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Inverse responses of species richness and niche specialization to human development

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Abstract

Aim: Humans impact biodiversity by altering land use and introducing nonnative species. Yet the extent to which coexistence processes, such as competition and niche shifts, mediate these relationships is not clear. This study compares how human development influences wetland plant diversity by examining patterns of species richness, niche specialization and nonnative species occurrences along a human development gradient.

Location: Alberta, Canada.

Taxon: Plants.

Methods: We computed species richness and niche specialization (a measure of the range of human development extents over which a species occurs) from species occurrence data across 1582 wetlands. We tested associations between human development extent and species richness, niche specialization and nonnative species using linear mixed models. We used nonmetric multidimensional scaling ordination to examine whether community composition differed among wetlands surrounded by different human development extents.

Results: Species richness and niche specialization show contrasting relationships with human development: richness was highest and niche specialization was lowest at intermediate human development extents, suggesting that competitive ability and environmental filtering may contribute to low richness at low and high development extents, respectively. Wetlands surrounded by the highest and lowest human development extents had similar levels of richness and niche specialization, but differed in community composition. The proportion of nonnative species increased with increasing human development, alternatively suggesting that the substitution of native species by nonnatives in developed areas may contribute to reduced richness and influence community assembly.

Main conclusions: These findings demonstrate that human land development plays a major role in shaping species richness by influencing the number of nonnative species and the niche specialization of species inhabiting a wetland. Furthermore, these findings suggest that the proportion of nonnative species is an overlooked factor

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potentially influencing plant richness; including this variable may help clarify the inconsistent responses of diversity to human development over large spatiotemporal scales.

KEYWORDS

assembly rules, communities, diversity patterns, exotic species, human footprint, invasive, peatlands

1 | INTRODUCTION

Understanding patterns of species diversity is a central goal of ecology. Globally, humans are causing massive declines in biodiversity (Hallmann et al., 2017; IPBES, 2019; Marques et al., 2019), but local impacts on richness are debated (Cardinale et al., 2018; Gonzalez et al., 2016; Sax & Gaines, 2003; Vellend et al., 2013). Inconsistent responses of diversity to human activity may arise from methodological differences (Cardinale et al., 2018; Hillebrand et al., 2018), as well as characteristics of the disturbance (Newbold et al., 2016) and of the species themselves (Mayor et al., 2012). A better understanding of mechanisms underlying biodiversity responses to human activity may help to resolve some discrepancies, with important implications for conservation biology and monitoring programs.

Plant diversity is the outcome of processes occurring both at large (e.g. dispersal) and small (e.g. coexistence) spatial scales (HilleRisLambers et al., 2012; Velland, 2017), and research on this topic spans many biological and ecological subdisciplines. At large spatial scales, regional species pools provide the propagule source for local diversity (Cornell & Harrison, 2014). In local assemblages, diversity is maintained by processes that govern plant coexistence, which itself is generally determined by a species' ability to disperse to a suitable habitat and to persist there (Chesson, 2000; HilleRisLambers et al., 2012; Tilman & Pacala, 1993). Niche theory posits that, in the absence of competitors, a plant species inhabits a fundamental niche; the fundamental niche encompasses relatively broad ecological conditions determined by the species' morphology and physiology (Chase & Leibold, 2003; Hutchinson, 1957; Pocheville, 2015). As additional plant species are introduced, the range of ecological conditions over which this species can persist is often reduced, resulting in a narrower so-called 'realized niche'. If ecological conditions require specialized adaptations and if those adaptations have trade-offs that incur fitness costs, species are likely to have limited spatial distributions and highly specialized, or narrow, realized niches (Tilman, 2011). On the other hand, generalist species – those with characteristics that allow their persistence across a range of ecological conditions – will have broad distributions and low realized niche specialization but are unlikely to be found in stressful ecological conditions. While stressful ecological conditions might limit species richness, moderately harsh conditions, such as those with multiple limiting resources or intermittent disturbances, may promote high species richness by creating heterogeneous microhabitats (Chesson, 2000; Chesson & Huntly, 1997) or increasing

the number of niche axes on which a variety of species can coexist (Harpole & Tilman, 2007; Hutchinson, 1957).

Any anthropogenic activity that alters a process governing coexistence or dispersal, then, may influence plant diversity. Land transformation and the introduction of nonnative species are the major activities through which humans influence terrestrial diversity (IPBES, 2019; Newbold et al., 2015; Sanderson et al., 2002). Land transformation can reduce available habitat, fragment remaining habitat (i.e. breaking one large habitat patch into many smaller patches), and interfere with dispersal patterns (Fischer & Lindenmayer, 2007). The resulting smaller, more fragmented habitat area can support fewer individuals and species. Indeed, landscape fragmentation is thought to have negative impacts on the diversity of all taxa (Fischer & Lindenmayer, 2007; Fletcher et al., 2018; but see Fahrig et al., 2019) including plants (Ibáñez et al., 2014).

