



Negative per capita effects of purple loosestrife and reed canary grass on plant diversity of wetland communities

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ABSTRACT

Invasive plants can simplify plant community structure, alter ecosystem processes and undermine the ecosystem services that we derive from biotic diversity. Two invasive plants, purple loosestrife (*Lythrum salicaria*) and reed canary grass (*Phalaris arundinacea*), are becoming the dominant species in many wetlands across temperate North America. We used a horizontal, observational study to estimate per capita effects (PCEs) of purple loosestrife and reed canary grass on plant diversity in 24 wetland communities in the Pacific Northwest, USA. Four measures of diversity were used: the number of species (S), evenness of relative abundance (J), the Shannon–Wiener index (H') and Simpson's index (D). We show that (1) the PCEs on biotic diversity were similar for both invasive species among the four measures of diversity we examined; (2) the relationship between plant diversity and invasive plant abundance ranges from linear (constant slope) to negative exponential (variable slope), the latter signifying that the PCEs are density-dependent; (3) the PCEs were density-dependent for measures of diversity sensitive to the number of species (S, H', D) but not for the measure that relied solely upon relative abundance (J); and (4) invader abundance was not correlated with other potential influences on biodiversity (hydrology, soils, topography). These results indicate that both species are capable of reducing plant community diversity, and management strategies need to consider the simultaneous control of multiple species if the goal is to maintain diverse plant communities.

Keywords

Biological invasions, community structure, invasive plants, *Lythrum salicaria*, *Phalaris arundinacea*, weeds.

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INTRODUCTION

The increasing number, distribution and abundance of invasive plant species are reducing biological diversity worldwide (Vitousek *et al.*, 1997; Wilcove *et al.*, 1998; Mack *et al.*, 2000). Declines in plant diversity can alter ecosystem functions and services (Schulze & Mooney, 1994; Kinzig *et al.*, 2001). To respond effectively to invasive species problems, we require quantitative measures of the impact of invaders on diversity. The impact (I) of an invader depends on the invaders abundance (A), distribution (D) and per capita effect (E) according to the equation: $I = A \times D \times E$ (Parker *et al.*, 1999). Estimates of the abundance and distribution of invaders are widely reported, but estimates of per capita effects are rare (Parker *et al.*, 1999). Quantitative measures of the sign and strength of per capita effects are necessary to (1) understand how invasive organisms affect natural environments, (2) prioritize weed management actions, and (3) determine what levels of control are needed to achieve an acceptable level of impact. Here we

report results of a horizontal, observational study assessing how severely two invasive plants, purple loosestrife (*Lythrum salicaria* L. Lythraceae) and reed canary grass (*Phalaris arundinacea* L. Poaceae), reduce wetland plant diversity as invader abundance increases.

The expected response of biotic diversity to an introduced species depends on the relative abundance the invader attains in the community. The organism may be a 'weak invader' and may colonize and persist at low abundance with minimal influence on other species, thus incrementally increasing species richness (Ortega & Pearson, 2005). However, as a 'strong invader' increases in density, abundances of most other species are expected to decrease, increasing the probability of local extinctions, eventually reducing both species richness and evenness of abundance among species (Parker *et al.*, 1999; Myers & Bazely, 2003; Ortega & Pearson, 2005).

Community diversity and invader abundance can be linked in a complex positive feedback relationship whereby increases in

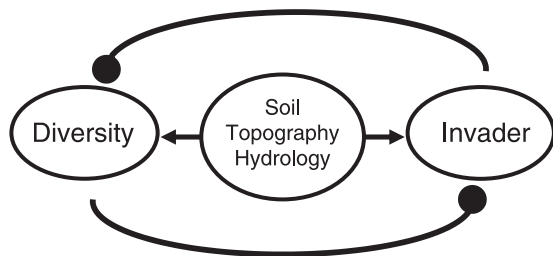


Figure 1 Signed diagram illustrating the relationship between invader abundance, biotic diversity and environmental variables that potentially influence diversity and invader abundance. Community diversity and invader abundance are linked in a complex positive feedback relationship whereby increases in invader abundance lead to decreases in diversity that in turn lead to increasing invader abundance.

invader abundance lead to decreases in diversity that in turn lead to increasing invader abundance (Fig. 1). In extreme cases, this positive feedback loop can lead to community collapse or ‘invasion meltdown’ (Simberloff & Von Holle, 1999). To investigate the feedback relationship, one needs to interrupt the feedback, controlling one factor and measuring the response of the other. Thus, some studies control diversity and measure the response of the invader, showing that increasing diversity sometimes decreases the abundance of an invader, i.e. increases the community’s resistance to invasion (Kinzig *et al.*, 2001). Other studies control the invader abundance and measure the response of diversity, showing that increasing invader abundance sometimes decreases diversity (Parker *et al.*, 1999; Goodell *et al.*, 2000). Taken together, these studies indicate how low diversity can be both a cause and/or a consequence of invasions: as increasing invader abundance decreases diversity, the decrease in diversity facilitates still further increase in invader abundance. For our study species, prior experiments conducted in an artificial garden and greenhouse environments show that increasing abundance of these invaders can decrease diversity (Weiher *et al.*, 1996; Green & Galatowitsch, 2002; Kercher & Zedler, 2004). Here we extend those studies by showing how increasing invader abundance can decrease diversity under natural field conditions. To isolate the effect of invader abundance on diversity, we show that three additional factors (hydrology, soils, topography) known to influence diversity did not covary with invader abundance.

Study organisms

Purple loosestrife and reed canary grass are two invasive emergent wetland plants that currently dominate vegetation in many wetlands across temperate North America (Galatowitsch *et al.*, 1999; Magee *et al.*, 1999; Blossey *et al.*, 2001). Both species are known to form dense monospecific stands that may negatively affect local wetland plant and animal communities (Galatowitsch *et al.*, 1999; Merigliano & Lesica, 1998; Blossey *et al.*, 2001).

Purple loosestrife is a tall perennial wetland plant native to Europe. Two thorough reviews of the biology, ecology and history of invasion in North America of purple loosestrife are found

in Thompson *et al.* (1987) and Mal *et al.* (1992). Purple loosestrife is an invasive species that is thought to displace native wetland vegetation in wetlands and riparian areas. Early reports of adverse effects published prior to 1998 have been criticized (Anderson, 1995; Hager & McCoy, 1998). Subsequent reports have not resolved whether loosestrife negatively affects wetland diversity. Two articles summarize what had been known to date as suspected and documented negative effects (Blossey, 1999; Blossey *et al.*, 2001). Direct evidence that purple loosestrife can dominate wetland plant assemblages and reduce species richness is provided by extended germination trials (Weiher *et al.*, 1996), tests of competitive response (Johansson & Keddy, 1991; Keddy *et al.*, 1998), removal studies using herbicides (Gabor *et al.*, 1996) and increases in plant diversity following biological control (Landis *et al.*, 2003). However, not all recent studies agree that purple loosestrife reduces the diversity of local wetland plant communities (Treberg & Husband, 1999; Farnsworth & Elis, 2001; Morrison, 2002; Hager & Vinebrook, 2004; Houlahan & Findlay, 2004). More research is needed to clarify the negative effects of purple loosestrife, specifically a representative sample to discover what levels of invader abundance decrease diversity and a random sample to discover how often invader abundance reaches these levels.

