



# Soil nutrients and variation in biomass rather than native species richness influence introduced plant richness in a semi-arid grassland

Morodoluwa Akin-Fajjiye\*, Amanda C. Schmidt, Lauchlan H. Fraser

*Department of Natural Resource Sciences, Thompson Rivers University, 805 TRU Way, Kamloops, British Columbia V2C 0C8, Canada*

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## Abstract

Several different hypotheses account for the success of introduced species in new environments. Experimental studies show a negative native-exotic richness relationship (NERR), while observational studies suggest that this relationship is usually positive. Increased resource availability and environmental variation can also enable introduced species to establish in new environments. We conducted an observational study in a semi-arid grassland in the Thompson-Nicola District of British Columbia to examine the biotic and abiotic factors that account for variation in introduced and native species richness.

In each of 12 sites, an  $8 \times 8$  m area was set up, containing 64,  $1\text{-m}^2$  plots. We identified and categorized plant species in each site into introduced and native species. We tested the relationship between introduced species richness and native species richness at the  $1\text{-m}^2$  sampling grain and at sampling grains up to  $64\text{ m}^2$ . We also analysed the relationship between native and introduced species, and within-plot biomass, and between native and introduced species and variation in biomass. For a representative subset of four sites, we tested the relationship between introduced and native species richness and nitrogen, phosphorus and potassium.

We found no NERR at the  $1\text{ m}^2$  sampling grain, nor for the other sampling grains up to  $64\text{ m}^2$ . Introduced species richness increased with phosphorus and nitrogen availability, and was also positively related to biomass heterogeneity.

Our results indicate that introduced species richness in these grasslands is likely influenced by phosphorus and nitrogen, and by variation in vegetation biomass, but not by native species. More non-native plants are likely to occupy nutrient-rich plots compared to nutrient-poor plots in these grasslands. Variation in biomass can leave gaps for the establishment of introduced species. These results should inform management considerations for the control of invasive species to optimize preservation of grasslands.

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**Keywords:** Nitrogen; Phosphorus; Introduced plant richness; Invasive plants; Native species richness; Semi-arid; Grasslands

## Introduction

Introduced or exotic plant invasions continue to be a widespread ecological issue due to their effects on native diversity, soil nutrient cycling, and community structure

\*Corresponding author.

E-mail address: [makinfajjiye@tru.ca](mailto:makinfajjiye@tru.ca) (M. Akin-Fajjiye).

among others (Bradley et al., 2019; David et al., 2017). Across many ecosystems, the factors that enable exotic plants to establish in a new environment can be biotic, i.e., due to the characteristics of the plant community in the new area, or abiotic, i.e., due to climatic, geological, or edaphic factors (Blumenthal, Mitchell, Pyšek, & Jarošík, 2009; Prather, Castillioni, Welti, Kaspari, & Souza, 2020). In preserved semi-arid grasslands with low disturbance, the factors that can affect the distribution of introduced plants have been rarely studied.

The biotic resistance hypothesis predicts that higher native diversity will lead to lower site invasibility, because available resources will be consumed by the native species, leading to more intense competition (Elton, 1958; Souza, Bunn, Simberloff, Lawton, & Sanders, 2011). Biotic resistance is said to work through complementarity, in which resources are used more exhaustively by a greater number of species leaving few open niches for invaders (Byun, de Blois, & Brisson, 2013; Fargione & Tilman, 2005). Another proposed mechanism is due to selection, such that the most dominant competitors are more likely to be present in more diverse species assemblages, and are able to resist the invader (Jones, Ramoneda, Rivett, & Bell, 2017). In both mechanisms, native species acquire a greater proportion of the resource, leaving few resources for incoming species. Studies of the native exotic richness relationship (NERR) at small scales (<10 m<sup>2</sup>), generally support these predictions (Callaway, Montesinos, Williams, & Maron, 2013; Kettenring, Whigham, Hazelton, Gallagher, & Weiner, 2015), while studies over broad scales (>1 km<sup>2</sup>) find a positive relationship between native and exotic species richness (Chen, Qian, Spyreas, & Crossland, 2010). At smaller scales, species are more likely to interact with one another such that incoming exotic species can be limited by existing native species, while at larger scales, environmental conditions may dictate the establishment and success of both native and exotic species (Fridley et al., 2007; Levine, Adler, & Yelenik, 2004). However, in a meta-analysis, Peng, Kinlock, Gurevitch, and Peng (2019) showed that the relationship between native and exotic species richness was positive across all scales in observational studies, while experimental studies showed a negative native-exotic richness relationship.

Another hypothesis used to explain the success of introduced species is the resource availability hypothesis (Blumenthal et al., 2009; Davis, Grime, & Thompson, 2000). Ecosystems with high nutrient availability have been shown to accumulate more invasive species compared to those with low nutrient availability (Funk, 2013). Additionally, low nutrient ecosystems can transition from having a low proportion of invaders to a high proportion when nutrients are introduced, indicating the likely effects of anthropogenic nutrient deposition (Huenneke, Hamburg, Koide, Mooney, & Vitousek, 1990). Abiotic influences on invasions have been observed under low and high resource environments (Funk & Vitousek, 2007; Huenneke et al.,

1990). Increases in nutrients in natural ecosystems can occur due to fossil fuel burning, nitrogen deposition and agricultural fertilization, and these human activities have continued to increase nitrogen creation and deposition worldwide (Li, Hou, Song, Yang, & Li, 2017; Matson, Lohse, & Hall, 2002). Soils in many ecosystems continue to accumulate phosphorus, although it still remains a limiting nutrient in many ecosystems including grasslands (Elser et al., 2007; Tilman & Lehman, 2001). One of the environmental issues that arise from nutrient enrichment is the proliferation of fast-growing invasive species, able to take advantage of increased nutrient availability and outcompete native species (Liu, Yang, & Zhu, 2018; Uddin & Robinson, 2017).

High nitrogen availability commonly leads to reduced species richness, increased invasive plant richness, and changes in plant composition in grasslands (Roscher et al., 2009; Scherer-Lorenzen, Venterink, & Buschmann, 2008). The rate of nitrogen entry into ecosystems is increasing with growing atmospheric deposition of nitrogen (Stevens, Dise, & Gowing, 2009). In Canada, total nitrogen deposition per year over the past 20 years was between 1.15–10.51 kg/ha, although deposition rates are decreasing in most ecozones (Hember, 2018). In other parts of the world, rates of between 5 and 25 kg/ha/yr have led to decreases in native species richness, while invasive species increase (Bobbink et al., 2010; Wragg, 2017). In terrestrial systems, phosphorus has been shown to be as important as nitrogen in causing native species losses and reducing species diversity (Elser et al., 2007). In many ecosystems, a synergistic association occurs between nitrogen and phosphorus, such that both nutrients can jointly affect biomass, richness and invasive species (Harpole et al., 2011). While potassium is relatively understudied compared to nitrogen and phosphorus, there are indications that it can also be limiting (Sardans & Peñuelas, 2015). Studies have linked the success of some invasive plants to potassium availability (Dassonville et al., 2008; Sardans et al., 2017).

The response of introduced plants to soil nutrients may have consequences for ecosystem structure and function. Higher numbers of introduced species can also affect ecosystem productivity, such that sites with a greater number of introduced species tend to have greater productivity (Vilà et al., 2011; Wilsey & Polley, 2006). One reason for this is that successful introduced species are able to acquire and use resources more efficiently than native species, leading to an increased productivity in areas with high introduced species richness (Leishman & Thomson, 2005; Levine et al., 2003). Maron et al. (2014) in a cross-continental grassland experiment found that plots seeded with exotics species displayed substantially greater biomass than those seeded with native species from the same species pool. Introduced species are also associated with increased vegetation and ecosystem heterogeneity in terrestrial and riparian ecosystems (Kumar, Stohlgren, & Chong, 2006; Tang et al., 2013).