Nonnative plants can have complicated effects on local diversity due to the myriad ways that nonnative species can alter the competitive landscape in which native plants have evolved (Levine et al., 2003, 2006; Vilà et al., 2011). For example, nonnative plants, especially those that naturalize (*sensu* Richardson et al., 2000) or are invasive, can increase soil resource availability (Pyšek et al., 2012) and increase fire frequency (Brooks et al., 2004), thus competitively displacing natives (Catford et al., 2018). Although the relationships between native and nonnative species are complex, invading species appear to generally conserve their niche dimensions in their new, nonnative habitats (Liu et al., 2020; Petitpierre et al., 2012) – though it remains unclear if this is also true for nonnative species that are not invasive. Since the global occurrence of nonnative species has increased by 40% since 1980 (IPBES, 2019), understanding how and why nonnative species affect natives species will be increasingly important for managing biodiversity.

Despite a robust literature documenting the processes underlying plant coexistence (HilleRisLambers et al., 2012) and a strong appreciation that human activity impacts global diversity (Hallmann et al., 2017; IPBES, 2019; Marques et al., 2019), the effects of human activity on local diversity are debated (Cardinale et al., 2018; Sax & Gaines, 2003; Vellend et al., 2013). Moreover, it is not clear how human activity impacts the small-scale processes that maintain coexistence and promote diversity (Tilianakis et al., 2008). For example, Mayor et al. (2012) found inconsistent responses of native and nonnative boreal plant species to human development extent (i.e. areal proportion of altered landscape); but it is not clear whether native, nonnative and total species richness will respond in the same



way to the same drivers. Similarly, native species in invaded communities should likely not be examined in isolation from their nonnative co-inhabitants, since native and nonnative species interact when co-inhabiting an area (Waller et al., 2020).

Our goal was to examine how human activity relates to local patterns of plant diversity and better understand which processes underlie the relationship between human activity and plant diversity. To do so, we examined how richness and niche specialization covaried across a human development gradient, and assessed the degree to which nonnative species contributed to the pattern in our study area. We paired a provincial scale assessment of wetland vascular plant species occurrences in Alberta with measures of human development extent. We tested the following predictions: (1) the highest wetland vascular plant species richness will occur at intermediate development extents, consistent with findings from other work (Mayor et al., 2012), and will be associated with broad realized niche breadths (i.e. low specialization) of resident species plus the additions of nonnative plants; (2) low richness at high development extents will be due to the replacement of native plants by nonnatives; (3) low richness at low human development extents will be associated with high niche specialization of resident species. We thus predict that species richness and niche specialization will show nonlinear and inverse responses to human development and that the occurrence of nonnative plant species will increase with increasing human development.

2 | MATERIALS AND METHODS

2.1 | Site selection

We used vegetation and human development data from the Alberta Biodiversity Monitoring Institute (ABMI) permanent sampling plots. We used wetland vegetation datasets from ABMI captured using two separate protocols: the 'terrestrial' and 'wetland' protocols. Wetlands sampled using the terrestrial protocol include bogs, fens, marshes and wet meadows that comprise a subset of monitoring plots uniformly distributed across a 20 km by 20 km grid that covers the Province. The wetland protocol was used to sample bogs, fens, marshes, wet meadows, and shallow open water wetlands having an open water surface area between 1 and 100 ha and water depth between 0.5 and 2.0 m at mid-summer. Thus, wetlands sampled with the wetland monitoring protocol generally had larger open water extents than wetlands sampled with the terrestrial monitoring program. Wetlands sampled with both protocols are classified based on the dominant vegetation community, and soil nutrient and moisture statuses. Detailed sampling protocols are available through ABMI (Alberta Biodiversity Monitoring Institute, 2014, 2016).

We focused our analyses on all ABMI wetlands sampled between 2007 and 2016 using either protocol (terrestrial or wetland) for which both vegetation data and human development data were available (see below). This dataset consisted of 1582 unique wetlands, of which 471 were resampled in two or three different years. For the wetlands sampled over multiple years, we used only the

sampling event that was closest to the median sample year (i.e. 2013) to reduce any potential variability in richness due to interannual climatic differences. Thus, our final dataset consisted of 554 wetlands sampled with the terrestrial protocol and 1028 wetlands sampled with the wetland protocol for a total of $n = 1582$ sites.

