DISPERAL, COMPETITION, AND SHIFTING PATTERNS OF DIVERSITY IN A DEGRADED OAK SAVANNA

ANDREW S. MACDOUGALL1,2,3 AND ROY TURKINGTON1,2

1Department of Botany, University of British Columbia, Vancouver, British Columbia, V6T 1Z4 Canada
2Biodiversity Research Center, University of British Columbia, Vancouver, British Columbia V6T 1Z4 Canada

Abstract. Diversity is a balance between processes that add and limit species (e.g., dispersal vs. competition), but reconciling their contributions remains a challenge. Recruitment-based models predict that dispersal barriers are most limiting for diversity, while competition-based models predict that dispersal matters only when competition is minimized. Testing these models is difficult because their influence varies with scale and site productivity. In a degraded oak savanna, we used plot-level (seed additions, burning) and site-level (proportions of regional functional groups found locally) analyses in areas with variable soil depth to examine how dispersal and competition influence diversity. At the plot level, added species persisted where they were formerly absent, but few established naturally despite fire-induced resource enrichment and nearby populations, revealing the importance of dispersal limitation for diversity. This result did not vary with soil depth or standing crop. Although competition could not prevent establishment in unburned plots, it significantly lowered survival, indicating that resource limitations exacerbate dispersal inefficiencies. At the site level, the concordance between regional and local diversity for native species was associated with soil depth heterogeneity, not dispersal or competition. This suggests that persistence is determined primarily by the influence of the environment on population demographics. Given that the formation of new populations is unlikely, those remaining appear to be confined to optimal habitat where they resist competitive or stochastic displacement, possibly explaining why species loss is rare despite substantial habitat loss and invasion. For exotics, there was no relationship between diversity and soil depth heterogeneity. Annuals with presumed dispersal capabilities were significantly overrepresented in all sites while perennial forbs, the largest regional functional group, were significantly underrepresented. We interpret the native-exotic discrepancies as reflecting the recent arrival of exotics (150 years ago), suggesting that local establishment occurs slowly even for species with regional prevalence. The accumulation lag may be explained by the need for founder populations to be demographically stable; otherwise persistence requires continual immigration favoring overrepresentation by dispersers. Our findings support the view that dispersal limitation restricts diversity within plant communities, but suggests that the impacts of environment on demographic performance ultimately determine the pattern and rate of community assembly.

Key words: British Columbia; competition; dispersal limitation; habitat loss; oak savanna; plant invasion; species coexistence.

INTRODUCTION

Given current declines in species diversity worldwide, it has never been more critical to understand the mechanisms that maintain diversity or cause its reduction. Diversity is regulated by the balance between processes that add species (e.g., dispersal) and those that constrain them (e.g., competition, environmental stress) (Ricklefs 1987, Loreau et al. 2003). Dispersal-based models predict that immigration sets the potential upper limits for local diversity but that these limits are rarely attained because of barriers that prevent its occurrence.

Competence-based models predict that dispersal is only important when competition is absent or weak (e.g., early in succession). Distinguishing the relative importance of these models for diversity has been difficult and subject to debate (Loreau and Mouquet 1999, Shurin 2000, Ricklefs 2004), especially in degraded systems where changes to both are substantial and covary (Seabloom et al. 2003, Yurkonis and Meiners 2004, MacDougall and Turkington 2005). Correlations between plant invasion and declines in native flora, for example, suggest competitive displacement by the exotic intruders. Because many invaded plant communities are also fragmented, however, species loss could actually be caused by reduced dispersal that prevents native species from offsetting naturally occurring population turnover. In this circumstance, conservation measures that tackle
the highly visible problem of invasion will miss the primary cause of species loss.

Disentangling the interaction of dispersal-based and competition-based processes is challenged by the spatial complexity and long time frames over which they operate (Srivastava 1999, Loreau 2000, Collins et al. 2002, Leibold and Miller 2004). Experimental approaches have long confirmed the significance of competition for community structure, including invasion resistance (Kennedy et al. 2002, Fargione et al. 2003), but the effects of competition can be highly localized due to variations in its intensity across broad environmental gradients (Byers and Noonburg 2003, Ricklefs 2004). Experimental and biogeographical studies have both demonstrated that many communities are dispersal limited, capable of absorbing many more species than currently occur without concomitant species loss (e.g., Sax et al. 2002, Foster and Tilman 2003). The experimental studies, however, have typically been limited in duration (<15 yr) making it unclear whether the results will persist beyond a single generation. The biogeographical studies have found that native flora in invaded areas can be precariously rare even though species loss has yet to occur, so that displacement by competition may be slow but inevitable (Sax et al. 2002, Davis 2003, Sax and Gaines 2003). These examples illustrate that competition and dispersal are both critical for determining diversity but reconciling their relative contributions remains a fundamental challenge (Smith and Shurin 2006). Because standard methods lack the resolution to detect how diversity is regulated through space and time, there is a need for integrative approaches that examine short-term local dynamics and the longer-term biogeographical context within which they operate (Ricklefs 2004, Davis et al. 2005a).