In this study, we examined the roles of biotic and abiotic factors in driving introduced species richness in a protected

semi-arid grassland. First, we examined the relationship between native and introduced plant species richness for evidence of biotic resistance. This was an observational study, therefore, based on the results of Peng et al. (2019) in which mean NERR was not negative, even at smaller grain sizes, we predicted that at the small grain at which data was collected in this study (1 m<sup>2</sup>), we would not find a negative NERR. We then tested the dependence of the relationship between introduced and native richness on increasing sampling grain across the grassland. Using a subset of sites for which soil nutrient information was available, we analyzed the relationship between introduced and native species richness, and soil nutrients (nitrogen, phosphorus and potassium), predicting a positive relationship between soil nutrients and introduced (but not native) plant richness. We examined the relationship between native and introduced species richness, and total biomass, and between mean native and introduced species richness per site and standard deviation and spatial heterogeneity of above ground live and litter biomass. We expected positive relationships between introduced richness and biomass due to potentially superior nutrient acquisition of the introduced plants compared to native plants, and a positive relationship between introduced species and biomass heterogeneity.

## Materials and methods

### Study location

Our study was conducted in the Lac Du Bois Grasslands Protected Area in the Thompson-Nicola District of British Columbia. The area is a semi-arid climatic region with hot and dry summers and cold winters. The average annual daily temperature for the region is 9.3 °C, the warmest month is July with average temperature of 21.5 °C, and the coldest is January with an average temperature of −2.8 °C. The range of average total precipitation is from 12.4 mm in February to 37.4 mm in June (Environment Canada, 2014). The grasslands in the park can be classified into three vegetation types: *Pseudoroegneria* – *Artemisia*, *Pseudoroegneria* – *Poa*, and *Pseudoroegneria* – *Festuca*, which dominate the lower, middle and upper grasslands, respectively (van Ryswyk, McLean, & Marchand, 1966). Between May and September, the lower grasslands have a mean temperature of 19.3 °C and a total rainfall of 96 mm, while the upper grasslands have a mean temperature of 15.4 °C and total rainfall of 145 mm (Schmidt, Fraser, Carlyle, & Bassett, 2012).

### Study design

We selected 12 sites (Fig. 1) along an elevation gradient in the grasslands (see Appendix A: Table A.1). These sites are part of the HerbDivNet coordinated experiment that

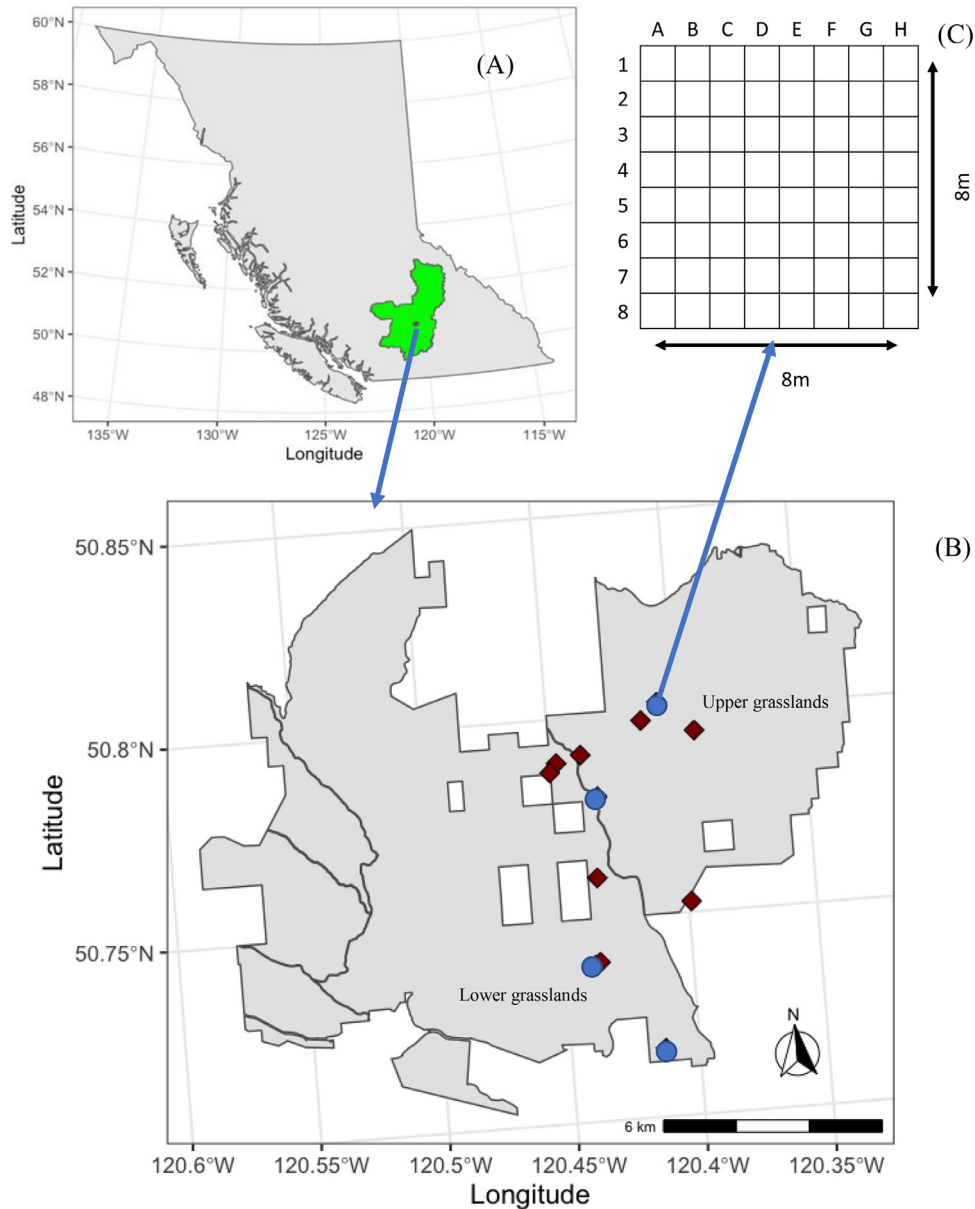
assessed the relationship between species richness and productivity (Fraser, Jentsch, & Sternberg, 2014). Each site measured, 8 × 8 m, and contained 64, 1-m<sup>2</sup> plots. The corners of each site were marked using four buried 20.3 cm (8') nails. The locations of all four corners of the sites were recorded using GPS. Elevation in each site was also obtained using GPS. We extracted temperature and precipitation data from WorldClim at the 30 s resolution (Fick & Hijmans, 2017).

### Plant and soil sampling

Plant sampling was done in late July and early August 2012. Plant species were identified and above-ground biomass harvested in each of the 1-m<sup>2</sup> plots in all 12 sites. Live biomass and litter were separated in the field and collected. We then determined if the plants were native or introduced to British Columbia using E-Flora BC: <http://eflora.bc.ca/> (Klinkenberg, 2020). Forage grasses that may have been intentionally introduced to these grasslands such as *Poa pratensis*, *Medicago sativa* and *Andropogon cristatum* were removed from further analysis. Biomass samples were oven-dried at 80 °C for 48 h and weighed. In each of the four sites for which nutrient data were available, each 1 m<sup>2</sup> plot was sampled for soil. After plant sampling was complete, a 10-cm deep soil core was taken from the center of each plot. The top layer of organic matter (0–2 cm) was removed from soil samples in the field. A subsample was sieved to <355 μm and analyzed for total nitrogen with a CE-440 Elemental Analyzer. Samples sieved to <5 mm were also sent to the British Columbia Ministry of Environment's Analytical Chemistry Laboratory in Victoria, British Columbia, Canada for soil nutrient analysis of potassium and phosphorus among other nutrients. Samples were prepared by very high-pressure (VHP) closed vessel microwave acid digestion. Sample extractions were done in concentrated nitric acid (0.2 g soil per 4 ml acid) at 230 °C and ~1500 psi in a Milestone “Ultrawave” single reaction chamber digester, then cooled and made up to 15 ml with 10% hydrochloric acid and analyzed using a Teledyne/Leeman Labs “Prodigy” dual view inductively coupled plasma-optical emission spectrometer (ICP-OES). Multiple sub-samples were oven-dried at 105 °C to obtain the ‘moisture factor’ used to correct the analysis results to an oven-dry basis.