2.2 | Vascular plant richness

To examine the floristic composition and species richness of Alberta wetlands, we merged data on vascular plant species occurrence (presence or absence) from the wetlands sampled under both the terrestrial and wetland protocols, yielding a total of 893 species. We classified species as native or nonnative based on the Alberta Conservation Information Management System (ACIMS) online database for vascular plants (ACIMS, 2020). For 37 species not found in the ACIMS database, nativity status was assigned based on the designation in the US Department of Agriculture PLANTS database (USDA & NRCS, 2020). Vascular plants were surveyed between the end of June and the beginning of August. Under the terrestrial protocol, vascular plants were surveyed within a central 1-ha plot at each site for 90 min. Under the wetland protocol, vascular plants were surveyed in 20-m² plots spaced at 25-m intervals along a transect running parallel to wetland moisture gradient; the vast majority of sites were sampled using five plots ($n = 896$ of 1028 sites sampled with the wetland protocol), though the number of plots sampled ranged from 2 to 8. Ten minutes was spent in each plot identifying vascular plant species. For both protocols, unknown plants were identified in the field after the allotted survey time or brought back to the lab for further identification by an expert botanist.

2.3 | Human development

The Alberta Human Footprint Monitoring Program identifies 21 categories of human development (i.e. any non-natural land cover) based on manually delineated polygons derived from SPOT6 satellite imagery and geospatial datasets (Alberta Environment & Parks, 2016). Human development datasets have been produced for years 2003–2017, although not for every site for every year. Development is broken down into six categories of activity (agriculture, commercial and industrial, energy and mining, forestry, residential and recreational, and transportation). For sites sampled using the terrestrial protocol, the relative area of human development (%) is examined in a 250-m radius circle (~0.196 km²) centred on the vegetation survey plot; thus, for terrestrial sites the area in which human development extent was assessed can overlap with the vegetation sampling plots. For sites sampled with the wetland protocol, the relative area of human development is determined for a 250-m buffer around the open water zone; thus, for wetland sites, the area in which human development extent was assessed can also overlap the vegetation sampling plots. To make wetlands sampled with each protocol comparable, we report the areal extent of human development as a percentage of the



total surveyed area at each site. For each vegetation sampling event, we paired human development data collected from the same year. If human development was not collected in the same year as the vegetation was sampled, we interpolated the human development collected during the closest year prior to and following vegetation sampling.

2.4 | Realized niche specialization

To calculate the realized human development niche specialization of vascular plant species, we adapted the methodology followed by Devictor et al. (2010) for presence/absence data. Briefly, sites were binned into deciles of human development extent. As the niche specialization calculation is based on species occurrence, to avoid bias, each bin was assigned the same number of sites. We excluded 170 species that we deemed to be 'rare' (≤ 3 occurrences in the dataset) to avoid including records that may have reflected potential misidentification or naming inconsistencies. For each of the remaining species ($n = 723$), we summed its occurrence in every bin and calculated the coefficient of variation for the distribution of its occurrence frequency across the binned human development gradient. We marked 0 occurrence for bins where a species did not occur so that each species was evaluated on all bins, thus representing the whole gradient. Thus, a species found within only a very narrow range of human development extents will occur only in one or a few bins and will have a high coefficient of variation, reflecting its high realized niche specialization towards human development. In contrast, a species that occurs across a broad range of human development extents will occur relatively more evenly across all human development bins; this species will have a lower coefficient of variation, reflecting its lower realized niche specialization. Finally, we averaged the niche specialization value of each species present at each site to calculate the mean community niche specialization for each wetland.

However, the distribution of sites across the human development gradient was left-skewed (i.e. there were more sites with no or little human development than with extensive human development), resulting in multiple bins with the same low average human development extent. That is, if bins 1, 2, and 3 all have 0% human development, a species' occurrence would be arbitrarily counted in any one of these three bins despite there being no ecological difference among the bins. To correct for this, we randomly selected a subset of wetlands with 0% human development such that when dividing the human development gradient into new bins of equal numbers of sites, the human development extent increments more closely aligned with deciles (i.e. 0%–10%, 10%–20% ... 90–100%). We created 1000 of these randomly truncated binned human development gradients, summed the occurrence of each plant species in each new bin for each random gradient, and calculated the coefficient of variation for each species as above. Finally, we assigned each species ($n = 723$) the mean niche specialization (coefficient of variation) calculated across the randomizations for which it was included (maximum = 1000 randomizations). There was a strong overall correlation between the niche specialization values calculated among

each of the 1000 randomizations (mean Spearman $\rho = 0.929 \pm 0.01$; Supporting Information S5).

