THE INFLUENCES OF DISPERSER BEHAVIOR, HOST AVAILABILITY, AND ENVIRONMENTAL CONDITIONS ON THE DISTRIBUTION OF OAK MISTLETOE [*PHORADENDRON LEUCARPUM* (RAF.) REVEAL & M. C. JOHNST.] IN EASTERN VIRGINIA AND NORTH CAROLINA

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ABSTRACT

THE INFLUENCES OF DISPERSER BEHAVIOR, HOST AVAILABILITY, AND ENVIRONMENTAL CONDITIONS ON THE DISTRIBUTION OF OAK MISTLETOE [*PHORADENDRON LEUCARPUM* (RAF.) REVEAL & M. C. JOHNST.] IN EASTERN VIRGINIA AND NORTH CAROLINA

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Mistletoes are shrubs that typically parasitize the branches of host trees and rely on avian frugivores for seed dispersal. Because mistletoes are restricted to a narrow range of suitable recruitment sites and avian frugivores are more visible than other guilds of seed dispersers, mistletoe-frugivore systems afford opportunities for assessing the roles of dispersal limitation and local environment in determining plant distribution. These mechanisms have been proposed as determinants of the observed association of oak mistletoe [*Phoradendron leucarpum* (Raf.) Reveal & M. C. Johnst.] with forested wetlands in eastern Virginia and North Carolina, USA. I tested the alternative hypothesis that variation in host availability drives this habitat relationship, instead finding a significant positive effect of forested wetland habitat on oak mistletoe occurrence after correcting for differences in host availability.

I used a community occupancy model to analyze avian occurrence data and estimate species-specific relationships between disperser occurrence and forested habitat type. I did not find statistically significant relationships between occurrence and forested wetland habitat for either of the two principal dispersers of oak mistletoe in the study area, the eastern bluebird (*Sialia sialis*) and cedar waxwing (*Bombycilla cedrorum*). While these results suggested avian dispersers to be more widespread with regards to habitat type than oak mistletoe, the potential remained for these species to show cryptic habitat specificity. As such, I looked at patterns of oak mistletoe genetic structure versus habitat type. Analyses showed evidence for gene flow across habitat types and the presence of a genetically distinct population of oak mistletoes restricted to hosts in the genus *Nyssa* L.

I used seed sowing experiments to quantify the roles of light availability and flood regime in determining the initial survival of oak mistletoe. These experiments allowed me to evaluate the potential for establishment limitation to determine variation in oak mistletoe occurrence across different forested habitats. I found support for

a relationship between manipulated local light availability conditions and seedling establishment rates. Variation in oak mistletoe establishment success across forested habitat types is a potentially important mechanism in determining observed habitat relationships in oak mistletoe.

I would like to dedicate this work to those of the past, present, and future
who share my love of the natural history of the southeastern United States.

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CHAPTER 1

INTRODUCTION

1.1 RATIONALE

Parasites have historically been neglected in some fields of ecology (Mittelbach 2012), but predictive theories on the spatial distribution of parasite populations have emerged from a substantial body of research (Poulin 2007). The mechanisms driving these patterns continue to draw the interest of researchers. Recent studies have attempted to explain the predictably aggregated spatial distribution of parasite populations using information on variation among hosts in their vulnerability to infection (Hernandez & Sukhdeo 2008, MacIntosh et al. 2010). Researchers viewing populations as metapopulations have also given attention to the influence of dispersal limitations on parasite distributions (Poulin 2007), with variation in dispersal rates and distances largely attributed to variation in host behavior (Blouin et al. 1995, Criscione & Blouin 2004). Due to the visibility of mistletoes and their dispersers, mistletoe-frugivore systems offer excellent opportunities for testing the generality of these and other mechanisms proposed as determinants of parasite distributions (Aukema 2003).

The mistletoe habit of being an obligate hemiparasitic shrub infecting host stems and branches has arisen independently in five different lineages within the plant order Santalales (Vidal-Russell & Nickrent 2008). As parasites, mistletoes exert a negative influence on host trees, acquiring water and nutrients from host xylem and in some cases photosynthates from host phloem (Bennetts et al. 1996, Norton & Carpenter 1998). When a tree species of economic importance is parasitized, information on mistletoe distribution and dispersal can be important for scientists and managers interested in mistletoe control (Bennetts et al. 1996, Gougherty 2013). Often, however, the negative effects of mistletoe on hosts are minor and overshadowed by the positive effects of mistletoes in ecological communities; relationships between mistletoes and both frugivores and pollinators can be considered mutualistic (Bennetts et al. 1996, Aukema 2003, 2004, Dickinson & McGowan 2005, Mellado & Zamora 2014b).

Here I used field surveys and planting experiments to examine the influences of avian frugivore behavior, host tree abundance, and environmental conditions on the distribution of oak mistletoe [*Phoradendron leucarpum* (Raf.) Reveal and M.C. Johnst.], a widely distributed mistletoe species in the family Viscaceae that is obligately dispersed by generalist avian frugivores (Panvini 1991, Reid 1991). The use of population genetics analyses for estimating gene flow among mistletoe populations was used to inform avian disperser behavior and habitat use. This work was conducted in the Coastal Plain and Piedmont regions of Virginia and North Carolina, a portion of the range of oak mistletoe where little formal work has been done on mistletoe ecology (Gougherty 2013, but see Baldwin Jr. & Speese 1957). I was especially interested in determining the relative importance of potential drivers of a mistletoe habitat relationship in the study area; this aspect of mistletoe distribution was here defined as variation in mistletoe occurrence across different forested habitat types.

1.2 MISTLETOE HOST ASSOCIATIONS

Some mistletoe species appear to be generalists in terms of host tree specialization when viewed across their entire range, but at the population-level relatively few tree species are parasitized (May 1971, Clay et al. 1985, Norton & Carpenter 1998, Aukema 2003, Mellado & Zamora 2014b). With the primary host tree species parasitized by a given mistletoe population often being the most common potential host at that location (Mellado & Zamora 2014b), the existence of mistletoe "host races" that are adapted to the locally preferred host species has been suggested (Clay et al. 1985, Panvini 1991). In many cases it is still unclear whether local host tree specialization is due primarily to physical or biochemical interactions between mistletoes and hosts (Mellado & Zamora 2014b), avian frugivore behavior (Norton & Carpenter 1998), or variation in susceptibility of host tree populations to infection (May 1971, Panvini 1991, Sallé et al. 1993, Mellado & Zamora 2014b).

The distribution of host trees has been found to be the most influential factor determining observed mistletoe habitat relationships in some systems (Gougherty 2013, Lira-Noriega and Peterson 2014). Host tree availability has been proposed to be responsible for the positive association between oak mistletoe and forested wetlands in the southeastern US (Weakley 2012). Quantifying host availability to test this hypothesis using field data required the identification of potential host trees; regional variation in the diversity of host species parasitized by oak mistletoe, along with host size, must be considered when making these identifications (Kuijt 2003). Studies documenting oak mistletoe host associations in the field did not account for variation in habitat type at sites hosting mistletoe (Reed & Reed 1951, Hemmerly et al. 1979, Rucker & Hemmerly 1976, Brown & Hemmerly 1979), yet interactions could exist between habitat type and potential determinants of these associations (Clay et al. 1985, Norton & Carpenter 1998, Aukema 2004).

1.3 MISTLETOE DISTRIBUTIONS

Numerous studies have found mistletoes to show clumped spatial distributions at the individual tree level (i.e. some individual trees with much higher infection rates than others; Panvini 1991, Martínez del Rio et al. 1996, Aukema & Martínez del Rio 2002, Aukema 2003, Gougherty 2013) and at larger spatial scales, such as among patches of forested habitat (Martínez del Rio et al. 1996, Aukema & Martínez del Rio 2002, Aukema 2003, 2004). Various factors may make some individual host trees more vulnerable to mistletoe infections than others (May 1971, Aukema & Martínez del Rio 2002, Kuijt 2003, Lira-Noriega & Peterson 2014, Mellado & Zamora 2014b). Mistletoe aggregations at various spatial levels have largely been attributed to a positive feedback mechanism where disperser frugivores are attracted to those trees or patches that are already infected with mistletoe and disperse seeds to nearby sites (Martínez del Rio et al. 1996, Aukema & Martínez del Rio 2002, Aukema 2003, 2004, Carlo & Aukema 2005, Thompson & Poindexterss 2005). Specialist frugivores have usually been implicated in such mechanisms, while generalist frugivores could also contribute to positive feedback processes (Mellado & Zamora 2014a). Mistletoes have been found to be clumped spatially at the within-tree level (Mellado & Zamora 2014a), and results from planting experiments suggest environmental conditions, branch thickness, and seed predation limit potential recruitment sites and cause frugivore species to have varying efficiencies as dispersers due to behavioral differences (Mellado & Zamora 2014b).

Even with the relatively high visibility of many mistletoes and their dispersers, the relative importance of environmental conditions, avian frugivore habitat relationships, and host tree availability in determining mistletoe distributions at scales larger than the within-tree or individual tree levels remains unclear in many cases (Panvini 1991, Aukema 2004). Many studies maintain the importance of considering host tree abundance and distribution when studying mistletoe distributions (Panvini 1991, Aukema 2003, 2004, Kuijt 2003, Thompson & Poindexterss 2005, Gougherty 2013, Lira-Noriega & Peterson 2014, Mellado & Zamora 2014b). Correlations between distributions of mistletoes and their avian frugivores led researchers to cite habitat choices of birds as another potentially determinant factor (Panvini 1991, Martínez del Rio et al. 1996, Aukema 2004, Lira-Noriega & Peterson 2014).

Relationships between mistletoe distributions and those of their avian dispersers may be functions of bird movement patterns, or alternatively, could be attributed to frugivores being attracted to sites that contain mistletoe fruits (Martínez del Rio et al. 1996, Lira-Noriega & Peterson 2014). If birds are driving mistletoe distributions, then other factors that determine the distributions of avian frugivores should also explain spatial patterns of mistletoe infections (Martínez del Rio et al. 1996, Lira-Noriega & Peterson 2014, Mellado & Zamora 2014b). Such a process has been suggested to be responsible for high rates of mistletoe infections in some urban areas (Gougherty 2013). Bird behavior has been cited as being responsible for mistletoe distribution patterns at the individual tree level, with higher infection rates on taller trees (Martínez del Rio et al. 1996, Aukema & Martínez del Rio 2002, Aukema 2003, Carlo & Aukema 2005, Mellado & Zamora 2014b) and female individuals in dioecious species (van Ommeren & Whitham 2002, Aukema 2003, Carlo & Aukema 2005) mirroring expected patterns in generalist frugivore behavior. Increased tree age has been cited as an alternative reason for higher infection rates on taller trees (Gougherty 2013).

Oak mistletoe is light-demanding (Panvini 1991, Mellado & Zamora 2014b) and most common in forest edge habitats. The affinity of oak mistletoe for forested wetland habitat in the study area could be driven by consistent differences in host tree quality due to local environmental conditions. Photosensitivity of oak mistletoe seeds with respect to germination was found in laboratory trials in the early 20th century (Gardner 1921), with light later proposed as an influential factor in determining observed spatial distribution patterns in this species (Eleuterius 1976). More recent work involved planting oak mistletoe seedlings in the field and maintained light availability as critical for seedling establishment (Randle et al. 2018). My work aimed to examine the generality of this result and the relative importance of light compared to other factors in determining oak mistletoe distributions.

1.4 MISTLETOE DISPERSAL BY AVIAN FRUGIVORES

As recruitment limitations are important drivers of various metrics in plant communities, seed dispersal is an important process in plant community ecology (Howe & Smallwood 1982, Tilman 1997, Wenny & Levey 1998, Norton & Carpenter 1998, Webb & Peart 2001, Wang & Smith 2002, Aukema 2003, Carlo & Aukema 2005). For plant species with very restricted suitable establishment sites, such as mistletoes, directed dispersal by frugivores can be especially important (Wenny & Levey 1998, Carlo & Aukema 2005). Primary seed dispersal, such as that accomplished by avian frugivores in mistletoe dispersal systems, is one process among many in the seed dispersal cycle (Howe & Smallwood 1982, Wang & Smith 2002). Other processes such as secondary seed dispersal, the post-dispersal movement of seeds, and seed predation can also be important for plant recruitment (Wang & Smith 2002, Mellado & Zamora 2014b) and are often confounded with primary seed dispersal when current plant distributions are used to make inference about the overall seed dispersal cycle.

The avian frugivore species essential for dispersing seeds of many mistletoe species are often classified as either specialists or generalists. Specialists depend on mistletoe fruits as the major portion of their diet for much of the year, while generalists feed on mistletoe fruits for only a portion of the year (Reid 1991, Aukema & Martínez del Rio 2002, Dickinson & McGowan 2005, Weinkam 2013) or in only some portions of their range (Reid 1991); many species may fall somewhere in between the two categories (Reid 1991, Aukema 2003). Mistletoe species in northern temperate areas often completely lack specialized frugivores in their local avifauna (Reid 1991, Mellado & Zamora 2014a) and mistletoe populations in these regions must rely on generalist frugivores for dispersal (Mellado & Zamora 2014a). Indeed, generalist frugivores have often been cited as being primarily responsible for starting new infections as they are more prone to foraging in uninfected trees and patches than are specialists (Martínez del Rio et al. 1996, Aukema & Martínez del Rio 2002, Aukema 2003, 2004, Carlo & Aukema 2005, Thompson & Poindexterss 2005). By starting new mistletoe infections some generalist frugivores may expand the foraging opportunities of mistletoe specialists (Carlo & Aukema 2005). While the importance of mistletoes as resources for specialist frugivorous species with diets composed primarily of mistletoe fruits is obvious, less is known about the importance of mistletoe fruits to generalist frugivore species (Mellado & Zamora 2014a). The importance of mistletoe fruits in generalist frugivore diets may vary among years due to variation in crops of mistletoe fruits and crops of other food resources (van Ommeren & Whitham 2002, Weinkam 2013).

Seeds of most mistletoes are covered in a material called viscin that adheres to host branches after seeds are defecated by avian frugivores or dispersed by birds via other external mechanisms, such as bill-wiping (Panvini 1991, Reid 1991, Aukema 2003, 2004, Mellado & Zamora 2014b). Seeds of the mistletoe species *Viscum album* and likely other generalist-dispersed mistletoe species do not require ingestion to germinate and establish, expanding the diversity of potential avian dispersers (Mellado & Zamora 2014a). Numerous studies have shown that rates of mistletoe seedling establishment are highest on host branches or portions of branches that are thinner in diameter (Reid 1991, Norton & Carpenter 1998, Mellado & Zamora 2014a, Mellado & Zamora 2014b), making certain disperser agents, especially smaller species that perch on thin branches, more effective at successful mistletoe dispersal than others (Reid 1991, Mellado & Zamora 2014a).

Frugivores have mutualistic relationships with plant species when seed dispersal is accomplished and seedlings successfully recruit into plant populations (van Ommeren & Whitham 2002, Aukema 2003, Mellado & Zamora 2014a). In mistletoe-frugivore systems the benefits to mistletoes are obvious, with directed dispersal to specific recruitment sites (Howe & Smallwood 1982, Norton & Carpenter 1998, Aukema & Martínez del Rio 2002, Aukema 2003) and long-distance gene flow (Panvini 1991) accomplished by avian dispersers. Many studies have found mistletoe abundance to be a strong predictor of frugivore distributions (Martínez del Rio et al. 1996, Aukema & Martínez del Rio 2002, van Ommeren & Whitham 2002, Aukema 2003, Lira-Noriega & Peterson 2014), suggesting the importance of mistletoe fruits to frugivores as a food source. Removal experiments have provided even stronger evidence of the importance of mistletoe fruits to avian dispersers. At the individual tree level, mistletoe removal caused reduced seed rain, presumable due to lower foraging rates by specialist frugivores (Aukema & Martínez del Rio 2002). Fruits of the mistletoe *P. villosum* are a very important winter food resource for the western bluebird (*Sialia mexicana*), a generalist frugivore. Removal of *P. villosum* shrubs at the scale of western bluebird winter territories caused changes in the formation and behavior of western bluebird social groups (Dickinson & McGowan 2005). An understanding of mechanisms determining mistletoe distributions could aid managers interested in maintaining this resource for avian frugivores (Renne et al. 2001).

As an evergreen species, oak mistletoe shows prominently among the branches of its deciduous tree hosts in the winter landscape of the southeastern US. This visibility is likely an advantageous trait given the importance of frugivorous birds to the dispersal of oak mistletoe (Sutton 1951, Gougherty 2013). I assumed two generalist avian frugivores known to include oak mistletoe fruits as substantial portions of their winter diet, the cedar waxwing (*Bombycilla cedrorum*; Sutton 1951, Eleuterius 1976) and eastern bluebird (*Sialia sialis*; Weinkam 2013), to be the primary dispersers of mistletoe seeds in the study area. I then quantified relationships between distributions of this mistletoe and these focal frugivore species (Panvini 1991, Martínez del Rio et al. 1996, Gougherty 2013).

1.5 METHODOLOGICAL JUSTIFICATIONS

When analyzing data from field surveys for plants or animals, failure to account for imperfect detection probability can bias estimates of species distributions and covariate relationships (MacKenzie et al. 2002, Tyre et al. 2003, Kéry et al 2008, Ruiz-Gutiérrez et al. 2010). Occupancy models (MacKenzie et al. 2002) are a popular way to estimate species distributions and covariate relationships using presence-absence data from repeated field surveys while accounting for imperfect detection. I used this approach to estimate relationships between avian frugivore occurrence and forested habitat type using point count data.

Even with evidence from occupancy models suggesting co-occurrence between two species, experimental studies provide much stronger evidence for species interactions than field survey data (James & McCulloch 1985, MacKenzie et al. 2004, Bailey et al. 2009, Richmond et al. 2010). Researchers studying mistletoe distribution have used seed sowing experiments (Clay et al. 1985, Mellado & Zamora 2014b) and quasi-experiments (Mellado & Zamora 2014a, Mellado & Zamora 2014b) to look at the effects of host tree species and environmental conditions on mistletoe germination and establishment success. Here I used quasi-experimental and experimental seed sowing methods to confirm results suggested by field survey data and occupancy models. I know of few other mistletoe studies that combine both observational and experimental approaches (Aukema & Martínez del Rio 2002, Mellado & Zamora 2014a).

Panvini (1991) suggested bird behavior as a potential mechanism limiting gene flow among oak mistletoe populations. I hypothesized that habitat specialization exhibited by populations or species of mistletoe dispersers in the study area would produce genetic structure among mistletoe populations. To test this hypothesis, I used microsatellite markers to examine fine-scale genetic differentiation across oak mistletoe populations occupying different habitat types.

CHAPTER 2

THE ROLE OF HOST AVAILABILITY IN DETERMINING THE DISTRIBUTION OF OAK MISTLETOE [*PHORADENDRON LEUCARPUM* (RAF.) REVEAL & M. C. JOHNST.] ACROSS POTENTIAL HOST TREE SPECIES AND HABITAT TYPES IN EASTERN VIRGINIA AND NORTH CAROLINA

2.1 INTRODUCTION

Mistletoes are hemiparasitic shrubs that typically parasitize the branches of host trees and rely on avian frugivores for seed dispersal (Calder & Bernhardt 1983). Because most mistletoes are restricted to a narrow range of suitable recruitment sites (Overton 1994, Alexander et al. 2012, Mellado & Zamora 2014b) and avian frugivores are more visible 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 & Aukema 2005, Roxburgh 2007, Caraballo-Ortiz et al. 2017). The presence and abundance of suitable host trees must be accounted for when making inferences about factors driving mistletoe distributions (Overton 1994, Norton & Carpenter 1998, Kuijt 2003, Aukema 2004). Regional variation in host usage by mistletoes should be considered when quantifying host availability, as with parasites in general (Poulin 2005, Stanko et al. 2006).

Regional host associations

Host availability could be the most important driver of mistletoe distributions in some systems (Caraballo-Ortiz et al. 2017). Accounting for regional variation in host usage, hereafter a “regional host association”, is necessary to avoid misidentifying available trees as potential hosts. Regional host associations can collectively be viewed as a disjunction between the diversity of hosts parasitized across the range of a mistletoe species and the smaller subsets of available host species parasitized at the level of a mistletoe population (May 1971, Kuijt 2003, Caraballo-Ortiz et al. 2017, Randle et al. 2018). Factors determining regional host associations largely remain unidentified (Kuijt 2003); variation in mistletoe-host compatibility (Paine 1950, May 1971, Clay et al. 1985), avian disperser behavior (Monteiro et al. 1992, Caraballo-Ortiz et al. 2017), and the phenology of gaseous cues released by hosts (Randle et al. 2018) have been proposed as drivers of such regional variation in some systems.

The identification of the mechanisms that determine regional mistletoe host associations using empirical data requires a consideration of variation in habitat type (Clay et al. 1985, Norton & Carpenter 1998, Aukema 2004). Regional variation in parasitism of a widespread host species could be related to differences in habitats used by the host or mistletoe. Habitat-specific variation in avian disperser behavior or environmental conditions could then drive the observed lack of parasitism in certain regions.

Regardless of variation in habitat usage shown by a mistletoe or its host, regional variation in assemblages of mistletoe seed dispersers could drive differences in mistletoe host associations (Jordano 1994, Bleher & Bohning-Gaese 2001, Renne et al. 2002, Yule & Bronstein 2018). Preferences for perching and foraging in different potential host tree species could vary across mistletoe seed dispersers because of host habitat (Monteiro et al. 1992, Bennetts et al. 1996, Martínez del Rio et al. 1996, Norton & Carpenter 1998, Kuijt 2003, Lira-Noriega & Peterson 2014, Mellado & Zamora 2014b) or variation in the fleshy fruit resources offered by hosts (van Ommeren & Whitham 2002, Kuijt 2003, Carlo & Aukema 2005, Caraballo-Ortiz et al. 2017). The effect of the distribution of fruit resources other than mistletoe is especially important to consider in areas where all mistletoe dispersers are generalist frugivores (Reid 1991, Carlo 2005, Mellado & Zamora 2014a, Caraballo-Ortiz et al. 2017, Donoso et al. 2017).

In some cases, host tree usage is proportional to host availability (Kuijt 2003, Mellado & Zamora 2014b), and positive relationships between the diversity of available trees and the diversity of mistletoe hosts have been observed (Kuijt 1969, Norton & Carpenter 1998). Such patterns suggest that some regional host associations could be largely driven by random chance (Kuijt 1969). The existence of genetically distinct mistletoe populations predisposed to parasitizing the most common available host species could also drive such patterns (Clay et al. 1985, Norton & Carpenter 1998). An alternative parasite-host pattern was found by Randle et al. (2018), who showed a difference between the species composition of mistletoe hosts and overall tree diversity at one site.

Oak mistletoe habitat and host relationships

The oak mistletoe [*Phoradendron leucarpum* (Raf.) Reveal & M. C. Johnst.] is a parasitic shrub that infects stems of a variety of woody plant species across the southern United States (US; Panvini 1991, Kuijt 2003) and for which seed dispersal is mediated by avian frugivores (Sutton 1951, Panvini 1991, Gougherty 2013). In the study area of eastern Virginia and North Carolina, oak mistletoe is more common in forested wetlands of the Coastal Plain than in other forested habitats (Weakley 2012), a distributional pattern I henceforth refer to as a habitat relationship. The factors most important in determining such patterns remain unidentified (Panvini 1991, Kuijt 2003, Hawkins 2010, Gougherty 2013).

Host tree availability has been proposed to explain the relationship between oak mistletoe and forested wetlands in the southeastern US (Weakley 2012), yet some host tree species such as red maple (*Acer rubrum* L.) occur in a variety of habitats. This implies that the habitat itself may serve as a factor independent of host species availability. Oak mistletoe is likely an important resource for avian frugivores wintering in forested wetlands of the region (Watson 2001, Aukema & Martínez del Rio 2002, Dickinson & McGowan 2005, Watson & Herring 2012). Given this potential relationship, understanding the relative roles of avian behavior, host availability, and environmental conditions in maintaining its presence in forested wetlands remains important.

Regional oak mistletoe host associations have been documented with empirical data (Reed & Reed 1951, Rucker & Hemmerly 1976, Hemmerly et al. 1979, Brown & Hemmerly 1979, Randle et al. 2018), yet the relative importance of potential driving factors in maintaining these associations remain largely unexplored (Kuijt 2003, Hawkins 2010). I split the study area into host association regions based partly on observed geographic variation in parasitism of widespread host species by oak mistletoe. Both the existence of genetic host races of oak mistletoe and their potential as drivers of regional host associations in other portions of its range have been suggested by results from common garden experiments (May 1971, Clay et al. 1985). I failed to find evidence for a correlation between genetically distinct oak mistletoe populations and host association regions in the study area (Chapter 3).

Especially evident was variation in parasitism of sweetgum (*Liquidambar styraciflua* L.) across host association regions in the study area despite the ubiquitous distribution of this tree species in forested wetlands (Weakley et al. 2012). The species composition and behavior of avian frugivores can be expected to be similar in forested wetlands across the relatively small area I am studying (Hamel 1992**,** Dickson et al. 1993, Wigley & Roberts 1994, Wakeley & Roberts 1996, Tikkanen et al. 2021). If differences in frugivore characteristics do exist across the study area, such variation is unlikely to be a determinant of regional host associations; many tree species parasitized by oak mistletoe in eastern Virginia and North Carolina do not offer fleshy fruit resources to generalist avian frugivores (Weakley et al. 2012). Such resources are generally absent in winter from those host species that do bear fleshy fruits during other seasons. A list of known host species from the study area is listed in the Appendix.

Relationships between host availability and oak mistletoe distribution

Oak mistletoe habitat relationships could be explained by frugivore behavior (Lamont & Southall 1982, Martínez del Rio et al. 1996, Aukema 2004, Krasylenko et al. 2020), with variation in local environmental conditions as another potential determining factor (Eleuterius 1976, Panvini 1991, Weakley et al. 2012). Survey data on the occurrence of avian frugivores in winter across the aforementioned plots suggest that avian seed dispersers are generalists with regards to forested habitat type, pointing to local environmental conditions as the most important factor determining oak mistletoe habitat relationships (Chapter 3). Here I tested the alternative hypothesis that such habitat relationships are explained by host tree availability (Gougherty 2013, Lira-Noriega and Peterson 2014). Unlike other studies of the relationship between host abundance and mistletoe occurrence, I acknowledged the existence of regional host associations and used region-specific lists of known host species when quantifying host availability. I also tested the importance of host availability as an alternative to other potential drivers of regional variation in parasitism of sweetgum by oak mistletoe.

2.2 METHODS

Oak mistletoe habitat relationships

I selected 96 circular plots with 25-m radii to survey for the presence or absence of oak mistletoe during one of five winters (Dec–Mar) from 2015–2020 (Fig. 1). I surveyed in winter when deciduous trees were leafless to maximize detection rates of the evergreen mistletoe shrubs. These plots were selected in the Coastal Plain and Piedmont of Virginia and North Carolina (NC) 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 oak mistletoe within each plot was 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 the imperfect detection of mistletoe at plots (Fadini & Cintra 2015, Caraballo-Ortiz et al. 2017).

I collected data on tree stems present within sub-plots to quantify host availability. All stems of tree species present within a 10 m x 10 m square sub-plot centered on the central point of each 25-m radius circular plot were identified to the species or genus level 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 oak mistletoe hosts in the study area and those such species commonly encountered are listed in the Appendix.

Sub-plot 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 oak mistletoe is rare or absent. Maps depicting the parasitism of 17 taxa that show more widespread occurrence in sub-plot data are provided in the Appendix. First, all plots were placed into 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 NC and as defined in Weakley et al. (2012). I expected these three regions to be related with geographic host associations as they are with plant community composition (Weakley et al. 2012), and to account for additional host association regions apparent in survey data (e.g. variation in parasitism of *Carya* spp.) I further split the inner Coastal Plain into two regions: one region from the James River watershed north and one region south of this watershed. Finally, the portions of both the inner and outer Coastal Plains within the Cape Fear and Lumber River watersheds in the southeastern section of the study area, hereafter referred to as the southeastern region, were split into a fifth region to account for a seemingly sharp shift in parasitism rates of the widespread tree sweetgum.

Species of potential host stems selected from sub-plot data were only those found to serve as hosts in the region containing the sub-plot. 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 parasitized trees at regional sites selected ad hoc in forested habitats; a total of 125 such sites were established across the study area (Fig. 2). Due to the scarcity of mistletoe in forested habitats near the northern edge of my study area, I included such data from two sites in southeastern Maryland. Basal area (BA) in m^2ha^{-1} for each region-specific potential host species was calculated and summed for each sub-plot 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 tree BA on mistletoe occurrence. Potential host tree BA was normalized to allow easy interpretation of the effect of habitat type after accounting for host tree availability. I used the 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 3 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 & 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).

Oak mistletoe host associations

To compare species-specific frequencies of infected trees to those frequencies expected if oak mistletoe was distributed across potential host tree species at random, I used a chi-square goodness-of-fit test with the function chisq.test in R (Caraballo-Ortiz et al. 2017; R Core Team 2021). Expected species-specific frequencies of infected trees were weighted by the proportion of BA each species represented in my survey of available hosts. To ensure expected frequencies were high enough I only included data on the 25 species with the highest BA.

I used the observed regional mistletoe-host association between oak mistletoe and sweetgum to examine the influence of host availability on such regional patterns. Sweetgum is widespread with regards to habitat and geography across the study area (Weakley et al. 2012) and individuals infected with oak mistletoe were frequently detected in a variety of forest types in the southeastern region. Despite sufficient effort, such detections were absent from portions of the study area north of this region.

I used a GLM with a Gamma error distribution to model the relationship between sub-plot sweetgum BA and a binary categorical predictor representing membership of the respective plot in the southeastern region or elsewhere in the study area. I compared this model with a null GLM lacking the region effect using AIC_c (Table 1; Burnham & Anderson 2002). If host availability determines regional oak mistletoe host associations, I expected a positive relationship between sub-plot-level sweetgum BA and plot membership in the southeastern region. This GLM and model comparison and the analyses described in the remainder of this section were conducted with the package AICcmodavg (Mazerolle 2020) within R (R Core Team 2021).

Regional variation in the proportion of forested habitat types occupied by either host or mistletoe species could increase the potential for avian frugivore behavior and local environmental conditions to play important roles in determining regional host associations. I modeled variation in sweetgum occurrence rates with GLMs and compared candidate models with AIC$_c$ (Table 1). The global model included an interaction between habitat type and region in their effects on the presence of sweetgum in sub-plots. I ran identical analyses with sub-plot data on the occurrence of red maple to compare results for a host used across the study area with results for the regionally parasitized sweetgum. Finally, I repeated these analyses with plot-level presence data on oak mistletoe to examine evidence for a difference in mistletoe habitat relationships between the southeastern region and the rest of the study area. Models of mistletoe occurrence included an additional term representing the effect of plot-specific potential host BA.

2.3 RESULTS

Oak mistletoe habitat relationships

I detected mistletoe at 38 survey plots on 599 individual trees and 7 host tree species and at 117 ad-hoc sites on an additional 23 host tree species; detected host species are listed in the Appendix. Three additional host taxa detected at ad-hoc sites were identified to only genus or sub-genus level. Single instances of the shrub *Cornus stricta* Lam. and the liana *Ampelopsis arborea* (L.) Koehne serving as hosts for oak 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 list of 16 host species from the inner Coastal Plain between the James and Cape Fear River watersheds. The most common host species was *Nyssa biflora* Walter with a total of 436 infected stems (24.22 ± 81.89 stems/25-m radius plot). Disregarding host species, 15.76 ± 57.34 trees were infected across plots. Red maple was parasitized at more plots (n = 26) than any other host species.

The 76 tree species and additional 13 taxa above the level of species detected across the study area are listed in the Appendix. The mean basal area of tree stems in sub-plots across the study area was 42.36 ± 27.63 m^2ha^{-1}. The tree species present at the highest proportion of sub-plots was red maple at 65%. *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 sub-plot area.

Eighty-five out of 96 sub-plots contained region-specific host species, with a mean host BA in sub-plots across the study area of 16.24 ± 22.91 m^2ha^{-1}. When regional host associations were unaccounted for, 89 plots contained at least one species that served as a host in the study area, and the mean sub-plot-level host stem BA was 19.07 ± 23.92 m^2ha^{-1}. The occurrence rate of oak mistletoe in forested wetland habitat was significantly more positive than the occurrence rate in forested upland habitat after accounting for host availability (GLM, Fig. 3).

Oak mistletoe host associations

Oak mistletoe was not randomly distributed across potential host tree species ($\chi^2 = 585.59$, df = 24, $P < .001$). Plot-level data on infected trees were dominated by two host species, with *N. biflora* and red maple together accounting for 97% of such detections. In contrast, these two tree species accounted for 14% and 19% of the total BA of potential host tree species across all sub-plots, respectively. Total BA values for the 25 potential host tree species with the highest BA are displayed in the Appendix. Remaining findings in this section pertain to determining the importance of potential host availability as a driver of observed regional variation in the association between sweetgum and oak mistletoe.

The mean sub-plot-level sweetgum BA was 2.22 ± 2.43 m^2ha^{-1} in the southeastern region and 7.35 ± 12.22 m^2ha^{-1} across other regions in the study area. Model comparison with AIC_c gave support to both a GLM of sweetgum BA that included only the intercept and a GLM that included a regional effect, with full model selection results provided in the Appendix. All candidate models of the occurrence of sweetgum in sub-plots received some support when ranked by AIC_c (Table 2); an interaction between the effects of habitat and a binary predictor representing whether a plot was in the southeastern region or not on this response was not strongly supported, with the GLM that included this interaction only receiving 12% of the AIC_c weight. I found more support for a relationship between the binary regional predictor described above and sweetgum occurrence, with candidate models that included this effect collectively accounting for 62% of the AIC_c weight and 24% of sub-plots in the southeastern region hosting sweetgum relative to 43% of sub-plots across the rest of the study area. Results from the ranking by AIC_c of these same models for red maple, parasitized across the study area, were similar to those for the regionally parasitized sweetgum in that an interaction between the effects of habitat and region received minimal support, with full model selection results provided in the Appendix. In contrast, such an interaction between the effects of habitat and region on the occurrence of oak mistletoe did receive strong support when candidate models were ranked by AIC_c, as the candidate model that included this interaction in addition to the effects of habitat, region, and potential host BA received 92% of the AIC_c weight (Table 3). Specifically, the best-supported model of mistletoe occurrence predicted a higher proportion of forested upland plots containing oak mistletoe in the southeastern region than in the rest of the study area (Fig. 4). It should be noted that region as a main effect appears to be an uninformative parameter in models of oak mistletoe occurrence (Arnold 2010).

2.4 DISCUSSION

I used plot survey data to examine the role of host availability in determining habitat relationships and regional host associations of oak mistletoe in eastern Virginia and North Carolina. I examined a specific regional host association that was unlikely to be driven by other factors such as avian frugivore behavior and local environmental conditions due to characteristics of the study area and the host tree species. In contrast, my study of the relationship between host availability and oak mistletoe habitat relationships left avian disperser foraging preferences and habitat-specific variation in environmental conditions as viable alternative drivers of this pattern. Concurrent work on this topic has given greater support to abiotic factors such as light availability than to avian disperser behavior in determining this phenomenon (Chapter 3, Chapter 4).

Host availability had previously been proposed as a potential driver of both habitat relationships and host associations for oak mistletoe in the eastern United States (Kuijt 2003, Weakley et al. 2012). Preliminary observations in the study area showed that some hosts were widespread with regards to both habitat and apparent host association regions, making host availability an unlikely factor in determining the distribution of oak mistletoe at these scales. Subsequent work presented here is the first, to my knowledge, to formally test the relationships between host availability and these phenomena 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 & Peterson 2014, Usta & Yilmaz 2021).

Accounting for regional variation in host use

My goal was to quantify the importance of host availability in determining the habitat relationships and regional host associations of oak mistletoe, yet the linkage between these two distributional phenomena had to be addressed. I thought it unlikely that host availability could drive the observed relationship between oak mistletoe and forested wetland habitat in the study area given the ubiquitous nature of some common host species. Without accounting for regional variation in host use by oak mistletoe, however, estimates of the relationship between host availability and mistletoe occurrence could be severely negatively biased. For instance, a tree species that was widespread geographically but parasitized only regionally could be abundant in a habitat type where oak mistletoe is rare, leading to the false inference that potential host availability is unrelated to the observed mistletoe habitat relationship.

Regional variation in host use by oak mistletoe has been noted by numerous workers who at a minimum overlapped in geographic scope with the study area (Baldwin & Speese 1957, Panvini 1991, Hawkins 2010). Here I partly defined host association regions based on physiographic regions due to known differences in plant community composition (Weakley et al. 2012). In two cases, the host association regions resulted from further splits of physiographic regions to account for shifts in parasitism of widespread tree taxa obvious in the data.

Oak mistletoe habitat relationships

The results supported the existence of a positive relationship between oak mistletoe occurrence and forested wetlands in the study area after accounting for both host availability and regional variation in host usage by oak mistletoe. Several factors remain as viable alternatives to host availability as drivers of this habitat association, including avian disperser behavior (Lamont & Southall 1982, Martínez del Rio et al. 1996, Aukema 2004, Caraballo-Ortiz et al. 2017) and local environmental conditions (Norton & Smith 1999, Roxburgh & Nicolson 2005, Mellado & Zamora 2014b, Lira-Noriega & Peterson 2014, Tikkanen et al. 2021). Several lines of evidence suggest that mistletoe dispersers in the study area freely disperse mistletoe seeds across habitat types, including a lack of a relationship between oak mistletoe genetic structure and habitat type (Chapter 3). Mistletoe samples used to test for this relationship came from only forested wetland and urban habitats, so I cannot speak to the existence of bird-mediated genetic structure across other habitat types.

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 to study its effect on mistletoe habitat relationships. There is evidence for a potential host-specific population of oak mistletoe in the eastern portion of the study area based on a population genetics study (Chapter 3), with the existence of a genetically distinct mistletoe population found only parasitizing host species in the genus *Nyssa*. This study also revealed that mistletoe populations found across several regions of the study area parasitizing a variety of host tree species were largely admixed.

The apparent widespread presence of generalist oak mistletoes in eastern portions of the study area makes it unlikely that host-specific populations could be driving the observed affinity of oak 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 & Zamora 2014b). 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 oak mistletoe populations in other portions of its range.

Oak mistletoe host associations

The results suggest that observed regional variation in the parasitism of sweetgum by oak mistletoe is not associated with variation in the availability of sweetgum stems. Furthermore, little support was found for regional variation in habitat type occupied by sweetgum, minimizing the likelihood of mistletoe disperser behavior or local environmental conditions to act as determinants of this regional host association. Instead, sweetgum was found to be more abundant and widespread in regions of the study area where it is not used as a host. Finally, the negligible support for a relationship between variation in sweetgum habitat type and host association region was similar to support found for such a relationship in red maple, a tree species parasitized across the study area.

While generalist mistletoes appear predominant among samples from forested wetland and urban habitats in the study area (Chapter 3), if host-specific populations are more common in other portions of the range of this mistletoe their host-specificity could determine regional host associations in such areas (Paine 1950, May 1971, Clay et al. 1985, Caraballo-Ortiz et al. 2017). Other potential drivers include variation in either local microenvironment conditions at scales finer than the habitat types examined here or the phenology of gaseous host cues (Randle et al. 2018).

Surprisingly, results from modeling presented here showed a higher likelihood of mistletoe occurrence in forested uplands in the southeastern region where sweetgum is commonly parasitized than across the remainder of the study area. In contrast to the lack of interaction between region and sweetgum habitat occupancy, this result maintains the potential for regional variation in avian disperser behavior or local environmental conditions to determine the observed regional host association (Clay et al. 1985, Norton & Carpenter 1998, Aukema 2004). If mistletoe is more common in forested uplands in the region where sweetgum is commonly parasitized, the sweetgum individuals in this region may be more prone to mistletoe infection due to avian disperser behavior or local environmental conditions specific to forested uplands. For instance, light availability has been proposed as an important factor determining mistletoe distributions in some systems (Panvini 1991, Mellado & Zamora 2014b) and there is evidence for a significantly positive relationship between light availability and oak mistletoe establishment (Chapter 4). If light is more available for mistletoes on sweetgum individuals in forested uplands than for such individuals in forested wetlands, the higher prevalence of oak mistletoe in these habitats in the southeastern region could make sweetgum trees more likely to be parasitized. The driver of this strongly supported interaction between the effects of habitat type and region on mistletoe occurrence in the study area is unknown. Increased light availability in forested uplands of the southeastern region due to abiotic factors seems a viable possibility.

Summary

Here I showed that factors other than host availability are responsible for the observed affinity of oak mistletoe for forested wetland habitat in eastern Virginia and North Carolina. I avoided potential biases in the estimates by accounting for regional variation in host use by oak mistletoe. Evidence to date suggests that variation in local environmental conditions is the most likely mechanism driving the distribution of oak mistletoe across different habitats in the study area. The existence of regional variation in host susceptibility remains an untested yet viable alternative hypothesis.

Similarly, I found that variation in host availability cannot explain regional variation in use of the widespread tree sweetgum by oak mistletoe. While several alternative hypotheses remain to be tested, my findings showed a regional shift in mistletoe distribution across habitat types that was related to a regional shift in parasitism of sweetgum. A greater occurrence of oak mistletoe in forested uplands in the southern region of the study area could make sweetgum individuals more suitable hosts in this region through changes in habitat-specific disperser behavior or abiotic conditions. Work remains to determine if this relationship between habitat occupancy of oak mistletoe and parasitism of sweetgum is restricted to the area examined in this study. Future studies of mechanisms driving regional variation in the use of widespread host species by generalist parasitic plants could include variation in parasite habitat relationships as a viable hypothesis and reveal the generality of this phenomenon.

