Dominance not richness determines invasibility of tallgrass prairie

Melinda D. Smith, Julia C. Wilcox, Theresa Kelly and Alan K. Knapp

Many recent studies suggest that more diverse communities are more resistant to invasion. Community characteristics that most strongly influence invasion are uncertain, however, due to covariation of diversity with competition and crowding. We examined separately the effects of species richness and dominance on invasion by an exotic legume, *Melilotus officinalis*, in intact, native Kansas grassland. We manipulated dominance of C₄ grasses by reducing their abundance (i.e. ramet densities) by ~ 25 and 50%. In addition, richness was reduced by removing species that were mainly rare and uncommon as might be expected with environmental changes such as drought and fragmentation. In both years of the study (2001–2002), invasibility, measured as peak establishment of *Melilotus*, was not affected by a 3-fold reduction in species richness, nor was there an interaction between loss of species and reduced dominance on invasion. In contrast, reductions in abundance of the dominants significantly reduced invasibility of the grassland plots in both years. Because the abundance of dominants was highly correlated with measures of competition (i.e. ratio of dominant biomass to total biomass) and crowding (total stem densities), this pattern was opposite to that expected if competition were indeed limiting invasion. Rather, invasion appeared to be facilitated by the dominant species, most likely because reduced dominance increased environmental stress. Our results suggest that dominance is the key community characteristic determining invasibility, because highly competitive and space-filling species can either enhance or reduce susceptibility to invasion depending on whether dominants create a more competitive environment or alleviate stressful conditions.
community, particularly the role of diversity in influencing invasion. Diverse plant communities are hypothesized to be more resistant to invasion due to more intense competition and fewer resource opportunities that result from more complete resource use (Elton 1958, Shea and Chesson 2002). Both theory and experiments provide support for this hypothesis by demonstrating greater resistance to invasion with increasing diversity (Knops et al. 1999, Stachowicz et al. 1999, Tilman 1999, Levine 2000, Naeem et al. 2000, Prieur-Richard et al. 2000, Symstad 2000, Lyons and Schwartz 2001, Moore et al. 2001, Kennedy et al. 2002, Troumbis et al. 2002) and evenness (Wiley and Polley 2002) at small spatial scales and in relatively homogeneous systems. However, an opposite pattern or a lack of relationship also has been found in other experiments (Robinson et al. 1995, Burke and Grime 1996, Palmer and Maurer 1997, Crawley et al. 1999, Lavorel et al. 1999, Foster et al. 2002) and in observational studies at larger spatial scales (Knops et al. 1995, Wiser et al. 1998, Lonsdale 1999, Smith and Knapp 1999, Stohlgren et al. 1999, Levine 2000).

These conflicting patterns may result from uncontrolled (extrinsic) factors (e.g., disturbance, productivity, resource availability, or size of the species pool), which covary with diversity and confound observed patterns of invasion in observational studies and in some experiments (Levine and D’Antonio 1999, Naeem et al. 2000, Wardle 2001, Shea and Chesson 2002). An alternative explanation may be that extrinsic factors are more important than diversity in determining invasion at larger spatial scales (Kennedy et al. 2002). At smaller spatial scales where extrinsic factors are held constant (i.e. plot or field), biotic factors appear to be most important for invasion by defining the competitive space that potential invaders encounter (Kennedy et al. 2002) or by controlling resource opportunities that invaders can exploit (Shea and Chesson 2002). Indeed, experiments in which diversity is directly manipulated and extrinsic factors are controlled suggest that more diverse communities are more resistant to invasion due to increased neighborhood crowding and competition for limiting resources (Stachowicz et al. 1999, Naeem et al. 2000, Kennedy et al. 2002).

