent cover of *R. catharctica* was not related to average light level (p =0.10), however, there was a negative relationship between percent cover of *R. catharctica* and light heterogeneity at upper quantiles (p =0.09, p =0.046, p =0.061, p =0.036 for the 0.9, 0.8, 0.7, and 0.6 quantiles, respectively, Fig. 3). There was no relationship between species richness and light heterogeneity, contrary to our expectations. The total size of mature *R. catharctica* shrubs, our assessment of propagule pressure, was positively related to the abundance of *R. catharctica* seedlings at the landscape scale (p =0.002), supporting the "large scale propagule" hypothesis.

Discussion

Our analysis showed a scale-dependent relationship between diversity and *R. catharctica* invasion when controlling for estimated propagule pressure. Among small patches, the negative relationship between species richness and invasibility reflected the negative relationship between native cover and invasibility, and the positive relationship between species richness and native cover (Fig. 4). This supports the idea that diverse communities decrease invasibility at small scales through resource competition (Knops et al. 1999, Stachowicz et al. 1999, Naeem et al. 2000, Dukes 2001).

The relationship between light, a limiting resource in shady understories, and *R. catharctica* invasion was positive at this small scale, in agreement with other studies that have shown that gross resource supply affects invasion (Burke and Grime 1996, Davis and Pelsor 2001). Because we measured canopy openness above the forest understory plants, the degree of shading of *R. catharctica* seedlings by other forest understory plants is unknown. Increased cover of these native plants would lead to more shading of *R. catharctica* seedlings as well as increased competition for belowground resources and physical space, which would explain the negative
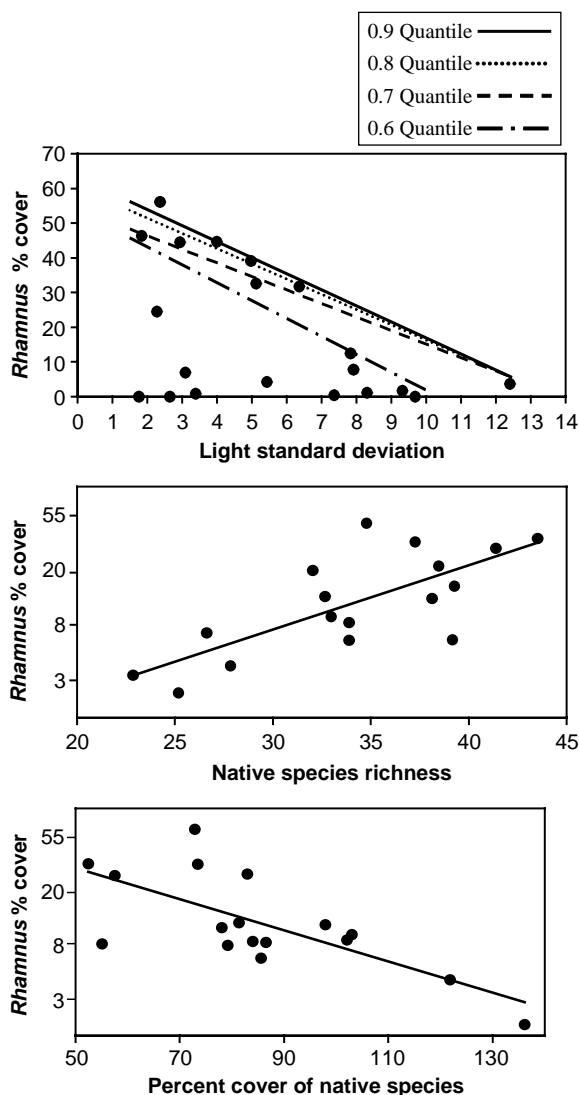
Fig. 3. Landscape–scale response of average percent cover of *R. cathartica* to light heterogeneity (the standard deviation of percent canopy openness), native percent cover, and total species richness. Light heterogeneity was analyzed with quantile regression, which is robust to non-normal error distributions (Cade and Noon 2003), so no transformation was used for this analysis. The graphs for native cover and species richness are leverage plots from the multiple regression full model including native cover, species richness, size of nearby *R. cathartica* trees within 5 m, and light. The natural log transformation of *R. cathartica* cover was used for the multiple regression analysis to approximate normality.
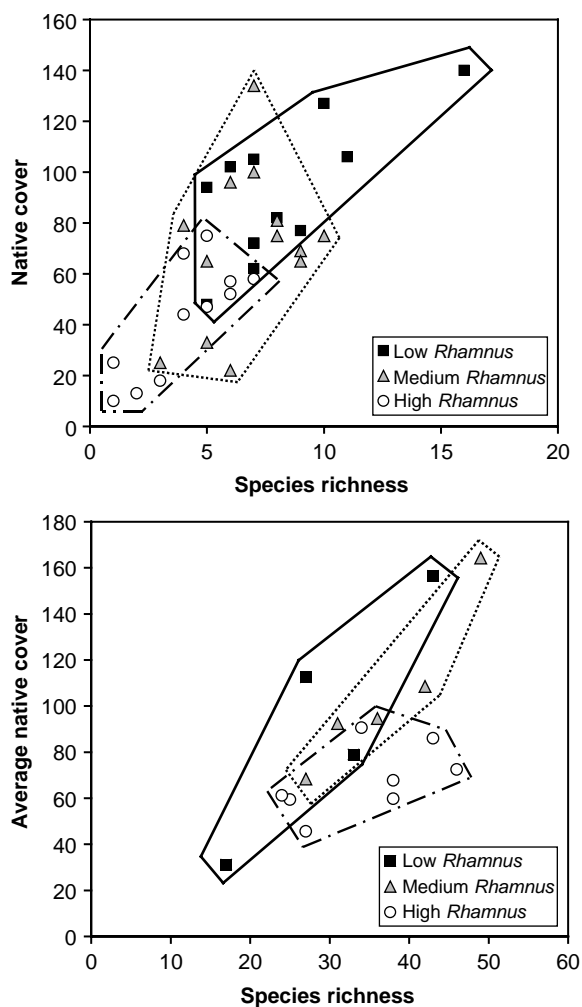
Fig. 4. The top graph shows the patch scale relationship between percent cover of native species and native species richness, with the abundance of *R. cathartica* seedlings indicated by different shapes. Combined data from two stands (both "high" invasion sites) was chosen to illustrate the association of low *R. cathartica* seedling abundance with low native cover and species richness, and the association of high *R. cathartica* seedling abundance with low native cover and species richness. In this graph, the average percent cover of *R. cathartica* was 4–20% in "low" plots, 30–45% in "medium" plots, and 50–100% in "high" plots. The bottom graph shows the landscape scale relationship between average percent cover of native species and native species richness, with the average abundance of *R. cathartica* seedlings indicated by different shapes. At the landscape scale, the average percent cover of *R. cathartica* was 0.5–2% in "low" sites, 4–13% in "medium" sites, and 24–56% in "high" sites. Sites with low, medium, and high abundance of *R. cathartica* seedlings tend to cluster in different areas of these two graphs, as predicted in Fig. 1.