Reed canary grass is a perennial wetland plant. Its origin is currently in dispute, and some believe it has mixed origins stemming from hybridization of North American and European populations (Galatowitsch *et al.*, 1999; Lavergne & Molofsky, 2004). Its competitive ability and rapid growth make reed canary grass both a useful forage plant and an aggressive invader (see review in Lavergne & Molofsky, 2004). Studies in mesocosms have shown that it is capable of out-competing other wetland species, particularly when nutrient concentrations are elevated (Green & Galatowitsch, 2002; Kercher & Zedler, 2004; Mahaney *et al.*, 2004) and under conditions of increased sedimentation (Mahaney *et al.*, 2004). Reed canary grass is associated with reduction of native plant species in a survey of 58 wetlands in south-western Ontario (Houlahan & Findlay, 2004). In addition, presence of reed canary grass (often approaching 75–100% cover) impedes revegetation efforts in prairie pothole wetlands in the midwestern USA (Mullhouse & Galatowitsch, 2003). In a study of 96 randomly chosen wetlands in north-west Oregon, reed canary grass was present in 93% of the sites (Magee *et al.*, 1999). In a subset of 43 wetlands, canary grass was found in 813 of 1026 plots (79%) and when present had a mean cover of 67% (Magee & Kentula, 2005). Unlike purple loosestrife, all studies of reed canary grass concur that it is capable of reducing plant diversity.

Study sites

This study was based on a representative sample of 24 wetland field sites chosen to span a range in the abundance of each invader (Fig. 2, see Appendix S1 for site information). Sixteen sites were established in the Willamette Valley, Oregon, four study sites were established on islands within the Columbia River Estuary, and an additional four sites were located east of the Cascade Mountain Range along the Columbia and Snake Rivers. Twenty

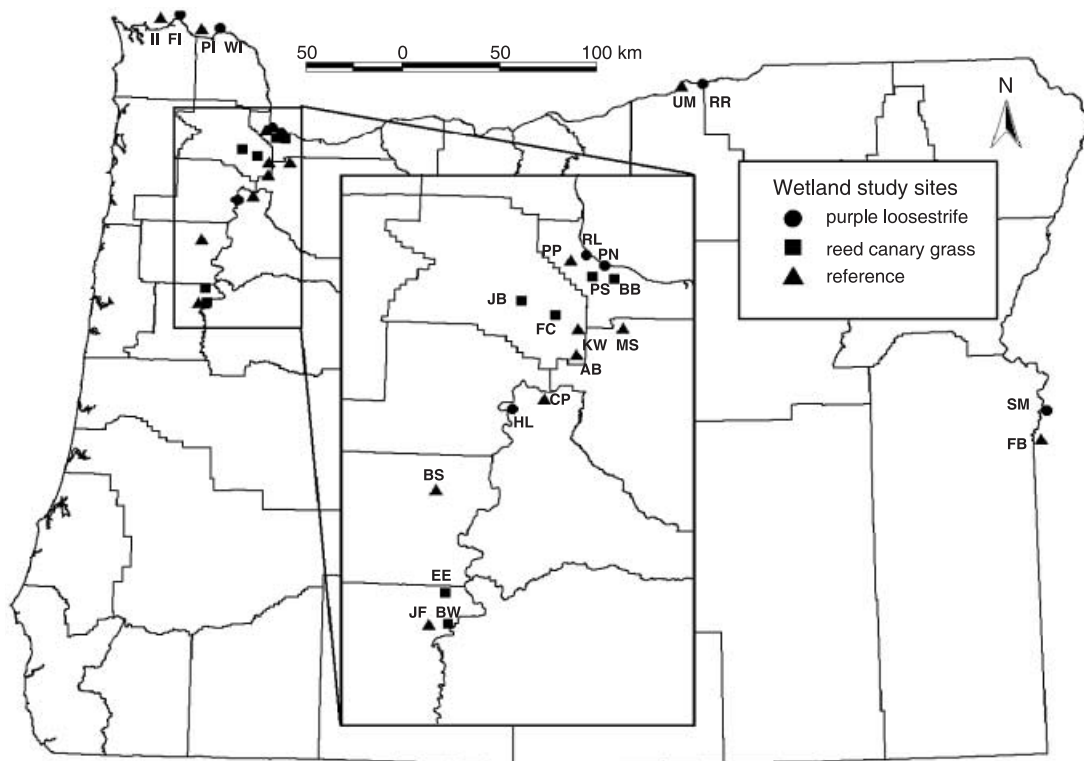


Figure 2 Map of wetland study site locations in the Pacific Northwest. Acronyms are used for site identification (see Appendix S1). All sites are in the state of Oregon except Simplot Marsh (SM) and Fort Boise (FB), which are in Idaho, and Puget Island (PI), which is in Washington. Thin lines denote county boundaries.

sites are seasonally flooded emergent palustrine wetlands and the four estuary sites are tidally influenced freshwater wetlands inundated on a monthly cycle. The plant community at all sites was dominated by herbaceous vegetation and at none of the sites was the vegetation being actively managed. Sites were selected based on: (1) wetland type, (2) abundance of purple loosestrife or reed canary grass, (3) area and shape of invasive-species stand, (4) accessibility, (5) permission to sample, and (6) probability that the site would not be modified during the study. We could not choose sites based on a stratified random selection method because the necessary data did not exist. Instead, we employed a quasi-experimental approach using site matching along with assessing the covariance between invader abundance and potentially influential environmental variables.

Relationship between environment and plant diversity

Environmental variables that are correlated with invasive plant abundance may influence plant diversity. To control for these potential environmental effects, the wetlands were characterized by (1) hydrologic regime, (2) wetland microtopography, and (3) soil characteristics. The environmental data were used to assess whether covarying environmental factors may be responsible for the observed patterns of diversity. A result of no relationship between the abundance of the invasive species and the environmental factors strengthens the evidence that the invasive species are the cause of the diversity patterns observed.