### Data analysis

We used linear models with a Poisson distribution within the glmmTMB package (Brooks et al., 2017) in R (R Core Team, 2019) to model the relationship between introduced species richness and native species richness in the 768 1 m<sup>2</sup> plots in our study. We used site as a random factor, and controlled for possible spatial autocorrelation in our model that may arise from the structure of our data. We used a similar

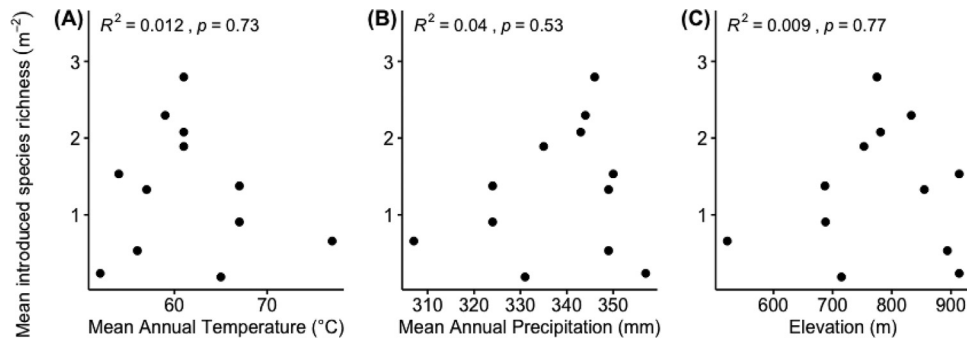


**Fig. 1.** The experimental design and site locations with the Thompson-Nicola Regional District in British Columbia. Panel (A) shows a map of British Columbia, within the Thompson-Nicola Regional District in green, and the dark dot indicating the Lac Du Bois grasslands. Panel (B) shows the Lac Du Bois grasslands, with the location of the twelve sites. Blue circles show the four locations from which vegetation and soil nutrient were sampled. Dark red diamonds show the eight locations from which only vegetation was sampled. Panel (C) shows an  $8 \times 8$  m site within which 64  $1 \times 1$  m plots were nested. Site columns were labelled A-H and rows were labelled 1–8. White spaces represent private property. Map plotted using data from the bmaps package (Teucher, Hazlitt, & Albers, 2018), which presents spatial data in the BC Albers projection.

model to test the relationship between both introduced and native species richness and above-ground live and litter biomass.

We then examined how the relationship between introduced species richness varied with increasing sampling grain, from  $1 \text{ m}^2$  to  $64 \text{ m}^2$  (after Fraser et al. (2015)). For each of the 8 grain sizes, we calculated the number of introduced species and the number of native species encountered in each site, such that each site provided one data point. We

enlarged the quadrats outwards from each of the four different corners of each site by 1 m in length and width to encompass eight progressively larger grain sizes, and thus constructed four different datasets on introduced and native species richness for the eight grains. We then built 8 regression models (one for each grain) to test the relationship between introduced and native richness. We constructed three new regression models, using data from a different site corner and thus orientation. We averaged parameter



**Fig. 2.** Relationship between mean introduced species richness and abiotic variables in the study sites. Plots show model coefficients of determination and  $p$  values.

estimates and coefficients of determination across the 4 orientations for each grain size.

For each site, we calculated the standard deviation of above ground live and litter biomass, and tested the relationship between mean introduced and native species richness and the standard deviation of both biomass measures. We estimated spatial heterogeneity in each site by constructing semi-variograms of the spatial structure of above-ground live and litter biomass. We fit variogram models using a modified version of the “autofitVariogram” function from the “automap” package (Hiemstra, 2013), which fits spherical, exponential, Matern, and Gaussian variogram models, and selects the model with the lowest sum of squares error. From the final variogram model, we obtained the nugget ( $C_0$ ) and the partial sill ( $C$ ). The nugget represents random variation, while the partial sill represents the amount of variation that is due to spatial heterogeneity (Li & Reynolds, 1995). We calculated the spatial heterogeneity proportion (SHP) as  $C/(C_0+C)$  (Oliver & Webster, 2014). We tested the relationship between mean introduced and native species richness and the SHP of both above ground live and litter biomass.

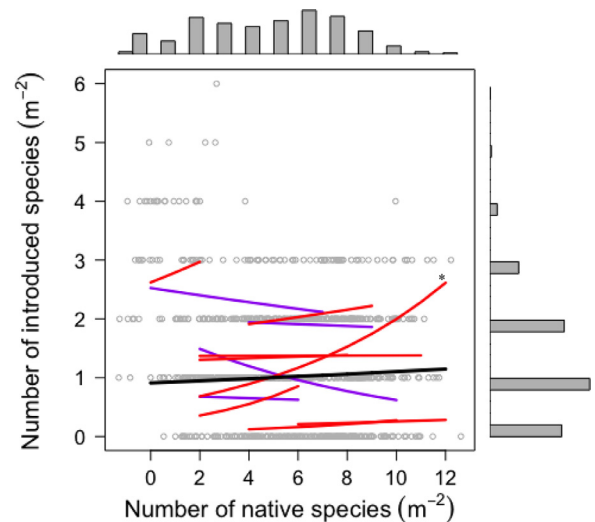
From the 12 study sites, we selected four sites for further analysis. Two of these were low-biomass sites, and had the lowest elevations, one was a medium-elevation high-biomass site, while one was a medium-biomass, high-elevation site, thus encompassing the productivity and elevation range of the study region. Using these four sites for which we obtained soil nutrient data, we analysed the relationship between introduced species richness and soil nitrogen, phosphorus and potassium, using a three-way interaction model, with site as a random factor, and controlling for possible spatial autocorrelation, to examine the influence of the three nutrients on introduced species richness. Using a similar model, we tested the relationship between native species richness and all three soil nutrients.

## Results

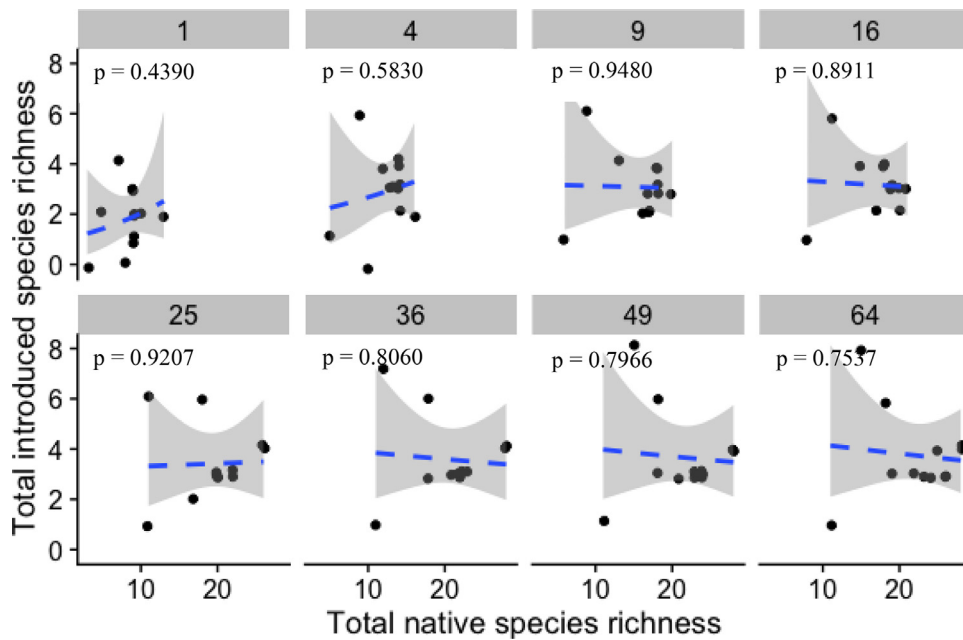
We found a total of 12 introduced potentially problematic species across all the 12 sites. Eleven of these species were

present in the four sites selected for nutrient analysis. The most common were *Taraxacum officinale* and *Tragopogon dubius*, which were present in 267 and 230 plots respectively out of the 768 plots (see Appendix A: Table A.2). Mean introduced species richness was not related to temperature, elevation or precipitation (Fig. 2).

