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Ecological processes affecting weed communities in Nova Scotian wild blueberry fields

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ABSTRACT

Ecological gradients and processes are known to play a key role in determining weed community composition in agroecosystems. The present study investigated whether climatic, topographical, and soil edaphic factors were associated with weed species occurrences and abundances in wild blueberry fields. A plant survey of 165 wild blueberry fields in the Canadian province of Nova Scotia was conducted and combined with climatic, topographical, and soil edaphic data collected from Federal databases. Linear mixed models and multivariate analyses were used to disentangle the relationship between weed species occurrences, species-species interactions, and environmental covariates in wild blueberry fields. The surrounding weed species diversity in fields had the strongest association with wild blueberry stem density with increasing species richness driving a decrease in stem density regardless of weed density. Weed diversity was affected by accumulated growing degree days, topographical position index, and topographical wetness index. The occurrence and abundance of many common weed species was positively associated with wild blueberry and accumulated growing degree days. The relative importance of niche-based assembly rules for overall weed species composition in wild blueberry fields, however, was minimal. Yet several species showed high correlation with environmental cofactors. These results stress the importance of local stochasticity and species-species interactions in determining weed communities in wild blueberry fields and the challenge with predicting weed communities in perennial agroecosystems.

1. Introduction

Wild blueberry is a deciduous perennial shrub native to North America and the most economically important fruit crop in Canada (Statistics Canada.., 2022). Within wild blueberry fields, *Vaccinium angustifolium* Ait. and *V. myrtilloides* Michx. form the majority of commercial stands (Strik and Yarborough, 2005). Wild blueberry is low-growing with a deep taproot and new shoots arising from a rhizome network. Viable seeds are produced, however, its seedbank longevity and persistence is minimal and seedlings likely do not contribute to patch expansion in fields (Jensen and Yarborough, 2004; Drummond, 2019). Wild blueberries are managed on a unique two-year production cycle where shoots are pruned to ground level by mowing or burning in the first year, termed the non-bearing year, and then emerged shoots are left to flower and produce berries in the second year, termed the bearing year. Weeds are a significant limiting factor in wild blueberry production and contribute to variations in yield and fruit quality (Jensen and Yarborough, 2004; McCully et al., 1991). Wild blueberry is an early successional species and fields are typically developed from natural vegetation stands, abandoned farmland, and cleared forests (Hall, 1959). Therefore, weed management in wild blueberry must strike a balance between maintaining the agroecosystem in an early successional phase while ecological succession progresses.

Weed management in wild blueberry is complicated by the two-year production cycle, the perennial nature of the crop, and the reliance on rhizome growth for clonal expansion. Weed management typically consists of mowing every other year and a few select broad-spectrum herbicides applied in the non-bearing year with little variation in weed management practices across the major North American production regions (Bell et al., 1999; Scherm et al., 2001; Jensen and

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Yarborough, 2004; Rose et al., 2013). In contrast to the majority of annual cropping systems, weed communities in wild blueberry fields are often dominated by native woody and herbaceous perennials that are not considered weeds in other cropping systems (Jensen and Yarborough, 2004). The historical reliance on burning and mowing in the production cycle has selected for several species including bunchberry (*Cornus canadensis* L.), fireweed (*Chamaenerion angustifolium* (L.) Scop.), cow wheat (*Melampyrum lineare* (Desr.)), and spreading dogbane (*Apocynum androsaemifolium* L.) which are well adapted to frequent disturbance and commonly associated with a post-forest-fire plant community (Lynham et al., 1998). The now wide-spread use of selective herbicides, however, has shifted weed communities to include those tolerant of commonly applied herbicides. Further shifts in wild blueberry management practices, including the deregistration of atrazine (Anonymous, 2003), increase in herbicide-resistant species (Li et al., 2014; Laforest et al., 2022), and weed-seed dispersal on equipment (Boyd and White, 2009), has had unintended consequences on weed communities in wild blueberry fields. Species richness of both annual and perennial grasses and broadleaves more than doubled from the period of 1984–2020 (McCully et al., 1991; Lyu et al., 2021). This trend towards increased richness has allowed more species reliant on seed dispersal to colonize wild blueberry fields and is characteristic of a plant community progressing to later successional stages. This increases the relative importance of local environmental factors for determining which species successfully invade and colonize a particular wild blueberry field.

The majority of weed research focuses on the explicit control and removal of weeds in agricultural settings and pays little attention to the ecological processes governing weed population assembly nor the consequences of weed removal on the agroecosystem. In contrast to annual cropping systems which are maintained in a constant state of primary and secondary succession by tillage and herbicides (Smith, 2015), many wild blueberry fields are decades old which allows for ecological succession processes to shape weed communities. Yet understanding and anticipating how ecological processes alter weed population assembly in agricultural fields remains poorly understood. Joint species distribution models are advanced multivariate analyses developed from the community ecology literature that shows promise as a tool to unravel how weed communities are shaped by ecological processes in agricultural systems (Thorson et al., 2015; Ovaskainen et al., 2017). These models account for species-species interactions and how species interact with environmental cofactors to model species occurrences and abundances. Further, these models can provide predictive tools for anticipating weed population shifts under changing environmental conditions (Schliep et al., 2018). These analyses to study weed populations and ecological processes across broad geographic areas may provide researchers and producers tools to monitor and anticipate weed challenges in response to environmental change.

In the present study we sought to identify climatic, topographical, and soil edaphic factors associated with wild blueberry stem density and weed species communities within wild blueberry fields in the province of Nova Scotia, one of the largest producers of wild blueberries in Canada. Nova Scotia is surrounded by the moderating forces of the Gulf of Saint Lawrence, the Bay of Fundy, and the Atlantic ocean and has a relatively mild climate with highly varied geography. The primary wild blueberry producing regions are in the southern shore of Nova Scotia classified as a coastal uplands ecodistrict and along the north coast classified as Nova Scotia highlands and Maritime lowlands ecodistricts (Webb and Marshall, 1999). There is, however, little year-to-year and geographic variation in producers' specific weed management practices (Rose et al., 2013; USDA-NAAS, 2023). Further, high levels of within-field genetic diversity and the effects of management practices on specific genotypes has a large role in determining wild blueberry stem density which is negatively correlated to productivity and yield in wild blueberry production systems (Beers et al., 2019; Barai et al., 2022). Therefore, we hypothesized that weed species occurrences and their abundances would be associated with wild blueberry stem density, used as a proxy for management intensity, in addition to environmental, topographical, and edaphic factors. We used a recently completed vegetation survey of 165 wild blueberry fields across the province of Nova Scotia and linked it with readily available climatic, topographical, and edaphic data to evaluate relationships between factors, species, and species co-occurrence patterns using univariate and multivariate analyses.