We take such an integrative approach in an invaded, fragmented, and fire-suppressed oak savanna on southeastern Vancouver Island in British Columbia, Canada. We use separate experimental and biogeographical analyses to examine the relative importance of local-scale (competition, disturbance, soil depth heterogeneity) and regional-scale (dispersal) processes for present-day diversity in savanna remnants. Using experimental seed additions and burning, we test if recruitment by native forbs is more limited by dispersal, by competition from the invasive perennial grasses that presently dominate, or some combination of the two. Using a comparison of the proportion of species within plant functional groups at regional and local levels, we test (1) if functional groups from the regional species pool with assumed abilities to disperse or compete are over- or underrepresented in local site remnants, and (2) whether these trends differ for exotic and native species. For natives, we predicted that perennial forb species would be significantly underrepresented in all remnant sites due to the long-term effects of fire suppression and competition. For exotics, we predicted complete concordance between regional and local pools due to the prevalence of these species on the landscape generally.

METHODS

The study was conducted in a sub-Mediterranean oak (Quercus garryana) savanna ecosystem of southwestern British Columbia, Canada (Fuchs 2001). This ecosystem reaches its northern distributional limit in British Columbia, extending from northern California in the rain shadow of the Coast Mountains. Like all post-glacial plant communities, dispersal from regional sources underlies its assembly (e.g., Fig. 1A) but its current impact on local diversity is unknown. The flora is closely affiliated with the California Floristic Province (CFP) and possesses the high percentage of perennial forbs and annuals that characterize species of the CFP associated with a Mediterranean climate (Raven and Axelrod 1978, Hickman 1993). In British Columbia, however, it is unclear whether species pools at finer spatial scales (i.e., remnant sites) bear this distinctive floristic signature or whether membership reflects local environmental factors and habitat change interacting with relative competitive ability. Currently, remnant savanna is fire suppressed and dominated by exotics, suggesting competitive suppression of the native flora that is less abundant, has reduced ranges, and more 10% of which are considered at risk provincially or nationally in Canada (Fuchs 2001). It is also, however, highly fragmented with >95% habitat loss, so that native species may be more constrained by an inability to disperse among remnants.

Field experiment

A factorial seed addition and burning “pulse” experiment was conducted in an 18-ha oak savanna reserve in the Cowichan Valley on southeastern Vancouver Island (48°48′ N, 123°38′ W). The reserve is dominated by exotic perennial C3 grasses (Poa pratensis, Dactylis glomerata) but also contains numerous obligate and non-obligate native plant species (obligate means that distributions in British Columbia are confined solely to oak savanna habitat, as defined by Fuchs 2001). In May 2000, 10 blocks (3 × 3 m) were placed along a gradient of soil depth (range: 5 cm to >85 cm) and species diversity in savanna openings unobstructed by the oak canopy (described in MacDougall 2005). Prior to treatment, the blocks were divided into four 0.75 × 0.75 m plots and assessed for species cover, ground-level light (percentage of full light; quantum sensor, Li-Cor, Lincoln, Nebraska, USA), soil moisture (Hydrosense TDR meter, Campbell Scientific, Logan, Utah, USA), aboveground grass and litter biomass, and percentage of bare soil. Light and soil moisture were monitored every two months during the first three years of the experiment. Relative abundance was visually estimated using a 0.75 × 0.75 m frame divided into 16 segments that guided the visual estimation. Grass and litter biomass were determined by clipping, sorting, and oven-drying (at
70°C for two days) all aboveground biomass in 10 × 10 cm subplots in May of each year. Soil samples from the top 5 cm of each plot were taken before, one week after, and two years after burning, extracted with 1 mol/L KCl, and analyzed for NO₃ and NH₄ (mg/kg soil).

In each plot, seed bank composition was determined from soil cores (10 cm diameter, 7 cm deep) taken in early July 2000 and cold-stored in plastic bags at 5°C. In October 2000, the core samples were sifted to remove roots and tubers and spread over sand-filled trays in a heated greenhouse. For eight months, all seedlings were counted, identified to species, and removed from the trays as they emerged. Identification of seedlings to species aided subsequent seedling identification in the field (e.g., differentiating between seedlings vs. tillers for *Poa pratensis*).

Plots in each block were randomly assigned to one of four treatments: control, burning only, seed addition only, or burning plus seed addition. Burning was applied twice: in late July and in early October 2000. The July burn occurred during seed set by the dominant exotic grasses. The October burn removed the post-burn regrowth, although little had occurred. An additional 0.25 m was burned around the plots to reduce edge effects.

Seeds of nine native obligate forb species (Table 1) were hand-broadcast over the 20 “addition” plots several days after burning. A 10th species was also