2.5 | Comparisons among human development levels

To compare wetlands surrounded by different human development extents, we selected wetlands surrounded by 0% ($n = 435$), 45%–55% ($n = 53$), and $\geq 90\%$ ($n = 125$) total human development extent, and categorized them as low, intermediate and high human development levels, respectively. To distinguish analyses using the defined human development rankings (e.g. comparing floristic composition among sites with low, intermediate, high human development levels) from those using the continuous gradient of human development, we refer to the former as human development levels and the latter as human development extent.

2.6 | Statistical analyses

We examined relationships between human development and both plant richness and mean community-level niche specialization for 723 vascular plant species at $n = 1582$ sites. To do so, we created mixed effects models using the lmer function in the lme4 (Bates et al., 2015) package in R version 3.6.0 (R Core Team, 2018). Separate models were created for richness and niche specialization (both untransformed). Data and model residuals were visually inspected to determine that they met the test assumptions. In both models, the percent cover of human development was the predictor and we included protocol (i.e. wetland or terrestrial) as a fixed effect. Despite determining that both protocols estimate species richness with similar accuracy (as determined by estimating true richness with Chao estimators; Supporting Information S1), we included protocol as a fixed effect to account for potential differences in the response variable due to sampling methodology (i.e. vegetation of wetlands sampled using the terrestrial protocol was surveyed at $\sim 100 \text{ m}^2 \text{ min}^{-1}$ while the vegetation of wetlands sampled using the wetland protocol was surveyed at $\sim 2 \text{ m}^2 \text{ min}^{-1}$) and ecology (i.e. wetlands with open water zones were sampled with the wetland protocol while wetlands without open water zones were sampled with the terrestrial protocol). We included sampling year as a random effect to account for any differences in response due to interannual climatic variation. We first compared models that included plant species richness (or niche specialization) as a linear versus second order polynomial fit of human development using AIC and chose the model that minimized AIC. We compared linear and polynomial models because our a priori hypothesis, based on previous work (Mayor et al., 2012), was that a second order polynomial model would be the best fit for relationships between human development and richness. Visual inspection of the relationships did not warrant testing other polynomial models. Next, for models of species richness, we compared whether



previous models were improved by including the proportion of nonnative species as a supplementary explanatory variable along with its interaction effect with human development to see how it could improve the overall fit of the models, and again chose the model that minimized AIC. We tested for spatial autocorrelation of final models residuals by calculating Moran's I statistic with the Moran.I function in the ape package (Paradis & Schliep, 2019). Correlograms were also computed using correlog function in the pgirmess package (Giraudoux, 2018).

To examine whether the floristic composition differed among communities surrounded by low, intermediate, and high human development levels, we performed a Nonmetric Multidimensional Scaling (NMDS) analysis with Raup-Crick distances using the metaMDS function in the vegan (Oksanen et al., 2018) package in R. We assessed whether sites in each human development level exhibited a significantly distinct floristic assemblage using permutational multivariate analysis of variance (PERMANOVA) with the adonis2 function in the vegan package (Oksanen et al., 2018) in R. Differences in composition detected by adonis2 can be attributable to different mean composition or composition variances; to test whether sites in each human development level exhibited different variances, we also performed a dispersion test using the betadisper function in the vegan package (Oksanen et al., 2018) in R.

3 | RESULTS

Across 1582 wetlands in Alberta, there was a peaked, unimodal response of vascular plant species richness across a human development gradient (marginal- $R^2 = 0.19$, conditional- $R^2 = 0.21$, all predictors $p < 0.001$; Δ AIC versus linear model = 88.67; Figure 1a; Figure S2). Species richness was initially positively correlated with human development extent, peaked around 40% human development, and was negatively correlated with human development extents over about 50% (Figure 1a). In contrast, vascular plant niche specialization exhibited a U-shaped response to the same human development gradient (marginal- $R^2 = 0.14$, conditional- $R^2 = 0.16$, $p < 0.001$ for disturbance extent and $p = 0.002$ for Protocol, Δ AIC versus linear model = 101.63; Figure 1b and Figures S2 and S3). All models displayed low spatial autocorrelation in their residuals (Supporting Information S2).