Wardle (2001) argued that variation in dominant species abundance could explain conflicting relationships observed between diversity and invasion in grasslands, a focal system of many recent invasion studies. In highly productive sites where dominance is strong, dominant species competitively exclude sub-ordinate (uncommon and rare) species and suppress potential invaders. This could produce a positive relationship between diversity and invasion when sites that vary in productivity and abundance of dominant species are included in examinations of invasibility, a scenario common to observational studies (Levine and D’Antonio 1999, Smith and Knapp 1999). Naeem et al. (2000) suggested that experimental studies in which diversity is directly manipulated and that are conducted at smaller spatial scales remove such covariation. However, these experiments often employ synthetic communities comprised of random assemblages of species. Here the chance of including the most competitive or space-filling species increases as diversity increases (i.e. the sampling effect, Wardle 2001). As a result, crowding and competition covary with diversity (Kennedy et al. 2002), making it difficult to separate the effects of diversity per se from such biotic factors as the composition or abundance of resident species. Thus, despite evidence for diversity, competition and crowding increasing resistance to invasion at smaller spatial scales, it is still unclear which of these community characteristics most strongly influences invasibility.

The goal of this study was to examine the effects of species richness and dominance (abundance of competitive species) on invasibility while holding constant extrinsic factors, such as propagule supply, productivity and disturbance. We measured invasion by an exotic legume species, Melilotus officinalis L., in response to experimentally manipulated levels of plant species richness and dominance in intact, mesic grassland (tallgrass prairie) plots over a two-year period. The capacity of tallgrass prairie plant communities to respond rapidly to a variety of perturbations (Tilman and El Haddi 1992, Steinauer and Collins 1995, Turner and Knapp 1996) makes it an excellent system to examine the immediate consequences of manipulations of richness and dominance. In addition, these communities are characterized by steep rank-abundance relationships, where a few C_4 grasses species dominate (control resources and competitively exclude other species) and a suite of sub-ordinate C_3 grass and forb species comprise a bulk of the diversity but are generally found at lower abundance (Collins and Steinauer 1998, Smith and Knapp 2003).

By directly manipulating the dominance, but not the presence, of key C_4 grasses, we controlled crowding and competition effects that covary with diversity, and examined these effects on invasion independent of other community characteristics. We also manipulated species richness by eliminating plant species from experimental plots based inversely on their probability of occurrence in the community, so that rare and uncommon species were removed before more abundant species. Drought, fragmentation or altered disturbance regimes are known to cause this type of nonrandom loss of species from grasslands (Smith and Knapp 2003). Thus, our intent was to simulate a realistic pattern of species loss in the field. This experimental design also allowed us to decouple diversity effects from the sampling effect (Wardle 2001), because the most common and dominant species were never lost from the communities and were present at all richness levels (Smith and Knapp 2003).
We hypothesized that both decreased richness and reduced dominance would increase invasion. We expected that the loss of less common and rare plant species from grassland plots would increase susceptibility to invasion by creating open niches and making available resources previously unavailable (MacArthur 1972, Davis et al. 2000), whereas communities with lower abundance of dominant species would be less competitive and crowded and thus less resistant to invasion by non-resident species. However, we expected that reduced dominance, by more strongly influencing resources (light, space) important for establishment at local scales (Foster et al. 2002), would more strongly impact invasion than richness. We used seedling establishment as our measure of invasibility of the experimental plots. Although seedling germination and establishment are only the first steps in the invasion process (Crawley 1987), there is strong evidence for this phase of life history, rather than survivorship, being of critical importance in regulating species distributions and invasion in grasslands (Gross and Werner 1982, Foster 1999, 2002).

Methods
In May 2000, we established 72 1.0 × 0.5 m plots on a relatively homogeneous upland site in an infrequently burned (~ every 4 years) watershed at the Konza Prairie Biological Station (Manhattan, KS, USA). The site had been burned several weeks prior. Plots were laid out in a grid with rows of plots separated by 1 m, and plots within rows separated by 0.5 m. Vegetation of the site was dominated by a few warm-season (C₄) grass species, mainly Andropogon gerardii Vitman and Sorghastrum nutans (L.) Nash and to a lesser extent Bouteloua curtipendula (Michx.) Torr., A. scoparius Michx. and Panicum virgatum L. Numerous less common and rare warm- and cool-season (C₃) grass and forb species made up the bulk of the diversity. Exotic species are relatively uncommon at Konza Prairie, comprising only ~9% of the species in grassland sites (Smith and Knapp 1999), and were absent from the study site.

