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Asiatic bittersweet presence and cover over 20 years in upland hardwood forests after hurricane disturbance

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Abstract. Invasive exotic plants are one of the most challenging problems facing forest land managers. Many invasive species are shade intolerant and typically do not invade forest sites with dense tree canopies. In contrast, Asiatic bittersweet (*Celastrus orbiculatus* Thunb.), a shade-tolerant exotic liana, is capable of colonizing and successfully growing in forest sites and has proven to be an aggressive competitor of native vegetation in the eastern USA. We investigated changes in the presence and cover of bittersweet after a hurricane-created major canopy disturbance in a southeastern USA upland hardwood forest over 20 yr. Bittersweet was present frequently in mesic but rarely in xeric forest sites. Bittersweet increased rapidly for the first 9 yr after a hurricane within disturbed sites; its presence then increased slowly to year 20. Bittersweet was more frequently found within *versus* outside wind-felled tree gaps; its presence was greater west and south of gap centers within gaps but was greater east and north of centers outside gaps in the unaffected forest. We attributed these location-based differences in presence to differences in available soil moisture. Bittersweet was present in extremely low light environments. As with presence, the rate of increase in bittersweet cover slowed after 9 yr after a hurricane. Results of this long-term study will provide forest managers with information to evaluate the potential response of bittersweet to forest management treatments such as timber harvest.

Key words: Asiatic bittersweet, forest gaps, invasive species, soil moisture

Invasive exotic plants are one of the most challenging problems facing forest land managers (Larson *et al*. 2011; Crowley *et al*. 2017). Many invasive species are shade intolerant and typically do not invade forest sites with dense tree canopies (Martin *et al*. 2009). In contrast, Asiatic bittersweet (*Celastrus orbiculatus* Thunb.), a shade-tolerant exotic liana, is capable of colonizing and successfully growing in forest sites and has proven to be an aggressive competitor of native vegetation in the eastern USA (Patterson 1974; Albright *et al*. 2009). Bittersweet vines climb, choke, deform, and sometimes kill native trees (Ladwig and Meiners 2009; Horton and Francis 2014). Bittersweet vines have spiny projections that enable them to cling tenaciously to tree stems and climb rapidly into the forest canopy. Height growth can exceed 3.0 m/yr (Silveri *et al*. 2001). These attributes make bittersweet a highly opportunistic species capable of colonizing and accruing biomass in many eastern forest sites (Webster *et al*. 2006). Land management treatments, including prescribed fire, livestock grazing, herbicide application, and cutting, have achieved only limited success in controlling the spread of bittersweet (Webster *et al*. 2006; Rebbeck 2012).

Bittersweet presence and cover may be strongly influenced by site quality, particularly available soil moisture, which may produce unique bittersweet responses within and around forest gaps (Coomes and Grubb 2000; Johnson *et al*. 2019). For example, Berg (2002) found that macroscale available soil moisture, aliased by a measure of topographic shading by surrounding landforms (McNab 1993), was positively related to shrub and vine species cover in forest gaps. Although within-gap effects of variation in the soil moisture regime

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have been documented (Morrissey *et al*. 2010), less is known about long-term vegetation change in response to moisture variation among gaps. Bittersweet accrues biomass and survives best when soil moisture levels are moderate, that is, sites are classified as mesic and not xeric or hydric (Leicht-Young *et al*. 2007). Adding to bittersweet's attributes as an aggressive competitor, individual plant biomass growth and mortality rates have been shown to be insensitive to increasing levels of plant competition (Leicht-Young *et al*. 2011).

Bittersweet has been shown to be highly plastic in response to varied levels of received light and is noted for being shade tolerant (Leicht-Young *et al*. 2007). McNab and Loftis (2002) suggested that the presence of bittersweet is not strongly related to changes in received light. However, Leicht-Young *et al*. (2007) reported increasing bittersweet plant survivorship and biomass as light levels increased. McNab and Loftis (2002) found that bittersweet presence was positively related to gap creation. Residual canopy trees are frequently left after gap formation; larger gaps are seldom clear-felled by natural disturbances (Berg 2002). Residual overstory and mid-story trees reduce the amount of light reaching the forest floor and may change vine and shrub presence and foliage cover probabilities (Grayson *et al*. 2012). Residual tree canopies may also facilitate the spread of bittersweet by serving as a growing-medium vector; bittersweet vines can reach into the upper tree canopy and spread progressively among residual trees (Fike and Niering 1999; Horton and Francis 2014).

