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Species richness is a surrogate for rare plant occurrence, but not conservation value, in boreal plant communities

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Abstract

Rare species are an ecologically important component of biological communities, but may be at risk of decline as a result of human disturbance and other sources of environmental change. Rare species are also ecologically idiosyncratic, making their occurrence difficult to predict a priori, and leading to efforts to find surrogate measures of rare species occurrence to inform conservation decisions. Using floristic data collected at 602 sites in the western Canadian boreal forest, we studied relationships between rare species occurrence, species richness and habitat type, with rarity defined according to the classification system developed by Rabinowitz (in: Synge (ed) The biological aspects of rare plant conservation, Wiley, Somerset, 1981). Relative to similar studies in other temperate regions, we found that a smaller proportion of species were classified as rare in our study region, and that common species dominate the flora. Regional-scale relationships were positive between richness and the occurrence of rare species; however, due to variation in these relationships among habitat types, richness is not a suitable surrogate for a site's conservation value with respect to species rarity.

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Introduction

Natural ecosystems are increasingly under pressure as human activity disturbs, alters, and converts large tracts of land for economic and social purposes, leading to concerns about biodiversity loss. Preserving biodiversity under increasing anthropogenic pressures requires an understanding of which species are most at risk of decline. Rare species are often perceived to be susceptible to decline based on attributes such as small population size and highly specific habitat requirements, which increase vulnerability to extinction (Davies et al. 2004); this is reflected in the widely-used International Union for the Conservation of Nature (IUCN) criteria for assessing species conservation status, where these and other aspects of rarity factor heavily into assessing extinction risk (IUCN 2012). Although they may encompass only a small proportion of the biomass in a given ecosystem, rare species often comprise a disproportionate amount of the overall diversity of ecological communities (Rabinowitz et al. 1986; Goerck 1997), play significant roles in ecosystem function (Mouillot et al. 2013; Jain et al. 2014), and may provide resilience against ecological change and invasion by exotic species (Walker et al. 1999; Lyons and Schwartz 2001). The loss of rare species therefore has the potential to disproportionately impact ecosystem diversity and function.

Rare species as a group are heterogeneous, and even quantifying rarity within a single ecosystem is challenging, though the system developed by Rabinowitz et al. (1981, 1986) based on species' geographic range, population size and habitat specificity, is often recognized as a benchmark. Because rare species vary widely in their ecological associations and habitat requirements, predicting their occurrence across the landscape is challenging. A further difficulty is that the ecology and distribution of many rare species are not well understood, and obtaining data to further our understanding of these can be time, labour, and cost-intensive. Owing to these difficulties, efforts have been made to find surrogates that can predict the occurrence of rare species. One avenue that has been investigated across a variety of ecosystems and taxonomic groups is the relationship between species richness and the abundance of rare species (White et al. 1984; Wheeler 1988; Prendergast et al. 1993; Kaye et al. 1997; Lawler et al. 2003; Vanderpoorten and Engels 2003; Gjerde et al. 2004; Stohlgren et al. 2005; Locky and Bayley 2006; Pearman and Weber 2007). These studies assess the degree to which taxonomic richness, which is relatively straightforward to measure, correlates with the occurrence of rare species. From a conservation planning perspective these relationships are also of interest, as sites that encompass both high levels of richness and an abundance of rare species constitute clear priority areas for conservation. Global scale assessments naturally focus on high-diversity regions and hotspots of endemism, such as the tropics and the Mediterranean Basin (Myers et al. 2000; Brooks et al. 2006), but understanding regional patterns of rarity and richness in less-diverse systems remains important for informing local conservation and management of biodiversity in these regions.

One such region is the boreal forest: while the boreal region remains relatively intact (Mittermeier et al. 2003), it is not exempt from growing anthropocentric pressures. For example, Canada's boreal ecosystems are affected by hydroelectrical developments, timber harvesting, oil and gas exploration and extraction, agriculture, and mineral and peat mining, and these activities occur predominantly in the southern portions of the region, where the majority of boreal biodiversity is also concentrated (Venier et al. 2014). In spite of such pressures, protected areas in the boreal forest comprise a low proportion of the landbase relative to other biomes globally, with 6.8% protected in Canada (Andrew et al. 2012) and

8.9% globally (Jenkins and Joppa 2009), compared to a worldwide average of 12.8% across all biomes. The combination of these factors raises concerns about how anthropogenic activity will affect the diversity and integrity of boreal ecosystems, as well as rare species they support. Few studies have focused on the relationships between biodiversity and rare species in the boreal forest (though see Locky and Bayley 2006; Zhang et al. 2014), perhaps because of its relatively low levels of richness and endemism compared to other regions (Mittermeier et al. 2003; Mills and Schwartz 2005). However, the combination of relatively limited protection and increasing human impacts warrants closer investigation of patterns of richness and rarity in boreal ecosystems.

