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Asian Bittersweet (*Celastrus orbiculatus*) Occurrence at Coarse and Fine Scales in North Carolina and Virginia

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ABSTRACT

Asian bittersweet (*Celastrus orbiculatus*) is a widespread, invasive, twining vine in eastern North American forests. Factors associated with its local occurrence are well known but seldom reported at geographic scales coarser than research locations. We evaluated its occurrence across a hierarchy of land units ranging from coarse (provinces), intermediate (landscapes), and fine (site) scales in North Carolina and Virginia. Chi-square tests indicated a significant difference in the proportion of plots with *C. orbiculatus* in mountain (5.5%) compared to piedmont (9.9%) provinces. Using groups of forest types (e.g., *Acer-Betula, Quercus-Pinus*) to represent landscape-scale land units, *C. orbiculatus* occurred in a greater proportion of plots classified as *Quercus-Carya.* At the fine scale of sample sites within landscapes, in plots where *C. orbiculatus* was present the soil moisture regime was classified as mesic significantly more often than xeric in both provinces. Foliage cover differed between mountain (9.6%) and piedmont provinces (5.1%), and among several forest type groups at the landscape scale but responded weakly to moisture regime. Our results show that the proportional occurrence of *C. orbiculatus* varied significantly among land units at each hierarchical level. We suggest that our land units, defined by physiography, tree communities and soil moisture regime, represent tentative ecosystems that can be included as spatial variables in models to improve predictions of the presence of *C. orbiculatus*, for example in response to a changing climate.

Key words: Forest Inventory and Analysis, foliage cover, forest type groups, invasive species, Oriental bittersweet, roundleaf bittersweet, soil moisture.

INTRODUCTION

Celastrus orbiculatus Thunb. (Celastraceae), also known as roundleaf bittersweet, Oriental bittersweet and Asian bittersweet, is a perennial, twining vine native to Japan and eastern China (Del Tredici 2014) that has received considerable study because of its use as a traditional medicine (Wang et al. 2012) and its pharmacological and phytochemical properties (Wu et al. 2012; Feng et al. 2023). From the early 1900s, *C. orbiculatus* was listed in a North Carolina plant catalog as a desirable ornamental because of its easy propagation, persistence when disturbed, rapid growth and attractive fruits for floral displays (Biltmore Nursery Catalog 1907; Del Tredici 2014). During the 20th century it has become naturalized throughout eastern North America (Del Tredici 2014), New Zealand (Williams and Timmins 2003), and Europe (Gudzinskas et al. 2020). In 1947, however, White and Bowden (1947) described *C. orbiculatus* as a potential invasive species in the eastern United States, where highly disturbed forests are particularly susceptible to alien species (Webster et al. 2006).

The invasive nature of *Celastrus orbiculatus* in forests beyond its endemic Asian range may

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be facilitated by the physiological and ecological characteristics of the species, such as its high tolerance to shade in the understory of forests (Patterson 1974; Martin et al. 2009). Beneath closed canopies of deciduous hardwoods it persists in a periodic cycle of limited stem growth (to a height of about 0.5 m) followed by dieback and regrowth (Greenberg et al. 2001; Leicht-Young et al. 2007). It has a longer growing season than the overstory trees, leafing out before the canopy in spring (McNab and Loftis 2002). When released from overstory shade following canopy disturbance, *C. orbiculatus* can quickly respond from a subsistence state to full growth (Patterson 1974). Its growth habit allows ascension to the canopy by twining around nearby supporting tree stems (McNab and Meeker 1987). In full sunlight, plants of this dioecious species annually produce either staminate or pistillate flowers and seed crops are typically abundant (Patterson 1974; Ellsworth et al. 2004). Rapid growth and high levels of pollen production by *C. orbiculatus* can reduce seed production by co-occurring populations of the native species (*C. scandens* L.) and endanger its status by overtopping and hybridization (Zaya et al. 2021). Seeds of *C. orbiculatus* have a high germination rate and seedlings can establish in an undisturbed forest floor (Ellsworth et al. 2004). The fleshy aril persists on stems during winter where it can be consumed by birds, which facilitates seed distribution (Dreyer et al. 1987; Greenberg 2001). Local-scale studies suggest *C. orbiculatus* is primarily associated with mesic habitats (Huebner and Tolin 2006, Pande et al. 2007, Berg et al. 2023); however, it can also occur on dry, sandy sites (Pavlovic and Leicht-Young 2011) and dredged soils of low fertility (Hoosein and Robinson 2019). Leaf extracts of *C. orbiculatus* can have allelopathic effects on competing vegetation (Pisula and Meiners 2010; Cipollini and Bohrer 2016). Coarse-scale mapping in the southern Lake Michigan region revealed its emerging presence, particularly in canopy gaps of mature *Quercus-Carya* forest types (Pavlovic and Leicht-Young 2011). In eastern North America, coarse-scale surveys based on Forest Inventory and Analysis (FIA) data revealed a general presence throughout with scattered areas of high density in northeastern (Kurtz 2013) and southeastern (Miller et al. 2010) forests.