Many investigators have linked vegetation presence and cover with gap size and position (gap center, gap edge, outside gap) within and around gaps (Yetter and Runkle 1986; Sipe and Bazzaz 1995; Van Der Meer *et al*. 1999), and these findings support gap partitioning. However, little is known about how shrub and vine presence and cover change relative to changes in light regimes within and outside gaps. Direction from gap center can serve as a surrogate for changes in light regimes and as a covariate related to plant colonization, survivorship, and growth (Berg 2002, 2004). Further, direction and distance from center within and outside gaps has been shown to be related to other essential plant resources such as soil moisture and nutrients (Gray *et al*. 2002; E. C. Berg, unpublished data). Brown (1996) found that height growth of tropical hardwoods decreased on a linear distance gradient from gap center to gap exterior and Van Couwenberghe *et al*. (2010) found that most European hardwood species regeneration densities were greatest at gap edge. However, Berg (2002) found that vine and shrub cover did not significantly change on a linear distance gradient from wind-created gap centers into the unaffected forest. Fahey and Puettmann (2008) found that understory plant composition did not substantially change in gaps compared with adjacent unaffected Douglas-fir forests along linear gradients aligned through gap centers.

The effects of eastern hardwood canopy disturbances on invasive species presence and cover have been studied mostly in the context of either small one- or two-tree death openings (gap-phase disturbance) or logging disturbances. Larger wind-created openings ($>$ 0.1 ha) are common across USA Southern Appalachian landscapes of the Central Hardwood Region (Greenberg and McNab 1998, McNab *et al*. 2004), and can be an important factor in shaping vegetation colonization, growth, and survival (Runkle 1985). Anthropogenic and natural gap-producing disturbances, such as logging and hurricane-caused tree blowdown, have been shown to accelerate the spread of invasive vines (Horvitz *et al*. 1998; Silveri *et al*. 2001). Past research efforts have frequently reported the presence and cover of bittersweet over relatively short time periods (*i.e*., 2 to 3 yr). In the USA, eastern forest managers lack knowledge of changes in bittersweet presence, cover, and possible damage to tree regeneration over longer time periods; this information is particularly essential for regenerating forests after canopy tree disturbance until newly established regeneration reaches crown closure, a critical life stage, typically taking 7 to 15 yr after disturbance (Loftis 1991).

To determine how bittersweet presence and cover changed through time in response to spatial and forest structure gradients and the varied influences of site quality and level of disturbance, we investigated 20-yr bittersweet presence and cover located within and around gaps in a mixed-species mesophytic upland forest created by a tropical hurricane (Opal, 1995), an uncommon type of large-scale disturbance in the Southern Appalachians. We tested two hypotheses: (a) 20-yr bittersweet presence would change by direction from gap centers to edge within wind-created gaps and from gap edge into the unaffected forest; (b) 20-yr cover would change by direction from centers (as with presence). Testing these presence