2. Materials and methods

2.1. Site selection and plant community data collection

Here we provide a brief description of data collection; for a complete description of site selection and data collection see Lyu et al., (2021). A total of 165 bearing-year wild blueberry fields across the province of Nova Scotia were surveyed in 2017 (84 fields), 2018 (49 fields), and 2019 (32 fields) (Fig. 1). Bearing-year fields were selected as they are rarely treated with herbicides and therefore represent how the weed community would assemble in the absence of additional disturbance and in response to weed management in the previous year. All plant species, including wild blueberries and weeds were identified to species and their respective density, measured as emerged shoots, was counted in 20, 1 m quadrats placed in a 'W' pattern across each field. Wild blueberry stem density was determined as the number of emerged wild blueberry shoots in a quadrat regardless of genet status. No effort was made to distinguish between *Vaccinium angustifolium* and *Vaccinium myrtilloides* and both were considered wild blueberry for the survey. All other plants inside the quadrat were considered weeds and individual shoots counted. It is acknowledged that not all plants within wild blueberry fields have a negative impact on the crop and are therefore not technically weeds, however, we have used this terminology for simplicity. Field size was estimated from satellite images using the Draft Logic Google Maps Area Calculator as described by Esau et al., (2019) and distance between quadrats adjusted based on field size with greater distance between quadrats in larger fields and less distance between quadrats in smaller fields (McCully et al., 1991). Field locations were georeferenced.

2.2. Collection of edaphic, topographical and climatic variables

The Canadian Digital Elevation Model (CDEM) dataset was obtained from the open Canada data catalogue (Natural Resources Canada, 2015). The Digital Elevation Models (DEM) were downloaded for the Nova Scotia study area and all DEMs were mosaicked into a single DEM prior to preprocessing. Preprocessing of the DEM was performed through the Whitebox package (Lindsay, 2016) in R Studio and consisted of filling missing values, feature preserving smoothing, 3×3 mean filters and completed with the filling of single cell pits. The resulting DEM was then used as input to create DEM derivatives using the terrain analysis tools from the '*RSAGA*' package in R Studio (Brenning, 2008). All raster datasets resulting from the terrain analysis were exported in GeoTIFF format. The accumulated precipitation datasets were obtained from the open Canada data catalogue (dataset Agriculture and Agri-Food Canada., 2021a) as well as the growing degree days datasets (dataset Agriculture and Agri-Food Canada., 2021b). The accumulated precipitation and growing degree days (base 0) represents the accumulated precipitation and growing degree days during the growing season (May 1 – October 31) for each of the years 2017, 2018, and 2019. Base 0 was chosen as a growing degree day model for wild blueberry has been developed and validated with this base temperature for the region (White et al., 2012). The accumulated precipitation and growing degree days raster datasets were clipped to the study area from the original coverage using the Extract by Mask tool in the Spatial Analyst extension in ArcGIS Pro (version 2.6.3) (Esri Inc., 2020) followed by exporting the resulting raster datasets in GeoTIFF format for

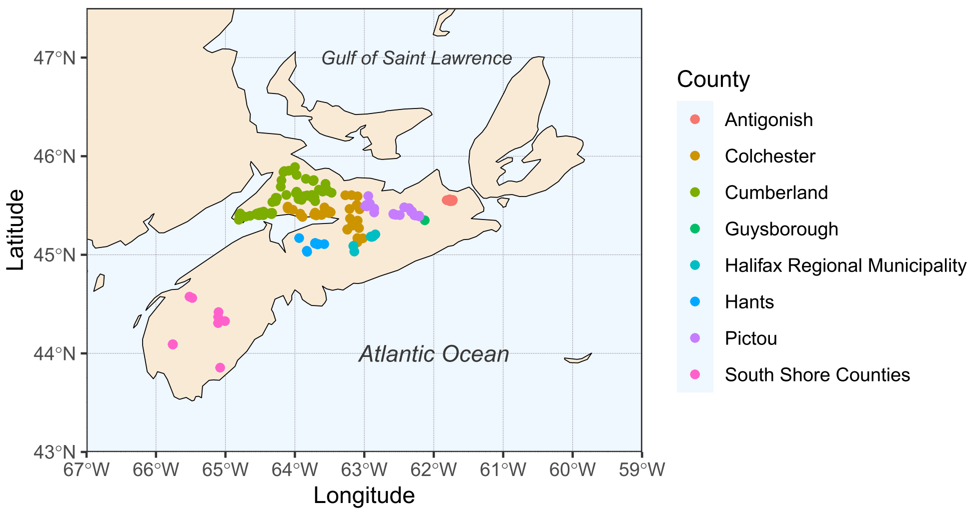

Fig. 1. Location of fields in the plant survey of wild blueberry fields in Nova Scotia, Canada. Fields are colour coded by county. See legend for colour descriptions.

use in R Studio. All raster datasets were compiled as a raster stack in R and the study sampling locations were imported into the R environment. The coordinates of the sampling locations were then used to extract the values from the raster stack to create a database of sampling location attributes with the raster values from the environmental and topographical data (Table 1). The soil dataset was obtained from the Canadian Soil Information System's (CanSIS) national soil database (NSDB) for the study area in Nova Scotia (dataset Agriculture and Agri-Food Canada., 2012). The soil databases for the study area were compiled from the NSDB's Component, Soil Map Unit File, Soil Name File and Soil Layer File. A mean topsoil value (0 – 15 cm) for each of the soil properties was calculated from the soils database and joined to the NS soil vector datasets in ArcGIS Pro. The sampling location vector dataset was intersected with the NS soil vector dataset to capture the mean soil properties for each of the sampling locations. The final sampling location dataset was exported from ArcGIS Pro to Excel and consisted of the sampling location data, environmental data, topographic data, and soil edaphic data on a field level basis.

Table 1
List of farm, environmental, topographical, and soil edaphic factors used for analyses. Units for each variable and additional notes are also included.

Variable	Units	Notes
Farm		
County	Antigonish	10 fields
	Colchester	39 fields
	Cumberland	66 fields
	Guysborough	1 field
	HRM[a]	9 fields
	Hants	9 fields
	Pictou	21 fields
	SSC[b]	10 fields
Field size	ha	Estimated as described by Esau et al., (2019)
VACAN[c]	stems m^{-b}	
Environmental		
GDD[d]	GDD accumulated during growing season - base 0°C	Average from May – Oct, 2017–2019
Precipitation	mm accumulated during growing season	Average from May – Oct, 2017–2019
Topographical		
Elevation	m above sea level	
Slope	%	
Topographical position index	Unitless	Compares the elevation of a point to the mean elevation of surrounding points
Topographical wetness index	Unitless	Measure of topographical control over hydrological processes
Edaphic		
Sand	%	0 – 15 cm layer
Silt	%	0 – 15 cm layer
Clay	%	0 – 15 cm layer
SOC	%	0 – 15 cm layer
pH	Unitless	0 – 15 cm layer

[a] Halifax Regional Municipality
[b] South Shore Counties
[c] Vaccinium angustifolium
[d] Growing degree days