Dominance and richness treatments
We determined levels of the dominance and richness treatments by first censusing the number of ramets (individual tillers) of each species in each plot at the beginning of the 2000 growing season. The range in dominance, i.e. total ramet densities of the three most abundant C₄ grasses (A. gerardii, S. nutans and B. curtipendula), for the plots was 173 to 519 ramets (average: 368.9 ± 87.5 SD). Average richness for the plots was 14.1 (± 2.0 SD) with a minimum of 10 species and a maximum of 18 species per plot. Based on these community characteristics, we selected dominance treatments of high (ambient), medium (~25% reduction in dominance) and low (~50% reduction). Richness treatments selected were 13–16 species (ambient), 10–12, 7–9, and 4–6 species for the most depauperate community. Only six plots had less than 12 species, thus richness was reduced to some extent in all the plots. Our assignment of the dominance and richness treatments to the plots (12 treatment combinations each with 6 replicates) was stratified and semi-random due to constraints of natural richness and dominance. We first divided the plots into the three dominance levels, so that high (ambient) dominance plots had at minimum 307 stems of the dominant C₄ grasses (average: 429.2 ± 53.8 SD), medium dominance plots had at minimum 243 stems (average: 378.5 ± 69.2 SD), and low density plots had at minimum 173 stems (average: 298.9 ± 83.3 SD). Each had similar initial average richness: high – 14.8 (range: 10–18 species), medium – 13.6 (10–18), and low – 13.9 (12–17). For each dominance treatment, six plots (of ~15 plots per dominance level) that had 13 or greater species were first randomly assigned to the high (13–16 species) richness treatment. The remaining plots were then assigned randomly to the other richness treatments. This resulted in an average initial richness of 15.4 (1.4 SD; range: 13–18) for the 13–16 richness treatment, 13.6 (1.7 SD; range: 10–17) for the 10–12 richness treatment, 14.3 (2.4 SD; range: 10–18) for the 7–9 richness treatment, and 13.1 (1.7 SD; range: 11–18) for the 4–6 richness treatment. Thus, for all but the ambient (high) richness treatment, average initial richness did not differ significantly among the richness reduction treatments. For each richness treatment, plots were then randomly assigned to a particular target richness value. In early June 2000, we reduced dominance and richness in the plots by clipping individuals and precisely applying herbicide (glyphosate) to the cut stem. This minimized non-target effects to neighbors. Dominance was reduced by permanently removing stems of mainly A. gerardii, S. nutans and B. curtipendula. In general, A. gerardii comprised 80% of the stems removed and S. nutans and B. curtipendula comprised 10–20% of stems removed. These proportions reflected natural abundance patterns observed in the plots (data not shown). For the richness treatments, plant species were selected for removal based on their frequency of occurrence at the study site; those that occurred least frequently were removed first and species that were more frequent were removed until a target richness level was achieved. Thus, the dominant and most frequent species were never removed completely from the study plots (Smith and Knapp 2003).

After all treatments were applied, ramet densities were recensused to confirm treatment levels. We reduced C₄
grass ramet densities in low dominance plots by 47% (average 137.7 ± 76.9 SD ramets per plot) and in medium dominance plots by 23% (average 86.3 ± 15.4 SD ramets per plot). In 2001, the plots required only minimal adjustments of the richness levels, and although total densities increased, the dominance treatments remained in place (Fig. 1A). At the end of the growing season (late August to mid September) each year, we harvested, dried and weighed all aboveground biomass of each species separately. Relative dominance, an estimate of competition in each plot, was calculated as ratio of the sum end-of-season biomass of the three dominant C₄ grasses, *A. gerardii*, *S. nutans* and *B. curtipendula* to total aboveground biomass.