Although the subcontinental occurrence of *Celastrus orbiculatus* is known in eastern North America (Miller et al. 2010; Kurtz 2013; McKenzie-Gopsill and MacDonald 2021), other than its association with mesic sites at local scales of investigation, relatively little has been reported on coarser scales of its distribution. Working in a small (5,000 ha) area of the Shawnee Hills ecoregion of southern Illinois, Pande et al. (2007) developed a mesoscale (landscape) prediction model of *C. orbiculatus* presence based on site-level topographic variables but cautioned against its application elsewhere because of different land use histories and disturbances. For example, *C. orbiculatus* has been reported to increase following logging (Silveri et al. 2001) or prescribed burning (Pavlovic et al. 2016). In the mountainous area of western North Carolina, Albright et al. (2009) concluded the presence of *C. orbiculatus* along roads and trails was better associated with distance from a likely point of origin in the vicinity of an early commercial nursery (Biltmore Nursery 1907) than with environmental factors. Merriam (2003) conducted an extensive roadside study of *C. orbiculatus* presence in relation to physiographical provinces in North Carolina and (without reference to habitats) reported the species was present primarily in the mountains (1.83% of sites), somewhat in the piedmont (0.39%), and rarely in the coastal plain (0.10%). Oswalt (2006) reported greater abundance of invasive species in the coastal plain province of South Carolina compared to the piedmont. Findings from these and other studies indicate a non-uniform distribution of some invasive species across a range of spatial scales. The objective of our study was to investigate the occurrence of *C. orbiculatus* from coarse to fine scales and test an overall hypothesis that its presence is independent of the presumed environment associated with each geographic scale. Our questions were: (1) Is *C. orbiculatus* a generalist species that occurs uniformly across a range of geographic scales? (2) Does the occurrence of *C. orbiculatus* differ between mesic and xeric environments? (3) Is the ground area covered by *C. orbiculatus* foliage associated with different soil moisture regimes? Our exploratory study utilized a large available database, which did not allow field sampling to check inferences of environments associated with land units of various scales.

MATERIALS AND METHODS

Field data

Preliminary assessment of *Celastrus orbiculatus* distribution in the 13 southeastern states based on publicly reported data (EDDMapS 2023) indicated it occurs throughout, but in widely varying frequencies. In South Carolina, for example, *C. orbiculatus* was reported in 15% of counties, but it was present in 40% of North Carolina counties. We judged *C. orbiculatus* occurrence data were sufficient for meaningful analysis only in North Carolina and Virginia (Figure 1). We used the invasive species data from FIA permanent plots from these two states inventoried between 2016–2021 following standard protocols (Rudis et al. 2006). Data collection spanned multiple years because FIA sample plots are inventoried on a rotating periodic basis, approximately once each five years. Each FIA plot location consists of a cluster of four smaller fixed-area subplots, each of which is 0.067 ha in area. Data used for this study were recorded on the subplots, which hereafter will be referred to as plots.

Attributes of the FIA data allowed classification of each plot into three hierarchical scales of land units: coarse, intermediate, or fine, represented respectively by FIA designated physiographic provinces, groups of forest types, and site moisture regimes. Physiographic provinces (hereafter provinces) are multi-state units of similar geology, climate, topography, and predominant types of natural and human disturbances, which are similar to the geomorphic areas mapped by Fenneman (1938). In the two-state study area of North Carolina and Virginia, FIA data are summarized and reported by three provinces: mountain, piedmont, and coastal plain, which had been coarsely delineated by FIA following county boundaries (Figure 1). Forests of provinces may be broadly characterized as predominantly deciduous, coniferous, or mixtures. Within provinces forests may be subdivided into relatively homogeneous land units of environmental conditions based on groups of characteristic tree species with similar physiological requirements (Gleason 1939). The FIA data for North Carolina and Virginia consisted of 10 groups of forest types (Table 2). For example, the *Quercus–Nyssa* group includes seven forest types typically found in swamps and periodically flooded areas of bottomland stream terraces with characteristic wet-site species including *Quercus nigra* L., *Nyssa sylvatica* Marshall, *Taxodium distichum* (L.) Rich., and associates common in continually wet environments. With one exception, FIA forest type groups define communities of canopy tree species that indicate land areas characterized by differing environments (e.g., temperature, moisture) and disturbance regimes (e.g., wind, fire). The *Quercus-Carya* group of forest types, however, includes species characteristic of site moisture regimes ranging from xeric (e.g., *Q. stellata* Wangenh., *Q. marilandica* Muenchh.) to mesic (e.g., *Liriodendron tulipifera* L., *Liquidambar styraciflua* L.). This forest type group thus represents mixed upland hardwood forests of the Central Hardwood Region (Fralish 2003) rather than an environmental condition of moisture or temperature manifested by a relatively homogeneous group of species with similar biological requirements, as for the other groups. We subdivided the large FIA *Quercus-Carya* group of 19 forest types into two subgroups: (1) mesic (*Quercus-Carya*-M) where many canopy species are mesophytic, particularly *L. tulipifera* (yellow-poplar) and *L. styraciflua* (sweetgum) and (2) xeric (*Quercus-Carya*-X) consisting primarily of upland xerophytic species of *Quercus* (oaks) and *Carya* (hickories) and a minority of mesophytic species.

