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Variation in establishment success for American mistletoe [*Phoradendron leucarpum* (Raf.) Reveal & M.C. Johnst. (Viscaceae)] appears most likely to predict its distribution in Virginia and North Carolina, United States

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Abstract

Dispersal limitation and variation in habitat suitability may determine an association of American mistletoe [*Phoradendron leucarpum* (Raf.) Reveal & M.C. Johnst. (Viscaceae)] with forested wetlands in Virginia and North Carolina, United States. Here, we first tested the alternative hypothesis that variation in host availability drives this habitat relationship. We used a generalized linear model to show a positive effect of forested wetland habitat on American mistletoe occurrence after accounting for both variation in host availability and differences among regions in host use. We then used seed sowing experiments to quantify how light availability and flood regime determine the viability of American mistletoe, allowing us to evaluate the potential for establishment limitation to determine this habitat relationship. Light availability predicted establishment rates but % canopy openness did not predict seed germination rates. Thus, variation in the ability for American mistletoe to establish across forested habitat types with different local light availabilities is a potentially important mechanism in determining its distribution.

Key words: oak mistletoe, establishment limitations, mistletoe habitat suitability, host availability, seed sowing experiment

Introduction

Mistletoes are hemiparasitic shrubs that typically parasitize above-ground portions of host trees and rely on avian frugivores for seed dispersal (Calder and Bernhardt 1983). Because most mistletoes are restricted to a narrow range of suitable recruitment sites (Overton 1994; Alexander et al. 2012; Mellado and Zamora 2014) and avian frugivores are more easily detected than other guilds of seed dispersers, mistletoe–frugivore systems afford opportunities for exploring the roles of dispersal limitations and environmental conditions in dictating plant distributions (Martínez del Rio et al. 1996; Carlo and Aukema 2005; Roxburgh 2007; Caraballo-Ortiz et al. 2017). As mistletoes are obligate hemiparasites, host presence and abundance must be controlled for when making inferences about factors driving mistletoe distributions (Overton 1994; Norton and Carpenter 1998; Kuijt 2003; Aukema 2004).

The American mistletoe [*Phoradendron leucarpum* (Raf.) Reveal & M.C. Johnst. (Viscaceae)] parasitizes a variety of woody plant species across the southern United States (Panvini 1991); many specimens from across the range with host information are listed in Kuijt (2003). In eastern Virginia and North Carolina, American mistletoe is more common in forested wetlands of the Coastal Plain than in other forested habitats (Weakley et al. 2012), a distributional pattern we henceforth refer to as a habitat relationship. Some tree species, such as red maple (*Acer rubrum* L.), occur in a variety of habitats and are parasitized across this region. This implies that factors other than host tree availability may drive this habitat relationship. Such factors include dispersal limitation mediated by frugivore behavior (Lamont and Southall 1982; Martínez del Rio et al. 1996; Aukema 2004; Krasylenko et al. 2020) and variation in local environmental conditions such as light availability and flood regime (Eleuterius 1976; Panvini 1991; Weakley et al. 2012).

Abiotic factors may affect the quality of hosts for mistletoes, such as drought-stressed trees serving as hosts for dwarf mistletoes (*Arceuthobium* M. Bieb. spp.) in the western United States (Page 1981). Potential host trees of upland forest stands may be of lower quality for light-demanding oak mistletoe seedlings (Eleuterius 1976) due to structural characteristics of younger stands (Esseen et al. 1996; Menzel et al. 2002; Weakley et al. 2012), namely, closed canopies dominated by evergreen trees providing dense shade to saplings of potential host species in the understory. While little is known about the general response of mistletoes to soil hydrological properties (Norton and Smith 1999), host trees growing in wetlands may be of higher quality for water-limited oak mistletoe shrubs (Panvini 1991) as evidenced by higher transpiration rates (Gregg and Ehleringer 1990; Yan 1992; Pauliukonis and Schneider 2001). Trees growing in flooded or compacted soils of wetlands or urban areas may have physiological responses to reduced soil O_2 (Larcher 1973) that make them higher quality hosts for oak mistletoe. Greater permeability of the vascular cambium in hydrophytic compared to mesophytic trees (Hook and Brown 1972) and the production of porous aerenchyma tissue in wetland plants (Larcher 1973; Keddy 2010) may enable mistletoe establishment.

Here, we tested the hypothesis that habitat relationships of American mistletoe are determined by host tree availability (Gougherty 2013; Lira-Noriega and Peterson 2014) and used region-specific lists of known host species when quantifying host availability. Failing to consider regional host associations could lead to the mis-identification of potential host trees, a bias recognized in general parasite ecology (Poulin 2005; Stanko et al. 2006). We also tested for a positive relationship between forested wetland habitat and oak mistletoe occurrence while controlling for variation in canopy openness measured at ground level. The lack of a relationship between habitat and mistletoe occurrence in such a model would provide evidence for light availability as an important factor determining mistletoe distribution. Given weaknesses of purely correlative studies at separating process from pattern (MacKenzie et al. 2004), we used experimental seed sowing methods to complement findings from occurrence models fit to field survey data.

Seed addition has been used in common garden experiments to test for host specificity in a variety of mistletoe–host systems (May 1971; Clay et al. 1985; Yan 1993; Overton 1994; Messias et al. 2014; Okubamichael et al. 2014; Caraballo-Ortiz et al. 2017). Seed sowing experiments have also been used to examine the effects of variation in abiotic conditions on mistletoe survival and establishment (Roxburgh and Nicolson 2008; Luo et al. 2016). Here, we simulated American mistletoe seed dispersal both to host trees experiencing different light availabilities in forests and to manipulated local light environments on potted host saplings exposed to varied soil moisture levels. The two principal avian dispersers of American mistletoe in eastern Virginia and North Carolina are the cedar waxwing (*Bombycilla cedrorum* Vieillot, 1808) and eastern bluebird (*Sialia sialis* (Linnaeus, 1758); Flanders et al. unpublished data), but handling of seeds by dispersers is not needed for germination in this species (May 1971; Randle et al. 2018). The potential importance of variation in local environmental conditions as a determinant of observed American mistletoe habitat relationships would be indicated by reduced establishment rates under abiotic conditions typical of forested uplands (Clark et al. 2007), such as low light availability and well-drained soil. Alternatively, a lack of support for relationships between American mistletoe establishment and abiotic factors would suggest dispersal limitation as the most likely mechanism driving these patterns.

Materials and methods

American mistletoe habitat relationships

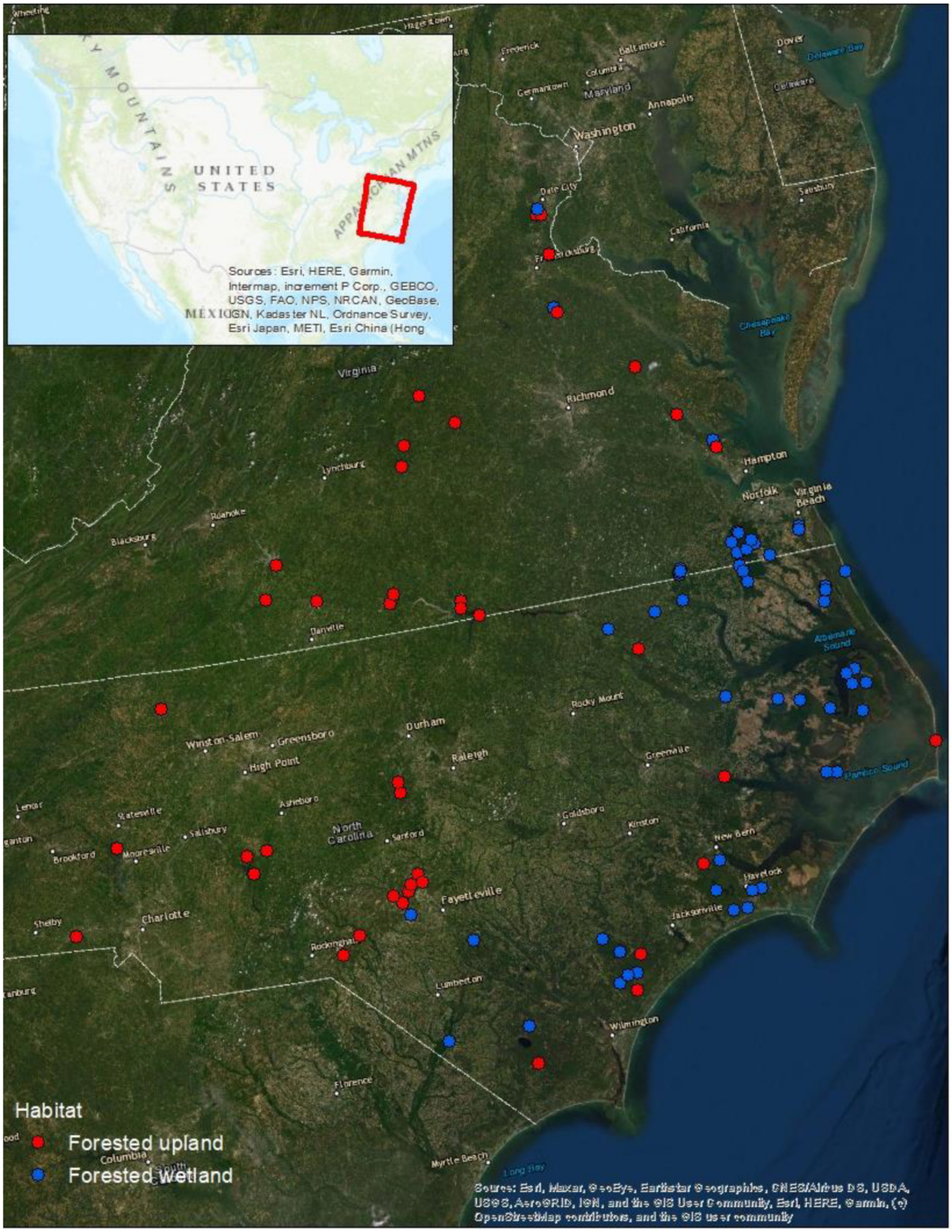
We selected 96 circular plots with 25 m radii (0.20 ha) to survey American mistletoe during one of five winters (December–March) 2015–2020 (Fig. 1). We surveyed in winter when deciduous trees were leafless to maximize rates of detection of evergreen mistletoe shrubs. Plots were selected in the Coastal Plain and Piedmont of Virginia and North Carolina using stratified random sampling, with forested wetlands serving as one stratum ($n = 54$) and all other forested habitats serving as the other ($n = 42$). The species and diameter at breast height (DBH) of all trees parasitized by American mistletoe within each plot were recorded. Most plots were visited 2–4 times per winter and were re-checked for the presence of mistletoe during repeat visits to account for imperfect detection of mistletoe at plots (Fadini and Cintra 2015; Caraballo-Ortiz et al. 2017). Images depicting the general morphology and habit of American mistletoe are available in the Appendix.

We collected data on tree stems present within subplots to quantify host availability. All stems of tree species present within a 10 m × 10 m square subplot at the center of each 25 m radius circular plot were identified to species or genus and DBH was recorded. Stems of tree species were measured even if multiple-stemmed saplings were encountered; woody species considered shrubs were not known as American mistletoe hosts and are listed in the Appendix.

Subplot data were assigned to a host association region based on location to avoid mis-identifying tree species as hosts in areas where parasitism of that species by American mistletoe is rare or absent. Maps depicting the parasitism of 17 taxa that show more widespread occurrence in subplot data are provided in the Appendix. First, all plots were placed into one of the three physiographic regions of the study area: outer Coastal Plain ($n = 46$), inner Coastal Plain ($n = 30$), and Piedmont ($n = 20$), with distinctions made based on counties in North Carolina and as defined in Weakley et al. (2012). We expected these three regions to be related with geographic host associations as they are with plant community composition (Weakley et al. 2012). To account for additional host association regions apparent in survey data (e.g., variation in parasitism of *Carya* spp.), we further split the inner Coastal Plain into two regions: one region south of the James River watershed and one region that included this watershed and the inner Coastal Plain to the north. Finally, the portions of both the inner and outer Coastal Plains within the Cape Fear and Lumber River watersheds in the southeastern section of our study area were split into a fifth region to account for a seemingly sharp shift in parasitism rates of the widespread tree sweetgum (*Liquidambar styraciflua* L.).

Stems selected as potential hosts from subplot data were only those of species found to serve as hosts in the region containing the subplot. The region-specific lists used for such selections came from both the identity of parasitized trees recorded at plots within the respective region and the species identity of trees parasitized at regional sites selected ad hoc in forested habitats; a total of 125 such sites were established

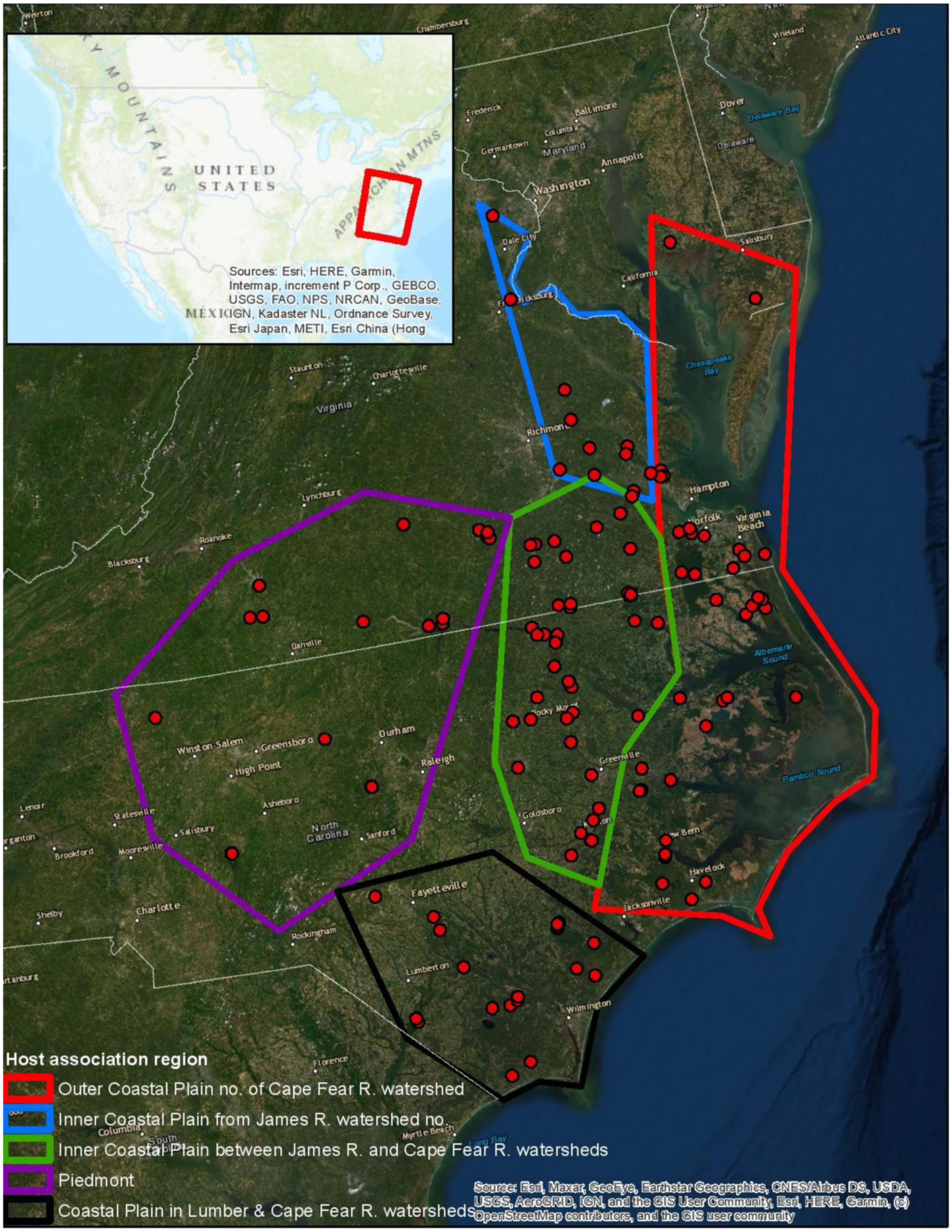
Fig. 1. Locations of survey plots in forested upland and forested wetland habitats; main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.



across the study area (Fig. 2). Due to the scarcity of mistletoe in forested habitats near the northern edge of our study area, we included such data from two sites in southeastern Maryland. Basal area (BA) in $m^2\ ha^{-1}$ for each region-specific potential host species was calculated and summed for each subplot to represent plot-specific host tree availability during subsequent analyses.

Generalized linear models (GLM; Bolker et al. 2009) were developed to estimate the effects of habitat type (forested wetland versus other forested habitats) and potential host

Fig. 2. Locations of 125 sites (red circles) that hosted mistletoe and were selected ad hoc across the study area; main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.



tree BA on mistletoe occurrence. Potential host tree BA was normalized for ease of interpretation of the effect of habitat type after accounting for host tree availability. We used package R2WinBUGS (Sturtz et al. 2005) in R (R Core Team 2021) to estimate posterior distributions in WinBUGS (Lunn et al. 2000) with uninformative prior distributions for all parameters and three Markov chain Monte Carlo (MCMC) chains run for 100 000 iterations with a burn-in of 20 000 and thinning by 4. Convergence for all parameters was assessed using trace plots and R-hat values (Gelman and Hill 2007). The effect of habitat was considered statistically significant if 95% credible intervals for habitat-specific intercept parameters did not overlap (Flanders et al. 2015).

Decisions on which region-specific host list should include data from ad hoc sites located near region boundaries were somewhat arbitrary. To determine whether such assignments affected model results, we removed data from such sites when determining host lists and re-ran the previously described GLM of the effects of habitat type on mistletoe occurrence after accounting for host availability. Plot-level host BA covariate values included in this model did not include contributions from peripheral tree species detected as hosts only near a boundary.

Habitat relationship versus canopy cover

Plot-level % canopy cover as a surrogate for light availability was quantified during the growing season following the winter in which the plot was surveyed for mistletoe. Convex densiometer readings were collected at the center of each plot and then averaged across all four cardinal directions (Jennings et al. 1999; Watts et al. 2011). We analyzed American mistletoe occurrence data using a model like that described previously to test for a relationship between habitat type and occurrence rate after accounting for host availability. Here, we included an additional parameter to represent the relationship between observed canopy openness and American mistletoe occurrence.