Hydrologic regime (duration of inundation) is the primary factor influencing the diversity of wetland plant communities (Van der Valk *et al.*, 1994; Magee *et al.*, 1999; Silvertown *et al.*, 1999; Azous & Cooke, 2000; Keddy, 2000; Mitsch & Gosselink, 2000) with the greatest number of plant species coexisting in seasonally flooded freshwater habitats (Keddy, 2000) like the wet meadows that are the focus of this study. Topographical variation and cyclic water level fluctuation create a landscape of waxing and waning soil oxygen concentrations. Plant roots need oxygen to respire, and standing water slows the rate at which plant roots obtain oxygen from the environment. In addition, water depth influences seed germination rates and photosynthetic ability (Keddy, 2000). Theoretically, habitats with greater topographical heterogeneity should provide a greater diversity of niches and thereby allow a greater number of species to coexist (Whittaker, 1965; Grime, 1973; Grubb, 1977). Therefore, reduced variation in microtopography should lead to a fewer number of plant species per unit area regardless of invasive species dominance.

Another factor that may influence plant diversity is soil fertility, where more fertile conditions tend to be associated with fewer species and greater biomass of the dominant species (Auclair *et al.*, 1976; Weiher *et al.*, 1996; Bedford *et al.*, 1999; Keddy, 2000). Nitrogen is considered the primary limiting nutrient for plant growth in emergent marsh ecosystems, followed by phosphorus (Bedford *et al.*, 1999; Keddy, 2000; Mitsch & Gosselink, 2000; Bridgman *et al.*, 2001). There is evidence that phosphorus may be limiting in some urban wetlands (Woo & Zedler, 2002).

Carbon, potassium and micronutrients (primarily Mn, Mg and Ca) may also be limiting nutrients for plant growth, but we found no prior literature that presents evidence that these nutrients are limiting in emergent wetland ecosystems.

Hypotheses

Based on prior evidence and field observations, we predicted that (1) both purple loosestrife and reed canary grass are capable of forming dense stands that can negatively affect community diversity; (2) as invader abundance increases, plant community diversity will decrease; and (3) the negative effect of canary grass is greater than that of purple loosestrife. Our analysis is based on (1) an observational survey of wetlands in the Pacific Northwest stratified to yield a range in invader abundance, (2) multiple measures of diversity, and (3) assessment of potentially confounding variables (hydrology, soils, topography) that might combine with invader abundance to influence diversity.

METHODS

Plant community sampling

Percentage plant cover was measured for each vascular plant species at each of the 24 sites during July 2001. Each sample universe was circular, with a 50-m radius (7854 m²). Thirty 1 m² plots were randomly selected from within 50 m of a centre point. This was done by randomly selecting a direction (1–360° with north at 360°) and a random distance between 0 and 2500 m, of which the square root of the result was the radial distance to the plot. This permitted sampling in proportion to area, which increases as the square of the radius with increasing radial distance from the centre of the circle. The percentage cover of each plant species was visually estimated in each plot to the nearest 1%. Due to overlapping canopy cover, the total cover for each plot sometimes exceeded 100%.

We sampled plant abundance non-destructively using the visual cover estimation method because many of the sites were mitigation wetlands, parks or other sensitive areas where we could not destructively sample biomass. To avoid the additional source of error introduced by multiple observers (Sykes *et al.*, 1983), the lead author sampled all sites. The observer was trained prior to making measurements by calibrating cover estimates using a series of figures where the percentage cover had been calculated. The observer tested against the figures again after measuring the sites to determine change in bias with experience.

Species identifications and nomenclature follow Hitchcock and Cronquist (1973). A voucher collection of the plant species sampled was assembled. Richard Halse (Department of Botany and Plant Pathology, Oregon State University) verified the voucher plant identifications and these specimens were deposited in the Oregon State University Herbarium.

Community structure

Sampling adequacy was analysed by constructing species–area curves for each site using multivariate analysis software (PC-ORD,

McCune & Mefford, 1999). The species–area curves were calculated using a nonparametric resampling procedure (jackknife). This procedure determines the number of unique species in 500 randomly selected ‘resampled’ combinations of subsamples (1 m² plots) for each increase in level of sampling area (1–30 plots) (McCune & Mefford, 1999; McCune & Grace, 2002). Then, the mean and standard deviation are calculated for each level of effort (stepwise increase of total area sampled). If the mean number of species reaches a plateau, it suggests fewer species are being added through each subsequent increase in sample area and therefore the majority of the species within the site have been sampled (McCune & Grace, 2002).

We qualitatively examined community structure between sites using rank-abundance diagrams. Rank-abundance diagrams plot mean species abundance against species rank (Whittaker, 1965; Magurran, 1988) thereby visually integrating the two diversity components, species richness and evenness (Fisher *et al.*, 1943; Peet, 1974; Magurran, 1988). The width of the curve represents the species richness of the site, and the slope indicates the degree of unevenness or dominance.

We quantitatively examined diversity using four standard nonparametric community diversity descriptors. These were species richness (S), Pielou’s evenness (J), Shannon–Wiener diversity index (H′) and Simpson’s index of diversity (D) (equations from Magurran, 1988). The indices S, H′ and D were transformed to Hill’s Series (N_a), where N₀ = S, N₁ = exp(H′) and N₂ = (1/D) (Hill, 1973). We first tested whether the abundance of the two invader species differently affected diversity. The summed residual error in linear regression models fit separately for each species was compared with the residual error in a full model that pooled the observations for both species (Snedecor & Cochran, 1967). The result of no significant difference in summed error between the separately fit models and the error in the pooled model indicates no difference between the effect of the abundance of the two invasive species and the diversity measure being examined. We then applied linear regression analysis to determine whether to reject the null hypothesis of no significant relationship between plant abundance and the measures of diversity. Data were transformed where necessary to improve normality and equality of variance before applying regression analyses.

We assessed the effect of dominant plant cover on native vascular plant species richness and abundance. Native species status was determined from Hitchcock and Cronquist (1973). Proportion of the number of native species per site and combined cover of all native plants per site were plotted against the mean abundance of the dominant plant to examine whether native plants were more negatively affected than introduced plants. As with the measures of diversity, regression analysis was used to determine whether the observed trends were significant.

We looked for negative patterns of association consistent with the hypothesis that the two species are competitors. The interaction was quantified as the correlation between the abundances of the two invasive species. Significance of the trend was tested by computing a correlation coefficient and by determining its significance using a *t*-test (Moore & McCabe, 2001).

Environmental variables

In March and April of 2001, a shallow well was sunk at each of the sites to measure water level throughout the year. Wells consisted of a 1.3-m PVC tube (5 cm inside diameter) with opposing perforations (1 cm diameter) at 10 cm intervals down each side. The bottom was capped and had two perforations. The tube was then wrapped with fibreglass window-screening (2 mm mesh) on the exterior to prevent sediment accumulation. The wells were installed to extend 1 m below the ground surface by digging a hole with a soil auger, inserting the well, and filling in with sand. Water levels were taken at monthly intervals over a span of 21 months.