When each plot was inventoried by FIA, the site was subjectively assigned a qualitative moisture regime class (i.e., hydric, mesic, or xeric) that represented the relative amount of soil moisture available to support vegetative growth during frost-free seasons. Hydric sites are permanently or seasonally saturated with water, mesic sites typically have adequate moisture throughout the growing season, and xeric sites usually experience one or more periods of moisture deficits, usually during late summer. We used moisture regime as an expression of site quality that integrated landform, topographic position, and soil characteristics at the plot, or local (fine) scale. A final FIA dataset attribute, percentage plot foliage cover (Daubenmire 1959), provided a measure of vegetative growth of *Celastrus orbiculatus* in response to the site environment, which included light as modified by the tree canopy. Therefore, our study examined the occurrence of *C. orbiculatus* in part of a multi-state region in relation to a three-level hierarchy. The coarse-to-fine hierarchy consisted of mapped

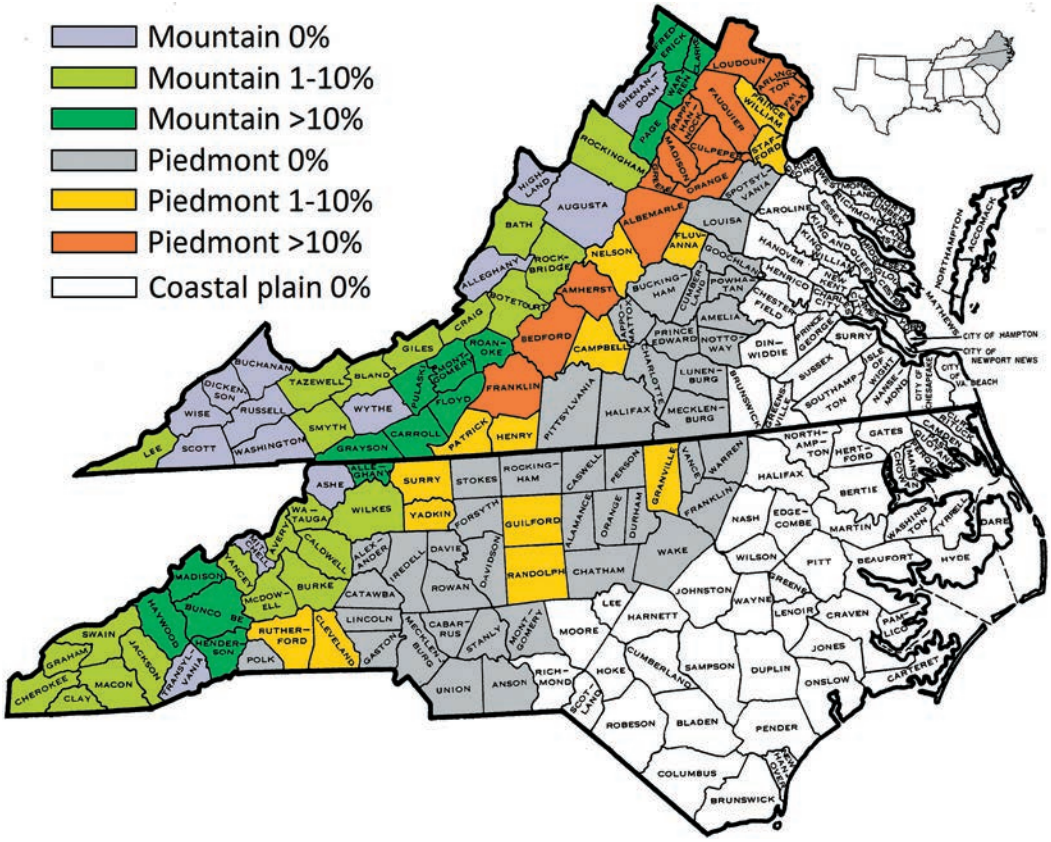

Figure 1. Mountain and piedmont provinces study area in North Carolina and Virginia and the percentage of FIA plots in each county occupied by *Celastrus orbiculatus* inventoried between 2016–2022.

provinces subdivided into repeating landscape scale units defined by smaller forest type groups based on tree inventory data that are further subdivided into soil moisture regimes classified onsite.

Data analysis

The occurrence of *Celastrus orbiculatus* in FIA plots associated with land units of province, landscape, and local areas was evaluated for differences with a sequence of chi-square tests of independence (McNab and Loftis 2002). Chi-square tests were based on frequency counts of individuals. Each FIA plot was classified according to the binary occurrence (e.g. either presence or absence) of *C. orbiculatus* and one (or more) criterion describing the plot location at each of the three geographical scales. For example, a single location criterion was used for both the province scale (e.g. either mountain or non-mountain (implying piedmont); excluding coastal plain as explained below) and local scale (e.g. either mesic or xeric soil moisture, excluding hydric as explained below). However, multiple criteria were required for the landscape scale because each FIA plot could be located in one of 11 forest type groups (e.g. Acer–Betula, *Quercus–Nyssa,* etc). A chi-square analysis tested for differences between the observed and expected frequencies of *C. orbiculatus* occurring at each scale. The expected frequencies of *C. orbiculatus* in each 2×2 classification category (e.g. presence or absence × mountain or piedmont) are the calculated values if the null hypothesis of independence (i.e. no difference) is accepted. Independence of *C. orbiculatus* occurrence and province can be interpreted to mean this species is present on the same proportion of the population of FIA plots in the mountains or piedmont. At the landscape scale, which used multiple criteria of

many forest type groups, when significant differences were found a series of pairwise post hoc tests were conducted using Fisher's exact test to determine which groups contributed to the overall chi-square significance (McDonald 2014). Because multiple, non-independent pairwise comparisons were made using the same dataset as for the overall test, significance levels were adjusted using the Bonferonni correction. Coverage percentages were log-transformed to increase normally of distributions (McDonald 2014). We used one-way analysis of variance (ANOVA) to determine if *C. orbiculatus* foliage cover percentage differed by province, landscape, and local scale land units. Tukey-Kramer tests were used to separate significant ANOVA differences among population means of all pairs of forest type groups at the landscape scale of land units. Welch's unequal variance t-tests were used to determine if either mesic or xeric plot moisture regimes had a significant effect on *C. orbiculatus* foliage cover. Significant difference was inferred when $p \leq 0.05$.