Field planting experiment to simulate dispersal to different local light environments

We conducted an American mistletoe seed sowing study in the field at two forested wetland sites in southeastern Virginia: Great Dismal Swamp National Wildlife Refuge (GDSNWR) and South Quay Sandhills State Natural Area Preserve (SQSNAP). At each site, stratified random sampling was used to select plots ($n = 26$ at GDSNWR, $n = 25$ at SQSNAP); maps of these plots are in the Appendix. The two strata for sampling consisted of portions of forested blocks <15 m from an edge ("edge" plots) and portions >15 m from an edge ("inner" plots) to ensure planting under a wide range of local light conditions (Gehlhausen et al. 2000). Mistletoe fruit collection and planting occurred during one of the three winter seasons (December–March) from the 2015–2016 winter season to that of 2017–2018.

Mistletoe seeds to be planted were collected from either GDSNWR or SQSNAP to match the plot location, with host-specific batches of seeds stored within intact fruits at 1.6 °C for no longer than 76 days ($n = 1090$ seeds, mean = 28 days, standard deviation (SD) = 18 days). Seeds were sown on the closest suitable host trees to the center of each plot. Suitable host trees were typically red maple, swamp tupelo (*Nyssa biflora* Walter), and ash spp. (*Fraxinus* L. spp.), the most frequently parasitized wetland trees in the region (Baldwin, Jr. and Speese 1957). The distribution of American mistletoe seeds planted at field plots across 11 host species and genera is in the Appendix. Five seeds per branch were planted on four to six branches per plot (mean = 4.3 branches, SD = 0.61 branches), with planting conducted on consistently thin branch sections (mean = 6.8 mm diameter, SD = 3.5 mm; Overton 1994; Mellado and Zamora 2014). The number of branches selected varied with the plot-specific availability of suitable branches within reach for planting, with planting heights ranging from 1 to 2.5 m. Seeds from mistletoe shrubs parasitizing different host species were allocated randomly to host branches during planting (Mellado and Zamora 2014), and the presence of mature mistletoe shrubs on each new host tree at the time of planting was recorded. During analyses of data on seed fates, the inclusion of random effects corresponding to plot and branch identity nested within plot in generalized linear mixed models (GLMMs) allowed us to account for the lack of independence among seeds planted on the same branch and in the same plot (Bolker et al. 2009).

We removed the exocarp from American mistletoe fruits prior to planting seeds and used either viscin ($n = 400$; May 1971; Mellado and Zamora 2014) or EcoGlue™ ($n = 690$; Willamette Valley Company, Eugene, OR, USA) to attach seeds on host branches. Images of American mistletoe fruits, mistletoe seeds affixed with viscin, and seeds affixed with EcoGlue™ are available in the Appendix. Surviving seedlings at each plot were monitored approximately every 3 months until we detected the emergence of foliage leaves on stems from either endophytic or epicotyl origins (Calvin 1966; Panvini 1991; Herrera et al. 1994). We used % canopy openness to represent light availability, and measurements were made during the first post-planting growing season at each branch location using a convex densiometer (Jennings et al. 1999; Watts et al. 2011).

We considered germinated seeds as those with green, emergent hypocotyls present after approximately 3 months and treated the binary germination state of each seed as a Bernoulli random variable (Mellado and Zamora 2014). Variation in germination rates was modeled as a function of fixed and random factors with GLMMs and a logit link (Bolker et al. 2009). We used a similar approach for analyzing data on the binary state of whether a seed remained for approximately 3 months or disappeared, also viewed as a Bernoulli random variable. In both cases, we used AIC_c (Akaike information criterion) to rank alternative models by their predictive power and derived model-averaged predictions of response rates across levels of factors deemed important as explanatory covariates (Burnham and Anderson 2002; Burnham et al. 2011). The GLMMs, model comparisons, and similar analyses described in the remainder of this section were run in R (R Core Team 2021) using the packages lme4 (Bates et al. 2015) and AICcmodavg (Mazerolle 2020).

The global model of variation in rates of seeds remaining to ∼3 months included the fixed effects of branch diameter, planting method (viscin or EcoGlue™), and site (GDSNWR or SQSNAP), and the random effects of plot identity and branch identity nested within plot (Table 1). Other candidate models compared to this global model using AIC_c included subsets of these fixed effects, but all models in the set included the random effects of plot and nested branch identities. Our set of models of variation in germination rates included combinations of the fixed effects of % canopy openness, planting method, and year of planting, while all models included the random effects of branch identity (Table 1). These models of

Table 1. Descriptions of models of variation in germination rates of American mistletoe seeds planted at field sites and rates of such seeds remaining to approximately 3 months.

Variable	Response: Seed remaining rate	Response: Germination rate
Branch diameter	Y	N
Planting method (G or N)	Y	Y
% canopy openness	N	Y
Year	N	Y
Site (GDSNWR or SQSNAP)	Y	N
Plot (random)	Y	N
Branch (random, nested in plot)	Y	Y

Note: "Y" indicates independent variables for which effects were included in at least some models of the respective response rate, while "N" indicates such variables that were not included in any models of that response. Other abbreviations used: "G" = glue, "N" = natural viscin, "GDSNWR" = Great Dismal Swamp National Wildlife Refuge, "SQSNAP" = South Quay Sandhills State Natural Area Preserve, "plmeth" = planting method, "stbrdiam" = standardized branch diameter, and "stlight" = standardized % canopy openness.

variation in germination rate did not include the random effects of plot identity, as we expected unmeasured factors likely to be accounted for with random plot effects, such as variation in plot-level seed predator abundance, to affect proportions of seeds remaining but not germination rates. Continuous covariate values were scaled by subtracting from the mean and dividing by the SD.

Controlled planting experiment under different light and flood regime conditions

We designed a controlled experiment to jointly estimate the effects of local light environment and flood regime on American mistletoe establishment. In winter 2016–2017, we transplanted 115 red maple saplings from a single population in Halifax County, NC, USA into pots containing natural soil from the site. These potted red maple saplings were transported to the Virginia Tech Hampton Roads Agricultural Research and Extension Center in the city of Virginia Beach, VA, USA and placed in plastic tubs (3–4 saplings per tub). From mid-April to mid-October 2017, tubs were subjected to one of three flood regime treatments: continuous, partial, and unflooded. Water in tubs subjected to the continuous flooding treatment ($n = 39$ saplings) was maintained near soil level over the entire growing season. Water in tubs subjected to the partial flooding treatment ($n = 38$ saplings) was maintained near soil level for 2 weeks at a time in between 2 week periods when natural precipitation was the sole water source. Drain holes were drilled in the bottom of tubs subjected to the unflooded treatment ($n = 38$ saplings), with growing season watering of approximately 500 mL per potted sapling per week only used to supplement natural precipitation during extremely dry periods, i.e., periods of less than 1 cm of precipitation per week. An image depicting one tub subjected to each treatment is available in the Appendix.

After maintaining the flood regime treatments during the 2017 growing season, we used the viscin planting method described above to adhere American mistletoe seeds collected from a single population in GDSNWR on the potted saplings the following winter. Two to ten seeds were planted on each sapling for a total of 599 seeds, with variation in planting rate a function of sapling size. We checked all seeds after 3 months and assessed germination rates as described above. Variation in the binary germination state of seeds was modeled as functions of fixed and random factors using alternative GLMMs ranked with AIC_c. Models varied in the inclusion of the fixed effect of flood regime treatment, but all included random effects corresponding to tub identity and sapling identity nested within tub to account for the lack of independence among seeds planted on the same sapling and in the same tub (Table 2; Bolker et al. 2009).

During the 2018 growing season, in addition to re-initiating flood regime treatments at the tub level, we subjected germinated mistletoe seeds to one of four light availability treatments. Light availability treatments were applied at the sapling level under a split-plot design, with saplings representing subplots within plastic tubs as main plots. Saplings hosting germinated mistletoe seeds in physical positions suitable for affixing sleeves of shade cloth (i.e., along internodes; $n = 34$ saplings) were randomly assigned one of three light availability treatments: broadcloth covering of seeds to create complete shade ($n = 15$ saplings, $n = 38$ seeds), 73% shade cloth covering (the Wetsel Seed Company, Inc., Harrisonburg, VA, USA) to create moderate shade ($n = 10$ saplings, $n = 33$ seeds), and a single layer of translucent white polyester tulle ($n = 9$ saplings, $n = 36$ seeds) as a control treatment (Randle et al. 2018). An image depicting such coverings and a diagram of the experiment are available in the Appendix.

We monitored the planted mistletoe seeds approximately every 3 months and recorded data on seedling survival to 18 months and the presence of leafy stems. As with data from the field planting experiment, we treated these data as Bernoulli random variables and analyzed rates of survival to 18 months and leafy stem development separately using GLMMs (Mellado and Zamora 2014). Models varied in their inclusion of the fixed effects of light availability and flood regime treatments and were ranked using AIC_c (Table 2). All models included random effects corresponding to tub identity and sapling identity nested within tub as described above for the analysis of germination rates.

Results

American mistletoe habitat relationships

We detected mistletoe at 38 survey plots on 599 individual trees and 7 host tree species, and on an additional 23 host tree species at 117 sites selected ad hoc in forested habitats (Table 3); all host species detected in this study are native trees, shrubs, or lianas. Three additional host taxa detected at ad hoc sites were identified to only genus or subgenus level. Single instances of the shrub swamp dogwood (*Cornus stricta* Lam.) and the liana peppervine (*Ampelopsis arborea* (L.) Koehne) serving as hosts for American mistletoe were also detected at ad hoc sites. The mean number of species on region-specific host lists was 12.4 ± 3.2 (mean ± SD) with the most diverse

Table 2. Descriptions of models of variation in rates of seed germination and seedling survival and leafy stem development for American mistletoes planted on potted host saplings.

Variable	Response: Germination rate	Seedling survival rate	Leafy stem development rate
Shade cloth treatment	N	Y	Y
Flooding treatment	Y	Y	Y
Tub (random)	Y	Y	Y
Sapling (random, nested in plot)	Y	Y	Y

Note: "Y" indicates independent variables for which effects were included in the global model of the respective response rate, while "N" indicates such variables that were not included in any models of that response. Other abbreviations used: "flooding" = flood regime treatment and "light" = shade cloth treatment.

list of 16 host species from the inner Coastal Plain between the James and Cape Fear River watersheds. The most common host species was *N. biflora* with a total of 436 infected stems (24.22 ± 81.89 stems/25 m radius plot). Irrespective of host species, 15.76 ± 57.34 trees were infected across all 38 plots. Red maple was parasitized by mistletoe at more plots (26 of 38) than any other host species.

The 76 tree species and additional 13 taxa (resolved taxonomically to genus) detected across the study area are listed in the Appendix. The mean BA of tree stems in subplots across the study area was 42.36 ± 27.63 m^2 ha^{-1}. The tree species present at the highest proportion of subplots was red maple at 65% (n = 96). *Pinus taeda* L. accounted for the largest BA across all subplots with a total of 645.83 m^2 across 0.96 ha surveyed or 6% of the total subplot area.

Eighty-five out of 96 subplots contained region-specific host species, with a mean host BA in subplots across the study area of 16.24 ± 22.91 m^2 ha^{-1}. When regional host associations were ignored, 89 plots contained at least one species that served as a host in the study area, and the mean subplot-level host stem BA was 19.07 ± 23.92 m^2 ha^{-1}. The rate of occurrence of American mistletoe in forested wetland habitat was statistically greater than the occurrence rate in forested upland habitat after accounting for host availability (GLM, Fig. 3). Excluding data from ad hoc sites near region boundaries somewhat altered regional host lists and plot-level host BA covariate values, but the statistical significance of the effect of wetland habitat in GLM results was unaffected.

Habitat relationship versus observed canopy openness

There was a positive relationship between forested wetland habitat and American mistletoe occurrence after accounting for both observed canopy openness and host availability. There was no effect of observed canopy openness on mistletoe occurrence (posterior mean = 0, lower credible interval = −0.73, and upper credible interval = 0.65) even though the 95% credible interval for the effect of potential host availability on mistletoe occurrence did not overlap 0 (posterior mean = 2.19, lower credible interval = 0.98, and upper credible interval = 3.63).

Field planting experiment to simulate dispersal to different local light environments

Of 1099 seeds planted in GDSNWR and SQSNAP, 71% remained after approximately 3 months. Planting method (viscin or glue) was an important predictor of variation in this rate, as candidate models that included the effect of planting method collectively received all AIC_c weight. While one model of variation in the proportion of seeds remaining that received support ($\Delta AIC_c = 2.02$) did include the effect of branch diameter, this covariate does not appear to be an important predictor of this response as models, including the effect, collectively received only 27% of the AIC_c weight. Of those seeds that remained after 3 months, 74% germinated. The candidate model of variation in germination rate that received all support when ranked with AIC_c included the effects of planting method and year of planting only. Full model selection results and model-averaged predictions of both rates of seeds remaining and seed germination are in the Appendix.

The 33 seedlings that survived 18 months occurred in 10 edge and 3 inner plots. A total of 13 seedlings that produced leafy stems occurred in 7 edge plots and 1 inner plot. The endophytic portions of American mistletoes penetrate host tissue and originate from a haustorial disk (Kuijt 1969), with leafy stems able to originate from both the epicotyl (Bray 1910) and from buds on the haustorial disk and endophyte (York 1909; Calvin 1966; May 1971). Leafy stems on seven seedlings arose from epicotyls, four seedlings had leafy stems developed from the endophytic system only, and two seedlings produced leafy stems from both the epicotyl and haustorial disk. An image showing a germinated American mistletoe seedling with a haustorial disk and leafy stems from different origins is available in the Appendix.

Controlled planting experiment under different light and flood regime conditions

Of 599 seeds planted, 360 remained on potted host saplings ~3 months after planting; 89% of these germinated. Germinated seedlings that outlived host tissue or that slipped onto non-host materials were disregarded during subsequent analyses, leaving 65 seeds available to establish on saplings subjected to continuous flooding (n = 25 saplings), 91 seeds available to establish on saplings subjected to partial flooding

Table 3. Species and genera of woody plants detected as hosts for American mistletoe in forested habitats at plots and sites selected ad hoc across the study area; commonly parasitized species were detected as hosts at greater than 24% of surveyed mistletoe populations, occasionally parasitized species were detected as hosts at between 6% and 24% of surveyed populations, and rarely parasitized species were detected as hosts at fewer than 6% of surveyed populations.

Host trees identified to species
Commonly parasitized
Acer rubrum L. (Aceraceae)
Fraxinus pennsylvanica Marshall (Oleaceae)
Nyssa biflora Walter (Nyssaceae)
Ulmus americana L. (Ulmaceae)
Host trees identified to species
Occasionally parasitized
Betula nigra L. (Betulaceae)
Fraxinus caroliniana P. Miller (Oleaceae)
Nyssa aquatica L. (Nyssaceae)
Nyssa sylvatica Marshall (Nyssaceae)
Quercus nigra L. (Fagaceae)
Quercus rubra L. (Fagaceae)
Host trees identified to species
Rarely parasitized
Acer saccharinum L. (Aceraceae)
Alnus serrulata (Aiton) Willdenow (Betulaceae)
Carpinus caroliniana Walter (Betulaceae)
Carya ovata (P. Miller) K. Koch (Juglandaceae)
Celtis laevigata Willdenow (Cannabaceae)
Fraxinus americana L. (Oleaceae)
Fraxinus profunda (Bush) Bush (Oleaceae)
Liquidambar styraciflua L. (Altingiaceae)
Persea palustris Rafinesque (Lauraceae)
Quercus falcata Michaux (Fagaceae)
Quercus laevis Walter (Fagaceae)
Quercus laurifolia Michaux (Fagaceae)
Quercus lyrata Walter (Fagaceae)
Quercus marilandica Muenchhausen (Fagaceae)
Quercus pagoda Rafinesque (Fagaceae)
Quercus palustris Muenchhausen (Fagaceae)
Quercus phellos L. (Fagaceae)
Quercus velutina Lamarck (Fagaceae)
Styrax americanus Lamarck (Styracaceae)
Ulmus alata Michaux (Ulmaceae)
Host trees identified to genus or subgenus
Occasionally parasitized
Carya Nutt. spp. (Juglandaceae)
Quercus (*Lobatae* subgenus) Loudon spp. (Fagaceae)
Host trees identified to genus or subgenus
Rarely parasitized
Celtis L. spp. (Cannabaceae)
Shrub species identified as host
Rarely parasitized
Cornus stricta Lamarck (Cornaceae)
Liana species identified as host
Rarely parasitized
Ampelopsis arborea (L.) Koehne (Vitaceae)

(n = 28 saplings), and 104 seeds available to establish on saplings left unflooded (n = 30 saplings).

One candidate model of variation in germination rates that received support when ranked by AIC_c ($\Delta AIC_c = 3.84$) included the effect of flood regime treatment, with model selection results in the Appendix. The model in this set that did not include this effect received 87% of the AIC_c weight, which we interpreted as only minimal support for a relationship between flood regime treatment and American mistletoe germination rates. A vast majority of leafy stems produced by seedlings that established on potted host saplings arose from the epicotyl, with only 9% of seedlings that produced leafy stems hosting such stems that traced to the endophytic system. All models of variation in both seedling survival to 18 months and leafy stem development received some support based on ΔAIC_c (Tables 4 and 5; Burnham et al. 2011). Models that included the effects of flood regime treatment collectively received 24% of the AIC_c weight across models of variation in survival and 13% of this weight across models of variation in leafy stem development. Models that included the effects of light treatment collectively received 74% of the AIC_c weight across models of variation in survival and 88% of this weight across models of variation in leafy stem development. We interpreted these results as strong support solely for a relationship between light availability and leafy stem development (Fig. 4).

Discussion

Host availability had previously been proposed as a potential driver of habitat relationships for American mistletoe in the eastern United States (Kuijt 2003; Weakley et al. 2012). Preliminary observations in our study area showed that some hosts were widespread with regards to habitat, making host availability an unlikely factor in determining the distribution of American mistletoe at this scale. Subsequent work presented here is the first, to our knowledge, to formally test the relationship between host availability and this phenomenon in the eastern United States. The use of data on the occurrences of both mistletoe and hosts from plots selected using stratified random sampling made this study unique among such investigations in temperate mistletoe systems (Lira-Noriega and Peterson 2014; Usta and Yilmaz 2021).

Regional variation in host use by American mistletoe has been noted by numerous workers, who at a minimum, overlapped in geographic scope with our study area (Baldwin, Jr. and Speese 1957; Panvini 1991; Hawkins 2010). Failing to account for such regional variation could lead to bias in estimates of the relationship between host availability and mistletoe occurrence. For instance, a tree species that was widespread geographically but parasitized only regionally could be abundant in a habitat type where American mistletoe is rare, leading to the false inference that potential host availability is unrelated to the observed mistletoe habitat relationship. Here, we partly defined host association regions based on physiographic regions to align with known differences in plant community composition (Weakley et al. 2012). In two cases, we had to further split a host association region

Fig. 3. Posterior distributions of predicted probabilities of mistletoe occurrence in forested upland and forested wetland habitats.