The microtopographical basin survey method used a surveyor grade differentially correcting GPS receiver (Trimble Navigation Limited, Sunnyvale, CA, USA) in conjunction with a rotating laser level (Latec Instruments Inc., Ontario, Canada) to obtain a digital elevation model (DEM, grid-based contour map) of each site. A laser level was set at each site and the distance to ground from the laser plane was measured at the well (usually within 2 m from centre). A laser sensing device and stadia rod (Crain Enterprises, Mound City, IL, USA) were used to map deviation from the laser level plane to the ground surface for multiple locations (50–100) at each site.

The data were then downloaded and differentially corrected using *PATHFINDER* software (version 4.1, Trimble). The GPS receiver, through real-time and post-processing differential correction, was able to locate the horizontal position of a given survey point within a calculated precision of < 1.0 m. Louhaichi *et al.* (2003) studied this technique and reported a vertical accuracy of 1–3 cm for agricultural fields. Using *ARCVIEW* (version 3.2, ESRI, Redlands, CA, USA), the elevation of each point was relativized to the elevation of the well. These point data were then used to interpolate an elevation grid with 1 × 1 m cells (7854 cells) for each site (Schooler, 2003).

The hydrological regimes were compared among sites using mean water depth (cm), maximum water depth (cm), range of water depth (cm), cumulative water volume (m³/year), cumulative area inundated (m²/year), maximum area inundated (m²), and the number of months to 50 and 90% drawdown. Elevation and topographical variation were included as separate variables as they may influence plant diversity independent from their role in defining intrasite flooding regimes. Elevation above sea level for each site was acquired from digital elevation models (USGS-DEM).

To assess soil characteristics, we collected soil samples from four randomly selected locations within wetland sites during June of 2002. Samples were taken by first removing the top 5 cm of soil from the centre of the plot using a spade. Then the next 5 cm (*c.* 2 L) was placed into a paper bag. Prior studies have found no significant difference in soil properties (organic C, N, pH, Ca and Mg) within small (0.25–0.35 ha) palustrine wetland sites among samples taken at the same depth (Stolt *et al.*, 2001). Therefore, we restricted soil sampling to the root zone at a single depth (5–10 cm below surface) within and across sites (Binkley & Vitousek, 1989).

The soil characteristics measured were: total nitrogen, nitrate, ammonium, mineralizable ammonium, total phosphorus, phosphate,

organic carbon, potassium, magnesium, calcium, manganese, conductivity, acidity and percentage of sand/silt/clay. Since variation of nutrients within a site may contribute to diversity, we also included the standard deviation of the soil variables in the analysis. Soil nutrient analyses were conducted by the Oregon State University Department of Crop and Soil Science Soils Laboratory, and physical soil properties were measured under the direction of Crop and Soil Science staff using their methods (Horneck *et al.*, 1989).

Data analysis

Random number generation and data entry were performed in Excel (Office XP, Microsoft 2002). Spatial data were collected using a Trimble Surveyor (XR Pro) global positioning system receiver (GPS) with real-time and post-processing differential correction capable of submetre spatial accuracy. Spatial data were differentially corrected using *PATHFINDER* Office software (version 2.70, Trimble 2000). *ARCVIEW* (version 3.2, ESRI 1999) was used to calculate basin topography. Linear regression and multiple regression analyses were performed using *S-PLUS* (version 6.1, Insightful 2002, Seattle, WA, USA). The community analysis software *PCORD* (version 4.17, MjM 2002, Gleneden Beach, OR, USA) was used to compute species–area curves and implement canonical correspondence analysis (CCA) ordination procedures.

CCA was used to determine whether the conditions of the reference uninvaded wetlands adequately represented those of the invaded wetlands. CCA is a direct gradient analysis method that seeks to structure one data matrix so as to maximize the strength of the relationships with a second matrix (McCune & Grace, 2002; Anderson & Willis, 2003). We used the method to constrain an ordination of the site characteristics by the abundance of purple loosestrife and reed canary grass. A Monte Carlo test was then used to evaluate whether the environmental variables were significantly related to the abundance of the invasive plant species. A finding of no significant difference among the correlations of the real data set and the randomized data sets suggests that the relationship between the matrices is not stronger than that expected by random chance and supports the hypothesis of no linear relationship between the two matrices (Ramsey & Schafer, 1997; McCune & Grace, 2002). The main data matrix consisted of the wetland habitat parameters and the second matrix contained the mean proportional cover of loosestrife and reed canary grass for the wetland sites. Since CCA incorporates linear regression, assumptions of normality and constant variance were examined for the abundances of invasive species in the second matrix. Normality was improved using an arcsine square-root transformation on the proportional cover data (McCune & Mefford, 1999).

RESULTS

The overall plant community composition of the 24 wetland sites consisted of 196 vascular plant species distributed within 36 families (see Appendix S2 for plant species information). The six

families with the most species recorded were the: Poaceae (23), Fabaceae (17), Asteraceae (17), Cyperaceae (17), Rosaceae (11) and Juncaceae (9). Native species comprised 60% of the regional wetland flora (118 species) while 34% (67) were exotic plant species. The origins (native or introduced) of 11 species (6%) were unknown.

Ten plant species were dominant (most abundant in the community) across the 24 wetland sites. Purple loosestrife was dominant at seven sites (13.8–91.7% cover), reed canary grass dominated six sites (18.8–94.7%) and the remaining 11 sites were dominated by eight other plant species (12.5–47.8%). These species were: *Alopecurus pratensis*, *Juncus effusus*, *Typha latifolia*, *Oenanthe sarmentosa*, *Eleocharis palustris*, *Scirpus microcarpus*, *Veronica americana* and *Carex obnupta* (see Appendix S3 for complete data set of plant abundance by site information).

Local variation in community structure

The species–area curves reached a plateau for the plant communities at the wetland sites, creating a reliable basis for comparing species richness among sites (Fig. 3). Rank-abundance diagrams of the plant community at the 24 wetland sites indicate that as the abundance of purple loosestrife and reed canary grass increase and approach 100% cover, species richness and evenness invariably decrease (Fig. 4). Sites not dominated by the invasive species tend to have a greater number of species and have more equitable distributions of abundances between species.

Comparison of regression models indicated that there was no difference between the effect of purple loosestrife and reed canary grass abundance on any of the four diversity measures (Table 1). Data were transformed (S, and D, natural log; H', square root) before analysis, which stabilized variances. Evenness (J) did not require transformation. Finding no difference between invader species in the effect of invader abundance on diversity, we pooled data for the two invader species in subsequent analyses.