RESULTS

The FIA data set for North Carolina and Virginia consisted of 14,308 plots distributed among three provinces (Table 1). Review of the FIA data revealed *Celastrus orbiculatus* was present on 619 (4.3%) of all inventoried plots. Further review indicated *C. orbiculatus* was present on 10 of the 5,652 plots (0.18%) in the coastal plain. The 10 coastal plain plots were in a municipal forest in coastal northeastern Virginia where *C. orbiculatus* became established likely from human influences, such as near roads or urban areas (Huebner and Tobin 2006). We excluded the coastal plain from further evaluation because the 10 plots with *C. orbiculatus* were insufficient for relevant and meaningful analysis. The remaining 8,656 FIA plots were distributed among three soil moisture regime categories: hydric, mesic, and xeric. Sixteen of the 8,656 plots (0.18%) were classified as hydric and were distributed nearly equally between the mountain and piedmont provinces; none of the 16 plots had *C. orbiculatus*. The hydric plots were judged too few for meaningful analysis and were reclassified as mesic in their respective province. An initial chi-square test of independence was performed using the entire dataset of 8,656 plots, without regard to province or landscape subdivisions, to assess the overall strength of the relationship between *C. orbiculatus* and soil moisture regimes. Summarization and analysis of the FIA field data indicated *C. orbiculatus* was found on plots classified as mesic (n=561) more often than expected (n=393) and on xeric plots (n=48) less often than expected (n=216). The relationship between these two variables was significant (χ^2=217.040, d.f.=1, p<0.001), indicating *C. orbiculatus* was more likely to occur on mesic sites compared to xeric. A series of follow-up chi-square tests were conducted to examine factors accounting for this significant difference at hierarchical scales of province, landscape, and site.

Province scale

The 8,656 FIA plots available for analysis were distributed as 5,682 (65.6%) sample plots in the mountains and 2,974 (34.4%) in the piedmont (Table 1). Although *Celastrus orbiculatus* was present on nearly the same number of plots in each province—314 plots in the mountains and 295 in the piedmont—the proportional occurrence in the piedmont (9.9%) was nearly double that of the mountains (5.5%). A chi-square test of independence revealed the difference in proportional occurrence between the provinces was significant, χ^2=57.603, d.f.=1, p=<0.001; indicating that *C. orbiculatus* was more likely to be present in piedmont plots compared to mountain plots. The significant difference of *C. orbiculatus* occurrence between the two provinces did not allow pooling mountain and piedmont data for the landscape scale of analysis.

Landscape scale

Eleven groups of forest types were represented in the total 8,566 FIA plots available for analysis, of which 5,682 plots were in the mountains and 2,974 plots in the piedmont (Table 2). Chi-square analysis of the *Celastrus orbiculatus* overall occurrence data among the 11 mountain forest type groups was significant (χ^2=365.519, d.f.=10, p<0.001), which indicated differences of occurrence among the groups. A series of post hoc Fisher's exact tests of pairwise comparisons among the 11 groups and the appropriate overall totals revealed significant differences for six groups (Table

Table 1. Frequency (% of row total) of *Celastrus orbiculatus* (Asian bittersweet) occurrence in Forest Inventory and Analysis (FIA) plots by province in North Carolina and Virginia.

FIA Province	FIA plots with *C. orbiculatusa*		Total
	Present (%)	Absent (%)	
Mountain	314 (5.5)	5,368 (94.5)	5,682
Piedmont	295 (9.9)	2,679 (90.1)	2,974
Subtotal	609 (7.0)	8,047 (93.0)	8,656
Coastal plain	10 (0.2)	5,642 (99.8)	5,652
Overall	619 (4.3)	13,689 (95.7)	14,308

[a]Plots inventoried 2016–2021.

2). The highest level of significance was associated with the two *Quercus-Carya* subgroups. For the mesic subgroup (*Quercus-Carya*-M), actual presence of *C. orbiculatus* inventoried in 133 plots was nearly double the expected presence in 71 plots. For the xeric subgroup, however, the opposite relationship was evident with an actual presence of *C. orbiculatus* in 85 plots compared to an expected presence in 177 plots.

In the piedmont province, a chi-square test of the nine groups with FIA plot data resulted in an overall significant difference (χ^2=201.459, d.f.=8, p<0.001) between actual and expected *Celastrus orbiculatus* occurrences (Table 2). A series of Fisher's exact tests of pairwise comparisons revealed four significant groups ($p \leq 0.05$). Most of the piedmont landscape significance difference was explained by the *Quercus-Carya*-M subgroup ($p<0.001$), where *C. orbiculatus* was inventoried on 141 plots but was expected to occur on only 77 plots. Three other forest type groups were significant at lower levels of probability. *C. orbiculatus* was present at half of the expected level in two relatively dry habitat groups, *Quercus-Pinus* and Southern Conifers. In the moist *Ulmus-Fraxinus* group, which typically occurs on moist river bottomlands, the vine was present at five times greater than the expected level.