---

**Table 1.** Summary details for the nine species used in the seed addition experiment.

<table>
<thead>
<tr>
<th>Species</th>
<th>Life form</th>
<th>Seed mass (mg)</th>
<th>Planting density</th>
<th>Soil depth (cm)</th>
<th>2000 cover (%)</th>
<th>2005 UB cover (%)</th>
<th>2005 B cover (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Achillea millefolium</em> L.</td>
<td>perennial</td>
<td>0.13</td>
<td>235</td>
<td>13.43 (0.44)</td>
<td>0</td>
<td>0</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Camassia quamash</em> (Pursh) Greene</td>
<td>perennial</td>
<td>4.91</td>
<td>541</td>
<td>18.23 (0.45)</td>
<td>0.09</td>
<td>3.0</td>
<td>4.3</td>
</tr>
<tr>
<td><em>Delphinium menziesii</em> DC.</td>
<td>perennial</td>
<td>0.94</td>
<td>65</td>
<td>12.84 (0.72)</td>
<td>0</td>
<td>0.9</td>
<td>1.2</td>
</tr>
<tr>
<td><em>Dodecatheon hendersonii</em> A. Gray</td>
<td>perennial</td>
<td>1.78</td>
<td>455</td>
<td>18.38 (0.49)</td>
<td>0.03</td>
<td>4.5</td>
<td>9.1</td>
</tr>
<tr>
<td><em>Eriophyllum lanatum</em> (Pursh) J. Forbes</td>
<td>perennial</td>
<td>0.53</td>
<td>321</td>
<td>13.24 (0.87)</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
</tr>
<tr>
<td><em>Erythronium oregonum</em> Applegate</td>
<td>perennial</td>
<td>6.11</td>
<td>121</td>
<td>23.8 (0.83)</td>
<td>0</td>
<td>0.4</td>
<td>1.4</td>
</tr>
<tr>
<td><em>Lomatium utriculatum</em> (Torr. &amp; A. Gray)</td>
<td>perennial</td>
<td>3.09</td>
<td>239</td>
<td>14.69 (0.45)</td>
<td>0</td>
<td>3.1</td>
<td>5.6</td>
</tr>
<tr>
<td>J.M. Coult. &amp; Rose</td>
<td></td>
<td>2.69</td>
<td>273</td>
<td>19.22 (0.50)</td>
<td>0</td>
<td>1.9</td>
<td>3.0</td>
</tr>
</tbody>
</table>

**Notes:** Seed mass (mg/seed) is the average from 100 seeds. Planting density is the number of seeds added per 0.6-m² plot. Soil depth is the average depth (cm) from all plots containing each species from the six site remnants of the Cowichan Valley (*n* = 184 plots). Abbreviations are: UB, unburned seed addition plots; B, burned seed addition plots. Nomenclature follows The Jepson Manual (Hickman 1993).

† Values in parentheses are standard errors.
Despite the presence of oak savanna in British Columbia, only a few remnants remain. Remnants range in size from 0.3% to 18.1 ha (Table 2; described further in MacDougall et al. 2006). The site pools were surveyed for species composition (visual estimation to 1% cover) and soil depth variability in May–June 2001 (n = 184 1-m² plots). The number of plots per site was roughly proportional to the size of the remnant (20–38 plots per site). Plots were selectively placed to represent the full range of soil depth variability found in each site, as randomly located plots consistently missed rarer microhabitats so that highly abundant species were over-sampled. Soil depth was determined by driving a steel rod to bedrock four times in each plot and averaging the outcome.

We used forward stepwise multiple regression to determine which of five independent variables (site, blocking, treatment, seed mass, number of added seed) and their interactions contributed significantly to seedling survival after five years. The cutoff point for variable addition was $P < 0.05$, although expanding the cutoff to $P < 0.10$ did not change the outcome. To stabilize the variance, establishment data were log transformed and percent cover data were arcsine transformed (Zar 1999). We then analyzed the data with an ANOVA using those variables identified by the stepwise procedure. Post-hoc comparisons were conducted with $t$ tests. Analyses were conducted using JMP (Sall et al. 2005).

**Biogeographical analysis**

We compared the relative proportion of species within plant functional groups between the regional savanna species pool and the six main local savanna remnants of the Cowichan Valley (Fig. 1B; Table 2). The Cowichan Valley is centrally located within the distributional range of oak savanna on Vancouver Island. Prior to the 1860s it contained approximately 30 000+ ha of oak savanna, of which $<~0.3\%$ remains. Remnants range in size from 2.9 to 18.1 ha (Table 2; described further in MacDougall et al. 2006). The site pools were surveyed for species composition (visual estimation to 1% cover) and soil depth variability in May–June 2001 ($n = 184$ 1-m² plots). The number of plots per site was roughly proportional to the size of the remnant (20–38 plots per site). Plots were selectively placed to represent the full range of soil depth variability found in each site, as randomly located plots consistently missed rarer microhabitats so that highly abundant species were over-sampled. Soil depth was determined by driving a steel rod to bedrock four times in each plot and averaging the outcome.

The analysis focused on the relative proportion of the four main native and exotic plant functional groups: annual and perennial grasses and forbs. We wanted to determine if the six local sites have “sampled” these functional groups based on their relative abundance in the regional species pool, or on the assumed relative ability of various functional groups to compete or disperse. We also asked whether native and exotic flora appear to be limited by the same processes. To do this we tested four models on the regional-site relationship that we assumed to reflect different mechanisms regulating local diversity: (i) a “regional” model where the relative abundance locally matches the relative abundance regionally (e.g., guild proportionality [Wilson 1989]), (ii) a “dispersal” model where annual species are overrepresented at the site level (annuals assumed to be the best dispersers because, on average, they exhibit “r-type” life history traits), (iii) a “competition” model where perennial grasses are overrepresented (these species are best able to acquire limiting resources in this savanna in the absence of fire [MacDougall and Turkington 2004]), and (iv) a “random” model where there is no detectable relationship. Models (ii) and (iii) are based on highly simplified assumptions about the relative abilities of annuals and perennials to disperse and compete, recognizing there is considerable variation for each within both groups (Stearns 1977, Rees 1995). Although species-specific trait data are unavailable to confirm these assumptions in British Columbia, they have been validated for the CFP generally (Baker 1972). Based on data for over 1600 species, annual herbaceous species were found have significantly smaller seeds and higher seed output, both of which were associated with higher dispersibility. Perennial herbaceous species dem-

<table>
<thead>
<tr>
<th>Species pool</th>
<th>Total remaining area (ha)</th>
<th>Number of species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Regional pool (British Columbia)</td>
<td>~1000†</td>
<td>310 144</td>
</tr>
<tr>
<td>Local pool (Cowichan Valley, BC)</td>
<td>~100‡</td>
<td>86 60</td>
</tr>
</tbody>
</table>

† Estimated area of remnant savanna in British Columbia (Erickson 2000).‡ Estimated area of remnant savanna in the Cowichan Valley of British Columbia derived from orthophotos (1:12 500 resolution).
onstrated the reverse trend (fewer and bigger seeds), and were assumed to be better competitors especially in sites with higher productivity.