Our primary objectives here are to evaluate richness-rarity relationships in boreal forest vascular plant communities, using Rabinowitz' classification system for defining rarity, with a secondary focus on richness-rarity patterns across different habitat types, and to determine the potential for richness to act as a surrogate for rarity. Based on results of similar studies, we anticipate that richness will predict the occurrence of rare species (Wheeler 1988; Prendergast 1993; Kaye et al. 1997; Locky and Bailey 2006; Pearman and Weber 2007; but see Gjerde et al. 2004; Stohlgren et al. 2005). If this is indeed the case, the question of whether richness is an appropriate surrogate for site conservation value may be less straightforward, depending on whether these relationships vary by rarity type or habitat type. Here, we test these predictions by comparing vascular plant richness and rarity in the Lower Athabasca region of Alberta, Canada.

Methods

Study area and data collection

The study was conducted in the Lower Athabasca Regional Planning area (LARP), which covers an area of 93 212 km^2 of northeast Alberta, Canada (Fig. 1). The LARP has been subjected to intensive industrial development over the past half century: active forest harvesting occurs throughout the region, and agriculture and grazing are common in the south, while oil and gas extraction is prevalent throughout the region, most notably in the Athabasca oil sands region near Fort McMurray. The rapid development of the oil sands and the resultant disturbances have led to concerns about the effects these developments might have on regional biodiversity and ecological processes (Rooney et al. 2012; Caners and Lieffers 2014; Muhly et al. 2015; Dabros et al. 2018; Mao et al. 2018; Filicetti and Nielsen 2018; Riva et al. 2018; Roberts et al. 2018).

The LARP is dominated by a mosaic of mixedwood, deciduous, and coniferous forest, with numerous wetlands and wetland complexes. Dominant tree species include trembling aspen (*Populus tremuloides*), white spruce (*Picea glauca*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), and tamarack (*Larix laricina*). The climate is cool continental: mean monthly temperatures in Fort McMurray, located centrally in the study area, range from − 17.4 °C in the coldest month to 17.1 °C in the warmest month (Environment Canada 2017). Mean annual precipitation is 419 mm, the majority of which falls as rain during the summer months (Environment Canada 2017).