2.3. Univariate analysis

All analyses were conducted in R v.4.0.3 (R Core Team, 2020). Weed species richness (R) and Shannon's diversity index (H), herein referred to as diversity, were calculated with the R-package '*vegan*' (Oksanen et al., 2022). Evenness (E) was calculated as $E = H/\ln(R)$. To determine the impact of explanatory variables on wild blueberry stem density, weed density, weed species richness, and weed Shannon diversity and evenness, independent linear mixed effects models were constructed, each with an explanatory variable (Table 1) as the sole fixed effect and field nested within county as the random effect except for the model relating explanatory variables to county which only included field as a random effect (Hofmeijer et al., 2021). Response variables were averaged per field prior to univariate analysis. As our objective was to evaluate how individual cofactors influenced a community trait, we did not consider interactions between fixed effects. Outliers, defined as data lying outside 3 × IQR, were removed prior to analysis to comply with model assumptions. To investigate how explanatory variables (Table 1) varied by Nova Scotian county, linear mixed effects models were constructed with county as the fixed effect and field as the random effect. All linear mixed effects models were constructed with the R-package "*nlme*" (Pinheiro et al., 2020). Lack of autocorrelation between fields was confirmed by plotting model residuals by x- and y-coordinates. ANOVA assumptions were evaluated with a Shapiro-Wilk test and visual inspection of model residuals. To compare the effect size of explanatory variables on wild blueberry stem density, weed density, weed species richness, Shannon diversity, and evenness the partial eta squared (η^2) of each explanatory variable was computed from linear mixed effects models as $\eta^2 = sum\ of\ squares_{effect}\ /\ sum\ of\ squares_{total}$ (Correll et al., 2022). η^2 is a measure of effect size of an ANOVA and indicates how much variance in a dependent variable is explained by the independent variable. In general, η^2 of 0.01–0.05 is a small effect, 0.06–0.13 a medium effect, and > 0.14 a large effect. Relationships between wild blueberry stem density, weed communities, and explanatory variables was investigated with linear regression.

2.4. Multivariate analysis

Hierarchical Modelling of Species Communities (HMSC; Ovaskainen and Abrego, 2020), a joint species distribution model, was used to investigate weed community structure across Nova Scotian wild blueberry fields. The initial dataset comprised the abundances of 183 weed species within 165 wild blueberry fields sampled with 20, 1 m quadrats. Rare species defined as those with less than 5 occurrences were removed resulting in 88 weed species ($n_s = 88$). Each quadrat within a field was considered a sampling unit. Due to missing values twelve fields were removed from the analysis ($n = 3060$ sampling units). The response variables ($n \times n_s$ matrix $\mathbf{Y}$ of HMSC; see Ovaskainen and Abrego, 2020) were the abundances of each of the 88 weed species within each sampling unit. To account for the zero-inflated nature of the data, we developed two-parallel models; one probit regression model for presence-absence (PA) and one lognormal Poisson regression model for abundance conditional on presence (ACOP). ACOP data were generated from abundance data by converting all zeros to missing data, log-transforming and scaling data to zero mean and unit variance within each species. Four explanatory variables, one environmental (growing degree day; GDD), one topographical (topographical wetness index; TWI), one edaphic factor (soil organic carbon; SOC), and wild blueberry stem density were selected for inclusion in the models (the $n \times n_c$ matrix $\mathbf{X}$ of HMSC; see Ovaskainen and Abrego, 2020; where n_c is the number of species-specific parameters to be estimated). Selection of environmental, topographical, and edaphic factors was as follows. Principle component analysis was run using the mean field values of explanatory variables in Table 1. The first two principal components explained > 35 % of total variation and were retained. Explanatory variables were selected by evaluating η^2 of explanatory variables calculated as explained in Section *2.3*. and inspection of principle component analysis biplots (Fig. A.1). To avoid highly correlated variables, only a single environmental, topographical, and edaphic factor was then selected. Wild blueberry stem density was selected as a proxy for management intensity as many agronomic management practices are known to directly influence this parameter (Eaton, 1994; Penney and McRae, 2000; Percival and Sanderson, 2004; Jensen and Yarborough, 2004). To account for the survey design, two random effects were included in the models. The first was a spatial random effect defined as the x- and y-coordinates of each field and the second defined as each quadrat within a field. The R-package '*Hmsc*' was used to fit the HMSC model assuming the default prior distributions (Tikhonov et al., 2020). The posterior distribution was sampled with four Markov Chain Monte Carlo (MCMC) chains, each run for 375,000 iterations, with a burn-in of 12, 500 iterations. Chains were thinned by 100 yielding 250 posterior samples per chain for a total of 100 posterior samples. Model convergence was assessed with the potential scale reduction factor (Gelman and Rubin, 1992). Explanatory power of the PA model was assessed with the species-specific Tjur's R^2 (Tjur, 2009) whereas species-specific R^2 was used for the ACOP model. Explanatory power was evaluated by generating model predictions fit to all data. To determine drivers of weed community structure in Nova Scotian wild blueberry fields, explained variance was partitioned to fixed and random effects in both models. Species-specific responses to fixed effects were examined that displayed positive or negative associations with ≥ 95 % posterior probability.

3. Results and discussion

3.1. Climatic, topographical, and edaphic factors of wild blueberry producing counties

Climatic, topographical, and edaphic factors of wild blueberry fields differed by Nova Scotian county (Table 2). Wild blueberry fields in the southern counties of Guysborough, Hants, Halifax Regional Municipality (HRM), and South Shore Counties (SSC) on average accumulated greater GDD, were at lower elevations, and had lower topographical wetness indices (TWI) than fields in the northern counties of Antigonish, Colchester, Cumberland, and Pictou (Table 2). Fields along the north shore of Nova Scotia, including those in Antigonish, Pictou and Colchester county, on average accumulated less precipitation than other counties (Table 2). Soil in fields from Colchester and Cumberland County were majority sand with the lowest percentage silt. Northern county soils had the greatest average clay content. North county fields on average had higher SOC and higher soil pH than south county fields (Table 2). Despite differences across counties in environmental factors, there was minimal variability in parameters across Nova Scotian wild blueberry fields. In general, elevation displayed the greatest variation and ranged from a low of 66 masl to a high of 161 masl (Table 2), which subsequently impacted the topographical position index (TPI).

3.2. Factors affecting wild blueberry stem density

Nova Scotian wild blueberry producing counties represent distinct microclimates across a geologically diverse landscape. Individual climatic, topographical, and edaphic factors were not strongly associated with wild blueberry stem density nor remaining vegetation density or diversity (Table 3). Rather, the interaction of multiple environmental factors at the county level had the largest effect on wild blueberry stem density and the remaining weed community supporting our initial hypothesis that plant species occurrences and abundances would be associated with environmental, topographical, and edaphic factors (Table 3). Fields in counties along Nova Scotia's south shore including Guysborough, Hants, HRM, and SSC, tended to have greater wild blueberry stem density, lower weed density, and higher weed diversity compared to counties along the north shore (Table 4). In addition, fields in these counties accumulated more GDD, were at lower elevations, and had soils with less sand, and lower soil pH and SOC compared to north shore county fields (Table 2). These results are consistent with previous studies demonstrating the importance of regional and location specific climatic, topographical, and soil edaphic factors on wild blueberry productivity and yield (Lavoie, 1968; Lapointe and Rochefort, 2001; Yarborough and Cote, 2014; Yarborough et al., 2017).

