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Eastern North American Liana Distributions Reveal Conservation and Climate Mitigation Potential

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ABSTRACT

Aim: We created the first high-resolution distribution maps for lianas at a continental scale to address critical knowledge gaps in invasive species management, forest carbon storage, and temperate forest ecology.

Location: The Nearctic realm and Eastern North America.

Methods: We developed a cascading modelling approach using Google Earth Engine that first classifies suitable climate envelopes at 5 km resolution across North America, then predicts occupancy within suitable areas at 250 m resolution using remotely sensed data, topography, and soil maps. We modelled four ecologically and economically important lianas capable of enshrouding forest canopies: Oriental bittersweet (*Celastrus orbiculatus*), kudzu (*Pueraria montana*), summer grape (*Vitis aestivalis*), and Chinese wisteria (*Wisteria sinensis*). These species represent native and nonnative species with contrasting dispersal mechanisms.

Results: Approximately 378.8 ± 36.4 million hectares are suitable for at least one of the focal species, with 57.9 ± 8.5 million hectares of forest likely occupied. Native and nonnative lianas exhibit differences in distribution patterns: while all lianas studied here are associated with urbanization and development, this pattern is particularly strong for species with limited seed dispersal (kudzu, wisteria), whereas the native grape and bird-dispersed nonnative bittersweet show broader distributions, challenging widespread assumptions about their climate-driven distributions and ability to spread across landscapes. However, given moderate SDM accuracy and potential sampling biases in presence records, area estimates should be interpreted as indicative rather than definitive.

Main Conclusions: Our computationally efficient cascading approach enables high-resolution species distribution modelling at scales previously prohibitive, particularly for range-restricted or invasive taxa. We demonstrate that urbanization drives non-native liana distributions, suggesting targeted management strategies. These maps provide immediate conservation applications for invasive species control, urban forest management, and potential carbon sequestration enhancement. Our publicly accessible models and workflow offer a proof-of-concept for functional group mapping applicable to understudied taxa globally.

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1 | Introduction

Managing lianas—or woody vines—could provide major climate mitigation benefits by way of increasing tree growth and carbon storage. The benefits of liana removal for tree growth have been documented in the tropics and could nearly double tree carbon sequestration rates in some cases (Schnitzer and Bongers 2011; Schnitzer et al. 2014; Finlayson et al. 2022). Once established, they hinder tree growth and can arrest succession—preserving ideal liana habitat and reducing the carbon storage capacity of forests (Putz and Mooney 1992; Gerwing and Farias 2000; Griscom and Ashton 2003; Finlayson et al. 2022). Although lianas, like trees, are woody plants that remove carbon dioxide from the atmosphere and therefore mitigate carbon emissions, current evidence suggests that lianas do not store enough carbon to compensate for the negative impact they impart on their hosts: they are structural parasites that invest little in structural support (Stevens 1987), opting instead to maximize leaf area, stem elongation, and fruit production (Putz 1983; Putz and Mooney 1992; Gerwing and Farias 2000). In a recent meta-analysis, researchers found that, after accounting for emissions from the decay of cut lianas, there is a net increase in carbon sequestration by tropical forests after thinning lianas (Finlayson et al. 2022). However, this evidence is primarily from tropical forest systems (e.g., Estrada-Villegas and Schnitzer 2018) and it is therefore critical to understand if temperate lianas have similar impacts on tree growth and carbon sequestration.

Eastern North American temperate forests (situated within the Nearctic realm *sensu* Dinerstein et al. 2017) sequester 12%–19% of annual U.S. fossil fuel emissions and represent a stable and increasing global carbon sink (McGarvey et al. 2015; Pacala et al. 2001). These forests also support diverse liana assemblages, with up to 28 species documented at individual sites and lianas present on the majority of canopy trees in some stands (Ladwig and Meiners 2009). Furthermore, non-native lianas are also problematic in the region, with several species appearing on invasive species watchlists and noxious weed lists across multiple states of the USA (Bennett 2022; NRCS 2024). However, liana ecology remains poorly understood relative to tropical systems with a relatively small body of literature reporting on the impact of temperate North American lianas over past decades (Matthews et al. 2016; Ladwig and Meiners 2009; Horton and Francis 2014; Siccama et al. 1976; Trimble and Tryon 1974), with essentially no published experimental studies. Similarly, there are very few published studies on lianas in other temperate regions such as the Mediterranean; for example, Garfi and Ficarrota (2003) or temperate or subtropical Asia for which we found no studies. Researchers have begun quantifying liana impacts on temperate tree carbon uptake, finding a 20% reduction in CO₂ removal rates (Peters et al. 2023) for shade-intolerant host trees, but such fundamental data were unavailable until 2023.

One approach to developing a better understanding of ecological phenomena such as lianas is through ecological niche modelling. Mapping the ecological niche of species or taxa offers significant benefits for policy, conservation, and understanding migration patterns. Since the early 2000s, these models have become a popular tool for understanding biogeography and informing conservation efforts (Peterson et al. 2000; Turner et al. 2003). For example, they can help us monitor or predict pest outbreaks

and changes in distribution through inferences based on predicted changes in climate and land use (Peterson 2003; Thuiller et al. 2005). Furthermore, Peterson (2003) and others have had some success in predicting the “invasion range” of certain taxa by using training data from their native range. This could be helpful for newly introduced species that have not yet reached an equilibrium with their new environment or for species for which there are minimal presence data in their non-native range. From a remote sensing standpoint, researchers have described “mapping” species rather than predicting distribution or suitable habitat, although the approaches are similar (Xie et al. 2008).

However, there is no consensus on terminology for these types of models and therefore different terms are often used interchangeably. Those most frequently used are Ecological Niche Models (ENMs), Habitat Suitability Models (HSMs), and Species Distribution Models (SDMs) (Bradley et al. 2012; Elith and Leathwick 2009). Importantly, we clarify the distinction between our HSMs and SDMs, as these terms are often used interchangeably throughout the literature (Bradley et al. 2012). We define our HSMs as models that attempt to predict (at a coarser resolution) where a species *could* survive. We define our SDMs as models that attempt to predict the current distribution of a species (i.e., where it actually occurs) at a higher resolution. This context is important for understanding our modelling approach, as we use both HSMs and SDMs in a cascading manner to first identify broadly suitable habitat and then predict current distribution within that habitat.

To determine if large scale liana management is worthwhile, we must therefore understand (1) where lianas are and (2) which landscape- and stand-level variables best describe their distribution. No map currently exists, though researchers have identified correlations between environmental conditions and tropical liana distributions (DeWalt et al. 2014; Schnitzer 2005; Hirzel et al. 2006). Temperate lianas tend to prefer fertile, moist, well-drained soils (Della-Bianca 1979) or “better sites” with an oak site index of 70 or higher (Smith 1984). In what we can tell is the northernmost liana study published in the Western hemisphere, Brice et al. (2014) linked liana presence around Montreal, Canada with urban heat islands. We unravel this problem by mapping and evaluating the distribution of four representative species of North American lianas that are capable of enshrouding forest canopies. We implement a novel cascading approach by first using coarse-grained (5km) bio-climatic variables to classify the suitable habitat ranges for individual lianas and subsequently combining these ranges to identify the area suitable to any of these species before using higher resolution (250 m) remotely sensed data to estimate their current distribution within that range.

Our goal is to map and understand the distribution of the following lianas with implications for forest management in Eastern North America: Oriental bittersweet (*Celastrus orbiculatus* Thunb.), kudzu (*Pueraria montana* (Loureiro) Merritt var. *lobata* (Willd.) Maesen & S. Almeida), summer grape (*Vitis aestivalis*), and Chinese wisteria (*Wisteria sinensis*). These four species in particular were selected because they are (1) frequent in Eastern North American forests, (2) known to cover forest canopies when given an opportunity, (3) represent both native and nonnative species, and (4) they

have contrasting dispersal mechanisms (Weakley et al. 2013; Bennett 2022; Forseth and Innis 2004). We note that summer grape, being the sole native species among these four, is representative of the large genus *Vitis*, with many species that often co-occur and have similar growth forms (Weakley et al. 2013; GBIF.org 2024). Additionally, we note that certain native species were not included in our selection. This is chiefly due to the lack of other native lianas in eastern North America that are known to cover forest canopies with the exception of other members of *Vitis* (e.g., *V. riparia*, *V. labrusca*). We have therefore excluded Virginia creeper (*Parthenocissus quinquefolia*) and poison ivy (*Toxicodendron radicans*) as they typically do not cover forest canopies (Weakley et al. 2013). We also do not include the non-native lianas English ivy (*Hedera helix*) or Japanese honeysuckle (*Lonicera japonica*) as they primarily occupy space on the ground, understory or tree trunks, and thus do not typically cover forest canopies (Weakley et al. 2013). In the case of wisteria, although we downloaded presence data specifically for “*W. sinensis*”, it is likely that these data include misidentified *W. floribunda* (Japanese wisteria) as well as cryptic hybrids of the two species (Trusty et al. 2007). For more information on why these species were selected and their ecological characteristics, see Appendix A.2. Secondly, we aim to compare the distributions in the context of their native status, method of introduction, and dispersal mechanisms. Finally, we provide the first preliminary estimate of the potential carbon sequestration benefits for several liana management scenarios in eastern North American forests.

We ask “what is the likely distribution and subsequent overlap for these lianas in Eastern North America, and what are the implications for forest management?” We hypothesize that environmental factors such as climate and land use play a significant role in shaping their distribution. Specifically, we predict that liana presence is positively correlated with urbanization (evidenced by nighttime light intensity or impervious surface percentage) as well as with warmer temperatures and higher precipitation levels. We aim to (1) predict and map the suitable ranges and occupied distribution for the aforementioned lianas, (2) combine predictions for all species to estimate liana infestation risk, (3) identify which variables best explain liana habitat and distribution, (4) compare the distributions of these lianas and propose hypotheses for the observed patterns, and (5) provide the first rough estimates for carbon sequestration benefits of liana removal in temperate forests. Our results provide a much needed point of reference for future studies on these species and temperate lianas broadly speaking and for agencies, municipalities, and practitioners that might be considering liana management as a means to conserve native species, restore forests with arrested succession due to lianas, or improve carbon capture and timber value.