Our study showed an overall non-significant relationship between native species richness and introduced species richness across all sites at a sampling grain of  $1 \text{ m}^2$  (slope = 0.0492,  $P = 0.411$ , SE = 0.0599; Fig. 3). The relationship was not significant within eleven out of the 12 sites and significantly positive in one site (Fig. 3, see Appendix A: Table A.3). The nonsignificant relationship between introduced species richness and native species richness in these grasslands was consistent from the  $1\text{-m}^2$  grain to the



**Fig. 3.** Introduced-native richness relationships in a British Columbia grassland. The black line represents the overall relationship across all 12 sites. Red lines represent positive within-site relationships, while purple lines represent negative within-site relationships. Bars on the side and top of graph represent the frequency distribution of introduced species richness and native species richness respectively. \* indicates the only within site significant relationship. Points show the values of introduced and native species for each plot within site.



**Fig. 4.** Relationship between the introduced and native species richness at varying sampling grains, (while maintaining the same extent). (Numbers 1–64 represent sampling grain in  $m^2$ ). P values are shown for each grain. See Appendix A: Table A.3 for the more information about model coefficients.

64- $m^2$  sampling grain, across the same landscape extent (Fig. 4, see Appendix A: Table A.4). In addition, there was no relationship between above ground biomass live and litter biomass and introduced richness (Live biomass: slope =  $-0.1494$ ,  $P = 0.0713$ , SE =  $0.0828$ ; Litter: slope =  $-0.0005$ ,  $P = 0.994$ , SE =  $0.0650$ ) (Figs 5A and C), but native species richness was negatively related to biomass (Live biomass: slope =  $-0.2037$ ,  $P < 0.001$ , SE =  $0.0559$ ; Litter: slope  $-0.2005$ ,  $P < 0.001$ , SE =  $0.0476$ ) (Fig. 5B and D). Introduced species richness increased as the standard deviation of above-ground live biomass increased (Fig. 6A), but did not respond to litter standard deviation (Fig. 6C), while native species was negatively related to above ground live biomass standard deviation (Fig. 6B), but was not related to litter standard deviation (Fig. 6D). There was no relationship between native and introduced species and spatial heterogeneity of above ground live and litter biomass (See Appendix A: Fig. A.1).

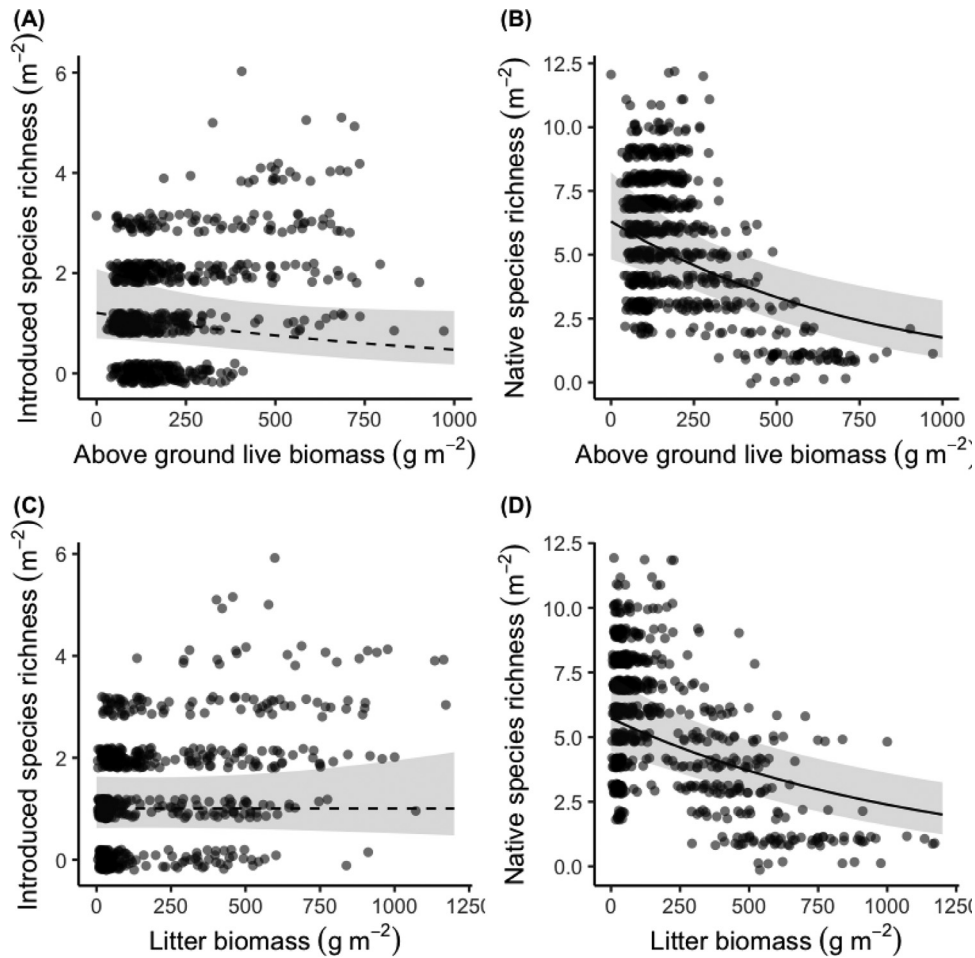
We confirmed that the four sites chosen for soil nutrient analysis displayed the same relationship between introduced and native species richness, i.e., not significant (slope =  $-0.0013$ ,  $P = 0.9872$ , SE =  $0.0809$ ). Introduced species richness was positively related to phosphorus and nitrogen, but not to potassium (Fig. 7A–C, See Appendix A: Table A.5). The interaction between nitrogen and phosphorus was also significant. To further observe the nature of this interaction, we split nitrogen into three groups: low ( $\leq 3000 \mu g$ ), medium ( $> 3000 \mu g$  and  $\leq 6000 \mu g$ ), and high ( $> 6000 \mu g$ ). We then tested the relationship between these nitrogen groups and phosphorus using similar linear regression models as described above. This revealed that as the

amount of nitrogen in the soil increased, the relationship between introduced richness and soil phosphorus transitioned from increasing to flat (See Appendix A: Fig. A.2). Introduced forbs responded positively to nitrogen, while introduced grasses did not respond to any nutrients (See Appendix A: Table A.6). We did not detect any relationship between native species richness and any of the soil nutrients (Fig. 7D–F, See Appendix A: Table A.5).

## Discussion

Introduced plant species richness was associated with native richness in the Lac Du Bois grasslands of British Columbia, a topologically diverse semi-arid grassland, in which gradients in precipitation, elevation and temperature shape the species distribution and thus many species interactions (Lee, Bradfield, Krzic, Newman, & Cumming, 2014; McCulloch, 2013). Although we found plants not native to British Columbia in all of the sites across the grasslands, we did not find support for a NERR. Rather, we found that richness of introduced species in this ecosystem was dependent on nitrogen and phosphorus in the soil, whereas native species did not respond to both nutrients. This result suggests that abiotic factors, particularly soil nutrients, rather than native species richness, account for the differences in the distribution of introduced species along the elevation gradient in this grassland.