We used data collected in 602 plots during the peak of the growing season (July–August), between 2012 and 2015. Sites spanned a wide geographic area, covering a north–south distance of 425 km (Fig. 1). Site selection followed a model-based sampling approach (Guisan et al. 2006), directed by a landscape model that predicted the occurrence
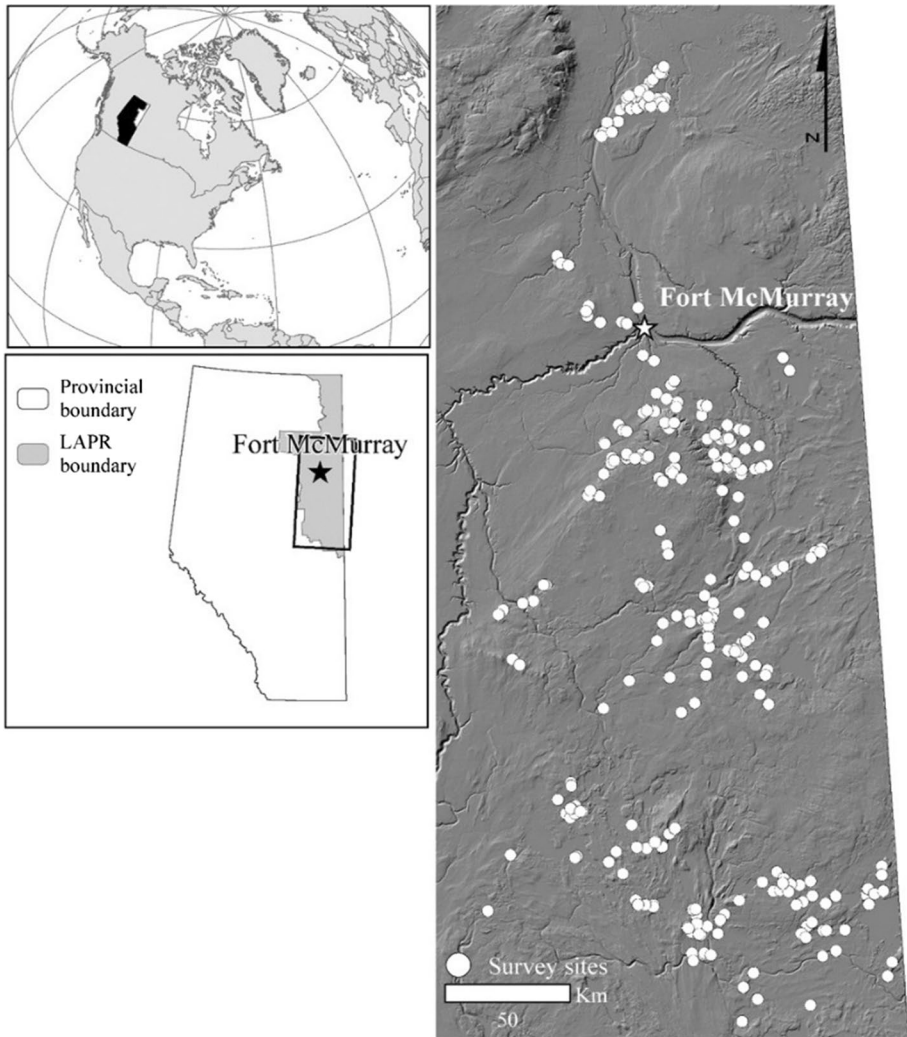
Fig. 1 Lower Athabasca regional planning area in northeast Alberta, Canada

of provincially rare species (those listed as S1 [critically imperiled] and S2 [imperiled]) within the LARP, described in Nielsen (2011). Sites with high, moderate, and low predicted probability of rare species occurrence were visited in each sampling year.

The following is a summary of data collection methods focused on elements pertinent to the analyses presented here; a comprehensive description of all field data collection methods is available in Grainger et al. (2013). Each site consisted of two 50×50 m (0.25 ha) plots less than 300 m apart and within 3 km of a paved or gravel road, placed in contrasting habitat types to maximize species detections. Plots were positioned in such a way that they encompassed, to the degree possible, a single habitat type. Plots were surveyed systematically by experienced surveyors with study-region specific training using a series of parallel belt transects. Transects were approximately 2 m wide, but the width was adapted based on vegetation density and sightlines. Each vascular plant species observed in the plot was

entered into an electronic tablet that automatically recorded the time to detection for each species. Surveys were time unlimited, allowing surveyors to tailor their pace in accordance with site complexity. Surveys were terminated once the surveyor was confident that they had thoroughly searched the plot (median search time = 95 min [effort of 0.038 min/m^2], range = 20–290 min). Unknown plants or those with particularly challenging taxonomy were pressed and sent to an expert at the Royal Alberta Museum for identification or verification.

Each plot was assigned an ecosite type using a modified version of the Alberta Ecosite Classification System developed by the Alberta Biodiversity Monitoring Institute, with 12 possible classifications (ABMI 2015, Table 1). Ecosites are defined by moisture and nutrient conditions and identified based on the presence of indicator plant species.

Data preparation and definitions of rarity components

Prairie species (which are at their range edge in the boreal region), hybrids, and species not native to Alberta were removed for the purposes of these analyses, as species in these groups could be erroneously classified as rare based on their low prevalence in the dataset (Online Appendix A, Table 1). We also removed all records identified only to genus or family, and all records with questionable identifications. Nomenclature was based on the best available information from the Flora of North America (Flora of North America Editorial Committee 1993+), VASCAN (Brouillet et al. 2010+), and the Integrated Taxonomic Integration System (ITIS 2017).