Table 1 Descriptions of models of variation in *Liquidambar styraciflua* basal area (BA) at sub-plots and the occurrence of *L. styraciflua*, *Acer rubrum*, and oak mistletoe at sub-plots. "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

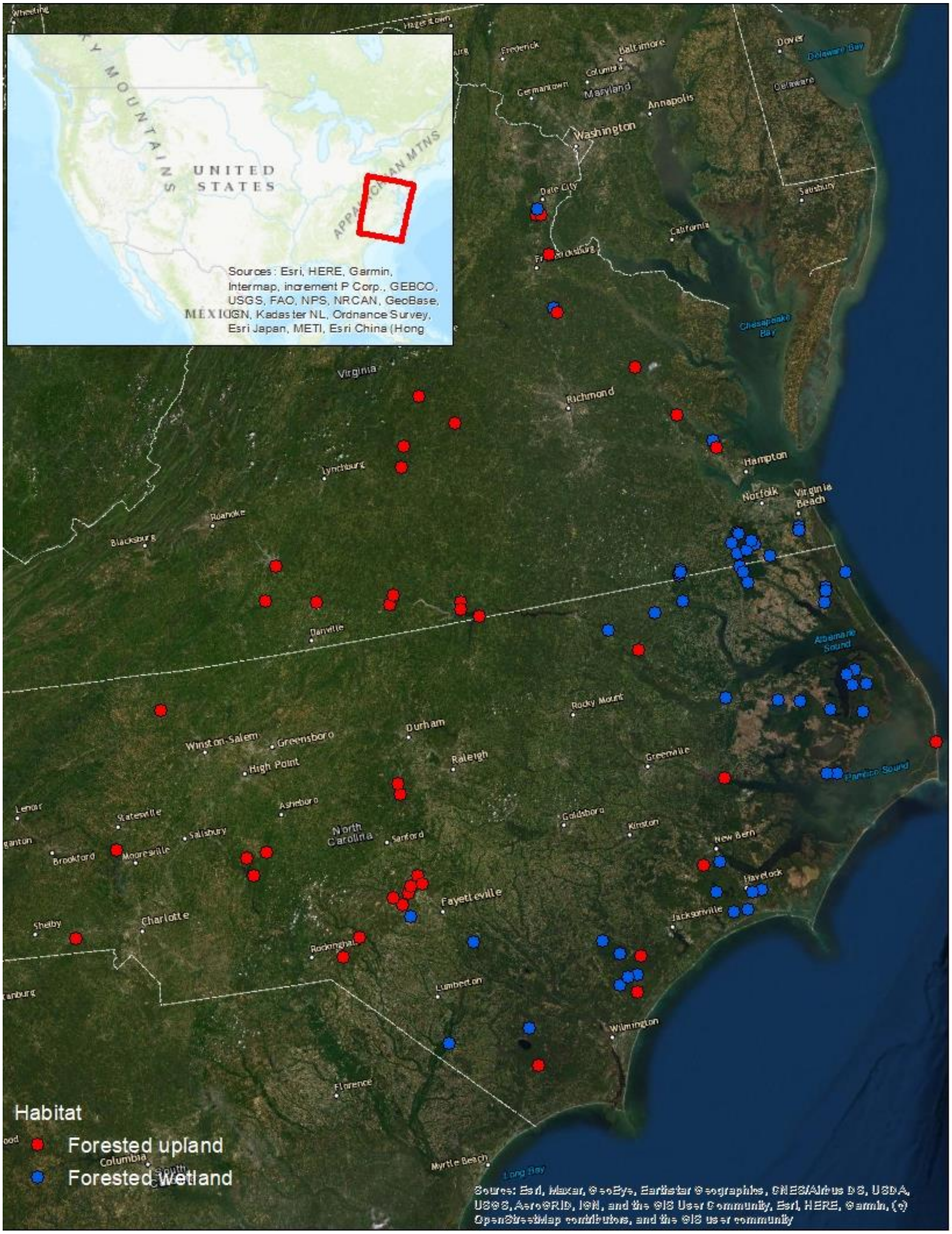
Variable	Response			
	Liquidambar styraciflua BA	*Liquidambar styraciflua* occurrence	*Acer rubrum* occurrence	Oak mistletoe occurrence
Region (southeastern region or other region in study area)	Y	Y	Y	Y
Habitat (forested wetland or forested upland)	N	Y	Y	Y
Region*habitat (interaction)	N	Y	Y	Y
Basal area (BA) of potential host species in sub-plot	N	N	N	Y

Table 2 Alternative generalized linear models for the relationships between *Liquidambar styraciflua* occurrence at plots and habitat type and region as ranked by AIC$_c$

Variables included in model	K	AIC$_c$	Delta AIC$_c$	AIC$_c$ weight	Cumulative weight	LL
Intercept + region	2	129.53	0	0.33	0.33	-62.7
Intercept (null)	1	130.04	0.51	0.26	0.59	-64
Intercept + region + hab	3	130.81	1.27	0.17	0.76	-62.27
Intercept + hab	2	131.54	2.01	0.12	0.88	-63.71
Intercept + region + hab + interaction	4	131.58	2.05	0.12	1	-61.57

Table 3 Alternative generalized linear models for the relationships between mistletoe occurrence at plots and region, habitat, and host availability as ranked by AIC$_c$

Variables included in model	K	AIC$_c$	Delta AIC$_c$	AIC$_c$ weight	Cumulative weight	LL
Intercept + region + hab + interaction + BA	5	77.16	0	0.92	0.92	-33.25
Intercept + hab + BA	3	82.93	5.77	0.05	0.97	-38.34
Intercept + region + hab + BA	4	83.85	6.69	0.03	1	-37.71
Intercept + BA	2	93.43	16.27	0	1	-44.65
Intercept + region + BA	3	94.6	17.44	0	1	-44.17
Intercept + region + hab + interaction	4	100.49	23.33	0	1	-46.03
Intercept + hab	2	101.73	24.57	0	1	-48.8
Intercept + region + hab	3	103.7	26.54	0	1	-48.72
Intercept (null)	1	130.93	53.77	0	1	-64.44
Intercept + region	2	132.99	55.83	0	1	-64.43



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Fig. 1 Locations of survey plots in forested upland and forested wetland habitats

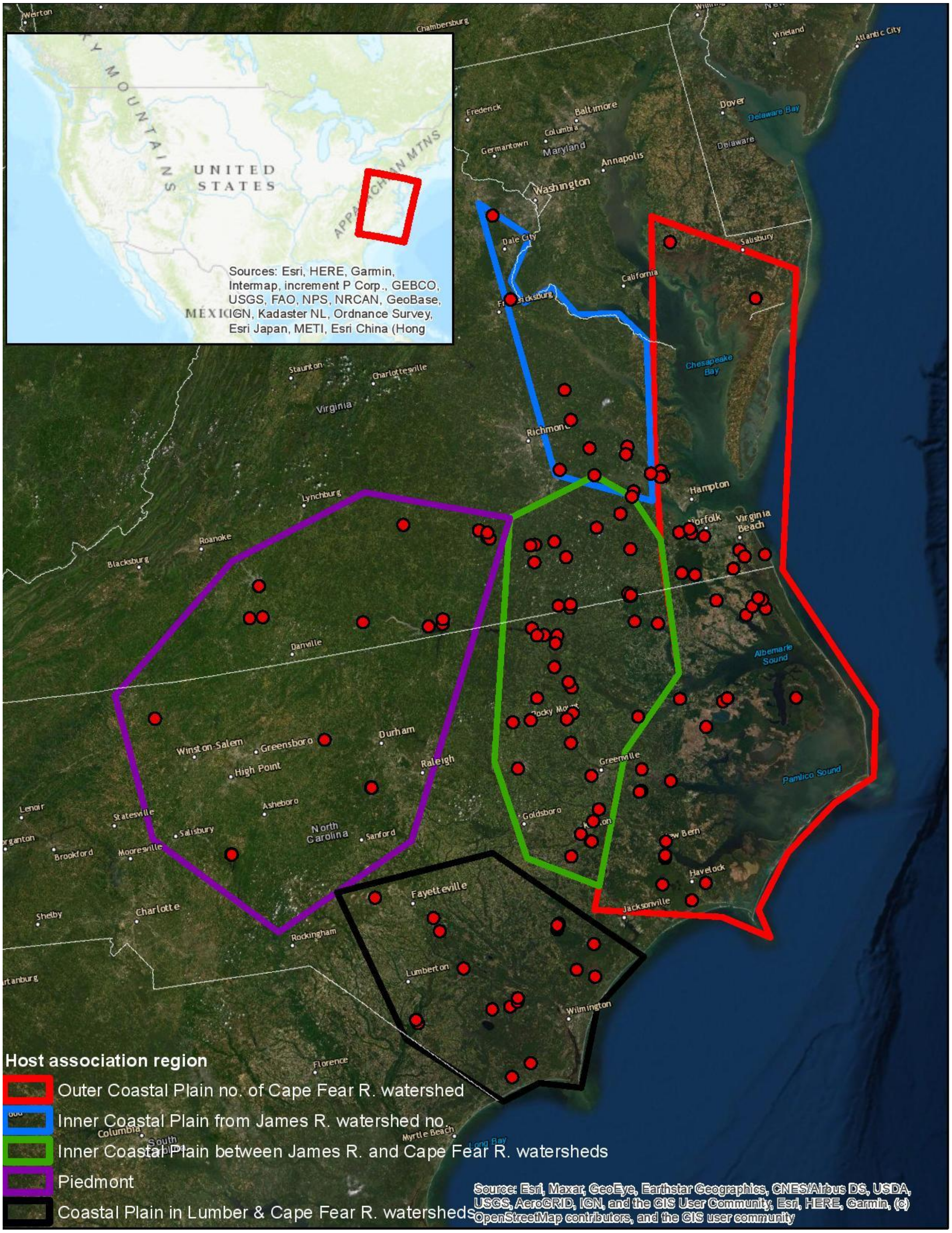


Fig. 2 Locations of 125 sites that hosted mistletoe and were selected ad hoc across the study area

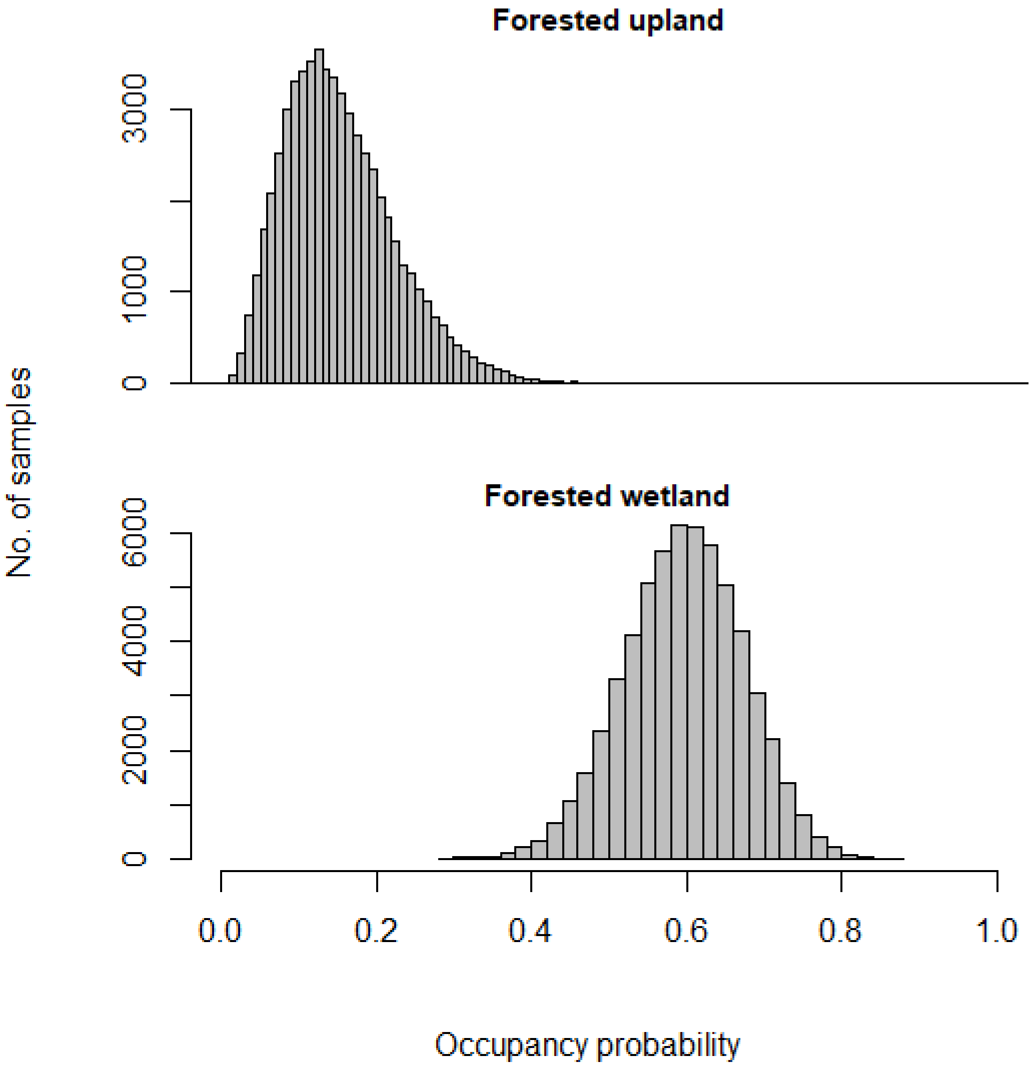


Fig. 3 Posterior distributions of predicted probabilities of mistletoe occurrence in forested upland and forested wetland habitats

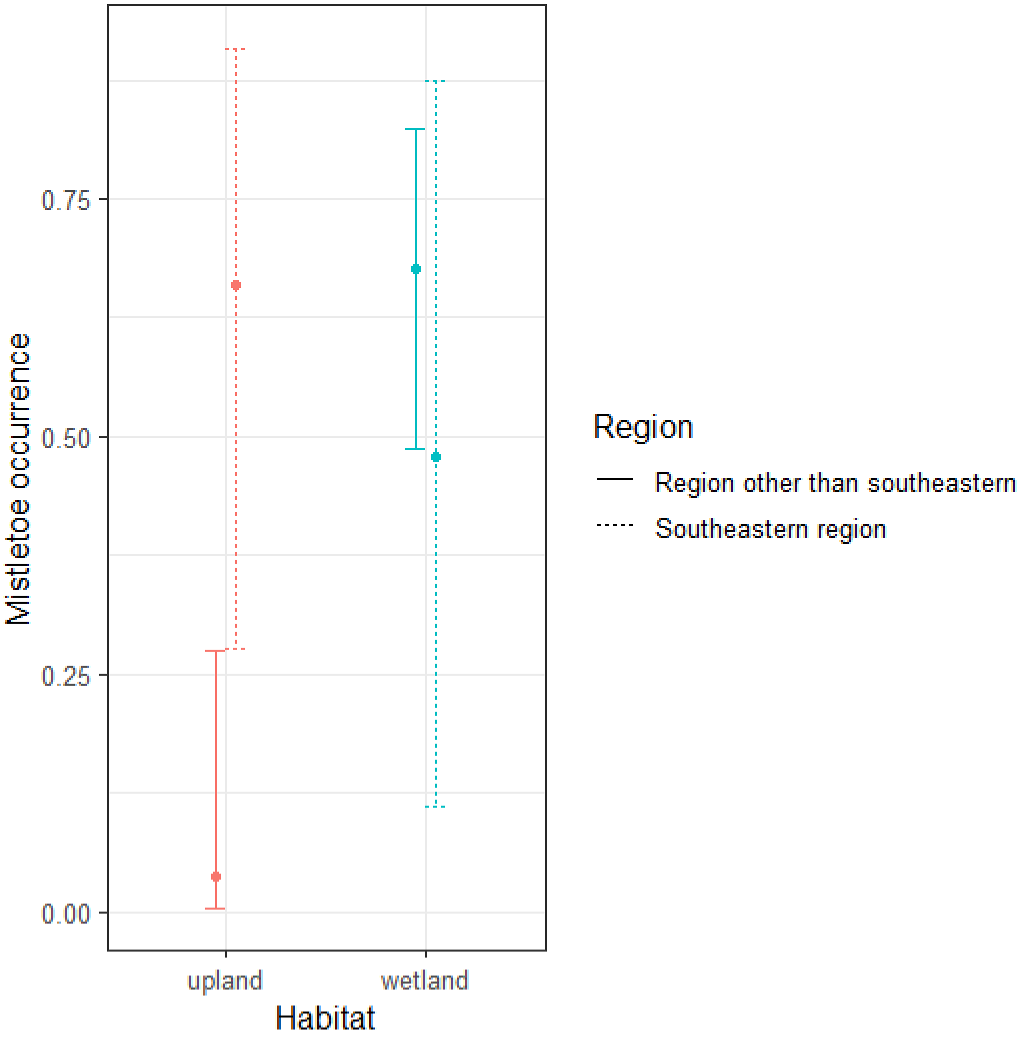


Fig. 4 Predicted rates of oak mistletoe occurrence from the top model of variation in mistletoe presence in plots across different habitats and regions as ranked by AIC$_c$; error bars represent 95% confidence intervals

CHAPTER 3

THE DISTRIBUTION OF OAK MISTLETOE [*PHORADENDRON LEUCARPUM* (RAF.) REVEAL & M. C. JOHNST.] IS MORE RESTRICTED WITH REGARDS TO HABITAT TYPE THAN THAT OF ITS AVIAN FRUGIVORE DISPERSERS

3.1 INTRODUCTION

The dispersal of propagules is critical to maintaining and structuring plant populations and communities (Schupp et al. 2010), yet its influence in determining plant distributions relative to other factors remains controversial (Levine & Murrell 2003, Alexander et al. 2012, Foster et al. 2011). Results from many seed augmentation experiments in the field suggests the presence of seed limitation, yet overall low seedling establishment maintains the likelihood that post-dispersal factors are more influential in determining plant distributions (Clark et al. 2007). Understanding the relative roles of dispersal and local environmental conditions in determining plant distributions is important for predicting the spread and persistence of plant species (Renne et al. 2001).

The visibility of dispersers and discrete establishment sites in many mistletoe-frugivore systems make such systems well-suited for testing hypotheses about determinants of plant distributions (Overton 1994, Levine & Murrell 2003). Despite this, the relative importance of environmental conditions, avian frugivore behavior, and host tree availability in determining mistletoe distributions remains unclear in many cases (Panvini 1991, Kuijt 2003, Aukema 2004, Caraballo-Ortiz et al. 2017). I was interested in determining what drives variation in oak mistletoe occurrence among forested habitat types, a distributional pattern I henceforth refer to as a habitat relationship.

In the Coastal Plain and Piedmont regions of Virginia and North Carolina in the southeastern United States (US), the study area of interest, oak mistletoe [*Phoradendron leucarpum* (Raf.) Reveal & M. C. Johnst.] is more common in forested wetlands of the Coastal Plain than in other forested habitats (Weakley et al. 2012) despite the widespread occurrence of potential host tree species such as red maple (*Acer rubrum* L.). Host trees available in urban areas under a variety of development intensities are also commonly parasitized in the region. Oak mistletoe is a food resource for avian frugivores wintering in the study area, and an understanding of factors responsible for current and future distribution of mistletoe is of interest for avian conservation (Watson 2001, Aukema & Martínez del Rio 2002, Dickinson & McGowan 2005, Watson & Herring 2012).

Habitat choices of avian seed dispersers have been cited as an influential factor determining distributions of mistletoe species (Martínez del Rio et al. 1996, Aukema 2004, Usta & Yilmaz 2021). While winter habitat relationships of avian frugivores that disperse oak mistletoe seeds are poorly known (Panvini 1991, Weinkam 2013), it is possible that variation in fruit availability drives these species to spend more time foraging in forested wetlands (Wigley & Roberts 1994, Wakeley & Roberts 1996, Usta & Yilmaz 2021) and urban areas (Thompson & Poindexterss 2005) than in other habitats (Renne et al. 2002). Differential seed dispersal rates among habitats could drive observed habitat relationships of oak mistletoe in the region of interest.

Weakley et al. (2012) suggested that regional silvicultural practices may reduce the suitability of upland forests relative to forested wetlands as oak mistletoe habitat by affecting the availability and quality of host trees. If avian dispersers choose hosts and non-hosts equally for perching, a positive relationship between host density and dispersal efficiency should exist for mistletoes in general (Overton 1994). While a relationship between oak mistletoe occurrence and forested wetland habitat was found even after accounting for host tree availability (Chapter 2), variation among habitats in local environmental conditions that affect host tree quality remains a viable mechanism driving such relationships (Roxburgh & Nicolson 2005, Mellado & Zamora 2014b, Lira-Noriega & Peterson 2014). I was interested in testing an alternative hypothesis that differential seed dispersal rates by avian frugivores across different habitat types is the most influential factor determining observed habitat relationships of oak mistletoe.

Presence-absence data on regional mistletoe dispersers identified using camera traps and other generalist frugivores from repeated surveys across a variety of forested habitat types were analyzed using occupancy models (MacKenzie et al. 2002) to estimate habitat relationships while accounting for imperfect detection rates. A Bayesian analysis allowed me to quantify similarities between estimates of habitat relationships for oak mistletoe and mistletoe dispersers (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015). Such comparisons tested the hypothesis that disperser behavior is an important driver of oak mistletoe distributions.

Understanding the distribution of mistletoe species that obligately depend on birds for seed dispersal has the potential to increase knowledge on avian behavior and habitat use (Stiles 1982, Aukema 2004, Mellado & Zamora

2014b). The successful spread of the invasive tree *Sapium sebiferum* (L.) Roxb. in the southeastern US has been partially attributed to variation among regions and habitats in avian disperser communities (Renne et al. 2002). Matula et al. (2015) interpreted the higher prevalence of the mistletoe *Loranthus europaeus* Jacq. on larger trees as a signal of the territorial behavior of the mistle thrush (*Turdus viscivorus*), an important disperser of mistletoe seeds in that system.

If avian disperser behavior is largely responsible for limited gene flow among populations of a mistletoe, the genetic structure of the mistletoe could be interpreted as a signal of otherwise largely cryptic patterns of avian disperser distributions (Loiselle et al. 1995, Aukema 2004, Mellado & Zamora 2014a). The presence of genetic structure in oak mistletoe associated with habitat types could indicate the existence of habitat-specific frugivore populations that would not be apparent in survey data of unmarked birds (Clay et al. 1985, Hamrick et al. 1993). If such habitat-specific winter populations exist, seemingly widespread avian species could play a role in determining oak mistletoe habitat relationships by limiting dispersal between different forested habitat types. Here I used genetic markers and oak mistletoe samples from different habitats in the Coastal Plain portion of the study area to look for a signal of such dispersal limitation between habitats.

3.2 METHODS

Avian frugivore occurrence sampling and analysis

Stratified random sampling was used to select 96 circular plots with 25-m radii to survey repeatedly for the presence or absence of mistletoe shrubs and avian frugivore species during the winter seasons (Dec–Mar) of 2015–2016 to that of 2019–2020 (Fig. 5). These plots were in the Coastal Plain and Piedmont regions of Virginia and North Carolina, with forested wetlands (54 plots) and all other forested habitats (42 plots) serving as two strata. I surveyed plots in winter when oak mistletoe provides fruits. Details of surveying plots for the occurrence of oak mistletoe and related variables and the analysis of the resulting presence-absence data were reported elsewhere (Chapter 2).

Repeated surveys for avian frugivores consisted of 10-min point counts conducted between official sunrise and 11:30 hrs EST during which all avian species detected using the ground or foliage within the plot were recorded. All plots were surveyed 2–4 times within a winter season (Dec–Mar). The subset of plots to be surveyed during a respective winter were chosen at random from the total set of active plots. I disregarded some date-specific presence-absence data on avian species under certain conditions to ensure my estimates reflected winter bird distributions. I filtered such data when 1) the avian species was considered to breed in the study area, 2) the breeding season of the avian species overlapped with the survey date, and 3) known habitat relationships of the species differed markedly between its breeding and non-breeding season. I referred to LeGrand et al. (2021) and Rottenborn & Brinkley (2007) for information on avian phenology and distribution in the study area.

Avian occurrence data that did not meet the above criteria were analyzed with a community occupancy model in a Bayesian framework (Dorazio & Royle 2005). As with single-species occupancy models (MacKenzie et al. 2002, 2006), community models use patterns of detection of a species from repeat surveys to account for imperfect detection and avoid detection-related biases in other parameter estimates. This assumes the occurrence state of the species is constant during the survey period; this assumption may be partially relaxed with shifts in interpretation of model parameters (Kendall 1999, MacKenzie 2005, MacKenzie et al. 2006, Kéry & Schaub 2012). Community models extend the estimation of parameters of interest to species with relatively little data by sharing information across similar species through the treatment of species as random effects (Dorazio & Royle 2005). These models have been shown to retain the flexibility necessary to estimate species-specific relationships between occurrence and explanatory variables (Kéry & Royle 2008).

The models I used allowed for the sharing of information across forest bird species and included species-specific effects of habitat type (forested wetland versus forested upland) on occurrence rate and both date and the quadratic effect of date on detection probability (Flanders et al. 2015). I included year-specific random intercepts in species-specific sub-models of detection rate to account for interannual variation in avian species abundance, acknowledging the relationship between abundance and detection probability (Royle & Nichols 2003). The species-specific effect of habitat on occurrence rate was considered statistically significant if 95% credible intervals for habitat-specific intercept parameters did not overlap. I used the package R2WinBUGS (Sturtz et al. 2005) in R 4.1.2 (R Core Team 2021) to estimate posterior distributions in WinBUGS (Lunn et al. 2000) with uninformative prior distributions for all parameters and 3 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 & Hill 2007).

The quantification of similarities between estimates of habitat relationships for oak mistletoe and for mistletoe seed dispersers required results from the previous fitting of a generalized linear model to mistletoe occurrence data from the same 25-m radius plots described above (Chapter 2). Specifically, I calculated the proportion of samples from the posterior distribution of the effect of wetland habitat on the occurrence of mistletoe that were greater than samples from the respective posterior distributions of such effects on the occurrence of a subset of avian species detected at plots (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015). If this proportion was less than 0.95, I considered the two estimates to not differ statistically. I selected a subset of avian species that represented potential mistletoe seed dispersers, including four frugivorous species detected eating oak mistletoe fruits in the region with remote cameras [eastern bluebird (*Sialia sialis*), cedar waxwing (*Bombycilla cedrorum*), gray catbird (*Dumetella carolinensis*), and tufted titmouse (*Baeolophus bicolor*)]. The other 15 avian species for which comparisons were made were considered frugivores based on a greater than 25% proportion of fruit in reported winter diets (Billerman et al. 2020). Forest bird species detected were categorized as frugivores or non-frugivores as listed in the Appendix.

Tissue sampling, genotyping, and molecular analyses

I used an extendable pole pruner to sample leaf tissue from accessible oak mistletoe shrubs (n = 517) at locations in forested wetland and urban habitats across eastern Virginia and North Carolina from January to December 2019 (Fig. 6); due to difficulties locating accessible mistletoe shrubs in forested wetlands in northern Virginia I also sampled from one wetland and one urban location in southeastern Maryland. I sampled approximately 20 mistletoes at each sampling location (mean = 19.88, SD = 0.59) from a total of 19 different host species; a list of these host species is in the Appendix. Five additional host taxa were identified to only the genus or sub-genus level. To test the hypothesis that dispersal limitation restricted mistletoe gene flow among habitat types, I chose paired sampling locations such that each location in urban habitat was as close as possible geographically to one sampling location in forested wetland habitat.

I grouped sampling locations based on geographic region: inner Coastal Plain south of the James River (9 locations), outer Coastal Plain south of the James River (13 locations), and Coastal Plain north of the James River (4 locations). These regions were based on observed geographic host associations as in a previous study of determinants of regional variation in host use (Chapter 2). Samples from locations in the same habitat type and region were treated as coming from the same population (mean = 86.17 samples per habitat within region, SD = 42; Table 5).

Leaf tissue samples were submitted to CD Genomics (Shirley, NY) to identify polymorphic microsatellite loci across individuals. First, a whole genome sequence for the non-model organism oak mistletoe was generated. A NEBNextR Ultra^{TM} DNA Library Prep Kit for Illumina (NEB, USA) was used to develop a library for DNA fragments from a sonicated 0.5 µg sample that were ligated to full-length adaptors for Illumina sequencing. Sizes of fragments purified using the AMPure XP system were quantified using the Agilent2100 Bioanalyzer and real-time PCR and the library was sequenced using Illumina NovaSeq6000 PE150. This library was searched for fragments with greater than five repetitions of a 3–5 base pair repeat unit using MISA (Beier et al. 2017). Primers were developed for such fragments using PRIMER3 with constraints of a minimum melting temperature of 55°C and optimal melting temperature of 57°C.

Potential markers were tested for amplification across 4 samples resulting in 46 loci that were screened for polymorphism using capillary electrophoresis and 8 mistletoe samples from across the study area. Eight markers (Table 4) were determined to be polymorphic and were genotyped across all samples. I used GenAlEx (Peakall & Smouse 2006, 2012) to format the fragment length data for analysis and GENEPOP (Rousset 2008) to test for Hardy-Weinberg equilibrium (HWE; dememorization 10000, batches 100, iterations per batch 5000), the presence of null alleles, and linkage disequilibrium. Because of significant pair-wise linkage disequilibrium, the marker c17395 was dropped; other markers were without significant pair-wise linkage at the 1% level after Holm-Bonferroni corrections.

Fragment length data from two population and locus combinations showed significant deviations from HWE due to heterozygote deficiencies (Table 5), while estimated null allele frequencies across all such combinations were low. Yule et al. (2016) found similar HWE deviations and null allele frequencies across populations of desert mistletoe (*Phoradendron californicum* Nutt.) using data from 10 microsatellite markers. As in that study, I failed to find a significant relationship between estimates of F_{IS} and the quantity of missing data from each population and locus combination, with such “blank” data interpreted as homozygotes under the hypothesis that null alleles are present (Dharmarajan et al. 2011). I also treated genotyping results as Bernoulli random variables with missing data or "blanks" treated as successes and ran locus-specific generalized linear models with a logit-link function to test for significant positive relationships between F_{IS} estimates and missing data rates. After adjusting for multiple tests with a Holm-Bonferroni correction, none of the seven locus-specific relationship estimates were statistically significant at alpha = .05. I concluded deviations from HWE were likely due to genetic structure within populations, also known as Wahlund effects, instead of the presence of null alleles (Dharmarajan et al. 2011, Yule et al. 2016).

I used the Bayesian clustering program STRUCTURE version 2.3.4 to estimate sample-specific proportions of ancestry from genetic populations under alternative hypotheses about the number of distinct populations present across all samples (K; Pritchard et al. 2000). I varied K from 1 to 10 and ran STRUCTURE independently 20 times under each hypothesis with $1x10^6$ iterations per run and the first $1x10^5$ iterations treated as burn-in values. I used Structure Harvester (Earl & vonHoldt 2012) to calculate the delta K statistic of Evanno et al. (2005) and selected the value of K best supported by the genetic data. Ancestry proportion estimates from independent runs of STRUCTURE under the value of K that optimized the delta K statistic of Evanno et al. (2005) were aligned optimally using the program CLUMPP (Jakobsson & Rosenberg 2007) and the Greedy algorithm with $1x10^4$ repeats. The package pophelper (Francis 2017) in R 3.6.2 was used to plot and label resulting optimized sample-specific ancestry proportions according to host association region, collection site, and host species.

A hierarchical analysis of molecular variance (AMOVA, Excoffier et al. 1992) was used to calculate the proportion of genetic variation aligned with habitat type nested within host association region. Such a correlation between habitat type and genetic structure could be a signal of dispersal limitation mediated by avian frugivore behavior (Clay et al. 1985, Hamrick et al. 1993). I ran a separate AMOVA to determine the degree to which oak mistletoe genetic variation could be attributed to variation in host species under the hypothesis that host races exist (May 1971, Clay et al. 1985). Whether examining genetic variation across habitats or host species nested within region, I used Arlequin version 3.5 (Excoffier & Lischer 2010) to quantify such structure using both F_{ST}-like differences in alleles and R_{ST}-like differences in fragment length.

A network analysis in EDENetworks version 2.18 (Kivelä et al. 2015) was used to visualize genetic relatedness among oak mistletoe populations without the injection of "a priori" information based on hypotheses about genetic isolation by habitat or host species. This software used pair-wise F_{ST} values to represent connectivity between site-specific and host-specific mistletoe populations and then to derive a minimum spanning tree.

EDENetworks was also used to visualize the resulting tree and color code population nodes based on habitat type or geographic region. To check for variation in clustering identified among populations I recreated such a minimum spanning tree 10 times in EDENetworks (Ashley et al. 2015).

3.3 RESULTS

Modeling avian frugivore habitat relationships

I detected the presence of 58 wintering forest bird species, 19 of which were frugivores, and analyzed occurrence data using a community occupancy model to estimate species-specific relationships between forested habitat type and occupancy while accounting for the imperfect detection of species. I found significantly positive relationships between forested wetland habitat and occupancy for six species including the rusty blackbird (*Euphagus carolinus*), a species of conservation concern (Greenberg & Matsuoka 2010), and two other frugivores: gray catbird (*Dumetella carolinensis*) and yellow-rumped warbler (*Setophaga coronata*; Table 6). Negative relationships between forested wetland habitat and occupancy were estimated for three avian species including the locally uncommon red-headed woodpecker (*Melanerpes erythrocephalus*) and the frugivorous tufted titmouse (*Baeolophus bicolor*). Posterior distributions of predicted occurrence rates of these nine avian species in forested upland and forested wetland habitat are shown in the Appendix. I estimated statistically significant relationships between date and detection probability for 10 species and quadratic effects of date on detection for three species (Table 6). Detection rates were highly variable across species and extremely low for some species, emphasizing the need to account for imperfect detection when estimating habitat relationships and comparing occupancy rates across forest bird species wintering in the southeastern US.

I did not find statistically significant positive relationships between forested wetland habitat and occupancy for either cedar waxwing or eastern bluebird, the two principal dispersers of oak mistletoe fruits. Posterior distributions of predicted occurrence rates of these two avian species in forested upland and forested wetland habitat are shown in the Appendix. Comparisons between estimates of this habitat relationship for avian frugivores and for oak mistletoe revealed 9 potential disperser species for which the effect was significantly lower than for mistletoe, including eastern bluebird (Fig. 7), suggesting that these dispersers are more widespread with regards to habitat than oak mistletoe. I found no significant differences between the estimated effect of forested wetland habitat for mistletoe and for the remaining 10 frugivore species, including cedar waxwing. Probabilities of differences between estimates of the relationship between forested wetland habitat and occurrence for oak mistletoe and avian frugivore species, along with posterior distributions of these effects, are given in the Appendix.

Population genetics analyses

A value of K = 4 was the optimal delta K (Evanno et al. 2005), suggesting the presence of four distinct genetic populations across the samples. Values of delta K calculated across different hypothesized numbers of oak mistletoe populations are shown in the Appendix. Optimized ancestry proportion estimates suggested many individuals are admixed (Figs. 8, 9, 10), with groupings of individuals strongly assigned to a particular cluster not aligned with host association regions or habitat type in most cases (Figs. 8, 10). Ancestry proportions for oak mistletoe samples grouped by host association region are shown in the Appendix. One exception was individuals from host association regions north of the James River (Fig. 10), many of which were strongly assigned to the same cluster. A distinct group of individuals strongly assigned to the same cluster was aligned with host species in the genus *Nyssa* L. regardless of habitat or region (Fig. 9), which I refer to as the “Nyssa” cluster below.

I verified the consistency of these patterns in cluster assignment by examining optimized ancestry proportion estimates from runs of STRUCTURE under alternative hypotheses about the number of genetic populations in existence. Such estimates from runs of STRUCTURE with K = 2 and K = 3 both maintained the existence of a genetically distinct group of mistletoes parasitizing *Nyssa* spp. I saw a decrease in the strength of the assignment of individuals from the northernmost host association region to the same cluster under these alternative hypotheses. An additional STRUCTURE analysis was conducted to both further examine the genetic similarity of mistletoes from the northernmost host association region and to check for hierarchical genetic structure at a level lower than that identified in the original analysis (Evanno et al. 2005). This second analysis used identical parameters as previously described but only included individuals whose estimated ancestry in the “Nyssa” cluster was less than 0.65. I failed to find support for a value of K greater than 1 using the delta K method of Evanno et al. 2005 when including only those samples outside of the “Nyssa” cluster; the values of delta K from these STRUCTURE runs are displayed in the Appendix. Across results from runs with different K values, this analysis suggested that all included individuals were largely admixed.

Results from AMOVA analyses supported the association between oak mistletoe genetic structure and host species revealed in patterns of ancestry proportions estimated by STRUCTURE. The proportion of genetic variation explained by host association region was consistently low across all models, as was the case for such variation explained by habitat type within host region (Table 7). In contrast, when genetic differences were calculated based on allele length, variation in host species within host region accounted for 10% of overall genetic variation. Further support for these patterns was provided by the shape of the minimum spanning trees created in EDENetworks and included in the Appendix. Links on these trees showed clustering among samples collected off hosts in the genus *Nyssa*, irrespective of geography. These results suggest that relatedness among other mistletoe samples is independent of habitat type or host association region.

3.4 DISCUSSION

Here I used survey data on the occurrence of avian species coupled with patterns of mistletoe genetic structure to show that dispersal limitation is unlikely to determine habitat relationships of oak mistletoe in the study area. Similarly, analyses of mistletoe occurrence data confirmed the affinity of oak mistletoe for forested wetland habitat in the study area even after accounting for host availability (Chapter 2). I found a relationship between light availability and oak mistletoe establishment in a separate planting study; these findings collectively suggest that local environmental conditions may be the most important factor driving oak mistletoe habitat relationships in the study area (Clark et al. 2007).

Lack of evidence for bird-mediated genetic isolation by habitat

The processes of seed dispersal and pollen dispersal are responsible for the transfer of genes between plant populations (Loveless & Hamrick 1984, Fenster 1991), thus playing important roles in determining the genetic structure of populations (Jordano et al. 2007). Pollen dispersal in oak mistletoe is likely mediated by small insects (Panvini 1991) and so can be expected to contribute little to gene flow between populations and sub-populations due to small movement ranges of such pollinators (Loveless & Hamrick 1984). However, seed dispersal rates and distances are known to vary widely from vector to vector (Jordano et al. 2007) and, in plants with animal-dispersed seeds, animal behavior can play a large role in determining gene flow between populations and sub-populations

(Westcott et al. 2005). Given the dependence of oak mistletoe individuals on frugivorous birds for seed dispersal in the southeastern US, information on the genetic structure of mistletoe populations in the region could inform on the behavior of these avian dispersers and their role in determining mistletoe distributions (Loiselle et al. 1995, Aukema 2004).

Two large-scale genetic analyses have been performed across substantial portions of the range of oak mistletoe. Panvini (1991) used allozyme variation to study genetic structure in populations across the southeastern US, with F_{st} estimates suggesting genetic isolation punctuated by long-range bird-mediated dispersal events. Hawkins (2010) used microsatellites to test the validity of four subspecies proposed across the range of oak mistletoe. Results of this range-wide analysis largely agreed with Panvini (1991) in terms of genetic differentiation and admixture between populations as shown by F_{st} estimates. Hawkins (2010) also tested the isolation by distance hypothesis (Wright 1943) using microsatellite data and failed to find strong support. Work presented here was a valuable extension to these previous studies as it looked specifically at correlations between oak mistletoe genetic structure and both habitat type and host species at an intermediate geographic scale (Aukema 2004).

The patterns of oak mistletoe genetic structure that I found did not show a signal of bird-mediated genetic isolation by habitat. While I failed to find support for the hypothesis that habitat specificity of mistletoe dispersers was driving oak mistletoe habitat relationships in the region, I did see a genetically distinct cluster of samples that parasitized hosts in the genus *Nyssa*. The potential barrier to gene flow between oak mistletoes on *Nyssa* spp. and those parasitizing other host species is unclear.

Relationship between genetic structure and host species

Regional variation in the parasitism of potential host species by oak mistletoe has been documented in the study area (Baldwin & Speese 1957, Panvini 1991, Hawkins 2010), with the existence of genetically distinct host races proposed as a potential driver of such variation in other portions of its range (May 1971, Clay et al. 1985). Results from the oak mistletoe population genetics work of Panvini (1991) left the possibility for the existence of host races open. A clustering analysis with ISSR marker data from oak mistletoe samples collected from a mixed-host population in Texas failed to reveal patterns indicative of host races (Randle pers. comm.). In contrast, I found a relationship between host species and genetic structure among oak mistletoe samples in the study area, specifically a distinct cluster of samples collected from hosts in the genus *Nyssa*.

The apparent lack of gene flow between oak mistletoes parasitizing *Nyssa* spp. and those parasitizing other host species in the study area is likely not caused by avian disperser behavior. There is no phenological overlap in the fruiting of oak mistletoe and any host species that offer fleshy fruits in the study area (Weakley et al. 2012). Thus, unlike in other systems (van Ommeren & Whitham 2002, Kuijt 2003, Carlo & Aukema 2005, Caraballo-Ortiz et al. 2017), there should be no resource-driven variation in attractiveness of potential host trees to generalist avian frugivores. Similarly, variation in attractiveness of hosts to avian dispersers based on host habitat preferences seems unlikely, as there is considerable overlap in habitats used by tree species hosting sampled mistletoes shown to differ genetically (Weakley et al. 2012).

Identification of an isolating mechanism strong enough to drive the formation of an oak mistletoe host race may require consideration of disperser communities and phenology in other portions of the range of this mistletoe. However, the maintenance of restricted gene flow between oak mistletoe populations parasitizing hosts in the genus *Nyssa* and those parasitizing other host species could be partially achieved through barriers to pollen dispersal as suggested by data in Yule et al. (2016) to explain similar genetic structure in *P. californicum*. This effect could be exacerbated if rates of between-tree seed dispersal are low in the system studied here, as were the rates used to parameterize a mistletoe metapopulation model able to simulate the distribution of the mistletoe *Phrygilanthus sonorae* Standl. (Overton 1994). Genetic isolation could also be achieved through pollen limitation coupled with differentiation such that the progeny of mistletoes on hosts in the genus *Nyssa* enjoy the highest establishment rates on *Nyssa* spp. hosts. This latter mechanism was partially shown for putative oak mistletoe host races by workers in and near Texas (May 1971, Clay et al. 1985).

Avian frugivore habitat relationships

Field studies of relationships between distributions of frugivores and mistletoes have historically failed to account for imperfect detection, with repeat surveys (Martínez del Rio et al. 1996, van Ommeren & Whitham 2002), spot-mapping (Bennetts et al. 1996), or presence-only datasets (Lira-Noriega & Peterson 2014) used to make inference about bird distributions. The use of a community occupancy model to estimate habitat relationships of oak mistletoe dispersers was novel as it formally accounted for imperfect detection, revealing low and variable detection rates capable of biasing such parameter estimates if unaccounted for (MacKenzie et al. 2002, Tyre et al. 2003, Kéry et al. 2008, Ruiz-Gutiérrez et al. 2010). I know of no other correlative studies examining relationships between mistletoe distributions and that of their avian dispersers conducted at as large a geographic scale as in this study.