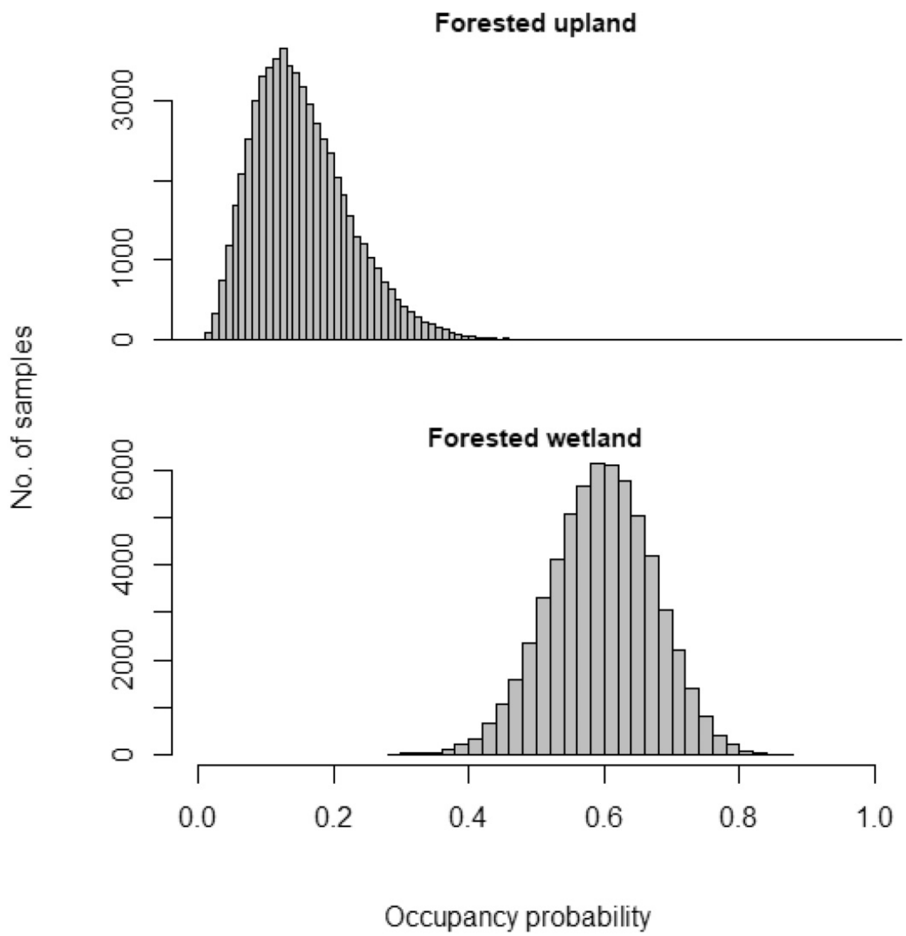


Table 4. Alternative generalized linear models (GLMs) for the relationships between rates of American mistletoe seedling survival to 18 months and the fixed effects of flood regime treatments and light availability treatments as ranked by Akaike information criterion (AIC_c).

Variables included in model	*K*	AIC_c	ΔAIC_c	AIC_c weight	Cumulative weight
Intercept + light	5	137.95	0	0.61	0.61
Intercept (null)	3	140.72	2.77	0.15	0.76
Intercept (null) + light + flooding	7	140.96	3.02	0.13	0.89
Intercept + flooding	5	141.45	3.50	0.11	1

Note: All models included the random effects of plastic tub and nested sapling identities.

Table 5. Alternative generalized linear models (GLMs) for the relationships between rates of American mistletoe leafy stem development and the fixed effects of flood regime treatments and light availability treatments as ranked by Akaike information criterion (AIC_c).

Variables included in model	*K*	AIC_c	ΔAIC_c	AIC_c weight	Cumulative weight
Intercept + light	5	129.86	0	0.78	0.78
Intercept + light + flooding	7	133.92	4.06	0.1	0.88
Intercept (null)	3	134.10	4.24	0.09	0.97
Intercept + flooding	5	136.57	6.71	0.03	1

Note: All models included the random effects of plastic tub and nested sapling identities.

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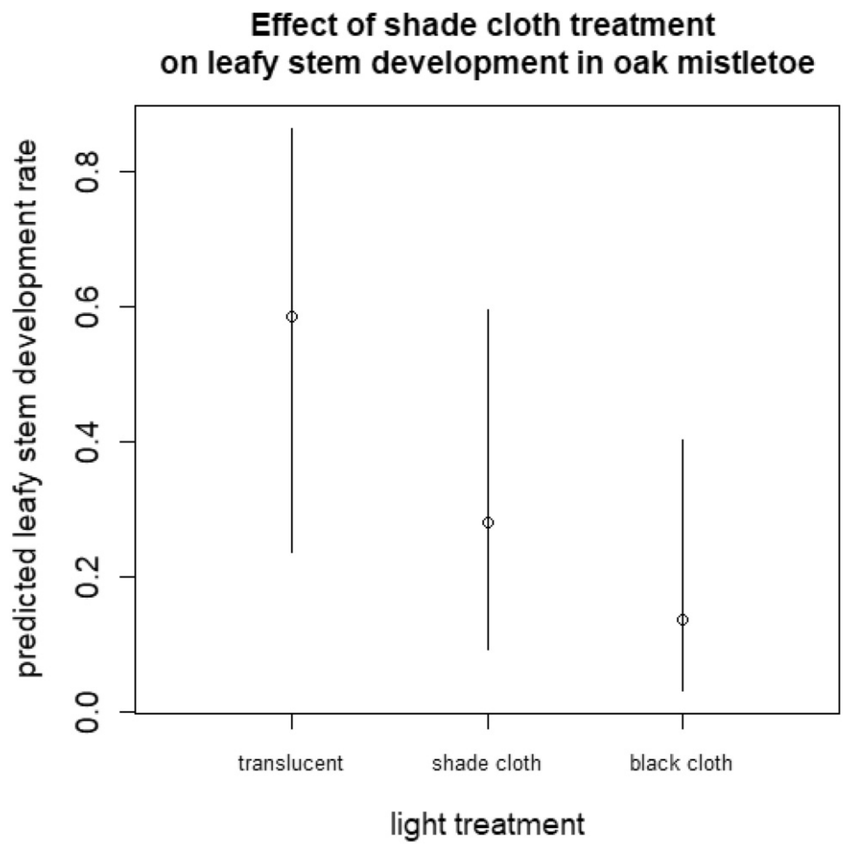
Fig. 4. Model-averaged predictions of rates of American mistletoe leafy stem development across light availability treatments; error bars represent 95% confidence intervals.



to account for shifts in parasitism of widespread tree taxa obvious in our data.

American mistletoe–habitat relationships

Our results supported the existence of a positive relationship between American mistletoe and forested wetlands after accounting for both host availability and regional variation in host use by American mistletoe. Several factors remain as viable alternatives to host availability as drivers of this habitat association, including avian disperser behavior (Lamont and Southall 1982; Martínez del Rio et al. 1996; Aukema 2004; Caraballo-Ortiz et al. 2017) and local environmental conditions (Norton and Smith 1999; Roxburgh and Nicolson 2005; Lira-Noriega and Peterson 2014; Mellado and Zamora 2014; Tikkanen et al. 2021). Several lines of evidence suggest that mistletoe dispersers in the study area, namely, the cedar waxwing (Sutton 1951; Eleuterius 1976) and eastern bluebird (Weinkam 2013), freely disperse mistletoe seeds across habitat types, including a lack of a relationship between American mistletoe genetic structure and habitat type (Flanders et al. unpublished data). Variation in compatibility between mistletoe and available hosts could drive mistletoe habitat relationships if a host-specific mistletoe population is predominant in an area and the preferred host is restricted to a certain habitat type (Caraballo-Ortiz et al. 2017). Host compatibility would need to be accounted for in these cases when quantifying host availability and its effect on mistletoe habitat relationships.

The apparent widespread presence of generalist American mistletoes in eastern portions of the study area makes it unlikely that host-specific populations could be driving the observed affinity of American mistletoe for forested wetlands. Host compatibility based on species identity alone should not be a barrier to parasitism of host tree species in forested uplands if those species are hosts for generalist mistletoe populations in other habitats. Genetic variation among host populations in their susceptibility to mistletoe infection could influence mistletoe distribution (Kuijt 1969; May 1971; Panvini 1991; Sallé et al. 1993; Mellado and Zamora 2014). The presence of such variation among hosts and any relationship with habitat type in the study area is an open question, as is the presence of predominant host-specific American mistletoe populations in other portions of its range.

Evidence for establishment limitation in American mistletoe

Planting experiments can provide evidence to support alternative hypotheses about the roles of dispersal limitation or establishment limitation in determining plant distributions (Clark et al. 2007). A lack of evidence for relationships between American mistletoe establishment and abiotic variables manipulated in planting experiments could result from three scenarios: (1) American mistletoe can establish across a range of local environmental conditions and variation in mistletoe occurrence across habitats is more likely driven by dispersal limitation, (2) the abiotic variables that limit American mistletoe establishment were not included in the experiment, or (3) sample sizes were too small to detect treatment effects. Instead, and more typical of studies of plant populations (Renne et al. 2001; Clark et al. 2007), we found evidence that establishment limitation outweighed dispersal limitation in determining the distribution of American mistletoe. Our findings support a relationship between local light availability, manipulated using shade cloth, and American mistletoe establishment on potted host saplings as measured by leafy stem development. Given the large, chlorophyllous seeds of American mistletoe (Calvin 1966; Kuijt 1969), an effect of light on its establishment is not unexpected.

Comparisons between planting experiments in the field and on potted host saplings

Red maple saplings subjected to flooding treatments exhibited visible changes in morphology like those responses to flood stress described in a previous greenhouse study (Day 1987). Yet, we did not find strong support for relationships between germination rates of American mistletoe seeds and both flood regime treatments when planted on potted host saplings and local light availability conditions when planted on host trees in the field. The former finding was expected, as American mistletoe seeds are known to readily germinate even on non-host material (Randle et al. 2018), and so we assumed that germination rates on hosts subjected to different hydrological conditions would be similar (May 1971). High germination rates have been found for the mistletoe *Viscum album* across a range of source populations and temperature regimes (Stanton et al. 2010). While American mistletoe seeds require light to germinate (Gardner 1921), our findings suggest that germination rates are not sensitive to variation in light availability under field conditions, at least for the range of light conditions tested.

The large variation in host branch diameter available for inoculation with American mistletoe seeds in the field allowed us to examine the relationship between this covariate and the proportion of seeds that remained after approximately 3 months. The inclusion of such an effect in models of this response variable was not strongly supported, which was a finding like those from a planting experiment using American mistletoe seeds from Texas and northern Mexico (May 1971). That study found seedlings with stem development from the endophytic system to outnumber seedlings with such development from the epicotyl, while we found the opposite pattern in results from our planting experiment on potted host saplings with roughly equal proportions of leafy stems developing from endophytic and epicotyl origins in our field planting experiment.

In contrast with the planting experiment on potted host saplings, we were unable to discern an effect of local light availability on American mistletoe establishment in the field because seedling survival rates were so low, typical of plant populations that are heavily influenced by post-dispersal factors (Clark et al. 2007). The much higher establishment rate for seeds planted on potted host saplings supports the existence of a positive relationship between light availability and American mistletoe establishment. Field sites were consistently shaded by canopy compared to the site where we conducted the controlled potted host experiment. Consistent with this observation was our finding that a majority of field planting plots where planted mistletoe seeds established were in areas near a forest edge where light is presumably less limiting.

Evidence for the importance of abiotic conditions in determining the distribution of other mistletoe species

The importance of environmental conditions, especially light availability (Panvini 1991; Shaw and Weiss 2000; Mellado and Zamora 2014), in determining mistletoe habitat relationships is suggested by studies that find differences between distributions of mistletoes and distributions of their dispersers and host trees (Lira-Noriega and Peterson 2014). As we have found for American mistletoe in eastern Virginia and North Carolina (Flanders et al. unpublished data), other studies have found mistletoe occurrence to be more restricted with regards to habitat type than that of the widespread and abundant avian species known to disperse their seeds (Norton and Smith 1999; Tikkanen et al. 2021). Even in systems where avian behavior is less well understood, the presence of reduced numbers of mistletoes in the apparently less preferred habitat type is an indication of some dispersal by birds into such habitats (Norton and Smith 1999). A small reduction in mistletoe establishment in less preferred habitat due to variation in abiotic conditions could lead to striking differences in oak mistletoe occurrence rates between habitats if dispersal distances are short (Reid 1989; Reid et al. 1995).

On smaller spatial scales, variation in mistletoe establishment and occurrence has been shown among hosts varying in size (Roxburgh and Nicolson 2008) and stand density (Matula et al. 2015; Usta and Yilmaz 2021). As an alternative to disperser behavior, establishment limitation under low light conditions could explain lower mistletoe occurrence on shorter host trees and those in denser stands (Matula et al. 2015). A negative relationship between mistletoe establishment and stand density could also indicate the importance of abiotic resources other than light in determining mistletoe distributions if reduced competition for such resources makes trees in open stands most suitable as hosts.

Future directions

Mistletoes are typically found in tree canopies (Calder and Bernhardt 1983), and despite logistical challenges, studies of relationships between mistletoe occurrence and light availability should involve data collected from locations within the canopy (Shaw and Weiss 2000). We did not find a relationship between American mistletoe and % canopy openness when measured at ground level. In certain forest types with reduced tree densities, there is likely a strong relationship between light availability experienced by American mistletoe shrubs and those light conditions measured at ground level. Quantifying light availability at canopy heights representative of the distribution of American mistletoe (Shaw and Weiss 2000) is likely necessary, however, to accurately determine the relationship between light and mistletoe occurrence.

Observations of non-fruiting American mistletoe individuals surviving in dense shade (Kuijt 1969) and physiological studies showing that American mistletoes can behave like a shade plant (Panvini 1991; Strong et al. 2000) suggest that low light availability may only reduce American mistletoe establishment and survival at a young age. Continued monitoring of the survival of American mistletoe seedlings growing under a variety of light conditions beyond the establishment and early growth phases studied here would inform on the ability of American mistletoe to persist under dense shade conditions. Such monitoring data focused on rates of flowering and fruiting could help answer whether a lack of such behavior observed in shrubs in deep shade is a response to light conditions or to age-related changes in host tissue.

Summary

Here, we showed that factors other than host availability are responsible for the observed affinity of American mistletoe for forested wetland habitat in eastern Virginia and North Carolina. We attempted to avoid potential biases by accounting for regional variation in host use by American mistletoe. Planting experiments provided evidence to support local light availability as an abiotic variable capable of explaining this pattern.

We took advantage of discrete establishment sites and quantifiable pre-planting seed rain of American mistletoe to interpret results of planting experiments. While extremely low survival rates of American mistletoe seedlings planted in the field made any relationships with local environmental conditions difficult to discern, we attribute most variation in counts of established seedlings on potted host saplings to treatment effects. We found evidence for a relationship between manipulated local light availability and rates of seedling establishment on host saplings. If dispersal limitation was the primary driver of variation in American mistletoe occurrence across habitats with different light availabilities, we would have expected a lack of such a relationship. While this finding provides support for establishment limitation as an important driver of variation in mistletoe occurrence across habitat types, data on light availability at potential mistletoe establishment sites within a variety of habitat types are needed to connect this finding to observed American mistletoe habitat relationships.

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The data that provided results for this study are available from the corresponding author upon request.

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Appendix A

Fig. A1. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across five regions that hosted subplots where *Liquidambar styraciflua* was detected. Fruit images represent locations where *L. styraciflua*, restricted as a host to one region, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

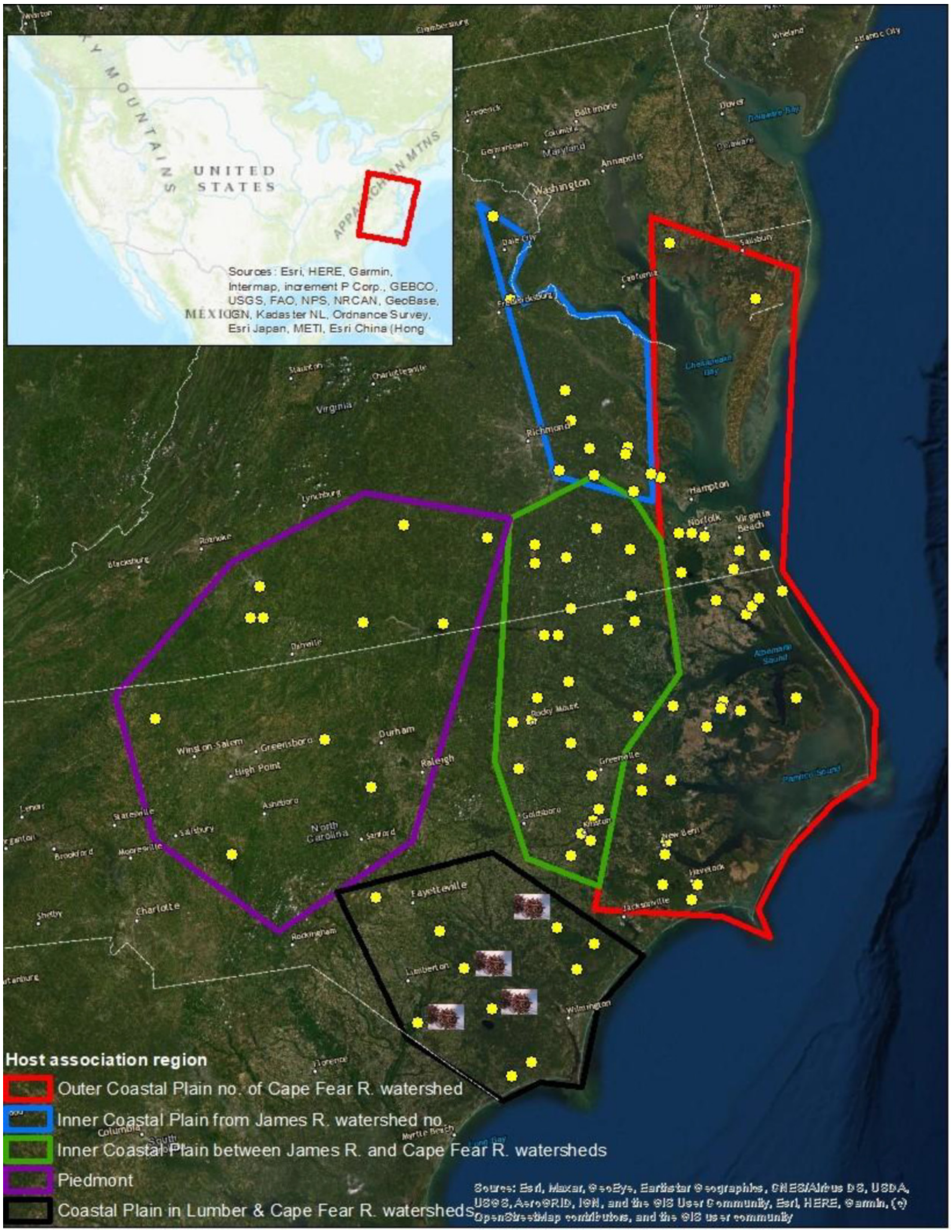

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Fig. A2. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across five regions that hosted subplots where *Acer rubrum* was detected. Images represent locations where *A. rubrum* was parasitized by mistletoe. Detected as a host in all five regions, we found a significant relationship between region and *A. rubrum* occurrence as a host across American mistletoe populations. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