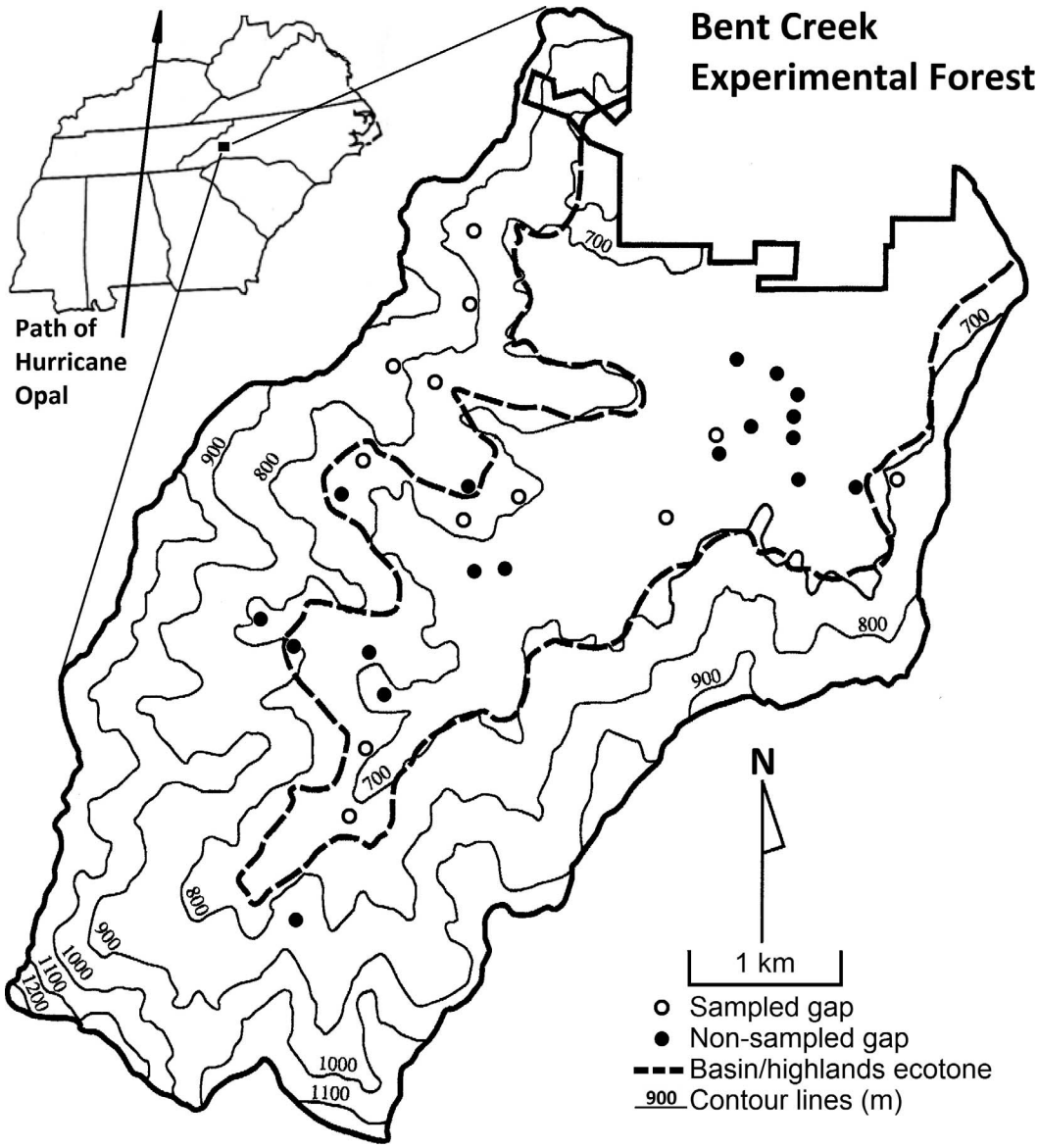

FIG. 1. Research area map.

and cover hypotheses should reveal the extent of gap partitioning for bittersweet.

Methods. HURRICANE DISTURBANCE AND SITE DESCRIPTION. Originating in the Gulf of Mexico, Hurricane Opal made landfall in western Florida and moved rapidly northward through Alabama and central Tennessee (Fig. 1). Wind from Hurricane Opal struck the Bent Creek watershed, which is encompassed by the Bent Creek Experimental Forest, about 16 km south of Asheville, NC (35.5°N, 82.6°W) in the Southern Appalachian region on the morning of October 5, 1995. Sustained wind from Opal averaged 8.9 m/sec, and maximum peak gusts of 25.9 m/sec were recorded at the nearby Asheville, NC airport. McNab *et al*. (2004) provide additional information on characteristics of this hurricane and the landscape distribution of $>$ 30 multiple tree canopy gaps in the experimental forest. Single-tree gaps were most common and averaged 57 m^2; multiple tree gaps averaged 117 m^2.

Approximately one-third of the gaps occurred in administrative areas not suitable for research activities or were harvested to salvage windthrown trees. Selected gaps for this investigation were restricted to the remaining openings being at least 0.1 ha in size. Also, at least six canopy trees/gap must have fallen as a result of the hurricane. Because we were also investigating tree regeneration survivorship sited within the same gaps (separate study), we sought a minimum gap size that would support the regeneration of all arborescent species. Beck (1988) commented on the 0.1-ha size as being a reasonable minimum for the successful colonization and development of the most shade-intolerant eastern hardwoods. By restricting this investigation to $>$ 0.1 ha, we ensured that all native hardwoods had sufficient light to colonize and grow successfully. Eleven gaps meeting the above criteria were located from October 1995 to June 1996 without regard to site environmental conditions. Although Opal-created gaps were located elsewhere, we restricted the pool of eligible sampling units to Bent Creek because the disturbance histories of the 11 gaps were known. Prior disturbances such as logging may have affected the spread of bittersweet and so we chose to limit our investigation to one drainage where histories were known.