Local scale

Of the 314 plots where *Celastrus orbiculatus* was present in the mountain province, 281 (89.5%) were classified as mesic (Table 3). In the piedmont 280 (94.9%) of 295 plots where *C. orbiculatus* was present were classified as mesic. Chi-square analysis indicated a significant difference (χ^2=6.165, d.f.=1, p=0.013) in the proportion of *C. orbiculatus* in mesic compared to xeric soil moisture regimes for the mountains and piedmont, which did not allow pooling data of the two provinces. Chi-square analysis by province revealed a significant difference in the proportion of *C. orbiculatus* occurrence among forest type groups for mountain (χ^2=19.642, d.f.=8, p=0.012) and piedmont (χ^2=29.375, d.f.=7, $p<0.001$). For mountain plots, post hoc Fisher's exact tests revealed much of the variation was explained by the presence of *C. orbiculatus* on more mesic plots of the relatively dry *Quercus-Carya*-X subgroup than expected. For piedmont plots, *C. orbiculatus* was present on more plots than expected for the mesic *Quercus-Carya*-M forest type subgroup and fewer for the dry *Quercus-Carya*-X subgroup.

Foliage cover

The growth response of *Celastrus orbiculatus* in relation to the environments of provinces, landscapes, and local scales was evaluated using percentage foliage cover recorded for the total 609 plots in the mountains and piedmont (Table 1). Foliage cover of *C. orbiculatus* was <10% for most FIA plots in both provinces; in nearly half of all plots, cover was classified as 1% (Figure 2). At the province level ANOVA tests indicated mean percentage foliage cover of *C. orbiculatus* was significantly greater ($p<0.001$) in the 314 mountain plots ($\bar{x}$=9.6%, sd=14.7%), compared with the 295 piedmont plots ($\bar{x}$=5.1%, sd=9.8%). ANOVA tests at the landscape level indicated significant differences of mean percentage foliage cover among forest types for both mountain (p=0.01) and piedmont ($p<0.001$)

Table 2. Number of Forest Inventory and Analysis (FIA) plots with presence or absence of *Celastrus orbiculatus* (Asian bittersweet) in forest type groups by province (mountain, piedmont) in North Carolina and Virginia inventoried 2016–2021. *P*-values are results by province of (1) a chi-square test of overall forest type group plot frequencies and (2) multiple Fisher's exact tests (with Bonferonni correction) of pairwise comparisons between each forest type group and the appropriate overall total.

FIA Forest type group[a]	Mountain plots with *C. orbiculatus*			Piedmont plots with *C. orbiculatus*		
	Present	Absent	*P*	Present	Absent	*P*
Acer-Betula	5	251	>0.05	0	0	Nt[b]
Juniperus virginiana	9	3	<0.001	2	0	>0.05
Miscellaneous	16	117	0.05	7	27	>0.05
Picea-Abies	0	16	>0.05	0	0	Nt
Pinus strobus	16	114	0.05	2	11	>0.05
Quercus-Carya-M	133	1,153	<0.001	141	637	<0.001
Quercus-Carya-X	85	3,110	<0.001	89	983	>0.05
Quercus-Nyssa	0	5	>0.05	0	13	>0.05
Quercus-Pinus	31	435	>0.05	16	341	<0.01
Southern pines	8	157	>0.05	20	650	<0.001
Ulmus-Fraxinus	11	7	<0.001	18	17	<0.001
Overall	314	5,368	<0.001	295	2,679	<0.001

[a]Environments associated with FIA forest type groups: *Acer–Betula* (maple–birch); moist, protected sites in high mountains. *Juniperus* virginiana (eastern red cedar); dry, exposed sites, usually abandoned fields. Miscellaneous—unusual compositions with no dominance by a species that does not fit elsewhere. *Picea–Abies* (red spruce–Fraser fir); exposed sites of high mountains. *P. strobus* (eastern white pine); naturally on fire excluded, moist to dry sites; planted on a wide range of site conditions of the mountain region. *Quercus–Carya*-M (oak–hickory, mesic); subgroup of forest types in the *Quercus-Carya* group that includes a majority of mesophytic species such as *Liriodendron tulipifera* (yellow-poplar) in mountains on protected slopes and coves, and *Liquidambar styraciflua* (sweetgum) in piedmont on mesic sites along large streams and river bottomlands. *Quercus–Carya*-X (oak–hickory, xeric); subgroup of forest types in the *Quercus-Carya* group that includes a minority of mesophytic species on exposed dry to xeric sites throughout. *Quercus–Nyssa* (oak–gum); swamps, floodplains, and stream bottoms. *Quercus–Pinus* (oak–pine); fire dependent xeric, exposed upper slopes and ridges. Southern pines—(*Pinus echinata, P. taeda, P. virginiana);* dry, exposed sites, abandoned fields or areas of commercial timber production where hardwood species have been controlled. *Ulmus-Fraxinus* (elm–ash); moist bottomlands.
[b]Nt=not tested; this group was not present.

provinces (Figure 3). There was considerable overlap of cover percentages among forest type groups and no clear differences were evident for either mountain or piedmont provinces.

Soil moisture regime had little effect on foliage cover of *C. orbiculatus*. Student's t-tests of mean *C. orbiculatus* cover percentages by forest type groups revealed a single significant effect ($p<0.05$) of plot soil moisture regime. In the piedmont province, mean foliage cover in xeric plots (7.8%) of the subgroup *Quercus-Carya*-X was greater than in mesic plots (4.9%).

DISCUSSION

Our study was designed to evaluate the premise that *C. orbiculatus* was distributed uniformly across discrete, coarse- to fine-scale land units in North Carolina and Virginia, and we hypothesized a greater presence of *C. orbiculatus* in mesic habitats compared to xeric. We found nonuniform distribution of *C. orbiculatus* for each of three hierarchical scales (i.e., province, landscape, local) and evidence of its association with mesic habits at each scale. Although a question not addressed in this study, our results suggest continued rapid expansion of this invasive species in the mountains and piedmont provinces of both states, where it had been reported as rare 30 years earlier (McNab and Meeker 1987).