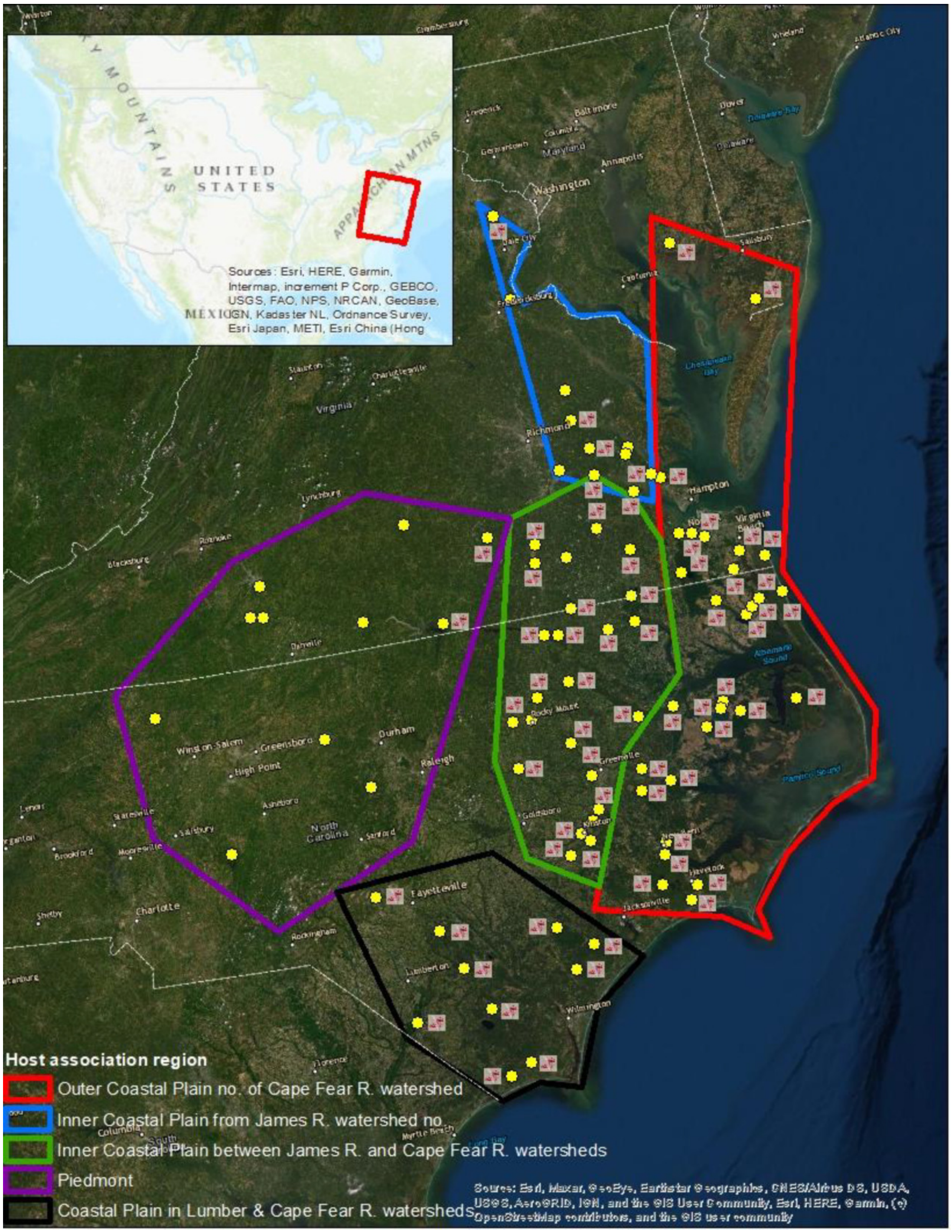

Fig. A3. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across four regions that hosted subplots where *Nyssa biflora* was detected. Images represent locations where *N. biflora* was parasitized by mistletoe. Detected as a host in all four regions, we found a significant relationship between region and *N. biflora* occurrence as a host across American mistletoe populations. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

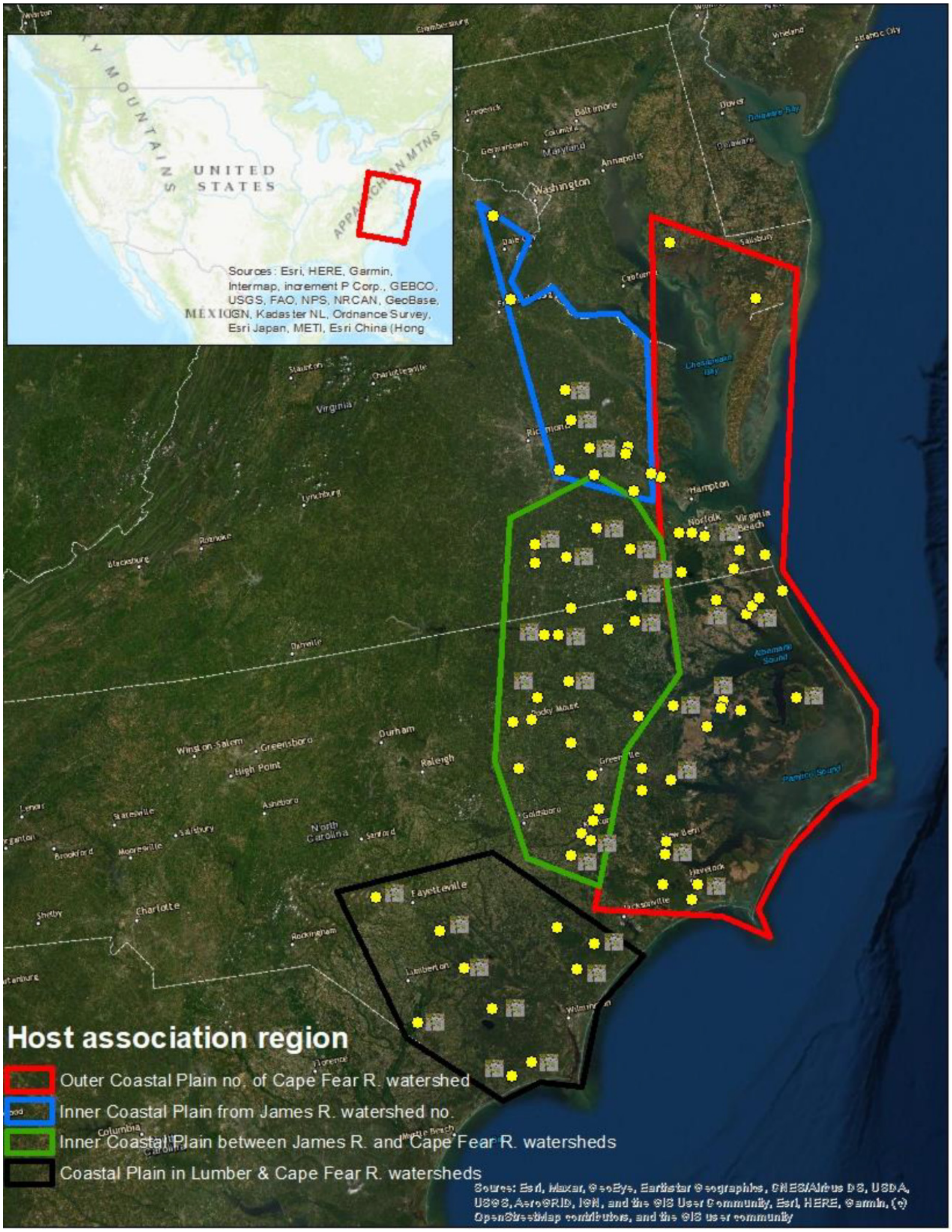

Fig. A4. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across three regions that hosted subplots where *Fraxinus caroliniana* was detected. Images represent locations where *F. caroliniana* was parasitized by mistletoe. Detected as a host in all three regions, we found a significant relationship between region and *F. caroliniana* occurrence as a host across American mistletoe populations. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

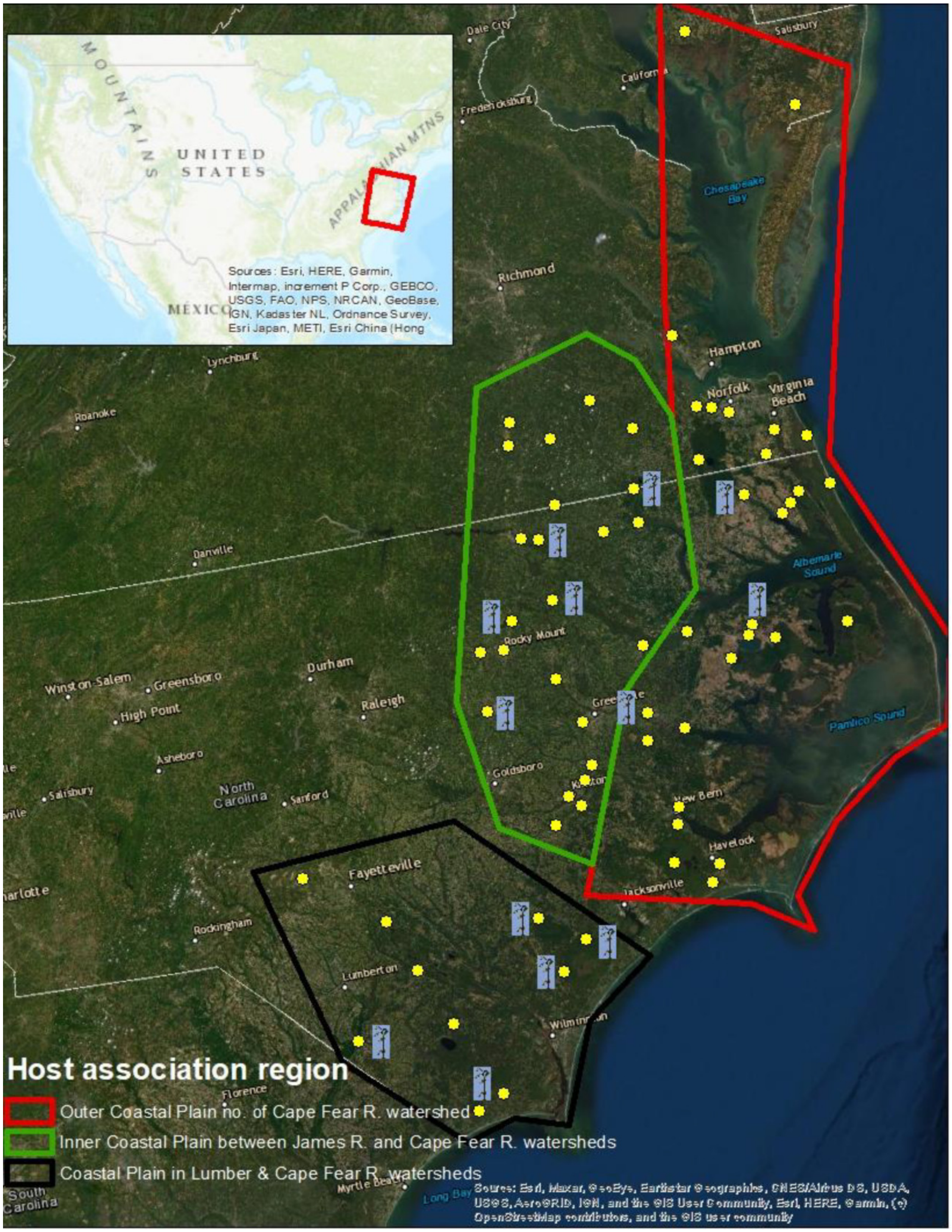

Fig. A5. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across three regions that hosted subplots where *Persea palustris* was detected. The image represents a location where *P. palustris*, restricted as a host to one region, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

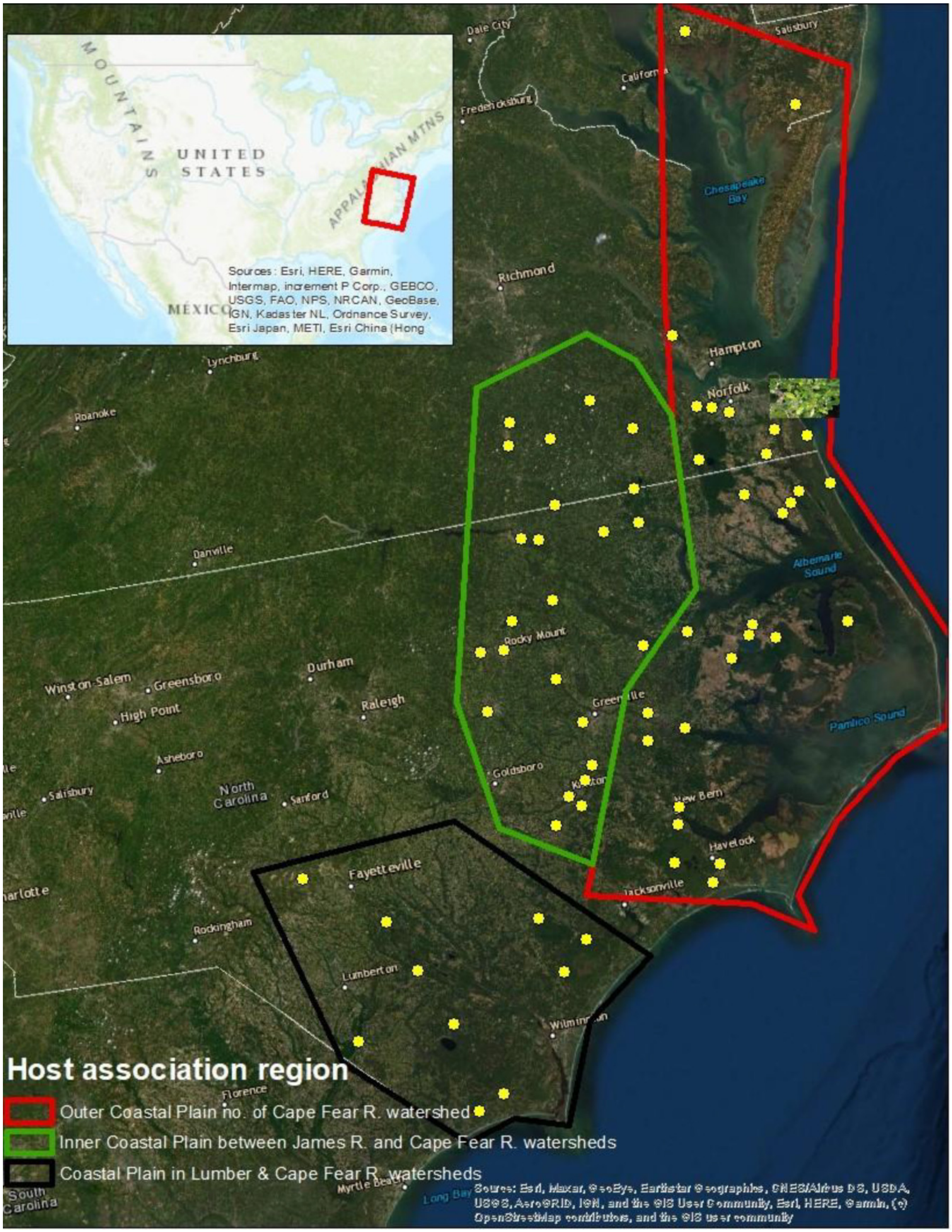

Fig. A6. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across two regions that hosted subplots where *Quercus rubra* was detected. Images represent locations where *Q. rubra*, restricted as a host to one region, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

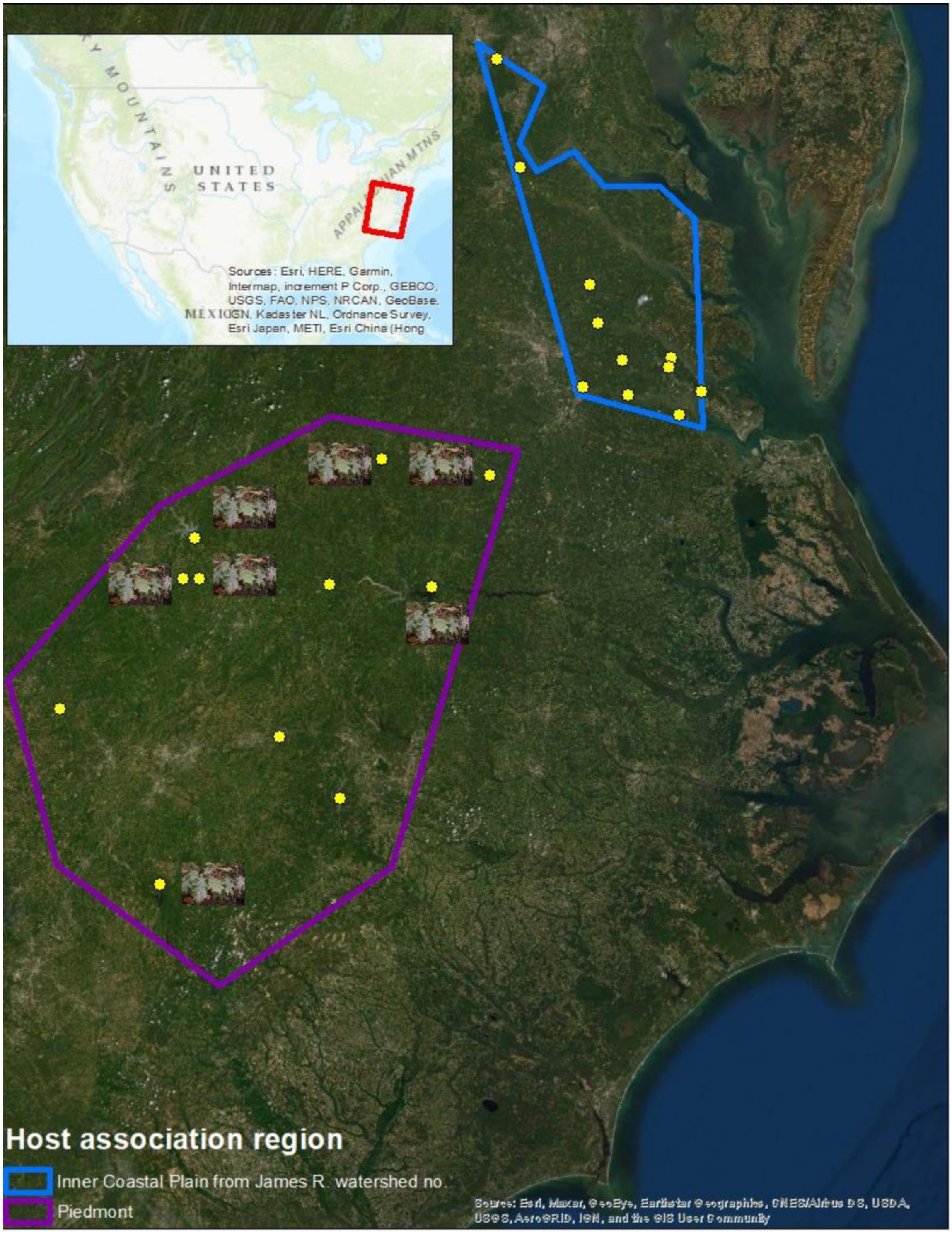

Fig. A7. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across two regions that hosted subplots where *Quercus velutina* was detected. The image represents a location where *Q. velutina*, restricted as a host to one region, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