### Invasibility

We added seeds of *Melilotus officinalis* (Fabaceae), an annual/biennial legume native to Eurasia, to plots to assess invasibility. Only one target invader was used to avoid confounding effects of competition that could occur between multiple target invaders. *Melilotus* invades grasslands throughout the Great Plains (Great Plains Flora Association 1986) and is considered a noxious weed in some areas. We chose *Melilotus* because, although found often at high local abundance in scattered populations on Konza Prairie (Smith and Knapp 1999, 2001), it was absent from the study site. Commercially grown seeds (Sharp Bros. Seed Co., Healy, KS) of uniform quality were used each year.

In June 2000, seeds of *Melilotus* were sown into each plot at a density of 300 seeds plot⁻¹ (equivalent to average 0.58 g plot⁻¹). In preliminary laboratory tests, we obtained germination rates in excess of 60% in microcosms (4 × 50 × 75 cm) consisting of blocks of intact, burned grassland sod obtained from the field (M. D. Smith unpubl.). Water (equivalent to 1 cm of rain) was gently added to all plots immediately after seed additions and three additional times during the first three weeks to stimulate germination. To determine if variation in propagule supply and spring environmental conditions altered patterns of invasion, seeds of *Melilotus* were added earlier (26 April) and at a higher density (600 seeds plot⁻¹, equivalent to average 1.26 g plot⁻¹) in 2001. Again, all plots were watered immediately after seed additions and five more times over the next two weeks to enhance germination. The number of seedlings that established was measured on 22 June, 2 July, 13 July, 23 August 2000 and on 24 May, 24 June, 7 July and 3 September 2001. Seedlings were not allowed to persist beyond establishment to avoid unwanted introductions to the site. Peak establishment (2000: 22 June, 2001: 24 May) was used as the measure of invasibility in subsequent analyses.

Since light is an important aboveground resource limiting growth and establishment in tallgrass prairie (Knapp and Seastedt 1986, Foster and Gross 1998, Foster 2001), light penetration (photon flux density; PFD) through the canopy was measured each time seedlings were counted. Using a Sunfleck ceptometer (Decagon, Pullman, WA), PFD was quantified above the canopy and at the soil surface in two locations in each plot on cloudless days. Light penetration at peak invader establishment was used as a measure of resource availability in the plots in subsequent analyses.

### Statistical analyses

Effects of dominance and richness treatments on light availability, dominance (ramet densities of three dominant C₄ grasses), and establishment of *Melilotus* seedlings were evaluated using two-way ANOVA for each year separately, and LSD tests detected differences in treatment means (Ott 1993). Simple linear regressions also were used to assess invasibility across the continuum of richness and C₄ grass ramet densities across the plots. For 2000 and 2001, separate multiple regression (backward elimination) analyses were used to evaluate the dependence of invasibility on richness, total ramet density (a measure of available space at the time of invasion), dominance, relative dominance, and light availability. The extent of collinearity was evaluated since there were inter-correlations among some of the predictor variables. Acceptable levels were judged using the following criteria: condition index < 30, variance inflation < 1/(1 − r²), and variance proportions not close to one. All analyses were performed using SAS statistical software (SAS version 8.1, SAS Institute, Inc. 1999). Significance levels were set at P ≤ 0.05.

### Results

#### Dominance and light availability

Experimental manipulations of dominance effectively reduced total ramet densities of the three most abundant C₄ grasses in 2000, with these reductions persisting in 2001 (Table 1, Fig. 1A). The dominance reductions were independent of the richness reduction treatments (Table 1). Dominance was similar across all richness levels, except in 2001 where total C₄ ramet densities differed with richness only for the low dominance treatment. Dominance was significantly lower in plots with 10–12 or 13–16 species when compared to those with only 4–6 species (data not shown). The dominance reduction treatments significantly altered light availability at the soil surface (Table 1). Light penetration increased by ~25% and 50% over that for the high dominance plots with equivalent reductions in ramet densities of the C₄
grasses (Fig. 1B). In 2001, light availability was still higher with reduced dominance, however differences between the dominance treatments were not as pronounced (Fig. 1B). Light availability was not affected by the richness treatments in either year of the study (Table 1).

