

ISSN: (Print) (Online) Journal homepage: <https://www.tandfonline.com/loi/tphy20>

Assessing poison ivy (*Toxicodendron radicans*) presence and functional traits in relation to land cover and biophysical factors

Lynn M. Resler , J. T. Fry , Scotland Leman & John G. Jelesko

To cite this article: Lynn M. Resler , J. T. Fry , Scotland Leman & John G. Jelesko (2021): Assessing poison ivy (*Toxicodendron radicans*) presence and functional traits in relation to land cover and biophysical factors, Physical Geography, DOI: [10.1080/02723646.2021.1883802](https://doi.org/10.1080/02723646.2021.1883802)

To link to this article: <https://doi.org/10.1080/02723646.2021.1883802>



Published online: 16 Feb 2021.



Submit your article to this journal 



View related articles 



View Crossmark data 

ARTICLE



Assessing poison ivy (*Toxicodendron radicans*) presence and functional traits in relation to land cover and biophysical factors

Lynn M. Resler ^b, J. T. Fry^b, Scotland Leman^c and John G. Jelesko  ^d

^aDepartment of Geography, Virginia Tech, Blacksburg, VA, USA; ^bDepartment of Statistics, Virginia Tech, Blacksburg, VA, USA; ^cDepartment of Statistics, Virginia Tech, Blacksburg, VA, USA; ^dSchool of Plant and Environmental Science, Virginia Tech, Blacksburg, VA, USA

ABSTRACT

Understanding species distributions remains central to research in ecology and biogeography. Emphasis is placed on the spatial presence/absence of plants as related to underlying environmental factors; however, distributions result from both abiotic factors and adaptations to the abiotic environment. We analyzed poison ivy (*Toxicodendron radicans* (L.) Kuntze), which has high intraspecies variability in the plant functional trait of growth habit, to assess implications of plant strategies for spatial distributions. Our objectives were to: 1) determine whether anthropogenic habitats are statistically overrepresented in poison ivy incidence and growth habits (shrub, climbing liana, crawling liana), and 2) model biophysical parameters that constitute preferred poison ivy habitat and the three growth habits. We collected poison ivy field data along a trail-transect with corresponding geospatially indexed parameters, subsequently analyzed using Bayesian spatial modeling. Model results revealed poison ivy preference for human-modified habitat; Developed and Planted/Cultivated land use categories showed the largest marginal posterior probabilities for crawling and climbing lianas. Increasing temperature and elevation preferentially benefit the climbing growth habit. Our results suggest that variability in functional traits may impact species geographic distributions by expanding niche breadth. Incorporation of functional traits may thus advance predictive niche models of species distributions.

ARTICLE HISTORY

Received 26 May 2020
Accepted 26 January 2021

KEYWORDS

Poison ivy; *Toxicodendron radicans*; spatial Gaussian model; functional traits; Appalachian Mountains; growth habit

Introduction

A fundamental goal of biogeographic research is to ascertain linkages between biotic and abiotic landscape elements (Cowell & Parker, 2004). Research examining plant species distributions with respect to environmental parameters has spanned centuries (e.g. Humboldt & Bonpland, 1805), and remains at the core of research in biogeography, ecology, and conservation science. In the discipline of geography, there is emphasis on understanding the spatial presence/absence of plants, particularly as related to underlying environmental factors. Species distribution modeling has become the primary

vehicle for meeting this challenge (Franklin, 2010). However, predictions remain problematic because species' niches, and hence, their distributions, result from dispersal limitation and species interactions in addition to adaptations to the abiotic environment (Soberón, 2007). These also vary across species ranges and through time. Grime (1977, 2006), for example, provided a broad framework for considering plant species distributions based on plant adaptive strategies, whereby plants make trade-offs in response to the environment, and have adaptations to biotic interactions along various resource and disturbance gradients. Although Grime (1977) emphasized interspecies variability, *intraspecific* variability, notably in plant functional traits (Yang et al., 2015), has been recognized as an important complication (Lecocq et al., 2019). Malanson and Resler (2015) noted that this concept could also be applied to intraspecific distributions.

Functional traits are morpho-physiological strategies that enable plants to succeed in their environment (Violle et al., 2007). Poison ivy (*Toxicodendron radicans* (L.) Kuntze) exhibits an exceptionally high degree of intraspecies variability in its functional traits (i.e. adaptive strategies), making it a model species for assessing the implications of intraspecific variation in plant strategies for spatial distributions. Poison ivy is a noxious, native North American plant with functional traits that enable it to grow across a broad geographic range and within diverse habitat types. Poison ivy is a perennial plant widely distributed east of the Rocky Mountains and south of the 44th parallel occupying areas within the Midwest, South, and eastern United States. It shows a high degree of morphological variation (Barkley, 1937) sufficient to assign nine subspecies that generally correspond to distinct geographical regions (Gillis, 1971). Poison ivy is dioecious and has both sexual and asexual reproductive modes. It is likely dispersed by a variety of animals, including birds (Martin et al., 1951; Penner et al., 1999). Foliage is consumed by a wide variety of native fauna (e.g. deer, rabbits, mice (Martin et al., 1951)) and non-native domesticated animals (e.g. goats (Popay & Field, 1996)) without any apparent discomfort. Within its range, it shows adaptability to a wide variety of habitats including rocky outcrops, mesic forests, swamplands, disturbed regions, and open areas (Weakley, 2015).

One of the primary traits mentioned in poison ivy systematics is the wide range of natural variation observed in primary anatomical characters (Barkley, 1937; Gillis, 1971). Growth habits of differing mechanical architecture can range from vertical climbing lianas (woody vines), ground crawling lianas, to less common erect branching shrubs. The vertical climbing growth habit is aided by aerial roots that emerge from the vertical climbing stems and attach to a variety of substrates such as living or dead tree trunks, fence posts, and rock or masonry. Supportive structures are advantageous to lianas, enabling energy resource investment into growing a large leaf area for photosynthesis, without over-expending for the development and maintenance of woody stem materials (Leight-Young, 2014). Climbing lianas give rise to long horizontal branches with many leaves and drupes. Aerial root density on these vertical climbing lianas can range from sparse to exceedingly dense. The ground crawling liana growth habit is characterized by stolons (i.e. horizontal branches along the ground and often hidden under leaf litter) that branch and produce single thin erect shoots from the nodes of branching stolons. The individual erect shoots produce relatively few leaves and drupes. The ground crawling liana growth habit can manifest either as a single stolon with one or more erect shoots (typically less than one meter in height) to large patches of what appear to be a single clonal network of branching stolons (i.e. ramets). The least common poison ivy growth

habit is the shrub growth habit consisting of a single, relatively thick erect stem with extensive vertical branches that typically grow more than a meter high.

Intraspecies variability in poison ivy growth form likely reflects an adaptive response to local resource availability and community interactions (Grime, 2006), which will differ among habitat type. In North American temperate forests, the climbing liana growth habit (including but not limited to poison ivy) demonstrates a preference for forest edge habitats (Fraver, 1994; Londré & Schnitzer, 2006; Ladwig & Meiners, 2010). Ground crawling poison ivy lianas are present in both non-forested and forested habitats. Forest disturbances that create canopy gap openings or edges result in localized concentrations of poison ivy climbing liana growth associated with increased light availability (Allen et al., 2005; Catling et al., 2002). Similarly, anthropogenic disturbances result in increased poison ivy abundance (Brice et al., 2014; Catling & King, 2007; Gillis, 1971; Tessier, 2010). However, as forest edges expand or gaps close, poison ivy persists as ground crawling lianas “sitting in wait” for future forest disturbance (Allen et al., 2005; Ladwig & Meiners, 2010a). The manifestation of different poison ivy growth habits in different environments suggests phenotypic plasticity. Indeed, a greenhouse common garden experiment confirmed that poison ivy displays differential biometric phenotypic responses to light and nutrient availability; however, this phenotypic plasticity is also significantly affected by accession-level (i.e. genetic) factors (Jelesko et al., 2017).

The high degree of intraspecific variation of growth habit in poison ivy may broaden its niche, with implications for its distribution. The purpose of this study was to assess poison ivy presence and growth habit in relation to biophysical and land cover parameters. By doing so, we can assess the implications of plant strategies for spatial distributions. Our objectives were to: 1) determine whether anthropogenic habitats (as determined by selected land cover/land use variables) are statistically overrepresented in poison ivy incidence and specific growth habits (shrub, climbing liana, crawling lianas), and 2) model primary biophysical parameters that constitute preferred poison ivy habitat and the three growth habits. Specifically, we were interested in determining whether modeled poison ivy populations prefer land cover categories representing human-modification, and if our selected biophysical parameters could differentiate among the major growth habits: crawling lianas, climbing lianas, and shrubs. We used a trail-transect to collect poison ivy field data with corresponding geospatially indexed parameters subsequently analyzed using Bayesian spatial modeling.