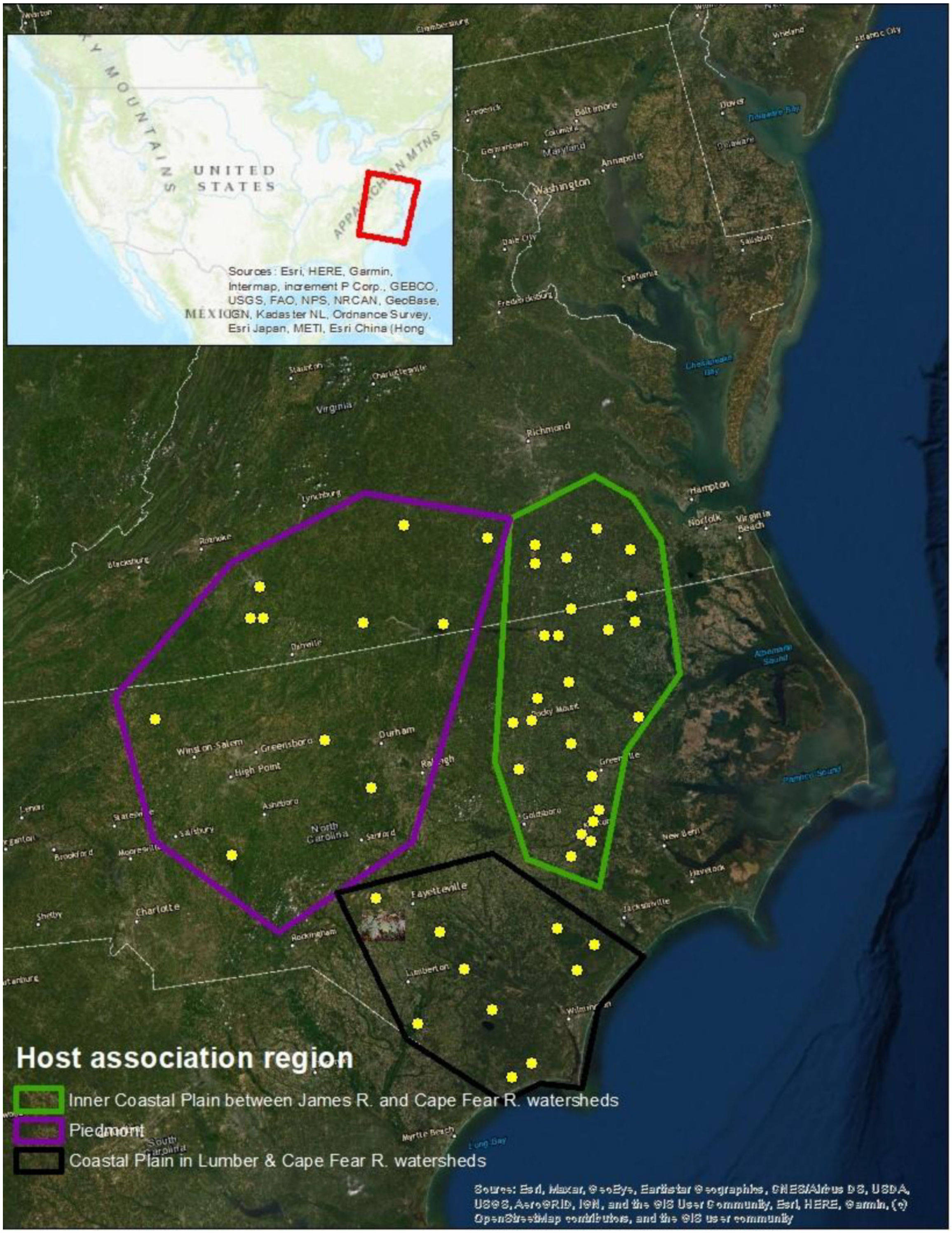

Fig. A8. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across four regions that hosted subplots where *Carya* spp. were detected. Images represent locations where *Carya* spp., restricted as hosts to three regions, were parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

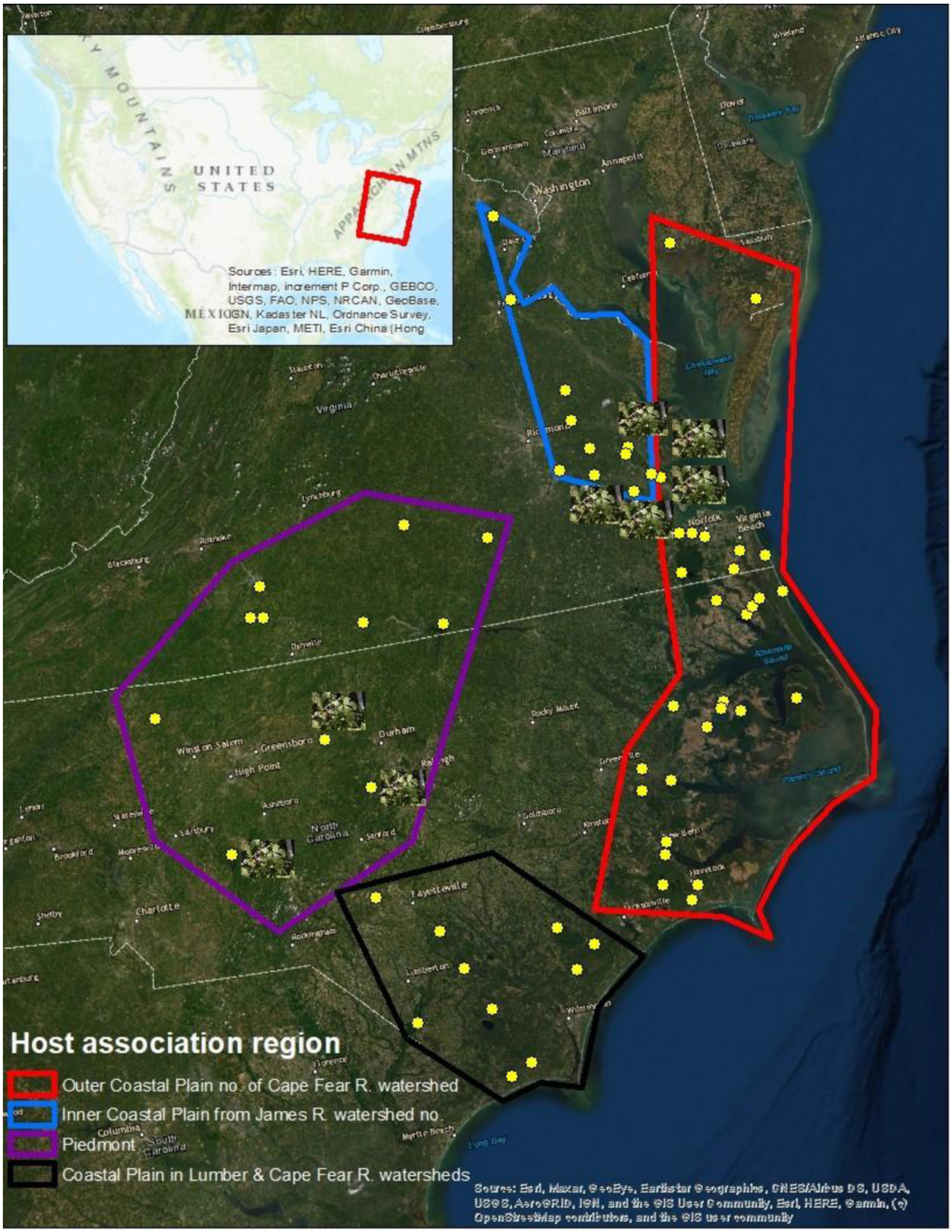

Fig. A9. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across three regions that hosted subplots where *Ulmus alata* was detected. Images represent locations where *U. alata*, restricted as a host to two regions, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

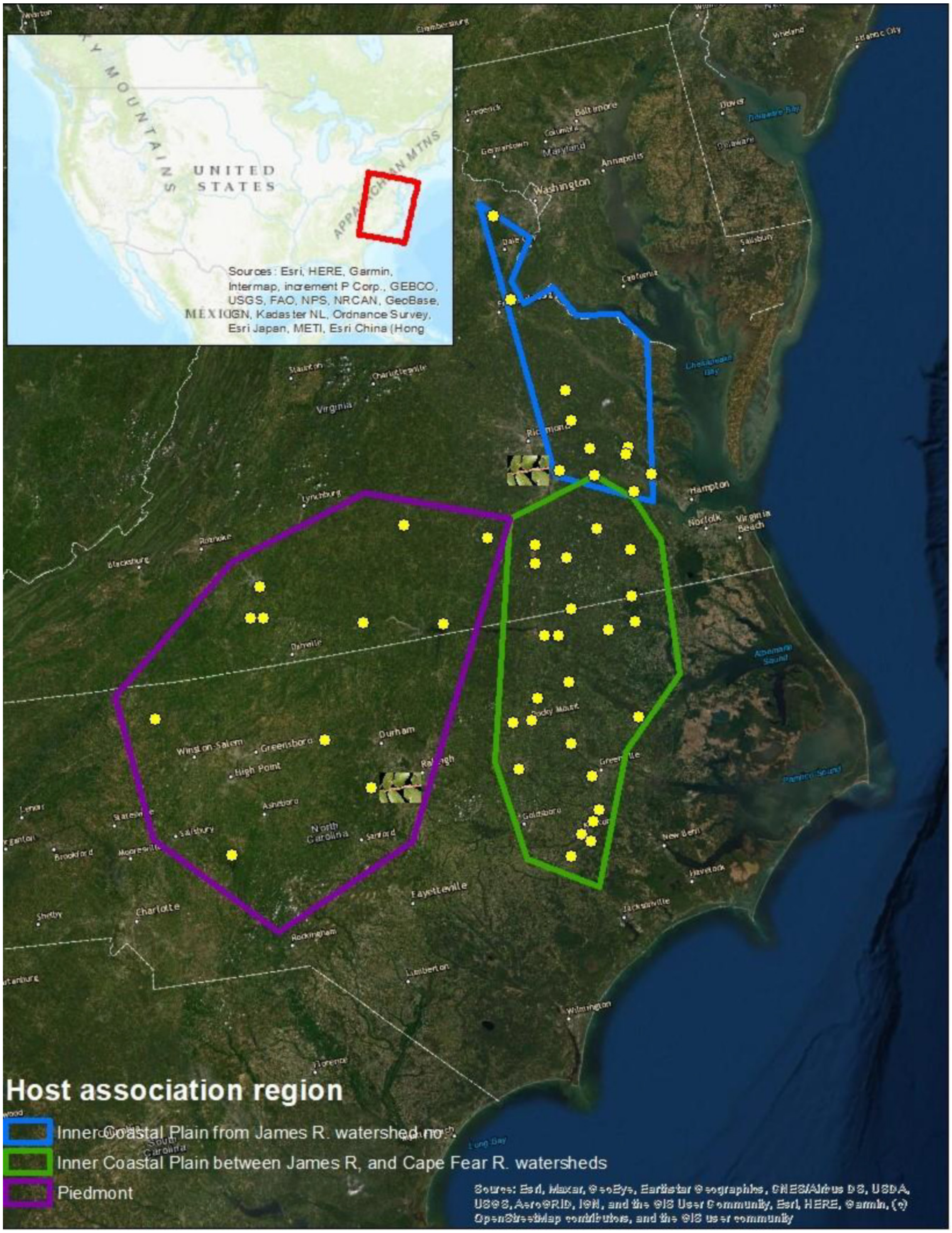

Fig. A10. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across three regions that hosted subplots where *Quercus laurifolia* was detected. Images represent locations where *Q. laurifolia*, restricted as a host to two regions, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

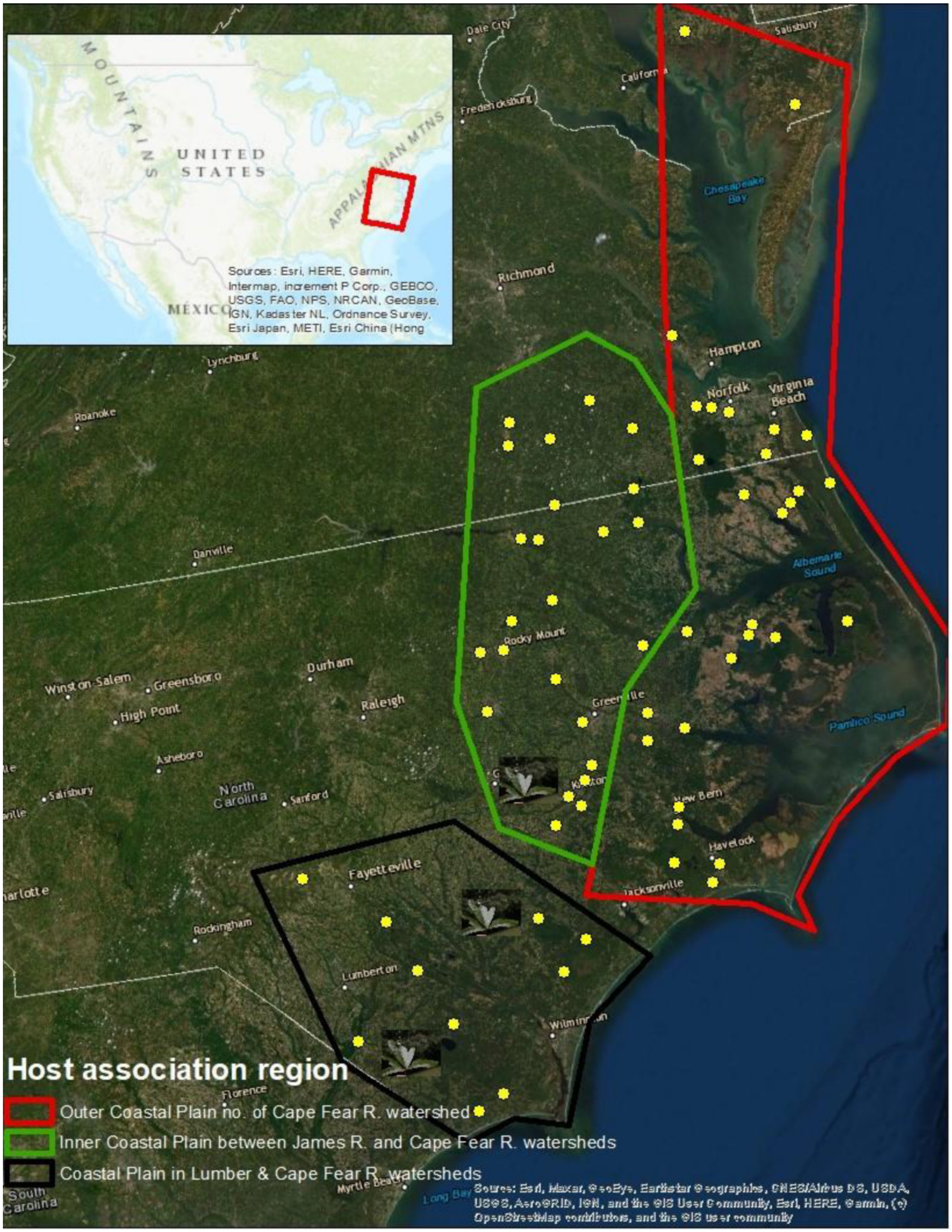

Fig. A11. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across five regions that hosted subplots where *Carpinus caroliniana* was detected. Images represent locations where *C. caroliniana*, restricted as a host to two regions, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