Following county, SOC and soil pH had the largest association with wild blueberry stem density relative to the remaining climatic, topographical, and edaphic factors (Table 3). Stem density declined with increasing SOC and soil pH (Fig. 2E, F). Yarborough et al., (2017) found that increasing SOC and soil pH were negatively correlated to wild blueberry floral buds stem^{-1}. Similarly, other studies have found wild blueberry fruit yield to be negatively correlated to SOC and pH (Farooque et al., 2012). Management recommendations within the region promote the use of sulphur to lower soil pH below 5.0 to reduce growth of weedy vegetation (Yarborough, 2012). Lowering pH to 4.0 through repeat applications of sulphur does not appear to negatively impact wild blueberry growth, nutrient uptake, or yield while reducing grass weed species growth (Smagula and Litten, 2003). As such, a link between wild blueberry stem density and soil pH is not surprising given the natural adaptation of the wild blueberry plant to low pH soils (Hall et al., 1964; Smagula and Litten, 2003). In contrast, SOC appeared to have a larger association with wild blueberry stem density than soil pH. Few studies have documented shifts in SOC or their impact on wild blueberry growth, development, and yield. Bacterial and fungal rhizosphere communities of wild blueberry have been shown to respond to

Table 2
Least square mean of farm size and climatic, topographical, and edaphic factors of wild blueberry fields in Nova Scotian counties. Standard error of the mean (SEM) and p-values are shown. Results of a contrast comparing north counties (Antigonish, Colchester, Cumberland, Pictou) to south counties (Guysborough, Hants, HRM, SSC) is also shown.

Covariance parameters			Size (ha)	GDD[a]	Precip[b]	Slope (%)	Ele[c] (masl)	TPI[d]	TWI[e]	Sand (%)	Silt (%)	Clay (%)	SOC[f]	pH
	ndf	*ddf*						*p-value*						
County	*7*	*157*	*0.17*	*< 0.01*	*< 0.01*	*< 0.01*	*< 0.01*	*0.92*	*0.09*	*< 0.01*	*< 0.01*	*< 0.01*	*< 0.01*	*< 0.01*
County								*Least square means*						
Antigonish			8.04	2727	716	3.36	125	0.22	14.3	39.5	45.5	15.0	1.2	5.3
Colchester			6.57	2663	736	3.12	124	0.10	14.0	54.7	34.5	10.8	1.4	5.0
Cumberland			6.44	2676	750	3.81	93	0.26	13.9	50.0	38.0	12.0	0.9	4.9
Guysborough			6.89	2631	738	5.83	66	0.26	13.6	52.5	40.0	7.5	0.6	4.5
HRM			3.52	2600	732	4.29	156	0.19	13.3	35.6	51.1	13.3	0.7	4.5
Hants			4.61	2793	797	5.40	143	0.18	12.8	36.1	49.7	14.2	0.8	4.6
Pictou			4.13	2692	715	6.41	161	0.19	13.3	39.8	46.0	14.3	1.3	4.9
SSC			4.11	2883	776	2.69	114	0.41	13.8	43.2	46.9	9.9	0.6	4.5
SEM			±1.53	±14	±11	±0.92	±22	±0.20	±0.4	±2.9	±2.5	±0.9	±0.2	±0.1
								Contrasts						
North[g] vs south Counties[h]			*0.06*	*< 0.01*	*0.04*	*0.60*	*< 0.01*	*0.92*	*0.05*	*< 0.01*	*< 0.01*	*< 0.01*	*< 0.01*	*< 0.01*
North counties mean			6.30	2690	729	4.18	126	0.19	13.9	46.0	41.0	13.0	1.2	5.0
South counties mean			4.78	2727	761	4.55	120	0.26	13.4	41.9	46.9	11.2	0.7	4.5

[a] Average growing degree days, base 0, accumulated during the growing season (May – Oct) in 2017 – 2019
[b] Average precipitation (mm) accumulated during the growing season (May – Oct) in 2017 – 2019
[c] Elevation m above sea level (masl)
[d] Topographical positional index
[e] Topographical wetness index
[f] Soil organic carbon
[g] North counties – Antigonish, Colchester, Cumberland, Pictou
[h] South counties – Guysborough, Hants, HRM, SSC

Table 3
Effect size (η^2) of explanatory variables on wild blueberry (VACAN) stem density, and weed species density, richness, diversity and evenness within Nova Scotian wild blueberry fields. Values are effect size from ANOVA with p-values denoting significance (* <0.1; ** <0.05; *** <0.01; ns not significant).

Factor	VACAN	Weed density	Richness	Shannon	Evenness
Farm					
Field size	0.00 ns	0.00 ns	0.00 ns	0.00 ns	0.00 ns
Environmental					
GDD	0.00 ns	0.02 ns	0.06***	0.12***	0.12***
Precipitation	0.00 ns	0.01 ns	0.01 ns	0.00 ns	0.00 ns
Topographical					
Elevation	0.00 ns	0.02*	0.00 ns	0.02*	0.03**
Slope	0.00 ns	0.00 ns	0.00 ns	0.00 ns	0.00 ns
Topographical position index	0.00 ns	0.00 ns	0.04***	0.05***	0.03**
Topographical wetness index	0.00 ns	0.00 ns	0.00 ns	0.00 ns	0.00 ns
Edaphic					
Sand	0.00 ns	0.02*	0.00 ns	0.00 ns	0.00 ns
Silt	0.00 ns	0.00 ns	0.00 ns	0.00 ns	0.00 ns
Clay	0.00 ns	0.02**	0.00 ns	0.00 ns	0.00 ns
SOC	0.05***	0.00 ns	0.00 ns	0.00 ns	0.00 ns
pH	0.02*	0.00 ns	0.00 ns	0.00 ns	0.00 ns
Plant community					
Weed density	0.02***				
Richness	0.15***				
Shannon	0.12***				
Evenness	0.04***				

SOC and it is thought Ericaceae may rely on specialized-mycorrhizal fungi, ericoid mycorrhiza (ErM), for nutrient acquisition (Yurgel et al., 2017; Morvan et al., 2020). Wild blueberry is inefficient at acquiring inorganic nitrogen compared to common weed species (Marty et al., 2019), as such ErM may be particularly important for nutrient mobilization in acidic soils with low nutrient availability. Mycorrhizal fungi are also important for increasing plant species co-existence through reduced competition and niche-overlap (Wagg and McKenzie-Gopsill, 2022). Therefore, as soil pH and SOC declines and subsequent nutrient availability declines, mycorrhizal fungal associations may have

Table 4
Least square mean of wild blueberry stem density (VACAN, stems m^{-2}), and weed density (plants m^{-2}), weed species richness (species m^{-2}), Shannon diversity of weeds and weed evenness in wild blueberry fields in Nova Scotian counties. Standard error of the mean (SEM) and p-values are shown. Results of contrast comparing north counties (Antigonish, Colchester, Cumberland, Pictou) to south counties (Guysborough, Hants, HRM, SSC) is also shown.