Materials and methods

Study area and field data collection

We conducted fieldwork between May and June 2016 along a 100 km segment of the Appalachian Trail (AT) in Southwest Virginia (Figure 1), (hereafter referred to as the “AT-transect”). The AT-transect extended from the Mills Gap Overlook in Botetourt County (~37.48°N; 79.68°W) to the Niday shelter in Craig County, VA (~37.39°N; 80.26°W). This section of the AT was selected because it represents diverse landforms and habitats, ranging from mesic deciduous forests to open landscapes, that characterize poison ivy habitat in Virginia (Weakley, 2015). Additionally, the AT-transect access points were in convenient proximity to logistical support from Virginia Tech. The

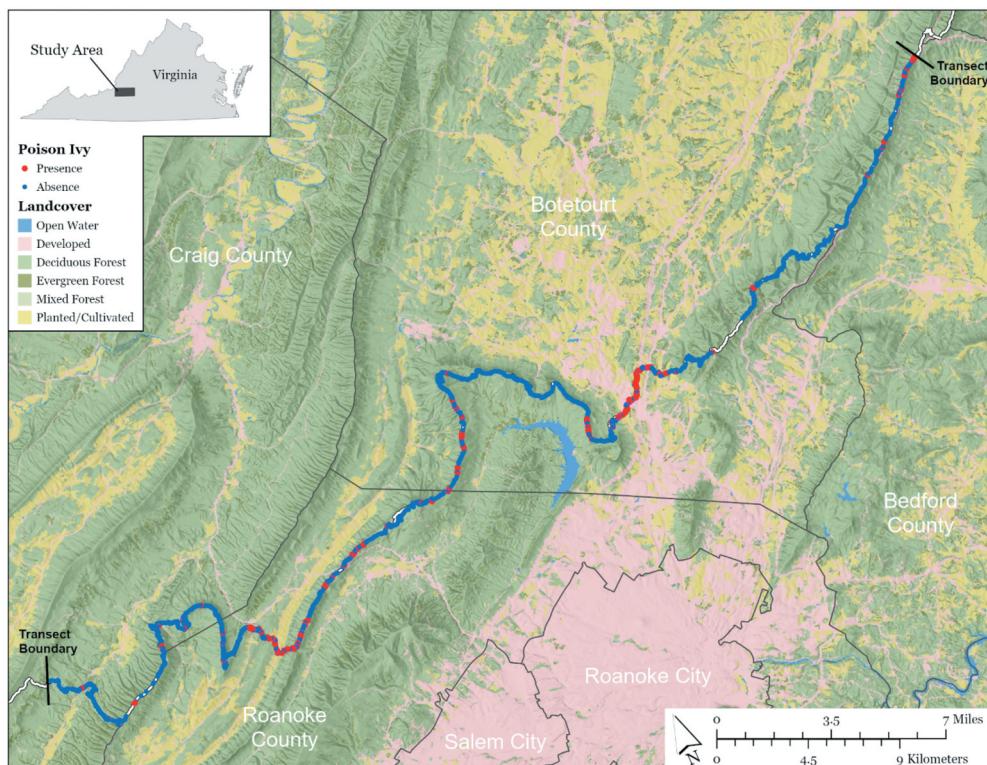


Figure 1. Poison ivy presence and absence along the study area transect, in southwestern VA associated land cover categories.

transect lies within the Ridge and Valley physiographic province of Virginia, which is characterized by parallel, southwest to northeast trending ridges and valleys. Shale, siltstone, sandstone, chert, and carbonates form parent material throughout the province (McNab & Avers, 1994). Ridges are often associated with rocky outcrops composed of erosion-resistant sandstone of the Tuscarora formation (Virginia Division of Mineral Resources, 1993). Elevation of the study transect ranged from 352 m to 968 m above sea level, averaging 654 m.

Poison ivy presence/absence and growth habit information was recorded for each of the 1,937 AT “white blaze markers” encountered along the transect. The Appalachian Trail Conservancy positions white blaze markers on trees, rocks, posts or guardrails to mark the authentic AT. Distance between white blazes varies, but typically ranges 50 m to 1 km (Appalachian Trail Conservancy). With the exception of two intervals when the IvyMap software unknowingly malfunctioned, all recognized white blazes were recorded and evaluated for poison ivy presence/absence and growth habit.

Sampling along the AT-transect using white blazes as locales of data collection allowed us to measure poison ivy characteristics across a gradient of land cover types (Deciduous, Mixed, and Evergreen Forest; and Developed and Planted/Cultivated land). Our transect sampling approach minimized a priori investigator sampling bias, and allowed sampling in locations both where poison ivy was absent, and where naturally recruited poison ivy

plants manifested each of the three growth habits (shrub, climbing liana, and crawling liana).

To facilitate field data collection, we used a custom Android smartphone app (IvyMap, version 1.0) developed as a Virginia Tech Computer Science undergraduate senior capstone course project for data collection (source code is publicly available on GitHub <https://github.com/McBrosa/IvyMap>). The program utilized the smartphone internal global positioning system (GPS) receiver to record the coordinates of each poison ivy sampling location. Using this app enabled efficient data collection with a customized interface that allowed us to simultaneously record: 1) the spatial X,Y,Z coordinates at each white blaze marker, and 2) whether poison ivy was either absent or present within a two-meter radius ($\text{area } 12.57 \text{ m}^2$) of the tree/post/rock centered on the white blaze marker. The two-meter radius around the object with a white blaze marker generally included the hard-packed trail, and thus limited (to varying degrees depending upon proximity of the trail to the white blaze) the available area for poison ivy to be detected at the white blaze. If poison ivy was present (as determined by the presence of any part of the plant within the plot), we additionally recorded which of three growth habits (i.e. shrub, ground crawling liana, or vertical climbing liana) was present. Climbing lianas were classified by a growth habit that attached to a vertical substrate, such trees, fence posts, or rocks using aerial roots. Ground crawling lianas were defined as single-stemmed erect freestanding shoots less than one meter in height attached to (typically hidden below leaf litter) ground crawling stolons. Shrubs were defined as erect shoots attaining a height equal to or greater than one meter, requiring a substantially thickened stem (relative to the ground crawling lianas) emerging from the ground. If more than one growth habit was present at a white blaze, then both growth habits were recorded as separate records. Thus, presence/absence records were a minimal estimation of poison ivy plant abundance for each growth habit encountered at a white blaze marker.

Biophysical variables and land cover

We derived several biophysical and land cover variables to analyze poison ivy presence and growth habit. Terrain variables were obtained from 1/3 arc-second (approximately 10 m) USGS digital elevation models (DEMs) to derive elevation, aspect, surface curvature, slope angle, and potential solar radiation (WH/m^2) using ArcGIS (v.10.3) Spatial Analyst. Surface curvature refers to the convexity or concavity on a cell-by-cell basis (positive and negative curvature, respectively) and reflects exposure (convex, positive curvature) or areas where moisture may be retained in concavities (negative curvature). Soil variables were obtained from Gridded SSURGO Database (Soil Survey Staff) and included slope profile, surface soil texture, soil series, soil depth to bedrock, soil water storage capacity, and drainage class. These terrain variables are indicative of the general trends in vegetation composition and structure found within our study area.

We used thirty-year climate normal (1981–2010) Precipitation-Elevation Regressions on Independent Slopes Model (PRISM, <https://prism.oregonstate.edu/>) climate data (800 m resolution) to characterize climate for the study region. For each data point, we collected temporal (monthly resolution; during the potential growing season Mar–Oct) variables: solar radiation, mean temperature, and precipitation. Interpolation techniques for the PRISM models account for spatially varying elevation relationships (Daly et al., 2008).

To capture dominant land cover categories within our study area, we downloaded the 2011 National Land Cover Database (NLCD) from the Multi-Resolution Land Characteristics Consortium (<http://www.mrlc.gov/>). We were interested in broad land cover categories that represented forested landscapes (primarily secondary forest growth, Fleming, 2012). In preparation for statistical analysis, we combined NLCD “Developed Open Space”, “Developed Low Intensity” and “Developed Medium-Low Intensity” land cover classes into one “Developed” class for analysis. Similarly, “Hay/Pasture” and “Cultivated Crops” were combined into the representative grouping “Planted/Cultivated”. Forest classes included Mixed Forest, Deciduous Forest, and (coniferous) Evergreen Forest. Our combined developed class was characterized primarily by open space development, with single family housing units and less than 20% impervious surface cover. Planted/Cultivated land cover was defined by >20% agricultural land, including land used for livestock grazing or crop production. Evergreen Forest cover is defined by >75% tree species maintaining their leaves year-round (Multi-Resolution Land Characteristics Consortium (MRLC). National Land Cover Database, 2016). In our study region, the Evergreen Forest class is composed mostly of conifer tree species, including naturally occurring *Pinus rigida* Mill. (pitch pine), *P. virginiana* Mill. (Virginia pine), and *P. pungens* Lamb. (Table Mountain pine), which specialize at growing in dry, rocky outcrops (Weakley et al., 2017). Deciduous Forest cover within our study area was comprised of Eastern Deciduous hardwood species, including *Acer rubrum* L. (red maple), *Carya* spp. (hickory), *Liriodendron tulipifera* (tulip poplar), and *Quercus* spp. (oaks), including *Quercus alba* L. (white oak), *Q. velutina* Lam. (black oak), *Q. montana* Willd. (chestnut oak), *Q. coccinea* Münchh (scarlet oak), and *Q. rubra* L. (northern red oak) (Braun, 1950; Dyer, 2006). Finally, Mixed Forest land cover represents a combination of the tree species that comprise Deciduous and Evergreen classes, occupying no more than 75% of total tree cover.

In total, we modeled poison ivy presence and growth habits, while controlling for the following 13 variables: elevation, curvature, slope, soil series, bedrock depth, water storage, Sine(aspect), Cosine(aspect), temperature, precipitation, solar radiation, land cover, and soil texture. These variables were incorporated into the model as linear effects to describe the probability of presence for each growth habit. Additionally, latitude and longitude were used to account for the spatial correlation among locations.

In order to linearize and standardize our variables, we: 1) first transformed slope aspect ($=a$) into the two orthogonal variables $\{\text{Sine}(a), \text{Cosine}(a)\}$, and then 2) all continuous variables were centered (mean = 0) and scaled (standard deviation = 1). Some locations along the transect had missing values for soil texture (127 locations), bedrock depth (153 locations), and water storage (153 locations). Since the models that we fit required no missing values, we imputed the values using a Bayesian approach. In other words, we assigned each missing value a prior distribution and averaged over the possible values that the missing value could have been. Prior distributions, or simply “priors”, are a key part of Bayesian inference that enable the probability of a related event to be calculated based on the understanding of parameters *before* observing any data. Priors are then combined with the probability distribution of new data to yield a *posterior*

distribution, which conveys belief about what the parameters are *after* observing the data (Gelman, 2002). Missing quantities were not associated with the presence or absence of poison ivy, meaning that the presence or absence could not be used to predict which values are missing (details in [Appendix A](#)).