Table 3. Number of Forest Inventory and Analysis (FIA) plots with presence of *Celastrus orbiculatus* (Asian bittersweet) in forest type groups classified by soil moisture regime (mesic, xeric) in provinces (mountain, piedmont) of North Carolina and Virginia inventoried 2016–2021. *P*-values are results by province of (1) a chi-square test of all overall forest type group plot frequencies and (2) multiple Fisher's exact tests (with Bonferonni correction) of pairwise comparisons between each forest type group and the appropriate overall total.

FIA Forest type group[a]	Mountain plots with *C. orbiculatus*			Piedmont plots with *C. orbiculatus*		
	Mesic	Xeric	*P*	Mesic	Xeric	*P*
Acer-Betula	5	0	>0.05	0	0	Nt[b]
Juniperus virginiana	9	0	>0.05	2	0	>0.05
Miscellaneous	16	0	>0.05	7	0	>0.05
Picea-Abies	0	0	Nt	0	0	Nt
Pinus strobus	15	1	>0.05	2	0	>0.05
Quercus-Carya-M[c]	123	10	>0.05	140	1	<0.001
Quercus-Carya-X[c]	66	19	<0.001	75	14	<0.001
Quercus-Nyssa	0	0	Nt	0	0	Nt
Quercus-Pinus	29	2	>0.05	16	0	>0.05
Southern pines	7	1	>0.05	20	0	>0.05
Ulmus-Fraxinus	11	0	>0.05	18	0	>0.05
Overall	281	33	0.05	280	15	<0.001

[a]See table 2 for description of forest type groups and associated environments.
[b]Nt=not tested because *C. orbiculatus* was not present or forest type group did not occur.
[c]Group subdivided by dominance of mesic (M) or xeric (X) canopy species.

The significant results of the province scale analysis revealed that *Celastrus orbiculatus* was present on a smaller proportion of sample plots in the mountains (5.5%) compared to the piedmont (9.9%). Our results are the opposite of earlier findings based on roadside surveys in North Carolina by Merriam (2003) who reported a greater occurrence of *C. orbiculatus* in mountain sites (1.8%) compared to relatively few (0.4%) piedmont sites. However, our finding of significant differences at the coarse scale of analysis supports results from a similar study by Oswalt (2006) of many invasive species on FIA plots in the piedmont of South Carolina. Although *C. orbiculatus* was not found in South Carolina in 2006, Oswalt considered the piedmont as a "hot spot" for invasion by alien species because of more favorable "... land use, site productivity, length of growing season, forest type characteristics or other environmental differences." Interestingly, Oswalt (2006) reported stronger results of invasive species presence if FIA plots were classified by regional ecosystems (Keys et al. 1995) rather than provinces (as in our study). In a study of invasive species (including *C. orbiculatus*) in relation to provinces in Virginia, Small and Chamberlain (2015) concluded the piedmont was more susceptible than the mountains because of several centuries of periodic, extensive land disturbances, particularly cycles of forests cleared for agriculture, followed by abandonment and old-field succession (Webster et al. 2006). Although without empirical explanatory evidence, our findings of increased *C. orbiculatus* in the piedmont compared to the mountains agrees with reports from other studies.

We used groups of similar forest types to represent different intermediate-scale land units within each province. Our findings agree with several reports of a strong relationship between *Quercus-Carya* forest types (Pavlovic and Leicht-Young 2011 Novais et. al. 2023) and the probability of *Celastrus orbiculatus* presence in FIA plots of both provinces (Merriam 2003; Small and Chamberlain 2015). We found the proportion of FIA plots with *C. orbiculatus* was greater where species of *Liriodendron tulipifera* or *Liquidambar styraciflua* were present (i.e., *Quercus-Carya*-M) and less where species of *Quercus* were dominant in forest type groups (i.e., Quercus-Carya-X). Because *L. tulipifera* and *L. styraciflua* are classified as mesophytic pioneer species,