County	VACAN	Weed density	Richness	Shannon	Evenness
Antigonish	189	93	3.2	0.63	0.47
Colchester	241	109	2.8	0.52	0.41
Cumberland	263	105	2.6	0.45	0.41
Guysborough	160	32	2.5	0.61	0.59
HRM	321	102	2.0	0.31	0.30
Hants	327	189	4.3	0.76	0.48
Pictou	250	136	3.3	0.60	0.48
SSC	277	103	3.4	0.67	0.48
SEM	±25	±18	±0.3	±0.08	±0.05
p-value	*< 0.01*	*< 0.01*	*< 0.01*	*< 0.01*	*0.13*
			Contrasts		
North vs South Counties	*< 0.01*	*0.01*	*< 0.01*	*< 0.01*	*0.20*
North counties mean	236	111	3.0	0.55	0.44
South counties mean	271	107	3.1	0.59	0.46

increased importance for wild blueberry ensuring adequate nutrient supply for increasing productivity. This may provide an explanation for the observed link between wild blueberry stem density, SOC, and soil pH in Nova Scotian fields.

The diversity of the associated weed community had by far the strongest association with wild blueberry stem density whereas weed density had little impact. The richness and Shannon diversity of the weed community had a stronger associationwith wild blueberry stem density than weed density or evenness (Table 3; Fig. 2A, B, C, D). Wild blueberry stem density declined as species richness, Shannon diversity and evenness increased (Fig. 2B, C, D). Greater significance of weed richness and diversity relative to weed density on wild blueberry stem density is interesting in that this effect is often expressed in modern

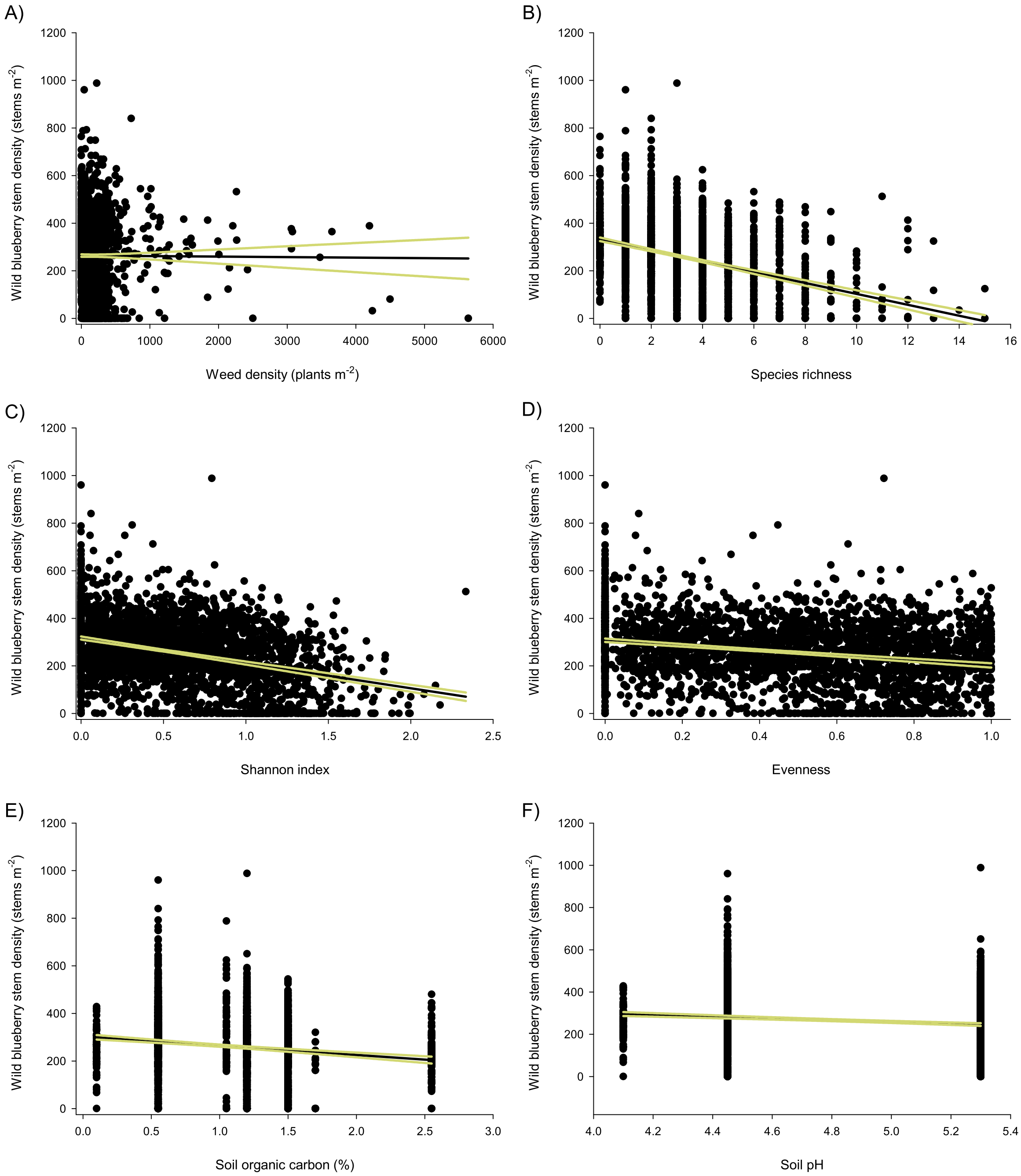

Fig. 2. The relationship between wild blueberry steam density (stems m^{-2}) and (A) weed density (plants m^{-2}), (B) species richness, (C) Shannon diversity index, (D) species evenness, (E) soil organic carbon (%), and (F) soil pH in Nova Scotian wild blueberry fields. Linear regression lines and 95 % confidence intervals are also shown.

weed control trials in wild blueberry. For example, many studies focused on management of a single weed species rarely report significant increases in wild blueberry stem density when the species is controlled or suppressed (Boyd and White, 2010; Boyd et al., 2014; Hughes et al., 2016; White, 2019). In contrast, early weed management research in wild blueberry reported large increases in wild blueberry stem density when several weed species were simultaneously controlled by broad-spectrum herbicides such as hexazinone, atrazine, or terbacil (Jensen and Kimball, 1985; Jensen, 1986; Yarborough and Ismail, 1985; Yarborough and Bhowmik, 1988). As such, increases in wild blueberry stem density from weed control will likely not occur in many fields dominated by a limited number of weeds as species richness is low and should be considered by both growers and researchers alike.

A dramatic decline in stem density was observed as species richness and Shannon diversity increased. Stem density is negatively correlated to floral buds stem^{-1}, which is in turn positively related to fruit yield (Yarborough et al., 2017; Barai et al., 2022). As such, these results are in concordance with previous studies demonstrating a positive link between weed diversity and crop yield in annual (Ferrero et al., 2017; Adeux et al., 2019) and perennial (Cierjacks et al., 2016) cropping systems. It has been suggested that increased weed diversity reduces competitive interactions through complementarity in root and canopy traits and resource requirements and acquisition (Smith et al., 2010; Storkey and Neve, 2018). The patchy distribution of wild blueberry plants within a field, its low-lying growth habit, and early-season root growth (Kaur et al., 2012) provide a variety of open niches for the surrounding weed community to exploit different resource pools and relax competitive interactions. In addition, increased weed diversity may provide greater floral resources for attracting wild pollinators post wild blueberry bloom which have been shown to improve productivity of the related *Vaccinium corymbosum* L. (Nicholson and Ricketts, 2019). Therefore, the relation between weed diversity and wild blueberry stem density may be tied to minimal niche overlap as species richness increases. The effects of biodiversity on trait complementarity is often more pronounced in resource-limited and heterogeneous environments (Wacker et al., 2008) such as the acidic sandy soils of wild blueberry fields. The combined interactions of niche exploitation and trait complementarity may provide a mechanism for the observed link between wild blueberry stem density and weed diversity in Nova Scotian fields.