2 | Methods

2.1 | Data Preparation

We began by downloading presence data from the Global Biodiversity Information Facility (GBIF.org 2024; Chamberlain et al. 2024) and constrained these data to the Nearctic

realm (minus the arctic circle: cutoff at 65.8252° latitude) per Dinerstein et al. (2017). We removed points from the centroids of state and national capitals (as points without true GPS information sometimes are set to the state or national capital of where they were documented), old observations (prior to 1945), and points with a documented GPS error of more than 30m using the CoordinateCleaner package in R (Zizka et al. 2019) and removed points that do not overlap with tree cover (classes 111–126) per the Copernicus Global Land Cover dataset (Buchhorn et al. 2020) using the Terra package in R (Hijmans 2024; R Core Team 2021). Next, all presence points were thinned slightly: no points are within 15m of another point. If there were more than 999 points after that initial thinning, we followed an example set by Pinkert et al. (2023), where presence data are thinned by iteratively eliminating points from randomly selected pairs that are less than 30, 45 ...50,000m apart until there are 999 points remaining across the entire study area. We took these steps to improve processing efficiency and reduce the potential effect of sampling bias or erroneous GPS points (Pinkert et al. 2023). For this suite of species, only Oriental bittersweet underwent additional thinning to 999 points whereas other species only underwent the initial thinning to remove points that were situated within 15m of another point. Final presence points for each species are as follows: Oriental bittersweet ($n = 999$), kudzu ($n = 530$), summer grape ($n = 396$), and Chinese wisteria ($n = 154$). However, although we follow an ecologically-informed approach as demonstrated by published workflows, we acknowledge that model performance for species with low final presence points might be more sensitive to the specific locations of these points compared to species with higher presence points. Nevertheless, we propose that the ecological implications of thinning presence records from sources such as GBIF, which is known to have serious sampling bias issues, would yield less biased results than if no attempt at thinning occurred. This is an important topic for ongoing research and discussion in the field of ecological niche modelling (Zizka et al. 2020, 2019; Pinkert et al. 2023).

For HSMs we used predictor variables that describe climate and region: (1) NASA's Earth Exchange Global Daily Downscaled Projections (Thrasher et al. 2022) from the ACCESS-CM2 model, which include temperature, humidity, wind, radiation, and precipitation, and (2) latitude and longitude. Longitude and latitude were included as predictors to account for spatial patterns and biogeographical processes not fully captured by the environmental variables. We calculated the annual means and mean of each meteorological season (winter: December, January, February; Spring: March, April, May; Summer: June, July, August; Fall: September, October, November). We also calculated the seasonality of temperature and precipitation. For temperature seasonality, we used the difference between maximum summer temperature (the maximum of daily near-surface air temperature) and minimum winter temperature (the minimum of daily near-surface air temperature). For precipitation seasonality, we used the ratio of summer and winter precipitation.

For SDMs, we used predictor variables that describe the physical characteristics or appearance of the landscape that vary at fine scales: (1) Spectral reflectance data using the median pixel values from cloud-masked Landsat 8 imagery (red, green, blue, near infrared, and shortwave infrared bands) from 2015 to 2021, (2) vegetation indices including Normalized Difference Vegetation

Index (NDVI; Rouse Jr et al. 1974 and Equation 1), Normalized Difference Moisture Index (NDMI or also known as NDWI; see Gao 1996 and Equation 2), Enhanced Vegetation Index (EVI; see Huete et al. 2002 and Equation 3), and a modified green leaf index (GLI), adapting the numerator from Woebbecke et al. (1995) and normalizing by total reflectance (Equation 4), (3) seasonal averages and seasonality (normalized difference of summer and winter values) for all reflectance bands and vegetation indices, (4) topographic variables including elevation, roughness, slope, aspect, eastness (sine of aspect), northness (cosine of aspect) derived from the Shuttle Radar Topography Mission (SRTM) digital elevation dataset (Jarvis et al. 2008), (5) topographic position index from SRTM Multi-Scale Topographic Position Index (mTPI) (Theobald et al. 2015), (6) nighttime lights (proxy for urbanization) from NASA/NOAA Visible Infrared Imaging Radiometer Suite (VIIRS) (Elvidge et al. 2021), (7) impervious surface percentage (from Copernicus Global Land Cover; see Buchhorn et al. 2020), (8) distance to forest edge (euclidean distance to the nearest non-forest pixel), (9) canopy height (derived from GEDI; see Potapov et al. 2021), (10) soil carbon OpenLandMap (Hengl and Wheeler 2018), and (11) soil moisture (Turek et al. 2023). Landsat imagery is collected every 16 days at a 30m resolution, and using these we calculated the mean reflectance values and vegetation indices for each meteorological season from 2015 to 2021. The equations for calculating NDVI, NDMI, EVI, and GLI are as follows:

$$\text{NDVI} = \frac{\text{NIR} - \text{RED}}{\text{NIR} + \text{RED}} \quad (1)$$

$$\text{NDMI} = \frac{\text{NIR} - \text{SWIR}}{\text{NIR} + \text{SWIR}} \quad (2)$$

$$\text{EVI} = 2.5 \times \frac{\text{NIR} - \text{RED}}{\text{NIR} + 6 \times \text{RED} - 7.5 \times \text{BLUE} + 1} \quad (3)$$

$$\text{GLI} = \frac{2 \times \text{GREEN} - \text{RED} - \text{BLUE}}{\text{RED} + \text{GREEN} + \text{BLUE}} \quad (4)$$

where NIR, RED, GREEN, BLUE, and SWIR correspond to Landsat bands 5, 4, 3, 2, and 6, respectively. We also included reflectance seasonality: the normalized difference of summer and winter reflectance.

Training data (described in the following section) and SDM predictor variables (and therefore the prediction output) were limited to pixels classified as tree cover per the Copernicus Global Land Cover database. The purpose of this is twofold. First, it reduces the number of erroneous training points (points from the center of highways, buildings, water bodies, etc.). Second, it allows for more confident and straightforward estimations and comparisons of forest occupancy by lianas, which is essential to our objective of understanding how lianas are distributed throughout and impact forests. HSM training data and predictor variables were not limited to tree cover, as the goal of HSMs is to identify broadly suitable habitat, which may include non-forested areas that could become forested in the future.

2.2 | Model Training

We ran Habitat Suitability Models (HSMs) and Species Distribution Models (SDMs) at resolutions of 5 km and 250 m,

respectively. As of 2025, all data used here are freely available through the Google Earth Engine (GEE) data catalogue to increase the reproducibility and transparency of our study. To see the broad context for our HSMs and SDMs, see Figure A1.

We trained and used Random Forest classifiers within Google Earth Engine via the Earth Engine Python API (using the `ee.Classifier.smileRandomForest` implementation) to fit models and generate continuous probability predictions and binary suitability/occupancy maps (Gorelick et al. 2017). Random forest is a machine learning algorithm that evaluates data using multiple decision trees made from random assortments of observations and independent variables (Breiman 2001a). In our case, every model contains 500 of these randomized decision trees ($nTrees = 500$). We used the default number of variables to be randomly sampled at each split (otherwise known as “mtry”), equal to the square root of the total number of predictors. Finally, making these models through GEE allows us to conduct the majority of our workflow in one place: model training, creating predictions, exporting results, and building confusion matrices, and sharing the results in an interactive web application.

Training and validation sets were randomly selected from spatial blocks, as described in the model validation section below and in Figure A1. We used a simple approach for generating pseudo-absence points following Crego et al. 2022, where we randomly sampled points across the study area (Nearctic realm for HSMs, suitable forest area for SDMs) without replacement until we had a number of points equal to the number of presence points. Aside from limiting pseudo-absence points to pixels with no presence data and randomly limiting the number of pseudo-absence points to equal the number of presence points, we did not do any post-processing of these pseudo-absence points for spatial autocorrelation nor did we apply any additional spatial filtering such as distance-based thinning. Models were ran five times, independently. Within each of these models, we followed a technique demonstrated by Crego et al. 2022 to select the best cutoff for classifying positive or negative outcomes (i.e., suitability for HSMs or occupancy for SDMs) based on which of 25 cutoffs (0.0, 0.04, 0.08, ..., 0.96, 1.0) maximizes the sum of sensitivity (True Positive Rate, TPR) and specificity (True Negative Rate, TNR). This allowed us to make an informed decision for classifying the outcome at every model iteration. For both HSMs and SDMs, we used this classification approach to estimate the area of suitable or occupied space for every model iteration for each species, allowing us to provide error-adjusted area estimates with standard error listed (Olofsson et al. 2014). The final models shown herein are summarized across model iterations and exported for each species: we use the most common classification (mode) for HSMs and average probability of occupancy for SDMs.

For HSMs, we computed the convex hull around the predicted suitable area to create a clean boundary. Once all HSMs were finalized, we combined them and computed the convex hull around this combined suitable area to create a clean boundary to represent the broadly suitable range for these species. This boundary is used for the footprint of all SDMs. Distribution models are made following the same steps described here but at a higher resolution (250 m) over a smaller geographic area and use a different suite of variables as described.

2.3 | Variable Selection

In an intermediate step, we conducted variable selection using variable importance rankings from the first five preliminary models alongside a correlation matrix (Spearman's correlation) for all variables. See [Supporting Information](#) for the full correlation matrix of all variables. When selecting variables for the final models, we set a high correlation threshold of 0.9, since random forest is reported to be robust when dealing with many variables and multicollinearity (Breiman 2001b; Hanberry 2024). For each pair of correlated variables, we kept the most important of the two per initial model results (GINI importance). We did this until there were no pairs of correlated variables remaining at our specified threshold. This step was repeated for distribution models. For any given model, we used 19 of the 43 possible variables for HSMs and 38–39 of the possible 72 variables for SDMs, depending on the species. Across all species, we used 33 unique variables for HSMs and 52 unique variables for SDMs (Table 1).