### Invasibility

Maximum establishment of *Melilotus* seedlings, our measure of community invasibility, was not affected by reduced richness in either year of the study regardless of whether data were analyzed with richness as a categorical variable or with realized (measured) levels of richness (Table 2, Fig. 2). These results indicate that invasion was independent of the number of resident species in these communities. In contrast, community invasibility was significantly affected by reduced dominance (Table 2). In 2000, the low density plots had ~30% fewer *Melilotus* seedlings establishing than the moderate or high dominance plots (Fig. 3A). A similar pattern of invasion was observed in 2001 (Fig. 3B), although the reduction in *Melilotus* establishment in low dominance plots was not significant (Table 2). Because there was a continuum of total dominant density for the plots the data were also analyzed with dominance as an independent regression variable (Fig. 3C, D). Results were consistent with the ANOVA analyses. The number of *Melilotus* seedlings establishing declined significantly with decreasing abundance of the dominant C4 grasses in both years (2000: $F_{1,70} = 26.13$, $P < 0.001$; 2001: $F_{1,70} = 6.26$, $P = 0.01$). Invasibility also was correlated with other biotic and abiotic factors that we measured. Establishment of *Melilotus* increased with increasing total ramet densities for the plots (2000: $r = 0.45$, $P < 0.001$; 2001: $r = 0.40$, $P < 0.001$), and with increasing competition, as measured as the ratio of end-of-season C4 grass biomass to total biomass (2000 only: $r = 0.32$, $P = 0.006$), but decreased with increasing light availability (2000: $r = -0.46$, $P < 0.001$; $r = -0.32$, $P = 0.006$). All of these measures also were significantly correlated with dominance, but only competition was correlated with richness (2000, $r = -0.38$, $P < 0.001$; 2001, $r = -0.31$, $P = 0.007$). Light availability decreased (2000, $r = -0.62$, $P < 0.001$; 2001, $r = -0.51$, $P < 0.001$), whereas competition (2000, $r = 0.65$, $P < 0.001$; 2001, $r = 0.64$, $P < 0.001$) and crowding, i.e. total ramet densities (2000: $r = 0.85$, $P < 0.001$; 2001: $r = 0.74$, $P < 0.001$), increased with dominant density.

### Table 1. Results from ANOVAs of effects of dominance (D) and richness (R) treatments on dominance (C4 grass ramet density) and light penetration (%) in tallgrass prairie for (A) 2000 and (B) 2001.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Dominance</th>
<th>Light penetration (%)</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>MS</td>
<td>F</td>
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<tr>
<td>A) 2000</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>11</td>
<td>98067.58</td>
<td>16.51</td>
</tr>
<tr>
<td>D</td>
<td>2</td>
<td>522063.04</td>
<td>84.55</td>
</tr>
<tr>
<td>R</td>
<td>3</td>
<td>1720.27</td>
<td>0.29</td>
</tr>
<tr>
<td>D × R</td>
<td>6</td>
<td>11576.08</td>
<td>1.95</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td>5938.31</td>
<td></td>
</tr>
<tr>
<td>B) 2001</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Model</td>
<td>11</td>
<td>102873.38</td>
<td>10.00</td>
</tr>
<tr>
<td>D</td>
<td>2</td>
<td>475060.50</td>
<td>46.20</td>
</tr>
<tr>
<td>R</td>
<td>3</td>
<td>4468.68</td>
<td>0.43</td>
</tr>
<tr>
<td>D × R</td>
<td>6</td>
<td>28013.32</td>
<td>2.72</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td>10282.38</td>
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</tbody>
</table>
In multiple regression (backward elimination) analyses, we included the following as predictors of invasibility: realized richness, total ramet density as an index of community crowding, dominance (C₄ grass ramet density), relative dominance (ratio of end-of-season C₄ biomass to total biomass) as an estimate of competition, and light availability. Light availability was not included in the final model due to collinearity (a variance inflation index $> 1/(1 - r^2)$ and variance proportion close to one).