Alternatively, intense management of wild blueberry fields may in turn result in a decline in weed community diversity and richness. For example, Hall et al., (2020) demonstrated that high intensity management of European vineyard inter-rows by herbicides or tillage was associated with reduced weed species richness in comparison to unmanaged inter-rows or those planted to cover crops. A multitude of studies, however, have documented that increased landscape diversity, environmental heterogeneity, and specific crop type rather than management intensity, is a primary driver of increased weed diversity in annual and perennial agroecosystems (Rew et al., 2005; Fried et al., 2008; Bourgeois et al., 2020). Future research should focus on improving our understanding of the effects of weed diversity on wild blueberry stem density, management intensity, and their relation to wild blueberry fruit yield.

3.3. Weed communities of Nova Scotia wild blueberry fields

A total of 183 weed species were identified within Nova Scotian wild blueberry fields. The most common species across all fields was *Rumex acetosella* L. followed by *Danthonia spicata* L., *Polytrichum commune* Hedw., *Festuca filiformis* Pourr., and *Euthamia graminifolia* (L.) Nutt. (Table 5). Weed density varied by county. South county fields tended to have lower average weed density but higher diversity than north county fields. For example, fields in SSC had below average weed density but the second highest Shannon diversity (Table 4). Similarly, fields in Hants county were the most diverse with the greatest species richness and Shannon index (Table 4). No differences in weed evenness was found between counties.

Weed species community varied by county and environmental and topographical factors. Similar to wild blueberry stem density, county was strongly associated on weed density, weed species richness, and Shannon diversity (Table 3). Average accumulated GDD had the second largest effect on weed species richness and Shannon diversity and the largest effect on weed species evenness (Table 3). Similarly, TPI affected weed diversity measures of species richness, Shannon diversity and evenness. In contrast, weed density was impacted by accumulated precipitation, elevation and TWI (Table 3).

Table 5
List of the most common weed species observed in a survey of Nova Scotian wild blueberry fields. Species are ranked by relative abundance. For a description of relative abundance calculation see lyu et al., (2021). EPPO code is also included.

Scientific name	EPPO code	Relative abundance
Rumex acetosella L.	RUMAA	39.80
Danthonia spicata L.	DANSP	18.56
Polytrichum commune Hedw.	PTYCO	16.99
Festuca filiformis Pourr.	FESPR	11.70
Euthamia graminifolia (L.) Nutt.	ETIGR	10.27
Agrostis hyemalis (Walter) BSP.	AGSGI	9.31
Panicum lanuginosum Ell.	DKTAC	7.02
Melampyrum lineare Desr.	MEALI	5.98
Cornus canadensis L.	CRWCA	5.48
Hieracium caespitosum Dumort	HIECA	4.93

3.4. Species-specific responses to explanatory variables

Weed species presence-absence and abundances were associated with explanatory variables in Nova Scotian wild blueberry fields. HMSC models achieved satisfactory convergence: the potential scale reduction factors of the β-parameter (the response of species to explanatory variables; see Ovaskainen et al., 2017) were on average 1.06 (maximum of 1.50) for the PA model and 1.00 (maximum of 1.02) for the ACOP model (Fig. A.2). The PA model had poor overall fit with a mean Tjur's R^2 of 0.09 whereas the ACOP model had greater fit with a mean R^2 of 0.18. Both the PA and ACOP models, however, had greater fit as presence and abundance increased (Fig. A.3).

Partitioning of variance to the explanatory variables in the PA model showed that fixed effects accounted for 46.2 % of mean explained variance in weed species occurrences (Fig. 3A). Wild blueberry stem density, a proxy for management intensity, accounted for the largest mean explained variance (20.4 %) in the PA model across all species, followed by GDD (9.8 %), TWI (8.2 %) and SOC (7.8 %). In general, however, fixed effects in the PA model explained minimal variance of the most prevalent species. For example, fixed effects explained 3 %, 9 %, 17 %, 2 %, and 78 % variation in the occurrence of *R. acetosella*, *D. spicata*, *P. commune*, *F. filiformis,* and *E. graminifolia*, respectively (Fig. 3A). In contrast, fixed effects accounted for larger explained variation in the ACOP model (77.6 %) (Fig. 3B). Wild blueberry stem density, GDD, TWI, and SOC described on average 20.2 %, 21.4 %, 17.1 %, 19.2 % of plant species abundances, respectively (Fig. 3B). Similarly for the most common species, the ACOP model explained greater variation in species abundances than the PA model with fixed effects accounting for 54 %, 70 %, 52 %, 52 %, and 67 % of variation in the abundances of *R. acetosella*, *D. spicata*, *P. commune*, *F. filiformis*, and *E. graminifolia,* respectively (Fig. 3B). Therefore, while species presence responded to wild blueberry stem density, a measure of management intensity, species abundances were less dependent on explanatory factors.

In general, species presence-absence was negatively associated with explanatory variables (Fig. 4). Wild blueberry stem density had the strongest association to species occurrence and was negatively associated with $>$ 60 % of species (Fig. 4A). Compared to wild blueberry stem density, relatively few species had a positive or negative response to either GDD, TWI or SOC. Similarly, species abundance had minimal responses to explanatory variables with 7 % responding negatively to wild blueberry stem density and 7 % responding positively to GDD (Fig. 4B). Of the most common species, the occurrence of *R. acetosella* responded negatively to wild blueberry stem density. This is in contrast to the abundance of *R. acetosella* which had a positive response to wild blueberry stem density (Fig. 4). *Rumex acetosella* attains higher ramet density and exhibits lower ramet mortality when growing in wild blueberry patches relative to bare soil patches (White et al., 2014) which may explain this positive response. The occurrence and abundance of *D. spicata* and *E. gramifolia* declined with increasing wild blueberry stem density, likely due to the fact that these species often occur most abundantly in bare soil patches between established wild blueberry patches (Scott White, personal observation).

