# Inverse responses of species richness and niche specialization to human development

Running title: Diversity and human development patterns

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2

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

# Keywords

Diversity patterns; communities; assembly rules; exotic species; invasive; human footprint; peatlands

# Introduction

Understanding patterns of species diversity is a central goal of ecology. Globally, humans are causing massive declines in biodiversity (*IPBES*, 2019; Hallmann et al., 2017; 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; D. 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; G. Evelyn 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 tradeoffs that incur fitness costs, species are likely to have limited spatial distributions and highly specialized, or narrow, realized niches (David 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; G. Evelyn 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 (Newbold et al., 2015; Sanderson et al., 2002; *IPBES*, 2019). 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 (J M Levine et al., 2003; Jonathan M. Levine et al., 2006; Vilà et al., 2011). For example, nonnative plants, especially those that 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 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 (*IPBES*, 2019; Hallmann et al., 2017; 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 which maintain coexistence and promote diversity (Tylianakis et al., 2008). For example, a recent study found inconsistent responses of native and nonnative boreal plant species to human development extent (i.e. areal proportion of altered landscape) (Mayor et al., 2012), but it is not clear whether native, nonnative, and total species richness will respond in the same way to the same drivers. Similarly, it is unlikely that native species in invaded communities should be examined in the absence of 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 non-linear and inverse responses to human development and that the occurrence of nonnative plant species will increase with increasing human development.

# Materials and Methods

## 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 with 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 generally include wetlands with 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 sampled two or three years. For these 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..

## Vascular plant richness

To examine the floristic composition and species richness of Albertan 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, n.d.). 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 80 minutes. 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 5 transects (n = 896 out of 1028 sites sampled with the wetland protocol), though the number of transects sampled ranged from 2 to 8.. Five 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.

## 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 from SPOT6 satellite imagery and geospatial datasets (Alberta Environment and 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 (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) centered 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.

## 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. 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), 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. We finally 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 *ρ* = 0.929 ± 0.01; Supporting Information (SI) 4).

## 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 ≥ 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.

## 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 to account for potential differences in the response variable due to sampling methodology. 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 vs 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, p. 0). 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.

# Results

Across 1582 wetlands in Alberta, there was a peaked, unimodal response of vascular plant species richness across a human development gradient (marginal-R² = 0.19, conditional-R² = 0.21, all predictors p < 0.001; ΔAIC vs linear model = 88.67; Figure 1a; SI 1). 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-R² = 0.14, conditional-R² = 0.16, p < 0.001 for disturbance extent and p = 0.002 for Protocol, ΔAIC vs linear model = 101.63; Figure 1b and SI 1, SI 2). All models displayed low spatial autocorrelation in their residuals (SI 1).