We conducted a 500-run Monte Carlo simulation to generate confidence intervals (α = 0.05) for each group in the regional species pool (Fig. 2A, I), using the relative proportions of the four functional groups as the basis for the simulation. Using maximum likelihood ratio and Pearson’s chi-square tests, we then tested whether the proportional distribution of the functional groups at the site level fell within the generated confidence intervals (Sall et al. 2005). Because there were no native annual grasses observed during the field surveys (although eight species occur in the regional pool), the analysis for native species was restricted to annual forbs and perennial forbs and grasses. A lack of significance was interpreted as support for the “regional” model (model i). For sites that differed significantly from the regional profile (Tables 3 and 4), we then determined which functional groups were over- and underrepresented based on whether their individual proportions fell above or below the generated confidence intervals. Overrepresentation by both annual grasses and annual forbs was interpreted as support for the “dispersal” model (ii), while overrepresentation by perennial grasses was interpreted as support for the “competition” model (iii). The “random” model (iv) was supported if all functional groups fall outside the generated confidence intervals.

**Fig. 2.** Relative proportion of species in the dominant plant functional groups for native species in the (A) regional species pool and (B–G) six site pools of the Cowichan Valley, British Columbia. (H) Distribution of soil depths from plots within each of the six sites. The right and left ends of each box indicate the 75th percentile and 25th percentile, respectively. The vertical line inside each box is the median; the solid square in each box is the mean. The whiskers are 95% confidence intervals. (I–O) Relative proportion of species in the dominant plant functional groups for exotic species in the (I) regional species pool and (J–O) the same six local sites. Error bars for the regional pools are from a 500-run Monte Carlo simulation.
RESULTS

Conditions in untreated plots

Eighteen species naturally recruited in the untreated plots, representing 17% of the species found on the reserve. Most were exotics (e.g., Galium aparine, Vicia spp.) or non-obligate natives (e.g., Sanicula crassicaulis). Total seedling numbers in these plots averaged 70 seedlings/plot (SE = 10.5). Five of nine species used in the seed addition mixture naturally established in at least one plot, but none had more than nine seedlings combined over the three survey years. Based on total seedlings numbers in 2002, the last time seedlings of all species were counted, natural recruitment by the added species represented only 0.5% of all recruitment even though most have large populations elsewhere in the reserve. Relative abundance in the established sward overstory did not determine the relative abundance of recruiting seedlings. There were few seedlings of the two most dominant species (Poa and Dactylis) (0.4% and 0.8% of total seedlings respectively). Poa recruited mostly by tillering.

Two microenvironmental variables differed significantly with soil depth. Late spring understory light levels were significantly lower in plots with deeper soils ($t_{1,9} = 3.38, P = 0.01$), in association with higher standing crop ($t_{1,9} = 3.59, P = 0.002$). Early summer soil moisture was significantly lower in plots with shallow soils ($t_{1,9} = 2.91, P = 0.02$). During the rest of the year, moisture levels did not differ (i.e., similarly moist in the winter, similarly dry in the late summer). Neither light or soil moisture differences were associated with the number of established seedlings for native nor exotic species in the control plots.

The most abundant taxa in the seed bank ($N = 6841$ seedlings) were small-seeded annuals. Most were exotics except for the non-obligate native Cardamine oligosperma. The average number of species per core did not differ significantly between sites with deep soil (13 species) and shallow soil (12 species) ($t_{1,9} = 0.45, P = 0.65$). Only 1.8% of all germinated seed (six species) were oak savanna obligates. In the deep soil plots, most obligate species were grasses (mostly Bromus carinatus).

Notes:

1. Native annual grasses are excluded because none were detected during the local surveys.

### Table 3. Results of Monte Carlo simulation (500 runs) for the regional species pool, including generated probabilities and 95% confidence intervals (CI).

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Native species</th>
<th>Exotic species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Regional pool (%)</td>
<td>No.</td>
</tr>
<tr>
<td>Grasses</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual</td>
<td>0.03</td>
<td>0</td>
</tr>
<tr>
<td>Perennial</td>
<td>0.15</td>
<td>80</td>
</tr>
<tr>
<td>Forbs</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual</td>
<td>0.34</td>
<td>184</td>
</tr>
<tr>
<td>Perennial</td>
<td>0.48</td>
<td>236</td>
</tr>
</tbody>
</table>

### Table 4. Results of the chi-square tests for the six site remnants, using two analyses: maximum likelihood ratio and Pearson’s.