In contrast to the majority of agroecosystems (Storkey et al., 2012), plant biodiversity of Nova Scotian wild blueberry fields appears to be increasing over time (McCully et al., 1991; Lyu et al., 2021). A similar trend is also occurring in wild blueberry fields in Maine (Ayers, 2020). In addition, the composition of weed communities in Nova Scotian wild blueberry fields appears unique in comparison with nearby regions with regional differences in density and diversity between counties. In Maine, Yarborough and Bhowmik (1988) observed various grass species including *Danthonia spicata*, as well as *Cornus canadensis* and *Apocynum androsaemifolium* to be the most common species in wild blueberry fields following sequential hexazinone applications. These species continue to be among the most common plants in wild blueberry fields in Maine

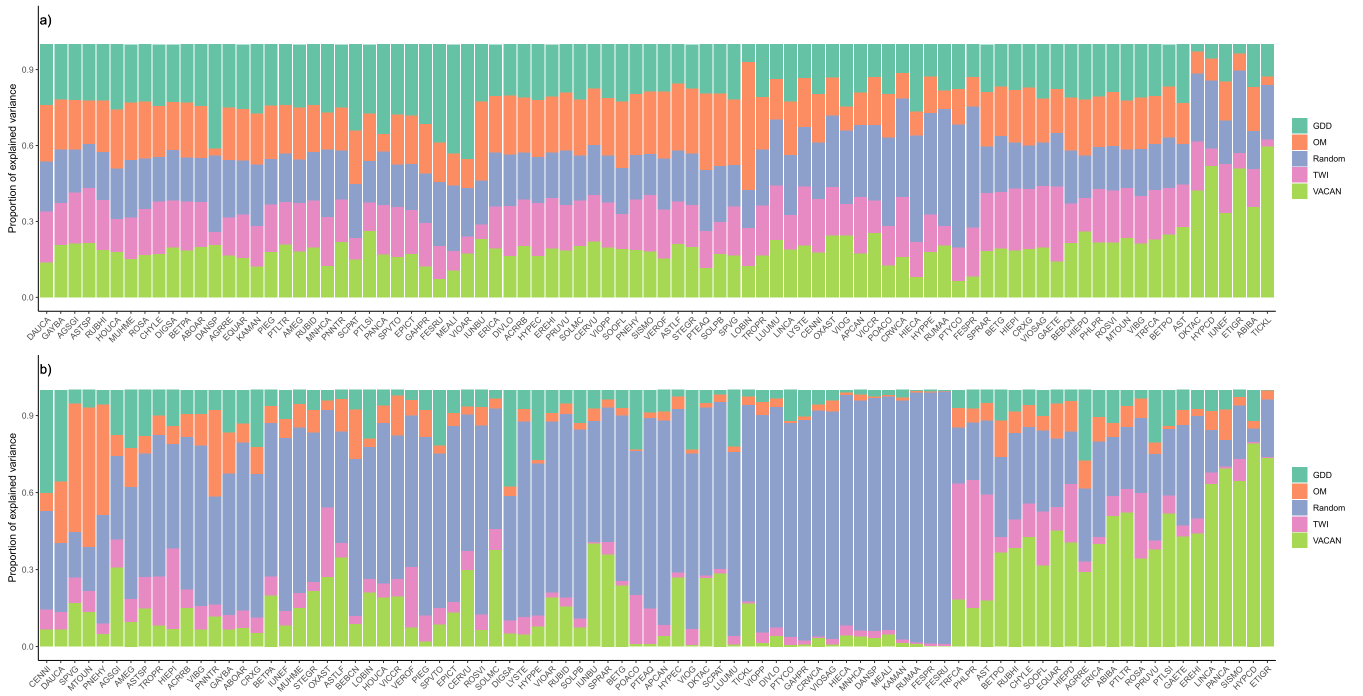

Fig. 3. Variance partitioning among explanatory variables for (A) presence absence (PA) and (B) abundance conditional on presence (ACOP) model. The heights of the bars correspond to the explanatory power achieved for each species, measured by Tjur R^2 for the PA and R^2 for the ACOP. Species are listed by EPPO code (see Table A.1). VACAN – Vaccinium angustifolium; GDD – growing degree day; TWI – topographical wetness index; SOC – soil organic carbon.

today (Ayers, 2020). In contrast, Lapointe and Rochefort (2001) found *Carex* spp., *Kalmia angustifolia* L., and *Comptonia peregrina* (L). Coult. were the most common species in a Québec survey following application of hexazinone. Lapointe and Rochefort (2001) suggested the species composition in Québec was likely due to maintenance of hexazinone susceptibility in weedy populations in the survey region. The unique selection and diversity of species found in Nova Scotian wild blueberry fields alludes to the importance of regional specific factors influencing species distributions.

The poor overall fit of the PA model, greater fit of the ACOP model and relative effect size of environmental covariates suggests that weed communities in wild blueberry fields are constructed largely at random with local extinction, dispersal, priority effects, and species-species interactions largely governed by producer management practices being more important than environmental factors. In addition, the nature of crop establishment in wild blueberry production systems where field selection is determined by the presence of native wild blueberry populations adds to the complexity and randomness of local weed community structure. Local extinction driven by herbicide use and population expansion driven by dispersal on harvesting equipment (Boyd and White, 2009) has been documented in wild blueberry fields and continues to be a significant source of novel plant introductions (Lyu et al., 2021). Similarly, relative timing of emergence and species-species interactions during any given year may dictate the composition of a weed community following alternating pruning and harvesting associated with the two-year wild blueberry production cycle. Although rarely acknowledged, it has been suggested that due to heavy disturbance associated with crop management, weed communities in agricultural settings filter at random (Maxwell and Luschei, 2004; Smith et al., 2015) with minimal roles for niche-based assembly rules (neutral theory). Wild blueberry is an early successional species whose abundance increases following clearing of forest land or during early stages of succession on abandoned farm land (Hall, 1959). Hall (1955) noted wild blueberry density rapidly declined following fire in a New Brunswick field and was replaced by a community dominated by *Dennstaedtia punctilobula* (Michx.) T.Moore, *Pteridium aquilinum* (L.) Kuhn. and *Danthonia spicata* if no further management occurred. The abundance of these species in Nova Scotian fields may be part of the natural progression of the agro-ecosystem and response to a combination of management and local environmental factors. Together this suggests that niche assembly processes may dictate the occurrence of plant species within wild blueberry fields at a broad geographic level and create the species pool from which to draw. Field level predictions, however, may be more challenging due to local stochasticity.

Due to shifts in management away from pruning by burning and limited alternatives for weed control, it has been suggested herbicides are now the primary selection pressure determining weed community assembly in wild blueberry fields (Jensen and Yarborough, 2004). The strong negative association between wild blueberry stem density, a measure of overall management intensity, and the majority of weed species in Nova Scotia wild blueberry fields supports this assertion. Standard weed management practices of Nova Scotian wild blueberry growers are not well documented, but tend to mirror other production regions in terms of reliance on a limited number of effective techniques. For example, producers in the nearby wild blueberry producing region of Maine rely on few weed management options with limited variability between producer practices (Rose et al., 2013). For example, four herbicide chemistries, flumioxazin (WSSA group 14), simazine (WSSA group 5), mesotrione (WSSA group 27), and glufosinate (WSSA group 10) were each applied to approximately 20 % of non-bearing year wild blueberry acreage in 2021 (USDA-NAAS, 2023). Further, herbicides are only applied to roughly 60 % of wild blueberry land in any given year (USDA-NAAS, 2023) with producers combing chemical weed control with pruning fields every other year (87 % of producers) or every three to four years (13 % of producers) and sulphur applications to lower pH (49 % of producers) for weed management (Rose et al., 2013). Weed species listed on the labels of the most commonly used herbicides in wild blueberry are mostly small seeded annual broadleaves and grasses and largely absent from our survey suggesting herbicides are effective at influencing populations of these weed species. Yet, the majority of weed species documented in Nova Scotian wild blueberry fields are not found on the labels of most herbicides and therefore chemical weed

Fig. 4. The responses of the weed species to explanatory variables for (A) presence absence and (B) abundance conditional on presence model. Responses that are positive are shown in red and those that are negative are shown in blue (≥ 95 % posterior probability). species are listed by EPPO code (Table A.1).

management practices per say may have had a limited role in directly shaping overall weed communities. Rather, the selection against many common agricultural weed species by herbicides in wild blueberry may allow for alternative species more dependent on environmental factors and which are adapted to frequent pruning to proliferate.