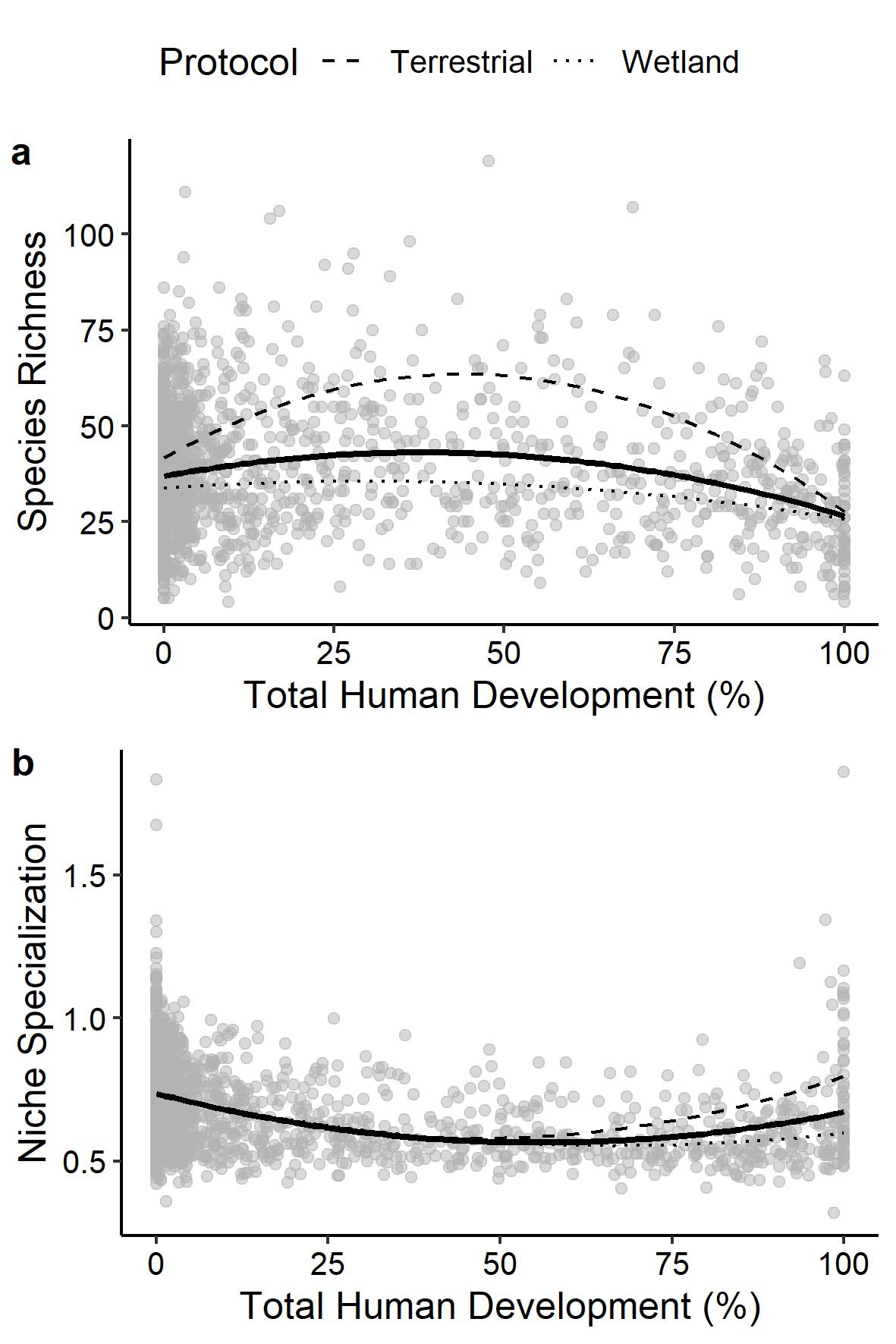


Figure 1: Vascular plant (a) species richness and (b) mean niche specialization show inverse relationships to human development across Albertan wetlands. Second order polynomial models were the best models for both richness and niche specialization. Solid lines in each panel represent the maximum likelihood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

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, R2 = 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 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, R2 = 0.26, p = 0.001; SI 2), though this may be due to different dispersions among the human development levels (df = 2, F = 4.06, p = 0.018).