2.4 | Model Validation

For separating training and testing sets, we followed a spatial block cross validation method described by Roberts et al. (2017) and exemplified using Google Earth Engine by Crego et al. (2022). We created a large grid over the study area composed of 100-km blocks and randomly selected 70% and 30% of those blocks from which we derived training and testing data, respectively (see Figure A1 for an example). We should note that the original example by Crego et al. (2022) used 200-km blocks, but we found that for species with potentially clumped or limited distributions (e.g., wisteria), this resulted in some model iterations having no presence points in the testing set. Therefore, we opted for smaller blocks to ensure that every model iteration had at least some presence points in the testing set and found that 100-km blocks were sufficient for this purpose and notably that GEE struggled to process smaller blocks as there were too many at this scale. However, it is possible that using smaller blocks might work for SDMs, which were limited to suitable habitat ranges and therefore had fewer blocks overall, but we did not explore this possibility further and opted to keep the same block size for both HSMs and SDMs for consistency. The grid used for HSMs consisted of around 2500 blocks, and the grid used for SDMs (over the combined suitable habitat ranges) consisted of around 450 blocks. As explained in further detail below, this approach allowed us to make more robust evaluations of model performance by ensuring that the model training data was different from the data used for validation.

We performed model validation for every model iteration. This allowed us to calculate metrics including Area Under the Receiver Operator Characteristic Curve (AUCROC; see Fielding and Bell 1997), Area Under the Precision Recall Curve (AUCPR; see Sofaer et al. 2019), and to build confusion matrices from each model iteration to calculate sensitivity (TPR), specificity (TNR), precision, and error-adjusted area estimates for every taxon.

In the case of mapping invasive or otherwise problematic species such as lianas, there is a higher cost for false negatives than

false positives. Therefore, we prioritize using the Area Under the Precision Recall Curve (AUCPR) as the most important metric for evaluating both HSMs and SDMs. The precision-recall curve plots precision (the proportion of true positives captured out of the total positives predicted by the model) against recall (TPR: the rate at which the model correctly predicts positive cases). The area under this curve provides a single value that explains how well the model correctly identifies liana presence.

2.5 | Model Interpretation and Results

For each species, we ran five model iterations from which we calculated error-adjusted area estimates by multiplying the predicted suitable or occupied area by the model's precision (user's accuracy: $TP/(TP + FP)$). This conservative adjustment accounts for commission errors (false positives) in our area estimates, following a simplified approach from Olofsson et al. (2014). We acknowledge this method does not account for omission errors (false negatives), which would increase area estimates. For each taxon, we calculated 95% confidence intervals on these error-adjusted areas using the t-distribution with four degrees of freedom, where the margin of error equals the critical t-value multiplied by the standard error of the five iterations. For delineating suitable areas, we used the mode (most common classification) from the five HSM iterations for each species and subsequently computed the convex hull of their union to estimate the total suitable area. Similarly, for summarizing occupied area, we averaged the probability of occupancy across the five SDM iterations for each species, then applied a binary cutoff at the mean best threshold (the cutoff maximizing the sum of sensitivity and specificity across iterations). We used the mode of these binary SDMs to estimate total area potentially occupied by lianas. For the combined multi-species estimates, we pooled the individual species' confidence intervals to provide an approximate measure of uncertainty, acknowledging that this does not fully account for spatial overlap among species' ranges. Finally, composite area estimates for liana presence should be interpreted with caution, since model accuracy varies among species, and overlapping distributions may lead to compounded uncertainties.

Liana abundance could be predicted either directly—requiring additional modelling steps and data preparation methods, for example, joint Species Distribution Models to model multiple taxa at once as in Pollock et al. (2014)—or by summing the distribution maps from multiple taxa as described by Thuiller et al. (2005). We have chosen the latter approach. Results will be organized and published in a GEE app for viewing by anyone with internet access (<https://ee-petersjdj.projects.earthengine.app/view/easternusalianas>).

After identifying the most important variables (per random forest's GINI importance metric), we collected a stratified random sample of pixels for each classification value. For HSMs, we sampled 1500 pixels classified as positive (i.e., suitable) and 1500 pixels classified as negative ($n = 3000$). For SDMs, we collected a stratified sample of 100 pixels across likelihood values: 0, 0.1, 0.2 ... 1 ($700 > n > 900$). For data exploration purposes, we fit a binary logistic regression (binomial for HSMs or quasi-binomial for SDMs) to help visualize each relationship. This allowed us to consider relationships between important variables and habitat

TABLE 1 | Environmental variables used in Habitat Suitability Models (HSM) and Species Distribution Models (SDM). Data sources reference Google Earth Engine (GEE) dataset identifiers.

Variable	Ecological proxy	Source	Resolution
HSM variables (climate)			
tmean	Annual mean temperature	NASA/GDDP-CMIP6	5 km
tmin	Annual minimum temperature	NASA/GDDP-CMIP6	5 km
tmax	Annual maximum temperature	NASA/GDDP-CMIP6	5 km
temp (seasonal)	Seasonal mean temperature	NASA/GDDP-CMIP6	5 km
tempMin (seasonal)*	Seasonal minimum temperature	NASA/GDDP-CMIP6	5 km
tempMax (seasonal)*	Seasonal maximum temperature	NASA/GDDP-CMIP6	5 km
tempSeasonality*	Temperature range (summer max—winter min)	Derived from NASA/GDDP-CMIP6	5 km
relHum*	Annual mean relative humidity	NASA/GDDP-CMIP6	5 km
relHum (seasonal)*	Seasonal relative humidity	NASA/GDDP-CMIP6	5 km
spHum	Annual mean specific humidity	NASA/GDDP-CMIP6	5 km
spHum (seasonal)*	Seasonal specific humidity	NASA/GDDP-CMIP6	5 km
precip*	Mean annual precipitation	NASA/GDDP-CMIP6	5 km
precip (seasonal)*	Seasonal precipitation	NASA/GDDP-CMIP6	5 km
rainSeasonality*	Warm vs. cool season precipitation ratio	Derived from NASA/GDDP-CMIP6	5 km
lwrad	Annual mean longwave radiation	NASA/GDDP-CMIP6	5 km
lwrad (seasonal)*	Seasonal longwave radiation	NASA/GDDP-CMIP6	5 km
wind*	Annual mean wind speed	NASA/GDDP-CMIP6	5 km
wind (seasonal)*	Seasonal wind speed	NASA/GDDP-CMIP6	5 km
long*	Geographic coordinates (Biogeographical patterns)	—	—
lat	Geographic coordinates (Biogeographical patterns)	—	—
SDM variables (forest structure and land cover)			
impSurface*	Urban cover fraction	COPERNICUS/Landcover/100 m/ Proba-V-C3/Global	100 m
distToEdge*	Distance to forest edge	Derived from COPERNICUS/Landcover	250 m
canHeight*	Canopy height	Users/potapovpeter/GEDI_V27	30 m
nighttime*	Anthropogenic light intensity	NOAA/VIIRS/DNB/ANNUAL_V21	500 m
SDM variables (spectral bands)			
nir (seasonal)*	Seasonal near-infrared reflectance	LANDSAT/LC08/C02/T1_L2 (SR_B5)	30 m
nirSeasonality*	NIR summer-winter difference	Derived from LANDSAT/LC08/C02/T1_L2	30 m
red (seasonal)*	Seasonal red reflectance	LANDSAT/LC08/C02/T1_L2 (SR_B4)	30 m
redSeasonality*	Red summer-winter difference	Derived from LANDSAT/LC08/C02/T1_L2	30 m
green (seasonal)	Seasonal green reflectance	LANDSAT/LC08/C02/T1_L2 (SR_B3)	30 m
greenSeasonality*	Green summer-winter difference	Derived from LANDSAT/LC08/C02/T1_L2	30 m
blue (seasonal)*	Seasonal blue reflectance	LANDSAT/LC08/C02/T1_L2 (SR_B2)	30 m

(Continues)

TABLE 1 | (Continued)

Variable	Ecological proxy	Source	Resolution
blueSeasonality	Blue summer-winter difference	Derived from LANDSAT/LC08/C02/T1_L2	30 m
SDM variables (vegetation indices)			
ndvi (seasonal)*	Seasonal vegetation greenness	Derived from LANDSAT/LC08/C02/T1_L2 (Equation 1)	30 m
ndviSeasonality*	NDVI summer-winter difference	Derived from LANDSAT/LC08/C02/T1_L2	30 m
ndmi (seasonal)*	Seasonal vegetation moisture	Derived from LANDSAT/LC08/C02/T1_L2 (Equation 2)	30 m
ndmiSeasonality*	NDMI summer-winter difference	Derived from LANDSAT/LC08/C02/T1_L2	30 m
evi (seasonal)*	Seasonal enhanced vegetation index	Derived from LANDSAT/LC08/C02/T1_L2 (Equation 3)	30 m
eviSeasonality*	EVI summer-winter difference	Derived from LANDSAT/LC08/C02/T1_L2	30 m
gli (seasonal)*	Seasonal green leaf index	Derived from LANDSAT/LC08/C02/T1_L2 (Equation 4)	30 m
gliSeasonality*	GLI summer-winter difference	Derived from LANDSAT/LC08/C02/T1_L2	30 m
SDM variables (topography)			
elevation*	Elevation above sea level	CGIAR/SRTM90_V4	90 m
slope*	Terrain slope	Derived from CGIAR/SRTM90_V4	90 m
aspect*	Terrain aspect	Derived from CGIAR/SRTM90_V4	90 m
northness*	North-facing terrain component	Derived from aspect	90 m
eastness*	East-facing terrain component	Derived from aspect	90 m
tpi*	Topographic Position Index	CSP/ERGo/1_0/Global/SRTM_mTPI	90 m
roughness*	Terrain roughness	Derived from CGIAR/SRTM90_V4	90 m
SDM variables (soil)			
soilMoisture15*	Volumetric water at 5–15 cm depth	ISRIC/SoilGrids250m/v2_0/wv0010	250 m
soilMoisture200*	Volumetric water at 100–200 cm depth	ISRIC/SoilGrids250m/v2_0/wv0010	250 m
soilCarbon10*	Soil organic carbon at 10 cm depth	OpenLandMap/SOL/SOL_ORGANIC-CARBON_USDA-6A1C_M/v02	250 m
soilCarbon200*	Soil organic carbon at 200 cm depth	OpenLandMap/SOL/SOL_ORGANIC-CARBON_USDA-6A1C_M/v02	250 m

Note: Variables marked with * were included in at least one species' final model after variable selection. Variables marked as "(seasonal)" include four variants with season suffixes: Win (winter), Spr (spring), Sum (summer), and Fal (fall). Landsat composites are median values from 2015 to 2021. Climate data use the ACCESS-CM2 model from GDDP-CMIP6.