Interestingly, wild blueberry stem density was positively associated with the occurrence of *Melampyrum lineare* and the abundance of *Rumex acetosella*. *Melampyrum lineare* is hemiparistic and is known to parasitize roots of *Vaccinium* spp. in Nova Scotia wild blueberry fields (Deveau, 2024). Preliminary studies have also demonstrated a negative effect of *M. lineare* presence on wild blueberry growth (Deveau and White, 2022) and the related *Melampyrum pratense* L. is known to parasitize *Vaccinium* spp., including *Vaccinium myrtillus* L. and *Vaccinium vitis-idaea* L. (Masselink, 1980). Therefore, the association between wild blueberry stem density and *M. lineare* in Nova Scotian fields is likely related to parasitism. The ubiquity of *Rumex acetosella*, as well as *Danthonia spicata*, and *Festuca filiformis* in Nova Scotian fields has been partially attributed to hexazinone tolerance and resistance (Jensen and Yarborough, 2004; Li et al., 2014; Lyu et al., 2021; Laforest et al., 2022) and may partially explain the association with wild blueberry stem density. Other management practices of wild blueberry production systems that would be incorporated in our measure of management intensity, such as pruning and fertilization, may also promote productivity of *R. acetosella* which is rosette forming and may escape pruning operations. *Rumex acetosella* populations can rapidly increase following heavy disturbance and changes to nutrient availability (Carson and Pickett., 1990; Penney et al., 2008) via an its extensive network of creeping roots and persistent seedbank (Stopps et al., 2011). Similar to wild blueberry, however, *R. acetosella* decreases in abundance following heavy disturbance in the absence of additional management (Lapointe and Rochefort, 2001; Penney et al., 2008). Therefore, wild blueberry and *R. acetosella* may occupy similar niche spaces in Nova Scotian fields and efforts to control *R. acetosella* chemically may be counteracted by efforts to increase wild blueberry growth. This may also explain why *R. acetosella* occurred in more Nova Scotian wild blueberry fields than any other weed in a survey conducted in 1984–1985 (McCully et al., 1991). While the occurrence of *R. acetosella* may be difficult to predict due to its ubiquity, these results suggest that *R. acetosella* will increase in abundance, and therefore management complexity, as stem density of a Nova Scotia wild blueberry field increases.

Weed communities in Nova Scotian wild blueberry fields were constructed largely at random with a strong management component, yet the occurrence and abundance of several common and problematic species was associated with environmental covariates. The positive association between *Danthonia spicata*, *Juncus bufonius* L., *Melampyrum lineare*, *Panicum capillare* L., and *Agrostis hyemalis* (Walter) Britton, Sterns & Poggenb. abundance and accumulated GDD demonstrates the importance of temperature during the growing season for these species. These species all spread by seed and, with the exception of *Danthonia spicata* and *Agrostis hyemalis*, are summer annuals. Soil temperature is the primary determinant of seed germination and emergence for annual species (Forcella et al., 1997) and increased temperature has been associated with earlier emergence and species-specific effects on biomass productivity in both C3 and C4 species (Lee, 2011; Ramesh et al., 2017). GDD accumulation has increased in the region through the combined effects of increased temperature and lengthening of the growing season (Qian et al., 2010) and is predicted to further increase over the next 50 years (Bootsma et al., 2005; Garbary and Hill, 2021). Therefore, as GDD accumulation increases, *Danthonia spicata*, *Juncus bufonius*, *Melampyrum lineare*, *Panicum capillare*, and *Agrostis hyemalis* may become an increasing management concern for Nova Scotian wild blueberry producers. Further, producers along the cooler north shore of Nova Scotia and within low-lying areas may face increasing weed pressure from these species as climate changes. Similarly, producers may face increasing challenges from species such as *Festuca filiformis* and *Panicum lanuginosum* Elliott which have a strong association with TWI, a long-term measure of soil moisture availability (Raduła et al., 2018), given the predicted increase in variability of precipitation in the region (Bootsma et al., 2005). In addition, novel species introductions and range shifts driven by changes in climate and management practices and not accounted for in the present study need to be considered and may add additional complexity to producers management programs. This emphasizes the increased need for continued weed surveillance despite a strong random component to weed community assembly in agricultural fields.

4. Conclusions

Our results demonstrate that the wild blueberry producing counties of Nova Scotia have varied and different microclimates. These microclimates, consisting of variations in accumulated GDD, TWI, and SOC, had a dramatic impact on species richness of the associated weed community of wild blueberry fields. The changes in weed species richness across counties were a driving factor determining wild blueberry productivity. This emphasizes and builds on the increasing evidence for the importance of weed diversity to agroecosystem productivity. Rotating management practices of wild blueberry fields such as resting or fallowing fields (Burgess, 2017), alternative use of burning and mowing (Lynham et al., 1998), and rotating use of selective herbicides (Jensen and Yarborough, 2004) can increase weed species richness (Smith et al., 2010). Increasing weed species richness while minimizing the dominance of any one species can relax competitive interactions and maximize wild blueberry productivity in the low-resource, highly stressful environments of Northeast North America.

Nova Scotian wild blueberry fields were highly diverse with nearly 200 different species recorded over the survey. The relative importance of environmental factors and niche-based assembly in wild blueberry fields, however, was minimal and only for those most common species. This stresses the importance of stochasticity, species-species interactions (neutral theory), and potentially management factors in determining local weed community structure in wild blueberry fields. The association between several species and climatic covariates, however, does allow us to prioritize which species and production regions may be impacted by climate change. Future studies should consider how management factors can be combined into joint-species distribution models with climatic, topographical, and soil edaphic factors to build a strong foundation for weed surveillance in wild blueberry fields.

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CRediT authorship contribution statement

A. McKenzie-Gopsill: co nceptualization, data curation, formal analysis, visualization, writing the original draft and review and editing the final verison. **S.N. White:** funding acquisition, methodology, supervision and reviewed and edited the final version. **H. Lyu:** investigation, data curation, and reviewing the final draft. **S. Hann:** data curation and reviewing and approving the final draft.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Scott N. White reports financial support was provided by Natural Sciences and Engineering Research Council of Canada. If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2025.109802.

Data Availability

Data will be made available on request.

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