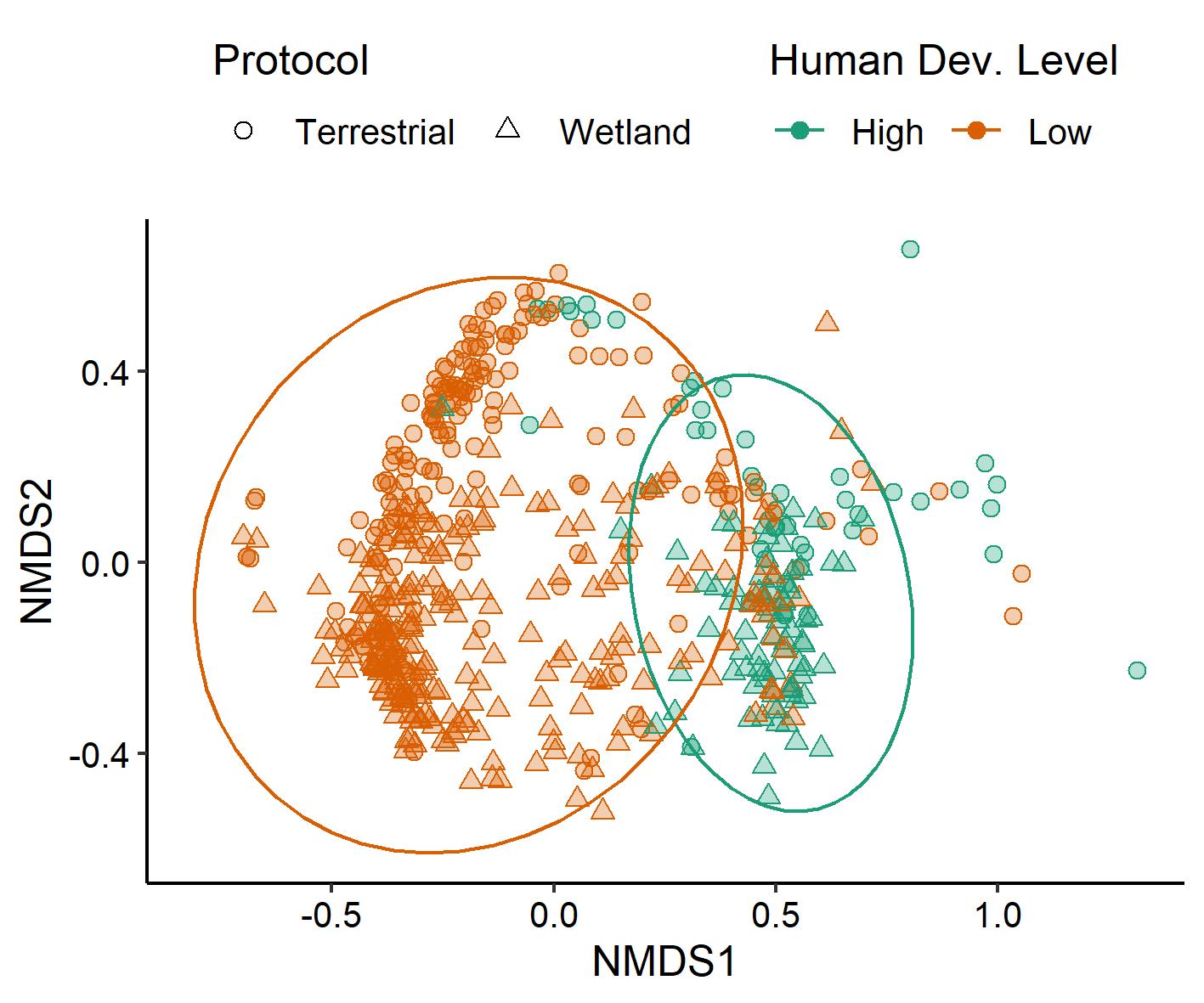


Figure 2. Ordination of vascular plant community compositions for wetlands in Alberta. Each point represents the community of one wetland inferred from NMDS analysis. Points are colored by human development level, point shapes (circles versus triangles) differentiate the sampling protocol and transparency is used to improve readability of stacked sites. The low human development level includes n = 435 wetlands with 0% total human development extent and the high human development level includes n = 125 wetlands with ≥90% human development extent. Ellipses represent 95% confidence intervals for the centroids of the human development levels. The final ordination converged with 7 dimensions; stress was 0.06.