Introduced species are expected to benefit from global climate change, due to their ability to succeed in novel environments (Dukes, 2010; Merow, Bois, Allen, Xie, &



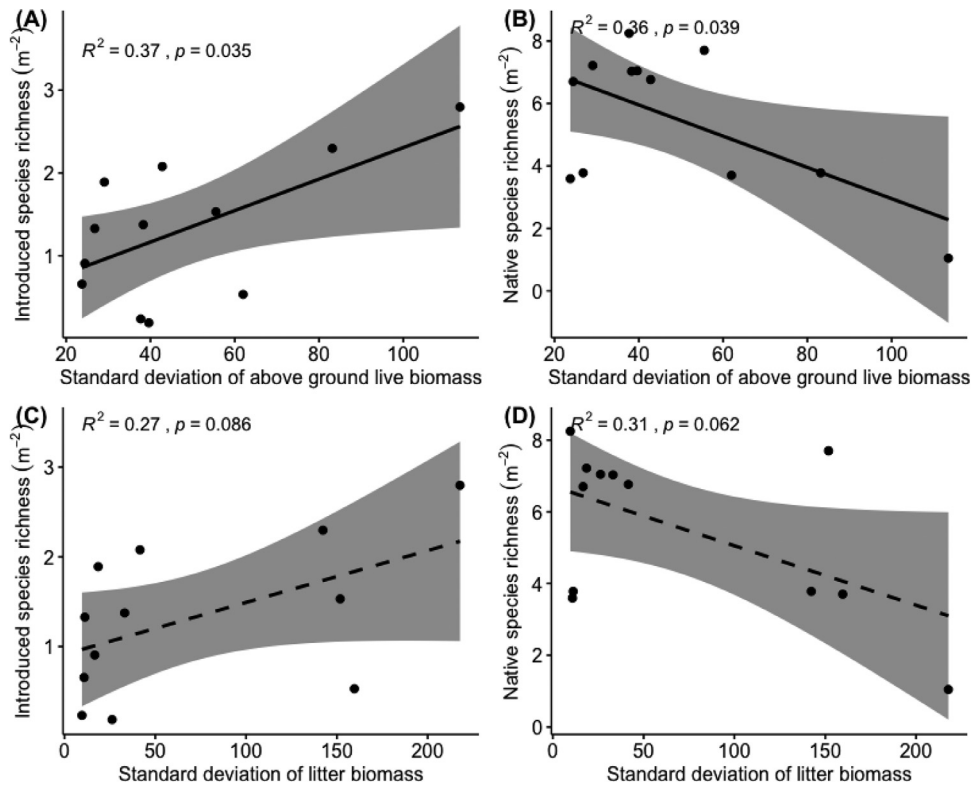
**Fig. 5.** Relationship between introduced species richness and above ground live and litter biomass (A and C respectively), and between native species richness and above ground live and litter biomass (B and D respectively) in twelve sites (64 plots each) in the Lac Du Bois grasslands. Plots show slope of models results and 95% confidence intervals. Data points are also shown. See results section for model results. Dashed lines = non-significant relationships, solid lines= significant relationships.

Silander, 2017). Surprisingly, we found that precipitation, temperature and elevation in our study region did not guide differences in introduced species richness. There is a substantial elevation gradient in our study region, resulting in a strong correlation between all three variables (See Appendix A: Fig. A.3). Introduced species may be equally accessible to all twelve sites, and they may be sufficiently adaptable to climatic conditions within the range of the study region.

Our overall result across all twelve sites contrasts with findings from many different ecosystems that have found a negative NERR (Byun et al., 2013; Going, Hillerislambers, & Levine, 2009; Kettenring et al., 2015). There are a few reasons why there may be no relationship between native and introduced species. (i) The relationship may not exist under conditions where competitive interactions are relaxed. For example, in nutrient-rich grassland prairies, under intense anthropogenic disturbance such as cultivation and grazing, competition may be relaxed due to continuous disruption, and a high diversity of native and introduced species can coexist (Perelman, Chaneton, Batista, Burkart, &

León, 2007). Thus, spatial or temporal heterogeneity in the availability of resources such as light or space may allow both native and introduced species to coexist. (ii) Aggressively growing invaders with extensive root networks or invaders that can exist under stress may still establish in the community despite high native richness (Collins, Jose, Daneshgar, & Ramsey, 2007). However, our study only measured species richness, and biotic resistance may extend to other metrics of native and introduced communities such as abundance or species diversity.

Several broad-scale analyses suggest that after controlling for spatial heterogeneity in ecological factors, a negative relationship between non-native and native richness emerges (Beaury, Finn, Corbin, Barr, & Bradley, 2020; Rejmánek, 2003). None of the ecological factors such as elevation, precipitation and temperature were significantly related to introduced species richness in these grasslands, however, none of the twelve 64 m<sup>2</sup> sites sampled at a 1 m<sup>2</sup> grain, displayed a significant negative relationship, while only one site displayed a significant positive relationship. A



**Fig. 6.** Relationship between introduced species richness and the standard deviation of above ground live and litter biomass (A and C respectively), and between native species richness and the standard deviation of above ground live and litter biomass (B and D respectively) in twelve sites in the Lac Du Bois grasslands. Plots show slope of models results and 95% confidence intervals. Data points are also shown. Dashed lines = non-significant relationships, solid lines= significant relationships.

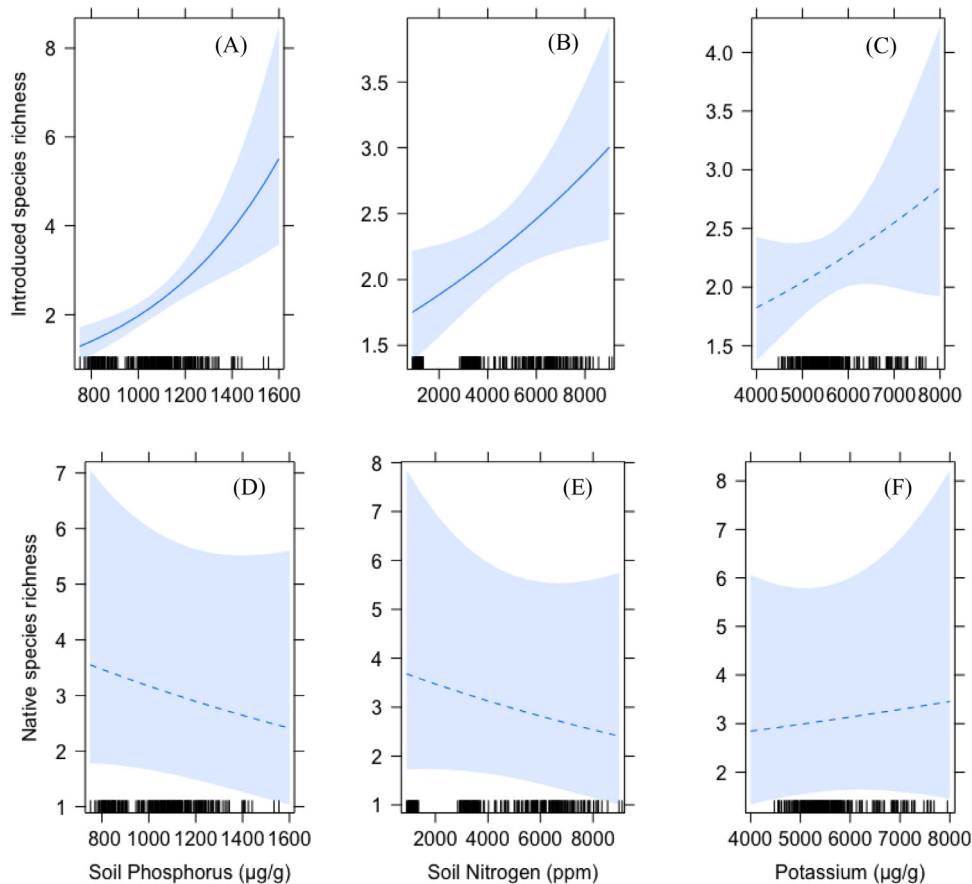
study at the 1 m<sup>2</sup> grain, found analogous results in which most of the NERRs were positive, but nonsignificant (Stohlgren, Barnett, & Kartesz, 2003). It is also thought that at the local scale, competitive exclusion by native plants should be strongest and should lead to exclusion of exotic species (Belote, Jones, Hood, & Wender, 2008; Shea & Chesson, 2002). The absence of a NERR may be due to a dearth of competitive interactions between native and exotic plants in the community (Cofer, Walck, & Hidayati, 2008).