Abbreviations: GDDP-CMIP6, Global Daily Downscaled Projections from coupled model intercomparison project phase 6; GEDI, global ecosystem dynamics investigation; mTPI, multiscale topographic position index; OLI, operational land imager; SRTM, shuttle radar topography mission; VIIRS DNB, visible infrared imaging radiometer suite day/night band.

suitability for the likelihood of occupancy by lianas, thereby providing additional nuance to consider alongside variable importance rankings.

2.6 | Estimating Potential Carbon Outcomes of Liana Management

To obtain rough estimates for the potential carbon sequestration benefits of removing lianas, we split our analysis into

three scenarios: forests that are (1) occupied by lianas (where any species predicted to be present for a pixel—wherein we estimated that any pixel predicted to be occupied means that 33% of trees in that pixel host a liana) with no differentiation of areas with potentially elevated abundance—effectively assuming a lower impact of lianas across their entire range, (2) hosting an elevated abundance of lianas (combined likelihood 2.0 or greater—wherein we estimated that 66% of trees in these pixels host a liana) or (3) highly infested (combined likelihood of 3.0 or greater—wherein we estimated that 90%

TABLE 2 | Model validation metrics for Habitat Suitability Models (HSM) and Species Distribution Models (SDM): Area Under the Receiver Operator Characteristic Curve (AUCROC), sensitivity (true positive rate), specificity (true negative rate), precision (proportion of true positives out of the total positives), and Area Under the Precision Recall Curve (AUCPR). Metrics shown are the mean across five model iterations.

Model	Species	AUCROC	Sensitivity	Specificity	Precision	AUCPR
HSM	Bittersweet	0.958	0.962	0.878	0.894	0.790
	Kudzu	0.980	0.988	0.916	0.928	0.802
	Grape	0.944	0.984	0.836	0.866	0.852
	Wisteria	0.972	0.964	0.934	0.940	0.898
SDM	Bittersweet	0.856	0.792	0.782	0.824	0.860
	Kudzu	0.882	0.784	0.818	0.838	0.886
	Grape	0.756	0.632	0.754	0.772	0.808
	Wisteria	0.896	0.828	0.822	0.842	0.890

of trees in these pixels host a liana). We did not discriminate between forest types (e.g., deciduous, evergreen, mixed) or tree species in our estimates. We then made several conservative assumptions: the number of trees per hectare of forest (400), the average carbon dioxide removal rate of a tree (we chose 18 kg CO₂ per year, though sources such as European Environment Agency (2023) suggest it may be as high as 21 kg per year), and the hindrance in tree growth due to lianas (20% reduction in tree growth rate, which is lower than typically assumed; see Finlayson et al. (2022) for a tropical forest review or Peters et al. (2023) for recent liana impact estimates from the eastern US). However, we emphasize that these are first-order estimates that are scenario-based approximations intended to scope the potential magnitude of carbon outcomes from liana management in temperate forests, and that more precise estimates would require more detailed data on tree species composition, age structure, and site-specific growth rates. In short, these estimates should not be interpreted as precise predictions. Using land cover classification data (see Buchhorn et al. 2020), and our assumption that there are 400 trees per hectare, we estimated that there are around 95 billion trees in the region predicted to be suitable for these four liana species. We also assumed that liana release will return a tree back to “normal” carbon sequestration rates (18 kg CO₂ per year). As a rough analogy to communicate our estimates in a more tangible manner, we compared the potential carbon sequestration benefits to the typical emissions from gasoline powered vehicles per EPA (2023). Under these assumptions, we estimated the total carbon dioxide removal outcomes for three liana management scenarios: removing all lianas, removing lianas from areas with elevated abundance, or removing lianas from infested areas.

3 | Results

3.1 | Model Validation Results

The True Positive Rate (TPR, or sensitivity) for HSMs ranged from 0.964 to 0.988, and the True Negative Rate (TNR) ranged from 0.836 to 0.934 (Table 2). According to most model validation metrics, HSMs were best at classifying suitable habitat

for kudzu, and worst for summer grape (Table 2). Our SDMs—which predict the current distribution of lianas at a higher resolution (250 m)—performed slightly worse than HSMs (Table 2). TPR and TNR for SDMs ranged from 0.632 to 0.828 and 0.754 to 0.822, respectively (Table 2).

AUCPR was relatively high for all taxa, indicating that these models are capturing the majority of the true positives (Table 2). HSMs with the highest AUCPR were Chinese wisteria and summer grape (0.898 and 0.852, respectively), whereas the lowest was Oriental bittersweet (0.790) (Table 2). Interestingly, SDMs with the highest AUCPR were for Chinese wisteria and kudzu (0.890 and 0.886, respectively), whereas summer grape was notably worse (0.808) (Table 2).

3.2 | Error-Adjusted Area Estimates

Our results suggest that there are 378.8 ± 36.4 million hectares (Mha) of suitable area for these lianas, with around 237.7 Mha of that area being forested as of 2019 (Buchhorn et al. 2020) (Figure 1). Further, we estimate that 57.9 ± 8.5 Mha of these forests are likely occupied by one of these lianas to some degree. The difference in suitable and occupied area is striking, indicating that their distribution is likely limited by factors beyond climate and broad habitat suitability. Combining SDMs, we observe that 32.9 Mha of these forests (13.8% of forests with suitable climate) are likely to harbour more than one of these lianas, indicating the potential for elevated liana abundance (sum of probability scores greater than 2). Similarly, we estimate that 0.81 Mha of these forests (0.34% of these forests) may be infested by lianas (sum of standardized probability scores greater than 3) (Figure 1).

The most widespread species according to our SDMs and calculated cutoffs for classification are Oriental bittersweet, which occupies an estimated 39.5 ± 14.6 Mha, followed by grape at 37.6 ± 9.9 Mha (Figure 1, Table 3). The least widespread species are kudzu at around 24.7 ± 4.6 Mha and wisteria at 25.1 ± 5.1 Mha (Figure 1, Table 3). Bittersweet has a noticeably higher uncertainty for occupied area relative to the other species: if its true occupied area is at the lower end of the estimate (around 24.82 Mha), it would be

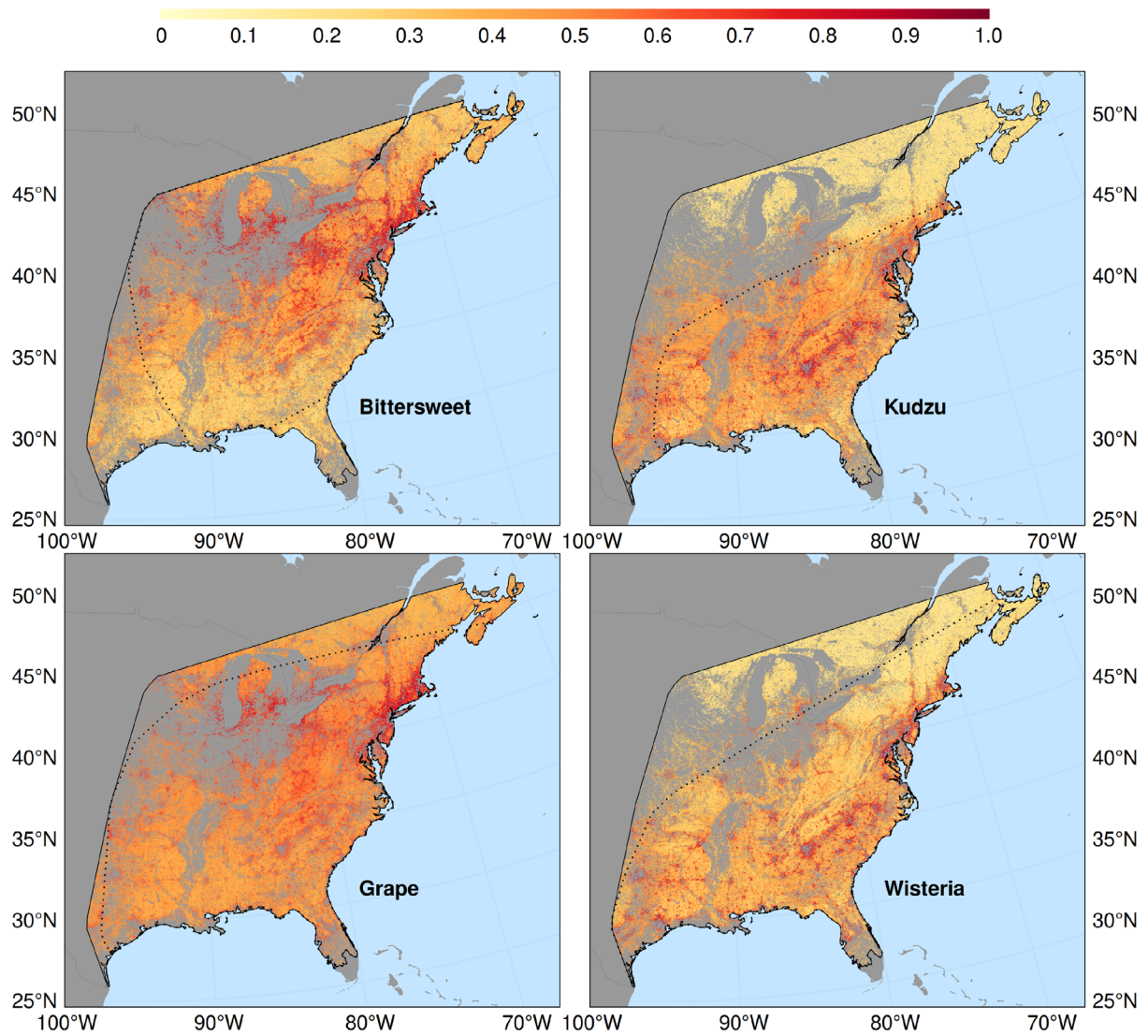


FIGURE 1 | Model predictions for the four liana species. Top left: Oriental bittersweet (*Celastrus orbiculatus*), top right: kudzu (*Pueraria montana*), bottom left: summer grape (*Vitis aestivalis*), bottom right: Wisteria (*Wisteria sinensis*). The broadly suitable habitat range for these four lianas (convex hull of combined models) is demonstrated with the outer black outline. The species-specific suitable range (convex hull of the HSM for that species) is demonstrated with a dotted black line. The prediction for current distribution (masked to forest) is displayed within the broadly suitable habitat range.