The analysis of survey data on avian occurrence revealed that only three frugivores showed a positive relationship between occupancy and forested wetland habitat, the preferred habitat of oak mistletoe in the study area (Chapter 2), with a negative estimate for this relationship found for the frugivorous tufted titmouse. To formally test this lack of coupling between habitat relationship estimates for oak mistletoe and for avian dispersers, I quantified overlap in posterior distributions of these parameter estimates. Such distributions for 8 out of the 19 frugivore species detected, including one of two principal oak mistletoe seed dispersers (eastern bluebird), showed a significant lack of overlap with the posterior distribution of the positive effect of forested wetland habitat on oak mistletoe occurrence. These results suggest that factors other than avian disperser behavior are most important in driving the association between oak mistletoe and forested wetland habitat.

A limited role of dispersal limitation in determining plant distributions has been shown for many plant species (Clark et al. 2007), including mistletoes at the scale of the range of a species (Tikkanen et al. 2021). As in this study, Norton & Smith (1999) concluded that disperser behavior was unlikely to drive variation in mistletoe infection rates between forested habitats, in contrast to studies attempting to explain variation in mistletoe occurrence between forested and open habitats where avian behavior was deemed more important. Another similarity was the presence, albeit at low occurrence rates, of mistletoe in a less preferred forested habitat type. Norton & Smith (1999) used this limited presence to infer that at least some dispersal must be occurring between habitats. I could similarly interpret the presence of oak mistletoe in forested uplands as evidence for some amount of dispersal into this habitat type, especially when coupled with the lack of evidence for oak mistletoe genetic isolation across habitat types in the study area.

Despite this evidence for oak mistletoe gene flow across habitat types, infrequent dispersal between trees could exacerbate the effects of habitat-specific variation in establishment rates on mistletoe habitat relationships (Reid 1989, Reid et al. 1995). I considered the cedar waxwing and eastern bluebird as the two principal dispersers of oak mistletoe fruits in the study area based on frugivory detections. The cedar waxwing is considered an effective seed disperser in general (Labbé & King 2020) and for mistletoes (Overton 1994), yet its flocking behavior could drive limited between-tree dispersal in oak mistletoe (Labbé & King 2020). While eastern bluebird behavior varies seasonally (Gowaty & Plissner 2020), individuals observed foraging on oak mistletoe fruits in the study area in winter also exhibited flocking behavior. Despite the widespread distribution of avian frugivores and lack of evidence for cryptic habitat specificity in the study area, limited seed dispersal between host trees by these dispersers could still play some role in maintaining oak mistletoe habitat relationships primarily driven by other factors.

Future research

I failed to find evidence for genetic isolation between oak mistletoe populations from forested wetlands and urban areas, both habitat types where the parasite is common in the study area. Samples are needed from the limited mistletoe presence in forested uplands to fully understand what is driving low rates of mistletoe occurrence in this habitat type. I assume analyses with such samples would result in patterns of genetic structure like those shown here. However, the potential existence of a genetically distinct group of mistletoes restricted to forested uplands could provide evidence for cryptic habitat specificity by avian seed dispersers.

Similarly, in this study, sampling for population genetics analyses occurred in the Coastal Plain region of Virginia and North Carolina, but oak mistletoe also occurs in the Piedmont region of the study area. The inclusion of oak mistletoe samples from the Piedmont is needed to test for the presence of genetic isolation by habitat in that region. If present, the genetic isolation of distinct oak mistletoe populations in forested uplands in the Piedmont or elsewhere could be maintained if mistletoes from populations inhabiting other habitat types were unable to invade these habitats due to local environmental conditions, such as low light availability in denser stands (Matula et al. 2015, Usta & Yilmaz 2021).

An understanding of the geographic extent of the potential cryptic host race identified here would require sampling of oak mistletoes from different host species across the range of the parasite. If detected beyond the study area, subsequent analyses could reveal the most likely geographic origin for genetically distinct oak mistletoes parasitizing *Nyssa* spp. (Hawkins 2010). The identification of such a location could provide insight into the factors responsible for the lack of gene flow between oak mistletoes on trees in the genus *Nyssa* and on other host species.

Differentiation of host races can lead to physiological adaptations such that establishment on the preferred host species is significantly higher than on other host species (May 1971, Clay et al. 1985). Such specialization can induce further genetic isolation and the maintenance of host races, although in stands of mixed host species other barriers to hybridization due to pollen dispersal are needed (Clay et al. 1985). Thus, given the genetic clustering of individuals collected from *Nyssa* spp. in the study area, a straightforward extension of my work is a common garden planting experiment to test for significant variation in establishment across host species (May 1971, Clay et al. 1985).

Conclusion

Host availability could drive mistletoe habitat relationships if a mistletoe race restricted to a habitat-specific host is the predominant mistletoe in an area. In contrast, in the study area, generalist oak mistletoes are widespread and I have shown the affinity of oak mistletoe for forested wetland habitat to be independent of host availability (Chapter 2). Results described here suggest that this mistletoe habitat relationship is also largely independent of avian disperser behavior, leaving local environmental conditions as the most likely driver of this pattern.

Table 4 Eight polymorphic microsatellite loci and repeat motifs, primer sequences, and specific melt temperatures

ID	SSR	Forward primer (5’-3’)	Tm(°C)	Reverse primer (5’-3’)	Tm(°C)	Size (bp)
c14652	(TGG)6	AATAAGCTCCAAAATTACGCTC	56.88	CAATATGCAAGGGAAGGTATG	57.15	140
c15116	(CGT)7	AAGTTCTCGTACTGCTTGGTG	57.16	TAGTAGAAGGTCTCCACCTTGG	57.49	137
c15928	(GGA)6	TACATATCAACCAAGAACGGAG	56.82	TTGATCTAAGCTTTCTCATTCG	56.48	255
c17395	(GCT)7	AGGTTTCAGGATCAGAGAACTG	57.52	CAATACCTGTGACGAATCAATC	57.09	254
c2003	(CTC)6	ACTCCCAAGTTCTTCTCACACT	57.03	AGGAGGATTTGCATTGACAT	57.04	243
c11123	(CCA)6	TTTTTACCTGCTTCGGTTACTC	57.66	TGATGTAGATCTCGCTCGTAAC	57.15	272
c12656	(TTA)5	GGGAAACATTTATGAAAGTGC	56.28	ATTCTCTCTAGCCTGAATGGAG	56.83	218
c13227	(TCC)6	ACAAGCTCTTACACACGCTTC	57.31	AATGCATTGGAGAAAGTAATTG	56.05	130

Table 5 Sample sizes (N), observed (HO) and expected (HE) proportions of heterozygotes, and number of alleles (A) for each locus and population combination. Asterisks denote combinations where HO differed significantly from expectation based on Hardy-Weinberg equilibrium, with such tests conducted in GENEPOP (Rousset 2008; dememorization 10000, batches 100, iterations per batch 5000)

Population		c13227			c14652			c15928			c15116			c11123			c12656			c2003		
	N	HO	HE	A	HO	HE	A	HO	HE	A	HO	HE	A	HO	HE	A	HO	HE	A	HO	HE	A
Outer CP so., urb	140	0.4	0.4	5	0.6	0.7	7	0.3	0.3	2	0.3	0.3	3	0.2	0.2	2	0.4	0.4	4	0.6	0.6	6
Outer CP so., for	120	0.4	0.4	4	0.6	0.6	8	0.3	0.3	3	0.5	0.5	3	0.3	0.3	2	0.5	0.5	3	0.6	0.6	4
Inner CP so., urb	80	0.4	0.4	5	0.4	0.5	6	0.3	0.3	2	0.2	0.3*	4	0.2	0.3	3	0.5	0.5	5	0.6	0.6	4
Inner CP so., for	100	0.5	0.6	6	0.6	0.7	7	0.3	0.3	2	0.4	0.4	4	0.3	0.3	3	0.4	0.4	4	0.5	0.6	6
CP no., urb	37	0.1	0.1	3	0.7	0.7	4	0.6	0.5	3	0.5	0.5	3	0.2	0.2	2	0.4	0.4	3	0.6	0.5	4
CP no., for	40	0.3	0.5	4	0.7	0.7	7	0.2	0.3	2	0.3	0.3	3	0.2	0.3	2	0.3	0.4	3	0.4	0.7*	5

Table 6 Posterior means of species-specific effects of forested wetland on occurrence and the linear and quadratic effects of date on detection for those wintering forest bird species detected during surveys and for which I estimated significant relationships. Statistically significant coefficient estimates had 95% credible intervals that did not overlap 0 and are here shown in bold

Species	Occupancy	Detection	
	Forested wetland	Date	Date^2
mourning dove (*Zenaida macroura*)	0.21	**0.96**	-0.16
red-shouldered hawk (*Buteo lineatus*)	**1.66**	0.15	-0.22
red-headed woodpecker (*Melanerpes erythrocephalus*)	**-2.1**	-0.49	-0.03
tufted titmouse (*Baeolophus bicolor*)	**-1.73**	**0.92**	0.26
golden-crowned kinglet (*Regulus satrapa*)	0.13	**-0.43**	0
white-breasted nuthatch (*Sitta carolinensis*)	**-1.43**	0.09	0.08
brown creeper (*Certhia americana*)	-0.42	**-0.8**	0.02
winter wren (*Troglodytes hiemalis*)	0.88	**-0.53**	0.01
Carolina wren (*Thryothorus ludovicianus*)	**1.56**	0.26	**0.25**
gray catbird (*Dumetella carolinensis*)	**2.14**	-0.37	0.06
hermit thrush (*Catharus guttatus*)	1.66	**-0.7**	0.01
American robin (*Turdus migratorius*)	1	**-0.63**	-0.09
American goldfinch (*Spinus tristis*)	-0.27	0.19	**0.36**
swamp sparrow (*Melospiza georgiana*)	**1.09**	-0.08	0.31
eastern towhee (*Pipilo erythrophthalmus*)	0.63	0.26	**0.34**
rusty blackbird (*Euphagus carolinus*)	**1.78**	0.44	-0.02
common grackle (*Quiscalus quiscula*)	0.87	**1.02**	-0.02
common yellowthroat (*Geothlypis trichas*)	0.63	**1.06**	0.38
pine warbler (*Setophaga pinus*)	-1.15	**1.26**	0.26
yellow-rumped warbler (myrtle) (*Setophaga coronata coronata*)	**2.68**	-0.1	0.02

Table 7 Results from analyses of molecular variance (AMOVA) for oak mistletoe (*Phoradendron leucarpum*) among habitat types (a, b) and host species (c, d) within host association regions quantified using either F_{ST}-like differences in alleles (a, c) or R_{ST}-like differences in fragment length (b, d)

(a)

Source of variation (F_{ST})	Sum of squares	Variance components	Percentage of variation	p-value
Among regions	19.33	0.0082	0.51	0.033
Among habitat types within regions	22.90	0.036	2.27	0
Within habitat types within regions	1563.92	1.55	97.21	0
Total	1606.15	1.60	100	

(b)

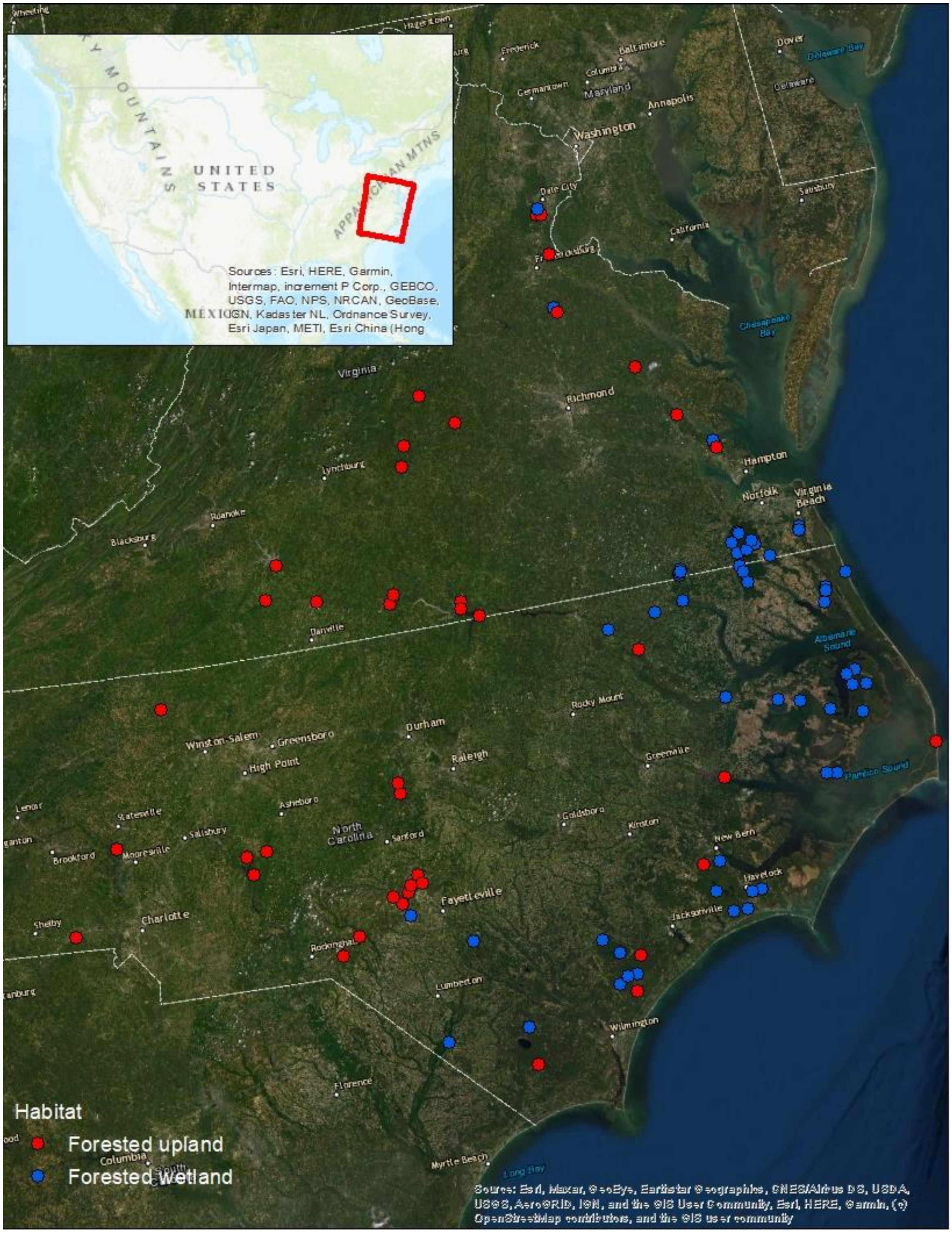
Source of variation (R_{ST})	Sum of squares	Variance components	Percentage of variation	p-value
Among regions	1154.51	-3.10	-1.63	0.55
Among habitat types within regions	4809.52	8.68	4.57	0
Within habitat types within regions	182084.73	184.20	97.06	0
Total	188048.75	189.78	100	

(c)

Source of variation (F_{ST})	Sum of squares	Variance components	Percentage of variation	p-value
Among regions	19.33	0.0047	0.29	0.01
Among host species within regions	101.90	0.075	4.71	0
Within host species within regions	1484.93	1.52	95.00	0
Total	1606.15	1.60	100	

(d)

Source of variation (R_{ST})	Sum of squares	Variance components	Percentage of variation	p-value
Among regions	1154.51	-4.46	-2.35	0.70
Among host species within regions	19340.52	19.85	10.45	0
Within host species within regions	167553.72	174.58	91.90	0
Total	188048.75	189.97	100	



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Fig. 5 Locations of survey plots in forested upland and forested wetland habitats

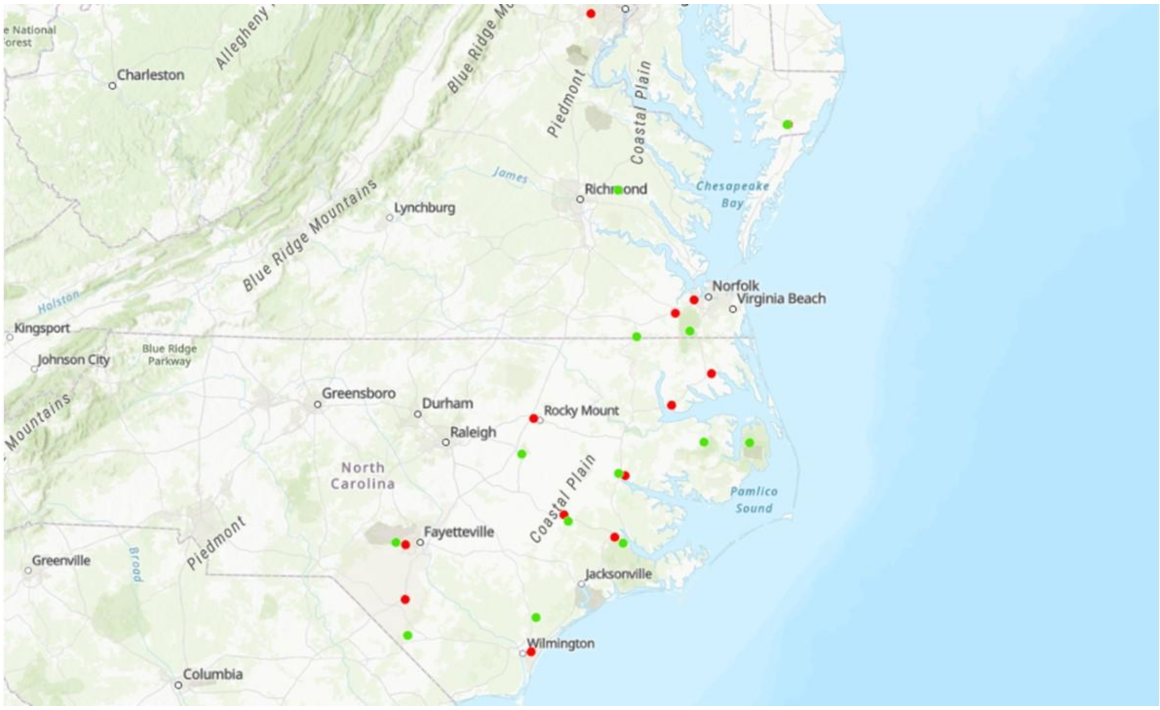


Fig. 6 Locations where oak mistletoe samples were collected for a population genetics study in the Coastal Plain of Virginia and North Carolina; locations colored red were in urban habitat, locations colored green were in forested wetland habitat

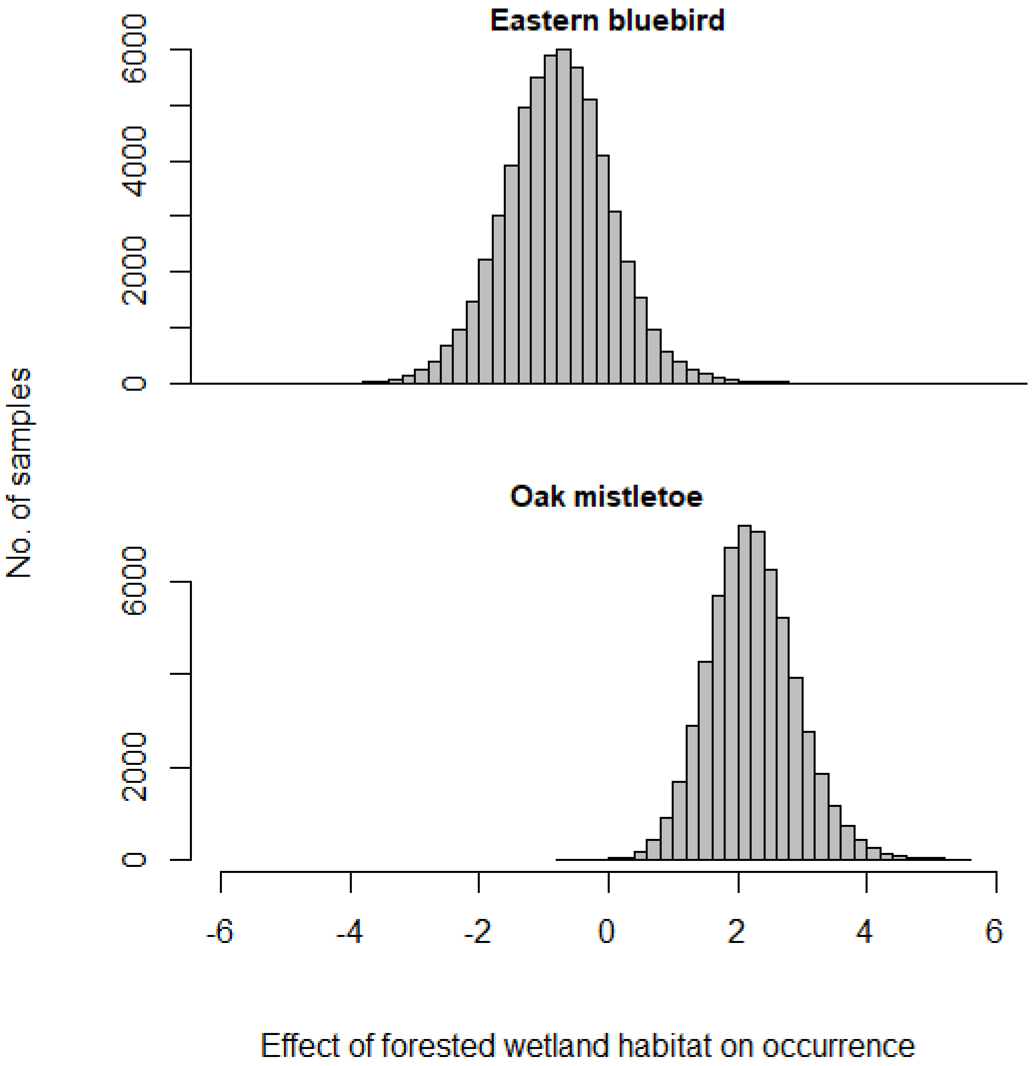


Fig. 7 Posterior distributions of the effects of forested wetland habitat on the occurrence of oak mistletoe (*Phoradendron leucarpum*) and eastern bluebird (*Sialia sialis*). These effects were deemed statistically different as greater than 95% of the samples from the posterior of this relationship for oak mistletoe were greater than such samples for eastern bluebird (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015)

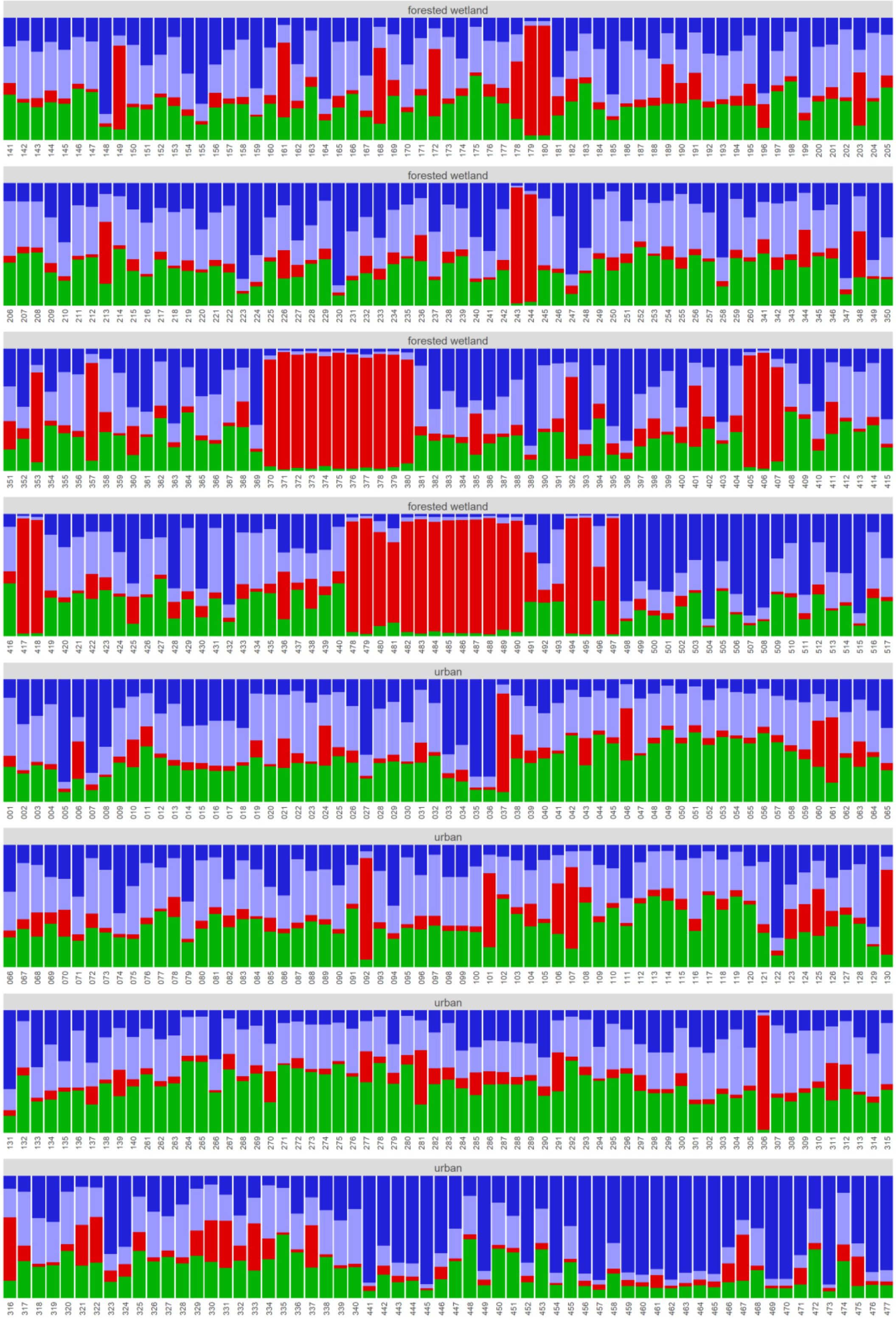


Fig. 8 Proportions of ancestry from four inferred populations represented by dark blue, light blue, red, and green colors for oak mistletoe samples (vertical lines with unique numeric identification) grouped by forested wetland and urban habitats as estimated by STRUCTURE (Pritchard et al. 2000) and optimally aligned across runs with CLUMPP (Jakobsson & Rosenberg 2007)

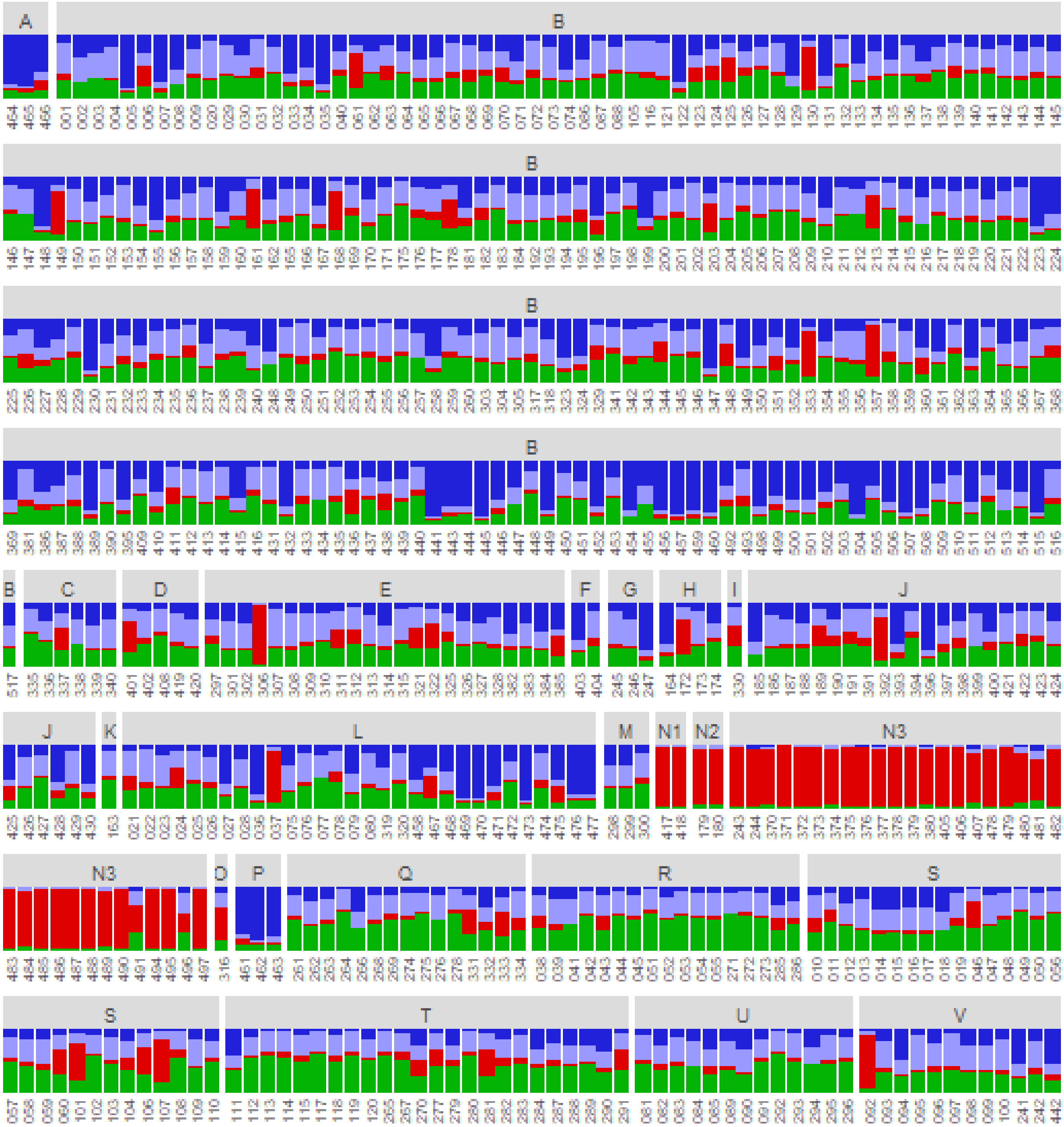


Fig. 9 Ancestry proportions for oak mistletoe samples grouped by host species as estimated by STRUCTURE (Pritchard et al. 2000) and optimally aligned across runs with CLUMPP (Jakobsson & Rosenberg 2007). Host species codes as follows: A = *Acer saccharinum*, B = *Acer rubrum*, C = *Acer* spp., D = *Alnus serrulata*, E = *Betula nigra*, F = *Fraxinus pennsylvanica*, G = *F. profunda*, H = *Fraxinus* spp., I = *Liquidambar styraciflua*, J = *F. caroliniana*, K = *Quercus laurifolia*, L = *Gleditsia triacanthos*, M = *Q. phellos/laurifolia*, N1 = *Nyssa aquatica*, N2 = *N. sylvatica*, N3 = *N. biflora*, O = *Ulmus parviflora*, P = *Ulmus* spp., Q = *Quercus* (*Lobatae* sub-genus) spp., R = *Pyrus calleryana*, S = *Q. nigra*, T = *Q. phellos*, U = *U. alata*, V = *U. americana*

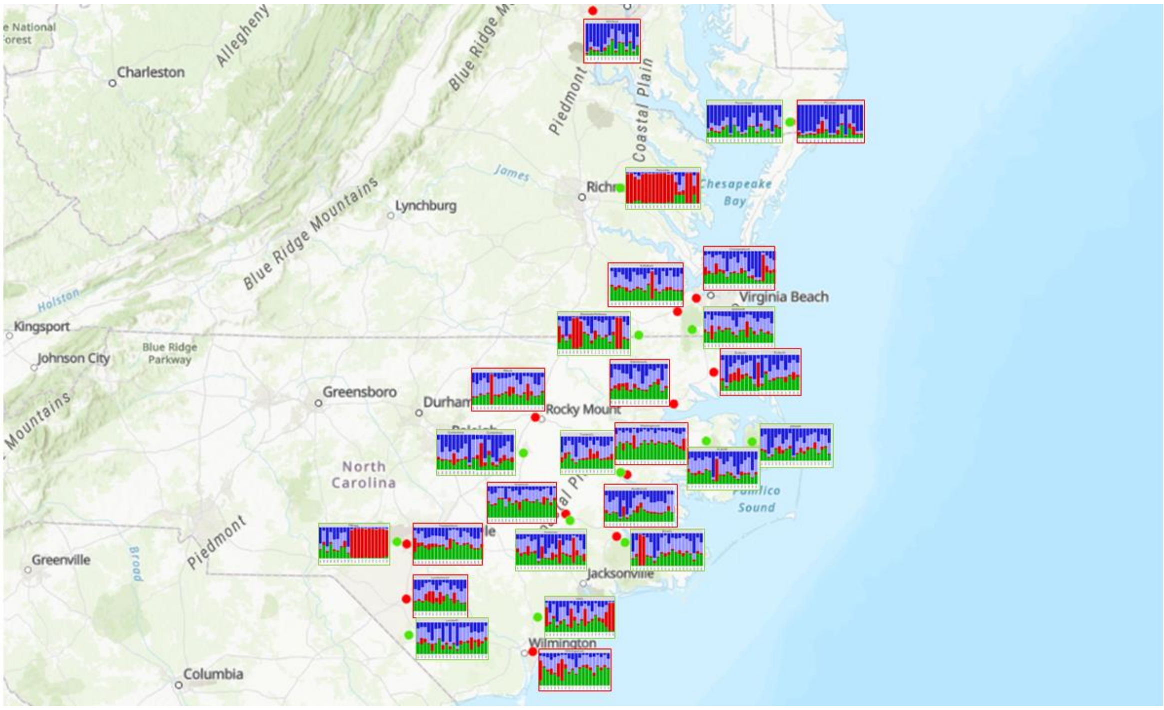


Fig. 10 Ancestry proportions for oak mistletoe samples grouped by sampling location and habitat type (locations colored red were in urban habitat, locations colored green were in forested wetland habitat) as estimated by STRUCTURE (Pritchard et al. 2000) and optimally aligned across runs with CLUMPP (Jakobsson & Rosenberg 2007)

CHAPTER 4

PLANTING EXPERIMENTS PROVIDE SUPPORT FOR A RELATIONSHIP BETWEEN LIGHT CONDITIONS AND ESTABLISHMENT OF A BIRD-DISPERSED MISTLETOE, *PHORADENDRON LEUCARPUM* (RAF.) REVEAL & M. C. JOHNST.

4.1 INTRODUCTION

The importance of local versus regional processes in determining plant community structure remains a controversial topic in plant ecology (Harvey et al. 1983, Tuomisto et al. 2003, Collins & Carson 2004, Gilbert & Lechowicz 2004, Lu et al. 2011, Alexander et al. 2012, Foster et al. 2011). An intermediate viewpoint holds that regional dispersal limitation provides an explanation for similar species that coexist despite direct competition for local resources (Hutchinson 1959, Tilman 1997). This intermediate viewpoint has been supported by empirical results (Tilman 1997, Turnbull et al. 2000) and incorporated in seed dispersal theory (Nathan & Muller-Landau 2000). The high visibility of many mistletoe species coupled with both their dependence on avian frugivores for seed dispersal and discreteness of establishment sites (Overton 1994, Alexander et al. 2012, Mellado & Zamora 2014b) makes the study of their ecology especially suitable for addressing this question (Martínez del Rio et al. 1996, Carlo & Aukema 2005, Roxburgh 2007, Caraballo-Ortiz et al. 2017).

Seed addition experiments can be used to determine the degree to which dispersal limitation or establishment limitation drive plant distribution and abundance (Clark et al. 2007). Such experiments are often conducted in the field or in a controlled setting that mimics field conditions to avoid ignoring unidentified environmental factors driving patterns (Renne et al. 2001, Levine & Murrell 2003, Clark et al. 2007). Several factors related to field settings often lead to small effect sizes and ambiguous results, including high seedling mortality and incomplete knowledge about the pre-existing seed bank (Clark et al. 2007). The latter problem does not exist in seed addition experiments for mistletoe species, as the seed bank is not hidden in soil and is more easily quantified prior to seed sowing.

The oak mistletoe [*Phoradendron leucarpum* (Raf.) Reveal & M. C. Johnst.] is a stem parasite distributed across the southern United States (Kuijt 2003). This winter-fruiting evergreen shrub is dependent on avian frugivores for seed dispersal beyond the host tree of origin (Sutton 1951, Gougherty 2013), after which a glue-like substance called viscin maintains attachment of the seed to the host stem. As with other mistletoes, the endophyte system acquires resources from hosts via a haustorium, which forms a disk on the host stem prior to penetration (Kuijt 1969).

In the Coastal Plain and Piedmont regions of Virginia and North Carolina, the study area of interest, oak mistletoe is more common in forested wetlands of the Coastal Plain than in other forested habitats (Weakley et al. 2012). However, some potential host tree species such as red maple (*Acer rubrum* L.) occur in a variety of forested habitats in the region. Such variation in infection intensity across host tree species and habitat remains unexplained (Panvini 1991, Kuijt 2003, Hawkins 2010, Weakley et al. 2012).

Avian seed disperser behavior has been shown to be an important factor driving the distribution of mistletoes (Martínez del Rio et al. 1996, Aukema 2004) and could play a role in determining patterns of oak mistletoe occurrence (Panvini 1991, Weinkam 2013). Evidence from avian survey data and oak mistletoe population genetics suggest that dispersal limitation is unlikely to play a large role in the affinity of oak mistletoe for forested wetland habitat in eastern Virginia and North Carolina (Chapter 3). Alternatively, observed oak mistletoe habitat relationships in the region could be driven by consistent differences in host tree quality attributed to local environmental conditions.

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 hydrology (Norton & Smith 1999), host trees growing in wetlands may be of higher quality for water-limited oak mistletoe shrubs (Panvini 1991) due to greater water availability as evidenced by higher transpiration rates (Gregg & Ehleringer 1990, Yan 1992, Pauliukonis & Schneider 2001). Physiological responses of trees growing in flooded or compacted soils to reduced soil O_2 (Larcher 1973) may make individuals in wetlands or urban areas higher quality hosts for oak mistletoe. Greater permeability of the vascular cambium in hydrophytic trees compared to mesophytic trees (Hook & Brown 1972) and the production of porous aerenchyma tissue in wetland plants (Larcher 1973, Keddy 2010) are examples of such mechanisms.

I have previously shown the presence of a positive relationship between oak mistletoe occurrence and forested wetland habitat in eastern Virginia and North Carolina even after accounting for host availability (Chapter 2). Here I tested for the presence of such a relationship after accounting for variation in canopy openness measured at ground level. The lack of a significant relationship between habitat and mistletoe occurrence in such a model would provide evidence for light availability as a driver of mistletoe distribution, assuming such canopy openness measurements are related to light availability at mistletoe establishment sites. Given weaknesses of purely correlative studies at separating process from pattern (MacKenzie et al. 2004), I used experimental seed sowing methods to complement findings from occurrence models fit to field survey data.

Seed addition has been used in common garden experiment settings 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 & Nicolson 2008, Luo et al. 2016). Here I simulated oak mistletoe seed dispersal at both field sites and potted host trees across a range of light availability and flood regime treatments. Reduced establishment rates under abiotic conditions typical of forested uplands would indicate the potential importance of variation in local environment as a determinant of observed oak mistletoe habitat relationships (Clark et al. 2007). Alternatively, a lack of support for relationships between oak mistletoe establishment and abiotic factors would maintain dispersal limitation as a viable mechanism for driving these patterns.

4.2 METHODS

Habitat relationship versus canopy cover

I used stratified random sampling to select 96 circular plots with 25-m radii in forested wetland and forested upland habitats of the study area (Fig. 11). Plots were surveyed for the presence or absence of oak mistletoe shrubs during one of five winter seasons (Dec –Mar) from the 2015 –2016 winter season to that of 2019 –2020. More details on the survey protocol and the quantification of host availability can be found elsewhere (Chapter 2).

Plot-level percent 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). I analyzed oak mistletoe occurrence data using a model very similar to that used previously to show a relationship between habitat type and occurrence rate after accounting for host availability (Chapter 2). Here I included an additional parameter to represent the relationship between observed canopy openness and oak mistletoe occurrence.

Field planting experiment to simulate dispersal to different local light environments

I conducted an oak mistletoe seed sowing study in the field at two forested wetland sites in southeastern Virginia with mistletoe: 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 within 15 m of an edge (“edge” plots) and portions greater than 15 m from an edge (“inner” plots) to ensure planting under a wide range of local light conditions (Gehlhausen et al. 2000). Mistletoe seed collection and planting at a given plot occurred during one of the three winter seasons (Dec –Mar) 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, sd = 18 days). The central point of each plot was visited and the closest suitable host trees to this point were used for seed sowing. Suitable host trees were typically individuals of red maple, swamp tupelo (*Nyssa biflora* Walter), and ash spp. (*Fraxinus* L. spp.), the most frequently parasitized wetland trees in the region (Baldwin, Jr. & Speese 1957). The distribution of oak 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 done on consistently thin branch sections (mean = 6.8 mm diameter, sd = 3.5 mm; Overton 1994, Mellado & Zamora 2014b). The number of branches selected varied with the plot-specific availability of suitable branches within reach for planting. Seeds from mistletoe shrubs parasitizing different host species were allocated randomly to host branches during planting (Mellado & Zamora 2014b) 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 identity and branch identity nested within plot in generalized linear mixed models (GLMMs) allowed me to account for the lack of independence among seeds planted on the same branch and in the same plot (Bolker et al. 2009).

I removed the exocarp from oak mistletoe fruits prior to planting seeds and used either viscin (n = 400; May 1971, Mellado & Zamora 2014b) or EcoGlue^{TM} (n = 690; Willamette Valley Company, Eugene, Oregon) for adhering the seeds to host branches. Surviving seedlings at each plot were monitored approximately every three months until the emergence of leafy stems were detected (Herrera et al. 1994). I used percent 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).

I considered germinated seeds as those with green, emergent hypocotyls present after approximately three months and treated the binary germination state of each seed as a Bernoulli random variable (Mellado & Zamora 2014b). Variation in germination rates was modeled as a function of fixed and random factors with GLMMs and a logit link (Bolker et al. 2009). I used a similar approach for analyzing data on the binary state of whether a seed remained for approximately three months or disappeared, also viewed as a Bernoulli random variable. In both cases, I used AIC$_c$ 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 & Anderson 2002, Burnham et al. 2011). The GLMMs, model comparisons, and similar analyses described in the remainder of this Methods 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 approximately three months included the fixed effects of branch diameter, planting method (glue or natural viscin), and site (GDSNWR or SQSNAP), and the random effects of plot identity and branch identity nested within plot (Table 8). 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. The set of models of variation in germination rates included combinations of the fixed effects of percent canopy openness, planting method, and year of planting, while all models included the random effects of branch identity (Table 8). These models of variation in germination rate did not include the random effects of plot identity, as I 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 standard deviation.