We found that the proportion of nonnative species was positively associated with human development (Figure 3; marginal R2 = 0.40, conditional R2 = 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 (SI 3). Including an interaction between nonnative species and human development extent improved the overall fit of models of richness (ΔAIC versus polynomial richness model = 59; SI 1). 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 ± 2% nonnative species (median ± IQR); wetland communities surrounded by intermediate human development levels were composed of 14 ± 19% nonnative species; and wetland communities surrounded by high human development levels were composed of 36 ± 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 (SI 1).

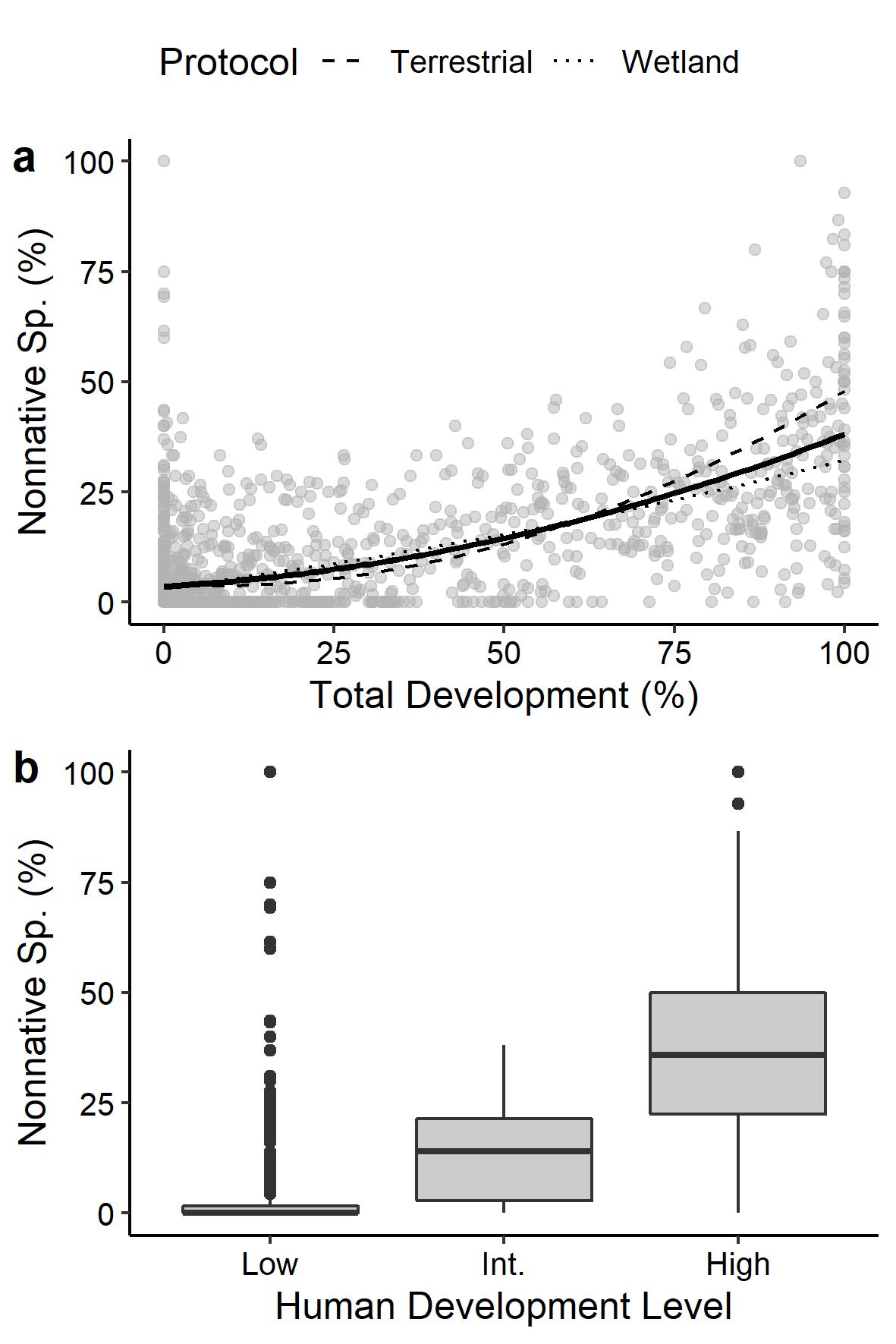


Figure 3: The proportion of nonnative vascular plant species (a) increases with the areal extent of human development surrounding wetlands in Alberta, and (b) differs significantly across sites with low, intermediate (Int.) and high human development levels. In *a*, the solid line represents the mean relationship of the two protocols (wetland and terrestrial) and the lighter 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 time 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 ± IQR).

# Discussion

## 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. Although this peak was gentle, it is notable that the peak was detectable even across diverse wetland classes and across a range of environmental conditions. 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 a 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 which 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, G. E. Hutchinson, 1959; G. Evelyn Hutchinson, 1957). We speculate that species in these focal wetlands exhibit tradeoffs between competitive ability (i.e. resource acquisition) and dispersal ability (i.e. competition-colonization tradeoff; Cadotte, 2007; Chesson, 2000). Though there are many limitations on data availability at large spatial scale, 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.

Albertan wetlands – which are primarily peatlands (Ficken et al., 2019; D. Vitt, 1996) – that are exposed to little direct human influence may have relatively low nutrient availability (D. H. Vitt, 2006) and 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; D. H. Vitt, 2006). In contrast to wetlands surrounded by low human development extents, wetlands surrounded by high human development extents may be more eutrophic and turbid (Sarneel 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; D. H. Vitt, 2006). 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 which 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.