All measures of diversity decreased with increasing abundance of the dominant plant species. Regression analysis indicated that trends were significant (Table 2). Analyses were conducted on transformed data when necessary to meet assumptions of

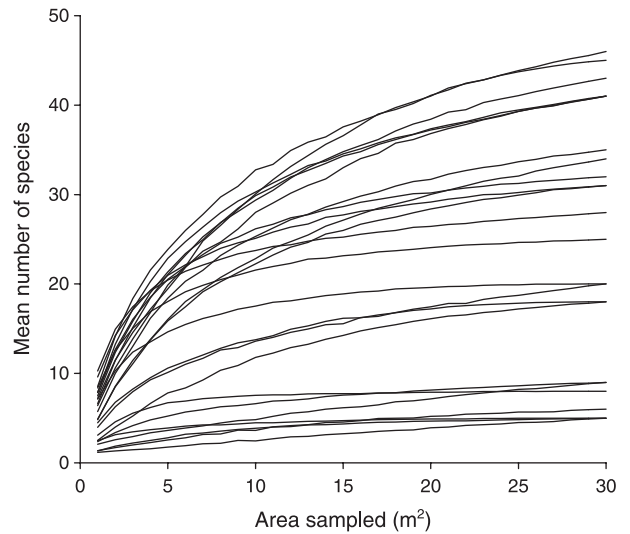


Figure 3 Assessment of sampling adequacy for plant diversity measurement. Species accumulation curves for the plant community approach a plateau with increasing sampling effort indicating progressively fewer species are gained with each incremental increase in sampling effort. This indicates that the sample effort was adequate to identify most of the species in the site, creating a reliable basis for comparing diversity among sites.

constant variance and linearity (S, and D, natural log; H', square root). The data for S, H' and D are plotted as Hill's Series values without transformation for ease of interpretation and to facilitate comparison between diversity measures (Fig. 5a–c).

Species richness (N₀) ranged from 4 to 46 species (Fig. 5a). Fanno Creek (FC), an urban site (within city boundary) dominated by reed canary grass (95% canopy cover), included only three other plant species all of which were introduced including blackberry (*Rubus discolor*), bedstraw (*Galium aparine*) and nightshade (*Solanum dulcamara*). An urban site, Pickle Pond (PP), and a rural site, Champoeg State Park (CP), tied for a total of 46 plant species despite CP being dominated by the introduced grass, short-awned foxtail (*A. pratensis* (48%)) and PP

Table 1 Tests of difference between effect of abundance (x) on diversity for purple loosestrife and reed canary grass. Absence of significant difference indicates that the response is similar for both species

Y variable	Model	R ²	d.f.	SSE	MSE	F	d.f.	P
S canary grass (ln)	-0.021x + 3.63	0.82	10	1.4624	0.1462	0.132	1,20	0.72
S loosestrife (ln)	-0.022x + 3.70	0.86	10	0.9039	0.0904			
Pooled	-0.022x + 3.67	0.84	22	2.3820	0.1083			
H' canary grass (sqrt)	-0.013x + 1.72	0.91	10	0.2622	0.0262	2.000	1,20	0.17
H' loosestrife (sqrt)	-0.013x + 1.78	0.88	10	0.2643	0.0264			
Pooled	-0.013x + 1.76	0.89	22	0.5792	0.0263			
D canary grass (ln)	-0.027x + 2.39	0.87	10	1.6456	0.1646	0.878	1,20	0.36
D loosestrife (ln)	-0.026x + 2.51	0.8	10	1.8783	0.1878			
Pooled	-0.026x + 2.46	0.84	22	3.6787	0.1672			
J canary grass	-0.007x + 0.80	0.94	10	0.0528	0.0053	3.700	1,20	0.07
J loosestrife	-0.006x + 0.85	0.77	10	0.1401	0.0140			
Pooled	-0.007x + 0.84	0.85	22	0.2286	0.0104			

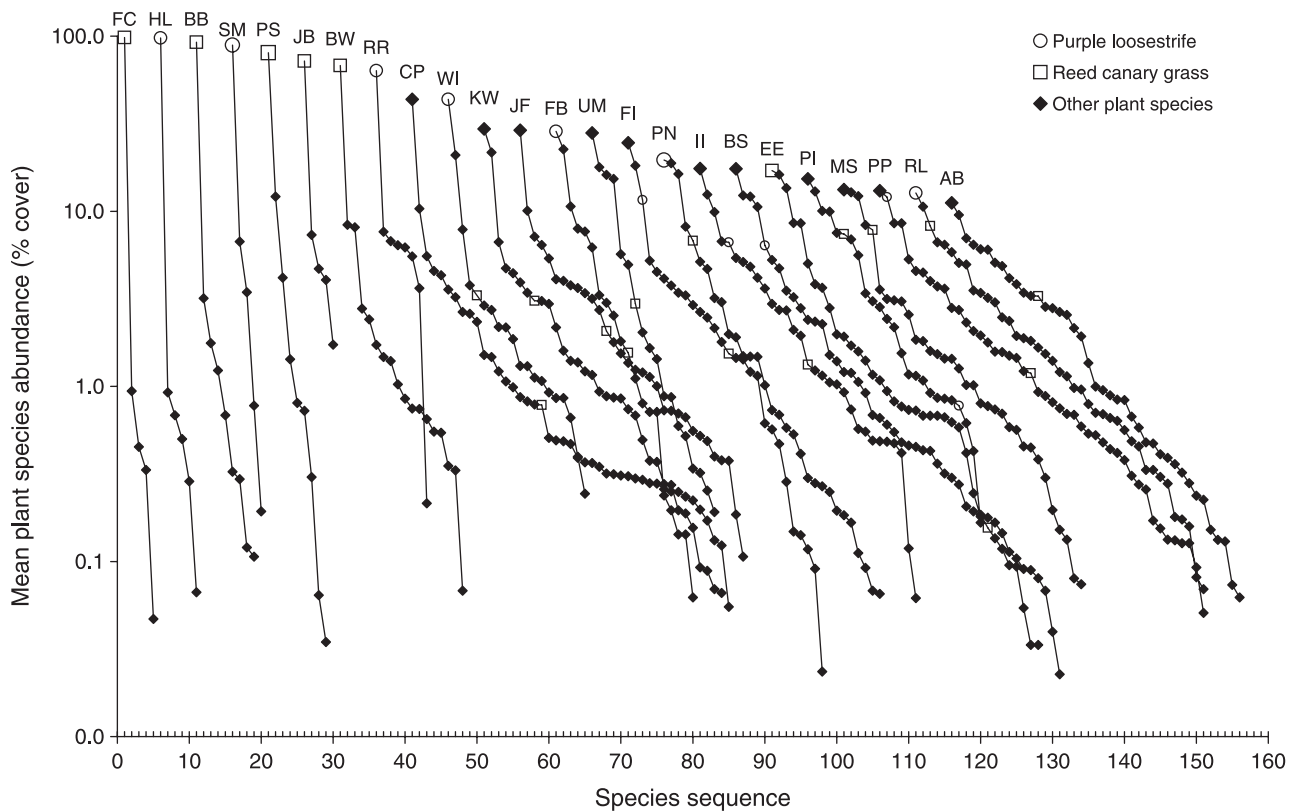


Figure 4 Rank-abundance curves for 24 wetlands in the Pacific Northwest. Mean percentage cover values of plant species are plotted for the sequences from the most to the least abundant species for each site. Means are computed from 301 m² plots per site. Curves are labelled according to site and are arranged in the order of decreasing abundance of the dominant plant species. Information regarding site acronyms can be found in Appendix S1. Circles are purple loosestrife, squares are reed canary grass, and diamonds are other species. The curves, separated by 5-unit intervals, start at various points on the species sequence in order to fit them into the same figure. Thus, the curve for Apache Bluff (AB) begins at point 120 and ends at point 156 on the species sequence. Rank-abundance curves allow the observer to visually integrate the species richness (spread of the curve) and evenness (slope of the curve) of the plant community. The curves show that as the abundance of the dominant species within a community decreases from left to right in the figure, species richness and evenness increase.