We found a significant difference in the plant species composition of wetlands surrounded by low and high human development levels (PERMANOVA $df = 1$, $F = 201.33$, $R^2 = 0.27$, $p = 0.001$; Figure 2) and no significant difference in dispersion between these groups (analysis of multivariate homogeneity of group dispersions; $df = 1$, $F = 2.71$, $p = 0.101$). These results indicate that despite similar levels of richness and niche specialization, wetland plant communities at low and high human development levels are compositionally distinct. We found that wetlands surrounded by low human development levels were typically inhabited by native plants characteristic of boreal peatlands such as *Carex pauciflora* (fewflower sedge), *Kalmia polifolia* (bog laurel), *Potamogeton*

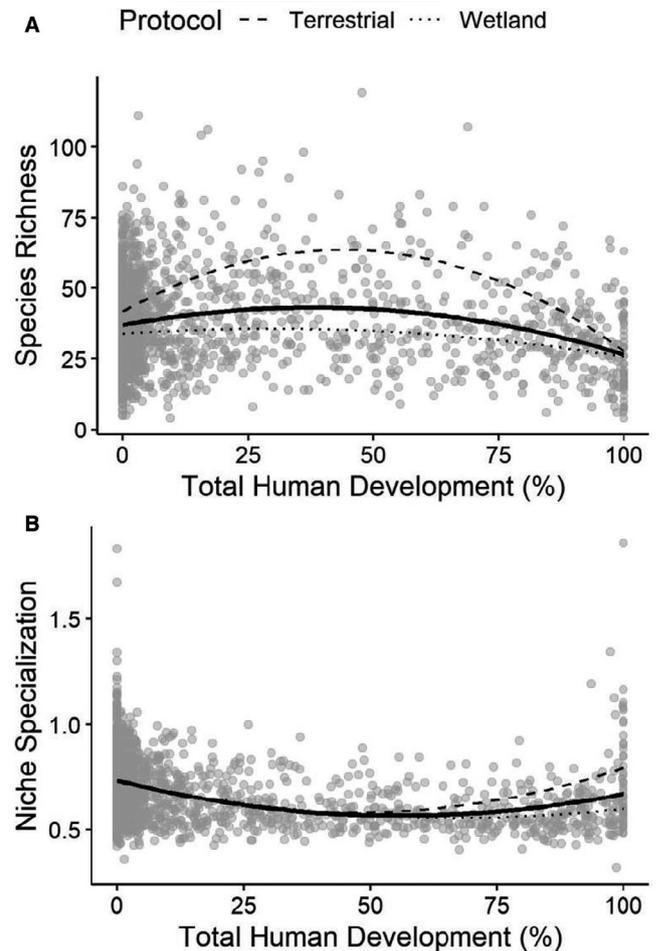


FIGURE 1 Vascular plant (a) species richness and (b) mean niche specialization show inverse relationships to human development across Alberta wetlands. Second order polynomial models were the best models for both richness and niche specialization. Solid lines in each panel represent the maximum likelihood fit of the two protocols (wetland and terrestrial) combined, and dashed lines represent the fit of each respective protocol from the fitted random effect model. See Section 2.3 for an explanation of the two protocols; see Section 2.6 for a description of model development and selection; see Supporting Information S2 for full statistical output

robbinsii (Robbins' pondweed), *Potamogeton amplifolius* (largeleaf pondweed) and *Scheuchzeria palustris* (rannoch-rush). In contrast, developed wetlands were typically inhabited by nonnative and agricultural species including *Brassica rapa* (field mustard; nonnative), *Chamaesyce serpyllifolia* (thymeleaf sandmat), *Fagopyrum esculentum* (common buckwheat; nonnative), *Fagopyrum tataricum* (green buckwheat; nonnative), and *Amaranthus retroflexus* (redroot amaranth; nonnative). The community composition of wetlands surrounded by intermediate human development levels overlapped with those of the high and low development wetlands (Figure S2); it was statistically distinct from the communities surrounded by low and high human development levels (PERMANOVA $df = 2$, $F = 107.5$, $R^2 = 0.26$, $p = 0.001$; Supporting Information S3), though this may be due to different dispersions among the human development levels ($df = 2$, $F = 4.06$, $p = 0.018$).