## 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. 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 become invasive (Catford et al., 2018). If some nonnative species colonize wetlands with lower levels of human development, we speculate that this would reduce species richness, thus 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 timepoint 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 an important pitfalls when e.g. 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 variables co-vary with human development and may also influence vascular plant richness. For example, 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; 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 also influence diversity. Additional work can 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 Albertan 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.

## Limitations

This study provides an important assessment of the relationships among wetland vascular plant richness, niche dimensions, human development, and nonnative species across a large geographical extent and across a range of wetland classes. However, these results should be interpreted in light of two important considerations. First, wetlands in our dataset were sampled under two different monitoring protocols which each used different methods; these wetlands were also surrounded by slightly different human development ranges. We attempted to account for these differences by including a “Protocol” covariate factor in all models. Still, the different sampling methods, particularly those used to measure vascular plant richness, may have affected the relationships we detected here. Second, our approach did not distinguish among human development types and it is unlikely that all types have the same ecological impact. For example, agricultural land cover and impervious surfaces (e.g. a road) will likely have very different impacts on the ecology of adjacent wetlands even when both human development types cover the same areal extent. Although previous work found that cumulative human development was an important driver of wetland plant community diversity in boreal wetlands (Ficken et al., 2019), a more detailed gradient encompasses enough sites of a precise metric of human impact would likely influence calculations of niche breadth related to human development and subsequently of the relationships we present in this study. Further studies with data sampled along different environmental and human development gradients would be useful to disentangle these potential limitations.

# Data availability statement

All data used in the study are freely available and downloadable on the Alberta Biodiversity Monitoring Institute (ABMI) website (www.abmi.ca/home/data-analytics/da-top/da-product-overview).

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# Biosketch

Cari D. Ficken is a plant ecologist who studies the impacts of disturbances on plant communities and ecosystem processes.

Martin Jeanmougin is a conservation scientist interested in bridging gaps between quantitative ecology, theoretical ecology and conservation sciences, embracing interdisciplinary approaches.

Author contributions: CF and MJ are considered as co-first authors because they contributed equally in the conception and design of the study, data analysis and drafted the manuscript together. JC and RR critically revised the manuscript and helped for final submission. All authors gave final approval for publication and agree to be held accountable for the work performed therein.

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