relationship we observed between native plant cover and *R. cathartica* invasion.

It is impossible to determine the strength of competition for each of these resources from the data we collected. Previous studies have shown that more diverse communities have increased shading (Knops et al. 1999, Naeem et al. 2000), nutrient uptake (Knops et al. 1999, Naeem et al. 2000), and occupied space (Stachowicz

et al. 1999), and decreased soil nitrogen solution concentrations (Reich et al. 2001) so any of these competitive mechanisms could potentially explain the patterns we observed.

Across a landscape, we observed a positive relationship between species richness and invasion, and a

negative relationship between native cover and invasion when controlling for propagule pressure. This result supports theoretical work showing that covarying extrinsic factors can affect native diversity and invasibility in the same way, which would lead to positive relationships between these factors at large scales (Shea and Chesson 2002, Byers and Noonburg 2003). In our survey, native species cover had to be incorporated in order to understand the large scale relationship between native diversity and *R. cathartica* invasion (Fig. 4).

Perhaps mixed results have been obtained by other studies (Stohlgren et al. 1998, 1999, Brown and Peet 2003) because native species cover is not always assessed. In agreement with our results, negative small scale and positive large scale relationships between diversity and invasion were present in Appalachian riparian areas (Brown and Peet 2003), but not in riparian or upland grasslands (Stohlgren et al. 1998). Negative relationships at both small and large scales between native cover and invasion have been obtained for upland, but not riparian, grasslands (Stohlgren et al. 1998, 1999). The measurement of landscape invasion patterns in these studies would have been affected by both propagule pressure and invasibility. If the importance of propagule pressure is greater in some landscapes than others, and if the relationship between exotic propagule pressure and native diversity varies, such discrepancies could result.

The highly significant impact of estimated propagule pressure at large scales in this study underscores the importance of this factor for invasion patterns. Although the landscape scale relationships between native cover, native diversity, and buckthorn abundance remain when propagule pressure is removed from the multiple regression, the R^2 decreases from 0.78 to 0.51 (analysis not shown). This decrease in R^2 is similar to the decrease when either diversity or native cover are removed, showing the necessity of including all three factors when examining invasion patterns.

Because our study controlled for propagule pressure, the positive relationship between diversity and invasion is due either to *R. cathartica* traits or to extrinsic factors that affect invasibility (Lonsdale 1999). Average light level had no effect on invasion, but light heterogeneity exhibited a negative upper limit in its relationship with invasion. This supports the idea that increased heterogeneity leads to decreases in any one microsite type, and therefore leads to decreases in the abundance of any one species requiring a particular microsite type. More heterogeneous areas, which had lower maximum buckthorn seedling densities, were expected to also have higher native diversity, but there was no relationship between heterogeneity and native diversity. Other extrinsic factors that may positively affect both native diversity and invasion are precipitation, temperature regimes, soil texture, and soil fertility. Minnesota's north–south temperature gradient and east–west precipitation gradient creates climatic variation between our sites.

The number of exotic plant species may be lower in forest understory communities than in other vegetation types (Brown and Peet 2003), however, those few invading species may have large impacts on the forest (Catling 1997). Therefore, it is important to study invasibility in the context of one or a few important invading species in these systems rather than focusing exclusively on exotic diversity. One caveat of this approach is that important invaders like *R. cathartica* may behave differently than other invaders (Levine and D'Antonio 1999); in fact, their success may be due to these differences. Consequently, this study does not demonstrate universality of scale-dependent relationships between diversity and invasion. It shows that these relationships can exist independently of propagule pressure, and provides impetus for future examination of important invaders in relation to propagule pressure and diversity.

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