Controlled planting experiment under different light and flood regime conditions

I designed a controlled experiment to jointly estimate the effects of local light environment and flood regime on oak mistletoe establishment. In winter 2016–17 I transplanted 115 red maple saplings from a single population in Halifax County, North Carolina into pots. These potted red maple saplings were transported to the Virginia Tech Hampton Roads Agricultural Research and Extension Center in the city of Virginia Beach, Virginia and placed in plastic tubs (3–4 saplings per tub). Beginning in 2017, tubs were subjected to one of three growing season (mid-April to mid-October) 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).

After maintaining the flood regime treatments during the 2017 growing season, I used the viscin planting method described above to adhere oak 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. I checked all seeds after 3 months and assessed germination rates as described in the previous section. 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 9; Bolker et al. 2009).

During the 2018 growing season, in addition to reinitiating flood regime treatments at the tub level, I subjected germinated mistletoe seeds to one of 4 light availability treatments. Light availability treatments were applied at the sapling level under a split-plot design, with saplings representing sub-plots within plastic tubs as main plots.

Saplings hosting germinated mistletoe seeds in physical positions suitable for affixing sleeves of light-altering cloth material (i.e. along internodes; n = 51 saplings) were randomly assigned one of four 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) to create moderate shade (n = 10 saplings, n = 33 seeds), and translucent tulle (n = 9 saplings, n = 36 seeds) and no covering (n = 17 saplings, n = 55 seeds) as control treatments (Randle et al. 2018).

I checked the planted mistletoe seeds approximately every 3 months for a total of 18 months and recorded data on seedling survival to 18 months and the presence of leafy stems. As with data from the field planting experiment, I treated this data as Bernoulli random variables and analyzed rates of survival to 18 months and leafy stem development separately using GLMMs (Mellado & Zamora 2014b). Models varied in their inclusion of the fixed effects of light availability and flood regime treatments and were ranked using AIC_c (Table 9). All models included random effects corresponding to tub identity and sapling identity nested within tub as described above for the analysis of germination rates. Random sapling effects accounted for unmeasured variation between saplings that received light availability treatments (n = 51) and those that did not (n = 32).

4.3 RESULTS

Habitat relationship versus canopy cover

I considered the association between oak mistletoe occurrence at survey plots and forested wetland habitat statistically significant as the 95% credible interval for this effect did not overlap 0 after accounting for both observed canopy openness and host availability (posterior mean = 2.27, lower credible interval = 0.95, upper credible interval = 3.74). While 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, upper credible interval = 3.63), the effect of observed canopy openness on mistletoe occurrence was deemed non-significant (posterior mean = 0, lower credible interval = -0.73, upper credible interval = 0.65).

Field planting experiment to simulate dispersal to different local light environments

Of 1099 seeds planted in GDSNWR and SQSNAP, 71% remained after approximately three months. Planting method (glue or natural viscin) 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 only collectively received 27% of the AIC_c weight. Of those seeds that remained after three 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 1 inner and 7 edge plots. Leafy stems on seven seedlings arose from epicotyls, four seedlings had leafy stems develop from the endophytic system only, and two seedlings produced leafy stems from both the epicotyl and haustorial disk.

Controlled planting experiment under different light and flood regime conditions

Of 599 planted seeds, 360 remained on potted host saplings approximately three 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 (n = 28 saplings), and 104 seeds available to establish on saplings left unflooded (n = 30 saplings). Sample sizes for light availability treatments were given in Methods.

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 I interpreted as only minimal support for a relationship between flood regime treatment and oak 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 delta AIC_c (Tables 10, 11; Burnham et al. 2011). Models that included the effects of flood regime treatment collectively received 30% of the AIC_c weight across models of variation in survival and 37% of this weight across models of variation in leafy stem development. Models that included the effects of light treatment collectively received 69% of the AIC_c weight across models of variation in survival and 82% of this weight across models of variation in leafy stem development. I interpreted these results as strong support solely for a relationship between light availability and leafy stem development (Figure 12).

4.4 DISCUSSION

The finding of a positive relationship between forested wetland habitat and oak mistletoe occurrence after accounting for ground-level canopy openness suggests that other factors are important determinants of the distribution of mistletoe in the study area. The widespread distribution of commonly parasitized tree species, coupled with similar patterns of habitat specificity shown by many frugivorous birds in the region leaves variation in abiotic conditions as a viable mechanism driving this pattern in oak mistletoe occurrence (Chapters 2, 3). Planting experiments described here provide evidence to support local light availability as an abiotic variable capable of limiting oak mistletoe establishment and driving its association with forested wetlands in eastern Virginia and North Carolina.

Evidence for establishment limitation in oak 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 oak mistletoe establishment and abiotic variables manipulated in planting experiments could result from three scenarios: 1) oak 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 oak mistletoe establishment were not included in the experiment, or 3) sample sizes were too small to detect treatment effects. Instead, and more typical of studied plant populations (Renne et al. 2001, Clark et al. 2007), I found evidence that establishment limitation outweighs dispersal limitation in determining the distribution of oak mistletoe. Results presented here support a relationship between local light availability conditions manipulated using shade cloth treatments and oak mistletoe establishment on potted host saplings as measured by leafy stem development.

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

Red maple saplings subjected to flooding treatments showed visible changes in morphology similar to those responses to flood stress described in a previous greenhouse study (Day 1987). Yet, I did not find strong support for relationships between germination rates of oak 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 oak mistletoe seeds are known to readily germinate even on non-host material (Randle et al. 2018) and so I assumed that germination rates on hosts subjected to different hydrological conditions would be similar (May 1971). While oak mistletoe seeds require light to germinate (Gardner 1921), results shown here suggest that germination rates are not sensitive to variation in light availability under field conditions.

The large variation in host branch diameter available for inoculation with oak mistletoe seeds in the field allowed me 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 similar to those from a planting experiment using oak 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 I found the opposite pattern in results from my planting experiment on potted host saplings with roughly equal proportions of leafy stems developing from the two origins in my field planting experiment.

In contrast with the planting experiment on potted host saplings, I was unable to discern an effect of local light availability conditions on oak mistletoe establishment in the field due to extremely low seedling survival rates, typical of plant populations heavily influenced by post-dispersal factors (Clark et al. 2007). The much higher establishment rate for seeds planted on potted host saplings than on host trees in the field supports the existence of a positive relationship between light availability and oak mistletoe establishment. Field sites had consistently lower levels of light availability than the site hosting the controlled experiment due to canopy shade, and a majority of field planting plots where I detected establishment among planted oak mistletoe seeds were near a forest edge.

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, Mellado & Zamora 2014b), 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 & Peterson 2014). As I have shown for oak mistletoe in eastern Virginia and North Carolina (Chapter 3), 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 & 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 & Smith 1999). A small reduction in mistletoe establishment success in the less preferred habitat type 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 & Nicolson 2008) and stand density (Matula et al. 2015, Usta & 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 & Bernhardt 1983), and despite logistical challenges, studies of relationships between mistletoe occurrence and light availability conditions should involve data collected from locations within the canopy (Shaw & Weiss 2000). I did not find a relationship between oak mistletoe occurrence and percent canopy closure measurements made at ground level. In certain sampled forest types with reduced tree densities I believe a correlation may exist between light availability conditions experienced by oak mistletoe shrubs in the canopy and those measured at ground level, but quantifying light availability at canopy heights representative of the distribution of oak mistletoe is necessary to determine the relationship between this abiotic variable and mistletoe occurrence.

Observations of non-fruiting oak mistletoe individuals surviving in dense shade (Kuijt 1969) and physiological studies showing that oak mistletoe can behave like a shade plant (Panvini 1991, Strong et al. 2000) suggest that low light availability may only reduce oak mistletoe establishment and survival at a young age. Continued monitoring of the survival of oak mistletoe seedlings growing under a variety of light availability conditions beyond the establishment and early growth phases studied here would inform on the ability of oak mistletoe to persist under dense shade conditions. Such monitoring data that informed 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.

Conclusion

I took advantage of the discrete establishment sites and easily quantifiable pre-planting seed rain of oak mistletoe when interpreting results from planting experiments. While extremely low survival rates of oak mistletoe seedlings planted in the field made any relationships with local environmental conditions difficult to discern, I could largely attribute variation in counts of established seedlings on potted host saplings to treatment effects. I found evidence for a relationship between manipulated local light availability and seedling establishment rates on such host saplings. If dispersal limitation was the primary driver of variation in oak mistletoe occurrence across habitats with different light availabilities, I 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 from different habitat types in my study area is needed to connect this finding to observed oak mistletoe habitat relationships in eastern Virginia and North Carolina.

Table 8 Descriptions of models of variation in germination rates of oak mistletoe seeds planted at field sites and rates of such seeds remaining to approximately three months. “Y” above 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 above: “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 percent canopy openness

Variable	Response	
	Seed remaining rate	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

Table 9_ Descriptions of models of variation in germination rates of oak mistletoe seeds planted on potted host saplings and rates of such seedlings surviving and developing leafy stems. “Y” above 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 above: “flooding” = flood regime treatment and “light” = shade cloth treatment

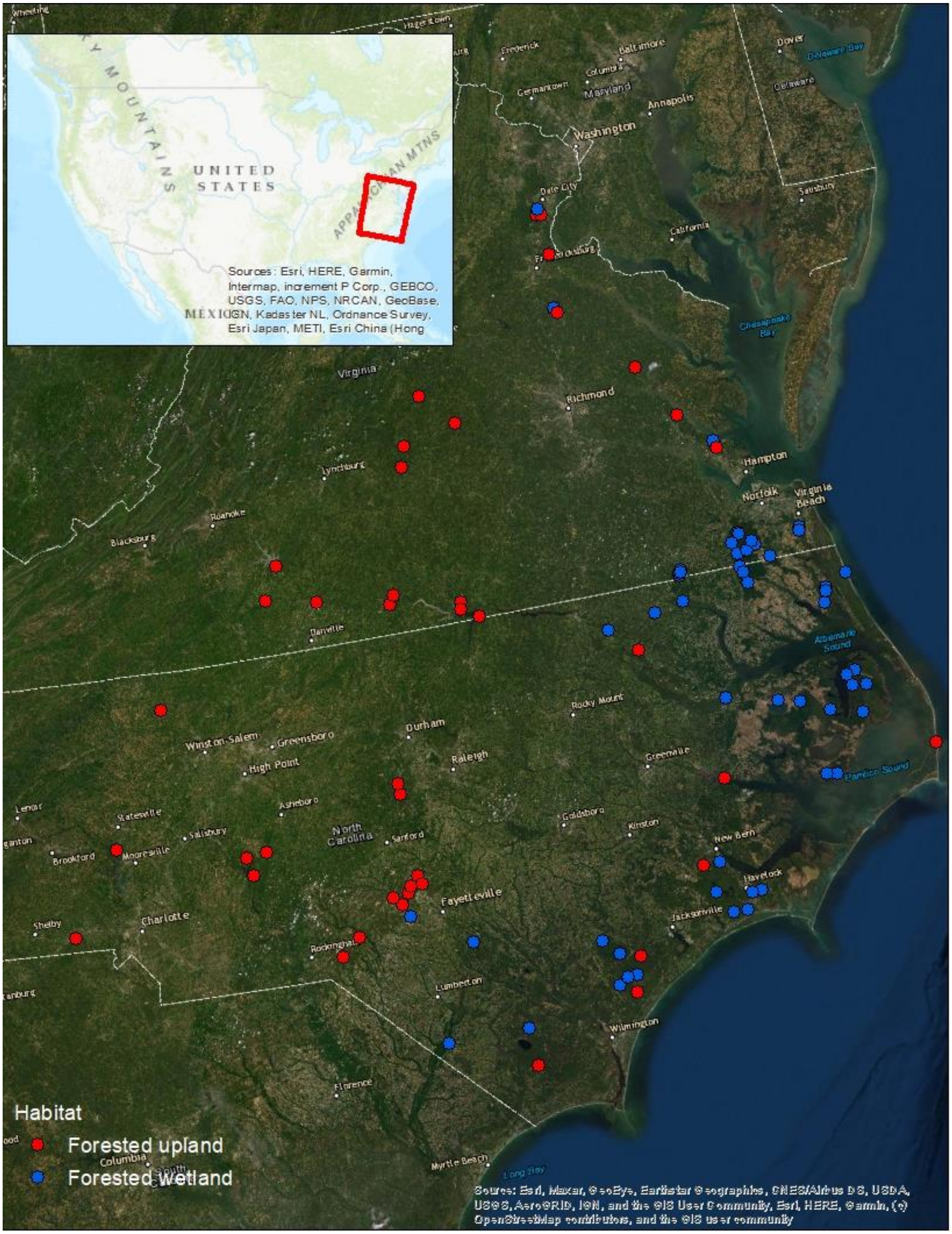
Variable	Response		
	Germination rate	Seedling survival rate	Leafy stem development rate
Shade cloth treatment	N	Y	Y
Flooding treatment	Y	Y	Y
Tub (random)	Y	Y	Y
Sapling (random, nested in plot)	Y	Y	Y

Table 10 Alternative generalized linear models for the relationships between rates of oak mistletoe seedling survival to 18 mo. and the fixed effects of flood regime treatments and light availability treatments as ranked by AIC$_c$. All models included the random effects of plastic tub and nested sapling identities

Variables included in model	K	AIC$_c$	Delta AIC$_c$	AIC$_c$ weight	Cumulative weight	LL
Intercept + light	6	321.96	0	0.48	0.48	-154.81
Intercept + light + flood	8	323.59	1.64	0.21	0.69	-153.51
Intercept (null)	3	323.59	1.64	0.21	0.91	-158.75
Intercept + flooding	5	325.23	3.27	0.09	1	-157.5

Table 11 Alternative generalized linear models for the relationships between rates of oak mistletoe leafy stem development and the fixed effects of flood regime treatments and light availability treatments as ranked by AIC_c. All models included the random effects of plastic tub and nested sapling identities

Variables included in model	K	AIC_C	Delta AIC_c	AIC_c weight	Cumulative weight	LL
Intercept + light	6	323.23	0	0.52	0.52	-155.45
Intercept + light + flood	8	324.33	1.1	0.3	0.82	-153.88
Intercept (null)	3	326.38	3.15	0.11	0.93	-160.14
Intercept + flooding	5	327.33	4.1	0.07	1	-158.55



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Fig. 11 Locations of survey plots in forested upland and forested wetland habitats

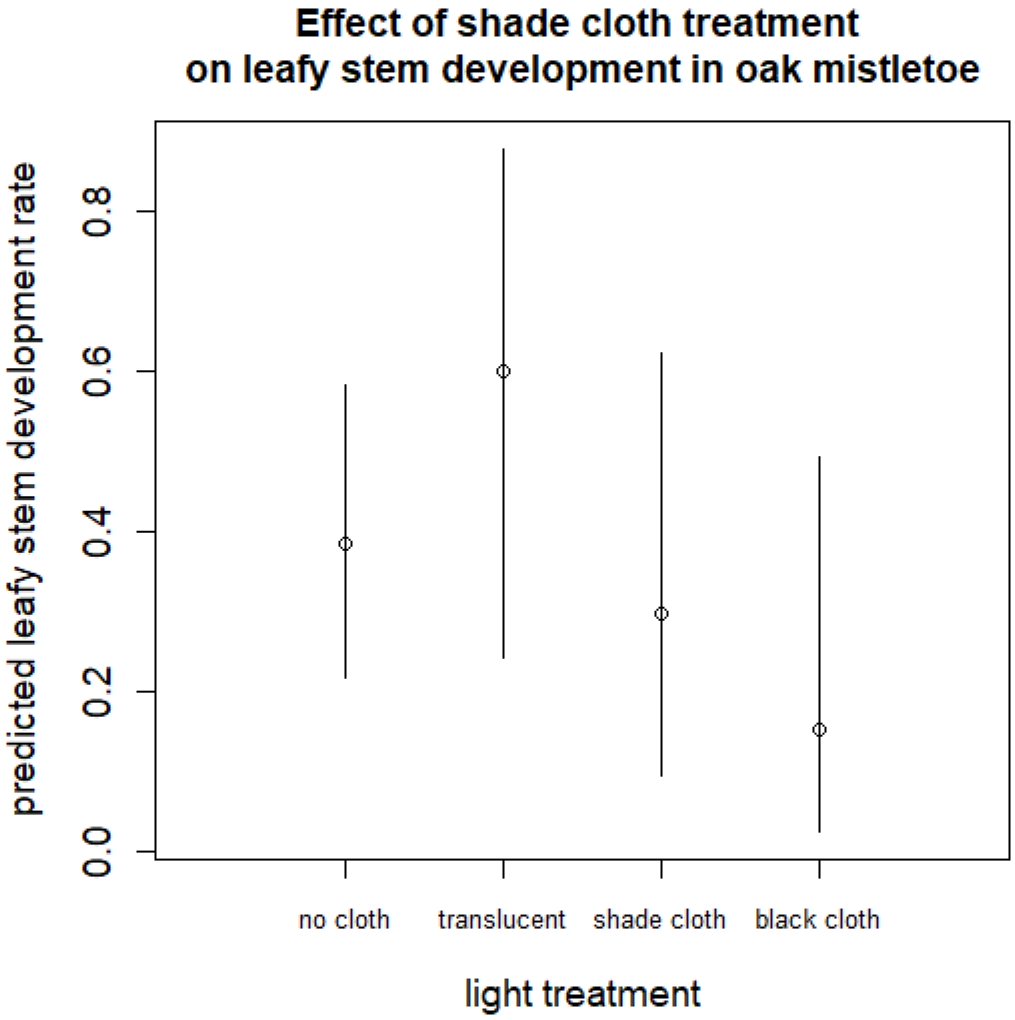


Fig. 12 Model-averaged predictions of rates of oak mistletoe leafy stem development across light availability treatments; error bars represent 95% confidence intervals

CHAPTER 5

CONCLUSION

Here I analyzed data from field surveys, planting experiments, and genetic markers to quantify the relative importance of potential drivers of the positive association between oak mistletoe and forested wetlands in eastern Virginia and North Carolina. I hereafter termed this pattern of oak mistletoe distribution a habitat relationship; the factors most influential in determining such patterns in oak mistletoe distribution remain unidentified (Panvini 1991, Kuijt 2003, Hawkins 2010, Gougherty 2013). The study of the effects of host availability, avian disperser behavior, and local environmental conditions on mistletoe habitat relationships requires consideration of mistletoe distribution at different spatial scales (Aukema 2004).

Effects of local environmental conditions can be viewed at the scale of variation in mistletoe occurrence across individual host trees or within host canopies (Mellado & Zamora 2014a, Mellado & Zamora 2014b). If forested habitats differ consistently in such an abiotic variable, then effects at such fine spatial scales could collectively determine a mistletoe habitat relationship. In the study area, collecting data on such environmental variables in situ proved difficult due to canopy heights and understory conditions. Results from analyses comparing such data to both oak mistletoe occurrence and the establishment of mistletoe seeds planted in the field were correlative in nature. These limitations led me to use experimental approaches to quantify relationships between abiotic factors and oak mistletoe establishment.

Study of the species identity of parasitized hosts at the scale of individual trees within a forest patch can reveal regional mistletoe-host associations (Baldwin & Speese 1957, Clay et al. 1985, May 1971, Aukema 2003, Martínez del Rio et al. 1996). I used an examination of variation in mistletoe occurrence across individual host trees to identify such patterns in the study area. As with habitat relationships, the relative influences of potential drivers of regional host associations are unknown (Kuijt 2003). Variation in mistletoe occurrence across habitats could influence regional host associations if mismatches exist between habitat relationships of mistletoe and a potential host tree species, making that tree species effectively out of reach of the parasite (Norton & Carpenter 1998).

Mistletoe-host associations are important to account for when examining the effect of host availability on mistletoe habitat relationships. Here I used data that took such regional variation in host usage into account to quantify the relationship between host availability and the observed affinity of oak mistletoe for forested wetlands in the study area. Both this effect and that of avian disperser behavior were estimated using data collected at the scale of survey plots within habitat patches, also the scale at which habitat relationships are realized. When viewed as a keystone resource (Watson 2001) the distribution of mistletoe at the forest patch scale can have implications for wildlife conservation (Panvini 1991, Martínez del Rio et al. 1996, Aukema 2004, Lira-Noriega & Peterson 2014, van Halder et al. 2019).

Relationships between host availability and oak mistletoe distribution across habitats and host species

The finding of a lack of relationship between an oak mistletoe habitat relationship and host availability was novel as I accounted for regional host associations when quantifying host abundance. Geographic host associations in the study area were evidenced by widespread tree species that were only parasitized regionally. A planting experiment by Randle et al. (2018) showed a relationship between the establishment of oak mistletoe seedlings from eastern Texas and various environmental conditions, including the presence of volatile compounds released by hosts. Those authors proposed that regional variation in the overlap between the phenology of the release of such potential gaseous cues and the dispersal of oak mistletoe seeds could explain host associations.

Correlations between regional mistletoe host diversity and overall tree diversity have been observed in general (Kuijt 1969) and in the case of oak mistletoe in the study area. The myriad of planted exotic trees in urban areas allows for a greater diversity of oak mistletoe hosts than in forested habitats. Such patterns suggest regional host associations could be driven by random dispersal constrained by host availability. Regional parasitism in my study area was observed for sweetgum (*Liquidambar styraciflua* L.), which co-occurs with and overlaps broadly in terms of habitat with the widespread host red maple (*Acer rubrum* L.). I showed that geographic variation in abundance and habitat relationships of sweetgum is not correlated with regional variation in its parasitism in the study area. This result suggests that host availability is not an important driver of this pattern.

Tree species parasitized by oak mistletoe in eastern Virginia and North Carolina do not offer fleshy fruit resources to avian frugivores in winter. Regional variation in the attractiveness of host trees as food resources to generalist frugivores should not exist in the study area at the time of mistletoe seed dispersal, reducing the likelihood that disperser behavior plays an important role in determining regional host associations. While sweetgum occurs in many habitats across the study area, I did find a correlation between regional variation in oak mistletoe habitat relationships and in the parasitism of sweetgum. The latter finding maintains the potential for disperser behavior or abiotic conditions to drive regional variation in this parasitism, and the generality of such an interaction between the habitat of a parasite and variation in its parasitism of a widespread host deserves further study.

I did not find evidence for a correlation between oak mistletoe genetic structure and geographic shifts in host associations in the study area. The potential remains for the existence of a genetically distinct oak mistletoe population predisposed to parasitizing the most common regional host (May 1971, Kuijt 2003). My work did not test hypothesized variation in susceptibility of host tree populations to mistletoe infection as a driver of regional host associations (May 1971, Panvini 1991, Sallé et al. 1993, Mellado & Zamora 2014b).

Relationship between avian disperser behavior and oak mistletoe habitat relationships

Both dispersal limitations (Howe & Smallwood 1982, Westcott et al. 2005, Jordano et al. 2007) and establishment limitations based on abiotic niche requirements (Hutchinson 1957) are believed to play roles in structuring plant communities (Tilman 1997, Nathan & Muller-Landau 2000, Tilman 2004). Similarly, mistletoe distributions may be determined by some combination of disperser behavior (Martínez del Rio et al. 1996, Aukema 2004) and environmental variation (Eleuterius 1976, Gregg & Ehleringer 1990, Yan 1992, Norton & Smith 1999), including host availability and suitability (Overton 1994, Aukema 2004, Caraballo-Ortiz et al. 2017). To test this, I examined the potential role of avian dispersers in determining oak mistletoe habitat relationships in eastern Virginia and North Carolina.

Motion-activated cameras were used to detect frugivory by potential oak mistletoe dispersers in the study area. This work confirmed the cedar waxwing (*Bombycilla cedrorum*) and eastern bluebird (*Sialia sialis*) as the primary avian frugivores consuming oak mistletoe fruits, of which only the cedar waxwing has been recognized as an important mistletoe disperser elsewhere to my knowledge (Overton 1994). Surpisingly, mammals were also frequently recorded eating mistletoe fruits. This frequency relative to such detections for avian species may be attributable to both reduced camera sensitivity and generally low camera heights. While it seems unlikely that mammals act as effective dispersers of oak mistletoe (Kuijt 2003), the importance of mammals in dispersing mistletoe seeds in other systems makes any effects of mammal frugivory on oak mistletoe distribution and abundance worthy of future study (Amico & Aizen 2000, Camargo et al. 2011, Génin & Rambeloarivony 2018).

I used community occupancy models to estimate avian frugivore habitat relationships using data from repeat point counts conducted at survey plots in forested habitats across the study area. The use of these estimates to study the relationship between avian disperser behavior and oak mistletoe distribution was novel amongst such studies in mistletoe ecology as I accounted for the imperfect detection of frugivores. Variable and often extremely low species-specific detection rate estimates provided evidence for the importance of accounting for imperfect detection to avoid bias when estimating habitat relationships for avian dispersers (MacKenzie et al. 2002, Tyre et al. 2003, Kéry et al 2008, Ruiz-Gutiérrez et al. 2010).

My analysis of field survey data showed discrepancies between habitat relationships of seemingly widespread avian dispersers and that of oak mistletoe. Because birds surveyed were unmarked, the potential for cryptic habitat specificity remained. Patterns of gene flow can inform on cryptic disperser behavior (Aukema 2004), so I examined oak mistletoe population genetics for evidence of dispersal limitation between habitat types (Ouborg 1999). Such disperser behavior could determine the observed positive relationship between forested wetland habitat and oak mistletoe occurrence. Instead, the only genetic structure evident indicated a lack of gene flow between mistletoe populations on different host tree species.

Effects of abiotic conditions on oak mistletoe distribution

The effects of abiotic variables on mistletoe range limits are widely recognized (Wagener 1957, Kuijt 2003, Aukema 2004, Mellado & Zamora 2014b, Tikkanen et al. 2021). Less is known about the importance of such variables relative to effects of disperser behavior in determining mistletoe distributions at finer spatial scales (Aukema 2004). Here I used a seed sowing experiment to quantify the effects of variation in light availability and flood regime on oak mistletoe seedling survival and establishment. Under the assumption that such variables differ consistently between forested habitat types, the existence of an effect would support the potential importance of that variable in determining the observed oak mistletoe habitat relationship in the study area.

Model selection supported the inclusion of the effect of light availability to explain variation in oak mistletoe establishment rates. Further experimental work is needed to confirm the existence of a non-linear relationship between light availability and oak mistletoe establishment, but such a hypothesis seems reasonable for a plant adapted to survive within canopies of open forests.

Establishment limitation seems more important than dispersal limitation in determining oak mistletoe distribution at the scale of habitat patches. I did not examine the distribution of oak mistletoe within tree canopies, and dispersal limitation may play a larger role in determining patterns at this finer spatial scale. Early survival of the mistletoe *Viscum album* subsp. *austriacum* (Wiesb.) Vollman has been shown to vary along with environmental variables across positions within host canopies (Mellado & Zamora 2014a, 2014b). Like my findings at a coarser scale, this finding for *V. a. austriacum* implies the importance of post-dispersal influences on mistletoe distributions within tree canopies.

Final remarks

Both avian dispersers and host trees appear more widespread with regards to habitat than oak mistletoe in the study area. Coupled with support for the effect of light availability on oak mistletoe establishment, these results suggest that post-dispersal effects are most important in determining the positive association of oak mistletoe with forested wetland habitat. Data on local light availabilities at potential oak mistletoe establishment sites in host canopies are needed to show significant variation in this abiotic variable across different forested habitat types.

Regional host associations do not appear capable of explaining the oak mistletoe habitat relationship observed in the study area. Such regional patterns could determine oak mistletoe habitat relationships in other portions of its range if the preferred host is restricted by habitat. I found support for an interaction between mistletoe habitat relationships and host usage, but the mechanisms driving both variation in mistletoe habitat relationships and this interaction deserve more study.

The discovery of a genetically distinct population of oak mistletoes restricted to hosts in the genus *Nyssa* L. was unexpected. Work remains to determine barriers to gene flow between these mistletoes and those on neighboring host trees of alternate species, including a common garden planting experiment to test for host species-specific establishment limitations. The result remains a testament to the discoveries that await future workers studying the ecology of the remaining wild portions of this populated region.

Overall, I hope my work can help instill an appreciation for our native leafy mistletoe in the southeastern US. Its presence adds colorful variation to the canopies of deciduous swamp trees in winter, and the enjoyment of stillness and quiet in such habitats at this season can be heightened by the welcome interruption of the noisy and nomadic flocks of frugivorous birds that the mistletoe resource helps support. Managers would be wise to consider conservation of oak mistletoe in forested wetlands and these results should aid such efforts.

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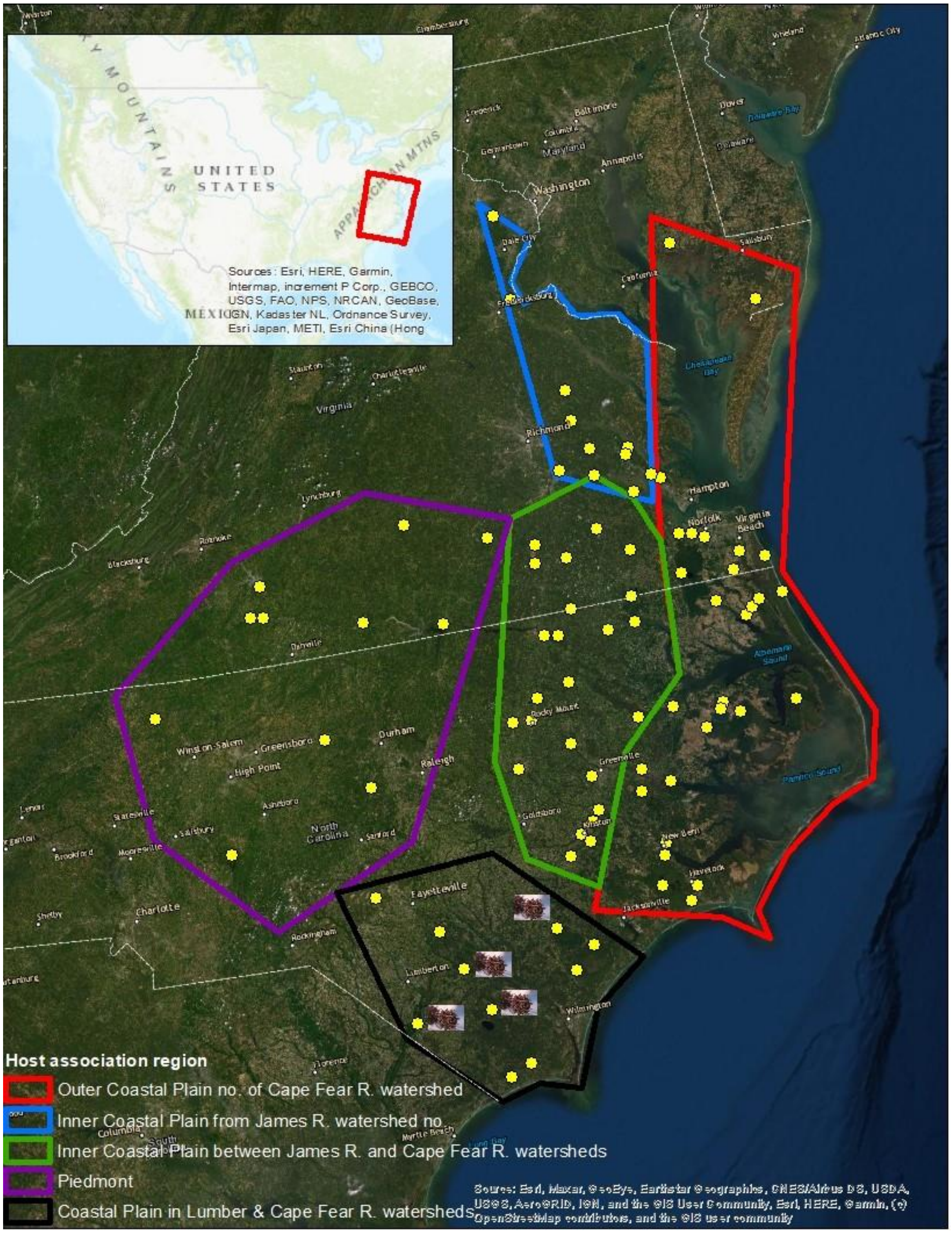
APPENDIX

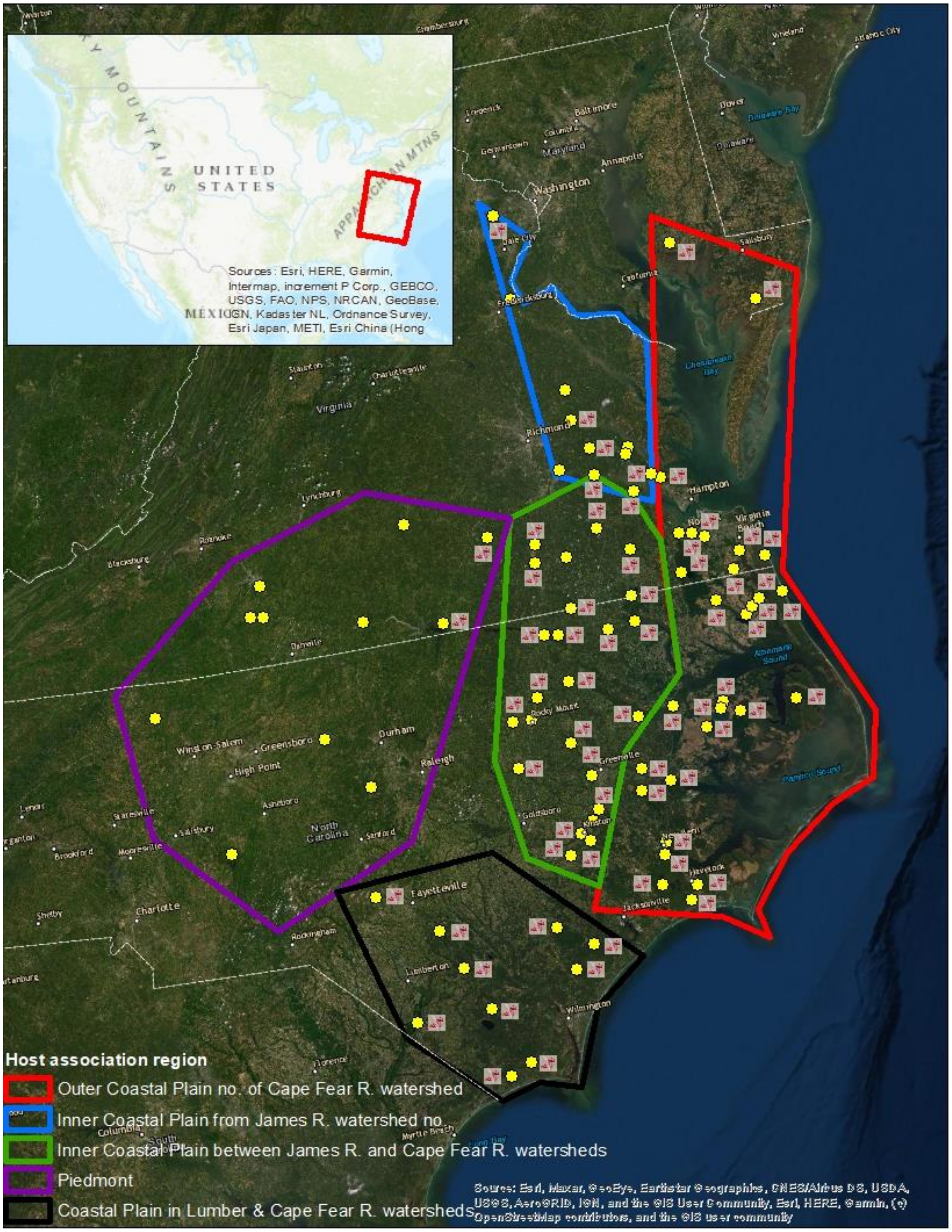
FIGURES



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Sources: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Fig. A1 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across five regions that hosted sub-plots where *Liquidambar styraciflua* was detected. Fruit images represent locations where *L. styraciflua*, restricted as a host to one region, was parasitized by mistletoe.



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Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Fig. A2 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across five regions that hosted sub-plots where *Acer rubrum* was detected. Images represent locations where *A. rubrum* was parasitized by mistletoe. Detected as a host in all five regions, I found a significant relationship between region and *A. rubrum* occurrence as a host across oak mistletoe populations.

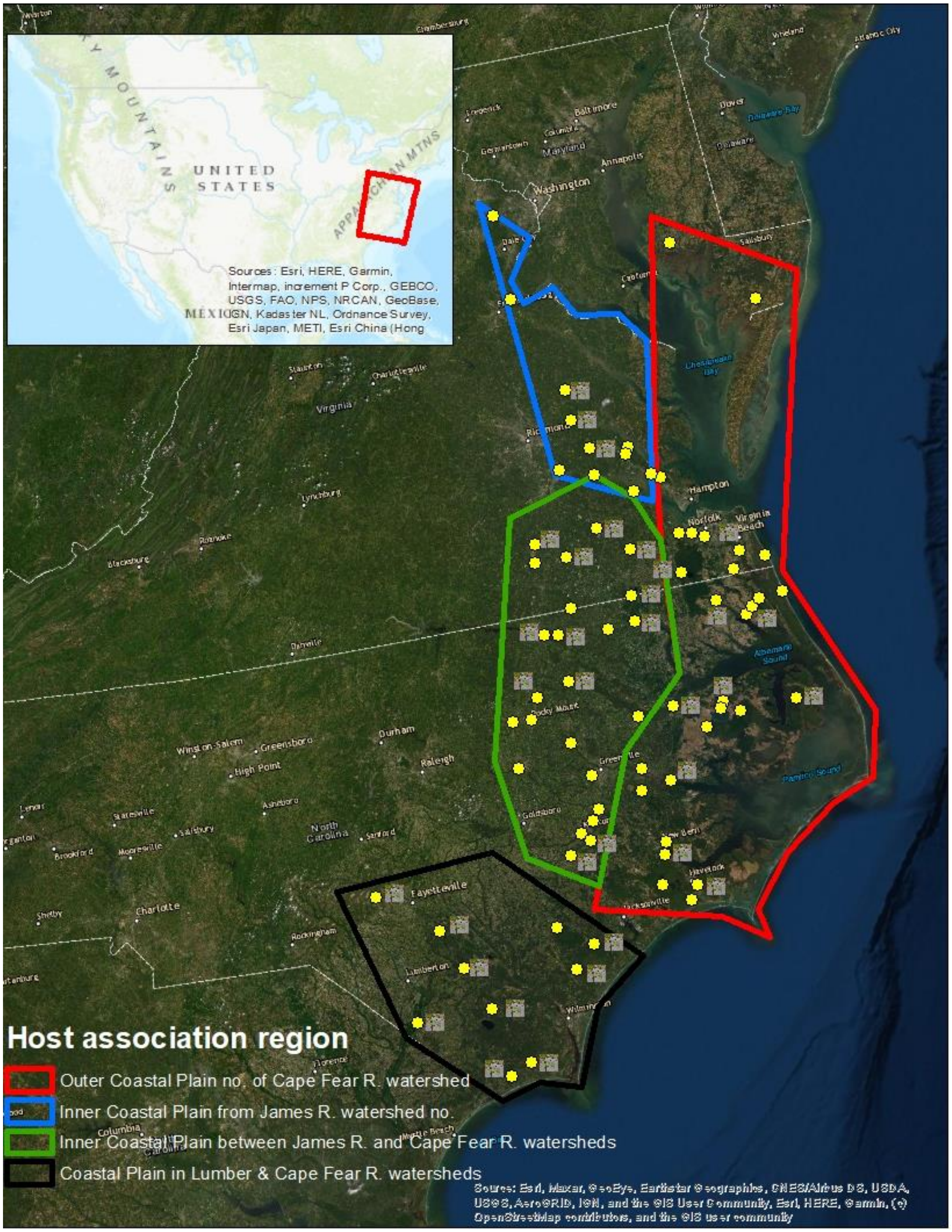

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Fig. A3 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across four regions that hosted sub-plots where *Nyssa biflora* was detected. Images represent locations where *N. biflora* was parasitized by mistletoe. Detected as a host in all four regions, I found a significant relationship between region and *N. biflora* occurrence as a host across oak mistletoe populations.