Statistical analysis

Given the inherent potential for poison ivy to show patchy spatial correlations, and with associated permissive landscape features, we utilized two Gaussian spatial models within a Bayesian framework to identify specific landscape and environmental parameters differentially associated with poison ivy characteristics. The first model uses the poison ivy presence/absence at each location as the response. The second, more granular model, uses the poison ivy growth habit as the response. Our models allow for the inference of the covariate effects while accounting for the dependence between locations. That is, locations are not assumed to be independent, but rather, the spatial dependence is inferred through the data. A standard Gaussian spatial model describes the propensity for poison ivy as normally distributed where the propensity at any location in close proximity will be more highly correlated than locations that are farther apart.

The Bayesian approach we adopt has several benefits. First, it provides distributions for each parameter, enabling us to know, for example, the probability that one parameter is larger or smaller than another. Second, for a complex model, it easily allows us to specify the model hierarchically; the complex model is a collection of smaller, simpler pieces. Lastly, the Bayesian approach allows us to average-over the missing values in the dataset.

Preliminarily, we investigated the features that were determinants of poison ivy presence using a clipped Gaussian Process (GP) model. Each location has a latent, normally distributed propensity for poison ivy that affects the probability of presence. The mean propensity at each location is a linear combination of the features with unknown parameters. Positive estimated parameters for the mean propensity are associated with an increase in propensity (and probability) of poison ivy presence as the feature increases. The correlation between pairwise locations is a function of the associated spatial distance, accounting for the spatial dependence. Statistical details of the model can be found in [Appendix A](#).

To extend the analysis to account for varying types of poison ivy, we modeled each categorical occurrence using the framework described within McCullough and Rossi (1994), which accounts for both spatial correlation between locations and correlation between the probability of observing each type at a given location. Each location has latent, normally distributed propensities for each of the three growth habits that affects the probability of observing a specific growth habit. Each habit propensity and each location has its own mean that is a linear combination of the features and unknown parameters. Positive estimated parameters for a particular location and habit are associated with an increase in the propensity (and probability) for that growth habit as the feature increases. Further, we account for the underlying correlation between both habit propensities and spatial correlation between locations ([Appendix A](#)).

Results

Poison ivy response to land cover types

Along the 100 km AT-transect, poison ivy was present at 228/1937 sampling plots ([Table 1](#)).

Ground crawling liana was the most frequently recorded growth habit (representing ~75.4% of total poison ivy) among the three poison ivy growth habits, in all land cover categories ([Table 1](#)). Climbing poison ivy (~18.4% of total poison ivy observations) and shrubs (~6.1% of total poison ivy) followed in abundance.

Poison ivy occurrence was not equally distributed along the 100 km transect, nor among land cover classes ([Figure 1](#)). Because poison ivy was recorded as either absent or present (as one of three growth habits) at each sampling site, this study reports the minimal incidence of poison ivy along the transect. Across all land cover categories, ground crawling lianas were more frequent than climbing lianas; and climbing lianas were more frequent than poison ivy shrubs ([Table 1](#)). The majority of white blaze sampling sites (87.5%) were classified as forested land use categories (Deciduous, Evergreen, or Mixed Forest), whereas the remaining 12.5% were located in more managed land use categories (Developed or Planted/Cultivated). However, Bayesian modeling of poison ivy presence across these land use categories indicated that poison ivy presence was not simply a stochastic process along the sampled AT.

The pattern observed in [Figure 1](#) is quantified in [Figure 2](#), with the Developed and Planted/Cultivated land use categories showing the largest marginal posterior probability values for the two most abundant poison ivy growth habits (ground crawling lianas and climbing lianas). Poison ivy showed comparable posterior marginal probabilities in Deciduous and Mixed Forest cover types that were consistently greater than the posterior marginal probabilities in Evergreen Forest cover ([Figure 2](#)). The differential poison ivy accumulation in land use types was additionally visualized for ground crawling lianas (i.e. the most abundant growth habit) as pairwise Bayesian contrasts, which show the distribution for the difference between two parameters ([Figure 3](#)).

Similar density values existed for Planted/Cultivated and Developed land cover types. Conversely, when Developed land cover was contrasted with Evergreen, Mixed, or Deciduous forest cover, there was a 99.7%, 89.3%, and 98.9% posterior probability, respectively ([Figure 3](#)), that the effect is larger for Developed land cover (in favor of poison ivy presence) than it is for the other land cover categories. Pairwise Bayesian contrasts also depict a similar trend when Planted/Cultivated land cover is contrasted with Evergreen, Mixed, and Deciduous land cover categories ([Figure 3](#)). Thus, poison ivy

Table 1. Census of poison ivy presence by land cover and growth habit.

Land Cover	Total White Blaze Markers Sampled By Land Cover	White Blaze Markers with Poison Ivy Present (Sorted by Growth Habit)				Totals
		Crawling	Climbing	Shrub		
Deciduous forest	1,461	92	20	6	118	
Evergreen forest	165	14	0	3	17	
Mixed forest	68	17	6	2	25	
Developed	190	33	8	2	43	
Planted/cultivated	53	16	8	1	25	
Totals	1937	172	42	14	228	

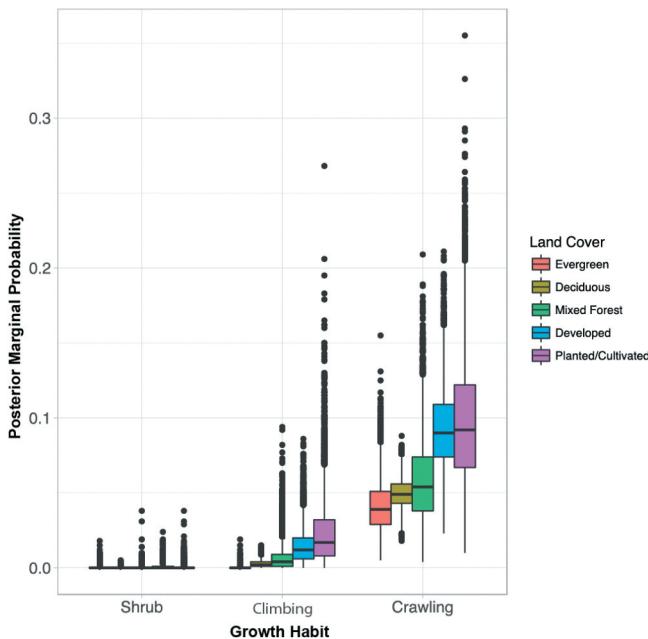


Figure 2. Poison ivy posterior probabilities by growth habit and land cover categories. Quantile box plots with outliers shown as dots.

incidence showed a clear preference for anthropogenic (Planted/Cultivated and Developed) land cover.

Biophysical parameters associated with poison ivy presence/absence and growth habits

The probability of poison ivy incidence (factored over the three growth habits) varied among the modelled biophysical variables (Figure 4(a)). For example, sampling points with north-east aspects (Figure 4(b)), and with higher temperatures had high probabilities of poison ivy incidence. The relationship between poison ivy incidence and other variables showed a relatively small effect size, and a large degree of uncertainty (e.g. precipitation, elevation, Figure 4(a)). The effects of slope (steepness) and surface curvature were negligible (Figure 4(a)).

In some cases, the responses of individual growth habits to the marginal effects of a given variable could be further differentiated. For example, both precipitation and solar radiation had strong positive effects on poison ivy crawling liana growth habit, and negative effects on poison ivy shrubs (Figure 5(a,b)). Poison ivy climbing lianas responded positively to increasing precipitation. Slope angle had a negative effect on all poison ivy growth habits ranging from weakly negative for crawling lianas to negligibly weak for shrubs (Figure 5(c)). Poison ivy crawling lianas showed a strong negative effect to increasing bedrock depth (Figure 5(d)), whereas shrubs showed a negligible positive effect, and climbing lianas seemed unaffected. The available soil water storage capacity had weak positive effects on poison ivy crawling lianas and climbing lianas (Figure 5(g))