We used Rabinowitz' (1981) system of classifying species based on a combination of their geographic range, population size, and habitat specificity. These three "axes" or metrics of rarity combine to create seven different types of rare species, and an eighth category (habitat generalists with large population and wide ranges) representing common species (Table 2). The first step to classifying species in Rabinowitz' system was to quantify each

Table 1 Twelve ecosite classes used to define the nutrient and moisture conditions for 602 field assessed 0.25 ha plots, based on ABMI (2015)

Nutrient/moisture code	Definition
NT	Not Treed
PX	Poor-Xeric (Jack pine forest)
PM	Poor-Mesic
PD	Poor-Hydric (Bog)
MX	Medium-Xeric
MM	Medium-Mesic
MG	Medium-Hygric
MD	Medium-Hydric (Poor Fen)
RG	Rich-Hygric
RD	Rich-Hydric (Rich Fen)
SD	Swamp
VD	Very Rich-Hydric (Marsh)

Generally speaking, the first letter of the code indicates nutrient status, and the second moisture levels, with the SD (swamp) ecosite being the exception to this pattern. In cases where the ecosite type encompassed a single habitat type, the habitat is shown in parentheses. Most ecosite types encompassed two or more different habitat types

Table 2 Rabinowitz rarity types, based on Rabinowitz (1981)

Geographic range		Wide		Narrow	
Population size		Large	Small	Large	Small
Habitat specificity	Generalists	GLW	GSW	GLN	GSN
	Specialists	SLW	SSW	SLN	SSN

The category GLW, generalist species with wide geographic ranges and large population sizes, represents the eighth category capturing common species

of the three metrics of rarity along continuous gradients. Thresholds were then established to separate each of these gradients into two discrete groups, allowing for classification of species into rarity types. We describe in more detail below each of the three rarity metrics.

Geographic range

Species' North American ranges, exclusive of Mexico, were determined based on the number of jurisdictions in which each species has been documented in Canada and the United States, using occurrence data from NatureServe, the US Department of Agriculture PLANTS database (USDA 2017), the Flora of North America (Flora of North America Editorial Committee 1993+), and VASCAN (Brouillet et al. 2010+). The area (km^2) of each jurisdiction was compiled from Canadian and US government sources (Government of Newfoundland and Labrador 2016; Statistics Canada 2016; United States Census Bureau 2016). Areas of all jurisdictions in which each species is present were then summed to provide an approximation of species' range.

To assess whether using full jurisdictional areas might overestimate species' ranges, we compared this approach to a Minimum Convex Polygon (MCP) method, where we generated an MCP for 5% of our species based on occurrence data (see Appendix B for detailed methods). While the raw range sizes differed substantially between the two approaches, the values were strongly positively correlated ($r = 0.89$). Because relative differences in range size among species were more important than absolute size for this analysis, we proceeded with the jurisdiction-based data.

Habitat specificity

Habitat specificity was assessed using the occurrence of species across the 12 ecosite types found in the study area (Table 1), under the assumption that species found in a small number of ecosites are more likely to be habitat specialists than those found in multiple ecosites. However, this assumption was confounded by species' overall prevalence within the study area, as prevalence was strongly and positively correlated with the number of ecosites in which a species was detected. To address this issue, we developed a metric for habitat specificity based on indicator values (IVs), using the methods developed by Dufrêne and Legendre (1997) for use in Indicator Species Analysis (ISA). While this is not a typical application of ISA methodology, its conceptual underpinnings make it suitable for assessing habitat specificity, as ISA is based on the strength of the association between species and various ad-hoc groups, in our case ecosites. These associations are quantified as IVs, where higher IVs indicate strong relationships between a particular species and a

given ecosite. We calculated IVs for each species in each ecosite type with the ISA function in PC-ORD Version 6 (McCune and Mefford 2011), using the modification developed by Tichý and Chytrý (2006) to control for differences in sample size among ecosite types. This modification also uses presence-absence of species rather than abundance, making it a suitable option for our dataset. We then calculated the evenness of the IVs for each species across the 12 ecosite types, using the method developed by Pielou (1966), which is widely applied in ecology. A high level of evenness in IVs across ecosites indicated generalist tendencies, while low evenness suggested strong affinities with one or few ecosites. Evenness measures were standardized between 0 and 1, and the inverse was taken so that higher values corresponded with higher specificity. The resulting values for each species were used as our metric of habitat specificity.