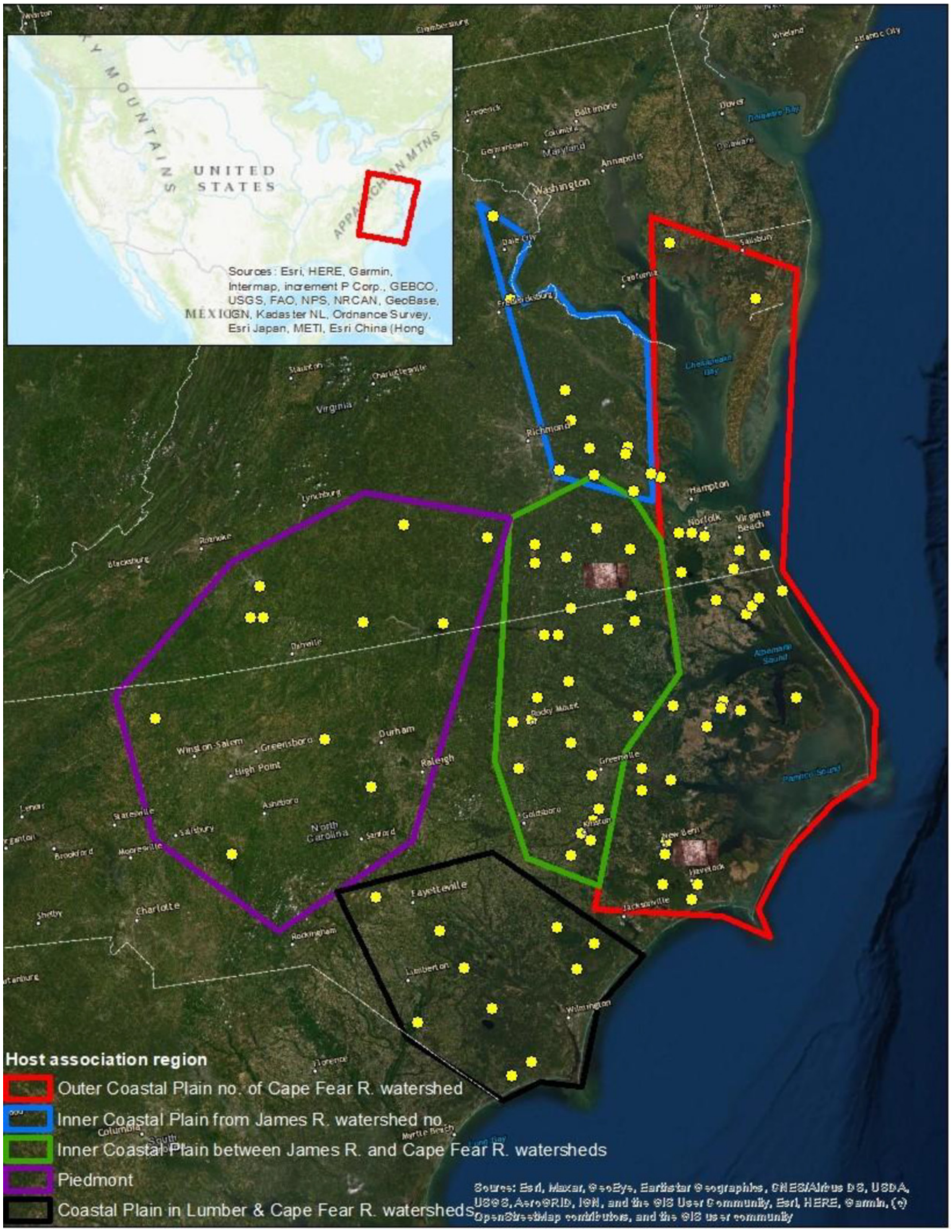

Fig. A12. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across four regions that hosted subplots where *Quercus nigra* was detected. Images represent locations where *Q. nigra*, restricted as a host to three regions, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

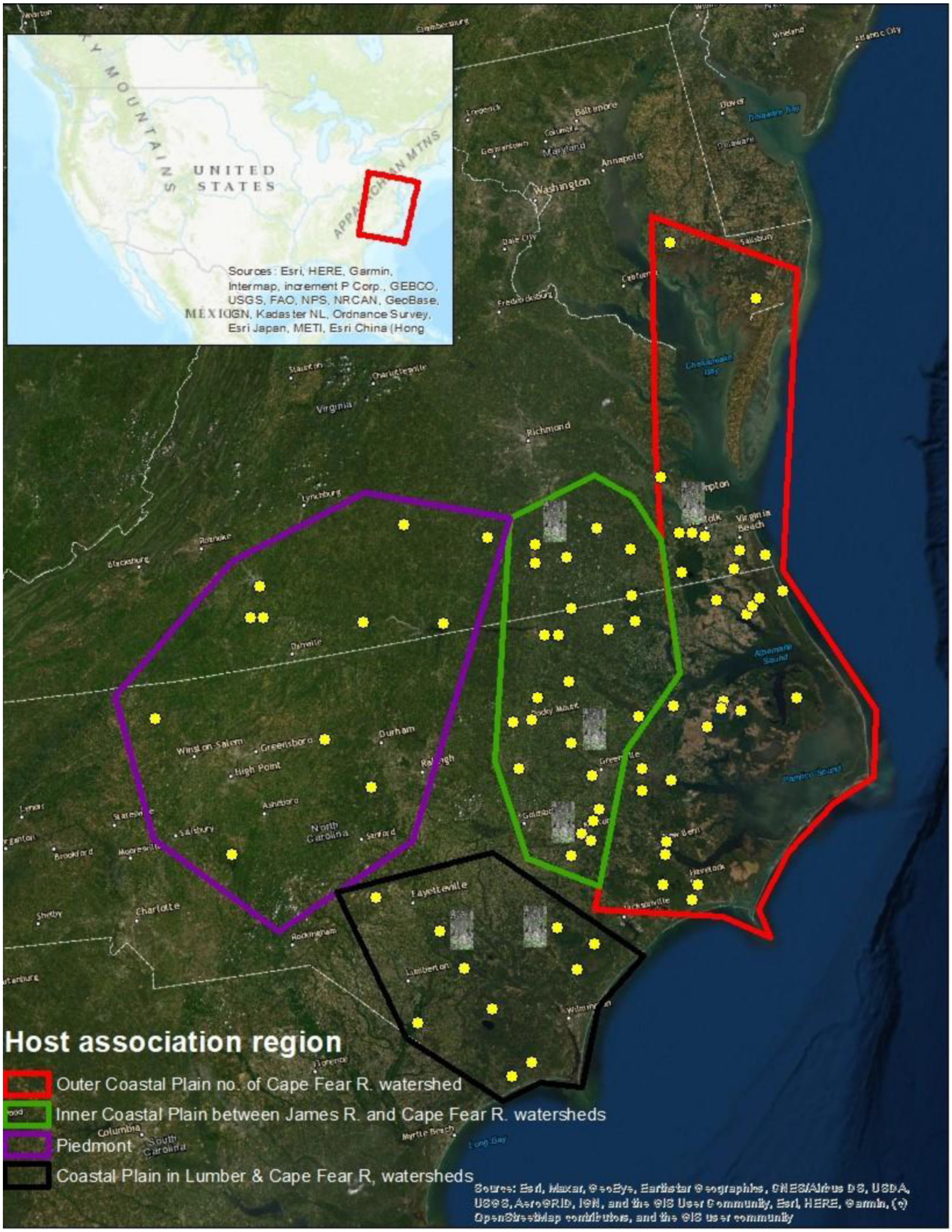

Fig. A13. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across four regions that hosted subplots where *Fraxinus pennsylvanica* was detected. Images represent locations where *F. pennsylvanica*, restricted as a host to three regions, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

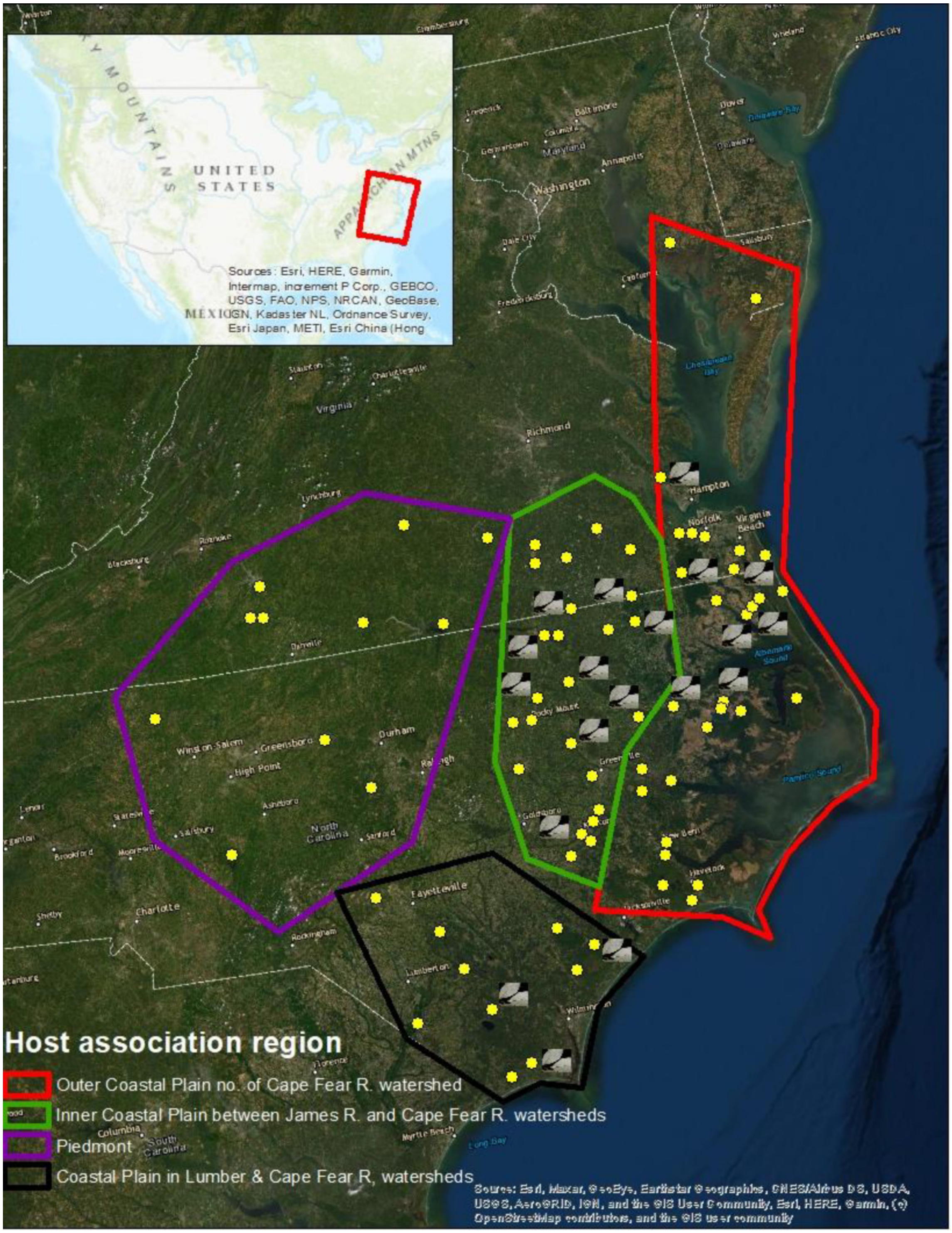

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Fig. A14. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across three regions that hosted subplots where *Quercus phellos* was detected. Images represent locations where *Q. phellos*, restricted as a host to two regions, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

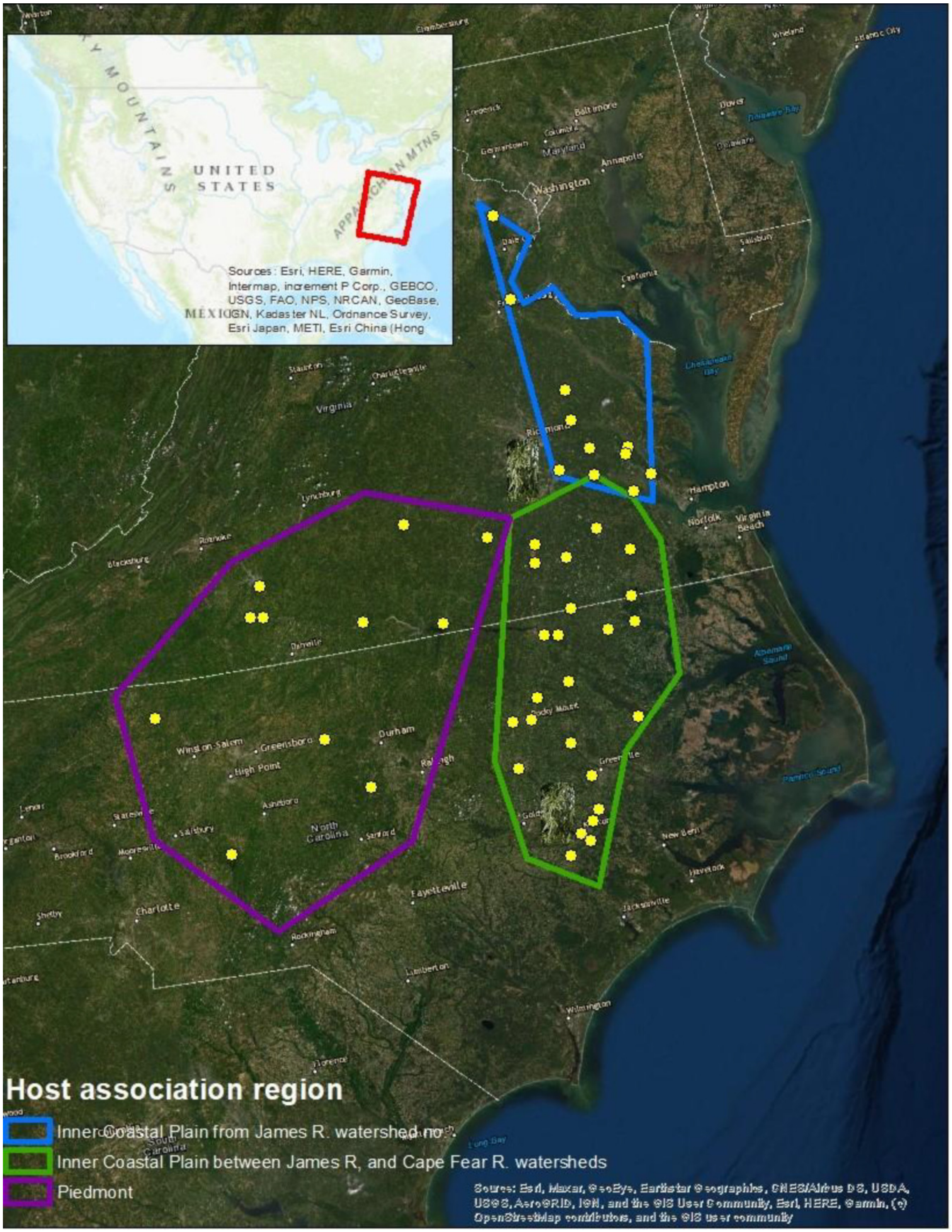

Fig. A15. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across three regions that hosted subplots where *Alnus serrulata* was detected. Images represent locations where *A. serrulata*, restricted as a host to two regions, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

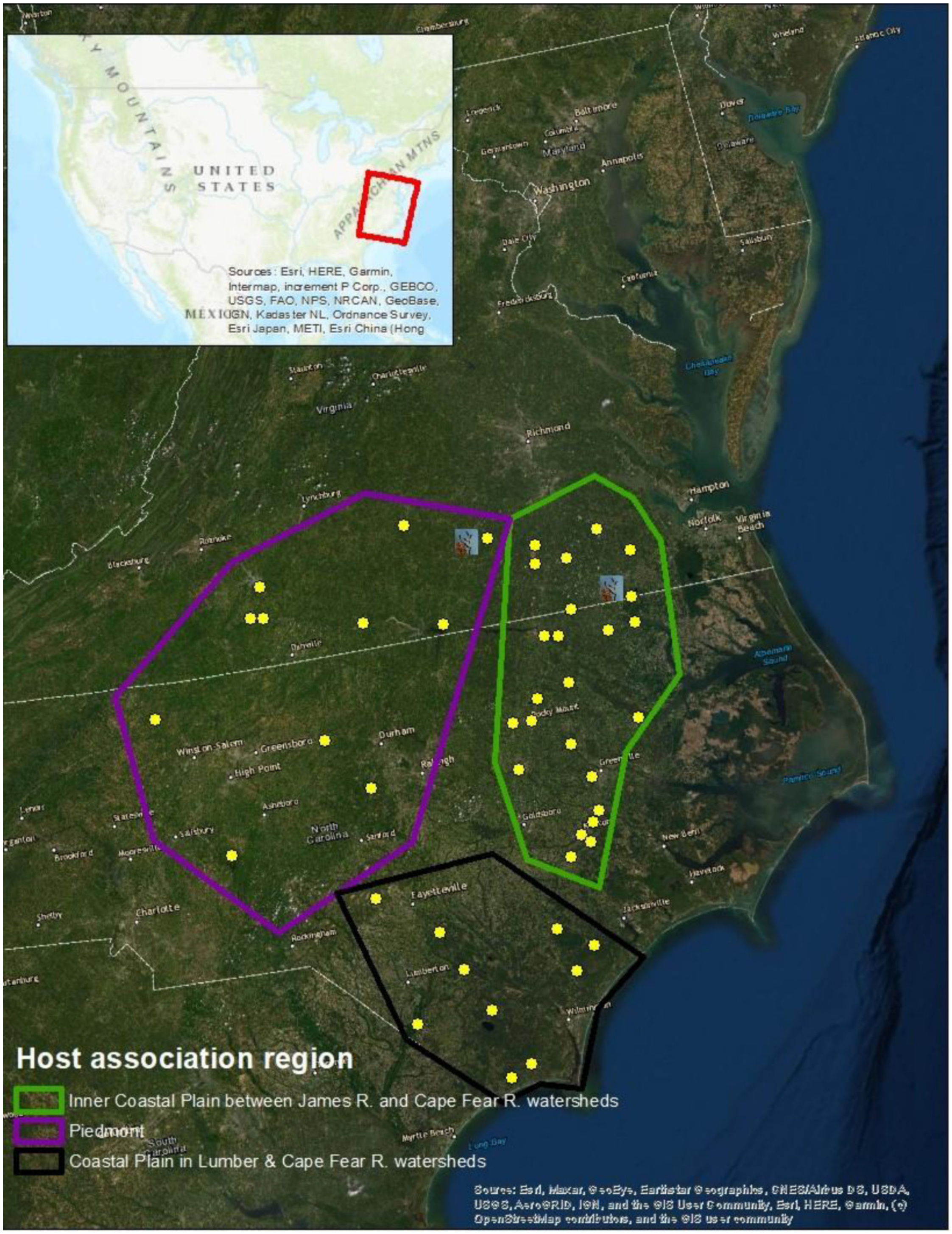

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Fig. A16. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across two regions that hosted subplots where *Fraxinus americana* was detected. The image represents a location where *F. americana*, restricted as a host to one region, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