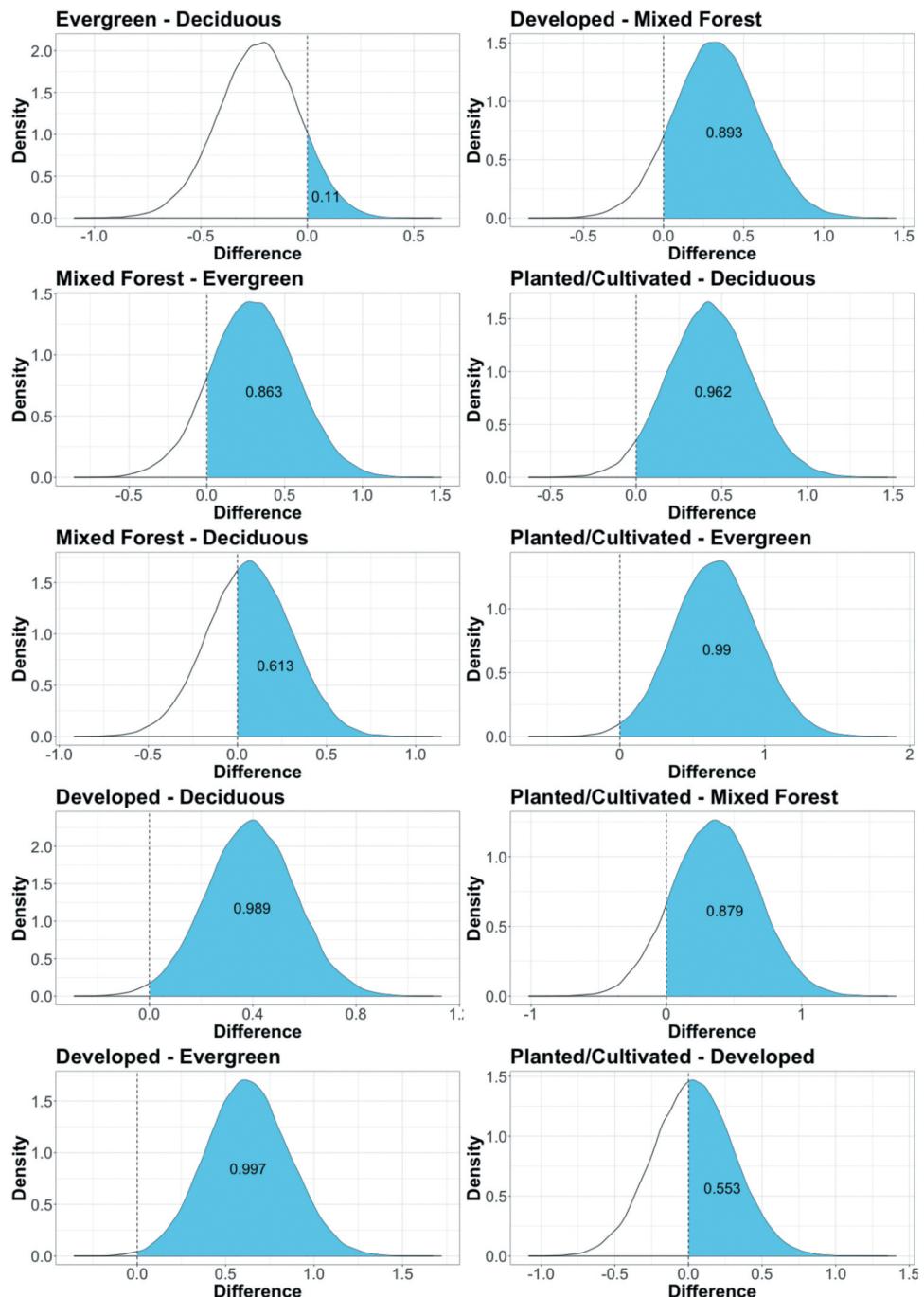


Figure 3. Pairwise Bayesian contrasts for land cover categories. Posterior pairwise contrasts between land cover group indicators. Larger density greater than zero for (group A – group B) suggests group A has a larger effect on positive poison ivy presence than group B. For example, “Developed – Mixed Forest” has 89.3% of the area (shaded) to the right of 0, meaning the probability is 89.3% that the effect (in favor of poison ivy) is larger for Developed.

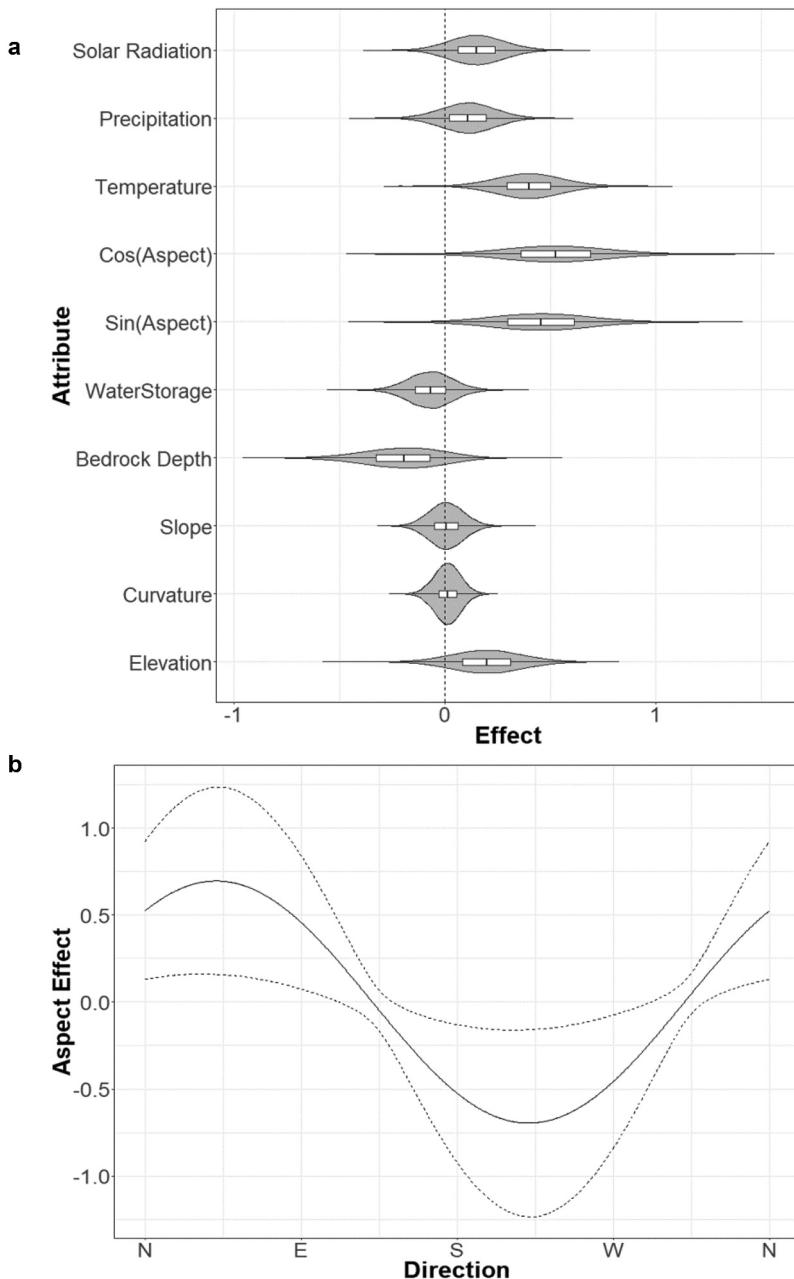


Figure 4. (A) Posterior distributions for selected biophysical effects on poison ivy presence/absence. The biophysical effects are the linear effects that each variable has on the inverse of Normal cumulative probability of poison ivy presence. For example, a value of zero implies that the variable has no effect on the probability of poison ivy presence. Increasing the value of a variable with a positive linear effect leads to an increase in the probability of poison ivy presence. In contrast, when the value of a variable is less than zero it indicates a negative linear effect on the probability of poison ivy presence. The shapes within the plots are smoothed histograms of the posterior distribution. Areas where the curve is taller are parameter estimates that are more likely. The total area within each ellipse is 100%. The area of the ellipse to the right of zero denotes the posterior probability that an increase in the variable value leads to an increase in the probability of presence; (B) Detail of aspect effects on poison ivy, showing probability of presence to be highest on north-east trending slopes. Solid line represents the posterior mean and dotted lines represent 90% credible intervals.

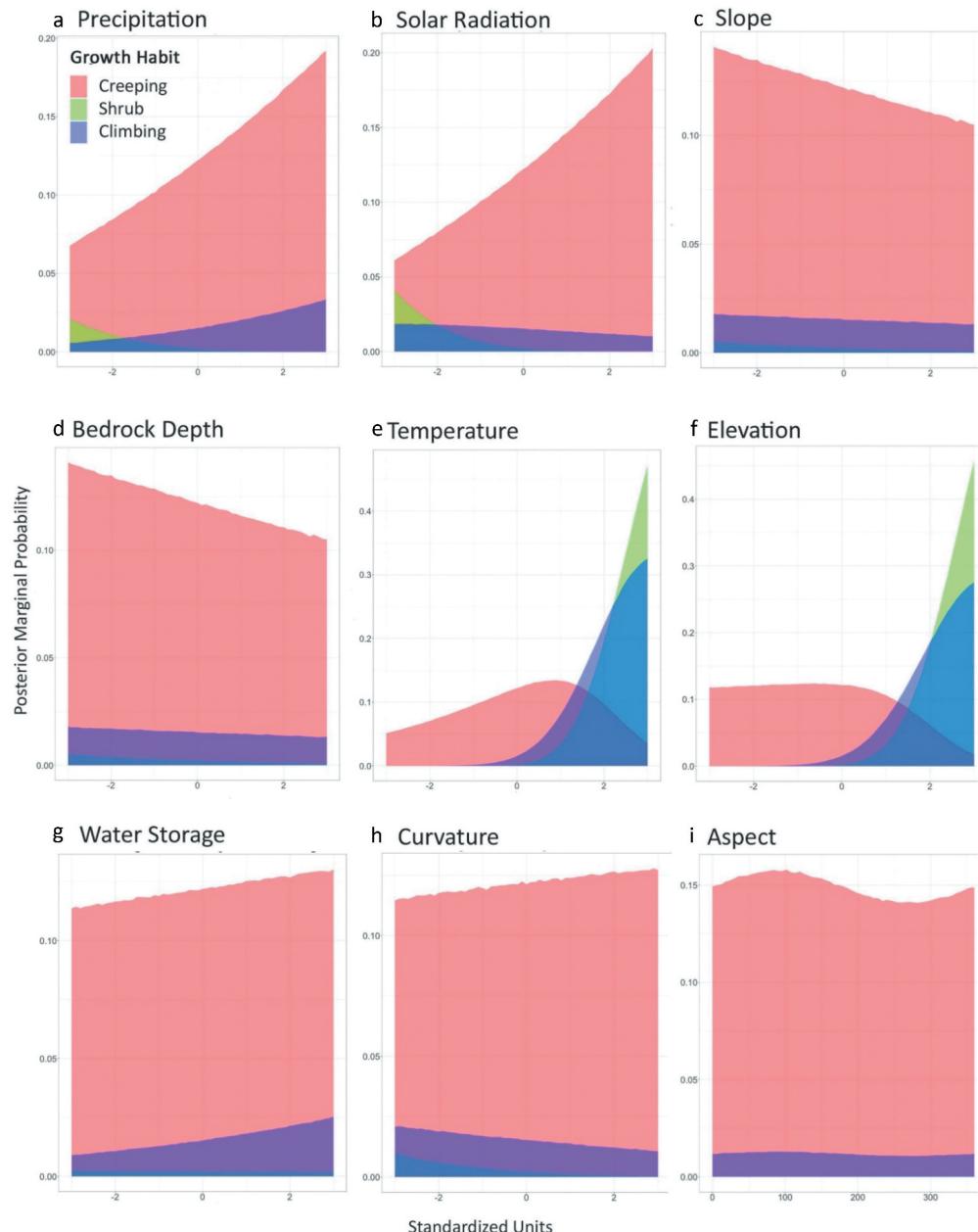


Figure 5. Land use and biophysical parameters associated with poison ivy growth habits. Note that for aspect (5i) x-axis scale is in degrees.

and seemingly no effect on shrubs. Poison ivy crawling lianas displayed a weak but consistent preference for north to eastward facing slopes compared to south to westward facing slopes ([Figure 4\(b\)](#), [Figure 5\(i\)](#)).