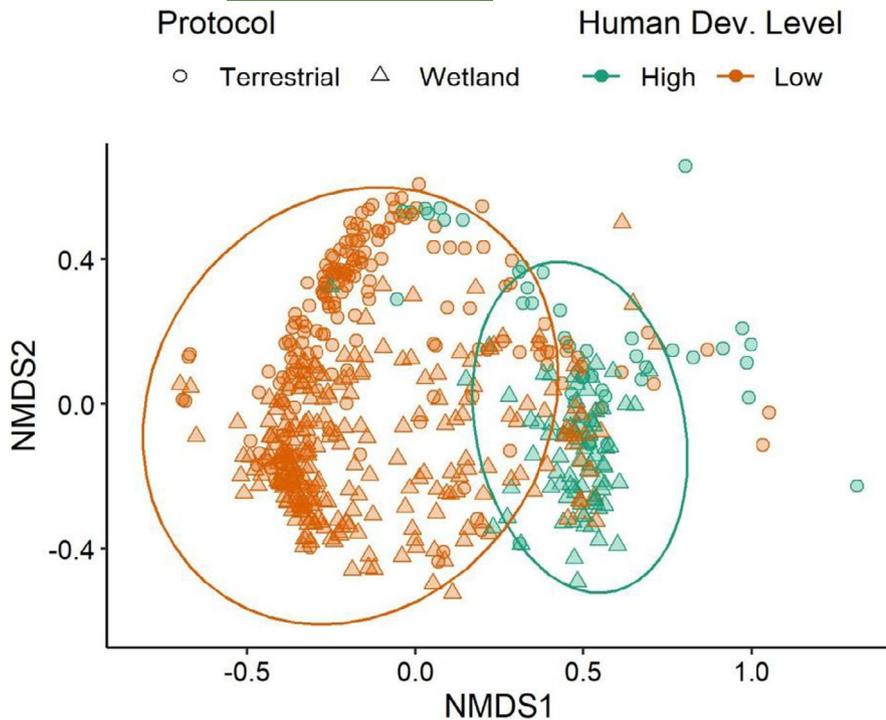


FIGURE 2 Ordination of vascular plant community compositions for wetlands in Alberta. Each point represents the community of one wetland inferred from NMDS analysis. Points are coloured by human development level, point shapes (circles versus triangles) differentiate the sampling protocol and transparency is used to improve readability of stacked sites. The low human development level includes $n = 435$ wetlands all with 0% total human development extent and the high human development level includes $n = 125$ wetlands all with $\geq 90\%$ human development extent. Ellipses represent 95% confidence intervals for the centroids of the communities within each human development level. The final ordination converged with seven dimensions; stress was 0.06

We found that the proportion of nonnative species was positively associated with human development (Figure 3; marginal $R^2 = 0.40$, conditional $R^2 = 0.40$, mean square = 6560.6, $df = 2$, $F = 521.85$, $p < 0.001$; ΔAIC vs. linear model = 7). This increase in the proportion of nonnative species was a result of reduced native species richness plus increased nonnative species richness (Supporting Information S4). Including an interaction between nonnative species and human development extent improved the overall fit of models of richness (ΔAIC versus polynomial richness model = 59; Supporting Information S2). The proportion of nonnative species differed significantly among wetland plant communities surrounded by low, intermediate, and high human development levels (Figure 3b). Wetland communities surrounded by low human development levels were composed of $0 \pm 2\%$ nonnative species (median \pm IQR); wetland communities surrounded by intermediate human development levels were composed of $14 \pm 19\%$ nonnative species; and wetland communities surrounded by high human development levels were composed of $36 \pm 28\%$ nonnative species (mixed model ANOVA $F = 158314.45$, $p < 0.001$). Species richness models which included the proportion of nonnative species and its interaction with human development outperformed models with human development alone (Supporting Information S2).

4 | DISCUSSION

4.1 | Richness, niche specialization and composition along a human development gradient

We found that richness peaked in wetlands surrounded by intermediate extents of human development, and was lower in wetlands surrounded by both low and high human development extents. This

peak was gentle, but it is notable that the peak was detectable even across the diverse wetland classes and range of environmental conditions encompassed in our study. Although we determined that the different protocols used in this study estimated richness with similar accuracy (Supporting Information S1), the different ecologies of wetlands sampled by each protocol may have contributed to its influence on richness estimates. Other studies have found various responses of diversity to spatial and temporal disturbances (e.g. Hall et al., 2012; Mackey & Currie, 2001), including a richness peak in plant communities surrounded by intermediate disturbance extents (Mayor et al., 2012). It is important to note, however, that neither a spatial nor a temporal disturbance gradient necessitates a peaked richness response (Fox, 2013; Mackey & Currie, 2001; Shea et al., 2004).

A unimodal richness-development relationship may occur if strong selective pressures restrict the number of species that can inhabit wetlands surrounded very high and very low development extents; only species with specific characteristics and/or life history strategies can inhabit these environments (i.e. those with a competitive advantage *sensu* niche theory, Hutchinson, 1957, 1959). We speculate that species in these focal wetlands experience trade-offs between competitive ability (i.e. resource acquisition) and dispersal ability (i.e. competition-colonization trade-off; Cadotte, 2007; Chesson, 2000). Although there are many limitations on data availability at large spatial scales, these speculations could be tested by calculating niche specialization based on different environmental gradients, rather than calculating niche specialization based on a human development, which itself encapsulates many different environmental conditions.