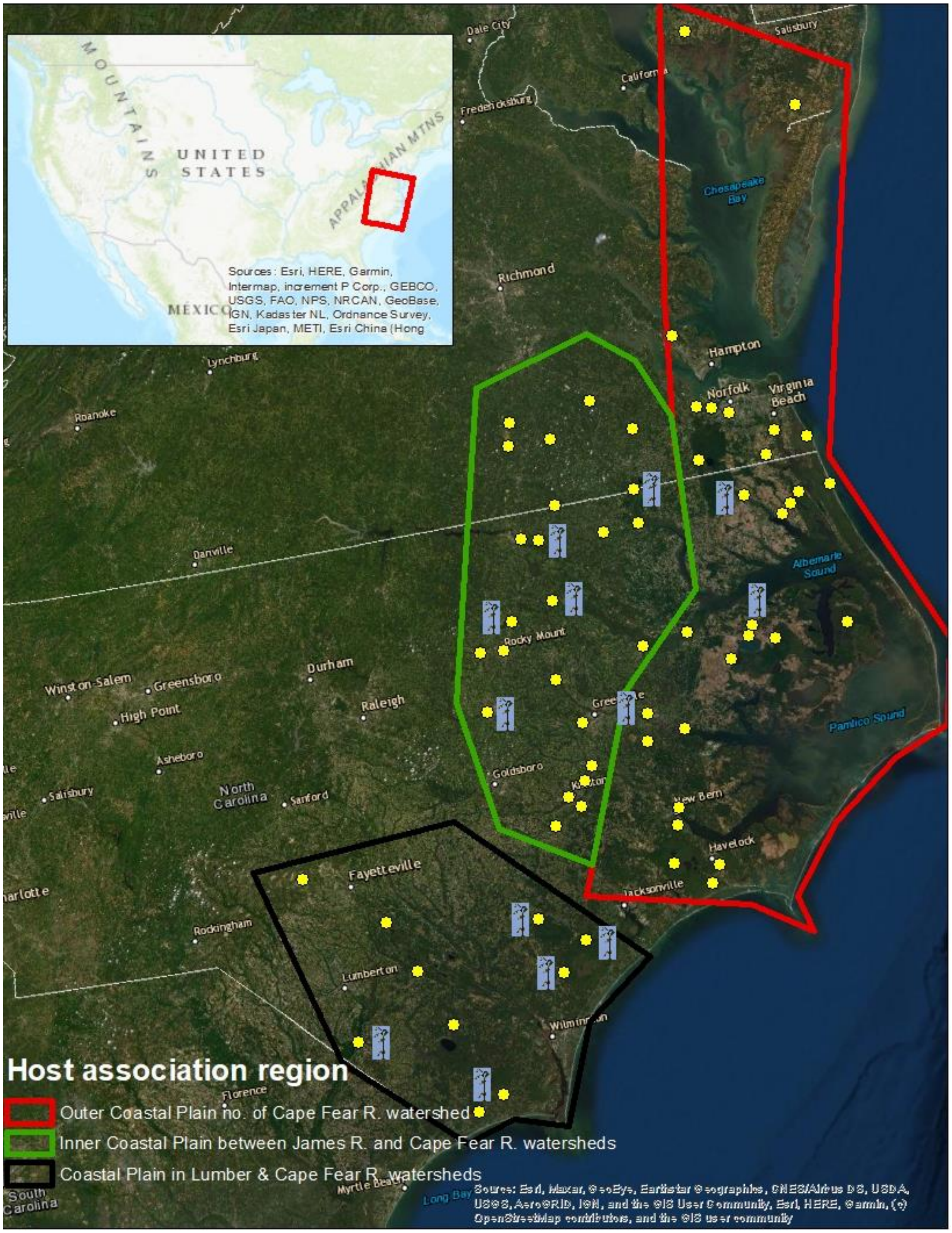
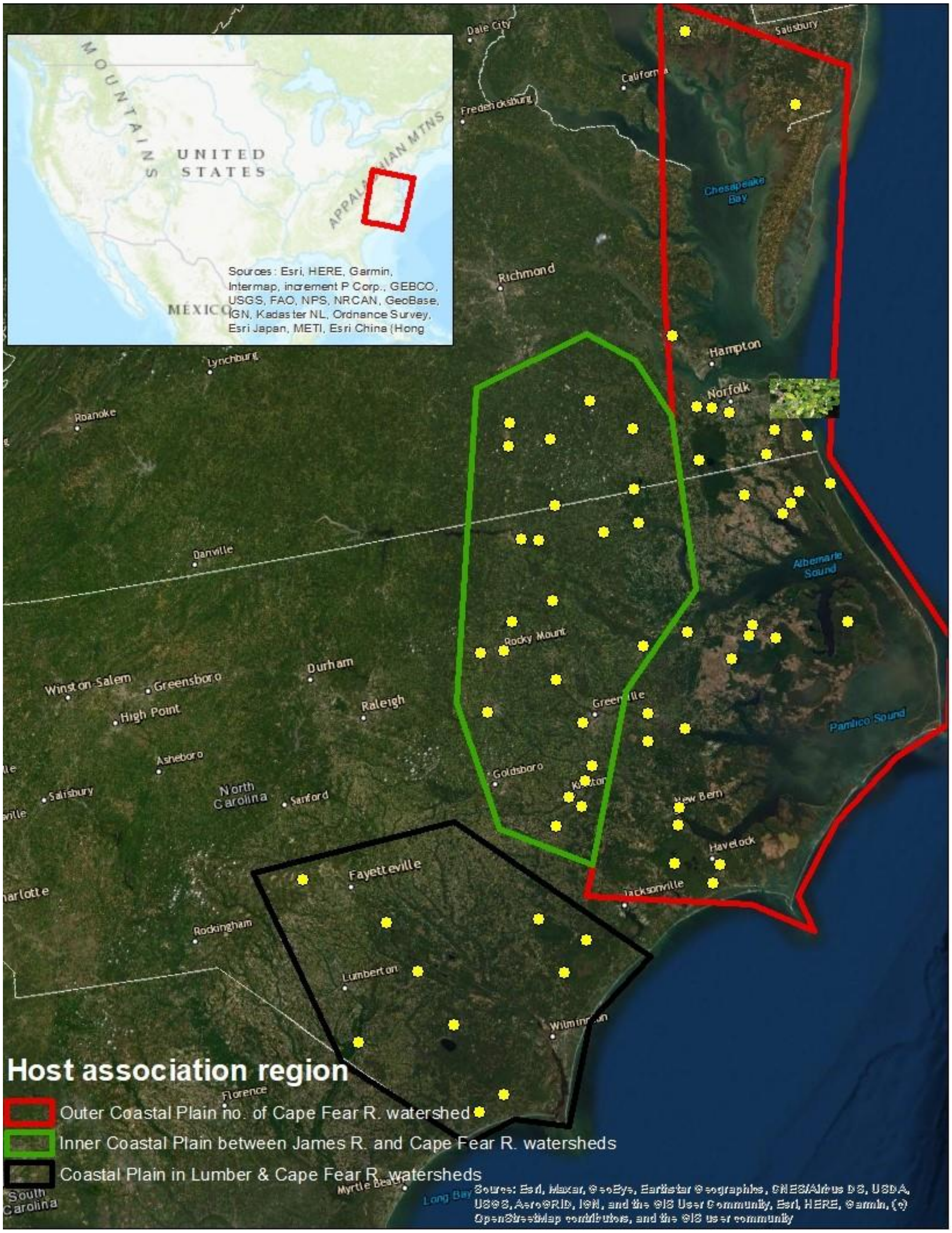


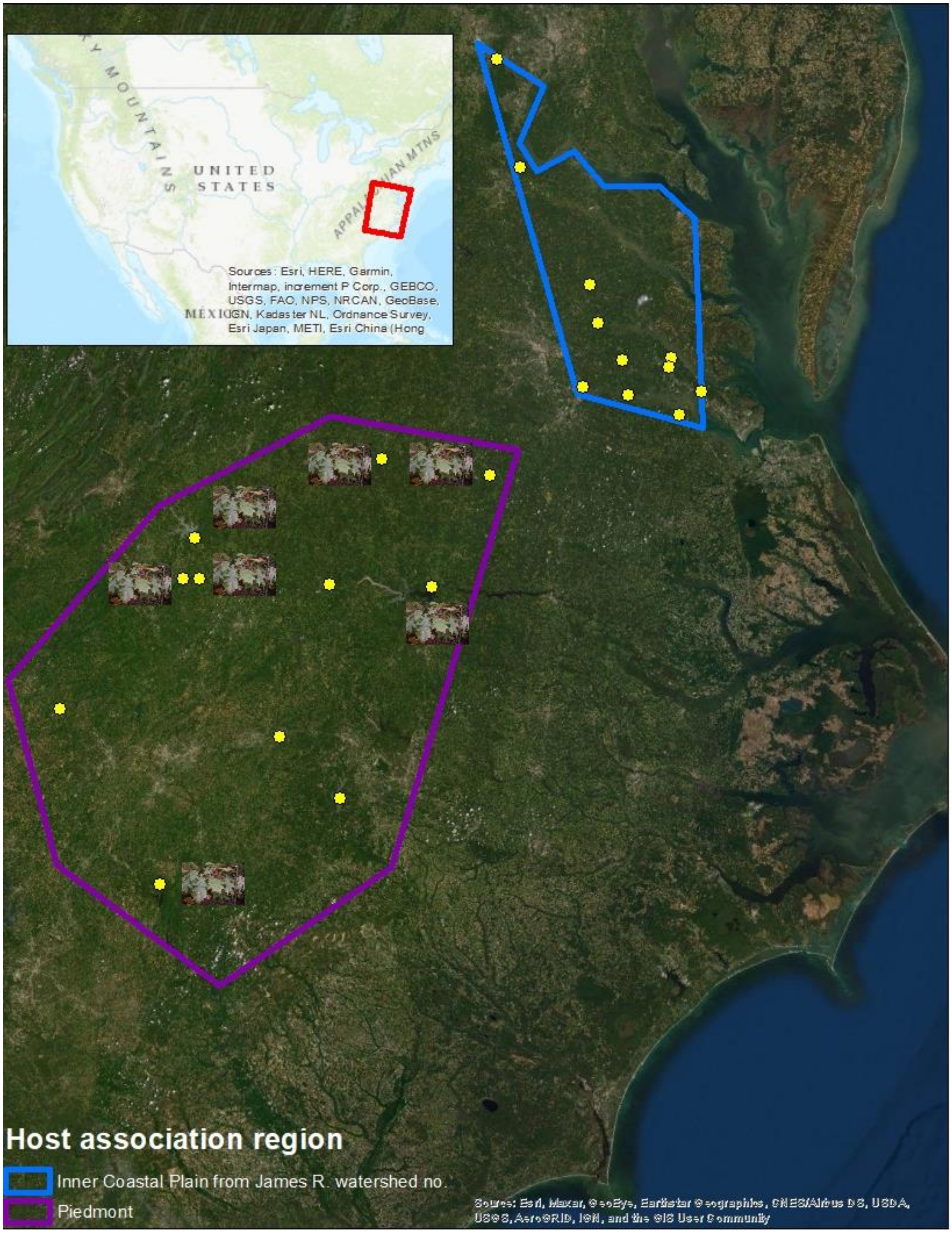
Fig. A4 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across three regions that hosted sub-plots where *Fraxinus caroliniana* was detected. Images represent locations where *F. caroliniana* was parasitized by mistletoe. Detected as a host in all three regions, I found a significant relationship between region and *F. caroliniana* occurrence as a host across oak mistletoe populations.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Fig. A5 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across three regions that hosted sub-plots where *Persea palustris* was detected. The image represents a location where *P. palustris*, restricted as a host to one region, was parasitized by mistletoe.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Fig. A6 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across two regions that hosted sub-plots where *Quercus rubra* was detected. Images represent locations where *Q. rubra*, restricted as a host to one region, was parasitized by mistletoe.

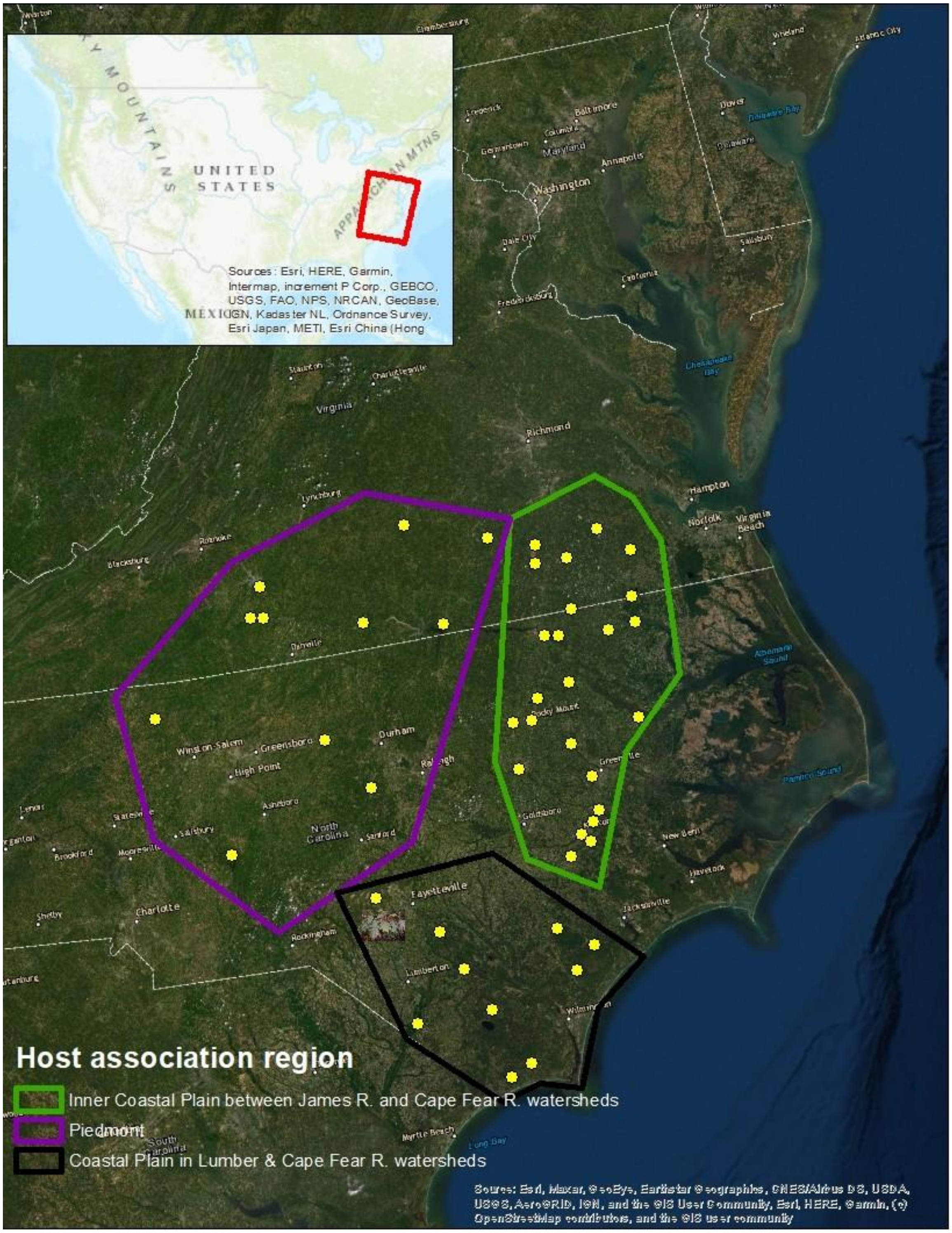


Fig. A7 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across two regions that hosted sub-plots where *Quercus velutina* was detected. The image represents a location where *Q. velutina*, restricted as a host to one region, was parasitized by mistletoe.

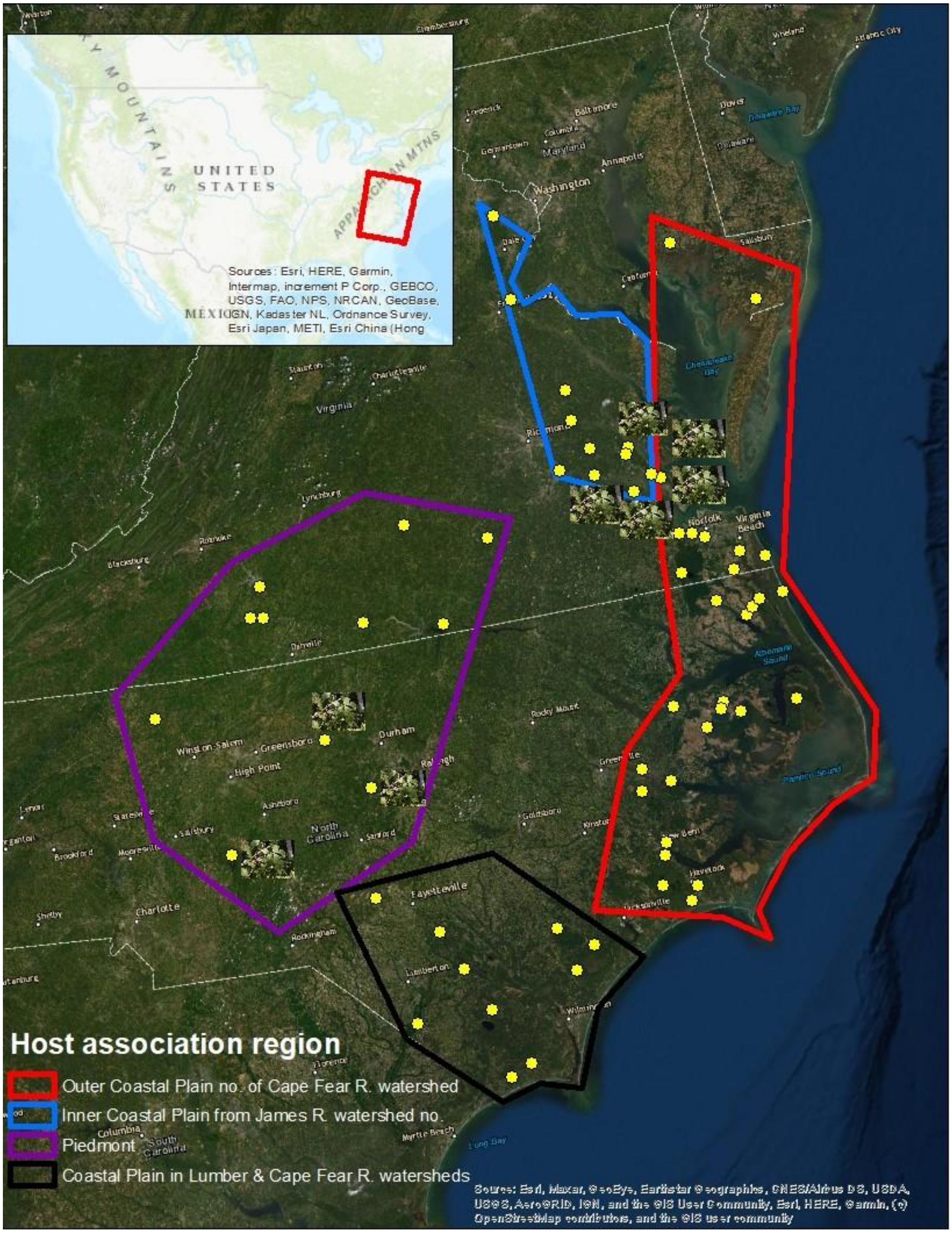


Fig. A8 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across four regions that hosted sub-plots where *Carya* spp. were detected. Images represent locations where *Carya* spp., restricted as hosts to three regions, were parasitized by mistletoe.

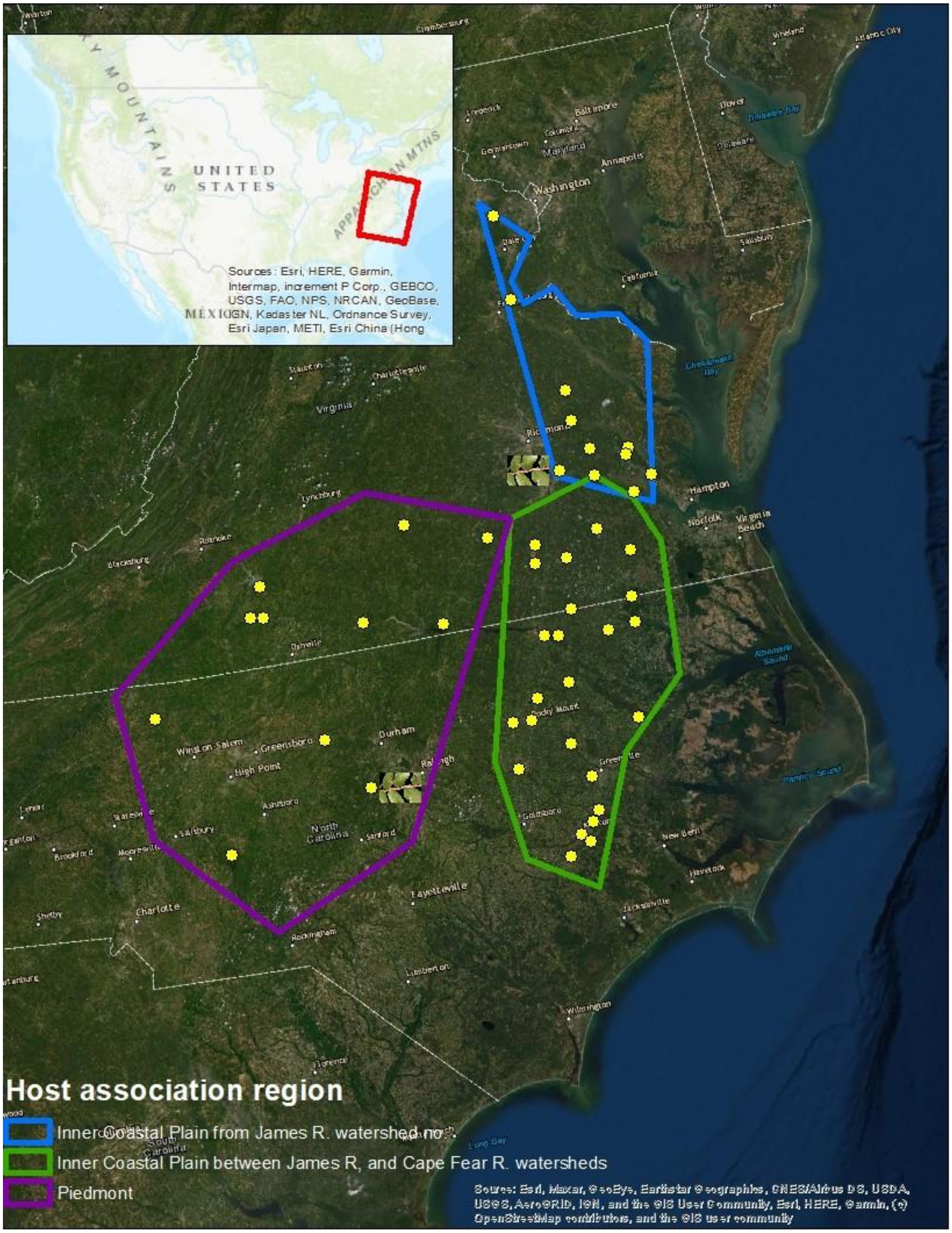


Fig. A9 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across three regions that hosted sub-plots where *Ulmus alata* was detected. Images represent locations where *U. alata*, restricted as a host to two regions, was parasitized by mistletoe.

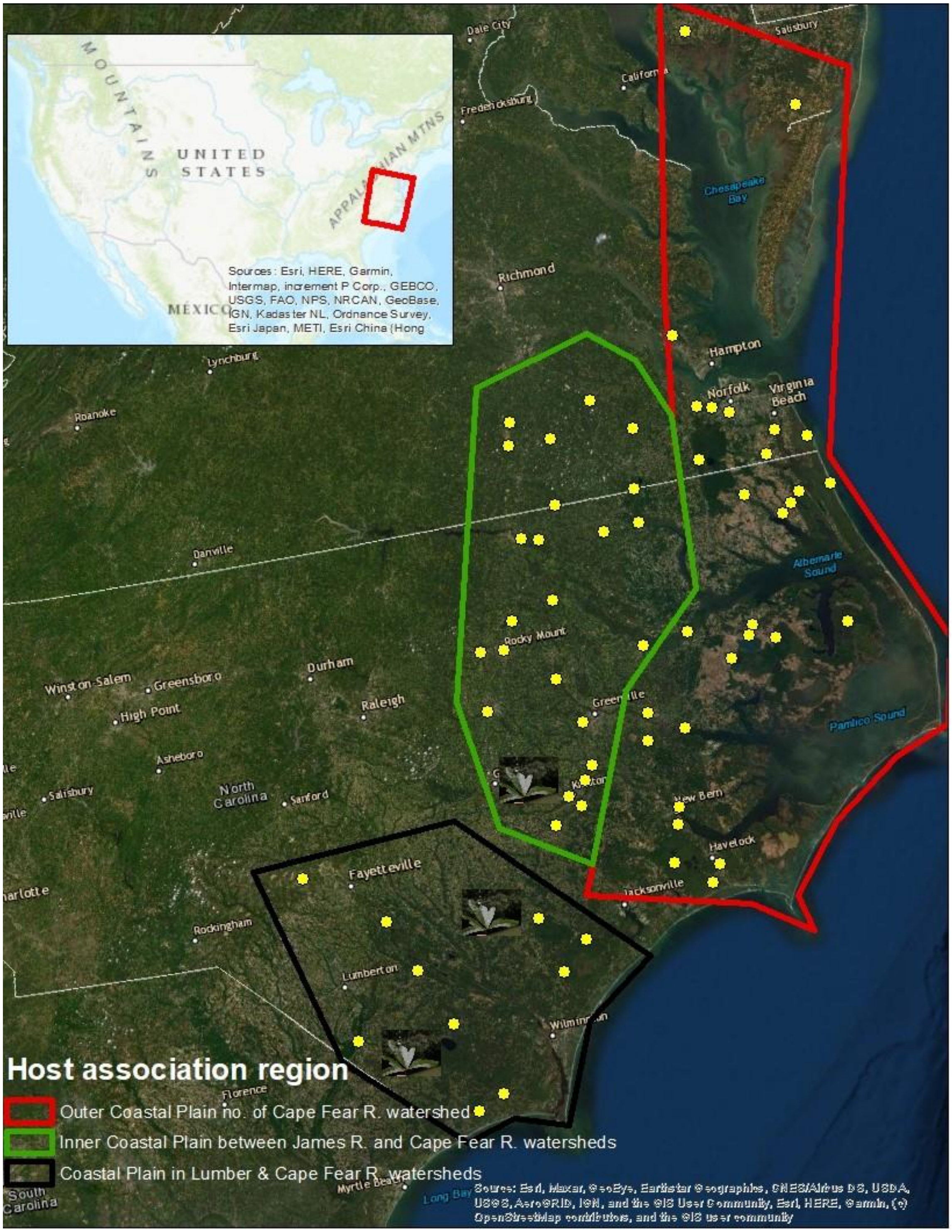
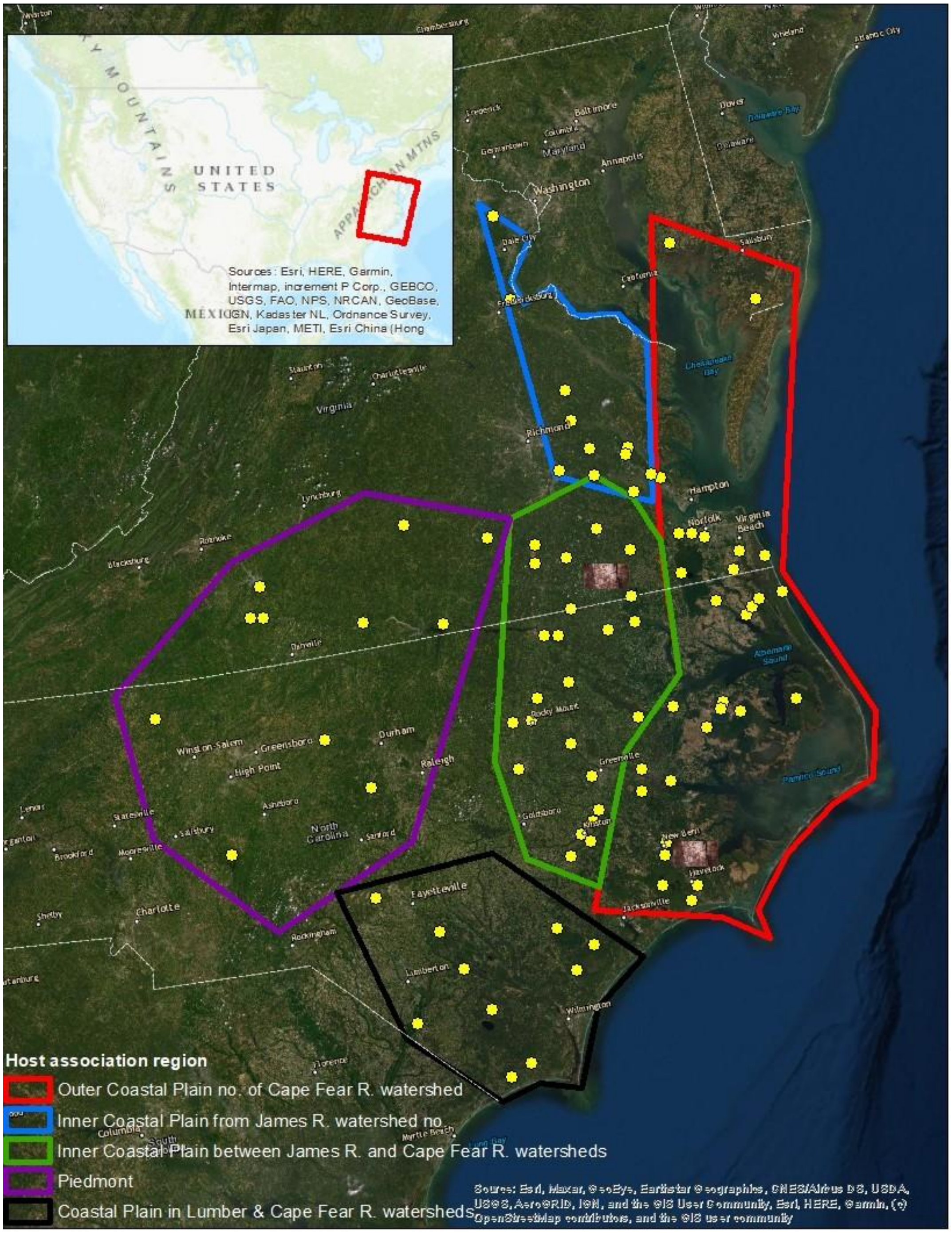


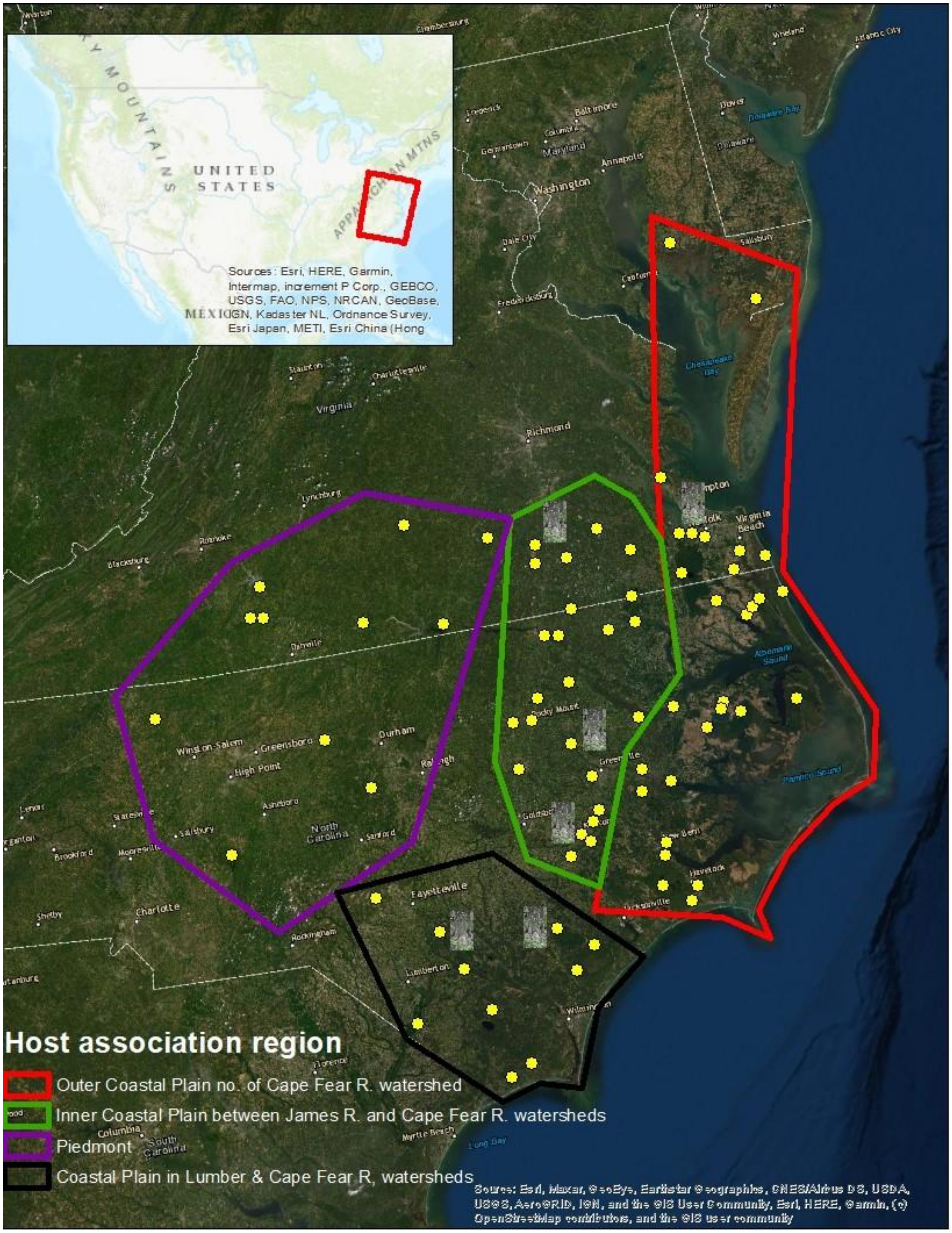
Fig. A10 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across three regions that hosted sub-plots where *Quercus laurifolia* was detected. Images represent locations where *Q. laurifolia*, restricted as a host to two regions, was parasitized by mistletoe.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Fig. A11 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across five regions that hosted sub-plots where *Carpinus caroliniana* was detected. Images represent locations where *C. caroliniana*, restricted as a host to two regions, was parasitized by mistletoe.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Fig. A12 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across four regions that hosted sub-plots where *Quercus nigra* was detected. Images represent locations where *Q. nigra*, restricted as a host to three regions, was parasitized by mistletoe.

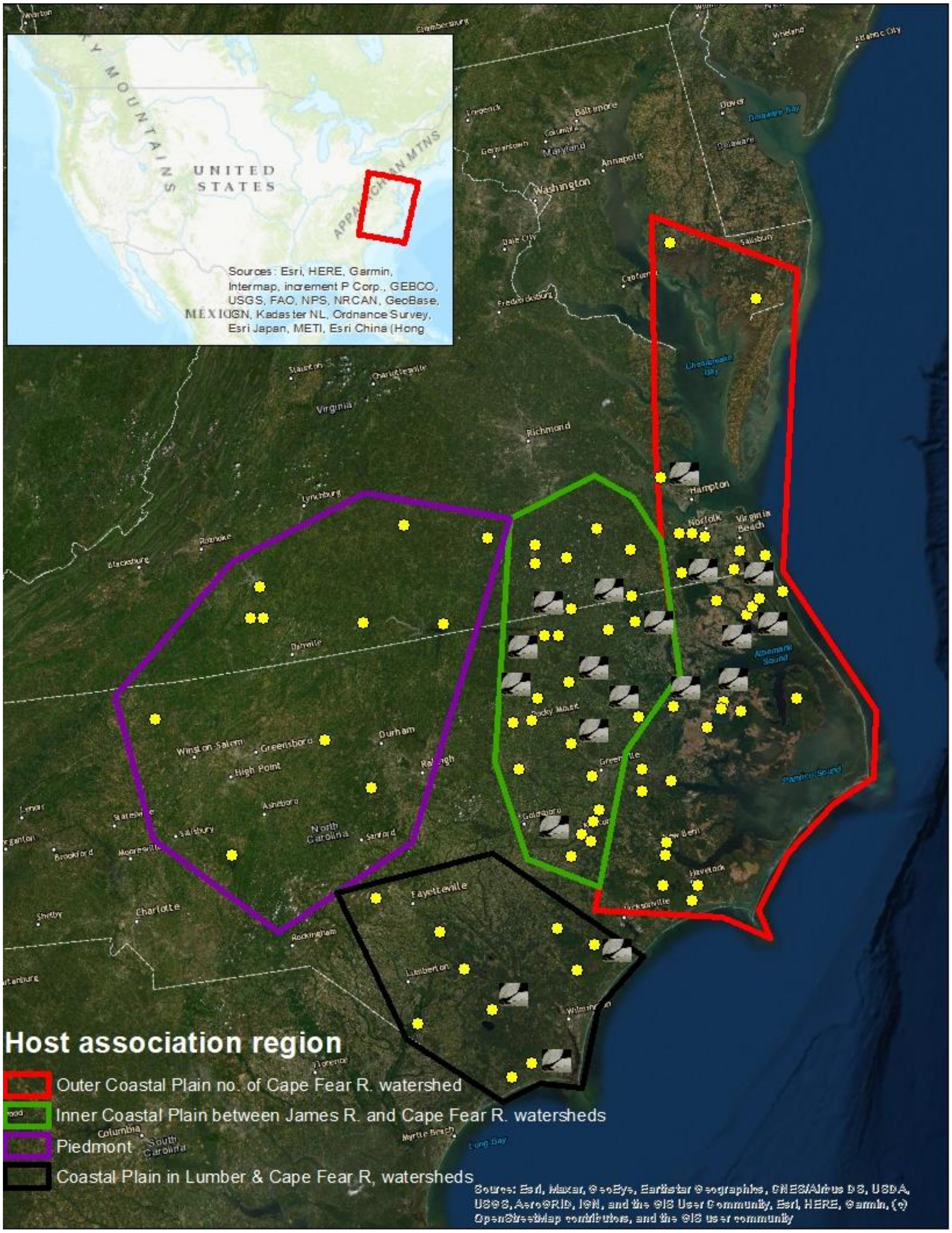


Fig. A13 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across four regions that hosted sub-plots where *Fraxinus pennsylvanica* was detected. Images represent locations where *F. pennsylvanica*, restricted as a host to three regions, was parasitized by mistletoe.

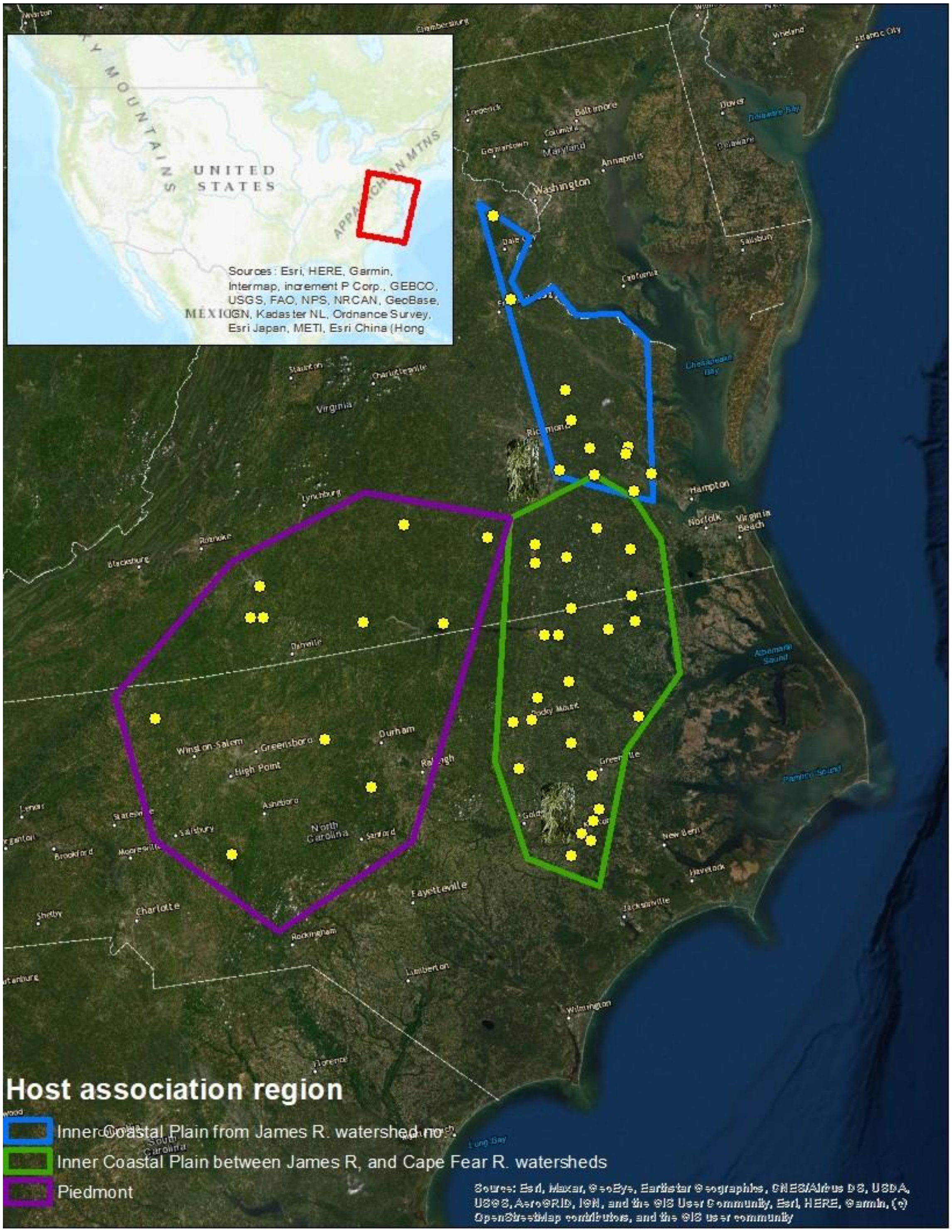


Fig. A14 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across three regions that hosted sub-plots where *Quercus phellos* was detected. Images represent locations where *Q. phellos*, restricted as a host to two regions, was parasitized by mistletoe.