<table>
<thead>
<tr>
<th>Site and test</th>
<th>Native species</th>
<th>Exotic species</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Chi-square</td>
<td>df</td>
</tr>
<tr>
<td>A</td>
<td>4.0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>3.6</td>
<td>2</td>
</tr>
<tr>
<td>B</td>
<td>4.8</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>5.0</td>
<td>2</td>
</tr>
<tr>
<td>C</td>
<td>12.3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>12.5</td>
<td>2</td>
</tr>
<tr>
<td>D</td>
<td>20.3</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>18.5</td>
<td>2</td>
</tr>
<tr>
<td>E</td>
<td>34.5</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>31.1</td>
<td>2</td>
</tr>
<tr>
<td>F</td>
<td>48.1</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>42.4</td>
<td>2</td>
</tr>
</tbody>
</table>

Note: Native annual grasses are excluded because none were detected during the local surveys.
In the shallow soil plots, most were perennial forbs (Camassia, Lomatium, and Ranunculus). Poa, the most abundant overstory species, was also the most abundant perennial grass species in the soil cores (deep soils, 10% of all germinating seed; shallow soils, 7%). Dactylis seed was uncommon in the seed bank (deep soils, 10% of all germinating seed; shallow soils, 7%). Dactylis seed was uncommon in the seed bank (deep soils, 0.3% of all seed). Most annuals emerged after one to four weeks. All native obligates except Bromus carinatus emerged after two to four months.

**Burning**

Burning transformed the microenvironment and recruitment dynamics of the plots. Two years after burning (May 2002), plots still had significantly less grass cover and litter, and significantly more light and bare soil, with deep soil plots being better illuminated and having less vegetation cover (Table 5). Soil moisture and levels of NO₃ and NH₄ were not significantly affected by burning (Table 5). Forty-four species naturally established in the burned but unseeded plots, mostly exotic annual grasses (e.g., Bromus spp.) and annual forbs found in high abundance in the seed bank (Fig. 3). Recruitment by native species increased in the burned plots compared to the unburned plots but most were non-obligates (Cardamine oligosperma, Sanicula crassicaulis). Natural establishment by native obligates in burned and unburned plots did not differ significantly (F₁,1₇₉ = 0.66, P = 0.42), with numbers averaging 2 seedlings/plot (total, all native obligate species) in the unburned plots and 5 seedlings/plot in the burned plots. Levels of natural establishment by the nine added species were unaffected by burning (Fig. 3).

**Seed additions**

The stepwise procedure identified five singular and interactive factors that best explained seedling establishment by the added species (Table 6). The most significant was the density of added seed; more seeds added initially meant more seedlings after five years. Seven of the added species established in the dense unburned grass despite low light, limited available N, dense litter, and no bare soil (Table 5). By 2005, the species with the highest establishment in all plots was the annual Plectritis congesta. It was the only species with higher seedling numbers in 2005 compared to 2002 (Fig. 4).

There were also significant effects of site and treatment on establishment after five years (Table 6), explained by higher seedling survival in burned plots with deeper soils. In these plots, there were significantly more seedlings after five years (26.5 ± 6.7 seedlings/plot, mean ± se) compared to seedling numbers in burn plots with shallow soils (13.2 ± 3.8 seedlings/plot) and compared to seedling numbers in unburned plots (deeper soils, 7.6 ± 2.0 seedlings/plot; shallow soils, 6.4 ± 1.6 seedlings/plot [t tests, α = 0.05]). Combined percent cover of the nine added species was also significantly higher in the burned plots on deep soils (t tests, α = 0.05), averaging 27.8% cover (se = 3.7). There were no significant differences in cover among the other three treatment × site combinations (burned-shallow, 14.4 ± 1.4%; unburned-deep, 8.4% ± 2.2%; unburned-shallow, 5.8% ± 1.7%). Seed mass had no statistically detectable effect on establishment in either treatment (F₁,8 = 0.31, P = 0.57), although the two species with the smallest seeds (Achillea and Eriophyllum) did not establish in the unburned plots.
Biogeographical analysis

A total of 119 species were observed during the site surveys, representing 26% of the total regional pool for British Columbia. Species richness in the six sites ranged from 44 to 64 species, with no significant relationship between richness and patch size ($F_{1,5} = 0.03, P = 0.88$). The percentage of exotic flora did not differ significantly among sites ($F_{1,5} = 2.73, P = 0.17$), ranging from 33% to 44% of the site-level species pools (Table 2).

The biogeographical results did not conform to the expectations that native perennial grasses would be most abundant at the site level (i.e., the competition model) or that there would be full concordance between regional and local pools for exotic species (i.e., the regional model). Only two local pools exhibited the regional signature, and both were for native species in sites with the greatest soil depth heterogeneity (Fig. 2B, C; Tables 3 and 4). Sites with limited soil depth did not conform statistically to any model for native species (Fig. 2D–G; Tables 3 and 4). In these sites, the percentage of perennial forbs decreased significantly with decreasing average soil depth ($F_{1,5} = 22.8, P = 0.005$).

Results for the exotic flora were consistent with the “dispersal” model for all sites regardless of soil depth variation and despite the prevalence of perennial forbs in the regional species pool (Fig. 2J–O; Tables 3 and 4). In each case, the proportion of annual grasses and forbs at the site level exceeded the 95% confidence intervals generated for the regional species pool. The proportion of perennial forbs, in contrast, fell below the confidence intervals.

Table 6. Results of the adjusted ANOVA model for number of established seedlings after five years, based on the variables identified by the forward stepwise regression procedure (summary statistics for the entire model: $R^2 = 0.39, F_{9,179} = 11.69, P < 0.0001$).