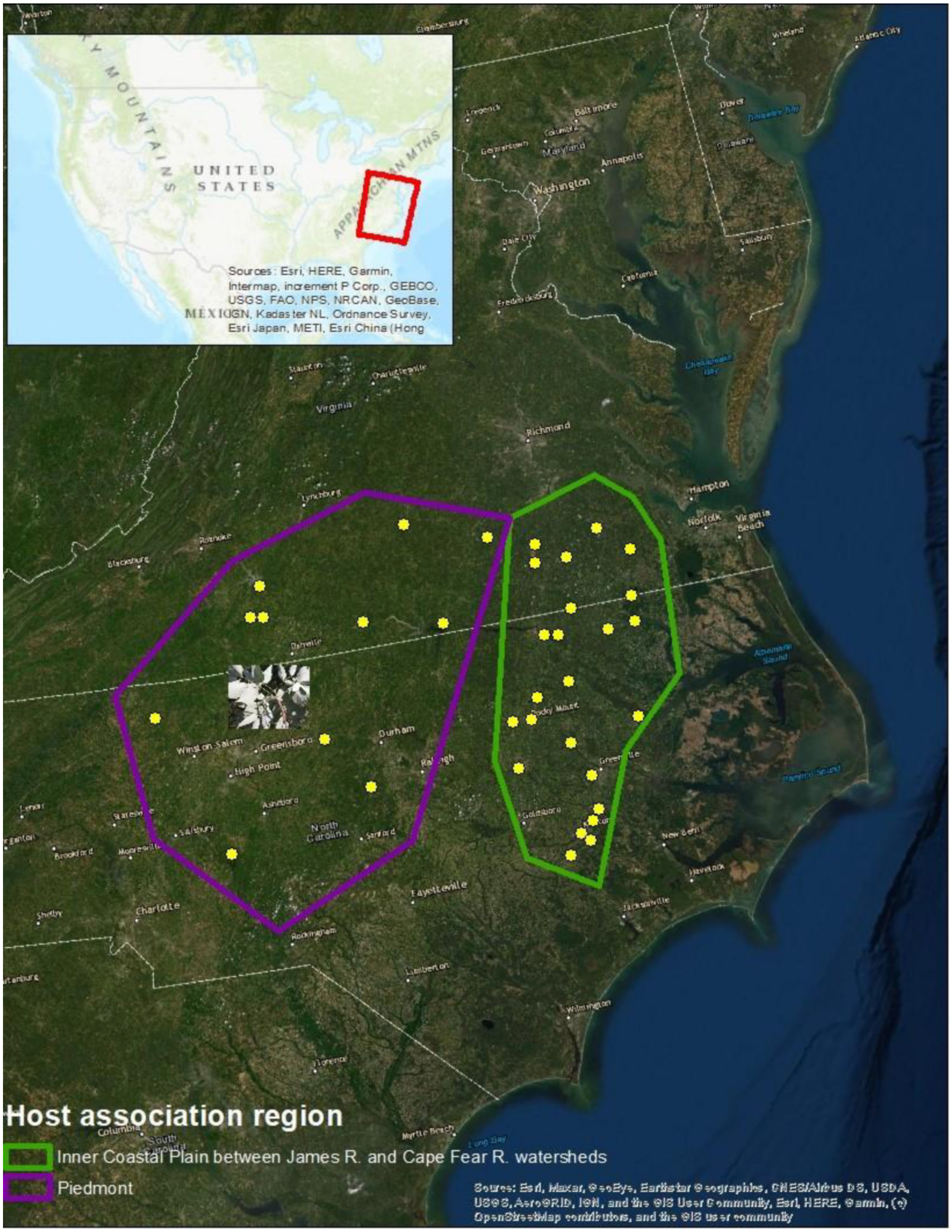

Fig. A17. Locations of American mistletoe populations detected during plot surveys and with ad hoc observations (yellow circles) across three regions that hosted subplots where *Fraxinus profunda* was detected. Images represent locations where *F. profunda*, restricted as a host to two regions, was parasitized by mistletoe. Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

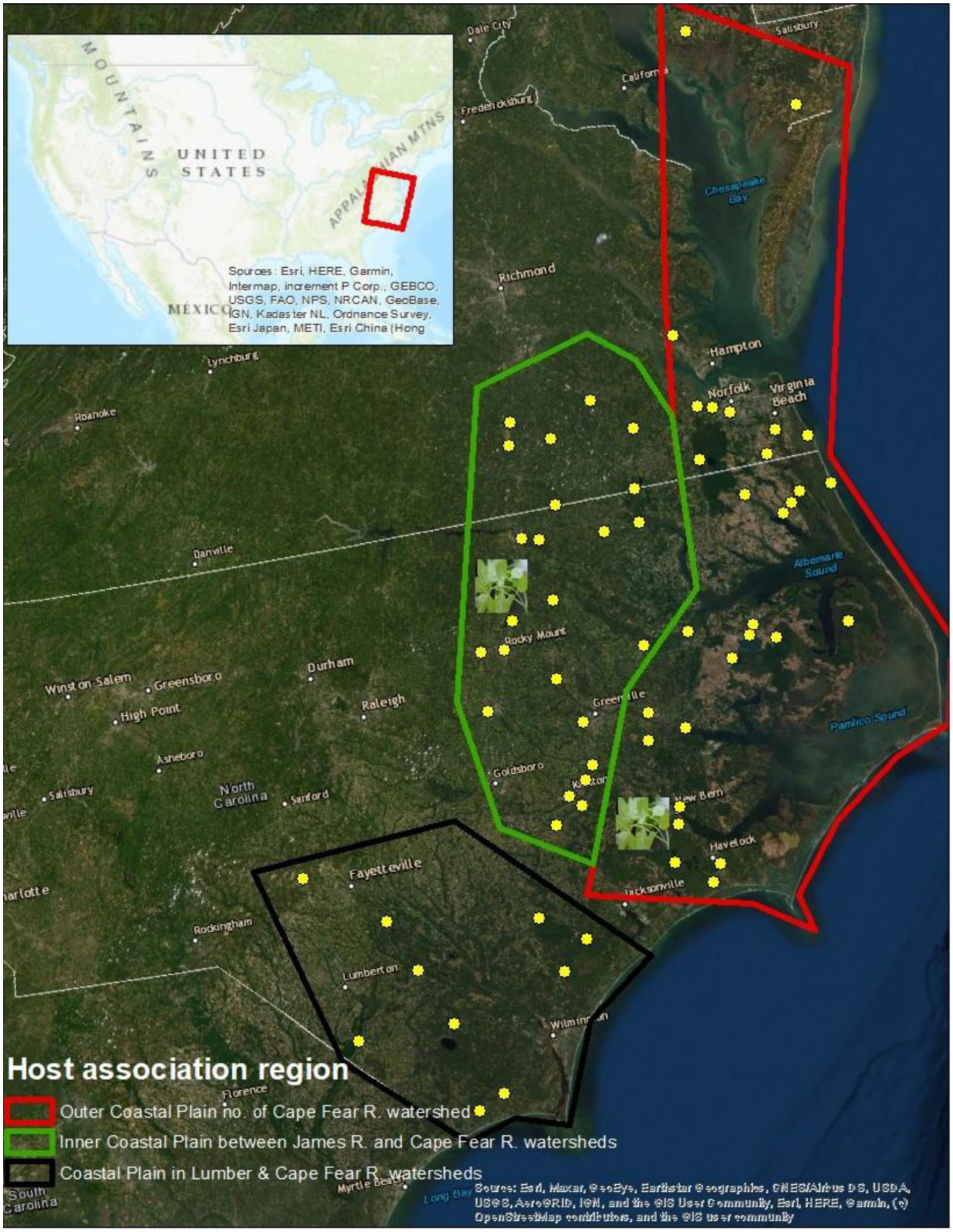

Fig. A18. Locations of 26 plots for planting American mistletoe seeds in Great Dismal Swamp National Wildlife Refuge, city of Suffolk, VA, USA; plots were in forested wetland habitat either within 15 m of an edge (edge strata) or greater than 15 m from an edge (inner strata). Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

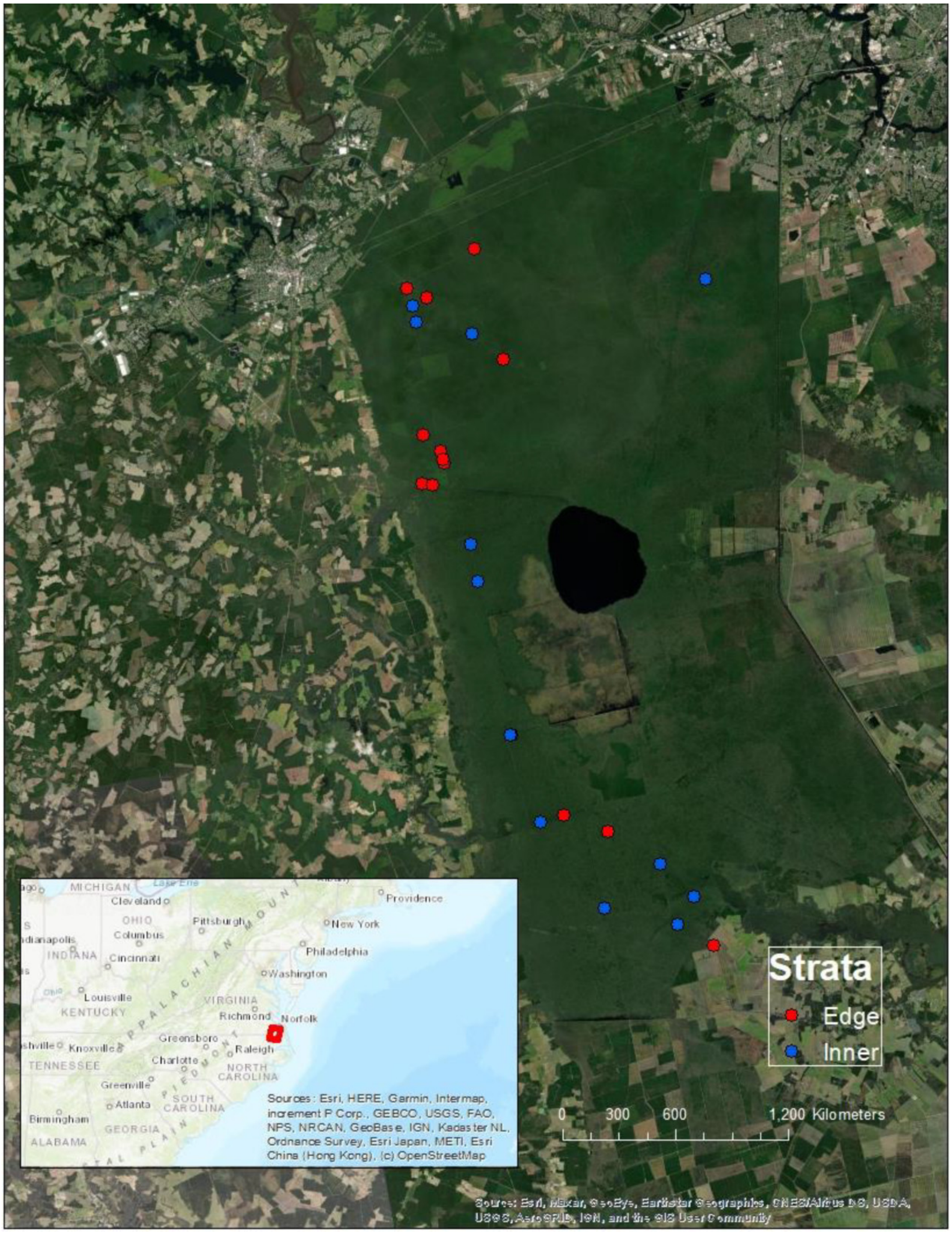

Fig. A19. Locations of 25 plots for planting American mistletoe seeds in South Quay Sandhills State Natural Area Preserve, city of Suffolk and Southampton Co., VA, USA; plots were in forested wetland habitat either within 15 m of an edge (edge strata) or greater than 15 m from an edge (inner strata). Main basemap sources: Esri, DigitalGlobe, GeoEye, i-cubed, USDA FSA, USGS, AEX, Getmapping, Aerogrid, IGN, IGP, swisstopo, and the GIS User Community; inset basemap sources: Esri, DeLorme, HERE, TomTom, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), swisstopo, MapmyIndia, and the GIS User Community.

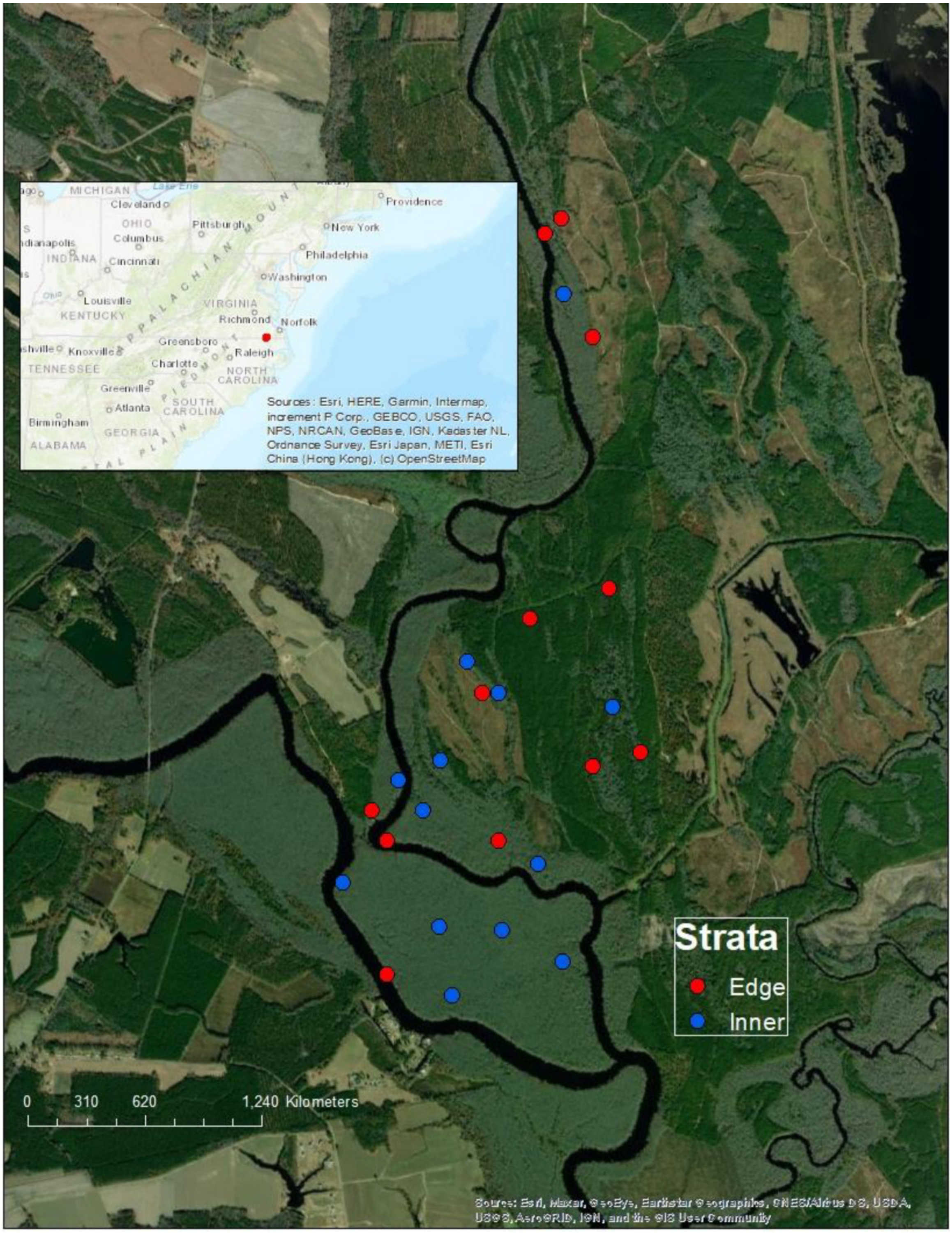

Fig. A20. Clockwise from upper left: American mistletoe, American mistletoe fruits, American mistletoe habit at edge of forested wetland, American mistletoe habit in urban habitat, germinated American mistletoe seeds affixed with glue, and germinated American mistletoe seeds affixed with natural viscin.

Fig. A21. Plastic tubs containing potted host tree saplings exposed to flood regime treatments; water level in tub pictured at left maintained near soil surface continuously, water level in tub pictured at center made to alternate between 2 week intervals of continuous flooding as described previously and 2 week intervals with natural precipitation as the sole water source, and water from natural precipitation into the tub pictured at right allowed to drain naturally.

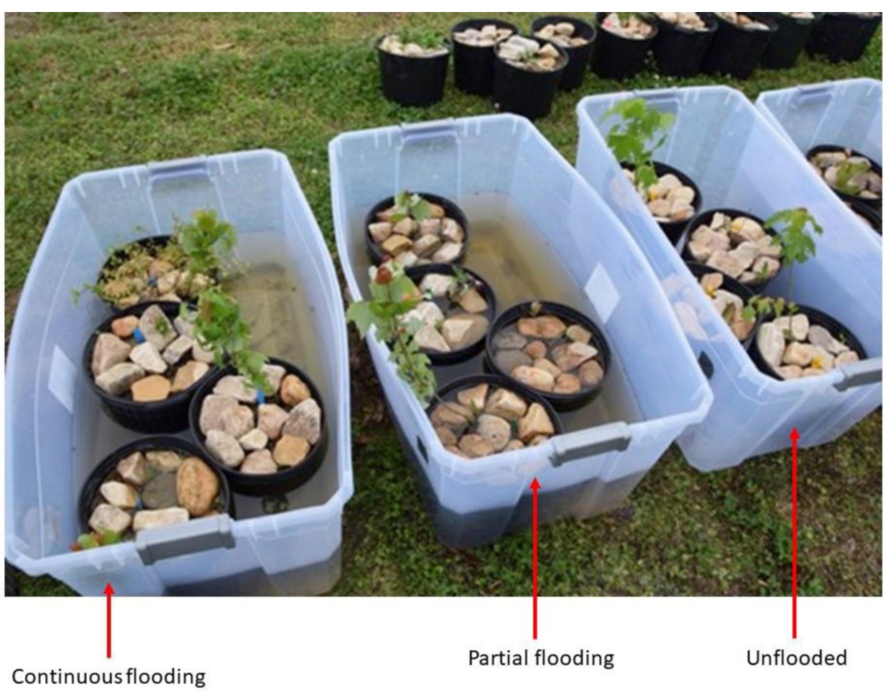

Fig. A22. Translucent tulle, 73% shade cloth, and broadcloth coverings used to manipulate local light availability for American mistletoe seedlings on potted host saplings.