Relative abundance

We used time to detection, on a plot level, as an indicator of species' abundance within plots, i.e., species that are present in high abundance are likely to be detected earlier in a survey than those that occur in small numbers. Records lacking time stamps due to equipment malfunctions were excluded, as were species that had more than one time stamp for a single plot. Because total survey time varied substantially among plots, detection times were standardised by the total plot survey time. Abundance was quantified for each species by taking the inverse of the median standardized time to detection for all observations of that species. The results of the abundance and habitat specificity methods were reviewed by two of the authors (J. Dennett and V. Crisfield), both of whom have extensive experience with boreal plant communities, to ensure that results were consistent with our understanding of species' ecology within the study region.

Rabinowitz rarity classification

Classifying species into Rabinowitz' rarity types required establishing thresholds to divide each of the three gradients into binary groups representing common and rare species. With no apparent biologically-meaningful breaks in the data, classification relied substantially on our knowledge of species' ecology. We split data for each rarity metric at the 25th/75th and 10th/90th percentiles to assess the viability of these as biologically-meaningful thresholds, and chose one of the two thresholds based on how they classified a subset of species that we had pre-assigned to particular categories based on their ecology. In all cases, we tended towards conservatism in our selection of thresholds in order to isolate truly rare species, not only from common species, but also from those that occupied intermediate positions along each gradient. Species for which we had fewer than three records were classified manually based on professional judgement and information available in floras and other botanical references. Twenty-six species were excluded owing to a lack of information with which to classify them.

Data analyses

Analysis 1: individual rarity metrics

Continuous rarity metrics were summarized by calculating the mean of each variable (range, abundance, and habitat specificity) among all species for each survey plot. Species

that had been detected only once were excluded, and all variables were log10-transformed to reduce the skewness of the data. Regression models were then created to relate each of the three individual rarity metrics to plot richness, with richness as the predictor. Both linear and non-linear responses were tested, and model fit (R^2) was used to select the best-supported model. Additionally, we used Kruskal–Wallis tests to assess differences in the three rarity metrics (response variables) among ecosites (predictor variable). Kruskal–Wallis was chosen because the data did not conform to the requirements of suitable parametric methods. The VD (marsh) ecosite was excluded from these analyses as it was only represented by two plots. Dunn's test was then used to perform pair-wise comparisons between all ecosite types, using a Bonferroni correction. All analyses were conducted in R Version 3.3.1 (R Development Core Team 2018; Jackman 2017; Zeileis et al. 2008; Ogle et al. 2019).

Analysis 2: Rabinowitz rarity types

We compared the occurrence of each of the eight Rabinowitz types (i.e., the number of species belonging to each type per plot) to plot-level species richness (predictor). Additionally, we aggregated all seven rare types and compared their combined occurrence to plot richness. Three of the rarity types (SSN, SSW, GSN) were too data poor for statistical analysis and were thus excluded. The remaining groups were analysed using either a generalized linear model (GLM) or a Poisson model, based on the normality and dispersion of model residuals. For types analysed using Poisson models, both Poisson GLMs and zero-inflated Poisson models were tested, with Vuong's test used to select the more appropriate model type.

Differences in the occurrence of rare species (all seven types combined; response variable) among ecosites (predictor) were analysed using Kruskal–Wallis tests, using the same methods as described in the previous Sect. (2.4.1). We analysed the occurrence of rare species by ecosite in two ways: (1) the number of rare species per plot, and (2) the percentage of total site flora comprised by rare species. In addition, we tested differences in species richness across ecosites using the same methods.

Results

A total of 31 398 species records were collected, representing 600 taxa. Following the removal of genus and family level records (55 records), prairie species (81 records), exotic species (592 records), hybrids (2 records), and records with obviously erroneous determinations (6 records), 460 vascular plant species were available for analysis; of these, 413 species were included in Analysis 1, and 433 species were included in Analysis 2 (Online Appendix A, Table 2).

Analysis 1: individual rarity metrics

On average, species tended to have large geographic ranges (mean of 13.9 million km^2 out of a total area of 19.8 million km^2; SD = 3.3), low habitat specificity (mean 0.37 out of a possible maximum of 1; SD = 0.23), and high relative abundance (mean 0.77 out of a possible maximum of 1; SD = 0.17), suggesting a strong tendency for the species pool in our study region to display characteristics of common species. Geographic range and

habitat specificity were best represented by a quadratic model, while relative abundance demonstrated a linear response. Relationships between richness and the three individual rarity metrics were all highly significant ($p < 0.001$), and were positive for range size, but negative for habitat specificity and abundance (Fig. 2). All three metrics differed significantly among ecosites (X^2 abundance $= 166.38$, X^2 range $= 164.77$, X^2 specificity $= 254.29$; df $= 10$ and $p < 0.001$ for all metrics; Online Appendix C Fig. 1).