TABLE 3 | Error-adjusted area estimates (million hectares) for HSMs (suitable habitat) and SDMs (area likely occupied), $\pm$ margin of error for 95% CI. Occupancy is the percent of forested area within the broadly suitable liana range (238 Mha) that is likely occupied per the SDM. Cutoffs are the best classification thresholds for each model, determined by maximizing the sum of sensitivity and specificity.

2–5 species	HSM		SDM		Occupancy (%)
	Area (Mha)	Cutoff	Area (Mha)	Cutoff	
Bittersweet	321.94 $\pm$ 42.86	0.412	39.46 $\pm$ 14.64	0.508	16.59 $\pm$ 6.15
Kudzu	179.70 $\pm$ 39.93	0.442	24.70 $\pm$ 4.59	0.532	10.38 $\pm$ 1.93
Grape	311.83 $\pm$ 21.99	0.402	37.58 $\pm$ 9.93	0.556	15.79 $\pm$ 4.17
Wisteria	263.16 $\pm$ 40.68	0.402	25.14 $\pm$ 5.14	0.500	10.56 $\pm$ 2.16

TABLE 4 | Top four most important variables, in order of mean importance, for Habitat Suitability Models (HSM) and Species Distribution Models (SDM).

Model	Species	Variable 1	Variable 2	Variable 3	Variable 4
HSM	Bittersweet	lwradSpr (11.7%)	spHumSum (11.5%)	long (9.9%)	tempMaxSum (9.6%)
	Kudzu	spHumFal (9.2%)	spHumSum (7.6%)	tempMinWin (6.9%)	precip (6.3%)
	Grape	spHumFal (9.9%)	lwradSum (9.5%)	long (9.2%)	precipWin (6.7%)
	Wisteria	lwradFal (8.6%)	lwradWin (7.9%)	spHumSum (7.7%)	relHumSpr (7.7%)
SDM	Bittersweet	nighttime (14.1%)	ndmiSpr (6.7%)	soilCarbon10 (6.1%)	gliSpr (4.9%)
	Kudzu	nighttime (11.3%)	impSurface (7.8%)	ndmiWin (7.3%)	ndmiSeasonality (6.6%)
	Grape	nighttime (11.7%)	soilMoisture200 (6.2%)	ndmiSpr (5.9%)	nirSpr (4.7%)
	Wisteria	nighttime (12.0%)	gliSum (6.5%)	impSurface (6.4%)	ndmiSeasonality (5.1%)

Note: Variables shown above are ranked by the mean importance across five model iterations. Relative importance (in parentheses) represents each variable's percentage contribution to total model importance.

Abbreviations: distToEdge, distance to forest edge; gli, green leaf index; impSurface, impervious surface; lwrad, longwave radiation; lwrad, surface downwelling longwave radiation; ndvi, Normalized Difference Vegetation Index; nighttime, nighttime lights; precip, precipitation; soilCarbon10, carbon estimate at 10 cm depth; soilMoisture200, volumetric water content estimated at 100–200 cm depth; spHum, specific humidity; temp, temperature; tmean, annual mean temperature.

much less widespread than grape (around 27.65–47.51 Mha) and closer to kudzu and wisteria (around 25 Mha).

3.3 | Drivers of Liana Suitability and Occupancy

Seasonal measures of downwelling longwave radiation (spring, summer, fall, and winter) were important for delineating the suitable habitat range for all four species. Measures of specific or relative humidity were also one of the most important predictors for delineating suitable habitat. Specifically, increased longwave radiation and humidity were positively correlated with habitat suitability for all species except Oriental bittersweet (Figure 3, Table 4). Additionally, longitude was an important variable for Oriental bittersweet and grape, and was negatively correlated with habitat suitability for all species except bittersweet (Figure 3, Table 4). Variables that were seemingly not as important as these listed above but were still in the top four most important variables for at least one species included annual or winter precipitation, maximum temperature of the summer months (Table 4). See [Supporting Information](#) for an exhaustive ranking of variable importance for HSMs and SDMs.

Nighttime lights were the top predictor for estimating the occupancy (SDMs) of all taxa within forested pixels of respective habitat ranges (Figure 4 Table 4). Second-most important variables varied by species, but included spring NDMI, impervious surface percentage, soil moisture, and summer GLI (Figure 4, Table 4). Specifically, the likelihood of liana occupancy was positively correlated with nighttime light intensity, impervious surface percentage, and NDMI seasonality and was negatively correlated with summer GLI and spring NDMI (Figure 4). Notably, impervious surface was a highly important predictor for kudzu and wisteria, but not for grape or bittersweet (Table 4). Additional important variables included soil carbon content, seasonal NDMI, and NIR band reflectance (Figure 4, Table 4).

3.4 | Rough Estimates for Liana Management as a Carbon Removal Strategy

Finally, we made rough estimates for the carbon dioxide removal outcomes for several liana management scenarios: removing all lianas, removing lianas from areas with potentially elevated abundance, or removing lianas from potentially infested areas. In our first and least conservative scenario we assumed that liana occupancy (of any level, over an estimated 95.2 Mha of forested areas; see Figure 2) causes a consistent reduction in tree growth (20%). As a reminder, for these occupied areas we assumed that one-third of trees therein are hosting a liana and that removing lianas results in a 20% increase in tree growth. In this case (where we estimated that 7.6 billion of around 95 billion trees in this suitable liana range host a liana and are negatively impacted), liana removal could result in an additional 28,000 metric tons of CO₂ being removed annually, or around a 1.63% increase by our estimates—equivalent to removing 5.9 million gasoline powered vehicles from the road.

In a more conservative scenario, we consider areas with a potentially elevated abundance of lianas (combined probability greater than 2, around 32.9 Mha of forested areas); see Figure 2. In this case, we make the same assumptions with the exception that we now assume that two-thirds of the trees in these areas are hosting a liana. We estimated that removing all lianas (from the estimated 8.7 billion occupied trees) could result in an additional 31,000 metric tons of CO₂ removed annually, or a 1.86% increase—equivalent to 6.8 million gasoline powered vehicles.

In a still more conservative scenario, we consider only the most infested areas (around 0.8 Mha of forested areas; see Figure 2). Here we assumed that 90% of trees host a liana and otherwise make the same assumptions about liana impact and release outcomes. We estimated that removing all lianas in more heavily infested forests (from an estimated 200 million occupied trees) could result in an additional 1000 metric tons of CO₂, a 0.06% increase—equivalent to over 230,000 gasoline-powered vehicles.

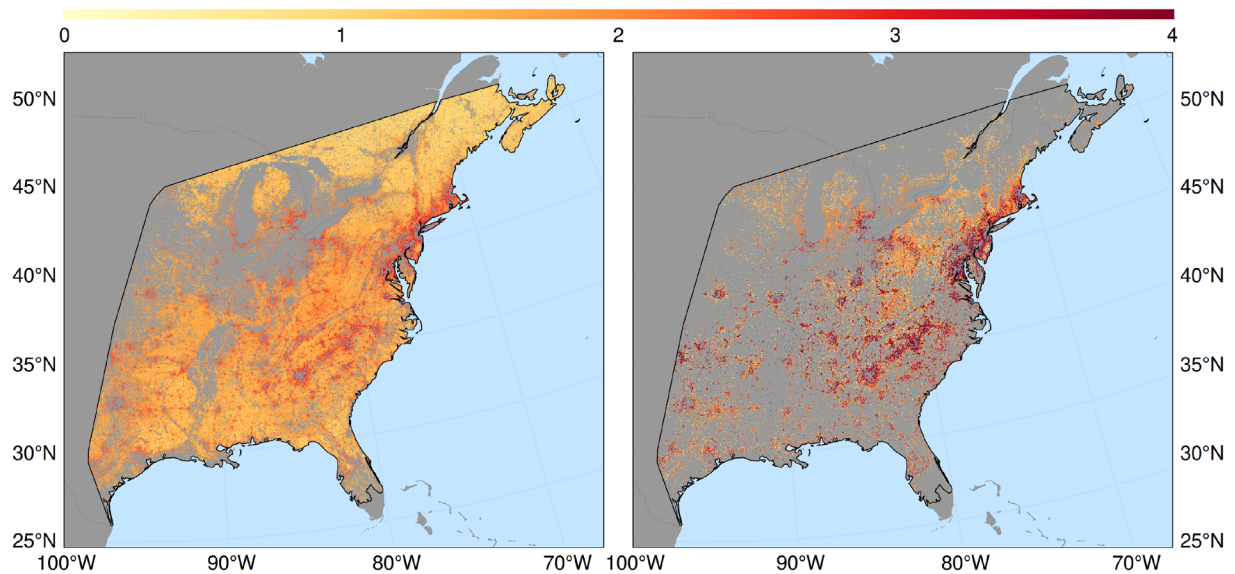


FIGURE 2 | Left: the overlap (sum) of distribution models (SDMs), which can be viewed as a proxy for liana infestation ranging from 0 to 4 combined probability. Right: the overlap of binary SDMs (per calculated thresholds) ranging from 0 to 4 species likely present. Suitable liana habitat is outlined in black.