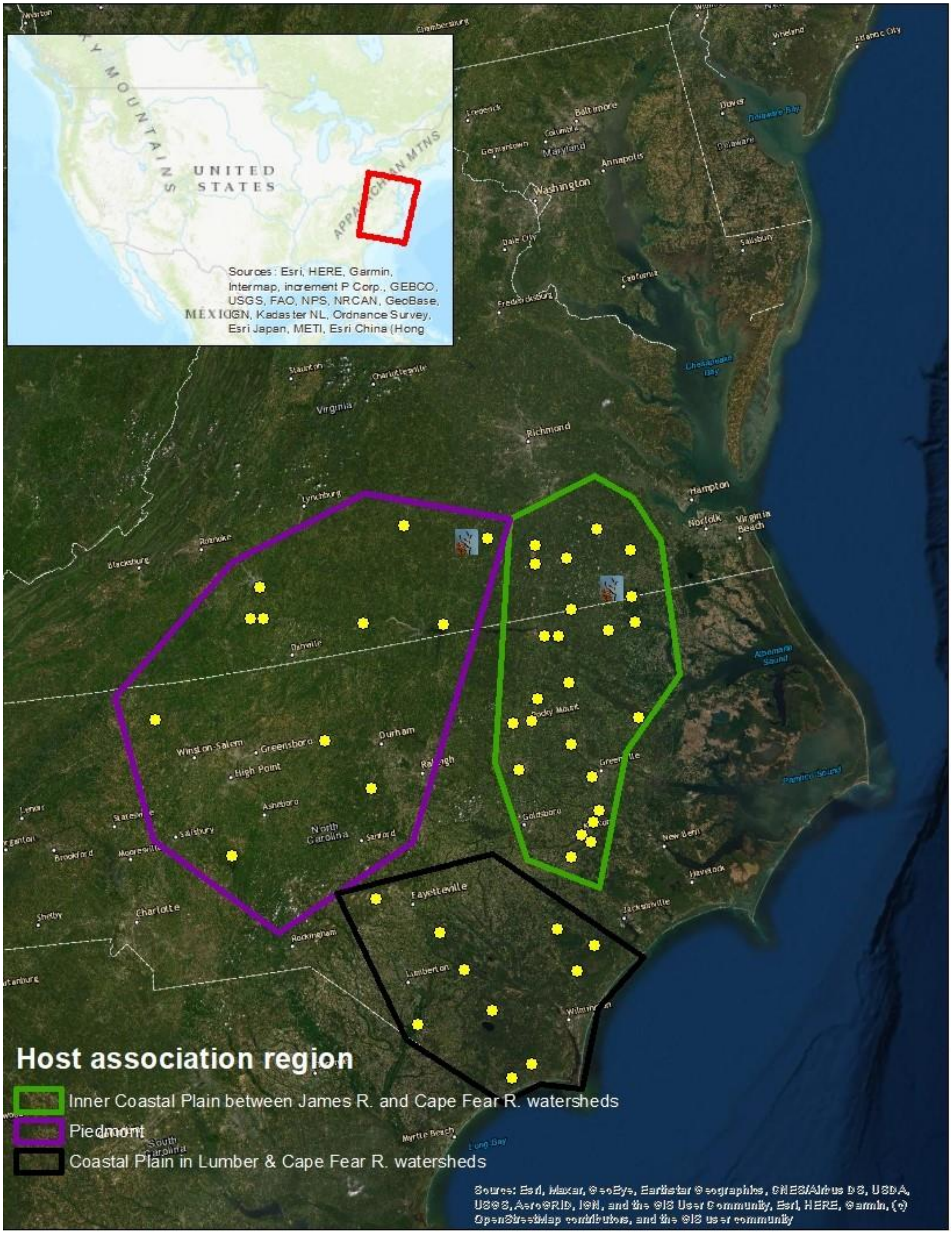
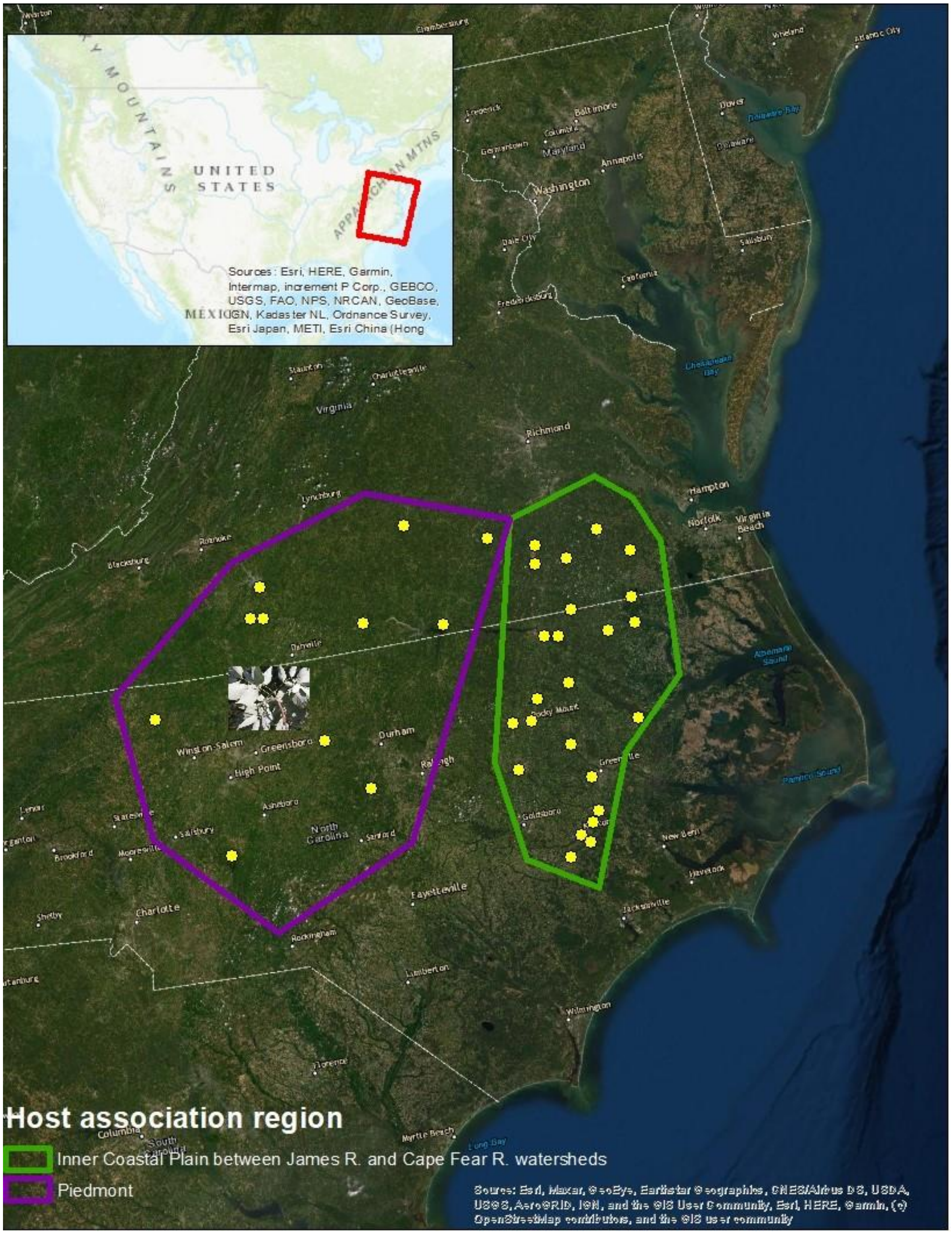


Fig. A15 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across three regions that hosted sub-plots where *Alnus serrulata* was detected. Images represent locations where *A. serrulata*, restricted as a host to two regions, was parasitized by mistletoe.



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community, Esri, HERE, Garmin, (c) OpenStreetMap contributors, and the GIS user community

Fig. A16 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across two regions that hosted sub-plots where *Fraxinus americana* was detected. The image represents a location where *F. americana*, restricted as a host to one region, was parasitized by mistletoe.

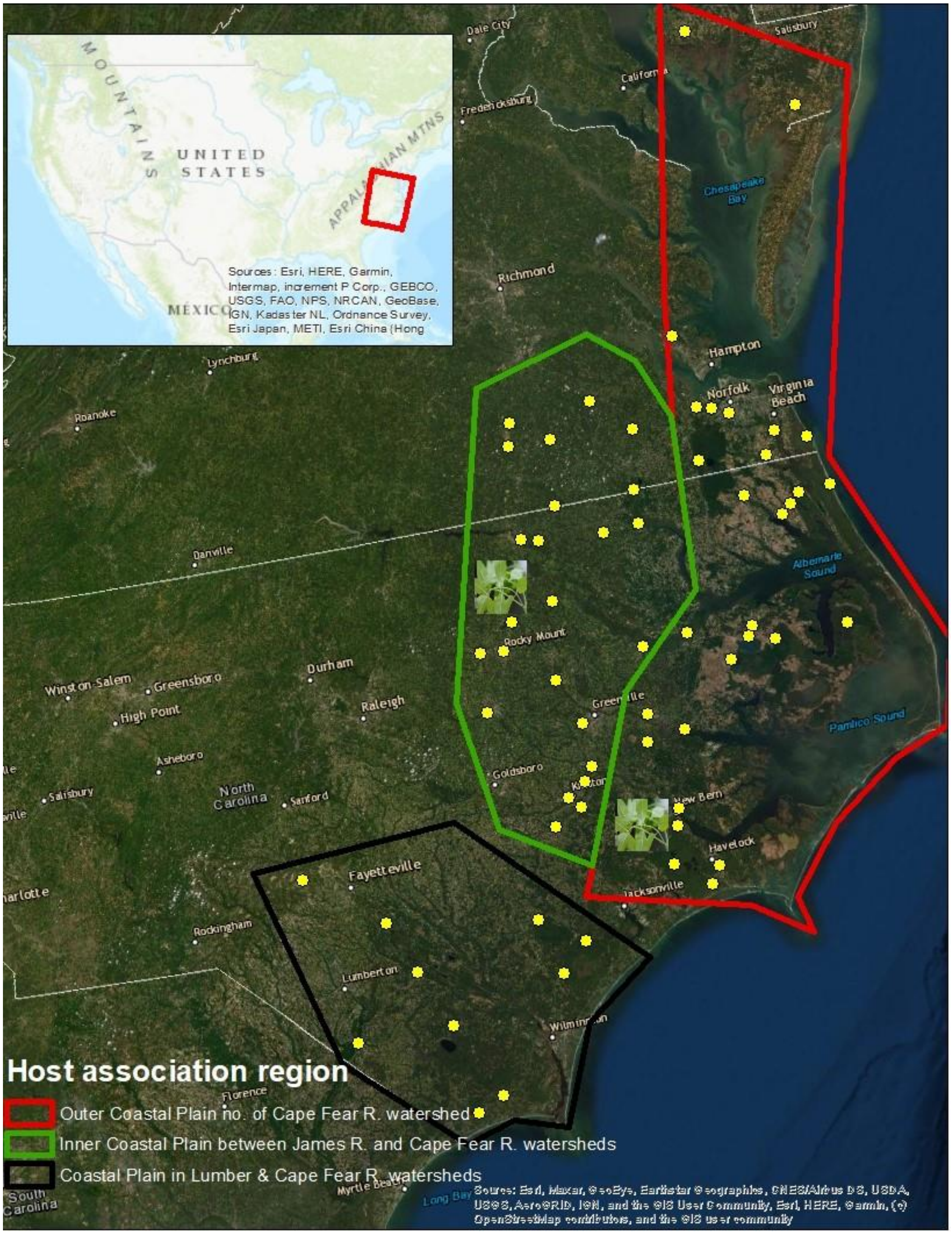


Fig. A17 Locations of oak mistletoe populations detected during plot surveys and with ad hoc observations across three regions that hosted sub-plots where *Fraxinus profunda* was detected. Images represent locations where *F. profunda*, restricted as a host to two regions, was parasitized by mistletoe.

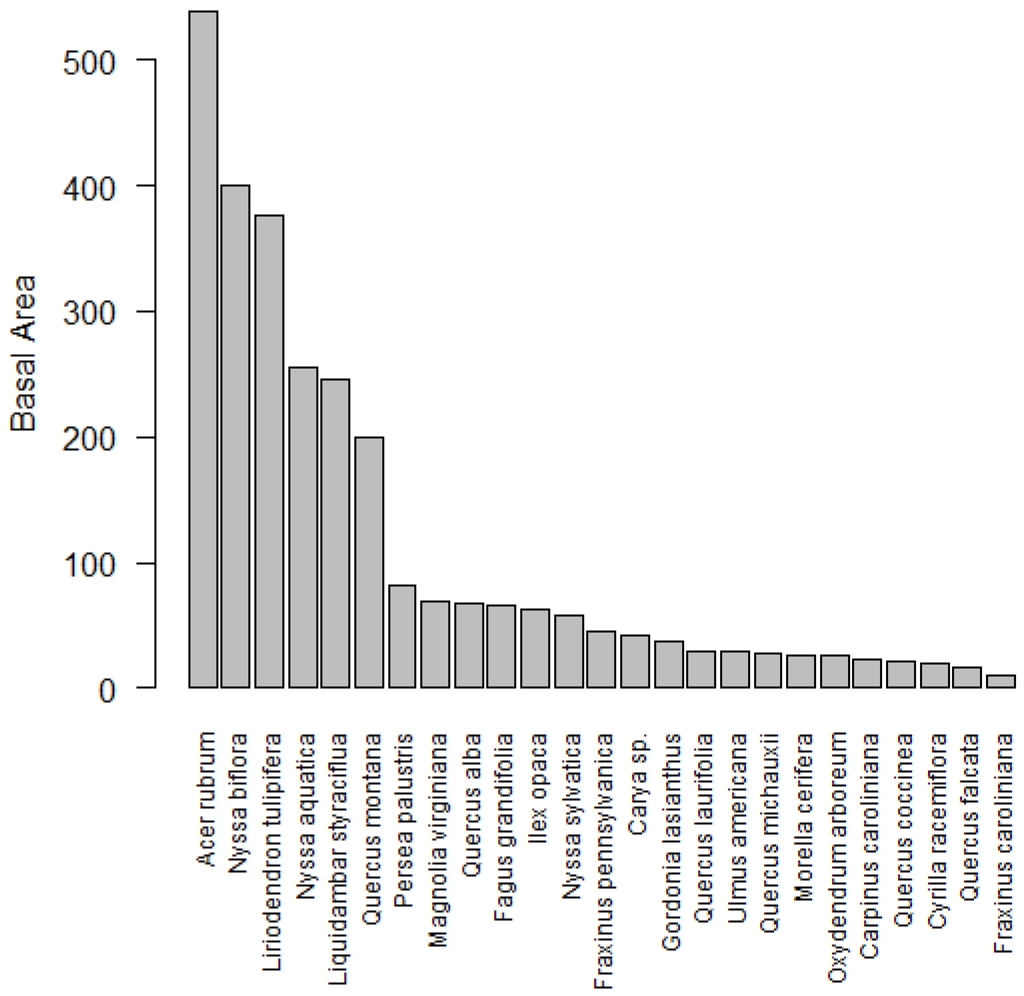


Fig. A18 Total basal area (BA; m^2) across all sub-plots for the 25 angiosperm tree species with the highest BA.

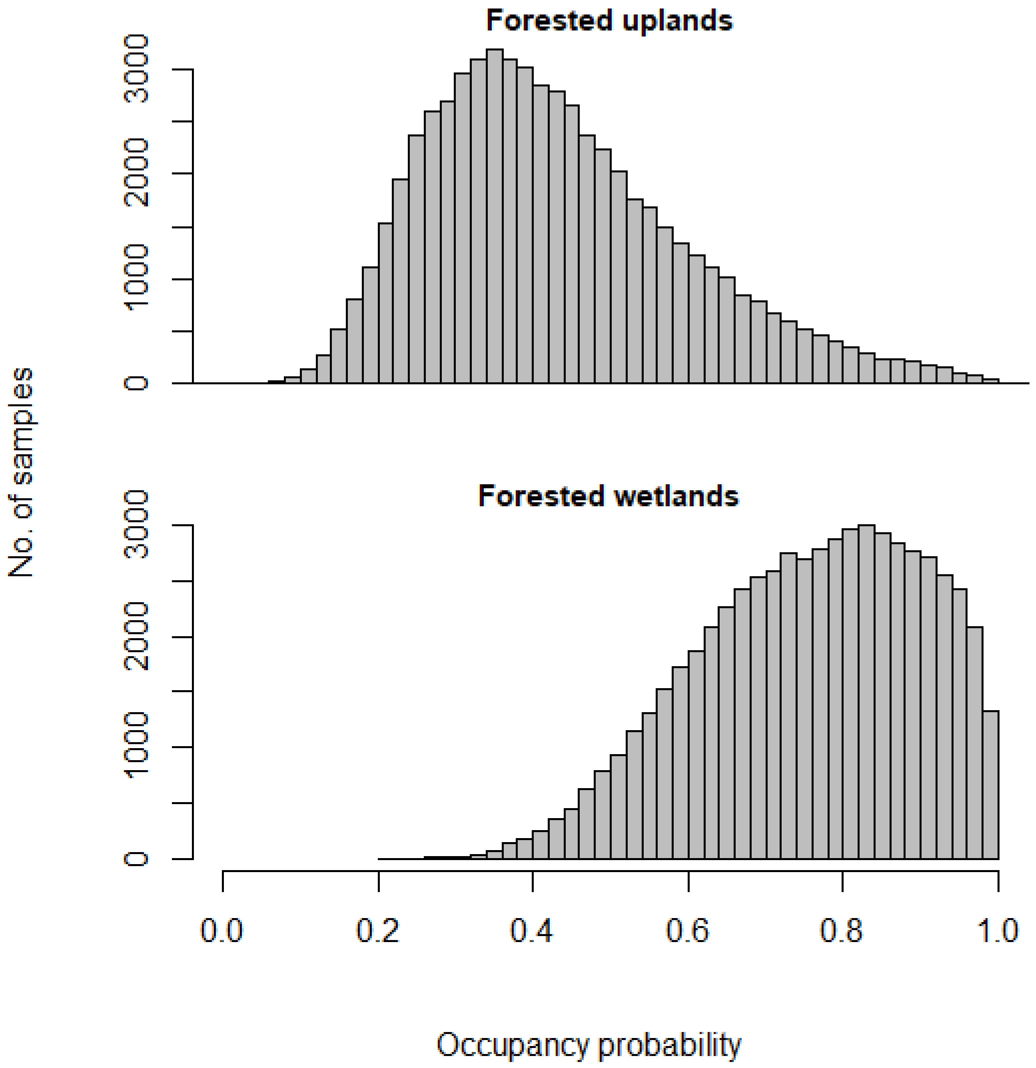


Fig. A19 Posterior distributions of predicted occurrence rates of red-shouldered hawk (*Buteo lineatus*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

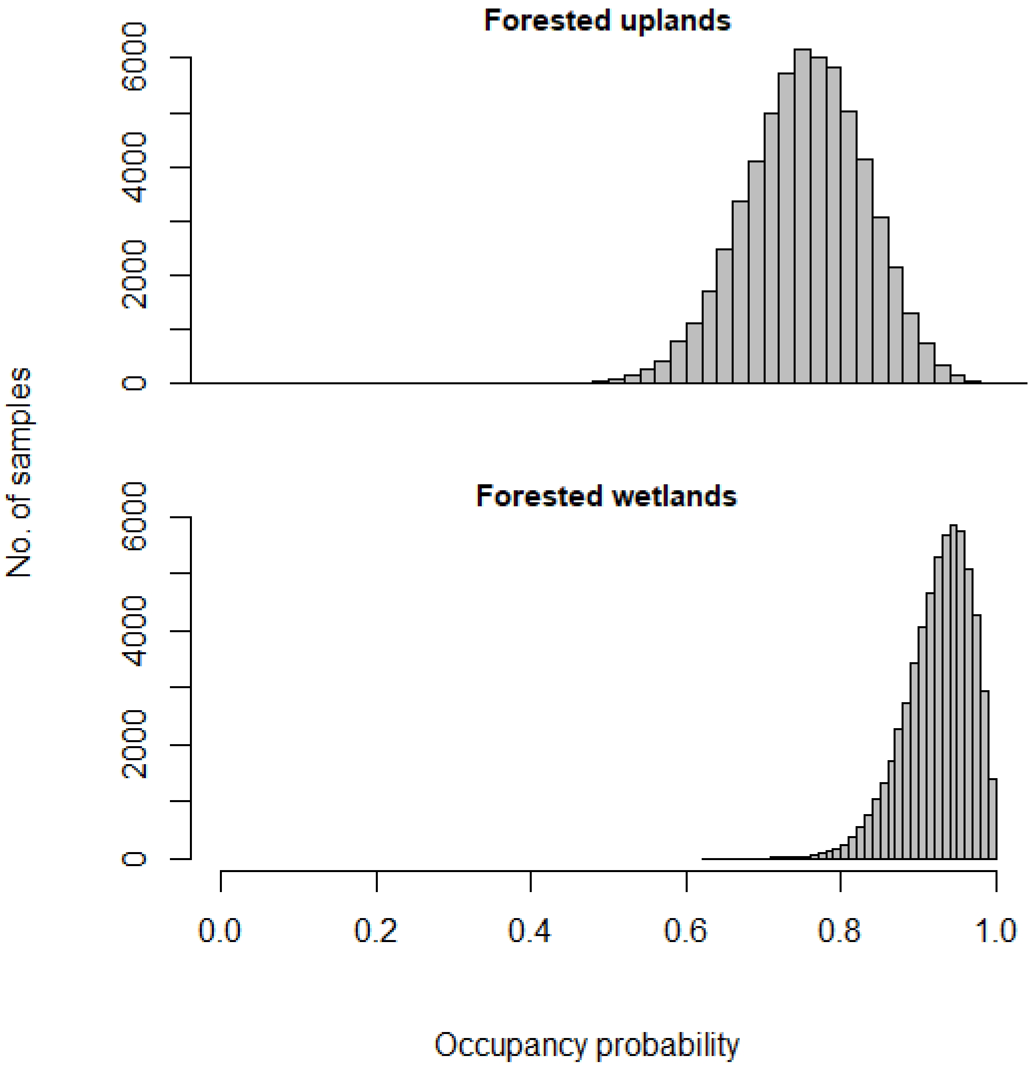


Fig. A20 Posterior distributions of predicted occurrence rates of Carolina wren (*Thryothorus ludovicianus*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

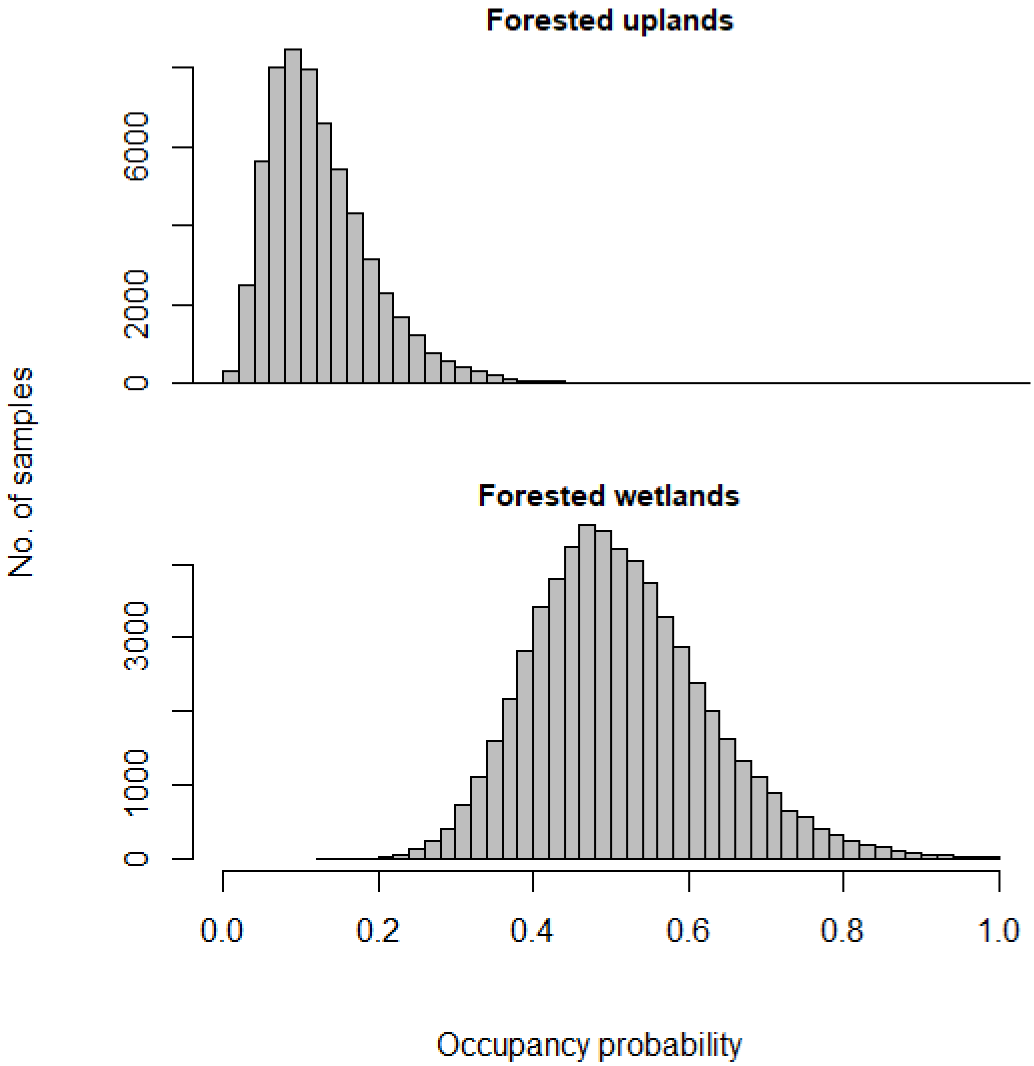


Fig. A21 Posterior distributions of predicted occurrence rates of gray catbird (*Dumetella carolinensis*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

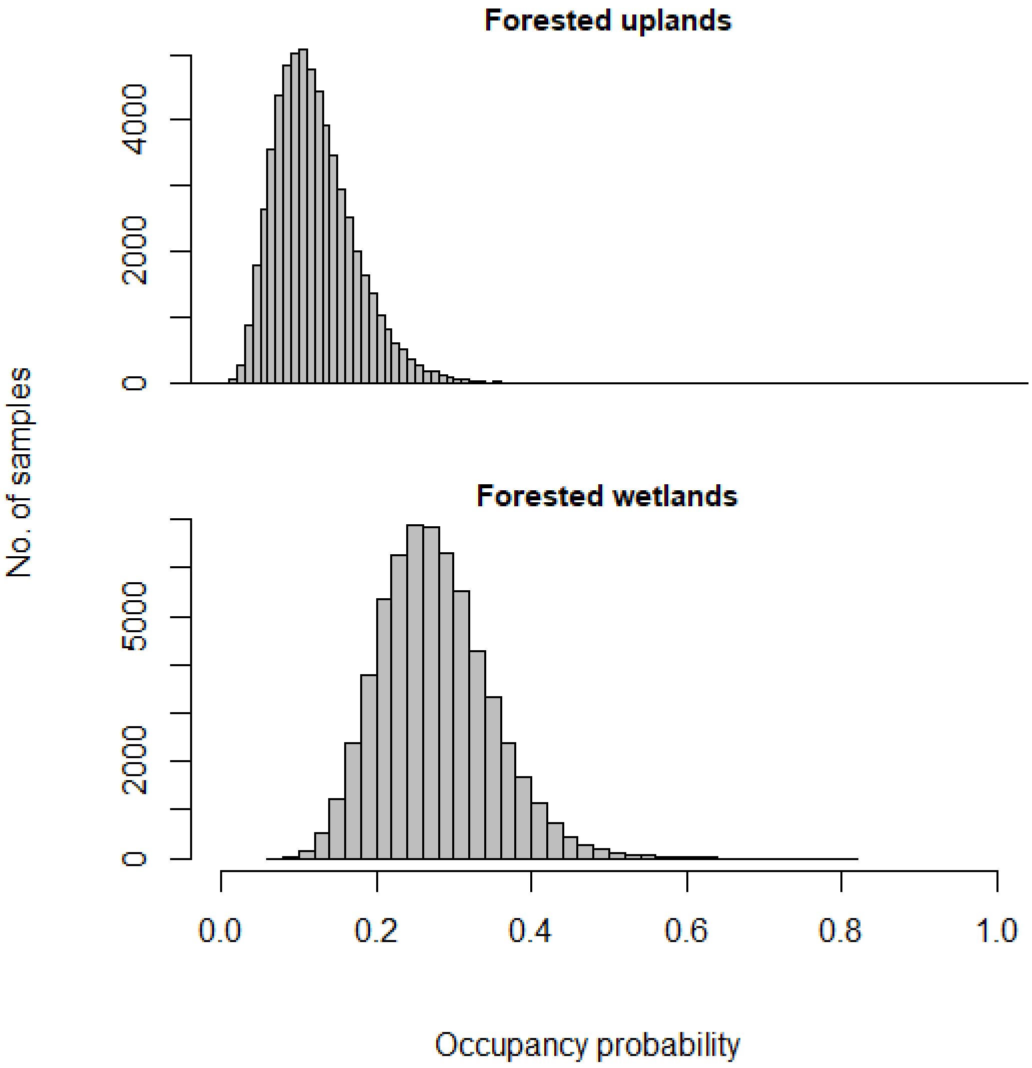


Fig. A22 Posterior distributions of predicted occurrence rates of swamp sparrow (*Melospiza georgiana*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

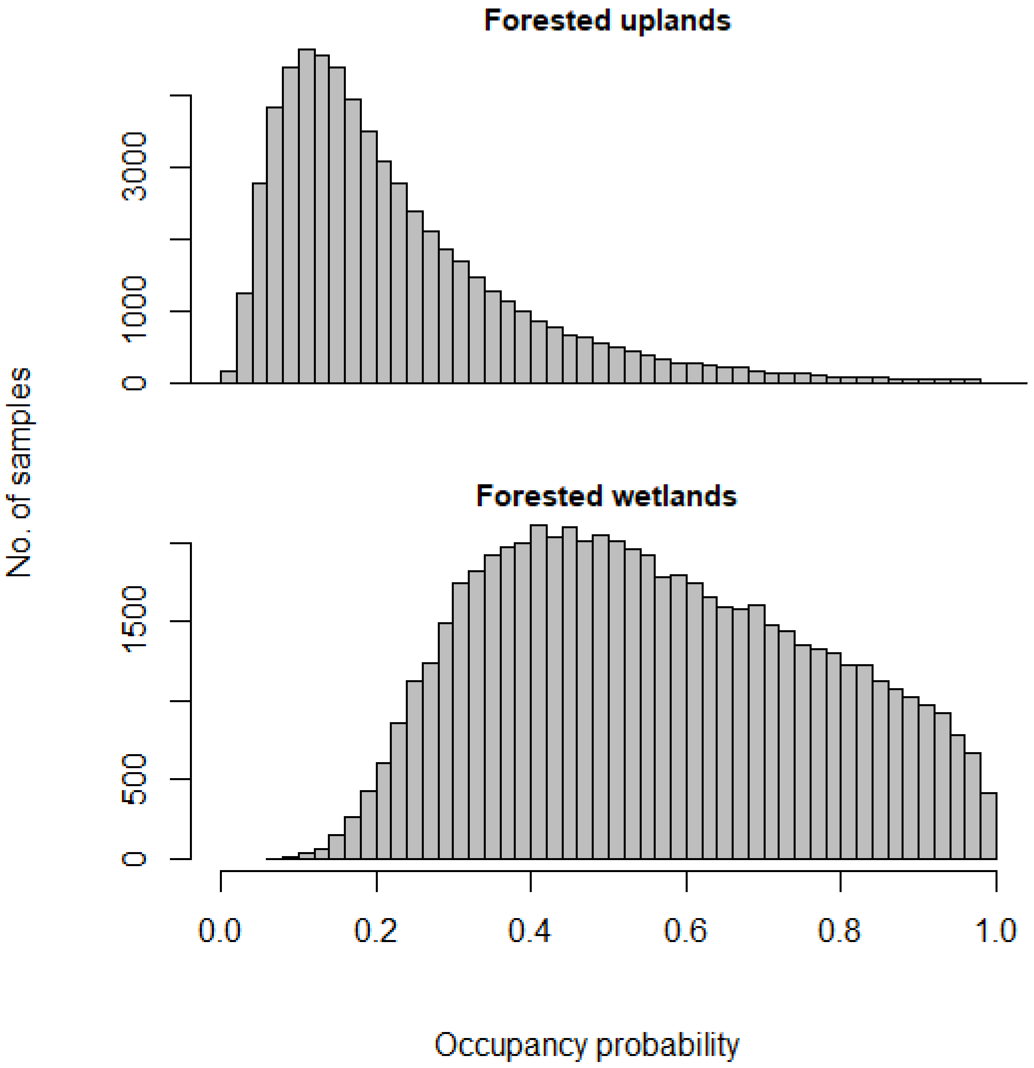


Fig. A23 Posterior distributions of predicted occurrence rates of rusty blackbird (*Euphagus carolinus*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

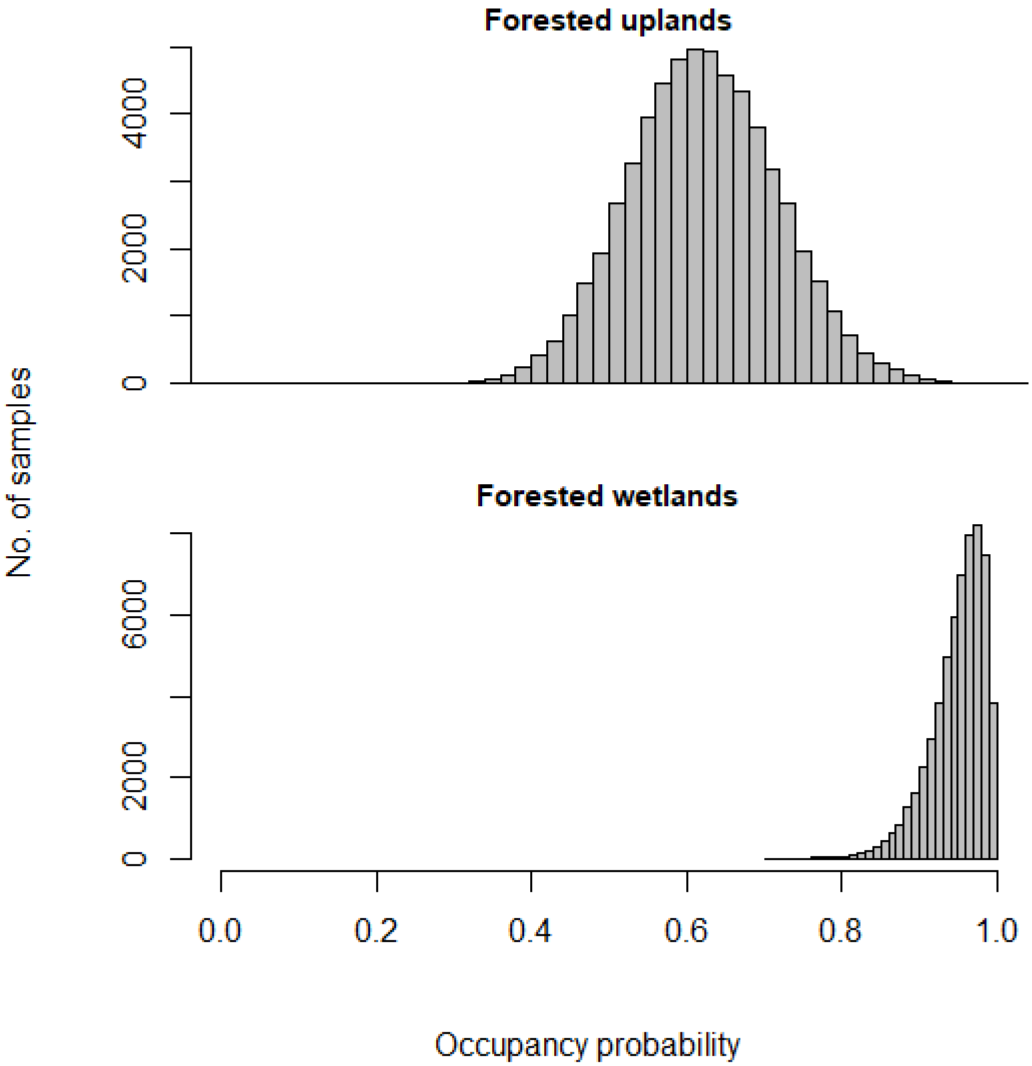


Fig. A24 Posterior distributions of predicted occurrence rates of yellow-rumped warbler (myrtle) (*Setophaga coronata coronata*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

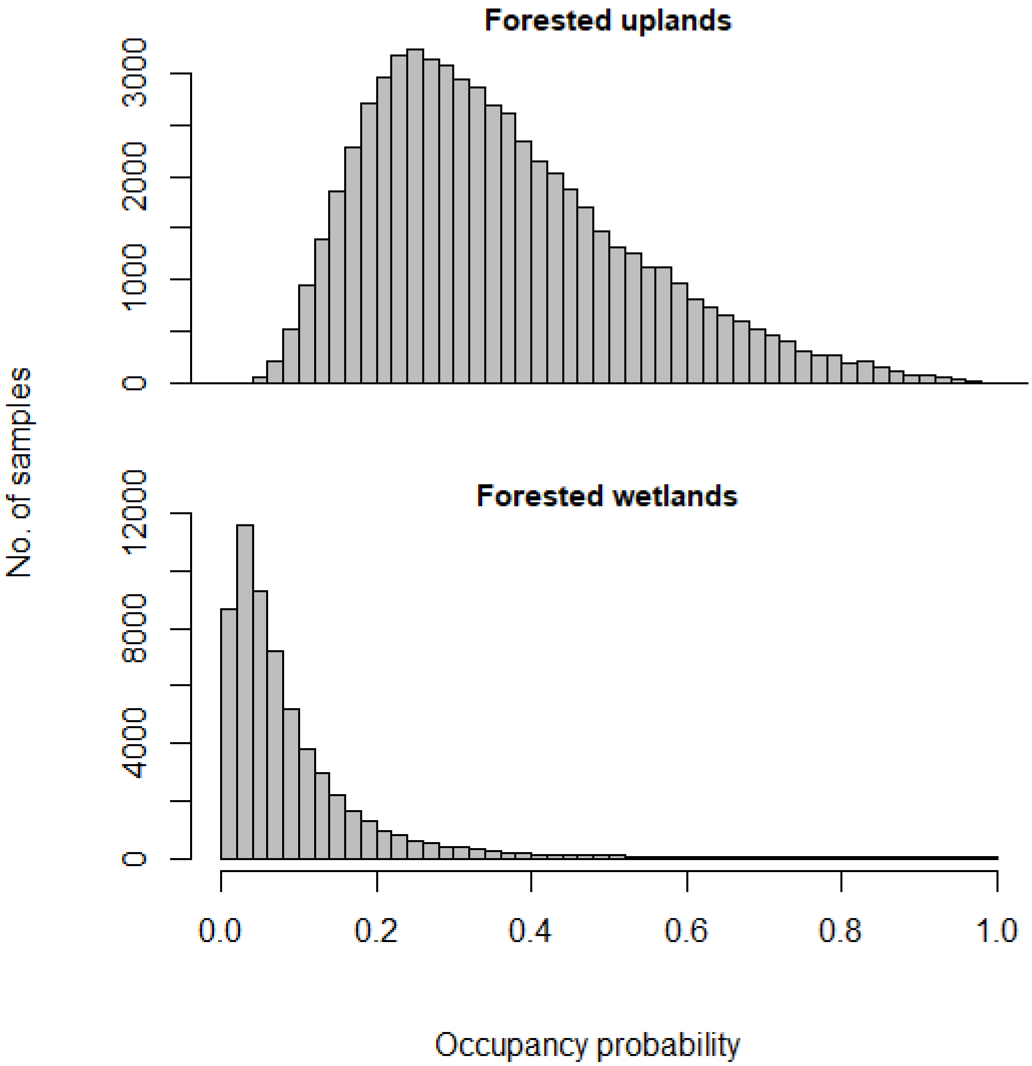


Fig. A25 Posterior distributions of predicted occurrence rates of red-headed woodpecker (*Melanerpes erythrocephalus*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

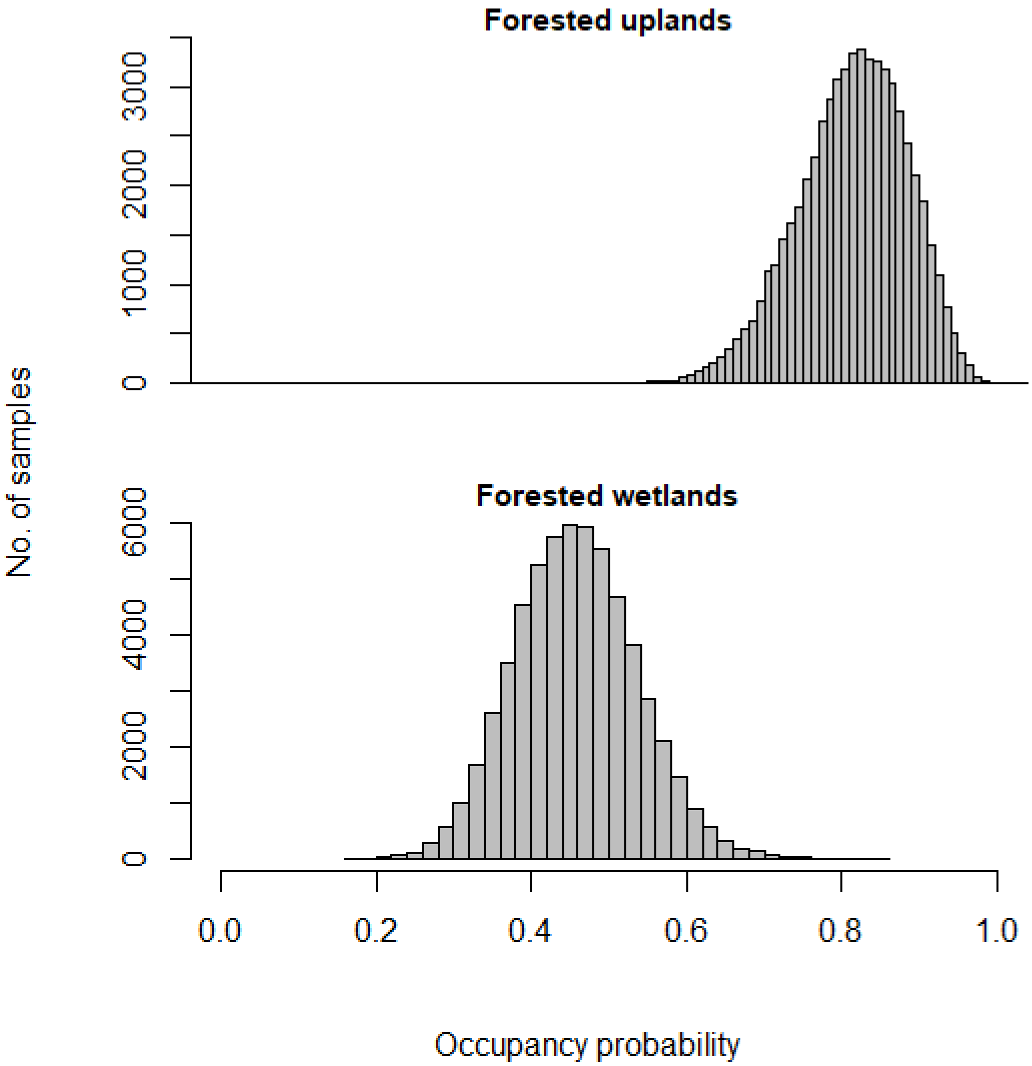


Fig. A26 Posterior distributions of predicted occurrence rates of tufted titmouse (*Baeolophus bicolor*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