Alberta wetlands – which are primarily peatlands (Ficken et al., 2019; Vitt, 1996) – that are exposed to little direct human influence may have relatively low nutrient availability (Vitt, 2006) and

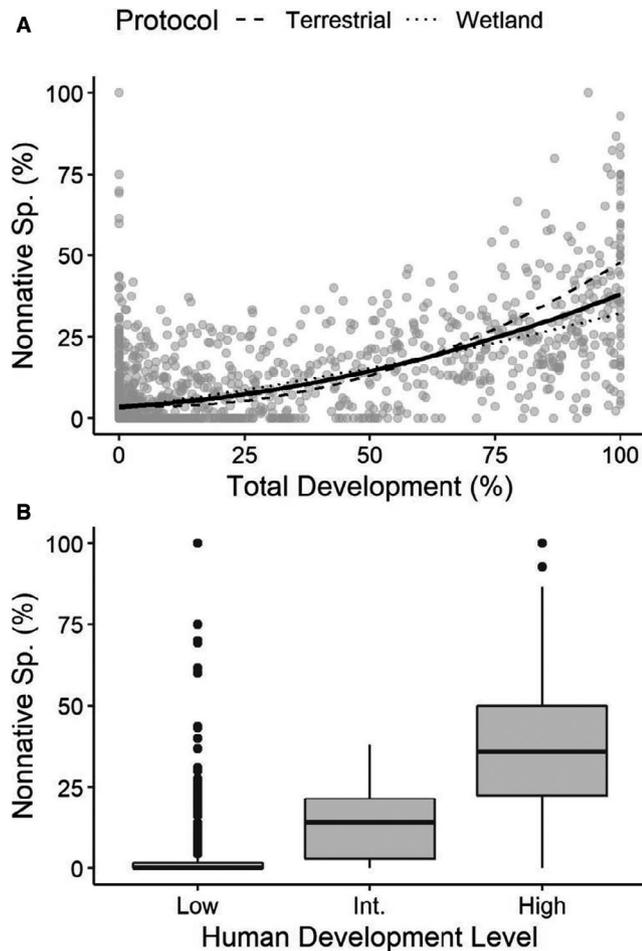


FIGURE 3 The proportion of nonnative vascular plant species (a) increases with the areal extent of human development surrounding wetlands in Alberta, and (b) differs significantly across sites with low, intermediate (Int.) and high human development levels. In (a), the solid line represents the mean relationship of the two protocols (wetland and terrestrial) and the dashed lines represent the respective protocols from the fitted random effect model. In (b) the solid thick horizontal lines depict the median proportion of nonnative species, the boxes extend to the first and third quartiles, and whiskers extend to 1.5 times the interquartile range. In (b), total richness (native + nonnative) was 34 ± 19 for low, 36 ± 26 for intermediate and 27 ± 18 for high human development levels (median \pm IQR)

experience infrequent natural disturbances (e.g. fire return interval of boreal peatlands ranges from tens to hundreds of years, Turetsky & St. Louis, 2006). Vascular plant species inhabiting wetlands surrounded by low development extents are likely limited by low nutrient availability (Turetsky & St. Louis, 2006; Vitt, 2006). In contrast with wetlands surrounded by low human development extents, wetlands surrounded by high human development extents may be more eutrophic and turbid (Sarneck et al., 2011) with patchy suitable habitat for obligate wetland vascular plants. Vascular plant species inhabiting wetlands surrounded by high development extents are thought to be limited by their ability to disperse in human-dominated landscapes (Turetsky & St. Louis, 2006; Vitt, 2006). Together, these conditions limit species richness under high and low human

development extents, whereas at intermediate human development these species coexist in low abundances with generalist species that have moderate competitive and dispersal abilities. However, different human development types likely have different magnitudes of impact on adjacent wetlands such that wetlands surrounded by the same proportion of developed landscape will be affected differently. In addition, wetlands remote from human activity will also experience low nonnative propagule pressure, which will likely limit the establishment of nonnative species and overall richness in these wetlands (Chadwell & Engelhardt, 2008).

If the characteristics that enable survival under stressful environmental conditions also incur fitness costs when the selection pressure is lessened (i.e. at intermediate development extents), the realized niche of species inhabiting wetlands with low and high human development should be lower than those inhabiting wetlands with intermediate human development (Carscadden et al., 2020; Chase & Leibold, 2003). In support of this, we found that wetland communities at the highest and lowest human development extents were both inhabited by species with relatively high niche specialization indices. However, even though wetlands surrounded by low and high human development extents were composed of species with similar niche breadths, community composition differed. We speculate that wetlands surrounded by intermediate human development exhibit a peak in species richness because they are inhabited both by distinct species that specialize on low and high development environments, as well as generalist species that inhabit wetlands across all human development levels.