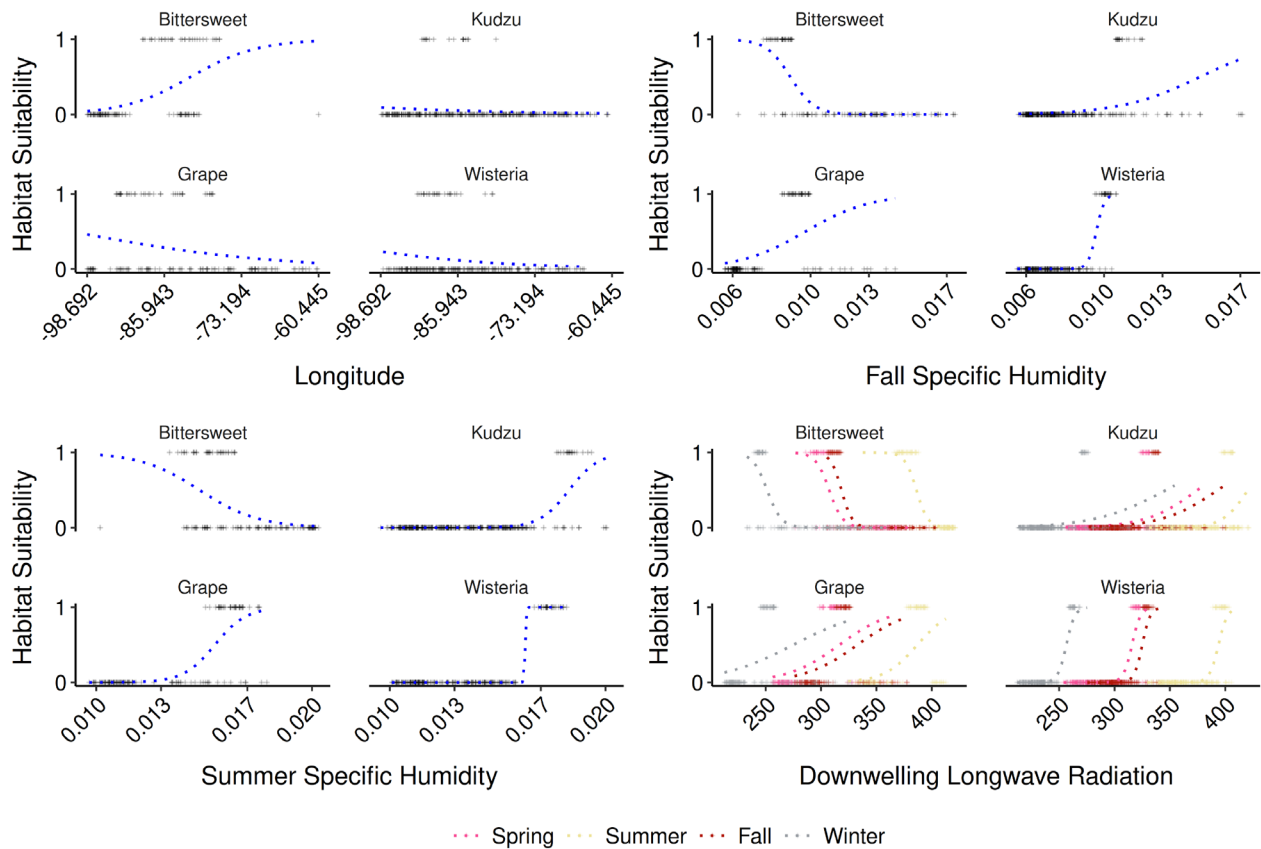


FIGURE 3 | Relationships between the most important HSM predictors and habitat suitability (suitable or unsuitable per classification results for all species). Lines are from an exploratory binomial generalized linear model of predictor variables at randomly selected pixels versus the model prediction (suitable or unsuitable habitat). All seasons were highly important for downwelling longwave radiation for one species or another and are thus shown here in different colours.

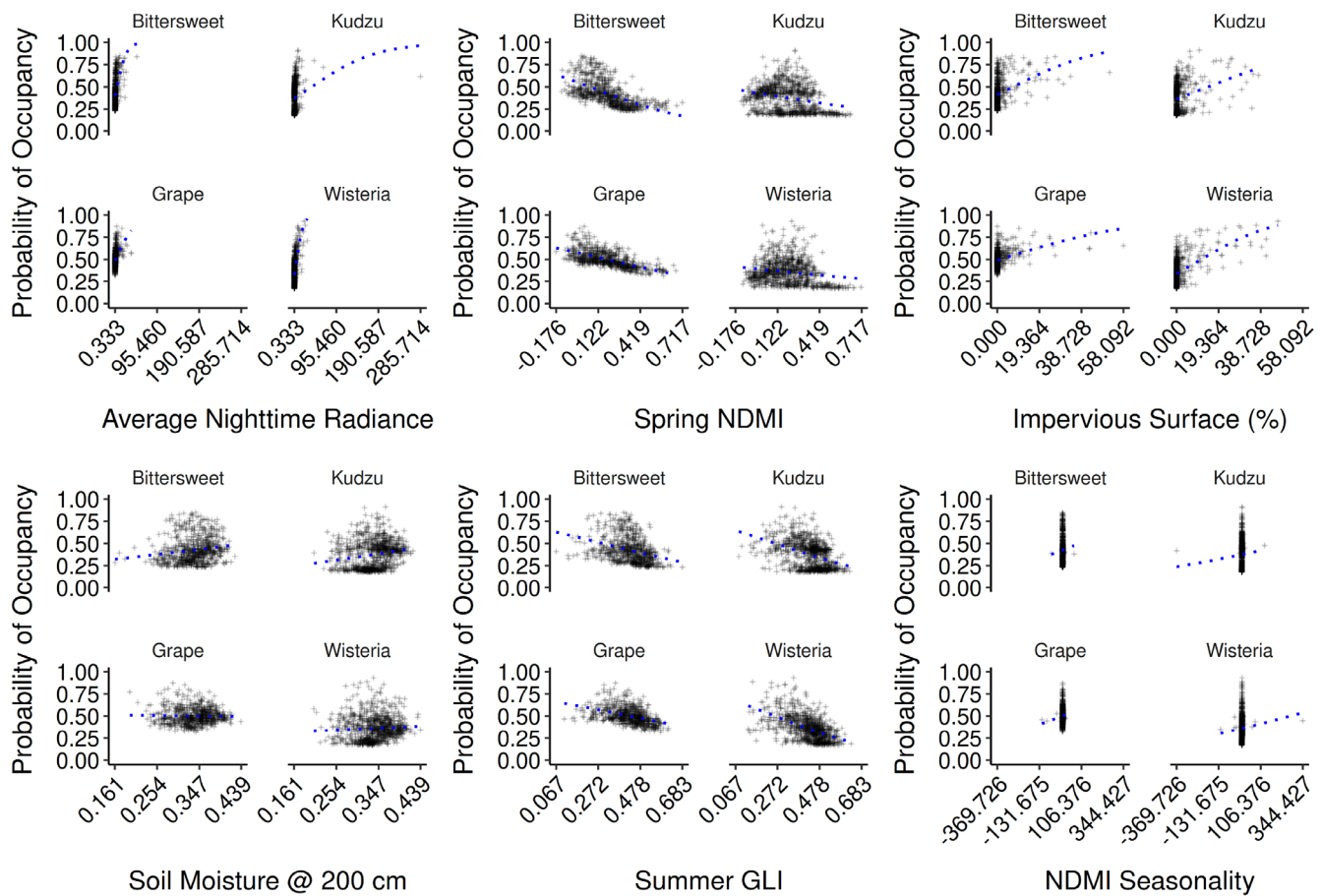


FIGURE 4 | Relationships between the most important SDM predictors and the predicted probability of occupancy. GLI, green leaf index; NDMI, Normalized Difference Moisture Index. Lines are from an exploratory quasi-binomial generalized linear model of predictor variables at randomly selected pixels versus the model prediction (probability of occupancy).

4 | Discussion

To our knowledge, we are the first to use habitat suitability models to limit the scope of Species Distribution Models. This approach is similar to those used by Pinkert et al. (2023) where they leverage expert range maps to aid global scale ecological modelling efforts. However, we expect that our approach is particularly useful for mapping taxonomic or functional groups that may be overlooked (such as lianas) and for nonnative plants for which updated expert range maps are lacking. Further, it allows us to use data-driven methods to determine the suitable habitat range for a taxon, which may be a more objective approach than using expert range maps (Herkt et al. 2017). This approach therefore allows for more variables to be considered at an increased spatial resolution than would otherwise be possible by first limiting the area of interest to the suitable habitat range of these species as determined by coarser variables that explain climate and geographic position. Importantly, a key finding of this work highlights that climate alone poorly predicts liana occupancy at this scale, with human activity and local landscape factors playing a more dominant role.

4.1 | Environmental Drivers of Liana Habitat Suitability and Occupancy

Our results indicate that downwelling longwave radiation (influenced by cloud cover and linked to water vapour and hydrologic cycles) and humidity (Table 4), are both positively correlated year-round with habitat suitability for eastern North American lianas (Figure 3). This contrasts with the tropics, where lianas have been documented to be more abundant in seasonally dry tropical forests, likely as a result of their capacity to compete well for water in these sites (Schnitzer 2005; van der Heijden and Phillips 2009). However, temperate studies like those by Trimble and Tryon (1979) and Smith (1984) have noted the link between the distribution of lianas (mainly *Vitis* spp.) and site productivity (i.e., those with better soils and more precipitation), aligning with our findings.