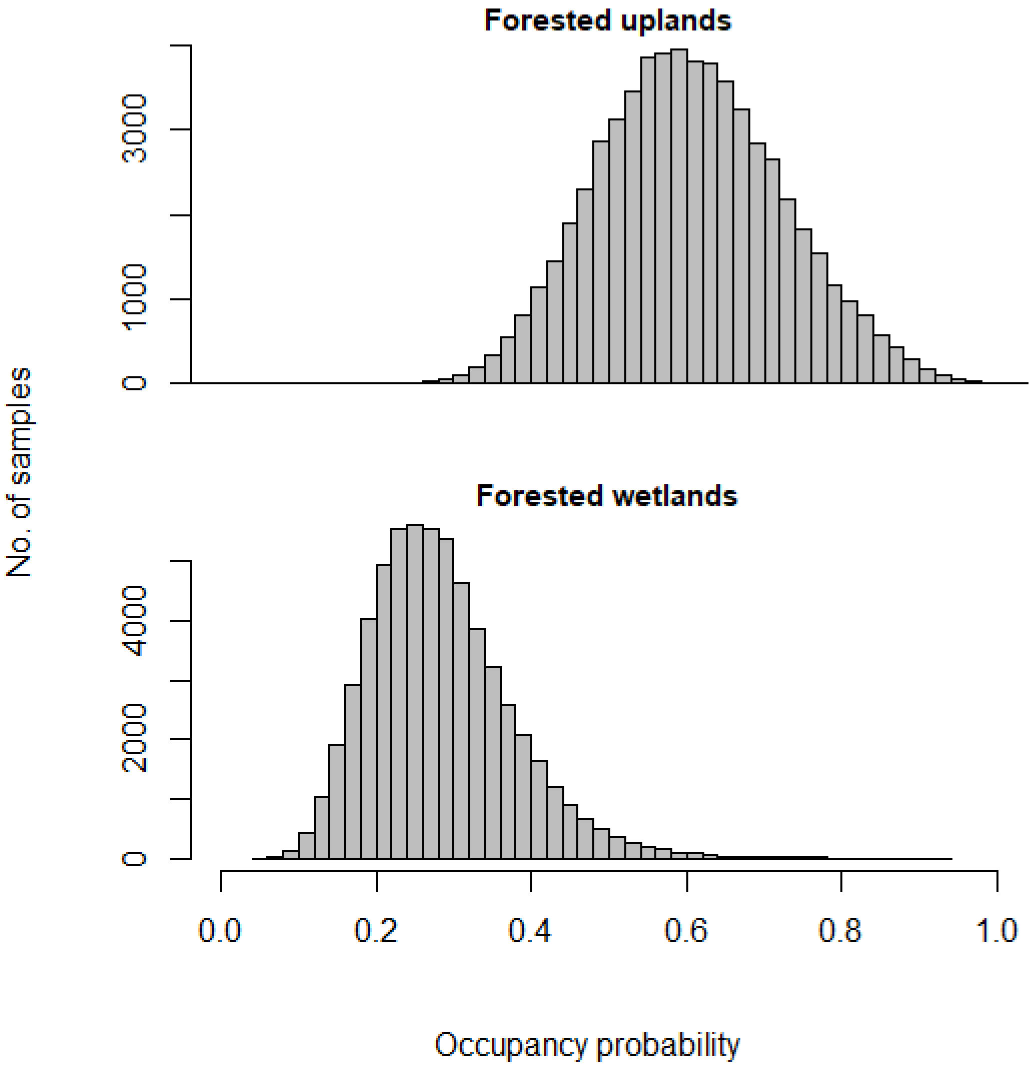


Fig. A27 Posterior distributions of predicted occurrence rates of white-breasted nuthatch (*Sitta carolinensis*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

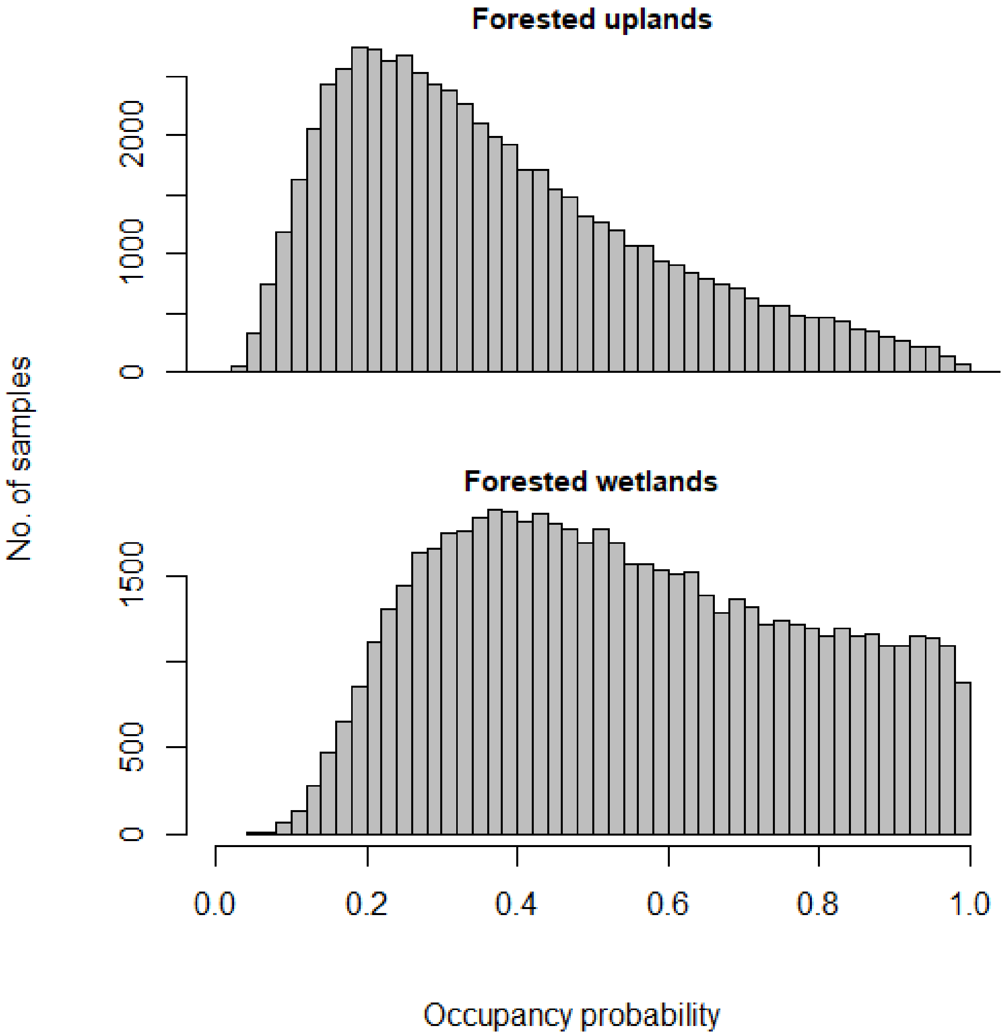


Fig. A28 Posterior distributions of predicted occurrence rates of cedar waxwing (*Bombycilla cedrorum*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

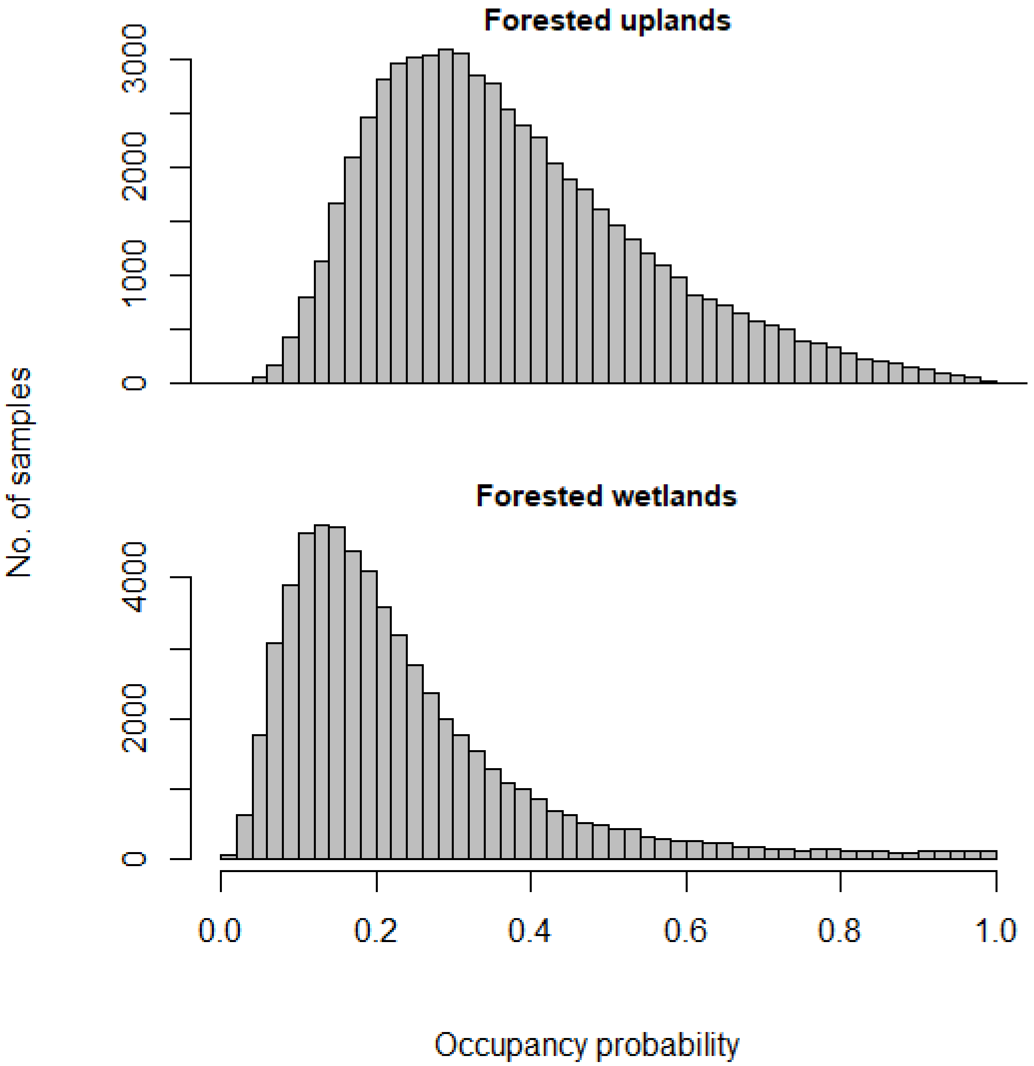


Fig. A29 Posterior distributions of predicted occurrence rates of eastern bluebird (*Sialia sialis*) in forested upland and forested wetland habitat in eastern Virginia and North Carolina.

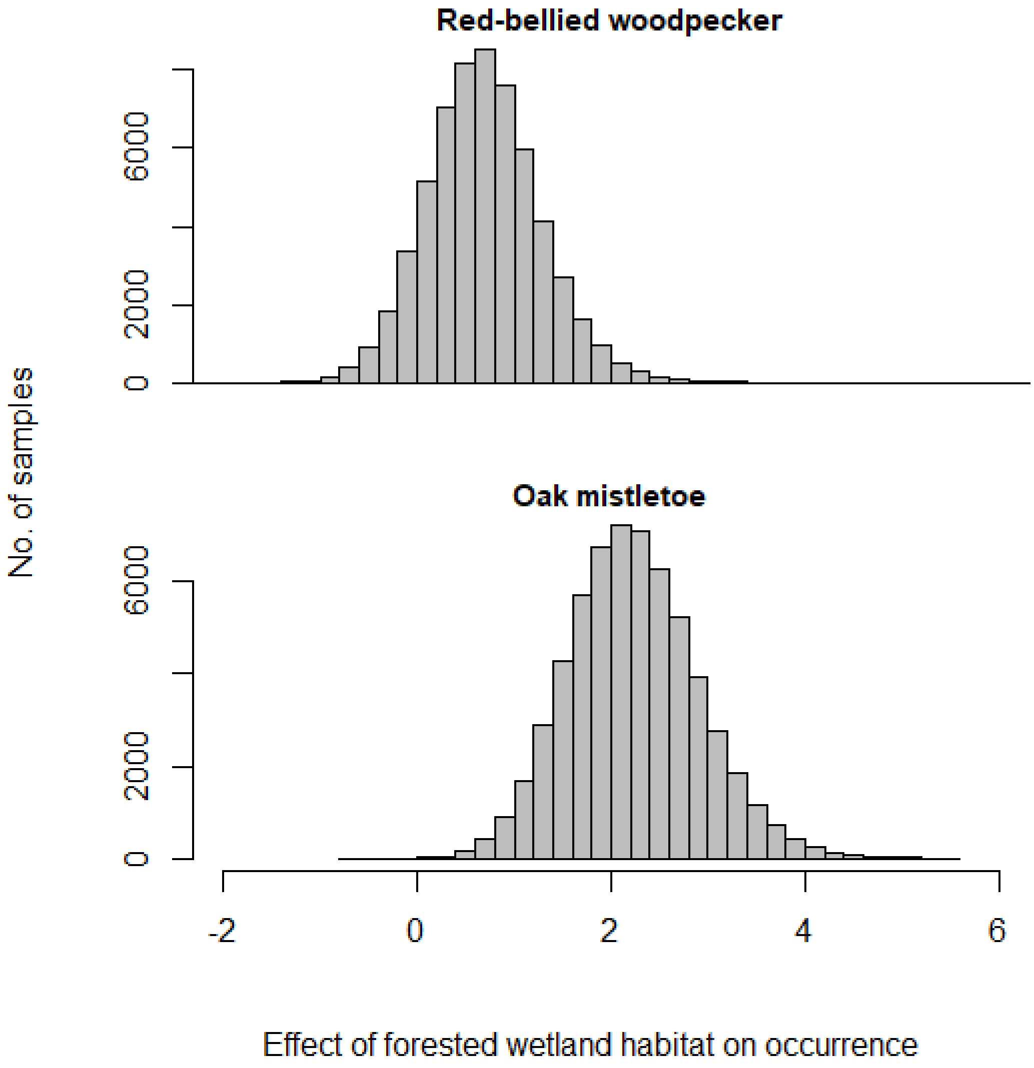


Fig. A30 Posterior distributions of the effects of forested wetland habitat on the occurrence of oak mistletoe (*Phoradendron leucarpum*) and red-bellied woodpecker (*Melanerpes carolinus*). These effects were deemed significantly different as greater than 95% of the samples from the posterior of this relationship for oak mistletoe were greater than such samples for red-bellied woodpecker (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015).

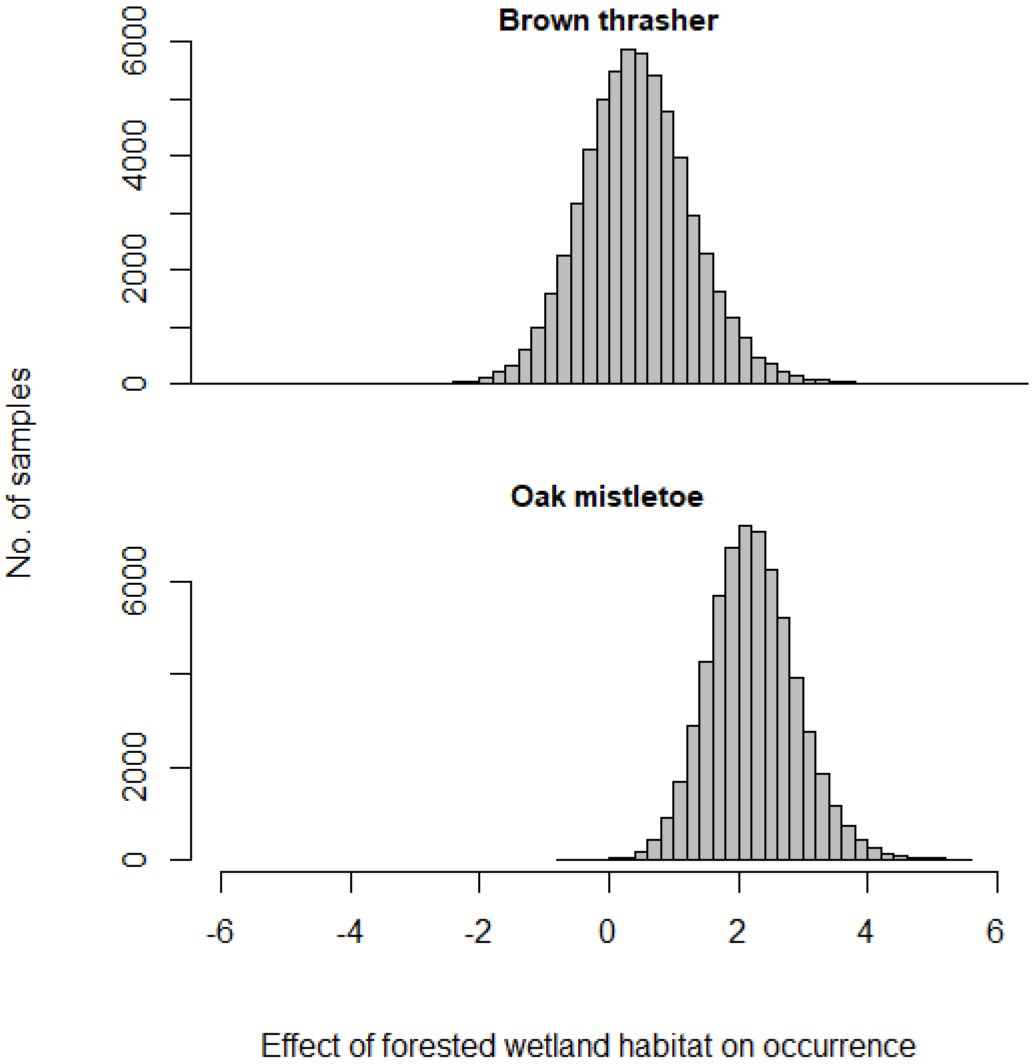


Fig. A31 Posterior distributions of the effects of forested wetland habitat on the occurrence of oak mistletoe (*Phoradendron leucarpum*) and brown thrasher (*Toxostoma rufum*). These effects were deemed statistically different as greater than 95% of the samples from the posterior of this relationship for oak mistletoe were greater than such samples for brown thrasher (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015).

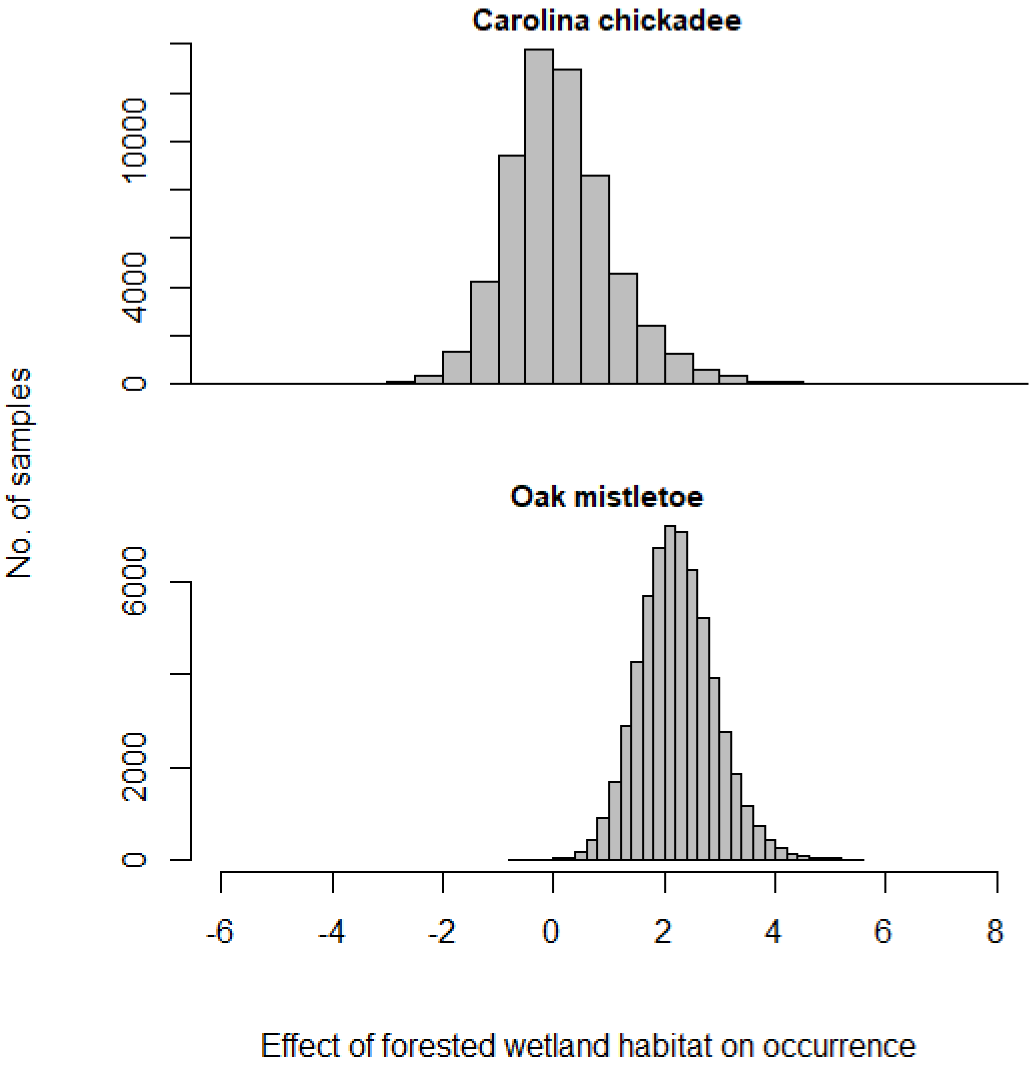


Fig. A32 Posterior distributions of the effects of forested wetland habitat on the occurrence of oak mistletoe (*Phoradendron leucarpum*) and Carolina chickadee (*Poecile carolinensis*). These effects were deemed statistically different as greater than 95% of the samples from the posterior of this relationship for oak mistletoe were greater than such samples for Carolina chickadee (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015).

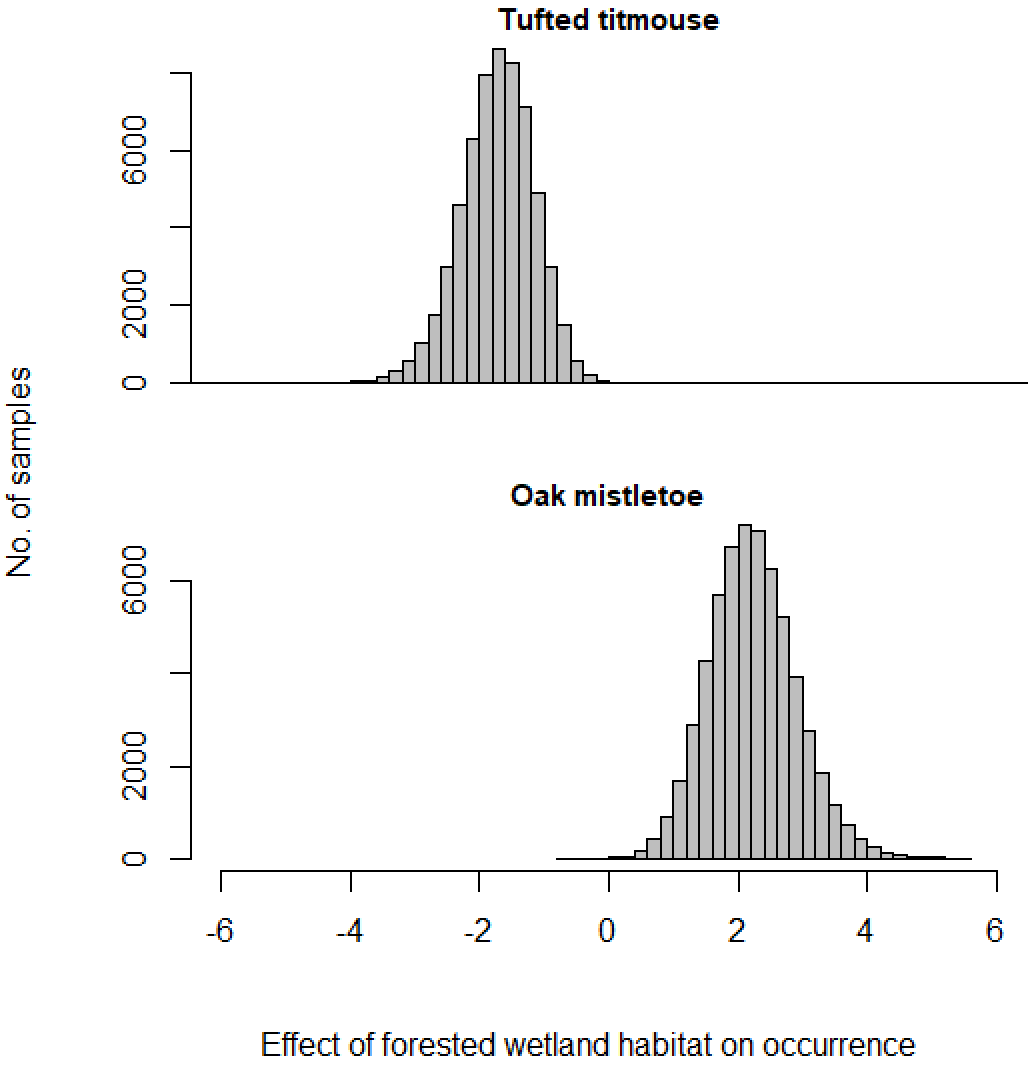


Fig. A33 Posterior distributions of the effects of forested wetland habitat on the occurrence of oak mistletoe (*Phoradendron leucarpum*) and tufted titmouse (*Baeolophus bicolor*). These effects were deemed statistically different as greater than 95% of the samples from the posterior of this relationship for oak mistletoe were greater than such samples for tufted titmouse (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015).

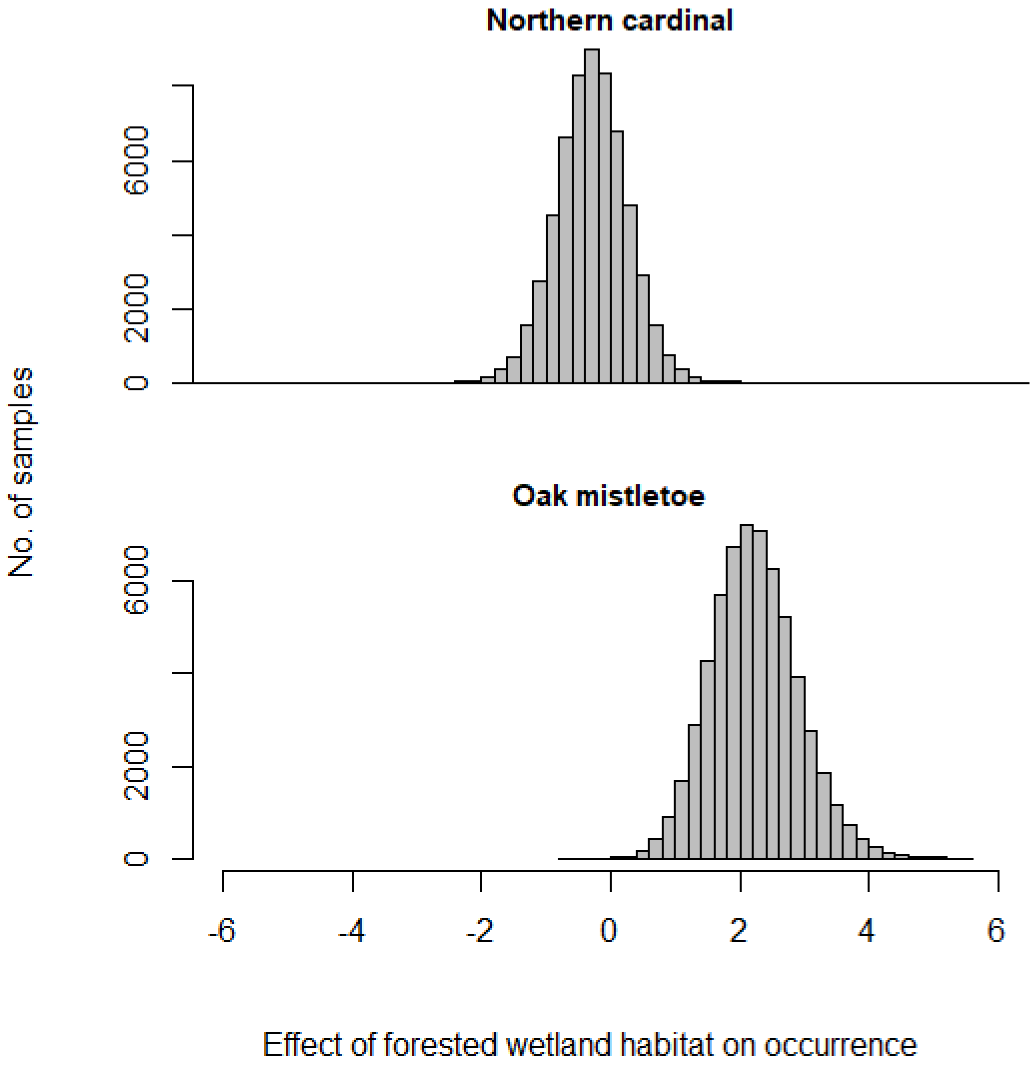


Fig. A34 Posterior distributions of the effects of forested wetland habitat on the occurrence of oak mistletoe (*Phoradendron leucarpum*) and northern cardinal (*Cardinalis cardinalis*). These effects were deemed statistically different as greater than 95% of the samples from the posterior of this relationship for oak mistletoe were greater than such samples for northern cardinal (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015).

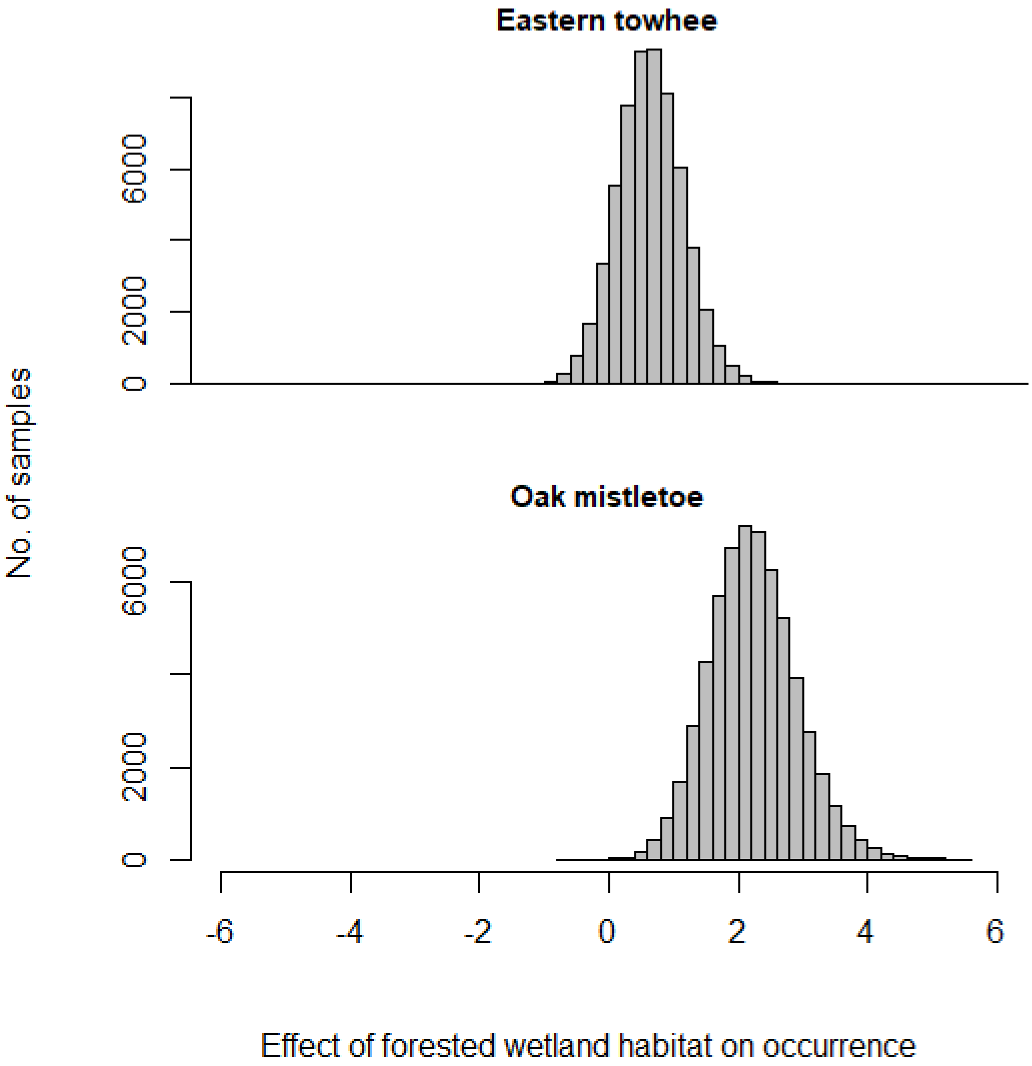


Fig. A35 Posterior distributions of the effects of forested wetland habitat on the occurrence of oak mistletoe (*Phoradendron leucarpum*) and eastern towhee (*Pipilo erythrophthalmus*). These effects were deemed statistically different as greater than 95% of the samples from the posterior of this relationship for oak mistletoe were greater than such samples for eastern towhee (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015).

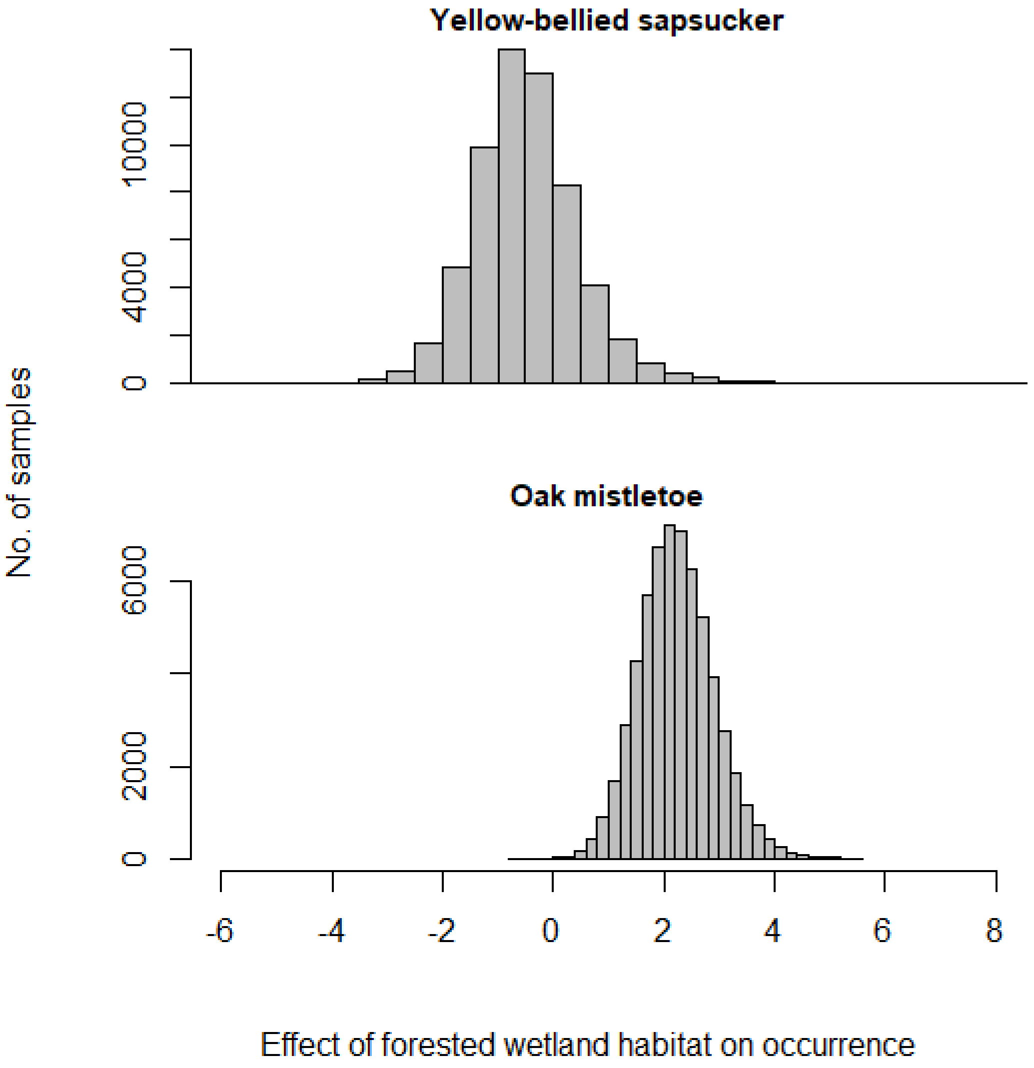


Fig. A36 Posterior distributions of the effects of forested wetland habitat on the occurrence of oak mistletoe (*Phoradendron leucarpum*) and yellow-bellied sapsucker (*Sphyrapicus varius*). These effects were deemed statistically different as greater than 95% of the samples from the posterior of this relationship for oak mistletoe were greater than such samples for eastern towhee (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015).

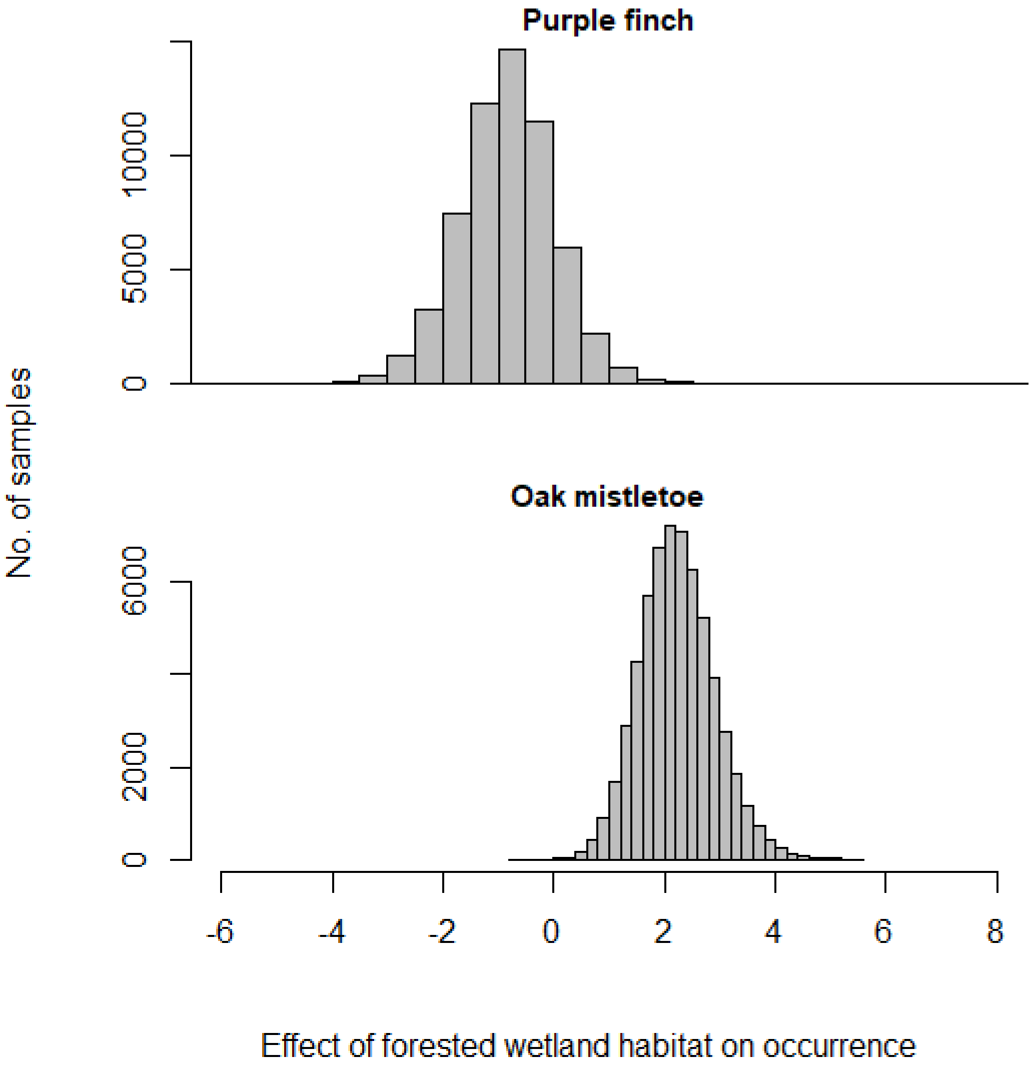


Fig. A37 Posterior distributions of the effects of forested wetland habitat on the occurrence of oak mistletoe (*Phoradendron leucarpum*) and purple finch (*Haemorhous purpureus*). These effects were deemed statistically different as greater than 95% of the samples from the posterior of this relationship for oak mistletoe were greater than such samples for purple finch (Ruiz-Gutiérrez et al. 2010, Flanders et al. 2015).

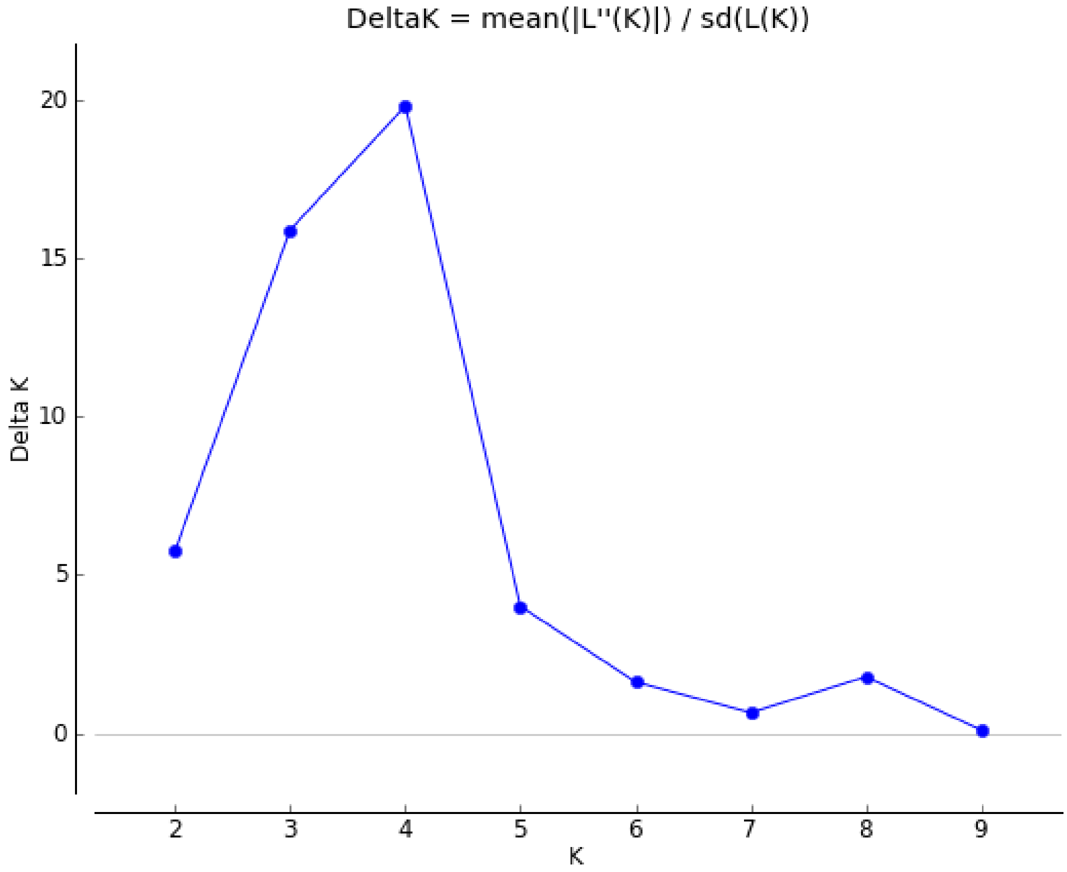


Fig. A38 The delta K statistic of Evanno et al. (2005) calculated using Structure Harvester (Earl & vonHoldt 2012) with results from runs of the program STRUCTURE (Pritchard et al. 2000) across different hypothesized numbers of oak mistletoe populations (K) in eastern Virginia and North Carolina.