Beyond the 1 m<sup>2</sup> sampling grain, we found a consistently non-significant relationship between native and introduced species richness. Many observational studies have reported a positive relationship, in contrast to the negative relationship documented in small-scale experimental studies. This contradictory result has been called the invasion paradox (Fridley et al., 2007; Peng et al., 2019) and has been ascribed to factors such as variation in study design and study systems (Tomasetto, Duncan, & Hulme, 2019), favourable environmental conditions for both invasive and native plants, or heterogeneity in abiotic factors, such that extrinsic factors that favour native species should also promote introduced species (Peng et al., 2019; Shea & Chesson, 2002). In our study, the lack of influence of sampling grain may be related to our finding that broad scale factors such as precipitation, elevation or temperature did not vary with introduced species richness. Peng et al. (2019) in a meta-analysis, found

no evidence of an invasion paradox, with a positive relationship between NERR and grain size, but considerable heterogeneity in NERR at grains below around 100 m<sup>2</sup>. The largest sampling grain in our study was 64 m<sup>2</sup>, and several studies have reported similar insignificant results at even smaller scales, at 0.01 m<sup>2</sup> (Brown & Peet, 2003) or 1 m<sup>2</sup> (Stohlgren et al., 2003).

Introduced species richness increased with phosphorus and nitrogen, with significant interaction between nitrogen and phosphorus, while native species did not respond to any nutrient. Introduced forbs, particularly responded to phosphorus while introduced grasses were unaffected by any nutrient. These results are consistent with a number of studies reporting higher exotic richness, in naturally or artificially enriched high-nutrient soils (Leishman, Thomson, & Cooke, 2010; Ostertag & Verville, 2002). Soil nitrogen can increase the density and biomass of introduced species to the detriment of native plants (Brooks, 2003), and may even alter competitive interactions to the advantage of introduced plants (Liu et al., 2018). Previous studies have also reported increased phosphorus availability in invaded soils suggesting that invasive plants may have an increased phosphorus utilization efficiency compared to native plants (Muth & Pigliucci, 2007; Zhang, Zhang, Wang, Zou, & Siemann, 2013). The interaction effect suggests possible colimitation on introduced plants between nitrogen and phosphorus in





**Fig. 7.** Relationship between introduced species richness and phosphorus, nitrogen and potassium (A - C), and between native species richness and phosphorus, nitrogen and potassium (D - F) in four selected sites. Blue lines in plots show slope of models results and the light blue band represents the 95% confidence intervals. Rugs at the base of plots show data points for each nutrient. Dashed lines = non-significant relationships, solid lines= significant relationships. See results section for the more information about model coefficients.

this ecosystem (Harpole et al., 2011; Niinemets & Kull, 2005). Low levels of both nitrogen and phosphorus limit introduced species richness, as is evident from the E1 site (See Appendix A: Table A.7, Fig. A.4), while introduced species can increase in response to soil phosphorus at low nitrogen levels. While we did not measure the fraction of soil nutrients available to the plants in this study, that native species did not respond to total soil nutrients strengthens our finding that introduced species are likely to better exploit an increase in soil nutrients.

Introduced species can differ from native species in traits that allow them to respond to resource availability or changes in environmental conditions, such that ecosystems with higher numbers of introduced species exhibit higher above-ground productivity compared to the native communities in the same region (Maron et al., 2014; McLeod et al., 2016). We did not find any relationship between introduced species and above-ground live and litter biomass in this study, but native species richness was negatively related to above-ground live biomass and litter. The biomass measurements incorporate both native and introduced species, therefore it is difficult to tease apart cause and effect. However, it is

possible, that higher litter biomass can impede the establishment of native species by forming a mechanical barrier between seed and soil (Xiong & Nilsson, 1999), while having no effects on introduced species. An experimental study by Sonkoly et al. (2020) found that litter did not affect germination of *Bromus tectorum* and *Bromus inermis*. It should be noted that *Bromus tectorum* and a congener *Bromus squarrosus* are prominent introduced species in our study region. The response of introduced seeds to litter may also depend on seed size (Sonkoly et al., 2020). Taken together, the results suggest that in high productivity plots, introduced species comprise a greater proportion of above-ground live and litter biomass compared to low productivity plots.

We also found that higher within-plot variation in above-ground biomass favoured introduced species establishment to the detriment of native species. Introduced communities are typically associated with higher environmental or resource variability, as introduced species are better able to profit from phases of high resource availability compared to natives (Parepa, Fischer, & Bossdorf, 2013; Tang et al., 2013). Heterogeneity in the distribution of above-ground live biomass may allow for more gaps in the vegetation that

can be exploited by introduced species. There was however no spatial component to the response of introduced species to biomass, as indicated by the lack of relationship between introduced richness and SHP.

Clearly, these findings are based on an observational study, and there may be other confounding factors that are unmeasured. Our results demonstrate the likely importance that nitrogen and phosphorus deposition can have on invasive plants in this ecosystem. Recent analyses have documented decreases in nitrogen deposition in Canada (Hember, 2018), but significant phosphorus accumulation in Canadian soils, particularly in areas with high livestock density (Reid & Schneider, 2019). Management of invasive species in this grassland should consider measures to control influx of soil nutrients to maintain the low numbers of exotic species.

## Conclusions

1. Introduction and establishment of exotic species in this grassland is not related to native species at different scales.
2. Areas with higher phosphorus and nitrogen will support a higher number of introduced species, indicating that invasive plants are likely to establish in areas with high nutrient availability.
3. Increases in introduced species is related to higher above ground biomass heterogeneity, and a higher proportion of introduced species related to total species is related to higher above ground biomass.

Data availability statement: The data used for this study are available at: <https://doi.org/10.6084/m9.figshare.14171180>

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.baae.2021.03.002.