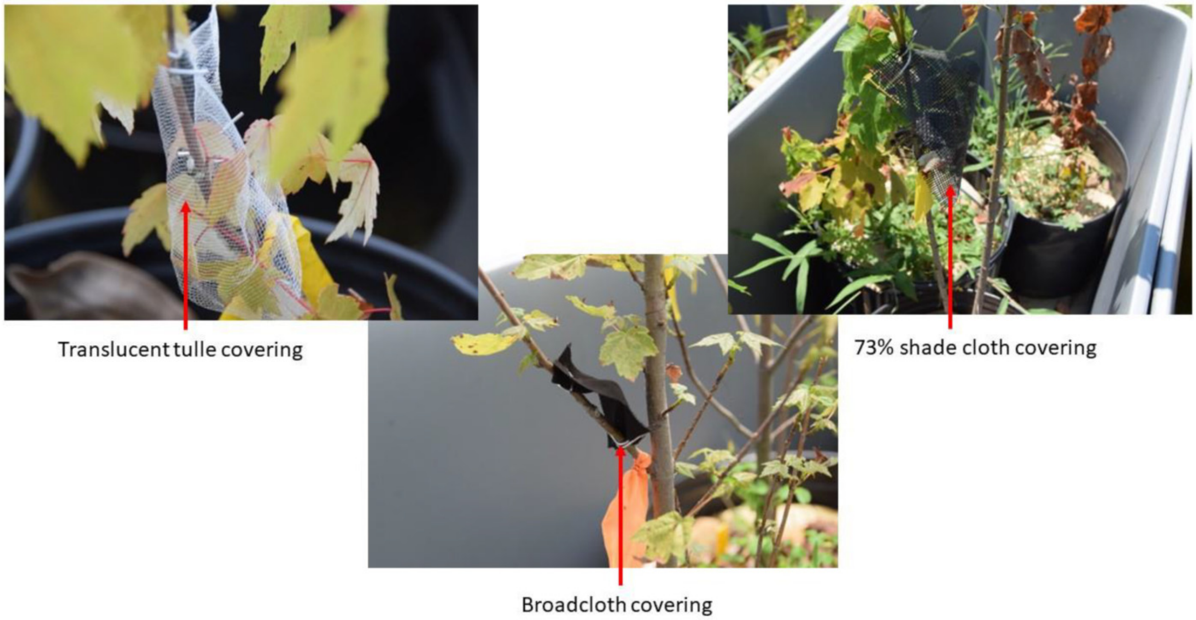

Fig. A23. Diagram of controlled planting experiment of American mistletoe seeds on potted host saplings; blue rectangles represent flooding treatment-specific plastic tubs, blue circles without parentheses represent potted host saplings present in each tub, blue circles with parentheses represent potted host saplings present in only some tubs, green dots represent planted American mistletoe seeds, and bracketed sets of images represent potential light availability treatments from which one was selected at random per suitable host sapling and applied to all germinated mistletoe seeds present.

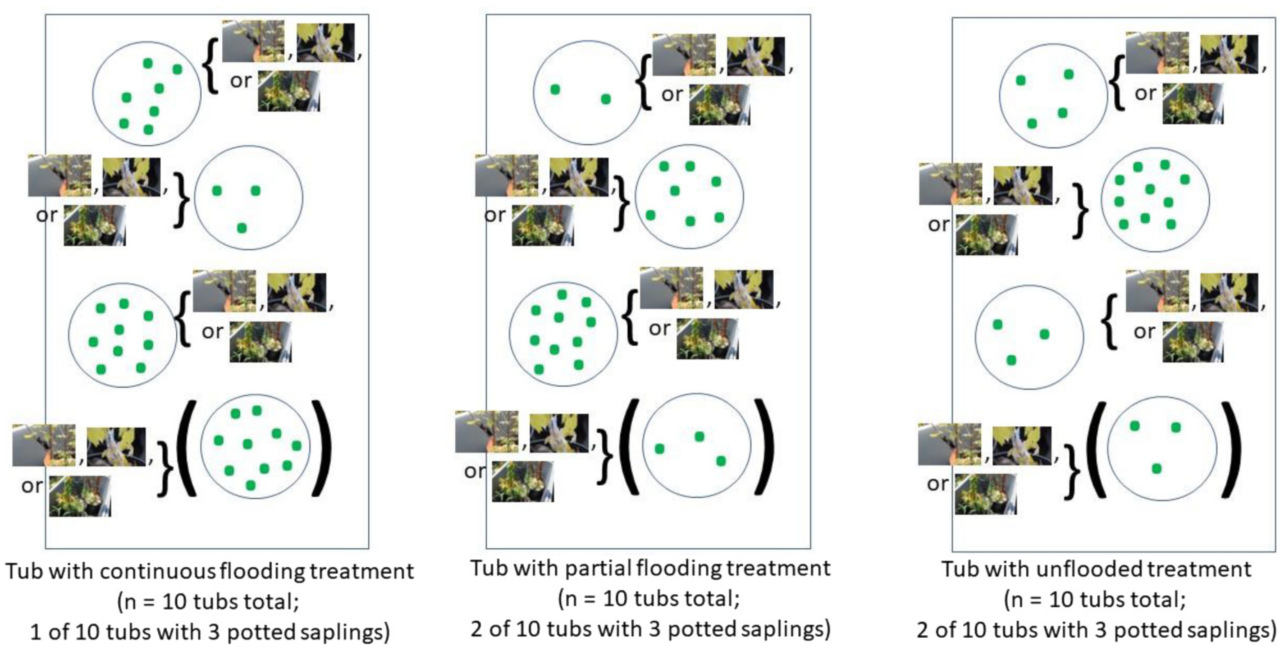

Fig. A24. American mistletoe seedlings planted on red maple hosts.

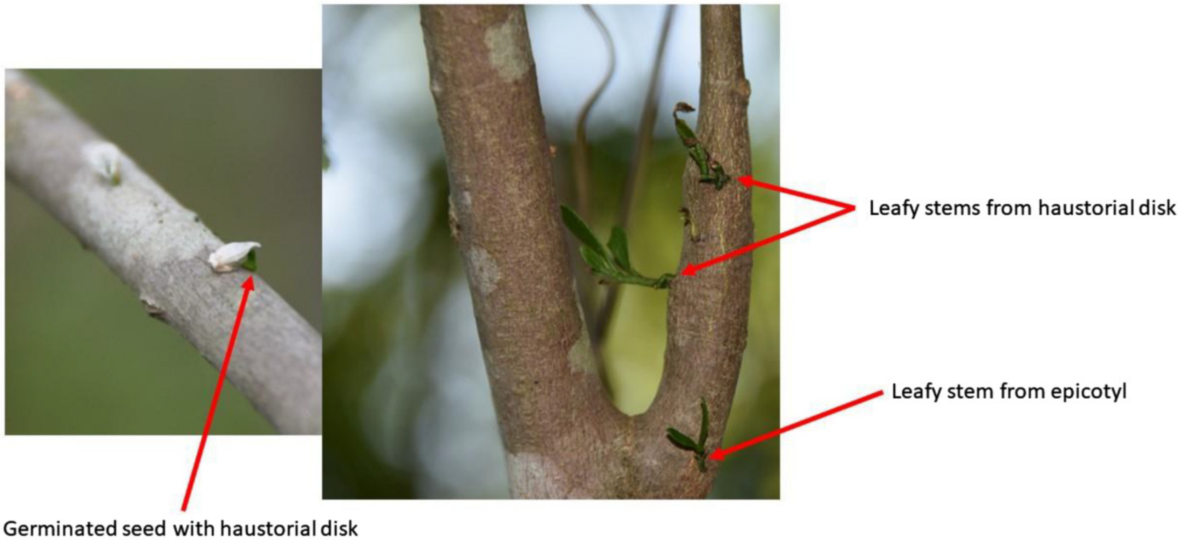

Fig. A25. Model-averaged predictions of proportions of American mistletoe seeds remaining approximately 3 months after planting across two alternative planting methods; error bars represent 95% confidence intervals.

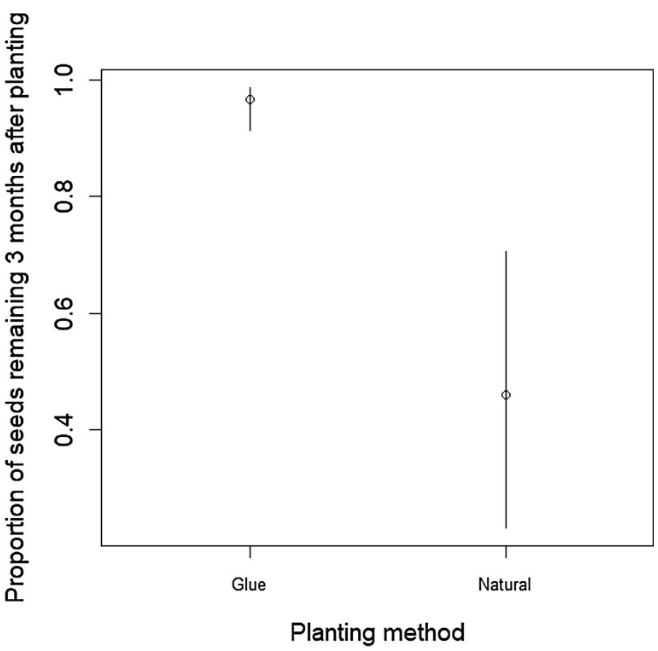

Fig. A26. Model-averaged predictions of American mistletoe germination rates across two alternative planting methods; error bars represent 95% confidence intervals.

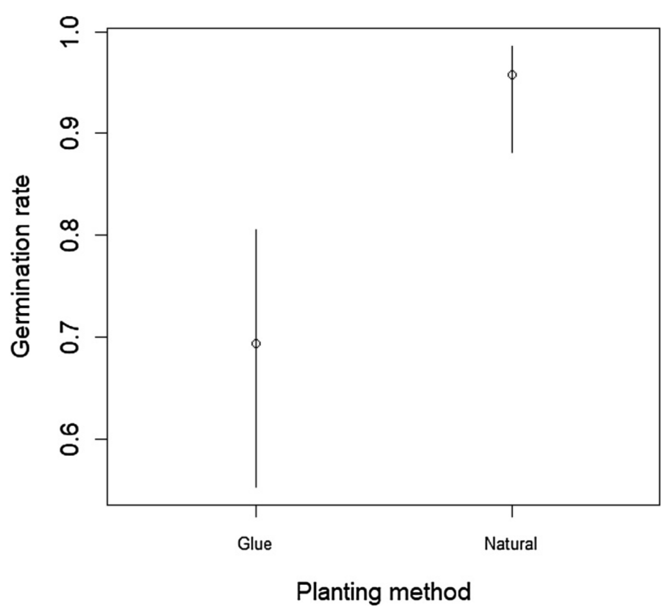

Table A1. List of shrub species commonly encountered in subplots but typically not recorded.

Woody plant taxa encountered but not typically recorded in subplots because considered shrubs
Aronia arbutifolia L. Persoon (Rosaceae)
Baccharis halimifolia L. (Asteraceae)
Clethra alnifolia L. (Clethraceae)
Cornus L. spp. other than *C. florida* L. (Cornaceae)
Elaeagnus L. spp. (Elaeagnaceae)
Eubotrys racemosus (L.) Nuttall (Ericaceae)
Ilex coriacea (Pursh) Chapman (Aquifoliaceae)
Ilex glabra (L.) A. Gray (Aquifoliaceae)
Ilex laevigata (Pursh) A. Gray (Aquifoliaceae)
Itea virginica L. (Iteaceae)
Lindera benzoin (L.) Blume (Lauraceae)
Lyonia ligustrina (L.) de Candolle (Ericaceae)
Lyonia lucida (Lamarck) K. Koche (Ericaceae)
Morella caroliniensis (P. Miller) Small (Myricaceae)
Rhododendron viscosum (L.) Torrey (Ericaceae)
Rosa L. spp. (Rosaceae)
Vaccinium L. spp. other than *V. arborea* Marshall (Ericaceae)
Viburnum L. spp. (Viburnaceae)

Table A2. Distribution of American mistletoe seeds planted at field plots across 11 host species and genera.

Species of tree selected for mistletoe seed sowing	Number of mistletoe seeds sowed
Acer rubrum L. (Aceraceae)	765
Nyssa biflora Walter (Nyssaceae)	140
Fraxinus L. spp. (Oleaceae)	85
Liquidambar styraciflua L. (Altingiaceae)	25
Nyssa aquatica L. (Nyssaceae)	25
Nyssa sylvatica Marshall (Nyssaceae)	20
Quercus nigra L. (Fagaceae)	10
Alnus serrulate (Aiton) Willdenow (Betulaceae)	5
Diospyros virginiana L. (Ebenaceae)	5
Oxydendrum arboreum (L.) de Candolle (Ericaceae)	5
Styrax americanus Lamarck (Styracaceae)	5

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Table A3. Species and genera of trees detected in subplots.

Sub-plot trees identified to species
Acer floridanum (Chapman) Pax (Aceraceae)
Acer negundo L. (Aceraceae)
Acer rubrum L. (Aceraceae)
Ailanthus altissima (P. Miller) Swingle (Simaroubaceae)
Alnus serrulata (Aiton) Willdenow (Betulaceae)
Amelanchier canadensis (L.) Medikus (Rosaceae)
Aralia spinosa L. (Araliaceae)
Asimina triloba (L.) Dunal (Annonaceae)
Betula nigra L. (Betulaceae)
Carpinus caroliniana Walter (Betulaceae)
Carya cordiformis (Wangenheim) K. Koch (Juglandaceae)
Carya glabra (P. Miller) Sweet (Juglandaceae)
Carya pallida (Ashe) Engler & Graebner (Juglandaceae)
Cephalanthus occidentalis L. (Rubiaceae)
Cercis canadensis L. (Fabaceae)
Chamaecyparis thyoides (L.) Britton, Sterns, & Poggenburg (Cupressaceae)
Cornus florida L. (Cornaceae)
Cyrilla racemiflora L. (Cyrillaceae)
Diospyros virginiana L. (Ebenaceae)
Euonymus americana L. (Celastraceae)
Fagus grandifolia Ehrhart (Fagaceae)
Fraxinus americana L. (Oleaceae)
Fraxinus caroliniana P. Miller (Oleaceae)
Fraxinus pennsylvanica Marshall (Oleaceae)
Fraxinus profunda (Bush) Bush (Oleaceae)
Gordonia lasianthus (L.) Ellis (Theaceae)
Ilex decidua Walter (Aquifoliaceae)
Ilex myrtifolia Walter (Aquifoliaceae)
Ilex opaca Aiton (Aquifoliaceae)
Ilex verticillata (L.) A. Gray (Aquifoliaceae)
Ilex vomitoria Aiton (Aquifoliaceae)
Juglans nigra L. (Juglandaceae)
Juniperus virginiana L. (Cupressaceae)
Kalmia latifolia L. (Ericaceae)
Ligustrum sinense Loureiro (Oleaceae)
Liquidambar styraciflua L. (Altingiaceae)
Liriodendron tulipifera L. (Magnoliaceae)
Magnolia acuminata (L.) L. (Magnoliaceae)
Magnolia virginiana L. (Magnoliaceae)
Morella cerifera (L.) Small (Myricaceae)
Nyssa aquatica L. (Nyssaceae)
Nyssa biflora Walter (Nyssaceae)
Nyssa sylvatica Marshall (Nyssaceae)
Ostrya virginiana (P. Miller) K. Koch (Betulaceae)
Oxydendrum arboreum (L.) de Candolle (Ericaceae)
Persea palustris Rafinesque (Lauraceae)

Table A3. (*concluded*).

Sub-plot trees identified to species
Pinus echinata P. Miller (Pinaceae)
Pinus palustris P. Miller (Pinaceae)
Pinus serotina Michaux (Pinaceae)
Pinus taeda L. (Pinaceae)
Pinus virginiana P. Miller (Pinaceae)
Platanus occidentalis L. (Platanaceae)
Populus heterophylla L. (Salicaceae)
Prunus serotina Ehrhart (Rosaceae)
Quercus alba L. (Fagaceae)
Quercus coccinea Muenchhausen (Fagaceae)
Quercus falcata Michaux (Fagaceae)
Quercus incana Bartram (Fagaceae)
Quercus laurifolia Michaux (Fagaceae)
Quercus michauxii Nuttall (Fagaceae)
Quercus montana Willdenow (Fagaceae)
Quercus nigra L. (Fagaceae)
Quercus phellos L. (Fagaceae)
Quercus rubra L. (Fagaceae)
Quercus velutina Lamarck (Fagaceae)
Quercus virginiana P. Miller (Fagaceae)
Rhododendron maximum L. (Ericaceae)
Rhus copallinum L. (Anacardiaceae)
Sassafras albidum (Nuttall) Nees (Lauraceae)
Stewartia malacodendron L. (Theaceae)
Styrax americanus Lamarck (Styracaceae)
Symplocos tinctoria (L.) L'Heritier (Symplocaceae)
Taxodium distichum (L.) L.C. Richard (Cupressaceae)
Toxicodendron vernix (L.) Kuntze (Anacardiaceae)
Ulmus alata Michaux (Ulmaceae)
Ulmus americana L. (Ulmaceae)
Sub-plot trees identified to taxa higher than species
Carya Nutt. spp. (Juglandaceae)
Chamaecyparis thyoides (L.) Britton, Sterns, & Poggenburg/*Juniperus virginiana* L. (Cupressaceae)
Fraxinus americana L./*pennsylvanica* Marshall (Oleaceae)
Fraxinus caroliniana P. Miller/*pennsylvanica* Marshall/*profunda* (Bush) Bush (Oleaceae)
Fraxinus L. spp. (Oleaceae)
Ilex verticillata (L.) A. Gray/*laevigata* (Pursh) A. Gray (Aquifoliaceae)
Morus L. spp. (Moraceae)
Pinus taeda L./*serotina* Michaux (Pinaceae)
Pinus virginiana P. Miller/*echinata* P. Miller (Pinaceae)
Quercus (*Lobatae* sub-genus) Loudon spp. (Fagaceae)
Quercus (*Quercus* sub-genus) L. spp. (Fagaceae)
Quercus L. spp. (Fagaceae)
Ulmus L. spp. (Ulmaceae)

Table A4. Alternative generalized linear models for the relationships between the proportion of American mistletoe seeds remaining approximately 3 months after planting and the fixed effects of planting method and branch diameter as ranked by AIC. All models included the fixed effect of site (Great Dismal Swamp National Wildlife Refuge versus South Quay Sandhills Natural Area Preserve) and the random effects of plot and nested branch identities.

Variables included in model	*K*	AIC_c	ΔAIC_c	AIC_c weight	Cumulative weight
Site + planting method	5	1011.2	0	0.73	0.73
Site + planting method + branch diameter	6	1013.22	2.02	0.27	1
Site (null)	4	1064.1	52.89	0	1
Site + branch diameter	5	1065.27	54.06	0	1

Table A5. Alternative generalized linear models for the relationships between American mistletoe seed germination rates and the fixed effects of planting method, year of planting, and % canopy openness as ranked by AIC. All models included the random effect of branch identity.

Variables included in model	*K*	AIC_c	ΔAIC_c	AIC_c weight	Cumulative weight
Intercept + planting method + year	5	701.06	0	1	1
Intercept + year	4	713.96	12.9	0	1
Intercept + year + light	5	715.3	14.24	0	1
Intercept + planting method	3	754.78	53.72	0	1
Intercept + planting method + light	4	756.8	55.74	0	1
Intercept (null)	2	765.3	64.25	0	1
Intercept + light	3	767.26	66.2	0	1

Table A6. Alternative generalized linear models for the relationship between American mistletoe seed germination rates and the fixed effect of flood regime treatments as ranked by AIC. All models included the random effects of plastic tub and nested sapling identities.

Variables included in model	*K*	AIC_c	ΔAIC_c	AIC_c weight	Cumulative weight
Intercept (null)	3	248.13	0	0.87	0.87
Intercept + flooding	5	251.97	3.84	0.13	1