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>$F$</th>
<th>$P$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Added seed density</td>
<td>1</td>
<td>29.4</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Treatment</td>
<td>1</td>
<td>15.3</td>
<td>0.0002</td>
</tr>
<tr>
<td>Site</td>
<td>1</td>
<td>5.4</td>
<td>0.021</td>
</tr>
<tr>
<td>Treatment × seed density</td>
<td>1</td>
<td>1.2</td>
<td>0.27</td>
</tr>
<tr>
<td>Site × seed density</td>
<td>1</td>
<td>0.02</td>
<td>0.88</td>
</tr>
<tr>
<td>Error</td>
<td>179</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Fig. 4. Seedling survival over the three survey periods for the nine added species. Numbers in the year 2000 are initial seed densities. Error bars are not included for clarity of presentation. Note that *Plectritis* is an annual species.
DISCUSSION

The combined experimental and biogeographical data provide insight on diversity maintenance that would be difficult to obtain with singular analyses. At the plot level, dominance by exotics suggests the prevalence of competition but the distribution of many native plants is also influenced by an inability to disperse widely and in large numbers. The exotic grass sward is unsaturated, capable of supporting more species, indicating that vacant recruitment space exists despite the low levels of available light and bare soil associated with fire suppression. At the site level, however, it appears that the influence of the environment on the demographic performance of populations, rather than recruitment limitation or competition, better explains the persistence of native plants. The degree to which local native communities matched the regional diversity signature was associated with soil depth heterogeneity in each site, not the relative ability of species to disperse or compete. Also, there was no indication that high levels of dispersal, as is expected for exotics generally, are driving the rapid accumulation of all functional groups in local communities. Instead, site-level pools were overrepresented by exotic annuals with presumed dispersal capabilities while perennial forbs, the largest exotic functional group regionally, were significantly underrepresented.

We interpret these findings to indicate that increased immigration could extend the plot-level distribution of many species in this system, but the demographic stability of these populations may be constrained in the long-run by the underlying environmental conditions, slowing the rate by which species locally accumulate (Pulliam 1988, 2000). We presume demographic stability (i.e., where reproduction matches or exceeds mortality) to be critical because it reduces the likelihood of population turnover, thereby eliminating the need for poor dispersers to immigrate repeatedly. At the same time, high densities of seed input, as is expected for exotics generally, is likely necessary but not sufficient for population establishment unless founder populations establish in optimal habitat (i.e., areas that support demographically stable populations for any given species [Snyder and Chesson 2003]). Given the small size of these remnants and the likelihood that optimal habitat will be limited in extent, this may be unlikely for most establishment events (e.g., Pulliam 2000, Tilman 2004). Once established, however, demographically stable populations should be resistant to competitive displacement due to their high fitness, which may also explain the persistence of native species in remnant areas despite rarely forming new populations (i.e., the only remaining populations of native plants are those confined to optimal habitat). Although speculative, these interpretations are consistent with modeled systems where dispersal, relative competitive ability, and spatial heterogeneity interact to determine local diversity rather than any one factor in isolation (e.g., Amarase-kare and Nisbet 2001, Levine and Rees 2002, Mouquet and Loreau 2003). They are also consistent with recent studies from other similarly degraded systems where native species continue to persist despite decades of fragmentation, invasion, and reduced population sizes (e.g., Helm et al. 2006, Herben et al. 2006).

Plot-level interactions between dispersal and competition

Given the high levels of exotic dominance and limited resources in this system (MacDougall and Turkington 2004, 2005), we predicted there would be almost no establishment by experimentally added native species in the unburned plots, especially because most were absent from areas where seed was added. We also predicted that potentially high levels of natural recruitment would occur in the unseeded burn plots given the large population sizes of some of the added species nearby in the reserve. Both predictions were rejected.

Instead, the results demonstrated that the exotic sward could limit, but not prevent, the establishment of most species despite constraints on resource availability. The dynamics of recruitment resembled a weighted lottery where more seed meant more establishment but the probability of success was partially contingent on life history differences in the presence of high competition (e.g., small-seeded species did not establish in unburned plots). The positive effect of fire on the establishment of added seed indicates that competition is a substantial impediment to recruitment, but its effects are more probabilistic than absolute. This means that competition lowers the odds that establishment will occur and raises the number of incoming seeds required for successful establishment. By contrast, naturally occurring establishment by native obligates, not just those added as seed, was extremely low despite the reduction of the grass sward by fire. Total seedling numbers increased significantly with burning, but most were exotic ruderals from the seed bank. The ability of added native species to persist where they are currently absent, and their inability to naturally capitalize on conditions of resource enrichment despite nearby populations, reveals the importance of dispersal limitation for constraining diversity in this system, a finding consistent with other studies using similar methods (e.g., Partel et al. 1996, Tilman 1997, Turnbull et al. 1999, Zobel et al. 2000, Foster et al. 2004). The causes of dispersal limitation are uncertain but assumed to reflect the effects of naturally occurring dispersal inefficiencies by perennial forbs, reduced reproductive output caused by increased competition in the absence of fire, and habitat fragmentation (MacDougall and Turkington 2005).