As predicted, the most important variable for predicting forests occupied by lianas was nighttime lights, a proxy for urbanization (Figure 4, Table 4). Although this may be influenced by citizen scientists' proclivity to sample along urban forest edges, leading to over-representation in these areas, this nevertheless aligns with what we know: lianas are light- and edge-loving plants (Putz and

Mooney 1992; Schnitzer et al. 2015). We also expect that our thinning approach used for cleaning occupancy data (see Section 2) has mitigated some of this potential bias. Next, vegetation indices were important, but had generally negative correlations with the likelihood of occupancy (Figure 4, Table 4). This is contrary to what would be expected, as lianas have been shown to have higher reflectance and NDVI than trees Heijden et al. (2022), Guzmán et al. (2018), Chandler et al. (2021), Visser et al. (2021). In this case, our SDMs seem to capture environmental factors linked to liana habitat (edges, disturbance, and development) rather than the spectral characteristics of the lianas themselves (Figure 4, Table 4). Put another way, we expect that reflectance near forest edges is contaminated by signatures from soil, roads, impervious surfaces, or otherwise non-forest surfaces, which would explain the decrease in vegetation indices.

4.2 | Liana Distributions and Implications

Our results demonstrate that the distribution of these four lianas is strongly linked to proximity to urbanization and forest edges as represented by nighttime lights, distance to forest edges, impervious surface, and mixed signals in vegetation indices near forest edges (Figure 4, Table 4). This finding is consistent with what we know of lianas: they are linked to partial disturbance, evidenced by their association with urbanization and maintained forest edges (Schnitzer and Bongers 2011; Brice et al. 2014; Matthews et al. 2016). This is the first time this has been mapped and demonstrated at this scale and resolution.

We estimate that over 200 million hectares (Mha) of forested land are suitable for at least one of the four lianas studied herein (Figure 1). When considering SDMs (that predict occupancy at a 250 m resolution), we estimate that over 50 Mha of that area is likely already occupied by lianas, with around 30 Mha potentially harbouring an “elevated” abundance of lianas (Figure 1). Visually, we observe that wisteria appears to be the most restricted to urban areas, followed by kudzu, whereas Oriental bittersweet and especially grape are relatively more likely to be found throughout their suitable habitat range, including in less urbanized areas (Figure 1). These findings, along with the interactive web map, could inform liana management for this region by way of highlighting places most in need of intervention that are easily accessible.

4.3 | Linking Liana Characteristics and History to Distribution Patterns and Potential Impact

It is important to clarify that lianas do provide benefits to ecosystems, such as food and habitat for wildlife, and they are an important component of many forests (Martin et al. 1961; Della-Bianca 1978; Greenberg et al. 2001). We do not suggest here that all lianas should be removed from forests or that these liana species are problematic in all instances. Management decisions must be made at the discretion of the land manager on a case by case basis and should consider the ecological value of lianas in addition to their potential negative impacts. Nevertheless, we continue here under the assumption that these lianas can be problematic in many parts of their suitable range where their abundance is higher than the baseline due to human

disturbance, and below we discuss observed patterns in their distribution and habitat suitability, as well as the implications of those patterns for forest management.

Climbing mechanism, distribution preferences, and vigour reflect the potential impact of lianas on the health and growth rate of their host tree as well as their distribution. For example, while all four species studied here can enshroud a forest canopy under the right conditions, Oriental bittersweet and Wisteria can also twine and girdle stems of their hosts, leading directly to host mortality (McNab and Meeker 1987; Lutz 1943; Weakley et al. 2013; Leicht-Young et al. 2010). Similarly, while kudzu can cover forest canopies, it appears limited to roadsides and urban edges in the southeastern US—likely because that’s where it was historically planted and its poor seed dispersal (Forseth and Innis 2004; Figure 1). In a recently published study on kudzu, Profetto and Howard (2021) points out that heavy kudzu infestation was found only adjacent to roads, old agricultural fields, or abandoned homesteads. This raises the question of whether kudzu is actively reducing biodiversity, or if it grows in areas where biodiversity has been reduced as a result of previous human actions. Additionally, Goodenough (2010) called for resisting the temptation to label native and non-native plants as good and bad, respectively, as not all non-native species are detrimental. Therefore, while kudzu is considered by many to be a dangerous invader (Forseth and Innis 2004; Blaustein 2001), we lend confirmation to the growing realization that the reputation of kudzu is likely due to its visibility since kudzu is less widespread compared to the other species studied here, despite being introduced to North America in the late 1800s (Blaustein 2001).

Regarding their introduction, these four species again display similarities and distinctions. Grapevines, represented here by a common species (*Vitis aestivalis*), for example, are a genus of native lianas that have been present in North America for millennia and are bird-dispersed (Della-Bianca 1979; Martin et al. 1961). In contrast, Oriental bittersweet is an introduced liana that is also bird-dispersed (Greenberg et al. 2001; Martin et al. 1961), which may contribute to the relatively high uncertainty in area estimations for Oriental bittersweet compared to other species like kudzu or wisteria (Table 3). Nevertheless, the similarity between these two species is reflected in their distribution patterns (Figure 1), though we note that the SDM for grape performed worse than others—potentially due to its broader niche, difficulty in remote sensing identification, data limitations, or other factors (Table 2). Both are widespread and likeliest to be found near forest edges but are not necessarily linked entirely to urbanization—evidenced by the fact that impervious surface was not as important for these two species as compared to kudzu and wisteria (Figure 1, Table 4). This suggests that they may be more closely associated with forest edges including agricultural edges or canopy gaps within forests (Figure 1). That is not to say that these species are not linked to urbanization, but rather that they are more widespread and not as restricted to urban areas as kudzu or wisteria (Figure 1). In the case of the latter species, kudzu and wisteria are both introduced lianas that are not bird-dispersed (they are both legumes) and are more restricted to urban areas (Figure 1). In particular, millions of kudzu seedlings were given to farmers and landowners from the 1920s to 1940s, with incentives up to \$20 per hectare to plant them (Blaustein 2001). Regarding wisteria, this genus of non-native

lianas was introduced sometime in the early 1800s (Wells and Brown 2023). Trusty et al. (2007) found that wisteria is primarily dispersed by human activity. Therefore, it is likely that horticulture and maintenance of permanent forest edges is a key driver of the current distribution patterns for kudzu and wisteria, whereas grape and bittersweet can additionally disperse via birds and are therefore more widespread.

4.4 | Implications for Conservation: Liana Management in Temperate Forests

Non-native lianas (Oriental bittersweet, kudzu, and wisteria) appear to be more restricted to urban edges than native lianas (represented here by summer grape) (Figure 1). Furthermore, native lianas like wild grapevines are relatively easy to treat compared to others. In the case of grapevines, this is due to their inability to re-sprout and survive in shade (Ladwig and Meiners 2010; Trimble and Tryon 1974). Regardless, care must be taken to not eradicate all lianas due to their value to wildlife via food, materials, and habitat (Martin et al. 1961; Della-Bianca 1978; Greenberg et al. 2001). More research is needed to quantify what constitutes a problematic liana infestation: developing a method for estimating site-specific baselines for liana abundance and subsequently determining the threshold at which lianas could be considered “super abundant” is a critical next step. Further, although these edge-restricted non-native lianas may appear highly abundant due to their visibility, we suspect that they are likely less widespread than is typically assumed. Therefore, focusing management efforts on forest edges may be a feasible liana management strategy with inherent biodiversity safeguards—with another caveat that lianas may provide buffering to problematic edge effects by functioning as “green walls” (Susca et al. 2022). Additional research on this topic is needed to determine the best management strategies for lianas in temperate forests.

Our results suggest that the near-eradication of lianas in the eastern US could result in these forests removing an additional 30,000 metric tons of CO₂ annually, or as much as a 2% increase, by our estimates. However, we note that this 2% estimate should be considered a theoretical maximum; and in the most conservative and simplest scenario where only the most infested areas are treated, liana removal might still result in a 0.06% increase in CO₂ removal for these forests. While this sounds miniscule, it is equivalent to the estimated annual emissions of around 230,000 gasoline powered vehicles. Such a scenario would also be more feasible, as it would require treating around 800,000 Mha (rather than several million) of forested land, which is around 0.34% of the total forested area within the suitable habitat range for these lianas and is likely to be more cost effective as these areas are likely near urban centers and therefore easily accessible. This is a rough estimate but suggests potential for liana management—particularly in fragmented urban forests or urban forest edges—as a practical piece of the growing mosaic of solutions for climate change mitigation. We anticipate that these estimates are relevant for other temperate forests as well, or that additional work to map lianas in temperate or subtropical forests such as English ivy (*Hedera helix*) in the Mediterranean (e.g., Garfi and Ficarrotta 2003; Madrigal-González et al. 2018) or subtropical or temperate Asian forests could be similarly useful to inform management strategies in those regions.

4.5 | Limitations and Future Directions

There are several limitations that should be considered when interpreting results. First, while we made efforts to clean and vet occurrence data, there is always an element of sample bias and a possibility of misidentification or erroneous coordinates. Second, we did not make any adjustments to pseudo-absences beyond ensuring that they were not placed in a pixel with presence data, and we acknowledge that there are more sophisticated methods for selecting pseudo-absences that may improve model performance in some cases (Barbet-Massin et al. 2012). Third, regarding variable importance rankings, we used GINI importance, the default for Google Earth Engine's random forest implementation, which may be biased toward continuous predictors but nonetheless indicates the relative contribution of each variable to model predictions (Strobl et al. 2007). Fourth, while we focus here on four representative liana species that can shroud forest canopies in temperate North America, we acknowledge that any competing vegetation will have some impact on tree growth and carbon sequestration, and, similarly, other liana species not included here that may have different distribution patterns and impacts on forests. Fifth, species with limited occurrence data (e.g., wisteria) may have less reliable models or may be overfit to the training data. Sixth, our carbon benefit estimates are based on general assumptions evidenced by the current body of literature (e.g., Peters et al. 2023; Finlayson et al. 2022; Schnitzer et al. 2014; Tobin et al. 2012) such as average tree density, average CO₂ removal rates, the degree to which lianas hinder tree growth, and the degree to which liana removal increases growth of the host tree; these assumptions may not hold true in all cases and should be refined as more detailed information becomes available. Seventh, we note that our decision to focus on species rather than some genera (such as *Vitis* and *Wisteria*) is done in an attempt to balance interpretability and model complexity; however, this may overlook intra-genus variability and could introduce some error inherent in occupancy data, as many grape species look very similar, and due to the ability of Chinese and Japanese wisteria to hybridize and become naturalized (Trusty et al. 2007). However, we expect that our decision to focus on singular, common species likely tightens our results compared to the alternative of modelling at the genus level. Finally, we only modelled four liana species that are capable of shrouding forest canopies, though there are more species in temperate North America that may have different distribution patterns and varied impacts on forests (such as additional species of *Vitis* spp.). This resulted in our specific focus on forested pixels, which tightens our estimates but may also overlook areas in non-forested but suitable early successional habitats. Future research includes mapping all North American lianas following the approach demonstrated herein, as well as in situ liana removal experiments to quantify outcomes of releasing North American forests from lianas.