4.2 | Ecological patterns, human development and nonnative species

High extents of human development are associated with a number of other changes to the biotic and abiotic environment (Carlson & Arthur, 2000; Imhoff et al., 2010), though this will vary depending on the type of human development and our approach did not differentiate between different types. Still, our results indicate that wetland communities in highly developed landscapes were composed of a higher proportion of nonnative species than those in undeveloped landscapes. Previous work has examined the relationships between human development and species richness separately for native and nonnative terrestrial species (Mayor et al., 2012), but co-occurring native and nonnative species are unlikely to be ecologically independent when they inhabit the same wetland. This increase in the proportion of nonnative species presents an alternative explanation for why species richness is low at high development extents. At high development extents, richness may be low if the environment requires highly specialized traits that increase niche specialization and reduce realized niche breadth, as we originally hypothesized (see above discussion). Alternatively, richness may be low if nonnative species replace or displace native species (Catford et al., 2018; Pyšek et al., 2012) in ratios greater than 1:1. This species replacement pattern could be helped by the fact that humans tend to settle

in environments that facilitate nonnative establishment and the potential success of invasive species (Gallien et al., 2019).

Even without any expansion of human development, the distribution of a nonnative species can expand from the initial point of introduction if some nonnative species naturalize or become invasive. While some nonnative species may have no impact on native richness (e.g. small annuals of disturbed wet mud), others may colonize wetlands with lower levels of human development, reducing native richness through competitive exclusion (Catford et al., 2018) and flattening the curve we observed. Invasion would also reduce the observed peak in mean community niche specialization at high development extents by expanding the realized niche breadth of these invasive species inhabiting high development wetlands. This suggests that the observed unimodal relationship between wetland vascular plant species richness and human development could be contingent upon the time of observation relative to the time point of invasion (Diamond, 1975; Richardson et al., 2000; Theoharides & Dukes, 2007). Hence, the presence of nonnative species – particularly those with characteristics that enable invasion – may be an important factor that indicates non-equilibrium situations of diversity patterns that are known to be important pitfalls when, for example, assembly rules are inferred from diversity patterns (Chase, 2003; Münkemüller et al., 2020).

Although we focused on only two drivers of richness – human development and nonnative species – a number of other environmental and wetland variables co-vary with human development and may also influence vascular plant richness. Including these variables as covariates would likely reduce the amount of unexplained variance in our models. Habitat area can be an important determinant of plant richness (Kreft et al., 2008; Shi et al., 2010; Smith & Haukos, 2002), although this is not always the case in wetlands (Oertli et al., 2002); however, because boreal peatlands often form large, continuous complexes that are difficult to discretize (Devito et al., 2005) we were not able to include this covariate in our models. Our approach also did not distinguish among human development types, which likely differ in ecological impact. For example, agricultural land cover and impervious surfaces (e.g. roads) will likely have different impacts on the ecology of adjacent wetlands even when both human development types cover the same areal extent. Thus, a more detailed gradient of precise human development types could influence calculations of niche breadth related to human development and subsequently of the relationships we present in this study. Moreover, previous work has found that reduced species richness is associated with increased nitrogen deposition (Payne et al., 2017) – another environmental variable associated with human development (though the effect of nitrogen on species richness is inconsistent; Peñuelas et al., 2013; Pescott & Jitlal, 2020; Sasaki et al., 2010; Seastedt & Vaccaro, 2001). Indeed, where humans settle on a landscape is non-random (Antrop, 2004; Pickett & Cadenasso, 1995; Vandam et al., 2013) and these confounding variables may influence diversity. Additional work is hence needed to disentangle the relative importance of different variables associated with human development. More broadly, however, since nonnative species clearly

contribute to the observed patterns in species richness and niche specialization in Alberta wetlands, care should be taken to understand when broad biogeographical patterns are driven by nonnative species, native species, or both, and also when the introduction of a nonnative species moves the community away from steady state. Particularly in the case of mixed responses of species diversity to disturbance gradients (Fox, 2013; Huston, 2014; Mackey & Currie, 2001; Mayor et al., 2012; Sheil & Burslem, 2013) or time (Cardinale et al., 2018; Sax & Gaines, 2003; Vellend et al., 2013), differentiating the responses of native, nonnative and invasive species may help clarify these relationships.

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CONFLICTS OF INTEREST

We do not have any conflict of interest to declare.

DATA AVAILABILITY STATEMENT

Data of the study can be found in the Dryad data deposit <https://doi.org/10.5061/dryad.b2rbnzsfw>, except for human disturbance data that need a data sharing agreement with ABMI. Precisions can be asked to the corresponding author.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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