Analysis 2: Rabinowitz rarity types

Based on our review of the spread of data and potential thresholds for each gradient, the 10th percentile was selected as a threshold for relative abundance and geographic range, while the 25th percentile was selected for habitat specificity. Species that scored below these thresholds were classified as rare for the respective metric. Common species (GLW) were by far the most speciose of the eight types, accounting for 288 of the 433 species included in this analysis. Common species also dominated most plots, accounting for the majority of species present: while representing 67% of the species in the analysis, common species accounted for a mean of 94% of the flora in each plot.

Relationships between richness and plot level occurrence of species belonging to the five analysed rarity types were all significant ($p < 0.05$); however, explanatory power (pseudo R^2) varied substantially (Table 3, Fig. 3). The relationship between richness and the seven combined rarity types was positive and significant, but with very low explanatory power. The occurrence of rare species, both as a raw count and as a percentage of total site flora, differed significantly among ecosites (X^2 count of rare species $= 93.931$, X^2 percent rare species $= 101.96$; df $= 10$ and $p < 0.001$ for both metrics; Online Appendix C Fig. 2). Species richness also differed significantly among ecosite types ($X^2 = 158.67$, df $= 10$, $p < 0.001$; Online Appendix C Fig. 2).
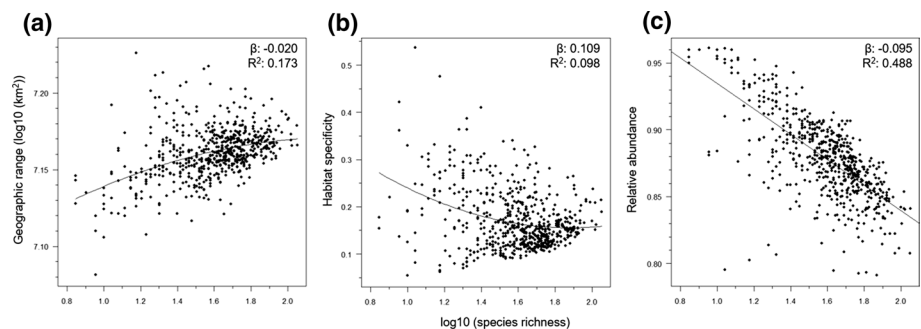

Fig. 2 Regressions of relationships between species richness (log10 transformed) and **a** geographic range [log10 (km^2)], **b** habitat specificity, and **c** relative abundance. Habitat specificity and relative abundance are both represented by unitless metrics standardised between 0 and 1, with 0 indicating very low levels of abundance/specificity, and 1 representing very high levels of abundance/specificity. Individual points in each of the graphs represent mean values for that metric for all species detected within the 0.25 ha plot

Table 3 Parameters of generalized-linear, Poisson, or zero-inflated Poisson models of rarity type as a function of species richness

Rarity type	Model type	ΔAIC[a]	Pseudo R[2b]	β	SE	p
GLW	GLM	1804.4	0.345	0.930	0.008	<0.001
GLN	Poisson GLM	213.2	0.113	0.022	0.002	<0.001
GSW	Poisson GLM	144.1	0.183	0.034	0.002	<0.001
SLN	ZIP	2.9	0.197	0.013	0.006	0.035
SLW	ZIP	20.5	<0.001	0.012	0.002	<0.001
All rares	ZIP	33.9	0.012	0.020	0.001	<0.001

[a]Compared to a null model for the same type

[b]Calculated using the following *1-(log likelihood of best model/log likelihood of null model)*

Discussion

Analysis 2 demonstrated a generally positive relationship between local species richness and the occurrence of rare species; by contrast, Analysis 1 showed that when considered individually, two of the three rarity metrics (habitat specificity and relative abundance) had negative relationships with richness. This apparent contradiction can be explained by the high prevalence of common species as a proportion of both number of species in the species pool and records in the dataset. Thus, it was the common species that drove trends between plot richness and mean values for each of the rarity metrics, and the influence of rare species on these patterns was swamped by the much larger number of common species.