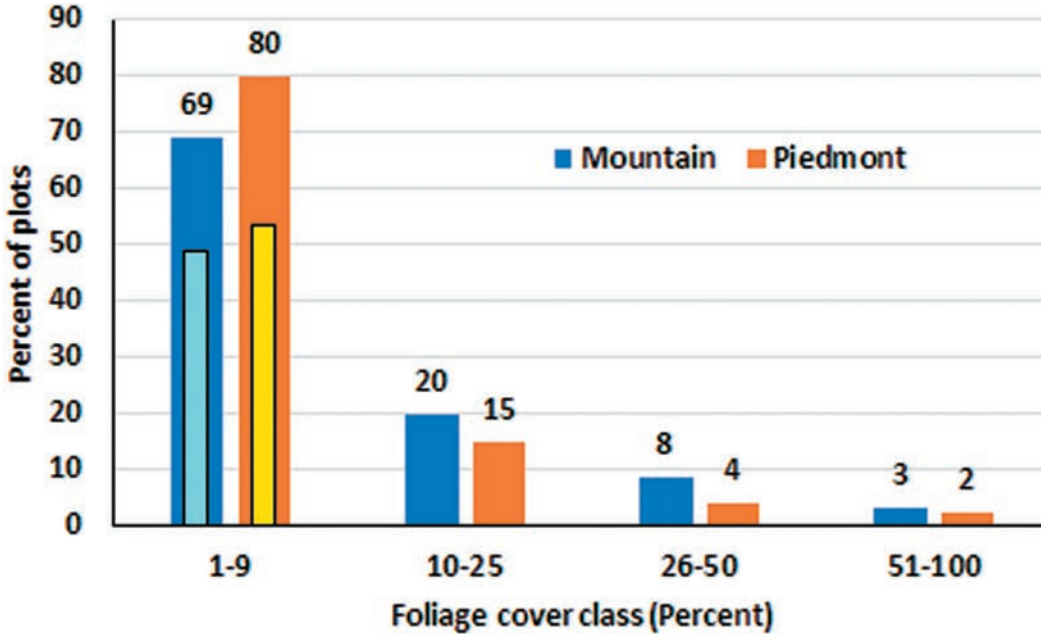

Figure 2. Distribution of *Celastrus orbiculatus* foliage cover classes by province in North Carolina and Virginia in FIA plots inventoried between 2016–2022. The small bar within the large bar of the 1-9% cover category represents the proportion of plots with 1% cover of *Celastrus orbiculatus* in the mountains (47.7%) and piedmont (53.2%).

their association with *C. orbiculatus* suggests a likely complex environment of moisture and disturbance favorable for invasion by this alien species. In the Appalachian Mountains of North Carolina, McNab and Loftis (2002) reported a negative relationship of *C. orbiculatus* with *Quercus* dominated forest stands on dry sites. Horton and Francis (2014) reported *C. orbiculatus* was present primarily on sites where *L. tulipifera* was present. In the piedmont of Virginia, Small and Chamberlain (2015) suggested that the long history of agricultural disturbance followed by abandonment facilitated establishment of *C. orbiculatus*. Malone (2011) reported the occurrence of *C. orbiculatus* on highly disturbed stream-side soils of the North Carolina piedmont. Kuhman et al. (2013) reported greater *C. orbiculatus* on old field sites in the North Carolina mountains. In the Mid-Atlantic states of the Southeast, Stapanian et al. (1998) found a significant positive correlation between the presence of alien species and disturbed sites. Our landscape scale analysis also suggests a strong positive relationship between *C. orbiculatus* and forest type groups associated with disturbed, mesic habitats.

As expected, the site level component of the FIA data (i.e., mesic or xeric moisture regime assessment of each plot) provided the strongest evidence of *Celastrus orbiculatus* presence in relation to environment. At each hierarchical level from province through landscape to site, *C. orbiculatus* was present on significantly greater proportions of plots classified as mesic compared to xeric. For example, in the 295 piedmont plots where *C. orbiculatus* occurred (Table 3), 94.9% were classified as mesic compared to 5.1% xeric. These results agree with findings reported by Kuhman et al. (2013) and Horton and Francis (2014) in North Carolina and Leicht-Young et al. (2007) in the Northeastern states.

We found foliage cover of *Celastrus orbiculatus* differed by province and forest type group. For both provinces, the trend of mean cover was greater in forest type groups with a conifer component (Figure 3). The conifers could indicate old-field succession on abandoned agricultural fields where *C. orbiculatus* became established and responded to residual soil amendments of potassium (Pavlovic and Leicht-Young 2011) and phosphorus (Lett et al. 2011). Another explanation of the