Poison ivy growth habits modeled markedly different responses to temperature and elevation. Crawling lianas indicated an optimum average temperature around one

positive standard deviation above the mean temperature (Figure 5(e)). Poison ivy crawling lianas seemed to prefer less than mean elevation, but beyond the mean elevation they were modeled to diminish with higher elevations (Figure 5(f)). In contrast to the crawling liana growth habit, both shrub and climbing lianas showed models with strong positive responses (i.e. increasing marginal posterior probabilities) to temperature (Figure 5(e)) and elevation (Figure 5(f)) above their respective means. Elevation and temperature effects were negatively correlated in the model ($r = -0.89$). However, this negative relationship was not accounted for in the separate marginal temperature and marginal elevation plots (Figure 5(e, f) respectively), which did not consider other variables in the model. The interaction of the marginal temperature and marginal elevation joint effects (in which both main effects were evaluated together) is visualized in Figure 6.

Poison ivy shrub and climbing lianas showed a very similar response surface where decreasing elevation combined with increasing temperatures increased their posterior probabilities (Figure 6). Interestingly, poison ivy crawling lianas showed a distinct and non-overlapping response surface to the joint marginal temperature and marginal elevation effects. Thus, poison ivy crawling liana growth habit responded to the combined effects of temperature and elevation quite differently than both poison ivy shrub and climbing lianas.

Impacts of soil series and texture on poison ivy

The analyses of association between soil classifications and poison ivy were limited by several factors. These included the relative overall paucity of poison ivy presence, uneven sampling of the three plant growth habits, and infrequent sampling of many soil

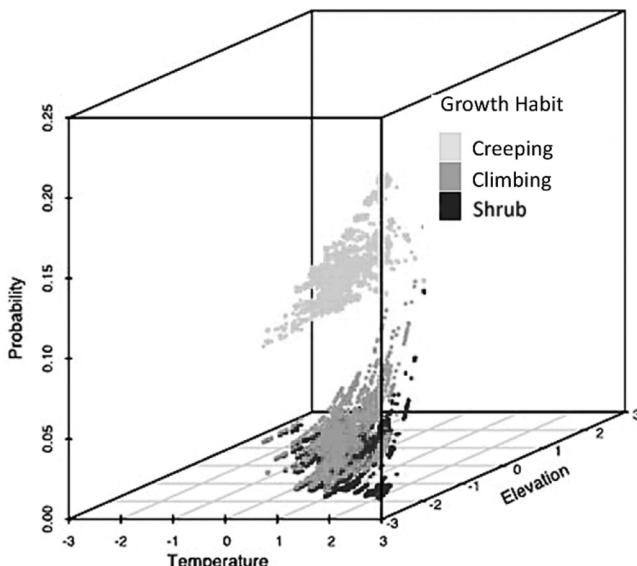


Figure 6. Poison ivy probability as a function of joint marginal temperature and marginal elevation effects.

classifications. For these reasons, modeling results for series and texture were primarily driven by the Bayesian priors and therefore largely uninformative.

Discussion

Although taxonomists have long recognized the manifestation of poison ivy's three distinct growth habits (Barkley, 1937; Gillis, 1971), ecologically oriented studies have emphasized single growth habits (e.g. Allen et al., 2005; Ladwig & Meiners, 2010b; Talley et al., 1996; Wilson et al., 2017) or total poison ivy incidence without differentiating among growth habits (Brice et al., 2014; Catling et al., 2002; Ladwig & Meiners, 2010a; Londré & Schnitzer, 2006; Rossell & Eggleston, 2017; Tessier, 2010). The present study is the first to evaluate both poison ivy presence and growth habit to assess the implications of plant strategies for spatial distributions. Here we discuss the major findings of the study as related to land cover and biophysical gradients.

Poison ivy presence and growth habit as related to land cover

Poison ivy exhibited an overall preference for human-modified (e.g. anthropogenic) habitat over forested land cover types. The direct impact in these human modified environments includes the partial or total destruction of plant biomass, and indirect climate-related effects, such as those resulting from land cover change. Within this context, the degree to which the AT-transect constituted a disturbed habitat varied. The trail itself was compacted soil or rock typically less than one meter wide. Trampling from hikers undoubtedly precluded poison ivy growth directly on the trail. However, disruption caused by the narrow trail was negligible to the overhead forest canopy, and thus did not change light conditions immediately on or adjacent to the trail itself (i.e. no appreciable trail-induced edge habitat formation). Given the position of the white blazes slightly off the trail, the AT-transect study area included a broader area than the trail itself. The study AT-transect traversed different environmental gradients (represented by the biophysical variables) and land cover types (represented by land cover categories). It ranged from a very low level of ecological disturbance (forested land cover, for example, comprised 87.4% of the study area), to high levels of disturbance (approximately 12.5% of the AT-transect). Areas with high levels of disturbance were characterized by the presence of pastureland, crops, powerline cuts, abandoned logging roads, roads with varying surfaces, and underpasses/bridges. Nevertheless, the Bayesian modeling demonstrated greater posterior probabilities for poison ivy presence (Figures 2 & 3) associated with anthropogenic disturbed habitats compared to forested land cover.

The association of poison ivy with disturbed habitat aligns with other research suggesting that anthropogenic, and other disturbance factors, result in increased poison ivy abundance (Brice et al., 2014; Catling & King, 2007; Gillis, 1971; Ladwig & Meiners, 2010a; Tessier, 2010). In the present study, the high probability of ground crawling poison ivy lianas in both Developed and Planted/Cultivated land covers is similar to previous reports of crawling poison ivy lianas increasing in both frequency and percent cover in the early herbaceous plant stage of abandoned agricultural field succession (Catling & King, 2007; Ladwig & Meiners, 2010a). These findings are also complementary to studies showing that poison ivy abundance levels are greater at forest edges where

“disturbance” of forest continuity is an inherent characteristic (Fraver, 1994; Londré & Schnitzer, 2006).

Based on counts alone, ground crawling liana was the most frequently recorded among the three poison ivy growth habits, in all land cover categories (Table 1). Within forested land cover (Deciduous, Mixed, and Evergreen) specifically, poison ivy ground crawling lianas were 4.7-fold more frequent than the climbing liana growth habit (Table 1). This finding is notable because despite the availability of trees for vertical climbing, poison ivy was frequently not functioning as climbing lianas on many nearby trees. The majority of white blaze markers in forested land cover were situated on trees; the recorded crawling lianas thus were within two meters of at least one climbing structure. Although we did not record the total number of encountered poison ivy ground crawling lianas at each white blaze, anecdotally, most ground crawling lianas were present as patches of multiple thin erect shoots emanating from the leaf litter. In a few instances, the leaf litter was pushed aside revealing a network of erect ramets at the nodes of branching stolons (Jelesko, personal communication). This observed pattern contrasts with the very closely related North American species poison oak (*Toxicodendron diversilobum* (Torr. & A. Gray) Greene) that will initiate a climbing growth habit if a vertical substrate is available (Gentry, 1991). Thus, although plasticity is a factor in morphological variation between both species, they functionally differ in their response to the presence of forest cover.

Biophysical factors

Factors such as rainfall, soil properties, temperature, and landform structure drive biological adaptions and interactions, and thus, plant distributions and community assembly. Given the intraspecific variability in growth habit response to selected variables, our results suggest that intraspecific variability in growth habit may enable poison ivy to occupy the broad niche that it does; that is, to occupy a wide range of environmental conditions beyond those characterized primarily by disturbance. When considering variables independently (Figure 5), growth habit responses to elevation, temperature, and to a lesser degree precipitation and curvature, could be differentiated. Although no single environmental parameter was associated with a particular poison ivy growth habit, the data from this study indicate that manifestation of the three growth habits was not consistent with a stochastic process.

Light

Bayesian modeling identified a small but consistent bias in poison ivy presence associated with north and east trending slopes and solar radiation (Figure 4(b), Figure 5(i)). Both slope angle and aspect (orientation) have a fundamental effect on the spatial and temporal trends of shortwave radiation received at a surface (Barry, 2008). In a study on microclimatic differences among clearcuts, forest edges, and forest interiors, Chen et al. (1993) reported that total amounts of shortwave radiation received on east- and west-facing study sites were similar, although radiation fluxes varied substantially among study site orientations over the course of a day, with flux peaking before noon on east-facing sites. Fraver (1994) showed highest abundance of poison ivy closest to the forest edge opening on north-facing forest edges (10 m from edge) compared to south-facing

forest edges where abundance peaked at 20 m from edge and where light penetrates more deeply into forest openings. Our results thus suggest that the timing of light, specifically morning light availability, may be important. Alternatively, additional microclimatic influences not measured in this study could be influential (e.g. slope-specific temperatures and soil moisture conditions). Poison ivy's positive effect with solar radiation is likely interrelated to its overall preference for non-forested land covers, where solar radiation was higher (averaging 142,543 WH/m² in Planted/Cultivated and Developed land covers, compared to 138,816 WH/m² for all forested land covers, combined). Although not measured, albedo of human-modified land cover is likely impactful (e.g. Chen et al., 1993). Shrubs contrasted to crawling lianas by exhibiting a negative response to solar radiation (Figure 5), possibly indicative of a valid growth preference for shrubs, or perhaps due to the small sample size of the shrub growth habit. Among the 14 shrub observations, 11 were in forested land covers, characterized by less total solar radiation compared to the human-modified sites.