## References

- Beaury, E. M., Finn, J. T., Corbin, J. D., Barr, V., & Bradley, B. A. (2020). Biotic resistance to invasion is ubiquitous across ecosystems of the United States. *Ecology letters*, 23, 476–482.
- Belote, R. T., Jones, R. H., Hood, S. M., & Wender, B. W. (2008). Diversity–invasibility across an experimental disturbance gradient in Appalachian forests. *Ecology*, 89, 183–192.
- Blumenthal, D., Mitchell, C. E., Pyšek, P., & Jarošík, V. (2009). Synergy between pathogen release and resource availability in plant invasion. *Proceedings of the National Academy of Sciences*, 106, 7899–7904.
- Bobbink, R., Hicks, K., Galloway, J., Spranger, T., Alkemade, R., Ashmore, M., et al. (2010). Global assessment of nitrogen deposition effects on terrestrial plant diversity: A synthesis. *Ecological Applications*, 20, 30–59.
- Bradley, B. A., Laginhas, B. B., Whitlock, R., Allen, J. M., Bates, A. E., Bernatchez, G., et al. (2019). Disentangling the abundance–Impact relationship for invasive species. *Proceedings of the National Academy of Sciences*, 116, 9919–9924.
- Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., et al. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, 9, 378–400.
- Brooks, M. L. (2003). Effects of increased soil nitrogen on the dominance of alien annual plants in the Mojave Desert. *Journal of Applied Ecology*, 40, 344–353.
- Brown, R. L., & Peet, R. K. (2003). Diversity and invasibility of Southern Appalachian plant communities. *Ecology*, 84, 32–39.
- Byun, C., de Blois, S., & Brisson, J. (2013). Plant functional group identity and diversity determine biotic resistance to invasion by an exotic grass. *Journal of Ecology*, 101, 128–139.
- Callaway, R. M., Montesinos, D., Williams, K., & Maron, J. L. (2013). Native congeners provide biotic resistance to invasive *Potentilla* through soil biota. *Ecology*, 94, 1223–1229.
- Chen, H., Qian, H., Spyreas, G., & Crossland, M. (2010). Native–exotic species richness relationships across spatial scales and biotic homogenization in wetland plant communities of Illinois, USA. *Diversity and Distributions*, 16, 737–743.
- Cofer, M. S., Walck, J. L., & Hidayati, S. N. (2008). Species richness and exotic species invasion in Middle Tennessee Cedar Glades in relation to abiotic and biotic factors. *The Journal of the Torrey Botanical Society*, 135, 540–553.

- Collins, A., Jose, S., Daneshgar, P., & Ramsey, C. (2007). Elton's hypothesis revisited: An experimental test using cogongrass. *Biological Invasions*, 9, 433–443.
- Dassonville, N., Vanderhoeven, S., Vanparys, V., Hayez, M., Gruber, W., & Meerts, P. (2008). Impacts of alien invasive plants on soil nutrients are correlated with initial site conditions in NW Europe. *Oecologia*, 157, 131–140.
- David, P., Thebault, E., Anneville, O., Duyck, P.-F., Chapuis, E., & Loeuille, N. (2017). Impacts of invasive species on food webs: A review of empirical data. *Advances in Ecological Research*, 1–60.
- Davis, M. A., Grime, J. P., & Thompson, K. (2000). Fluctuating resources in plant communities: A general theory of invasibility. *Journal of Ecology*, 88, 528–534.
- Dukes, J. S. (2010). Responses of invasive species to a changing climate and atmosphere. In D. M. Richardson (Ed.), *Fifty years of invasion ecology* (pp. 345–357). Blackwell Publishing Ltd.
- Elser, J. J., Bracken, M. E., Cleland, E. E., Gruner, D. S., Harpole, W. S., Hillebrand, H., et al. (2007). Global analysis of nitrogen and phosphorus limitation of primary producers in freshwater, marine and terrestrial ecosystems. *Ecology Letters*, 10, 1135–1142.
- Elton, C. S. (1958). *The ecology of invasions by plants and animals*. Methuen.
- Environment Canada. (2014). *Canadian Climate Normals 1981–2010*.
- Fargione, J. E., & Tilman, D. (2005). Diversity decreases invasion via both sampling and complementarity effects. *Ecology Letters*, 8, 604–611.
- Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology*, 37, 4302–4315.
- Fraser, L. H., Jentsch, A., & Sternberg, M. (2014). What drives plant species diversity? A global distributed test of the unimodal relationship between herbaceous species richness and plant biomass. *Journal of Vegetation Science*, 25, 1160–1166.
- Fraser, L. H., Pither, J., Jentsch, A., Sternberg, M., Zobel, M., Askarizadeh, D., et al. (2015). Worldwide evidence of a unimodal relationship between productivity and plant species richness. *Science*, 349, 302–305.
- Fridley, J. D., Stachowicz, J. J., Naeem, S., Sax, D., Seabloom, E., Smith, M., et al. (2007). The Invasion Paradox: Reconciling pattern and process in species invasions. *Ecology*, 88, 3–17.
- Funk, J. L. (2013). The physiology of invasive plants in low-resource environments. *Conservation Physiology*, 1, 1–17.
- Funk, J. L., & Vitousek, P. M. (2007). Resource-use efficiency and plant invasion in low-resource systems. *Nature*, 446, 1079–1081.
- Going, B. M., Hillerislambers, J., & Levine, J. M. (2009). Abiotic and biotic resistance to grass invasion in serpentine annual plant communities. *Oecologia*, 159, 839–847.
- Harpole, W. S., Ngai, J. T., Cleland, E. E., Seabloom, E. W., Borer, E. T., Bracken, M. E., et al. (2011). Nutrient co-limitation of primary producer communities. *Ecology Letters*, 14, 852–862.
- Hember, R. A. (2018). Spatially and temporally continuous estimates of annual total nitrogen deposition over North America, 1860–2013. *Data in Brief*, 17, 134–140.
- Hiemstra, P. (2013). Package 'automap' Version 1.0-14.
- Huenneke, L. F., Hamburg, S. P., Koide, R., Mooney, H. A., & Vitousek, P. M. (1990). Effects of soil resources on plant invasion and community structure in Californian serpentine grassland. *Ecology*, 71, 478–491.
- Jones, M. L., Ramoneda, J., Rivett, D. W., & Bell, T. (2017). Biotic resistance shapes the influence of propagule pressure on invasion success in bacterial communities. *Ecology*, 98, 1743–1749.
- Kettenring, K. M., Whigham, D. F., Hazelton, E. L., Gallagher, S. K., & Weiner, H. M. (2015). Biotic resistance, disturbance, and mode of colonization impact the invasion of a widespread, introduced wetland grass. *Ecological Applications*, 25, 466–480.
- Klinkenberg, B. (2020). *E-Flora BC: Electronic atlas of the plants of British Columbia. Lab for advanced spatial analysis*. Department of Geography, University of British Columbia.
- Kumar, S., Stohlgren, T. J., & Chong, G. W. (2006). Spatial heterogeneity influences native and nonnative plant species richness. *Ecology*, 87, 3186–3199.
- Lee, R. N., Bradfield, G. E., Krzic, M., Newman, R. F., & Cumming, W. P. (2014). Plant community–soil relationships in a topographically diverse grassland in Southern interior British Columbia, Canada. *Botany*, 92, 837–845.
- Leishman, M. R., & Thomson, V. P. (2005). Experimental evidence for the effects of additional water, nutrients and physical disturbance on invasive plants in low fertility Hawkesbury Sandstone soils, Sydney, Australia. *Journal of Ecology*, 93, 38–49.
- Leishman, M. R., Thomson, V. P., & Cooke, J. (2010). Native and exotic invasive plants have fundamentally similar carbon capture strategies. *Journal of Ecology*, 98, 28–42.
- Levine, J. M., Adler, P. B., & Yelenik, S. G. (2004). A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters*, 7, 975–989.
- Levine, J. M., Vila, M., Antonio, C. M. D., Dukes, J. S., Grigulis, K., & Lavorel, S. (2003). Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London. Series B*, 270, 775–781.
- Li, H., & Reynolds, J. (1995). On definition and quantification of heterogeneity. *Oikos*, 280–284.
- Li, Y., Hou, L., Song, B., Yang, L., & Li, L. (2017). Effects of increased nitrogen and phosphorus deposition on offspring performance of two dominant species in a temperate steppe ecosystem. *Scientific Reports*, 7, 40951.
- Liu, G., Yang, Y.-B., & Zhu, Z.-H. (2018). Elevated nitrogen allows the weak invasive plant *Galinsoga quadriradiata* to become more vigorous with respect to inter-specific competition. *Scientific Reports*, 8, 3136.
- Maron, J. L., Auge, H., Pearson, D. E., Korell, L., Hensen, I., Suding, K. N., et al. (2014). Staged invasions across disparate grasslands: Effects of seed provenance, consumers and disturbance on productivity and species richness. *Ecology Letters*, 17, 499–507.
- Matson, P., Lohse, K., & Hall, S. (2002). The globalization of nitrogen deposition: Consequences for terrestrial ecosystems. *Ambio*, 31, 113–119.
- McCulloch, J. A. (2013). *Effects of changing precipitation patterns and clipping on the shrub-steppe grassland plant communities of the Southern Interior of British Columbia*. Kamloops, BC, Canada: Department of Natural Resource Science: Thompson Rivers University.