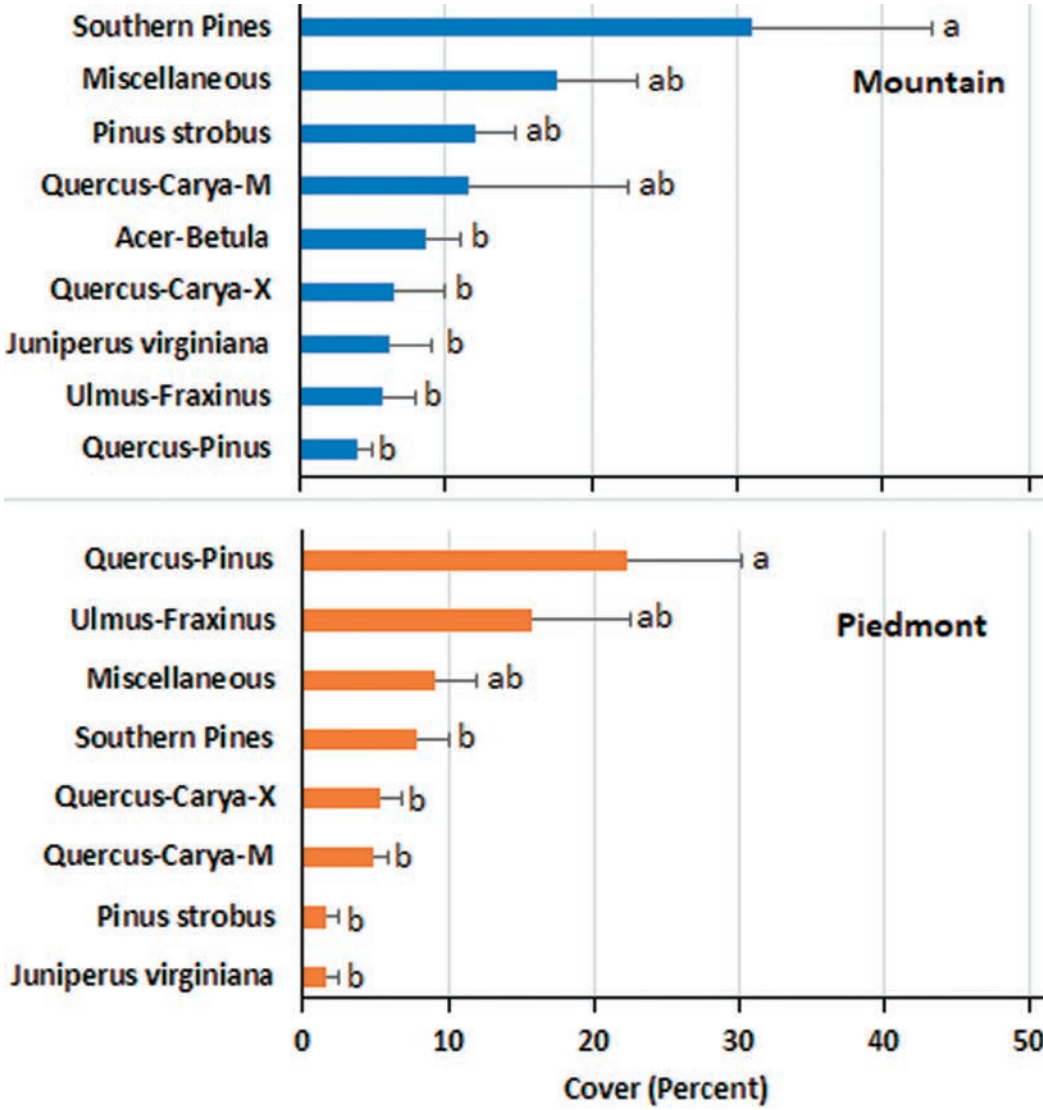

Figure 3. Mean percentage foliage cover of *Celastrus orbiculatus* by province and forest type group in North Carolina, and Virginia. Error bars represent 95% confidence intervals of the means. The number of plots in each forest type group is shown in Table 3.

greater cover could be increased light reaching the forest floor through less dense needle-foliage of conifer canopies or silvicultural activities such as thinning (Oshima and Takahashi 2020). Lett et al. (2011) reported that mycorrhizal fungi can increase foliage cover of *C. orbiculatus* by supplementing acquisition of phosphorus in infertile soils. In deciduous forests with high deer populations, browsing can reduce foliage and potentially the occurrence of *C. orbiculatus* (Rossell et al. 2007). In our study, estimated cover of *C. orbiculatus* could have been affected by density of the overstory tree canopy on the FIA plots. A dense canopy may reduce light penetration to the forest floor, but not enough to prevent survival of shade-tolerant, small *C. orbiculatus* plants. In support of this scenario is our overall finding that plot soil moisture regime had relatively little effect on cover of *C. orbiculatus*. The only significant effect was for the xeric subgroup of *Quercus-Carya*-X where cover of *C. orbiculatus*

was greater on xeric plots than for mesic. This seemingly opposite intuitive relationship could be explained by a less dense tree canopy responding to xeric conditions, which would increase light reaching the forest floor thereby increasing ground-level leaf cover of *C. orbiculatus*. We are unaware of results from other studies reporting experimental treatments affecting foliage cover of *C. orbiculatus*.

Perhaps the most important finding of our study was the association of *Celastrus orbiculatus* with forest type groups. Although many local-scale, site studies have noted an apparent relationship of *C. orbiculatus* with *Quercus-Carya* forest types, ours is among the few studies that reports an empirical significant relationship of increased frequency with mesic forest types and decreased presence with xeric types. Another interesting finding was that foliage cover of C. orbiculatus was only 1% on nearly half of all plots where the species occurred in both provinces (Figure 2). This could indicate several field situations, such as newly established seedlings. More likely, however, these occurrences are small older seedlings resulting from bird distributed seeds established in the shaded forest floor beneath closed canopies that are "waiting" for canopy disturbance and release from suppression (Greenberg et. al. 2001). Considering both presence and cover of *C. orbiculatus* in relation to site moisture regime, our findings suggest it establishes and maintains greatest presence on mesic sites, but subsequent growth and foliage cover is weakly associated with moisture availability. Further confirmation of the association of *C. orbiculatus* with certain forest types and determining plot conditions associated with 1% foliage cover will facilitate research to model occurrence of this species and increase efficiency of planning and executing field inventories.

In summary, our findings support the notion that *Celastrus orbiculatus* is a generalist species of mesic sites that can persist in a range of habitats (Merriam 2003; Pavlovic and Leicht-Young 2011). Results from our study provide new information that supplements current understanding of the distribution of *C. orbiculatus* across a range of environmental scales and conditions in North Carolina and Virginia. Perhaps our most surprising finding was the increasing occurrence of *C. orbiculatus* in the piedmont, which supports findings by Oswalt (2006) who inventoried many invasive species there. Not surprising, however, was the association of *C. orbiculatus* with mesic environments, which confirmed our initial premise about habitats favored by the species. A strength of our observational study was use of the large, high-quality FIA dataset for the analysis. Our findings identify relationships between *C. orbiculatus* and land units of differing scale, which we suggest can tentatively be regarded as ecosystems. In support of the ecosystem notion, Oswalt (2006) reported results like ours for many invasive species when the South Carolina piedmont was delineated as an ecoregion. Our findings may be particularly useful to resource managers for planning surveys to monitor this invasive species and formulating plans for control measures in relation to climate changes.

DATA AVAILABILITY

The field data files for this study are freely available for downloading from USDA Forest Service, Forest Inventory and Analysis (FIA 2021). The FIA DataMart allows anyone to download raw FIA data in comma delimited tables, databases, and other formats.

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