There was an inconsistent relationship between recruitment success and underlying environmental conditions associated with soil depth variability. Theory predicts that dispersal should be more limiting for diversity at low productivity and competition more limiting at high productivity. It also predicts that the
effects of disturbance on recruitment will be most significant at high productivity due to the reduction in competition and greater levels of resource availability (Partel et al. 2000, Foster et al. 2004, Foster and Dickson 2004, Huston 2004). Our results support the second prediction but not the first. Despite significant differences in standing crop, light, and soil moisture, recruitment success in unburned plots was significantly higher seedling survival. The mechanism explaining this response to burning is the combined effects of higher diversity on shallower soils, which include species that rapidly suppresses light availability following fire, and the sensitivity of the C₃ grasses to burning, which leads to higher levels of light and bare soil in areas where these grasses dominate (i.e., deep soils; MacDougall and Turkington 2005). What is unclear, however, is the cause of the pre-disturbance pattern of diversity (i.e., more native species on shallower soils) given that seeds of many species can establish everywhere. It is assumed that diversity is constrained in areas of high productivity by competition (e.g., Huston 1994, Waide et al. 1999), but the success of the seed additions in areas with deep soils suggest that competition cannot be the sole limiting factor. At the same time, however, dispersal inefficiency cannot explain patterns of diversity, because all points along the gradient were found to be unsaturated with species. Instead, it appears that feedbacks between the dampening effect of competition on seed production and the inability of native species to widely disperse despite high seed outputs combine to determine plot-level diversity in the absence of burning. Although competition from the dominant grasses is not an absolute barrier to establishment, it has been shown to significantly decrease reproductive effort by native species (MacDougall and Turkington 2005). Because more seed means more recruitment success, establishment will be greater in areas where the dominant grasses are less prevalent (shallow soils) because more seed is being produced. The rarity of dispersal means that most seed falls in close proximity to adult plants, creating a feedback loop that reinforces population persistence in established areas but limits range expansion. If true, it indicates that dispersal and competition interact to control diversity at the plot level, even though dominance by exotic grasses suggests that competition alone is prevalent.

Site-level patterns of diversity

Although the results of this and other similar experimental studies reveal that competition cannot solely limit diversity with high dispersal, the relevance of such findings for site-level patterns of diversity is unclear (Turnbull et al. 2000). It has long been understood that populations can be maintained outside of a species’ “fundamental niche” due to mass effects (Shmida and Ellner 1984, Pulliam 2000). However, because turnover rates for these populations can be high, mass effects do not necessarily lead to species accumulation in local plant communities (Leibold and Miller 2004). The more fundamental question, therefore, is what determines whether newly established populations become demographically stable (and are thus less likely to turnover), and do these same processes similarly limit native and exotic species?

Two patterns are apparent when comparing the proportions of species within functional groups at regional vs. local levels that may provide insight into these questions. Both point to soil-depth heterogeneity, and its possible influence on the demographic performance of founder populations, as a key determinant for how dispersal and competition influence the accumulation of species in communities. They also suggest that native and exotic species are similarly limited by these factors. For the native species, there was no evidence of over- or underrepresentation of functional groups, but only in sites with the widest range of soil depth heterogeneity. As heterogeneity diminishes, significant differences emerge between the regional and local pools as native perennial forbs became locally underrepresented in sites lacking deep soils. For the exotic species, by contrast, there was a significant overrepresentation of annual species in all sites, with no detectable impact of soil depth heterogeneity. Both of these results are contrary to our initial expectations.

What could cause these patterns? Recent theoretical and empirical work indicates that the functional identity of an invading species can determine establishment success and, therefore, community assembly (Wilson 1999, Fargione et al. 2003, Tilman 2004). The more functionally similar an invader is to species already present in the community, the less likely it is to successfully establish due to significant overlap in strategies of resource acquisition. This effect is predicted to become increasingly important as communities assemble, so that intra-group competition ultimately caps the numbers of species that accumulate in each functional group. Although our experimental work demonstrates the importance of competition for establishment, it did not show it to be an absolute barrier for establishment for most of the life history strategies represented in the seed addition mixture. Further, a companion experiment in this savanna has shown that fire suppression, rather than intra-group competition, is more limiting for community membership (MacDougall and Turkington 2005). Recruitment, and therefore coexistence, appears to depend more on species being functionally similar than functionally different due to the suppressive effects of competition in the absence of fire (i.e., environmental filters created by fire suppression are more limiting than biotic ones created by competition). Functional similarity, therefore, is unlikely to solely explain patterns of site-level diversity in this system.

Instead, it appears that species-specific habitat optimality, and its influence on the demographical stability of plant populations, better explains for how site-level diversity is created and maintained. For native species,
evidence comes from the significant connection between environmental heterogeneity and the site-level expression of regional diversity. It is generally understood that population performance will vary widely depending on underlying levels of resource availability, and that all species are predicted to be competitively superior under some “optimal” combination of environmental conditions (or at least be most resistant to its effects) (Pulliam 1988, 2000). Given our experimental evidence showing that new native plant populations rarely form (see also Soons et al. 2005, Herben et al. 2006), it seems likely that those persisting are confined to areas of optimal habitat where their reproduction exceeds mortality. Although buffeted by the competitive impacts of invasive species, such populations would not be easily displaced by competition because of their high fitness. Persistence would be reinforced by seed inputs that, based on the experimental results, appear to mostly fall in close proximity to adults. Although this prediction requires empirical confirmation, it would explain why native species loss appears to have been minimal in this savanna despite decades of invasion and habitat fragmentation, and why the full compliment of regional functional groups is lacking in remnants with limited habitat heterogeneity. It could also underlie similar observations from other systems where the long-term effects of invasion have not resulted in substantial species loss (Davis 2003, Sax and Gaines 2003, Gurevitch and Padilla 2004).