The Bent Creek Experimental Forest occupies most of a 2,500-ha watershed characterized by two predominant ecosystems: (a) an intermountain basin of hilly terrain that is bordered by (b) steep highlands of mountainous topography (Fig. 1). Of the 11 gaps, 6 were located in xeric–subxeric (dry) sites typically associated with the basin and 5 were in mesic–submesic (wet) sites common to the uplands. The dry-site gaps were located within oak–hickory (typified by *Quercus coccinea* [scarlet oak], *Quercus alba* [white oak], and pignut hickory [*Carya glabra*]) vegetation communities on Ultisol soils. The wet-site gaps were located within acidic and rich-cove hardwood sites, typified by *Quercus rubra* (northern red oak), *Liriodendron tulipifera* (yellow-poplar), and *Fraxinus americana* (white ash) on Inceptisols. Selected gap elevations ranged from 670 m to 850 m. The frost-free growing season is from approximately May 1 to mid-October. Annual precipitation ranges from 120 cm at 670-m elevation to 150 cm at 850-m elevation. Soils are derived from gneisses and schists, with occasional intrusions of mafic minerals found in amphibolite deposits. All soils are $>$ 80 cm deep and acidic; pH of dry sites and acidic coves was $<$ 4.7, and the pH of rich coves ranged from 5.0 to 5.3. Hurricane-created windfall trees mostly were uprooted and did not snap off from the bole. All selected gaps supported some residual hardwood overstory and mid-canopy trees; residual tree distribution was highly variable.

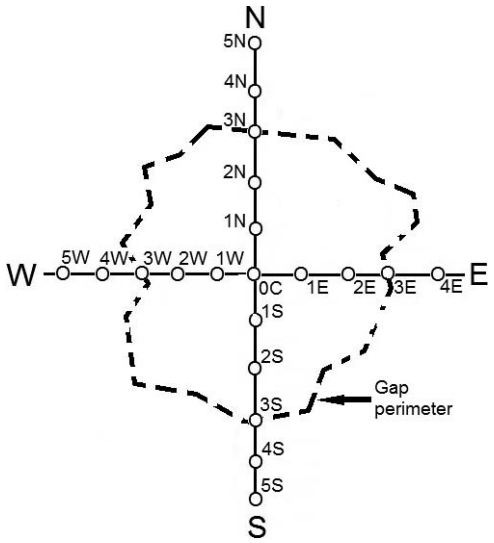

FIG. 2. Example of gap sample design. Gap perimeter = boundary of the extended gap. Quadrat locations are specified, for example, "4S" = fourth quadrat south of gap center.

SAMPLE DESIGN. Runkle's (1992) definition of the extended gap was used to determine gap perimeters (Fig. 2). Sampling points were installed from May to July 1996. Two horizontal perpendicular axes were located within each gap: north–south and east–west. Axes intersected at gap center. Axis orientation was changed for four gaps where realignment provided the opportunity to establish a linear distance gradient along the entire length of the gaps. For these gaps, the "north" azimuth from gap centers varied from 325.0° to 346.0°. Bittersweet was observed in only one of these four gaps through the 20-yr project time frame; for this gap the north axis azimuth was 346.0° from center—a 14.0° departure from the cardinal directions. All gaps varied widely in dimensions; most were elliptical or oval in shape. Transect lines extended out from the center through the gaps and into the unaffected forest.

Sampling quadrats were located (a) at gap center; (b) at the north, south, east, and west gap

edges; (c) 7.3 m from gap edge toward center (transition quadrat—farthest from center within gaps); the linear distance from center to the transition quadrat was then divided evenly to set quadrat position; quadrats ranged from 7.3 m to 10.67 m apart; (d) progressively outward beyond gap edges 7.3 m apart; the most extreme points were installed where ground-level solar radiation, measured with a ceptometer, approximated that of forests unaffected by windthrow. This resulted in 15 to 32 established 0.0013-ha circular sampling quadrats per gap and a total of 241 for the study. Fig. 2 exemplifies the sampling scheme used in all 11 gaps.