Moisture

Soil water dynamics are influenced by climate, landforms and soil properties, such as organic matter, texture, and porosity. The marginal effects of moisture-related variables on poison ivy presence/absence (e.g. positive effect of precipitation, and negative effects by soil moisture storage capacity and bedrock depth) were consistent with Gillis (1971) assertion that poison ivy prefers moist, well-drained soils. Although our modeling results on soil texture and type were uninformative and thus not included, our study area was consistently characterized by well-drained soils (e.g. sandy loam, cobbly sandy loam). Furthermore, poison ivy presence, crawling, and climbing liana growth habits showed (to varying degrees) a positive response to precipitation. The positive effect of precipitation either factored over all three growth habits (Figure 4) or the dominant ground crawling growth habit (Figure 5(a)) contrasts to tropical lianas that show a negative correlation to total annual precipitation (DeWalt et al., 2010; Schnitzer, 2005; Swaine & Grace, 2007). This finding suggests the crawling poison ivy liana growth habit may utilize different ecophysiological adaptations (e.g. posited shallow roots) than dry tropical forest lianas whose strategies enable them to outperform trees during drought when evapotranspirative demand is high (Schnitzer, 2005). Where poison ivy was present, depth to bedrock was particularly negatively correlated with poison ivy crawling lianas, among the three growth habits, indicating a preference for shallow soils. Schenk (2008) and Poot & Lambers (2003) indicated that the roots of woody plants growing on thin soils above bedrock tend to use a foraging strategy whereby nutrients and water are sought along rock fractures, and within weathered bedrock. Soil depth to bedrock can also influence plant distributions by providing a perched water table that roots can exploit (Pérez, 2015). In our study, however, it is reasonable to hypothesize that the crawling lianas have shallow, energy efficient root systems that are conducive to exploiting resources in shallow soils.

Elevation and temperature

When factored across all growth habits, poison ivy responded positively to both elevation and temperature (Figure 4). However, the ground crawling lianas showed markedly different responses to elevation and temperature than both the climbing liana and

shrub growth habits (Figure 5). Posterior probabilities of poison ivy functioning as crawling lianas decreased above the average elevation. In contrast, climbing lianas and shrubs demonstrated marked increases in posterior probability beyond the average elevation (654 m above sea level) (Figure 5(e, f)). Gillis (1971) noted that poison ivy (no growth habit distinction) showed an elevational limit of 1070 m in the Smoky Mountains; our observations of crawling lianas were consistent with that estimate (maximum elevation crawling lianas were observed was 936.7 m). However, the modeling of both poison ivy climbing lianas and shrubs indicated a potential for growth at higher than average elevations. That shrubs and crawling lianas are showing a preference for both higher elevations and lower temperatures is unexpected, given the typical inverse relationship between temperature and elevation. Since plants do not respond directly to elevation, per se, but rather to changes in variables that are regulated by elevation (Hof et al., 2012), elevation is thus acting as a surrogate for abiotic (e.g. soils characteristics, solar radiation) or biotic variables (e.g. species cover) that could restrict the geographic distribution of resources for poison ivy. However, interpretation was limited by too few shrubs; hence, additional research is needed to determine why the shrub and climbing liana growth form may be favored at higher elevations.

Bayesian response surfaces to the *joint* marginal effects of temperature and elevation (Figure 6) provide some additional insights. Climbing and shrub growth habits exhibited similar response surfaces, whereas the joint effect response of crawling growth habit was recognizably different from the other two growth habits. Rydberg's poison ivy (*Toxicodendron rydbergii* (Small ex Rydb.) Greene) in more northern latitudes is characterized by ground crawling or shrub growth habits, and explicitly excludes climbing growth habit (*sensu* Gillis, 1971). However, Brice et al. (2014) reported that, in metropolitan areas on the Hochelaga Archipelago, Quebec, Canada, an urban heat island effect might explain the otherwise uncharacteristic climbing growth habit of poison ivy in urban forest patches. Similar to Brice et al. (2014), the present study modeled a strong positive correlation between the climbing poison ivy growth habit with increasing temperature, suggesting that temperature might be an abiotic environmental cue promoting a poison ivy climbing growth habit.

Increases in temperature, seasonality (i.e. differences between moist and dry seasons), and atmospheric CO₂ have been associated with widespread expansion of tropical liana abundance and diversity within the last several decades (e.g. Schnitzer, 2005; Schnitzer & Bongers, 2011). This trend is problematic for forests because lianas can compete aggressively with their host trees for above- and below-ground resources, resulting in slower growth rates, lower overall growth, and tree mortality. Increases in climbing liana density have thus decreased overall tropical forest biomass (e.g. Schnitzer et al., 2005; Van der Heijden & Phillips, 2009). Although studies documenting the expansion of lianas in temperate forests are fewer, the trend is documented (e.g. Allen, 2015). With increasing temperature, atmospheric CO₂ levels, and land use intensification, measurable change in mid-latitude forest structure is a possibility (Allen, 2015). At present, however, temperate forest liana density and diversity are comparatively lower than tropical forest liana density and diversity (Gentry, 1991). With respect to poison ivy specifically, in both an *in situ* forest and in environmental growth chambers, poison ivy responds to elevated atmospheric CO₂ levels by growing faster, accumulating more biomass, and shifting its urushiol congener composition to more allergenic congeners (Mohan et al., 2006; Ziska

et al., 2007). Thus, poison ivy may become both more vigorous, prevalent, and noxious with expected trends of climate change.

Observations on scale and sampling efficiency

Vegetation sampling methods are a trade-off between spatial grain and scale. This study utilized a trail-transect approach that combined fairly rapid (using the IvyMap cell phone application) sampling at a fine spatial grain (i.e. 12.57 m² plots at white blaze markers) along a 100 km trail-transect. This method enabled us to capture variability in poison ivy growth habit and occurrence along environmental gradients and across different land cover types. We found this sampling strategy to be resource efficient for our purpose, and akin to the methodology used by Rossell and Eggleston (2017) to census lianas across an elevational gradient. Regardless, evidence of fine-scale disturbances, such as canopy gaps and edges, was obscured by the coarse grain of the geospatial data. Fine resolution detail on disturbance history and local vegetation composition would add to the interpretations made in this study. However, research has indicated that exacting fine detail is not always useful because heterogeneity can obfuscate linkages. For example, Fleming (2012) notes that for complex soil classification schemes, broader interpretations are often more useful for plant ecologists because heterogeneity can make direct correlation between vegetation and specific soil types elusive. Furthermore, since multivariate analyses reflect synergies among variables that change along gradients, our model results may be capturing the influence of an unobserved interaction among measured or unmeasured variables. Thus, we recognize the possibility of unknown or unmeasured variables which could more precisely explain the relationships between poison ivy and environmental factors (i.e. deterministic uncertainty; Phillips, 1993; Phillips et al., 1996).

Conclusion

Overall, it is clear that the capacity of poison ivy to manifest different growth habits reveals complex differential landscape-scale abiotic and biotic interactions. Poison ivy has a clear preference for human-modified habitat, and each of the three growth habits has the same sequence of increasing likelihood across the land covers (i.e. lowest in forested land covers and highest in cultivated and developed land covers, Figure 2). However, increasing temperature and elevation may preferentially benefit the shrub and climbing growth habit, indicating potential for poison ivy with these growth habits to extend its range. Our results for poison ivy suggest that intraspecific variability in functional traits may impact species geographic distributions by expanding niche breadth. Since species' strategies for inhabiting certain environments can be expected to influence spatial distributions (e.g. Gianoli, 2015), knowledge about how functional traits are favored under different habitat conditions can expand current emphasis within geography and allied disciplines on predictive niche models that focus solely on species presence.

Acknowledgments

The IvyMap smartphone app was created by Anthony Barbee, Alisher Pazylbekov, Bing Qin, and Nathan Rosa in fulfillment of the group project requirement for the Virginia Tech computer science course “CS 4624 Multimedia, hypertext, and information access”. This was an undergraduate capstone course with Dr. Edward Fox as the instructor of record in the Computer Science Department at Virginia Tech. We are grateful to Drs. Roger Harris and Alexander Niemiera for contributing to field data collection. Stewart Scales contributed to the cartography for Figure 1. Thanks also to Tyler Trice for compiling the GIS database and preparing the biophysical variables for analysis. To George Malanson and Luis Daniel Llambí provided helpful feedback. Furthermore, this manuscript was greatly improved due to the detailed suggestions of Charles Lafon (Associate Editor) and two anonymous reviewers. This work was financially supported by a Virginia Tech College of Agriculture and Life Sciences Proposal Development Grant, and in part by the USDA NIFA Hatch project 1016199. No potential conflict of interest was reported by the authors.

ORCID

Lynn M. Resler  <http://orcid.org/0000-0002-5135-1797>
 John G. Jelesko  <http://orcid.org/0000-0002-7088-8020>

Disclosure statement

No potential conflict of interest was reported by the authors.