5 | Conclusions

We share the first publicly available map of lianas (represented by summer grape, wisteria, kudzu, and oriental bittersweet for temperate North America) at such a scale and resolution, leveraging a cascading modelling approach within Google Earth Engine whereby we classified suitable habitat ranges at 5 km

resolution across North America (i.e., HSM), and subsequently predicted the likelihood of occupancy within those suitable areas at 250m resolution using remotely sensed data, topography, and soil maps (i.e., SDM). Specifically, 32.9 Mha of forests in eastern North America likely harbour more than one of these lianas. Importantly, we found that these lianas, particularly non-native species, are strongly linked to urbanization and forest edges (evidenced by nighttime lights, distance to forest edge, and vegetation indices), whereas native lianas (represented here by the common summer grape, *Vitis aestivalis*) are additionally associated with interior forest habitats. We therefore propose that managing lianas along roadsides and urban edges may have the biggest reward per unit effort, in addition to providing inherent biodiversity safeguards via preserving native lianas in interior forests' natural canopy gaps or riparian edges. This work furthers our ecological understanding of temperate lianas with applications for forest management and decision-making for biodiversity conservation and restoration, as well as forest resilience and carbon storage. Finally, we present the first rough estimates of potential outcomes for large-scale liana management, with potential carbon benefits ranging from a 0.06% to as much as a 2% (as a theoretical maximum) increase in CO₂ removal for eastern North American forests, depending on the extent of management efforts. These estimates suggest that liana management may be a feasible and practical piece of the growing mosaic of solutions for climate change mitigation.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

Data used for this project are publicly available in the linked Dryad repository and our scripts are available through GitHub at <https://github.com/jacobdjpeterson/nearcticLianaMaps>.

Peer Review

For transparency, the peer review documents associated with this article are available at <https://doi.org/10.1111/ddi.70188>.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** ddi70188-sup-0001-DataS1.docx.

Appendix A

Supporting Information below include an example of the spatial block cross-validation grid used for model evaluation and species descriptions for the four focal liana species in this study.

Spatial Block Cross Validation Example

Species Descriptions

Bittersweet (*Celastrus orbiculatus* Thunb)

Oriental bittersweet is a woody, deciduous liana native to eastern Asia (China, Japan, and Korea) that was introduced to the US in the late 1800s or early 1900s (Rehder 1940; Tredici 2014; Patterson 1974). It inhabits well-drained floodplains, old fields, clearings, fence rows, and disturbed habitats (Virginia Botanical Associates 2024). Initially used as an ornamental, bittersweet is now considered a threat to native biodiversity (Tredici 2014). However, bittersweet does provide food for wildlife, which helps to explain its “invasiveness” (Brizicky 1964; Martin et al. 1961). Further, this liana can persist in shade but will grow vigorously with increased sunlight (Lynch 2009; Greenberg et al. 2001; Patterson 1974). Bittersweet climbs by twining around host trees and can girdle and kill mature stems through mechanical constriction (McNab and Meeker 1987; Lutz 1943). Finally, this liana could threaten sensitive or at-risk ecosystems due to its ability to tolerate shade and kill trees (Leicht-Young and Pavlovic 2012; Leicht-Young et al. 2013; McNab and Meeker 1987).

Kudzu (*Pueraria montana* (Loureiro) Merritt var. *lobata* (Willd.) Maesen & S. Almeida)

Native to eastern Asia, kudzu was introduced to the US in the late 1800s, where it was first used as an ornamental in the American South (Forseth and Teramura 1987; Blaustein 2001). Kudzu can grow in both shade and light, and is most often seen along road-cuts, clearings, and disturbed forests (Miller et al. 2010; Virginia Botanical Associates 2024). Starting in the 1920s–1940s, kudzu was recommended by the U.S. Government to combat soil erosion in the South. Touted as a wonder plant, millions of kudzu seedlings were given to farmers and landowners, with incentives up to \$20 per hectare to plant them (Blaustein 2001). As a legume, kudzu fixes nitrogen, which can aid soil fertility, provides excellent forage for wildlife, and its growth form offers good cover for many species to evade predation or seek shelter from weather (Grebner et al. 2022). Kudzu's presence has been correlated with reduced plant species richness, and often persists in previously disturbed areas such as roadsides

or old agricultural fields—raising the question of whether kudzu reduces biodiversity or simply thrives in degraded habitats (Profetto and Howard 2021).

Summer Grape (*Vitis aestivalis* Michx)

Summer grape (and wild grapevines in general) is a widespread native liana, being found in mesic to dry upland forests, floodplain forests, wet flatwoods, maritime forests, tidal swamps, dune scrub, shrubby clearings, and old fields (Virginia Botanical Associates 2024). In Appalachia, they are typically found in productive mesic sites, which is relevant for our field study discussed later in this proposal (Trimble and Tryon 1979; Smith 1984; Della-Bianca 1978). This liana provides fruit, habitat, and materials to many wildlife species (Della-Bianca 1978, 1979; Martin et al. 1961). They have also been noted for their impact on forest structure, tree mortality, and growth rates (Siccama et al. 1976; Smith 1984; Peters et al. 2023). This species is not typically a management concern but can become abundant in some areas such as high-graded or disturbed forests (Smith 1984).

Chinese Wisteria (*Wisteria sinensis* (Sims) Sweet)

Wisteria (*Wisteria* spp.) is a genus of woody climbers native to temperate eastern Asia and eastern North America (Weakley et al. 2013). It includes Chinese wisteria (*W. sinensis*), Japanese wisteria (*W. floribunda*), American wisteria (*W. frutescens*), and a Chinese-Japanese hybrid species (*W. xformosa*). Here, we have chosen to focus on Chinese wisteria since it appears to be the more common species in its genus in the eastern US. The exotic members of the genus were likely introduced in the early 1800s (Wells and Brown 2023). This species is capable of climbing trees and forming dense entanglements in addition to being able to twine and girdle young stems similar to bittersweet (NRCS 2024), p. 73 of Miller et al. (2010). These lianas are commonly cultivated and may spread to disturbed forests, forest edges, and fence rows (Virginia Botanical Associates 2024), but have become more widespread due to the ability of Chinese and Japanese wisteria to hybridize and become naturalized (Trusty et al. 2007). There is relatively little research on the ecological characteristics and functions of this genus, and most information must be obtained from grey literature: gardening books, forums, and blog posts (Wells and Brown 2023; Stone 2009; Valder 1998). Also a legume, Wisteria appears similar to kudzu in its growth habit and can create areas that are shrouded in it, with no treetops visible from outside (Miller 2006). Interestingly, wisteria can grow also as a small tree (Valder 1998). It spreads primarily through vegetative growth and by forming adventitious roots where stems contact soil, though it also produces viable seeds in brown, bean-like pods.

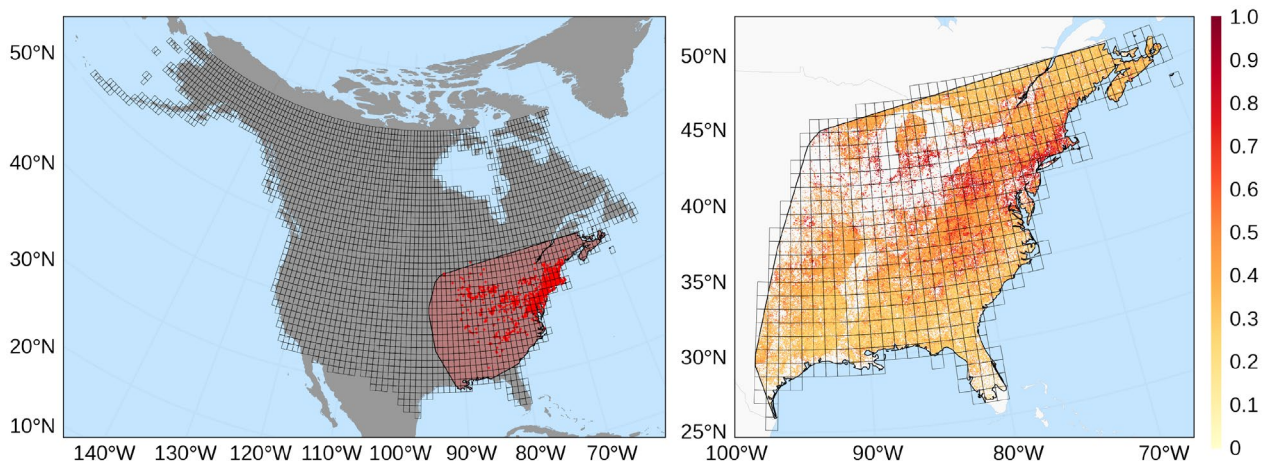


FIGURE A1 | Spatial block cross-validation example grid used to evaluate the Habitat Suitability Model (left) and Species Distribution Model (right) for Oriental bittersweet. Presence data for Oriental bittersweet are shown in red on the left panel. The grid is composed of 100-km blocks that used to separate training and testing sets for model evaluation, ensuring that the model's performance is assessed on spatially independent data.