Table 2 Regression tests for effect of plant abundance (x) on plant diversity. There is a significant negative association between dominant plant abundance and all measures of plant diversity

Y variable	Model	R^2	MSE	t	d.f.	P
S (ln)	$-0.026x + 4.01$	0.82	0.129	9.89	23	1.47×10^{-9}
H' (sqrt)	$-0.016x + 1.98$	0.91	0.020	15.28	23	3.39×10^{-13}
D (ln)	$-0.033x + 2.97$	0.93	0.069	17.46	23	2.21×10^{-14}
J	$-0.009x + 0.96$	0.90	0.007	14.13	23	1.62×10^{-12}

being a restored urban wetland (Rivergate Industrial District) with small amounts of both reed canary grass (2%) and purple loosestrife (14%). The number of species within each site decreased exponentially as the cover of the dominant species increased (Fig. 4a).

Hill's N_1 (exp(Shannon–Wiener index)) ranged from 1.1 (FC) to 24.0 (PP and AB) and was associated with cover of the dominant species in a negative exponential relationship (Fig. 5b). Hill's N_2 (reciprocal of Simpson's index) ranged from 1.0 (FC) to

18.8 (AB) and also decreased exponentially with increasing cover of the dominant species (Fig. 5c).

Pielou's Evenness ranged from 0.04 at Fanno Creek (FC) to 0.86 at Apache Bluff Wetland (AB). Apache Bluff is an urban wetland (Tualatin) dominated by short-awned foxtail (13%). As with species richness, evenness declined with the increasing abundance of the dominant species (Fig. 5d). However, the relationship was linear, indicating that the evenness of abundance between plant species is less sensitive to changes in the cover of dominant species when at low abundance than are the measures of diversity influenced by species richness.

We also examined whether native plant species richness and abundance were associated with increasing cover of the dominant species. Linear regression indicated that the *percentage of native plant species* (PNS) at each site did not decrease with increasing abundance (x) of the dominant plant species ($PNS = -0.27x + 65.6$, $R^2 = 0.16$, $MSE = 296.8$, $t_{23} = 2.04$, $P = 0.053$) (Fig. 6a). However, this low P value is heavily influenced by one reed canary grass-dominated site (FC) that contained only four introduced plant species. Removing this outlier increases the P value to 0.34 ($t_{22} = 0.98$). However, *abundance of native species*

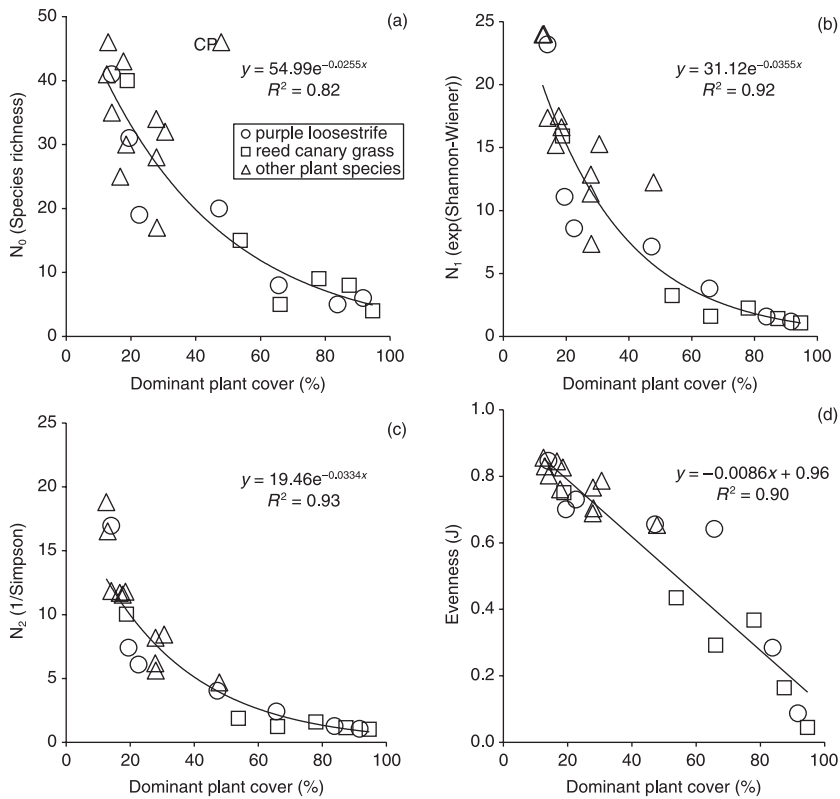


Figure 5 (a–d) All measures of diversity decrease with increasing abundance of the invasive plant species. Use of Hill’s Series facilitates direct comparison and suggests that rare species (N_0), species of intermediate abundance (N_1), and abundant species (N_2) are similarly affected by increasing abundance of a single dominant species. Linear regression after transformation to stabilize the variance and normalize the residuals (natural log of N_0 , N_1 , N_2) indicated all decreasing trends are significant ($P < 0.001$, d.f. = 23).

(ANS) declined exponentially with increasing cover of the dominant species ($\ln \text{ANS} = -0.04x + 4.85$, $R^2 = 0.74$, $\text{MSE} = 0.41$, $t_{23} = 7.97$, $P = 6.3 \times 10^{-8}$) (Fig. 6b). Abundance was transformed by the natural log before regression analysis to stabilize residuals, improve normality and make the relationship approximately linear. Untransformed data are presented for ease of interpretation.

Correlation analysis was used to determine the relationship between reed canary grass and purple loosestrife. The two species were negatively correlated ($r = -0.65$). The test for zero population correlation indicated that the negative relationship between purple loosestrife and reed canary grass was significant ($t_{22} = 4.0$, $P = 0.0006$).

We also used correlation to assess the accuracy of the percentage cover observations. The observer determined the percentage

cover of space occupied in a series of images both before and after determining plant cover in field plots. The test for zero population correlation indicated that the positive relationships were significant for both the before ($r = 0.98$, $t_{12} = 18.85$, $P < 0.0001$) and after ($r = 0.99$, $t_{12} = 31.15$, $P < 0.0001$) data.