References

- Allen, B. P. (2015). Patterns of Liana abundance, diversity and distribution in temperate forests. In N. Parthasarathy (Ed.), *Biodiversity of Lianas. Sustainable development and biodiversity* (Vol. 5, pp. 7–15). Springer, Cham. https://doi.org/10.1007/978-3-319-14592-1_2.
- Allen, B. P., Sharitz, R. R., & Goebel, P. C. (2005). Twelve years post-hurricane liana dynamics in an old-growth southeastern floodplain forest. *Forest Ecology and Management*, 218(1–3), 259–269. <https://doi.org/10.1016/j.foreco.2005.08.021>
- Appalachian Trail Conservancy. (2020). *Learn the basics*. Retrieved from <https://www.appalachiantrail.org/home/explore-the-trail/hiking-basics>.
- Barkley, F. A. (1937). A monographic study of *Rhus* and its immediate allies in North and Central America, including the West Indies. *Annals of the Missouri Botanical Garden*, 24(3), 265–498. <https://doi.org/10.2307/2394183>
- Barry, R. (2008). *Mountain weather and climate*. Cambridge University Press. <https://doi.org/10.1017/CBO9780511754753>
- Braun, E. L. (1950). *Deciduous forests of Eastern North America*. Blakiston.
- Brice, M. H., Bergeron, A., & Pellerin, S. (2014). Liana distribution in response to urbanization in temperate forests. *Ecoscience*, 21(2), 104–113. <https://doi.org/10.2980/21-2-3692>
- Carlin, B. P., & Louis, T. A. (2010). *Bayes and empirical Bayes methods for data analysis*. Chapman and Hall/CRC.
- Catling, P. M., & King, B. (2007). Natural recolonization of cultivated land by native prairie plants and its enhancement by removal of Scots Pine, *Pinus sylvestris*. *The Canadian Field-naturalist*, 121(2), 201–205. <https://doi.org/10.22621/cfn.v121i2.446>
- Catling, P. M., Sinclair, A., & Cuddy, D. (2002). Plant community composition and relationships of disturbed and undisturbed alvar woodland. *Canadian Field Naturalist*, 116(4), 571.

- Chen, J., Franklin, J. F., & Spies, T. A. (1993). Contrasting microclimates among clearcut, edge, and interior of old-growth Douglas-fir forest. *Agricultural and Forest Meteorology*, 63(3–4), 219–237. [https://doi.org/10.1016/0168-1923\(93\)90061-L](https://doi.org/10.1016/0168-1923(93)90061-L)
- Cowell, C. M., & Parker, A. J. (2004). Biogeography in the Annals. *Annals of the Association of American Geographers*, 94(2), 256–268. <https://doi.org/10.1111/j.1467-8306.2004.09402002.x>
- Daly, C., Halbleib, M., Smith, J. I., Gibson, W. P., Doggett, M. K., Taylor, G. H., Curtis, J., & Pasteris, P. P. (2008). Physiographically sensitive mapping of climatological temperature and precipitation across the conterminous United States. *International Journal of Climatology: A Journal of the Royal Meteorological Society*, 28(15), 2031–2064. <https://doi.org/10.1002/joc.1688>
- DeWalt, S. J., Schnitzer, S. A., Chave, J., Bongers, F., Burnham, R. J., Cai, Z. Q., Chuyong, G., Clark, D. B., Ewango, C. E. N., Gerwing, J. J., Gortaire, E., Hart, T., Ibarra-Manriquez, G., Ickes, K., Kenfack, D., Macia, M. J., Makana, J. R., Martinez-Ramos, M., Mascaro, J., Moses, S., ... Thomas, D. (2010). Annual rainfall and seasonality predict pan-tropical patterns of liana density and basal area. *Biotropica*, 42(3), 309–317. <https://doi.org/10.1111/j.1744-7429.2009.00589.x>
- Dyer, J. M. (2006). Revisiting the deciduous forests of eastern North America. *BioScience*, 56(4), 341–352. [https://doi.org/10.1641/0006-3568\(2006\)56\[341:RTDFOE\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2006)56[341:RTDFOE]2.0.CO;2)
- Fleming, G. P. (2012). The nature of the Virginia Flora. In A. S. Weakley, J. C. Ludwig, J. F. Townsend, & B. Crowder (Eds.), *Flora of Virginia* (pp. 24–75). Botanical Research Institute of Texas Press.
- Franklin, J. (2010). *Mapping species distributions: Spatial inference and prediction*. Cambridge University Press.
- Fraver, S. (1994). Vegetation responses along edge-to-interior gradients in the mixed hardwood forests of the Roanoke River Basin, North Carolina. *Conservation Biology*, 8(3), 822–832. <https://doi.org/10.1046/j.1523-1739.1994.08030822.x>
- Gelman, A. (2002). Prior distribution. In A. H. El-Shaarawi & W. W. Piegorsch (Eds.), *Encyclopedia of environmental statistics, volume 3* (pp. 1634–1637). John Wiley & Sons.
- Gentry, A. H. (1991). The distribution and evolution of climbing plants. In F. E. Putz & H. A. Mooney (Eds.), *The biology of vines* (pp. 3–49). Cambridge University Press.
- Gianoli, E. (2015). The behavioural ecology of climbing plants. *AoB PLANTS*, 7(plv013), 1–11. <https://doi.org/10.1093/aobpla/plv013>
- Gillis, W. T. (1971). The systematics and ecology of poison-ivy and the poison-oaks (*Toxicodendron*, *Anacardiaceae*). *Rhodora*, 73(793), 72–159, 161–237, 370–443, and 465–540. <https://www.jstor.org/stable/23310933>
- Grime, J. P. (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, 111(982), 1169–1194. <https://doi.org/10.1086/283244>
- Grime, J. P. (2006). *Plant strategies, vegetation processes, and ecosystem properties* (2nd ed.). John Wiley & Sons.
- Hof, A. R., Jansson, R., & Nilsson, C. (2012). The usefulness of elevation as a predictor variable in species distribution modelling. *Ecological Modelling*, 246, 86–90. <https://doi.org/10.1016/j.ecolmodel.2012.07.028>
- Humboldt, A. V., & Bonpland, A. (1805). *Essai sur la géographie des plantes*. Chez Levrault.
- Jelesko, J. G., Benhase, E. B., & Barney, J. N. (2017). Differential responses to light and nutrient availability by geographically isolated poison ivy accessions. *Northeastern Naturalist*, 24(2), 191–200. <https://doi.org/10.1656/045.024.0210>
- Ladwig, L. M., & Meiners, S. J. (2010a). Spatiotemporal dynamics of lianas during 50 years of succession to temperate forest. *Ecology*, 91(3), 671–680. <https://doi.org/10.1890/08-1738.1>
- Ladwig, L. M., & Meiners, S. J. (2010b). Liana host preference and implications for deciduous forest regeneration. *The Journal of the Torrey Botanical Society*, 137(1), 103–112. <https://doi.org/10.3159/09-RA-041.1>
- Lecocq, T., Harpke, A., Rasmont, P., & Schweiger, O. (2019). Integrating intraspecific differentiation in species distribution models: Consequences on projections of current and future

- climatically suitable areas of species. *Diversity and Distributions*, 25(7), 1088–1100. <https://doi.org/10.1111/ddi.12916>
- Leight-Young, S. A. (2014). Seeing the Lianas in the trees: Woody vines of the temperate zone. *Arnoldia*, 72(1), 2–12.
- Londré, R. A., & Schnitzer, S. A. (2006). The distribution of lianas and their change in abundance in temperate forests over the past 45 years. *Ecology*, 87(12), 2973–2978. [https://doi.org/10.1890/0012-9658\(2006\)87\[2973:TDOLAT\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2973:TDOLAT]2.0.CO;2)
- Malanson, G. P., & Resler, L. M. (2015). Neighborhood functions alter unbalanced facilitation on a stress gradient. *Journal of Theoretical Biology*, 365, 76–83. <https://doi.org/10.1016/j.jtbi.2014.10.005>
- Markiewitz, K. H., & Dawson, C. R. (1965). On the isolation of the allelogenically active components of the toxic principle of poison ivy. *The Journal of Organic Chemistry*, 30(5), 1610–1613. <https://doi.org/10.1021/jo01016a067>
- Martin, A. C., Zim, H. S., & Nelson, A. L. (1951). *American wildlife & plants*. Dover Publications.
- McCullough, R., & Rossi, P. E. (1994). An exact likelihood analysis of the multinomial probit model. *Journal of Econometrics*, 64(1–2), 207–240. [https://doi.org/10.1016/0304-4076\(94\)90064-7](https://doi.org/10.1016/0304-4076(94)90064-7)
- McNab, W. H., & Avers, P. E. (1994). *Ecological subregions of the United States, section descriptions*. Vol. 5. USDA Forest Service, Ecosystem Management. Retrieved from <https://www.fs.fed.us/land/pubs/ecoregions>
- Mohan, J. E., Ziska, L. H., Schlesinger, W. H., Thomas, R. B., Sicher, R. C., George, K., & Clark, J. S. (2006). Biomass and toxicity responses of poison ivy (*Toxicodendron radicans*) to elevated atmospheric CO₂. *Proceedings of the National Academy of Sciences*, 103(24), 9086–9089. <https://doi.org/10.1073/pnas.0602392103>
- Multi-Resolution Land Characteristics Consortium (MRLC). National Land Cover Database (2016). (*NLCD2016 Legend*). Retrieved from <https://www.mrlc.gov/data/legends/national-land-cover-database-2016-nlcd2016-legend>.
- Penner, R., Moodie, G. E., & Staniforth, R. J. (1999). The dispersal of fruits and seeds of Poison-ivy, *Toxicodendron radicans*, by Ruffed Grouse, *Bonasa umbellus*, and squirrels, *Tamiasciurus hudsonicus* and *Sciurus carolinensis*. *Canadian Field-Naturalist*, 113(4), 616–620.
- Pérez, F. L. (2015). Biogeomorphic influence of soil depth to bedrock, volcanic ash soils, and surface tephra on silversword distribution, Haleakalā Crater (Maui, Hawai‘i). *Geomorphology*, 243, 75–86. <https://doi.org/10.1016/j.geomorph.2015.04.029>
- Phillips, J. D. (1993). Chaotic evolution of some coastal plain soils. *Physical Geography*, 14(6), 566–580. <https://doi.org/10.1080/02723646.1993.10642498>
- Phillips, J. D., Perry, D., Garbee, A. R., Carey, K., Stein, D., Morde, M. B., & Sheehy, J. A. (1996). Deterministic uncertainty and complex pedogenesis in some Pleistocene dune soils. *Geoderma*, 73(3–4), 147–164. [https://doi.org/10.1016/0016-7061\(96\)00038-9](https://doi.org/10.1016/0016-7061(96)00038-9)
- Poot, P., & Lambers, H. (2003). Are trade-offs in allocation pattern and root morphology related to species abundance? A congeneric comparison between rare and common species in the south-western Australian flora. *Journal of Ecology*, 91(1), 58–67. <https://doi.org/10.1046/j.1365-2745.2003.00738.x>
- Popay, I., & Field, R. (1996). Grazing animals as weed control agents. *Weed Technology*, 10(1), 217–231. <https://doi.org/10.1017/S0890037X00045942>
- Rossell, I. M., & Eggleston, H. (2017). Elevational distribution of temperate lianas along trails in Pisgah National Forest. *Southeastern Naturalist*, 16(3), 443–450. <https://doi.org/10.1656/058.016.0310>
- Rowe, N., & Speck, T. (2005). Plant growth forms: An ecological and evolutionary perspective. *New Phytologist*, 166(1), 61–72. <https://doi.org/10.1111/j.1469-8137.2004.01309.x>
- Schenk, H. J. (2008). Soil depth, plant rooting strategies and species' niches. *New Phytologist*, 178 (2), 223–224. <https://doi.org/10.1111/j.1469-8137.2008.02427.x>
- Schnitzer, S. A. (2005). A mechanistic explanation for global patterns of liana abundance and distribution. *American Naturalist*, 166(2), 262–276. <https://doi.org/10.1086/431250>