For 2000, total ramet density and relative dominance were retained as significant predictors of invasion by *Melilotus* (Table 3). The parameter estimates for both were positive, which suggests that community crowding and competition by the dominant C₄ grasses each had independent and direct positive effects on community invasibility. In 2001, only total ramet density was retained as a significant predictor of *Melilotus* establishment. As in 2000, the parameter estimate for total ramet density was positive, indicating that crowding was the best predictor of invasibility.

**Discussion**

We examined the effects of species richness and dominance (abundance of highly competitive species) on invasibility of tallgrass prairie by separately manipulating these community characteristics in intact grassland plots. Counter to our expectations, establishment by the invading legume *Melilotus officinalis*, our measure of

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</thead>
<tbody>
<tr>
<td>Model</td>
<td>11</td>
<td>516.86</td>
<td>3.30</td>
<td>0.001</td>
<td>352.37</td>
<td>1.10</td>
<td>0.38</td>
</tr>
<tr>
<td>D</td>
<td>2</td>
<td>1876.68</td>
<td>11.98</td>
<td>&lt; 0.001</td>
<td>1083.58</td>
<td>3.37</td>
<td>0.04</td>
</tr>
<tr>
<td>R</td>
<td>3</td>
<td>173.07</td>
<td>1.10</td>
<td>0.35</td>
<td>43.15</td>
<td>0.13</td>
<td>0.94</td>
</tr>
<tr>
<td>D × R</td>
<td>6</td>
<td>235.48</td>
<td>1.50</td>
<td>0.19</td>
<td>263.25</td>
<td>0.82</td>
<td>0.56</td>
</tr>
<tr>
<td>Error</td>
<td>60</td>
<td>156.65</td>
<td></td>
<td></td>
<td>321.28</td>
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</table>

**Fig. 2.** Number of *Melilotus officinalis* invaders in response to richness reduction treatments (A–B) and as a function of realized richness in the plots (C–D) in 2000 (left) and 2001 (right). Note that twice as many seeds were added to plots in 2001 vs 2000. Closed circles = 4–6 richness treatment, open triangles = 7–9 richness treatment, closed squares = 10–12 richness treatment, open diamonds = 13–16 richness treatment.
invasibility in this system, was not influenced by non-random species loss in either year of the study. We found that establishment remained constant despite a 3-fold loss in the number of uncommon and rare species. This result contrasts with other studies that also have directly manipulated richness (Knops et al. 1999, Stachowicz et al. 1999, Levine 2000, Naeem et al. 2000, Prieur-Richard et al. 2000, Symstad 2000, Kennedy et al. 2002, Troumbis et al. 2002; but see Palmer and Mauer 1997, Crawley et al. 1999, Lavorel et al. 1999). The negative relationship between richness and invasion observed in these studies may be, in part, due to increased resource use, density and crowding with increasing richness (Stachowicz et al. 1999, Naeem et al. 2000, Dukes 2001, Kennedy et al. 2002), but also may be due to the sampling effect (Wardle 2001), in which the chance of including a highly productive, space-filling, or more competitive species increases as richness increases. Although the sampling effect is thought to be a likely process in communities shaped by stochastic assembly processes (Tilman et al. 1997), it is also viewed as an artifact of experiments that manipulate community richness by constructing synthetic communities comprised of random assemblages of species (Huston 1997, Wardle 1999, 2001).

Table 3. Parameter estimates from backward elimination multiple regression of the dependence of Melilotus establishment (invasibility) on realized richness, total ramet density as an index of crowding, dominance (total C₄ ramet density), relative dominance as a measure of competition (ratio of end-of-season biomass of dominant C₄ grasses to total biomass), and % light penetration in 2000 and 2001. Final models: 2000 $r^2 = 0.28$, $F_{2,70} = 13.27$, $P < 0.001$; 2001 $r^2 = 0.16$, $F_{1,70} = 13.00$, $P < 0.001$.