Abiotic factors potentially influencing plant community diversity

There was a negative correlation between the abundances of the two invasive species comprising the second matrix ($r = -0.39$). Axis 1 was primarily associated with the abundance of purple loosestrife ($r = -0.99$), whereas axis 2 was associated with the abundance of reed canary grass ($r = -0.86$). The Monte Carlo

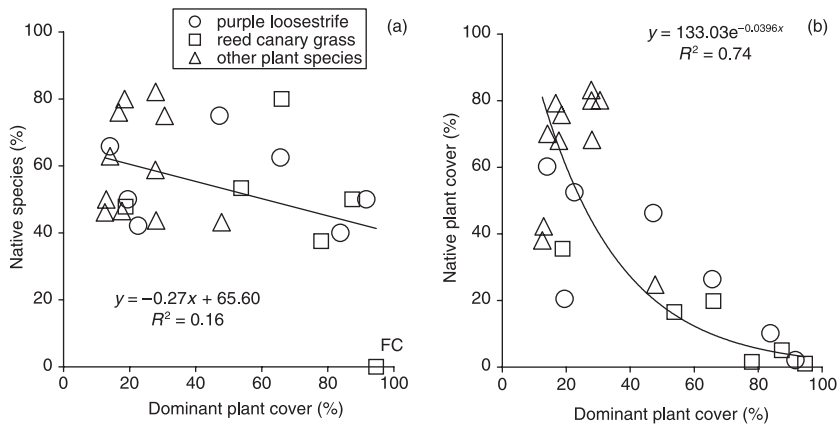


Figure 6 (a–b) Effect of invasive species on the number and relative abundance of native plant species. (a) The number of native and introduced plant species decreases at a similar rate with increasing cover of the dominant plants species ($t_{23} = 2.04$, $P = 0.053$). Note, when the outlier (FC) is excluded, the P value increases to 0.34 ($t_{22} = 0.98$). (b) Native plants comprise 65% of the cover (mean, $\text{SE} = 4.1$) in reference sites, and abundance decreases exponentially with increasing cover of the dominant plant species. Regression on natural log-transformed cover indicates that the trend is significant ($t_{23} = 7.97$, $P = 6.3 \times 10^{-8}$).

randomization procedure was run 100 times and the result was compared with that of the nonrandomized data. The Monte Carlo test statistic indicated that the relationship between loosestrife abundance (axis 1) and the environmental variables was not significantly greater than expected by chance ($P = 0.17$). The relationship between reed canary grass abundance (axis 2) and the environmental variables was also not statistically significant ($P = 0.47$).

DISCUSSION

The primary objective of this study was to measure and compare the per capita effects (PCEs) of two invasive plant species on wetland plant diversity. We have shown that (1) the relationship between plant diversity and invasive plant abundance ranges from linear (constant slope) to negative exponential (variable slope), the latter signifying that the PCEs are density-dependent; (2) the PCEs on biotic diversity were similar for both invasive species among the four measures of diversity we examined; (3) the PCEs were density-dependent for measures of diversity sensitive to the number of species (S, H', D), but not for the measure that relies solely on relative abundance (J); and (4) invader abundance was not correlated with other potential influences on plant diversity (hydrology, soils, topography).

One adverse effect of loosestrife and canary grass invasion is the negative effect on native plant species richness and abundance. During field sampling, we observed that native species richness appeared to be more greatly reduced than the number of introduced species in wetlands with high densities of loosestrife and canary grass. After plotting the proportion of native species against the percentage cover of the invasive species, we discerned no clear pattern that the *number* of native species was reduced more than that of the introduced species. However, the *abundance* of native species is exponentially reduced by the introduced invasive species, thus increasing risk of local extinction in the future. To take an extreme example, Fanno Creek (FC) was entirely devoid of native plant species.

In this study, we detected a strong negative association between invader density and plant diversity. Previous research underscored the uncertainty surrounding the impact of purple loosestrife on biotic diversity and this uncertainty has fostered criticism of biological control efforts. Prior to 1998, multiple papers report purple loosestrife's negative effect on community diversity (Rawinski & Malecki, 1984; Thompson *et al.*, 1987; Mal *et al.*, 1992), but subsequent papers criticize the results as inconsistent and inconclusive (Anderson, 1995; Hager & McCoy, 1998). The best evidence comes from an experimental study where loosestrife dominated wetland plant assemblages consisting of 20 selected plant species under conditions of low water fluctuation or high nutrient concentration (Weiher *et al.*, 1996).

Since Hager and McCoy's review (1998), six additional studies that examined the influence of purple loosestrife on plant community diversity (Treberg & Husband, 1999; Farnsworth & Ellis, 2001; Morrison, 2002; Landis *et al.*, 2003; Hager & Vinebrook, 2004; Houlahan & Findlay, 2004) have been published. Treberg and Husband (1999) studied 41 2 × 2 m plots at one site along

the Bar River, Ontario. They found no significant effect of presence of loosestrife or cover of loosestrife on mean species richness. Farnsworth and Ellis (2001) studied the effect of purple loosestrife abundance at five wetland sites in Connecticut. They examined species richness in 30 1 m² plots arrayed in a grid within each wetland and found no significant relationship between purple loosestrife density and species richness at the 1 m² scale. However, biomass of loosestrife was negatively correlated with biomass of other plant species. Morrison (2002) examined the effect of loosestrife on plant community diversity at two wetland sites in New York. At each site, nine 1 m² plots were established within three blocks. Within each block, one plot was an unmanipulated control, one plot had all vegetation removed and loosestrife was removed twice each year for 3 years, and one plot had all vegetation removed and was subsequently unmanipulated. Morrison detected no difference in species richness between any of the treatments after 3 years. Landis *et al.* (2003) examined the response of plant communities after the reduction in abundance of purple loosestrife by biological agents at five sites in Michigan. They measured species diversity within 1, 3.7 and 7.1 m² plots, first in 1995 before the biological control agents reduced biomass of loosestrife, then again in 2000 and 2001 after the agents reduced biomass by 61–95%. They found that plant species richness significantly increased after the decline of loosestrife biomass at all five sites. Hager and Vinebrook (2004) examined 10 recently invaded wetlands in south-eastern Minnesota. They sampled loosestrife abundance and plant richness in six 0.5 × 2.0 m (1 m²) plots in each wetland. Purple loosestrife was positively associated with species richness when invaded plots were compared to uninvaded plots. A survey by Houlahan and Findlay (2004) sampled 58 wetlands in south-western Ontario (mean size = 66.7 ha). They initially found a significant negative association between reed canary grass and purple loosestrife abundance and the number of native plant species, but the relationship for purple loosestrife disappeared when other predictor variables were included in the model. These six studies provide contradictory evidence that both supports and refutes the hypothesis that purple loosestrife abundance negatively affects plant community diversity.