Our analysis classified the majority of species as common (GLW), contradicting results from similar studies of British (Rabinowitz et al. 1986) and Norwegian (Sætersdal 1994) plant communities, where the majority of species were classified as rare. Rabinowitz et al. classified 57–64% of the British flora as rare (based on conservative and liberal classifications, respectively), while 63% of the species assessed by Sætersdal were determined to be rare at the regional level. By contrast, we classified only 33% of the species in our dataset as rare. This discrepancy is attributable in part to methodological differences; Rabinowitz et al. relied on professional judgement, while Sætersdal used phytosociological datasets as a basis for classification. That said, our decision to use conservative thresholds no doubt influenced species richness in each of the eight rarity types and limited the number of species that were classified as rare; however, we believe our decision is appropriate based on ecological characteristics of the boreal forest, and that differences between our results and the cited studies reflect differences in the ecology of the three study regions. The boreal region is a high-latitude, evolutionarily young landscape that is generally characterised by shallow ecological gradients with few barriers to species dispersal, all of which promote lower levels of endemism and a tendency towards larger geographic ranges (Cain 1944; Mills and Schwartz 2005; Zhang et al. 2015). The low number of habitat specialists is probably also attributable to the relatively moderate levels of environmental variation in our study area. While our study area was intermediate in size between those studied by Rabinowitz and Sætersdal, the latter two studies encompassed coastal habitats and mountain ranges, representing a much greater degree of contrast among habitats than what is found within the Lower Athabasca region, and thus requiring higher levels of habitat-specific adaptations such as tolerance for saline conditions or extreme cold. As for relative
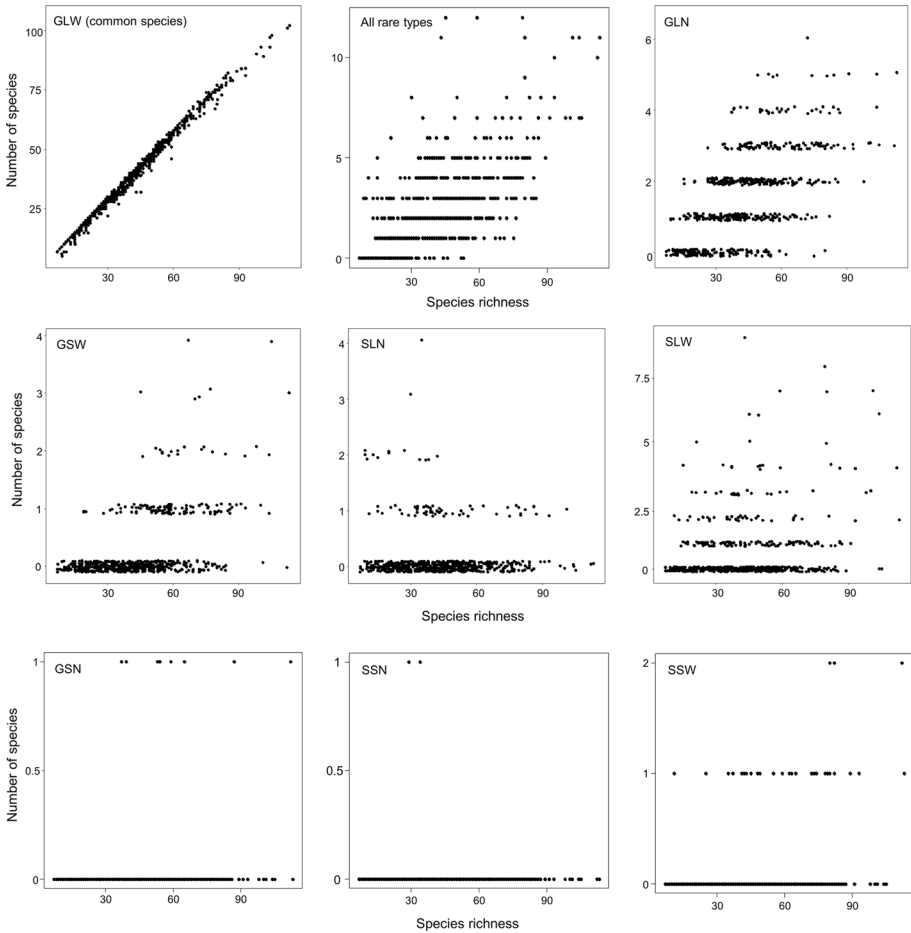
Fig. 3 Relationships between plot species richness and rarity types. The x-axis represents total plot species richness, and the y-axis the number of species (of each given category) per plot. Rarity type abbreviations indicate species' habitat specificity (generalist (G) or specialist (S)), relative abundance (large population (L) or small population (S)), and geographic range (wide (W) or narrow (N)). The upper lefthand panel (GLW) represents common species, the second represents the seven rarity types combined, and all other panels represent the seven types of rare plants