<table>
<thead>
<tr>
<th>Predictor variable</th>
<th>Invasibility</th>
<th>Parameter estimate</th>
<th>Partial correlation</th>
<th>P</th>
</tr>
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<tbody>
<tr>
<td>A) 2000 Realized richness</td>
<td>eliminated</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Total ramet density</td>
<td>0.03 (0.008)</td>
<td>0.49</td>
<td>&lt; 0.001</td>
<td>-</td>
</tr>
<tr>
<td>Dominance</td>
<td>eliminated</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Relative dominance</td>
<td>15.03 (7.86)</td>
<td>0.20</td>
<td>0.06</td>
<td>-</td>
</tr>
<tr>
<td>Light penetration (%)</td>
<td>eliminated</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>B) 2001 Realized richness</td>
<td>eliminated</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Total ramet density</td>
<td>0.03 (0.009)</td>
<td>0.40</td>
<td>&lt; 0.001</td>
<td>-</td>
</tr>
<tr>
<td>Dominance</td>
<td>eliminated</td>
<td>-</td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Relative dominance</td>
<td>eliminated</td>
<td>-</td>
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<tr>
<td>Light penetration (%)</td>
<td>eliminated</td>
<td>-</td>
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Fig. 3. Number of Melilotus officinalis invaders in response to dominance reduction treatments (A–B) and as a function of total C₄ grass (dominant) density in the plots (C–D) in 2000 (left) and 2001 (right). Note that twice as many seeds were added to plots in 2001 vs 2000. Closed circles = low dominance treatment, open triangles = medium dominance treatment, closed squares = high dominance treatment.
community. This allowed us to maintain the most dominant and productive species in all communities, irrespective of richness. In addition, the chance of including or excluding a more or less productive, rare and uncommon species was not related to community richness. Thus, the invasion patterns we observed were not influenced by the sampling effect (Smith and Knapp 2003). The lack of change in invasion resistance across the gradient of community richness we created, as well as the absence of an interaction between the richness and dominance reduction treatments, suggests that resource use, density and crowding were not related to richness in our experimental communities. Indeed, we found that light availability at peak Melilotus establishment, a key measure of aboveground resource availability, and total densities of all species were not affected by species loss. Thus, richness does not appear to be an important factor influencing invasion of intact, tallgrass prairie communities when factors known to covary with diversity are held constant.

In a study comparable to ours, Lyons and Schwartz (2001) found that loss of uncommon species decreased invasion resistance of an alpine meadow. In these short-statured, herbaceous communities, they hypothesized that invasion resistance decreased with species loss due to increased availability of limiting resources, particularly water, allowing for greater establishment by the target invader, Lolium multiflorum Lam. In contrast, uncommon and rare species in the present study did not appear to have disproportionate effects on key limiting resources for establishment, i.e. light or space availability, and thus their loss did not influence invasion resistance in this mesic grassland, at least in the short-term.

Although non-random loss of species had no impact on invasibility, reduced dominance of the C4 grasses significantly decreased invasion by Melilotus. This is counter to the pattern we expected. We hypothesized that reduced dominance would increase aboveground resource availability and decrease competition and crowding, which it did by increasing light availability and decreasing relative biomass of C4 grasses and total stem densities. However, these alterations did not result in increased establishment of Melilotus. Other studies have shown that susceptibility to invasion is strongly influenced by abundance of dominant species and regulated by light availability. For example, Burke and Grime (1996) found that invasion was highest in grassland sites that were disturbed. These sites not only contained the highest availability of bare ground (indicative of more available space and light) but also were those with the greatest damage to the dominants. They found that decreased abundance of the dominant species as a result of their disturbance treatments was key in determining invasion in their grassland plots. Similarly, Robinson and colleagues (1995) found that annual grassland communities with lower dominance (percent cover) of Bromus diandrus, the primary dominant in their study plots, as well as those subjected to greater disturbance, were more susceptible to invasion. In a successional Kansas grassland, invasion was found to be strongly influenced by variation in light availability across a natural gradient of plant diversity, with invasion increasing as light availability increased (Foster et al. 2002). Invasion also was lowest in sites with low diversity, which coincided with high dominance by a few grass species. In contrast, Wilsey and Polley (2002) found that invasion of synthetic grassland communities was enhanced with decreasing evenness (i.e. increasing dominance), but could find no change in resources among the different levels of evenness manipulated. Instead, they suggested that invasion may have been enhanced by within-plot variability in resources.