- Schnitzer, S. A., & Bongers, F. (2011). Increasing liana abundance and biomass in tropical forests: Emerging patterns and putative mechanisms. *Ecology Letters*, 14(4), 397–406. <https://doi.org/10.1111/j.1461-0248.2011.01590.x>
- Schnitzer, S. A., Kuzee, M. E., & Bongers, F. (2005). Disentangling above-and below-ground competition between lianas and trees in a tropical forest. *Journal of Ecology*, 93(6), 1115–1125. <https://doi.org/10.1111/j.1365-2745.2005.01056.x>
- Soberón, J. (2007). Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters*, 10(12), 1115–1123. <https://doi.org/10.1111/j.1461-0248.2007.01107.x>
- Soil Survey Staff. *Gridded Soil Survey Geographic (gSSURGO) Database for Virginia*. United States Department of Agriculture, Natural Resources Conservation Service. Retrieved from <https://gdg.sc.egov.usda.gov/>
- Swaine, M. D., & Grace, J. (2007). Lianas may be favoured by low rainfall: Evidence from Ghana. *Plant Ecology*, 192(2), 271–276. <https://doi.org/10.1007/s11258-007-9319-4>
- Talley, S. M., Lawton, R. O., & Setzer, W. N. (1996). Host preferences of *Rhus radicans* (Anacardiaceae) in a southern deciduous hardwood forest. *Ecology*, 77(4), 1271–1276. <https://doi.org/10.2307/2265596>
- Tessier, J. T. (2010). Effect of forest harvest on the vegetation of an urban park. *Northeastern Naturalist*, 17(2), 273–284. <https://doi.org/10.1656/045.017.0210>
- Van der Heijden, G. M. F., & Phillips, O. L. (2009). Liana infestation impacts tree growth in a lowland tropical moist forest. *Biogeosciences*, 6(10), 2217–2226. <https://doi.org/10.5194/bg-6-2217-2009>
- Violle, C., Navas, M. L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I., & Garnier, E. (2007). Let the concept of trait be functional! *Oikos*, 116(5), 882–892. <https://doi.org/10.1111/j.0030-1299.2007.15559.x>
- Virginia Division of Mineral Resources. (1993). Geologic map of Virginia: Virginia division of mineral resources. scale, 1:500,000.
- Weakley, A. S. (2015). *Flora of the southern and mid-Atlantic states*. University of North Carolina Herbarium, North Carolina Botanical Garden, University of North Carolina.
- Weakley, A. S., Ludwig, J. C., Townsend, J. F., Fleming, G. P., & Crowder, B. (2017). Flora of Virginia Mobile App. Flora of Virginia Project [Richmond, Virginia] and high country apps [Bozeman, Montana]. Available for Android and iOS mobile devices. In A. S. Weakley, J. C. Ludwig, J. F. Townsend, & B. Crowder (Eds.), *Flora of Virginia 2012*. Flora of Virginia Project. BRIT Press.
- Wilson, M., Freundlich, A., & Martine, C. (2017). Understory dominance and the new climax: Impacts of Japanese knotweed (*Fallopia japonica*) invasion on native plant diversity and recruitment in a riparian woodland. *Biodiversity Data Journal*, 5, e20577. <https://doi.org/10.3897/BDJ.5.e20577>
- Yang, Y., Zhu, Q., Peng, C., Wang, H., & Chen, H. (2015). From plant functional types to plant functional traits: A new paradigm in modelling global vegetation dynamics. *Progress in Physical Geography*, 39(4), 514–535. <https://doi.org/10.1177/030913315582018>
- Ziska, L. H., Sicher, R. C., George, K., & Mohan, J. E. (2007). Rising atmospheric carbon dioxide and potential impacts on the growth and toxicity of poison ivy (*Toxicodendron radicans*). *Weed Science*, 55(4), 288–292. <https://doi.org/10.1614/WS-06-190>

Appendix A. Statistical Details

Gaussian Spatial Models

Two novel Gaussian spatial models were implemented in a Bayesian framework to identify specific landscape and environmental parameters differentially associated with poison ivy characteristics. The first model uses the poison ivy presence/absence at each location as the response. The second, more granular, model uses the poison ivy growth habit as the response.

Given the inherent potential for poison ivy to show patchy spatial correlations, and with associated permissive landscape features, we developed a novel Gaussian spatial model for analyzing the transect data. Our model allows for the inference of the covariate effects while accounting for the dependence between locations. Preliminarily, we investigated the features that were determinants of poison ivy occurrences. Based on a clipped Gaussian Process (GP) model:

$$y_i = \begin{cases} 1 & \text{if } z_i \geq 0 \\ 0 & \text{if } z_i < 0 \end{cases}$$

$$z_i \sim \tilde{Normal}(X\beta, \Sigma)$$

$$\Sigma_{i,j} = \exp(-d_{i,j}/\lambda)$$

, we are able to determine which features (represented by the columns within X) are associated with the presence/absence of poison ivy. Specifically, covariates with inferred positive coefficients (elements of β) that are distinguished from zero are determinants of the presence of poison ivy; whereas negative values are associated with poison ivy absence. Diffused prior distributions were chosen as $\beta \sim \tilde{Normal}(0, 10I)$, and λ was fixed at its maximum likelihood estimate.

To extend the analysis to account for varying types of poison ivy, we modeled each categorical occurrence using the framework described within McCullough and Rossi (1994), which accounts for both spatial correlation between locations and correlation between the probability of observing each type at a given location. For model identifiability, we specifically modeled the latent differences from the baseline absentee group, so that elements of β represent the relative impact of covariates, from the baseline absentee group. For instance, a positive coefficient value (β_j) indicates that the probability of poison ivy presence increases as a function of the j^{th} covariate.

In order to differentiate growth habits (**S**: shrub, **V**: vertically climbing liana, and **C**: crawling stolon, **A**: absent), and explain the factors contribution to growth habitat, we extend our latent variable analysis to the four categories: z_{iC} , z_{iS} , z_{iV} , and z_{iA} , for each category. Similar to model 1, we define the differences: $w_{iC} = z_{iC} - z_{iA}$, $w_{iS} = z_{iS} - z_{iA}$, and $w_{iV} = z_{iV} - z_{iA}$ for each of the i ($= 1, \dots, N$) observations. Letting z_{iC} , z_{iS} , z_{iV} , and z_{iA} represent latent variables for each category, we define the differences: $w_{iC} = z_{iC} - z_{iA}$, $w_{iS} = z_{iS} - z_{iA}$, and $w_{iV} = z_{iV} - z_{iA}$ for each of the i ($= 1, \dots, N$) observations. Letting $w_i = (w_{iC}, w_{iS}, w_{iV})'$ and $W = (w_1, \dots, w_N)$ our model follows:

$$y_i = \begin{cases} \text{Cif } w_{iC} = \max(w_{iC}, w_{iS}, w_{iV}) \geq 0 \\ \text{Sif } w_{iS} = \max(w_{iC}, w_{iS}, w_{iV}) \geq 0 \\ \text{Vif } w_{iV} = \max(w_{iC}, w_{iS}, w_{iV}) \geq 0 \\ \text{Aif } \max(w_{iC}, w_{iS}, w_{iV}) < 0 \end{cases}$$

$$W \sim \tilde{Normal}((X\beta_C, X\beta_S, X\beta_V)', H \otimes T)$$

$$H_{ij} = \exp(-d_{i,j}/\lambda)$$

, where T , is a 3×3 covariance matrix for w_i , and \otimes represents the Kronecker product.

Diffused prior distributions were chosen as $(\beta_C, \beta_S, \beta_V) \sim \tilde{Normal}(0, 10I)$, $T \sim \tilde{Wishart}$, which provide identifiable estimates without heavily influencing the analysis. λ was fixed at its maximum likelihood estimate; however, we note that a full joint Bayesian analysis would yield nearly identical results but would increase computational intensity.

Missing Quantities

We utilized diffused prior distributions for missing quantities; specifically, we used *uniform* priors on discrete quantities, and diffused (relative to latent Gaussian Process model) *normal* distributions (=3). In order to mitigate any underlying subjectivity, we utilized an empirical Bayesian framework (Carlin & Louis, 2010) and centered our continuous prior distributions at their predictive expectations.