abundance, the preponderance of relatively large populations in our dataset may be attributable to high levels of clonality among boreal plants (Barrett and Helenurm 1987; van Groenendael et al. 1996), which has been found to be associated with higher levels of local abundance (Kolb et al. 2006). Thus, the geographic, climatic, and ecological characteristics of the boreal forest likely promote the dominance of species that are habitat generalists, have broad geographic ranges, and/or occur in high abundance.

In the Rabinowitz rarity analysis, we isolated rare species, allowing us to examine relationships between rare species and the surrounding plant community. Most rarity types had a positive relationship with richness, and based on the preponderance of common species in the dataset, it is unlikely that this relationship is an artefact of the contribution of rare species to total plot richness. We believe our results reflect a real biological relationship

that echoes results of similar studies (Wheeler 1988; Prendergast et al. 1993; Kaye et al. 1997; Locky and Bayley 2006; Pearman and Weber 2007), but the mechanisms behind this relationship are unclear. It is possible that, as an aggregate, rare species are ecologically similar to common species and respond similarly to common drivers of species richness such as productivity, soil microbes (van der Heijden et al. 2008), and disturbance. The causes of their uncommonness might therefore be unrelated to the determinants of community richness.

Although the observed strong, significant relationships between species richness and rarity support our initial prediction, we conclude that richness is not an appropriate surrogate for site conservation value in our study area, for two reasons. First, results of Analysis 1 suggest that the richest plots most effectively capture a large number of widespread habitat generalists. Second, the broad-scale correlation between richness and rare species masks a significant amount of variation among habitat types. For example, the PX (poor-xeric) ecosite, which is represented by jack pine-dominated communities on sandy soils, was among the most species-poor ecosites in our dataset (mean richness = 30 species per 0.25 ha), but had the highest occurrence of rare species as a proportion of overall plot flora, at 12%. Meanwhile, the RG (rich-hygric) ecosite, represented by a variety of rich, moist forest types, had roughly twice the average species richness as PX plots, but supported the same average number of rare species per plot. The PX ecosite is an ecologically-distinctive habitat in the LARP, and supports species not found in other habitat types in our study area, including slender lady's tresses (*Spiranthes lacera*), an orchid at the western limit of its range in Alberta (USDA 2018), as well as impoverished pinweed (*Lechea intermedia* var. *depauperata*), a narrow endemic (Lemke 2015). A regional-level approach, exclusive of habitat type and focused on richness, would underestimate the value of this ecologically significant habitat type, and thus be a poor tool for promoting the conservation of the above species and other rare species of relatively depauperate habitats. In fact, two of the perhaps most botanically significant sites in the LARP, La Saline Natural Area and the Athabasca Sand Dunes (which extend eastward across the border of Saskatchewan), are characterised more by their environmental uniqueness than by high levels of species richness. La Saline is fed by a salt spring, giving rise to salt-tolerant vegetation communities that are highly uncommon in the boreal forest and support numerous provincially rare species (Timoney and Robinson 1991), while the Athabasca Sand Dunes include areas of active sand dunes, a very unusual landscape feature in the boreal forest. The Athabasca Sand Dunes support approximately 10 narrowly endemic plant taxa (Lamb and Guedo 2012; but see Argus 2010), and, when considering the whole of Alberta, rank among the highest areas of endemism (Zhang et al. 2015). Neither of these sites is characterised by high levels of vascular plant richness; however, they both support rare species of provincial, national, and even global significance.

Conclusions

Unlike other studies using comparable methods, we found that most species in the boreal forest are common at the regional scale, which we attribute to many of the ecological and geographic characteristics of the boreal forest. Rare species were indeed more prevalent in richer plots, confirming one of our original hypotheses. However, we do not consider local richness to be an appropriate surrogate for site conservation value, because regional-scale trends obscure important ecosite-level patterns. Rather, predicting the occurrence of rare

species in the boreal requires a more nuanced approach, and conservation efforts will be more fruitful if they focus on the full range of habitat types present, rather than prioritizing the richest sites.

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