The decline in invasibility with decreasing dominance that we observed may have occurred for several reasons. The study site was burned at the beginning of the growing season (mid- to late-March) in both years of the study, and thus all plots lacked a litter layer. Light levels in the high (ambient) dominance plots also were relatively high (40%). Reduced abundance of the dominants further increased light availability by as much as 35%, perhaps to levels that negatively affected establishment. The expected positive effects of increased light and space availability resulting from reduced dominance were likely offset by increased stress at the time of establishment via increased canopy temperatures and evapotranspiration, and decreased soil moisture (Knapp and Seastedt 1986). Indeed, average light availability in the experimental plots (average: 46.3%, range: 21.3 to 80.0%) was double that observed in nearby, intact plots that were burned and varied naturally in dominance (average: 24.5%, n = 30 plots, range: 7.5% to 45.5%; Smith 2002). Decreased density of the dominant species also may have indirectly influenced invasion by increasing the apparancy of Melilotus seedlings to herbivores (Prieur-Richard et al. 2002). We observed mortality of seedlings as a result of herbivory in the study plots, but this was not directly quantified.

Regardless of which of these mechanisms were operating, invasion was not affected by richness but was facilitated by increased abundance of the dominant species in the grassland plots. Recently, Bruno and coauthors (2003) suggested that facilitation by dominant species might be an important, yet unrecognized, process influencing invasibility of communities. Under stressful conditions, dominant species may facilitate rather than compete with invading or colonizing species, because they provide specific environmental conditions or ameliorate harsh conditions. We hypothesize that our manipulations of the dominant species made
microclimatic conditions much harsher in low and moderate density plots than the high (ambient) density plots, and thus seedling establishment was facilitated by increased abundance of the dominants. Moreover, we observed similar patterns for natural recruitment of native species into the plots as observed for invasion by *Melilotus*; richness of colonizing species increased with dominance, but was unrelated to community richness (Smith 2002). This suggests that increased abundance of dominants also can facilitate establishment of a suite of other colonizing species in this grassland.

Bruno et al. (2003) also point out that facilitation by dominant species may change the shape of the relationship between richness and invasion by increasing richness of both native and exotic species under harsh conditions but then decreasing their richness when competition becomes intense. Our results indicate that variation in abundance of dominant species can strongly influence invasion independent of community richness. This suggests that for studies that manipulate richness by randomly constructing communities or by randomly removing species from intact communities, variation in the presence and/or abundance of dominant species could be driving observed relationships between richness and invasion.

Finally, because we focused on establishment of the invading species, it is unclear how important facilitation will be during other stages of the invasion process. Indeed, there is evidence that invasion resistance can vary depending on the life stage of the invading species (Prieur-Richard et al. 2000, Franzen 2001). In our grassland communities, dominant species may have an opposite effect on growth, persistence and reproduction of invaders once they are established, because the negative effects of competition may outweigh any positive effects related to improved microclimatic conditions for establishment. Patterns of invasion with natural variation in dominant species observed in intact, grassland plots (Smith and Knapp 1999) suggest that dominant species negatively affect persistence in invaders in the long-term. Thus, we contend that dominant species and their effects on other community characteristics and resources are key in determining resistance, as well as susceptibility, of communities to invasions. This emphasizes the need to examine the role of dominant species as competitors or facilitators in influencing diversity-invasibility relationships.

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