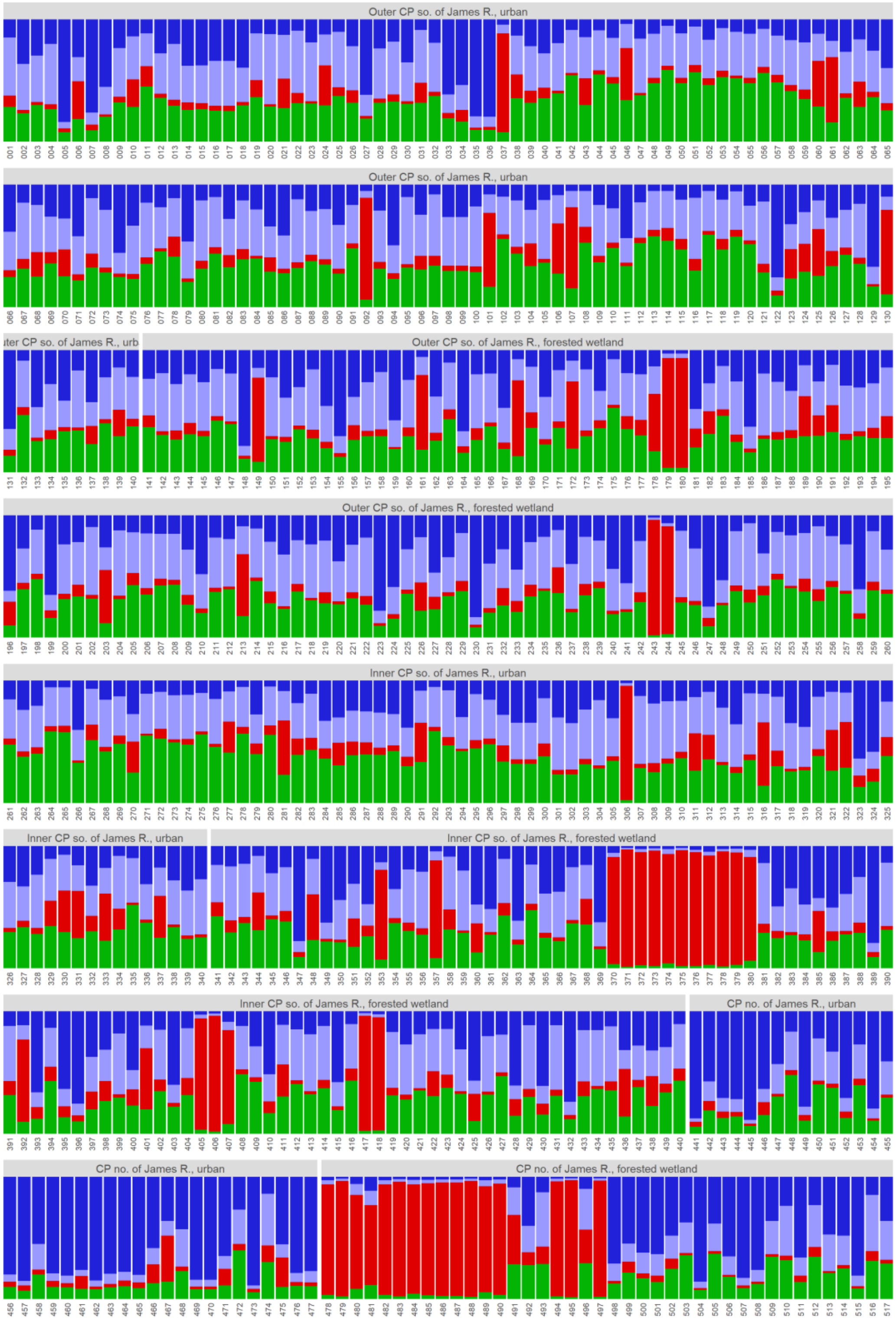


Fig. A39 Ancestry proportions for oak mistletoe samples grouped by host association region as estimated by STRUCTURE (Pritchard et al. 2000) and optimally aligned across runs with CLUMPP (Jakobsson & Rosenberg 2007).

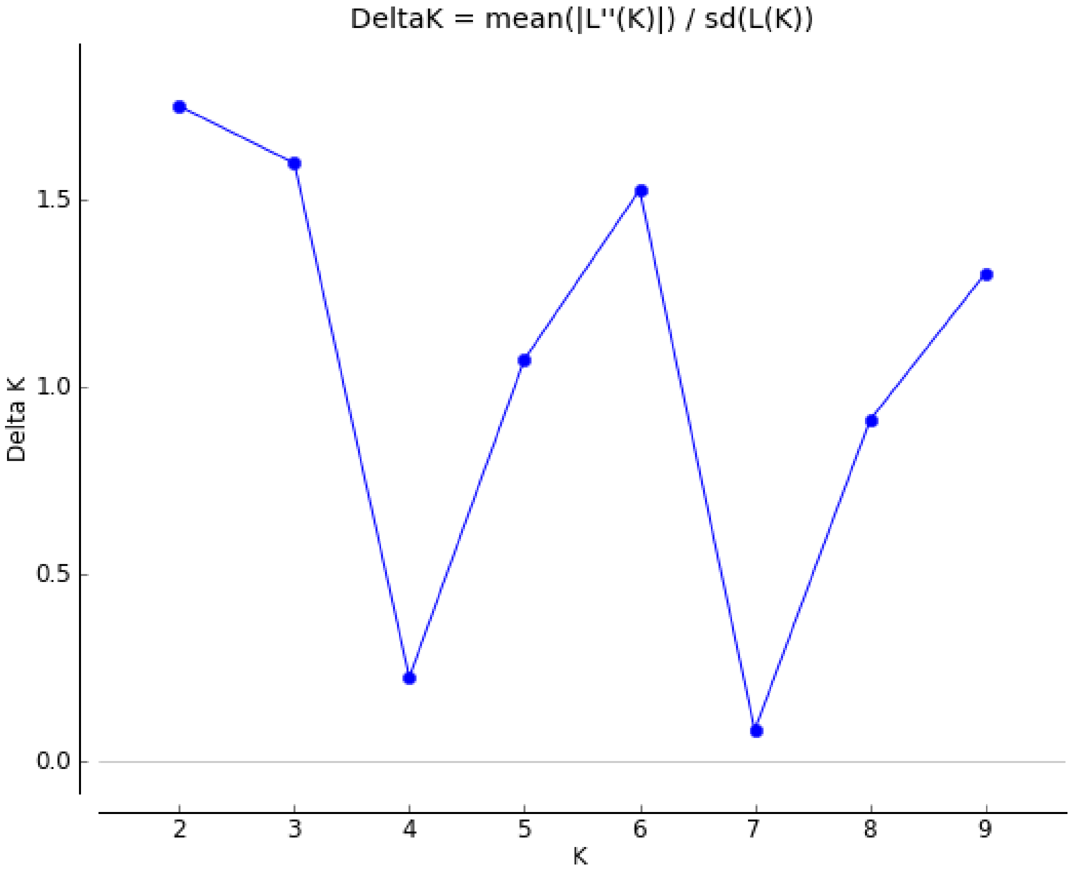


Fig. A40 The delta K statistic of Evanno et al. (2005) calculated using Structure Harvester (Earl & vonHoldt 2012) with results from runs of the program STRUCTURE (Pritchard et al. 2000) across different hypothesized numbers of oak mistletoe populations (K) in eastern Virginia and North Carolina. This analysis only included individuals whose previously estimated ancestry in the "Nyssa" cluster was less than 0.65.

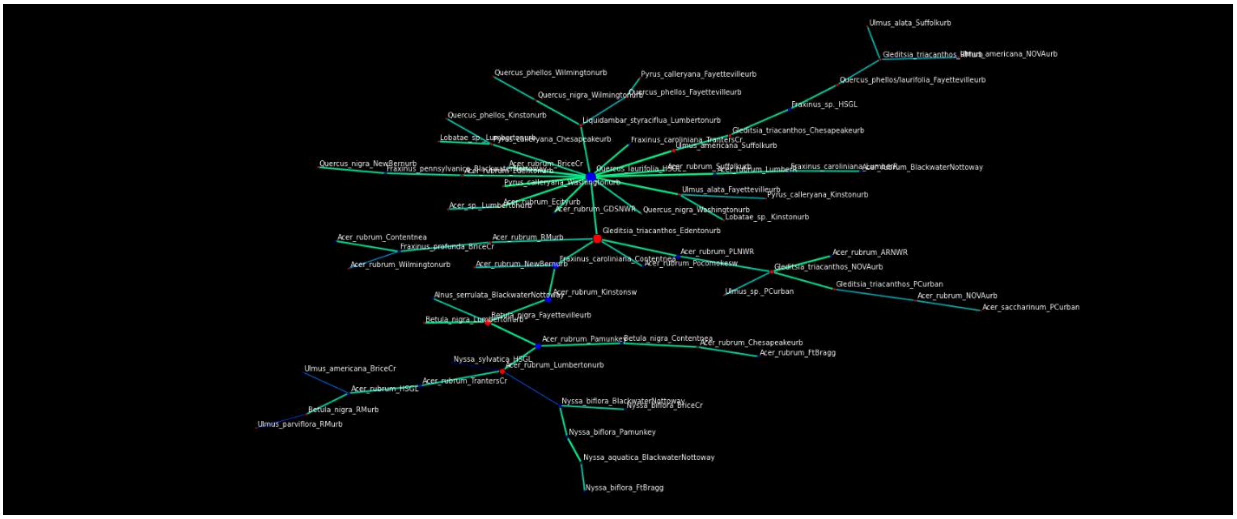


Fig. A41 Visualization of genetic relatedness between site and host-specific mistletoe populations with a minimum spanning tree created in EDENetworks version 2.18 (Kivelä et al. 2015). Thick lines between nodes that are colored green represent stronger links relative to thin lines colored blue that represent lower relatedness. Node size reflects the number of connections to other populations in the network, with populations from urban habitat colored red and populations from forested wetland habitat colored blue. Links on this tree suggest the lack of a relationship between clustering among mistletoe samples based on genetic distance and habitat type.

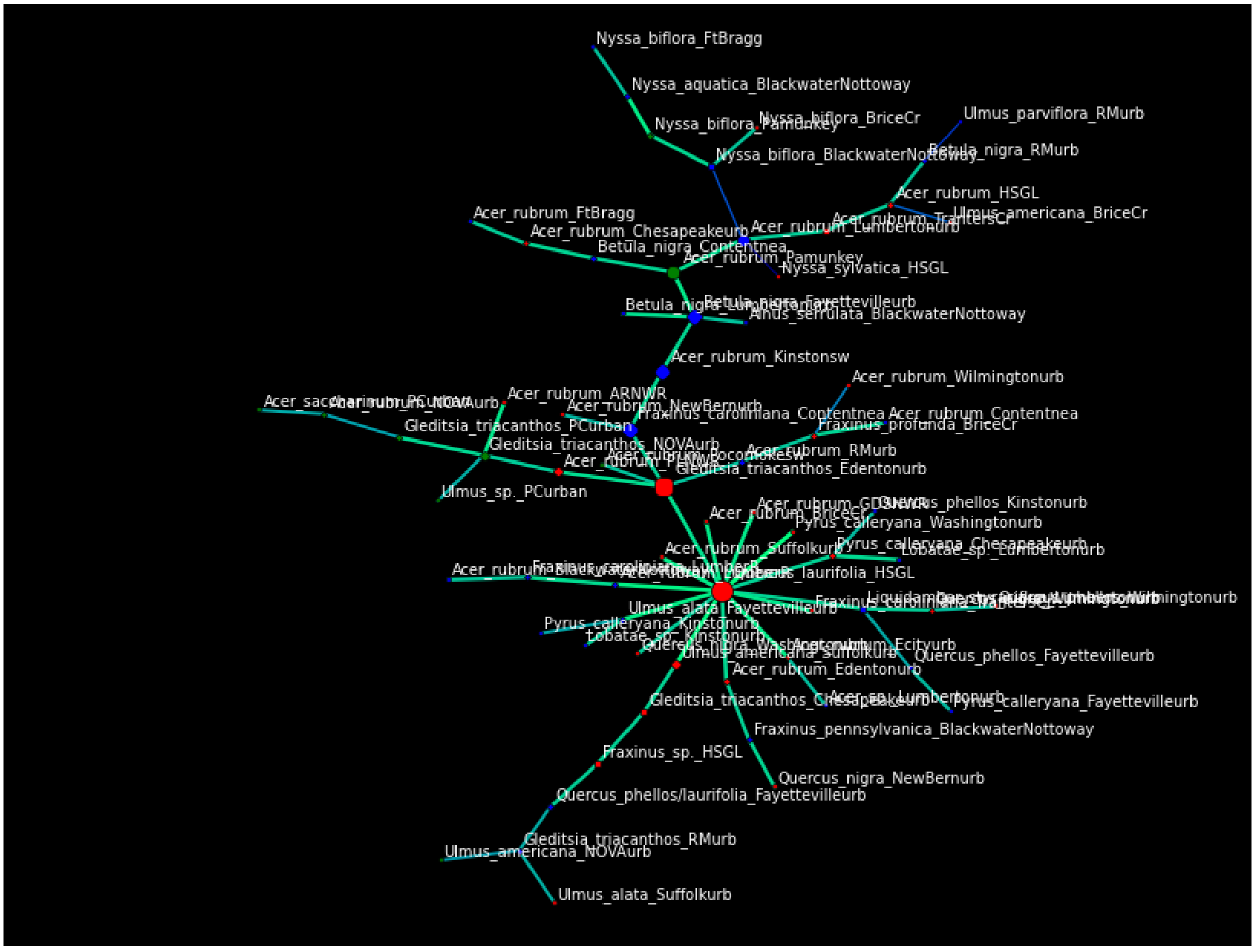


Fig. A42 Visualization of genetic relatedness between site and host-specific mistletoe populations with a minimum spanning tree created in EDENetworks version 2.18 (Kivelä et al. 2015). Thick, green lines between nodes represent stronger links relative to thin lines colored blue that represent lower relatedness. Node size reflects the number of connections to other populations in the network, with populations in the outer Coastal Plain south of the James River colored red, populations in the inner Coastal Plain south of the James River colored blue, and populations in the Coastal Plain north of the James River colored green. Links on this tree suggest clustering among mistletoe samples from *Nyssa* hosts based on genetic distance and the lack of a relationship between such clustering and geographic region.

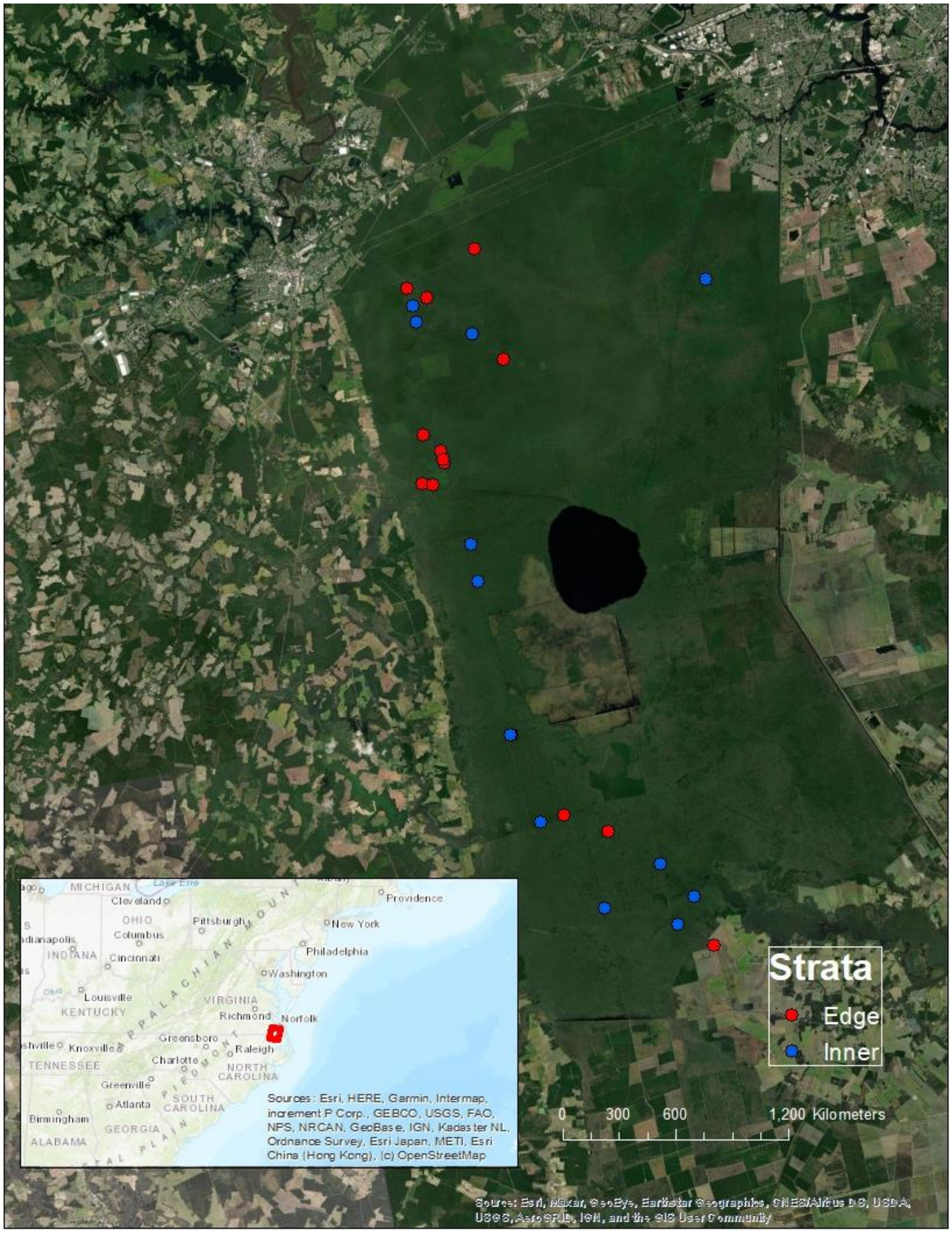
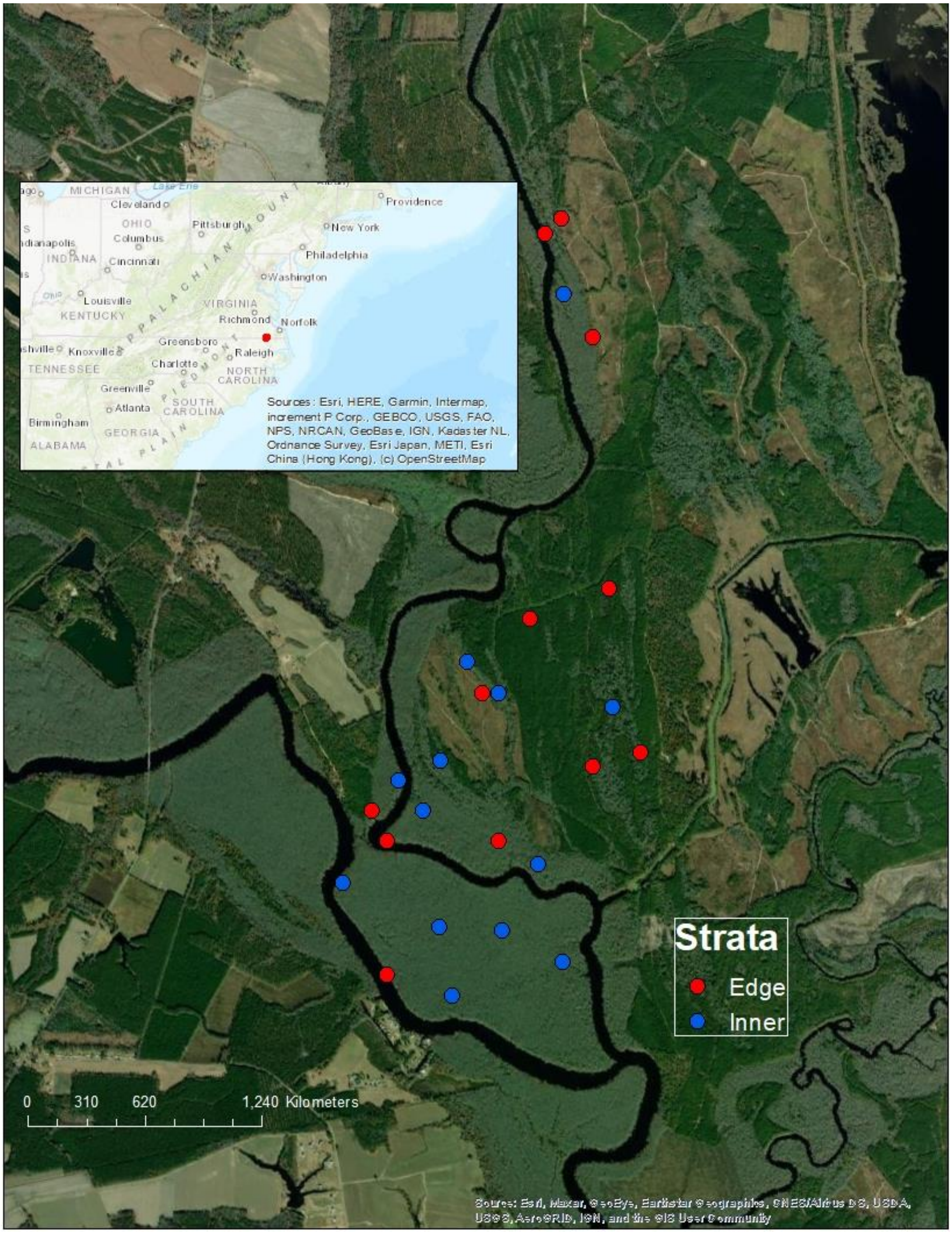


Fig. A43 Locations of 26 plots for planting oak mistletoe seeds in Great Dismal Swamp National Wildlife Refuge, city of Suffolk, VA, USA; plots were in forested wetland habitat either within 15 m of an edge (edge strata) or greater than 15 m from an edge (inner strata).



Sources: Esri, HERE, Garmin, Intermap, increment P Corp., GEBCO, USGS, FAO, NPS, NRCAN, GeoBase, IGN, Kadaster NL, Ordnance Survey, Esri Japan, METI, Esri China (Hong Kong), (c) OpenStreetMap

Source: Esri, Maxar, GeoEye, Earthstar Geographics, CNES/Airbus DS, USDA, USGS, AeroGRID, IGN, and the GIS User Community

Fig. A44 Locations of 25 plots for planting oak 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).

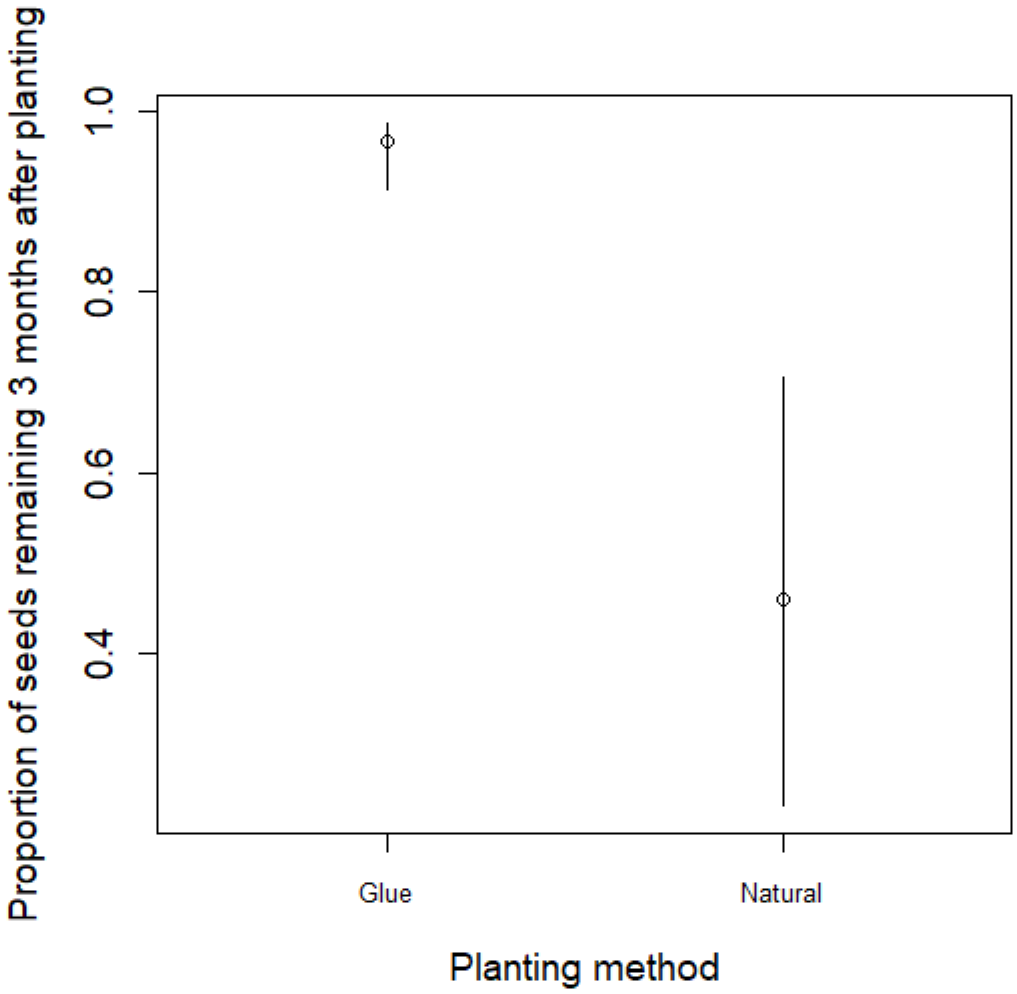


Fig. A45 Model-averaged predictions of proportions of oak mistletoe seeds remaining approximately 3 months after planting across two alternative planting methods; error bars represent 95% confidence intervals.

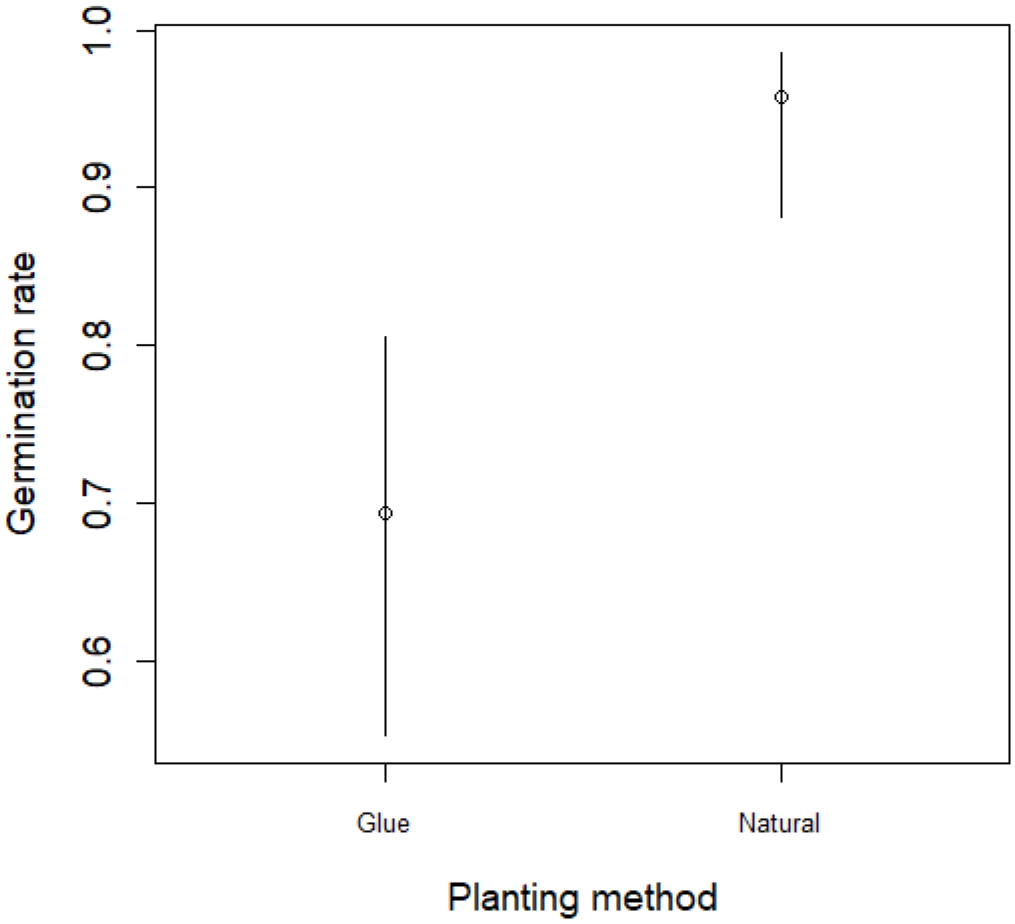


Fig. A46 Model-averaged predictions of oak mistletoe germination rates across two alternative planting methods; error bars represent 95% confidence intervals.

APPENDIX

TABLES

Table A1 Species and genera of woody plants detected as hosts for oak mistletoe in forested habitats at plots and sites selected ad hoc across the study area.

Host trees identified to species
Acer rubrum
Acer saccharinum
Alnus serrulata
Betula nigra
Carpinus caroliniana
Carya ovata
Celtis laevigata
Fraxinus americana
Fraxinus caroliniana
Fraxinus pennsylvanica
Fraxinus profunda
Liquidambar styraciflua
Nyssa aquatica
Nyssa biflora
Nyssa sylvatica
Persea palustris
Quercus falcata
Quercus laevis
Quercus laurifolia
Quercus lyrata
Quercus marilandica
Quercus nigra
Quercus pagoda
Quercus palustris
Quercus phellos
Quercus rubra
Quercus velutina
Styrax americanus
Ulmus alata
Ulmus americana
Host trees identified to genus or sub-genus
Carya sp.
Celtis sp.
Quercus (*Lobatae* sub-genus) sp.

Table A1 continued.
Shrub species identified as host
Cornus stricta
Liana species identified as host
Ampelopsis arborea

Table A2 Species and genera of trees detected in sub-plots.

Sub-plot trees identified to species
Acer floridanum
Acer negundo
Acer rubrum
Ailanthus altissima
Alnus serrulata
Amelanchier canadensis
Aralia spinosa
Asimina triloba
Betula nigra
Carpinus caroliniana
Carya cordiformis
Carya glabra
Carya pallida
Cephalanthus occidentalis
Cercis canadensis
Chamaecyparis thyoides
Cornus florida
Cyrilla racemiflora
Diospyros virginiana
Euonymus americana
Fagus grandifolia
Fraxinus americana
Fraxinus caroliniana
Fraxinus pennsylvanica
Fraxinus profunda
Gordonia lasianthus
Ilex decidua
Ilex myrtifolia
Ilex opaca
Ilex verticillata
Ilex vomitoria
Juglans nigra

Table A2 continued.

Juniperus virginiana
Kalmia latifolia
Ligustrum sinense
Liquidambar styraciflua
Liriodendron tulipifera
Magnolia acuminata
Magnolia virginiana
Morella cerifera
Nyssa aquatica
Nyssa biflora
Nyssa sylvatica
Ostrya virginiana
Oxydendrum arboreum
Persea palustris
Pinus echinata
Pinus palustris
Pinus serotina
Pinus taeda
Pinus virginiana
Platanus occidentalis
Populus heterophylla
Prunus serotina
Quercus alba
Quercus coccinea
Quercus falcata
Quercus incana
Quercus laurifolia
Quercus michauxii
Quercus montana
Quercus nigra
Quercus phellos
Quercus rubra
Quercus velutina
Quercus virginiana
Rhododendron maximum
Rhus copallinum
Sassafras albidum
Stewartia malacodendron
Styrax americanus
Symplocos tinctoria
Taxodium distichum
Toxicodendron vernix

Table A2 continued.

Ulmus alata
Ulmus americana
Sub-plot trees identified to taxa higher than species
Carya sp.
Chamaecyparis/Juniperus
Fraxinus americana/pennsylvanica
Fraxinus caroliniana/pennsylvanica/profunda
Fraxinus sp.
Ilex verticillata/laevigata
Morus sp.
Pinus taeda/serotina
Pinus virginiana/echinata
Quercus (*Lobatae* sub-genus) sp.
Quercus (*Quercus* sub-genus) sp.
Quercus sp.
Ulmus sp.

Table A3 Alternative generalized linear models for the relationship between *Liquidambar styraciflua* BA at sub-plots and region as ranked by AIC_c.

Variables included in model	K	AIC_c	Delta AIC_c	AIC_c weight	Cumulative weight	LL
Intercept (null)	2	197.37	0	0.52	0.52	-96.51
Intercept + region	3	197.55	0.18	0.48	1	-95.41

Table A4 Alternative generalized linear models for the relationships between *Acer rubrum* occurrence at plots and habitat type and region as ranked by AIC_c.

Variables included in model	K	AIC_c	Delta AIC_c	AIC_c weight	Cumulative weight	LL
Intercept + region	2	115.76	0	0.6	0.6	-55.81
Intercept + region + hab	3	117.18	1.42	0.29	0.89	-55.46
Intercept + region + hab + interaction	4	119.31	3.55	0.1	0.99	-55.43
Intercept (null)	1	125.59	9.84	0	1	-61.78
Intercept + hab	2	126.45	10.69	0	1	-61.16

Table A5 List of shrub species commonly encountered in sub-plots but typically not recorded.

Woody plant taxa encountered but not typically recorded in sub-plots because considered shrubs
Aronia arbutifolia
Baccharis halimifolia
Clethra alnifolia
Cornus spp. other than *C. florida*
Elaeagnus spp.
Eubotrys racemose
Ilex coriacea
Ilex glabra
Ilex laevigata
Itea verticillate
Lindera benzoin
Lyonia ligustrina
Lyonia lucida
Morella caroliniensis
Rhododendron viscosum
Rosa spp.
Vaccinium spp. other than *V. arborea*
Viburnum spp.

Table A6 Number of oak mistletoe samples collected from 19 host species and 5 hosts identified to the genus or sub-genus level.

Host species	Number of samples
Acer rubrum	260
Acer saccharinum	3
Acer sp.	6
Alnus serrulata	5
Betula nigra	23
Fraxinus caroliniana	26
Fraxinus pennsylvanica	2
Fraxinus profunda	3
Fraxinus sp.	4
Gleditsia triacanthos	30
Liquidambar styraciflua	1
Quercus (*Lobatae* sub-genus) sp.	15
Nyssa aquatica	2
Nyssa biflora	44
Nyssa sylvatica	2
Pyrus calleryana	17
Quercus laurifolia	1
Quercus nigra	29
Quercus phellos	24
Quercus phellos/laurifolia	3
Ulmus alata	13
Ulmus americana	12
Ulmus parviflora	1
Ulmus sp.	3

Table A7 Forest bird species detected on surveys conducted during winter seasons (Dec–Mar) of 2015-2016 to that of 2019-2020 in eastern Virginia and North Carolina. Species were classified as frugivores or non-frugivores based on reported winter diets (Billerman et al. 2020).

Frugivores	**Non-frugivores**
red-bellied woodpecker (*Melanerpes carolinus*)	wood duck (*Aix sponsa*)
yellow-bellied sapsucker (*Sphyrapicus varius*)	mourning dove (*Zenaida macroura*)
northern flicker (*Colaptes auratus*)	sharp-shinned hawk (*Accipiter striatus*)
pileated woodpecker (*Dryocopus pileatus*)	Cooper's hawk (*Accipiter cooperii*)
white-eyed vireo (*Vireo griseus*)	red-shouldered hawk (*Buteo lineatus*)
Carolina chickadee (*Poecile carolinensis*)	barred owl (*Strix varia*)
tufted titmouse (*Baeolophus bicolor*)	red-headed woodpecker (*Melanerpes erythrocephalus*)
cedar waxwing (*Bombycilla cedrorum*)	downy woodpecker (*Dryobates pubescens*)
gray catbird (*Dumetella carolinensis*)	red-cockaded woodpecker (*Dryobates borealis*)
brown thrasher (*Toxostoma rufum*)	hairy woodpecker (*Dryobates villosus*)
eastern bluebird (*Sialia sialis*)	Eastern phoebe (*Sayornis phoebe*)
hermit thrush (*Catharus guttatus*)	blue-headed vireo (*Vireo solitarius*)
American robin (*Turdus migratorius*)	blue jay (*Cyanocitta cristata*)
purple finch (*Haemorhous purpureus*)	common raven (*Corvus corax*)
fox sparrow (*Passerella iliaca*)	ruby-crowned kinglet (*Corthylio calendula*)
eastern towhee (*Pipilo erythrophthalmus*)	golden-crowned kinglet (*Regulus satrapa*)
rusty blackbird (*Euphagus carolinus*)	red-breasted nuthatch (*Sitta canadensis*)
yellow-rumped warbler (myrtle) (*Setophaga coronata coronata*)	white-breasted nuthatch (*Sitta carolinensis*)
northern cardinal (*Cardinalis cardinalis*)	brown-headed nuthatch (*Sitta pusilla*)
	brown creeper (*Certhia americana*)
	house wren (*Troglodytes aedon*)

Table A7 continued.

Frugivores	**Non-frugivores**
	winter wren (*Troglodytes hiemalis*)
	sedge wren (*Cistothorus stellaris*)
	Carolina wren (*Thryothorus ludovicianus*)
	house finch (*Haemorhous mexicanus*)
	pine siskin (*Spinus pinus*)
	American goldfinch (*Spinus tristis*)
	chipping sparrow (*Spizella passerina*)
	field sparrow (*Spizella pusilla*)
	dark-eyed junco (*Junco hyemalis*)
	white-throated sparrow (*Zonotrichia albicollis*)
	song sparrow (*Melospiza melodia*)
	swamp sparrow (*Melospiza georgiana*)
	red-winged blackbird (*Agelaius phoeniceus*)
	brown-headed cowbird (*Molothrus ater*)
	common grackle (*Quiscalus quiscula*)
	orange-crowned warbler (*Leiothlypis celata*)
	common yellowthroat (*Geothlypis trichas*)
	pine warbler (*Setophaga pinus*)

Table A8 Probabilities of differences between estimates of the relationship between forested wetland habitat and occurrence for oak mistletoe and avian frugivore species. Significant probabilities (> 0.95) indicated in bold.

Species	Pr(mistletoe coeff. > frugivore coeff.)
red-bellied woodpecker	**0.96**
yellow-bellied sapsucker	**0.98**
northern flicker	0.89
pileated woodpecker	0.86
white-eyed vireo	0.87
Carolina chickadee	**0.96**
tufted titmouse	**1**
cedar waxwing	0.87
gray catbird	0.54
brown thrasher	**0.95**
eastern bluebird	**0.99**
hermit thrush	0.7
American robin	0.86
purple finch	**0.99**
fox sparrow	0.91
eastern towhee	**0.97**
rusty blackbird	0.67
yellow-rumped warbler (myrtle)	0.35
northern cardinal	**0.99**

Table A9 Distribution of oak 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	765
Nyssa biflora	140
Fraxinus sp.	85
Liquidambar styraciflua	25
Nyssa aquatica	25
Nyssa sylvatica	20
Quercus nigra	10
Alnus serrulata	5
Diospyros virginiana	5
Oxydendrum arboreum	5
Styrax americanus	5

Table A10 Alternative generalized linear models for the relationships between the proportion of oak 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 vs. South Quay Sandhills Natural Area Preserve) and the random effects of plot and nested branch identities.

Variables included in model	K	AIC_c	Delta AIC_c	AIC_c weight	Cumulative weight	LL
Site + planting method	5	1011.2	0	0.73	0.73	-500.57
Site + planting method + branch diam.	6	1013.22	2.02	0.27	1	-500.57
Site (null)	4	1064.1	52.89	0	1	-528.03
Site + branch diameter	5	1065.27	54.06	0	1	-527.61

Table A11 Alternative generalized linear models for the relationships between oak mistletoe seed germination rates and the fixed effects of planting method, year of planting, and percent canopy openness as ranked by AIC. All models included the random effect of branch identity.

Variables included in model	K	AIC_c	Delta AIC_c	AIC_c weight	Cumulative weight	LL
Intercept + planting method + year	5	701.06	0	1	1	-345.49
Intercept + year	4	713.96	12.9	0	1	-352.95
Intercept + year + light	5	715.3	14.24	0	1	-352.61
Intercept + planting method	3	754.78	53.72	0	1	-374.37
Intercept + planting method + light	4	756.8	55.74	0	1	-374.37
Intercept (null)	2	765.3	64.25	0	1	-380.64
Intercept + light	3	767.26	66.2	0	1	-380.61

Table A12 Alternative generalized linear models for the relationship between oak 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	Delta AIC_c	AIC_c weight	Cumulative weight	LL
Intercept (null)	3	248.13	0	0.87	0.87	-121.03
Intercept + flooding	5	251.97	3.84	0.13	1	-120.9

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Great Dismal Swamp National Wildlife Refuge, Suffolk, VA

Monitoring pocosin habitat managed for Red-cockaded Woodpeckers (May–Aug 2014)

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