- McLeod, M. L., Cleveland, C. C., Lekberg, Y., Maron, J. L., Philippot, L., Bru, D., et al. (2016). Exotic invasive plants increase productivity, abundance of ammonia-oxidizing bacteria and nitrogen availability in intermountain grasslands. *Journal of Ecology*, *104*, 994–1002.
- Merow, C., Bois, S. T., Allen, J. M., Xie, Y., & Silander, J. A. (2017). Climate change both facilitates and inhibits invasive plant ranges in New England. *Proceedings of the National Academy of Sciences*, *114*, E3276–E3284.
- Muth, N. Z., & Pigliucci, M. (2007). Implementation of a novel framework for assessing species plasticity in biological invasions: Responses of *Centaurea* and *Crepis* to phosphorus and water availability. *Journal of Ecology*, 1001–1013.
- Niinemets, Ü., & Kull, K. (2005). Co-limitation of plant primary productivity by nitrogen and phosphorus in a species-rich wooded meadow on calcareous soils. *Acta Oecologica*, *28*, 345–356.
- Oliver, M., & Webster, R. (2014). A tutorial guide to geostatistics: Computing and modelling variograms and kriging. *Catena*, *113*, 56–69.
- Ostertag, R., & Verville, J. H. (2002). Fertilization with nitrogen and phosphorus increases abundance of non-native species in Hawaiian montane forests. *Plant Ecology*, *162*, 77–90.
- Parepa, M., Fischer, M., & Bossdorf, O. (2013). Environmental variability promotes plant invasion. *Nature Communications*, *4*.
- Peng, S., Kinlock, N. L., Gurevitch, J., & Peng, S. (2019). Correlation of native and exotic species richness: A global meta-analysis finds no invasion paradox across scales. *Ecology*, *100*, e02552.
- Perelman, S. B., Chaneton, E. J., Batista, W. B., Burkart, S. E., & León, R. J. C. (2007). Habitat stress, species pool size and biotic resistance influence exotic plant richness in the Flooding Pampa grasslands. *Journal of Ecology*, *95*, 662–673.
- Prather, R. M., Castillioni, K., Welti, E. A. R., Kaspari, M., & Souza, L. (2020). Abiotic factors and plant biomass, not plant diversity, strongly shape grassland arthropods under drought conditions. *Ecology*.
- R Core Team. (2019). *R: A language and environment for statistical computing (Version 3.5.2)*. Vienna, Austria: R Foundation for Statistical Computing 2018.
- Reid, K., & Schneider, K. D. (2019). Phosphorus accumulation in Canadian agricultural soils over 30yr. *Canadian Journal of Soil Science*, *99*, 520–532.
- Rejmánek, M. (2003). The rich get richer—responses. *Frontiers in Ecology and the Environment*, *1* 123–123.
- Roscher, C., Beßler, H., Oelmann, Y., Engels, C., Wilcke, W., & Schulze, E. D. (2009). Resources, recruitment limitation and invader species identity determine pattern of spontaneous invasion in experimental grasslands. *Journal of Ecology*, *97*, 32–47.
- Sardans, J., Bartrons, M., Margalef, O., Gargallo-Garriga, A., Janssens, I. A., Ciais, P., et al. (2017). Plant invasion is associated with higher plant—soil nutrient concentrations in nutrient-poor environments. *Global Change Biology*, *23*, 1282–1291.
- Sardans, J., & Peñuelas, J. (2015). Potassium: A neglected nutrient in global change. *Global Ecology and Biogeography*, *24*, 261–275.
- Scherer-Lorenzen, M., Venterink, H. O., & Buschmann, H. (2008). Nitrogen enrichment and plant invasions: The importance of nitrogen-fixing plants and anthropogenic eutrophication. *Biological Invasions*, 163–180.
- Schmidt, A. C., Fraser, L. H., Carlyle, C. N., & Bassett, E. R. (2012). Does cattle grazing affect ant abundance and diversity in temperate grasslands? *Rangeland Ecology & Management*, *65*, 292–298.
- Shea, K., & Chesson, P. (2002). Community ecology theory as a framework for biological invasions. *Trends in Ecology & Evolution*, *17*, 170–176.
- Sonkoly, J., Valkó, O., Balogh, N., Godó, L., Kelemen, A., Kiss, R., et al. (2020). Germination response of invasive plants to soil burial depth and litter accumulation is species-specific. *Journal of Vegetation Science*, *31*, 1081–1089.
- Souza, L., Bunn, W. A., Simberloff, D., Lawton, R. M., & Sanders, N. J. (2011). Biotic and abiotic influences on native and exotic richness relationship across spatial scales: Favourable environments for native species are highly invasible. *Functional Ecology*, *25*, 1106–1112.
- Stevens, C. J., Dise, N. B., & Gowing, D. J. (2009). Regional trends in soil acidification and exchangeable metal concentrations in relation to acid deposition rates. *Environmental Pollution*, *157*, 313–319.
- Stohlgren, T. J., Barnett, D. T., & Kartesz, J. T. (2003). The rich get richer: Patterns of plant invasions in the United States. *Frontiers in Ecology and the Environment*, *1*, 11–14.
- Tang, L., Gao, Y., Wang, C.-H., Li, B., Chen, J.-K., & Zhao, B. (2013). Habitat heterogeneity influences restoration efficacy: Implications of a habitat-specific management regime for an invaded marsh. *Estuarine, Coastal and Shelf Science*, *125*, 20–26.
- Teucher, A., Hazlitt, S., & Albers, S. (2018). Bcmaps: Map layers and spatial utilities for british columbia.
- Tilman, D., & Lehman, C. (2001). Human-caused environmental change: Impacts on plant diversity and evolution. *Proceedings of the National Academy of Sciences of the United States of America*, *98*, 5433–5440.
- Tomasetto, F., Duncan, R. P., & Hulme, P. E. (2019). Resolving the invasion paradox: Pervasive scale and study dependence in the native-alien species richness relationship. *Ecology Letters*, *22*, 1038–1046.
- Uddin, N., & Robinson, R. (2017). Can nutrient enrichment influence the invasion of *Phragmites australis*? *Science of The Total Environment*, 613–614.
- van Ryswyk, A., McLean, A., & Marchand, L. (1966). The climate, native vegetation, and soils of some grasslands at different elevations in British Columbia. *Canadian Journal of Plant Science*, *46*, 35–50.
- Vilà, M., Espinar, J. L., Hejda, M., Hulme, P. E., Jarošík, V., Maron, J. L., et al. (2011). Ecological impacts of invasive alien plants: A meta-analysis of their effects on species, communities and ecosystems. *Ecology Letters*, *14*, 702–708.
- Wilsey, B., & Polley, H. (2006). Aboveground productivity and root-shoot allocation differ between native and introduced grass species. *Oecologia*, *150*, 300–309.
- Wragg, P. D. (2017). Multiple nutrients control threatened grassland vegetation in Eastern South Africa. *South African Journal of Botany*, *112*, 225–236.
- Xiong, S., & Nilsson, C. (1999). The effects of plant litter on vegetation: A meta-analysis. *Journal of Ecology*, *87*, 984–994.
- Zhang, L., Zhang, Y., Wang, H., Zou, J., & Siemann, E. (2013). Chinese tallow trees (*Triadica sebifera*) from the invasive range outperform those from the native range with an active soil community or phosphorus fertilization. *PLoS One*, *8*, e74233.