These inconsistent results may be the result of (1) differences among studies in the spatial scale at which plant diversity was measured, (2) differences in the range of loosestrife abundance examined, and/or (3) environmental differences due to different study locations. We weigh each of the possibilities in turn. First, species richness is positively correlated with sample area (Whittaker, 1972; Magurran, 1988) and therefore the description of diversity varies with the spatial scale of observation. Four studies that found no decrease of plant diversity with increasing loosestrife abundance measured species richness at small spatial scales of 4 m² (Treberg & Husband, 1999) or 1 m² (Farnsworth & Ellis, 2001; Morrison, 2002; Hager & Vinebrook, 2004), whereas a study examining diversity at the 7.1 m² scale (Landis *et al.*, 2003) and this study (7854 m²) found that high densities of purple loosestrife were associated with reductions in wetland plant diversity. Second, the range of loosestrife densities might differ between studies. For example, the survey by Houlahan and Findlay

(2004) found no effect of purple loosestrife abundance on plant species richness in 58 wetlands in south-western Ontario. It is difficult to assess why they did not detect a reduction in diversity because they used a modified Brown–Blanquet abundance-estimation method where their highest abundance level was defined as ‘many individuals and dominant over > 20% total wetland area’. Therefore, at the two wetlands where loosestrife was scored in this category, the cover of purple loosestrife could have been 20–30%, in which case we might not expect to detect an effect, or loosestrife cover may have been 70–95%, where we would have expected to detect a difference (Fig. 5a). The ambiguity of their classification makes comparing results difficult. Third, the inconsistent results may be due to environmental differences, perhaps the result of different site locations. All of the other studies sampled wetlands in eastern regions of North America, whereas this study examined wetlands in western North America. Variation in environmental conditions between geographical regions might influence the negative effect of purple loosestrife on the diversity of plant communities.

Prior research on the negative effect of reed canary grass is less controversial. Mesocosm experiments (Green & Galatowitsch, 2002; Kercher & Zedler, 2004) and field observations (Werner & Zedler, 2002; Houlahan & Findlay, 2004) indicate that reed canary grass is capable of out-competing and displacing other wetland plants. Based on the consistency of these prior studies and personal field observations, we initially expected that reed canary grass would have a greater per capita negative effect on plant diversity than purple loosestrife (McEvoy & Coombs, 2000). We observed that canary grass creates a thick litter layer that impedes growth of other species where loosestrife does not produce a dense layer of litter. Contrary to expectations we did not find a difference in the negative effect on diversity between the two species. This may be due to the tall (2–3 m) dense stands that loosestrife produces where light reaching the substrate is reduced to a similar level as that under a layer of canary grass litter. However, although the per capita effects (E) are similar, the overall impact of canary grass is probably greater than that of purple loosestrife in the Pacific Northwest. Prior studies indicate that reed canary grass is more abundant (A) and more widely distributed (D) than purple loosestrife in wetlands in our area (Magee *et al.*, 1999; Magee & Kentula, 2005), which suggests that it is currently exerting a greater negative impact on biotic diversity than is purple loosestrife.

The distributions of purple loosestrife and reed canary grass overlap across much of temperate North America. They often coexist in wetlands, but we found that their abundances are negatively correlated. This suggests that (1) the two species are competing with each other, or (2) the two species respond in opposite ways to other environmental variables. Removing one will likely result in the increase of the other, and controlling one without controlling the other is unlikely to lead to an increase in diversity. A prior investigation of the effect of biological agents introduced for purple loosestrife control found that, although loosestrife abundance was reduced by 90%, plant diversity did not increase in the presence of high density stands of reed canary grass (Schooler, 1998). In addition, Morrison (2002) found that reed

canary grass increased in study plots where loosestrife was removed, which may be why she did not detect an increase of diversity with decreased loosestrife abundance. The replacement of one weed by another that is even harder to control is an example of a revenge effect: in our rush to solve local and acute pest problems we may be creating diffuse and chronic problems that are even harder to solve (Tenner, 1996; McEvoy & Coombs, 2000).

Our review of prior studies revealed sampling issues may have contributed to the inconsistent results on the environmental consequences of purple loosestrife invasion. We suggest future studies measuring biotic diversity need to address the five following issues. First, examination of diversity should include multiple measures to assess whether description of the results changes with the particular measure used. Second, studies should sample at a number of scales to determine how effect changes across scales. Third, adequacy of sampling effort needs to be examined using species area curves. Fourth, studies should account for the effects of environmental variables known to influence diversity. Finally, since purposefully infesting large areas and monitoring the outcome is not usually an option when studying invasive organisms, large-scale horizontal observational studies must be complemented by necessarily small-scale experimental studies to establish cause and effect relationships. Experiments might establish whether invaders potentially decrease diversity; observational studies might establish when, where and how strongly invaders actually decrease diversity. This information strengthens the conclusion that low diversity is a consequence of higher invader abundance rather than high invader abundance results from low diversity (Elton, 1958; Espinosa-García *et al.*, 2004; Zavaleta & Hulvey, 2004). Another method to determine cause and effect is through vertical field studies that track relationships among invasive species and biotic diversity over time at randomly selected sites while manipulating abundance of the invasive species. However, these studies are difficult to implement because selectively manipulating abundance of the invasive species across large spatial scales is difficult to accomplish. Classical biological control can be an effective means to selectively reduce populations of invasive plants (Landis *et al.*, 2003), but documenting negative effects should occur before the importation of potentially risky biological control agents (Hager & McCoy, 1998). It is difficult to establish causal relationships when examining the effects of invasive plants on biotic diversity. A robust assessment of effect requires evidence from both experimental and observational studies.

One difficulty of an observational study is determining cause and effect relationships. Underlying environmental variables, correlated with the abundance of the invasive species, may be responsible for the observed variation in plant diversity. To strengthen our conclusions, we measured alternative environmental variables likely to cause variation in plant diversity. We conclude that the variables of interest, purple loosestrife and reed canary grass abundance, are not correlated with various measures of topography, hydrology and soil properties. Therefore, patterns of plant species richness and abundance that are correlated with invasive species abundance are likely a result of the

effect of the invasive species and not the underlying environment. In addition, experimental studies document the ability of both invaders to decrease plant diversity (Weiher *et al.*, 1996; Green & Galatowitsch, 2002; Kercher & Zedler, 2004). The combination of this evidence strongly suggests that both purple loosestrife and reed canary grass are reducing the plant community diversity of wetlands in the Pacific Northwest USA.

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SUPPLEMENTARY MATERIAL

The following material is available online at www.blackwell-synergy.com/loi/ddi

Appendix S1 Study site information

Appendix S2 Plant species information

Appendix S3 Mean percentage cover for plant species at 24 wetland sites