For exotics, we interpret the overrepresentation of annuals as evidence that many are fugitive species, maintained by continuous dispersal but unlikely to persist if competitively superior exotic perennials eventually establish (Leibold and Miller 2004, Ozinga et al. 2005). The non-significance of underlying environmental variation tentatively supports this, as mass effects can create populations in a range of habitats including those where turnover is rapid but offset by continual immigration (Pulliam 2000). As a general principle, species accumulation in local communities will be constrained by the availability of habitat capable of supporting demographically stable populations for each immigrating species (Snyder and Chesson 2003). If founder populations do not become stabilized, persistence will be continually dependent on immigration that should favor overrepresentation by fugitives, as seen in this study. The establishment of superior competitors (i.e., perennial exotics), in contrast, would be constrained by their assumed inability to widely disperse, creating a time lag on their accumulation exacerbated by the limited amount of optimal habitat likely found in the small remnants (Hurtt and Pacala 1995, Snyder and Chesson 2003, Ozinga et al. 2005). As well, even though functional similarity may fail as the sole filter for local accumulation, it may create resistance to new additions thereby further slowing establishment (Hurtt and Pacala 1995, Tilman 2004). As shown experimentally, these competitive barriers are not insurmountable but require high seed inputs to increase rates of success. The perennial exotics most often observed during our site surveys tended to be wind-dispersed Asteraceae genera (Hypochaeris, Lactuca, Crepis, Cirsium, Sonchus), further supporting the hypothesis that the accumulation of exotic presently favors species with dispersal capabilities.

**Conclusion**

Our data lend support to three conclusions. First, they are consistent with findings that the processes that limit diversity vary with scale (e.g., Seabloom et al. 2005, Rajaniemi et al. 2006). At the plot level, immigration can greatly increase richness but is likely unable to fully dictate community composition due to the limiting effects of competition. At the same time, the present distribution of many native species cannot be solely explained by competitive displacement given the evidence that recruitment sites exist within the dense grass swards. At the site level, immigration sets the potential limits of site-level diversity but local antagonistic processes appear more likely to determine the degree to which these limits are expressed (Shurin 2000, Cottenie et al. 2001, Kneitel and Miller 2003, Resetarits 2005). Although an increasing number of studies are demonstrating that plant communities are dispersal-limited (Turnbull et al. 2000), such limitations in this savanna appear more relevant for determining the distribution of species within remnant areas (i.e., plot level) than for species presence or absence (i.e., site level). The variation in process with scale has significance for conservation management in this nationally endangered savanna, and may be generalizable to other systems. Within sites, conservation measures that target the more visible effects of increased competition (e.g., invasion) may fail if the less obvious impacts of reduced dispersal are not also addressed. Among sites, conservation measures that target the capture of extent populations may fail if they do not also consider patterns of underlying habitat heterogeneity and its impact on the demographic stability, given its apparent significance determining persistence despite severe habitat degradation (Cabeza et al. 2004, Wilsey et al. 2005).

Second, the data suggest that the assembly of species in these communities occurs slowly, perhaps on the order of millennia, based on the observed differences in regional-local relationships for natives and exotics. Native species have been accumulating in this region presumably since the early Holocene (8000 yr before present), while exotic species were first introduced in the early 1800s (MacDougall et al. 2004). Although exotic perennial taxa dominate almost all remnants, and are assumed to disperse at higher densities than native perennials, these taxa represent a small percentage of the total regional pool. We suggest that an accumulation lag for perennial exotics is created by the requirement for founder populations to be demographically stable, so that
relatively high immigration rates (compared to native perennials) are insufficient for rapid accumulation.

Third, our results indicate that present-day patterns of relative abundance, a common metric in diversity analyses, may not be fully indicative of the underlying processes determining community composition now and into the future. Abundance is contingent on the phase of community assembly being observed (Mouquet et al. 2003, Cadotte and Fukami 2005, Helm et al. 2006), which appears to be in its earliest stages in this savanna. We predict, however, that this pattern is unlikely to remain stable, and that perennial exotics will slowly increase at the site level in line with regional diversity patterns as demographically stable populations establish (Wiser et al. 1998). This would increase exotic diversity within site remnants, and also reconfigure patterns of relative abundance as the range of presently wide-ranging annuals becomes attenuated. If true, this highlights the need to examine the successional context of invasions (Davis et al. 2005b). Present-day patterns may be transient, and management efforts must target the anticipated future trends determined by the composition and diversity of the regional species pool combined with the habitat heterogeneity underlying local communities.

ACKNOWLEDGMENTS

We thank Scott Wilson, Jon Shurin, Diane Srivastava, Hans Roemer, Brenda Costanzo, Peter Arcege, Gary Bradfield, Scott Collins, Rob DeWreede, Judy Myers, Greg Henry, Ben Gilbert, Justine Karst, Richard Moe, Joe Boucher, Suzanne Caskanette, Rebecca Best, Kate Edwards, Tim Ennis, Irvin Banman, Mark Davis, and one anonymous reviewer. Funding for A. S. MacDougall was provided by the Natural Sciences and Engineering Research Council of Canada (NSERC), World Wildlife Fund, Mountain Landscape Co-op, and Nature Conservancy of Canada; funding for R. Turkington was provided by the NSERC Discovery Grant.

LITERATURE CITED


Andrew S. MacDougall and Roy Turkington1842 Ecology, Vol. 87, No. 7