Sample Measurements. We followed long-established advice for appropriate sample quadrat size, which varied between 10.0 m^2 (Kent and Coker 1995) and 16.0 m^2 (Shimwell 1971) for tall shrubs and vines, and installed 13.5-m^2 circular quadrats ranging from ground level to 2.0 m in height. Quadrats were installed from May through July 1996 to sample bittersweet presence and cover. Bittersweet was recorded as present if any part of a plant (stem or foliage) occurred in a quadrat, including plants that were rooted outside of the sample area, from ground to 2.0 m in height. Quadrats were examined for bittersweet initially in 1996, and periodically thereafter in 1997, 1998, 2001, 2005, and finally in 2016, after 20 yr. Cover was estimated during the growing season and recorded as the proportion of each quadrat occupied by bittersweet foliage. Estimates of presence and cover were made by the same person during each inventory. Variables (descriptions are in Table 1) were measured and tested as covariates in presence and cover models, including locations within or outside gaps in the unaffected forest, direction from gap centers, canopy cover, hurricane-created debris, pit and mound habitat, and site quality.

Rationale for Presence Model Construction. Unless otherwise noted, all bittersweet presence findings were based on random-intercept (quadrats clustered by gaps) logistic models produced with SAS PROC GLIMMIX (SAS Institute 2013). Many investigators have reported increases in invasive species presence and cover through time (Bellingham *et al*. 2005; Abe *et al*. 2020). Therefore, years since first posthurricane measurement (TIME, variable definitions in Table 1) was added to our presence model. Next, could disturbance history have influenced the spread of bittersweet? We found no discernible relationship of bittersweet presence with disturbance history (Table 2), either subjectively or through regression analysis of presence *versus* the estimated gap residual percent basal area after timber harvests in the 1940s ($P = 0.56$). Stand basal area had recovered after 1940s logging by 1980 (first sighting of bittersweet in Bent Creek) to near preharvest levels, so logging activity would likely not have facilitated the spread of bittersweet.

Previous research efforts reported higher bittersweet presence in mesic sites (Silveri *et al*. 2001), so we added a macrosite covariate (SITE) to our model to discover if this finding held true in our experiment. We used the tree species-based site classification system of McNab et al. (2002) to differentiate dry (xeric) *versus* wet (mesic) sites. McNab and Keyser (2020) reported significant differences in tree site index, a key metric of forest site quality, including available soil moisture, between xeric and mesic sites using this tree species-based site classification system. Several investigators have found differing plant responses by varied locations within gaps (Lu *et al*. 2018). We hypothesized that bittersweet presence would vary by changes in light and soil moisture resources indexed by location within and outside gaps. To establish the plant resource foundation of this hypothesis, we investigated changes in light quantity and soil moisture at installed quadrats. Because gap light index (GLI) was measured only twice (in 1998 and 2001) during the 20-yr response period (Table 1), we did not include it in our final presence model. However, GLI provided insights on bittersweet presence. We found GLI imputed with hemispherical photography to be greater north or east of gap centers in 1998 (ordinary least-squares analysis [OLS] $P = 0.0005$ for TRANSECT, Fig. 3) and 2001 (for simplicity, 2001 GLI is not shown in a figure; the relationship was essentially identical to that found in 1998). GLI was only slightly greater within *versus* outside gaps for most of the solar radiation measurements. We attributed these differences in radiation by direction from centers to shade patterns cast by canopy trees at gap edge; directions west and south of center were shaded for longer time periods than were directions east and north of center. Using the GLI data from Berg (unpublished data), we found bittersweet present in

Table 1. Variables used in analyses.

Variable	Mean (units)	Range or values	Explanation
Response			
COVER	0.07 m^2 at TIMECOUNT 0; 0.67 m^2 at TIMECOUNT 20	0.00–10.80	Square meters of bittersweet (*Celastrus orbiculatus*) cover found within a quadrat. Calculated by multiplying the proportion of the quadrat covered with bittersweet plants, that is, leaves and stems, × 13.5 m^2 (surface area of the quadrat).
PRESENCE	7.44% of quadrats contained bittersweet at TIMECOUNT 0; 30.77% at TIMECOUNT 20.	Dichotomous	Whether or not bittersweet was found within a 13.5-m^2 surface-area quadrat (maximum quadrat height = 2.0 m)—any bittersweet vegetation found within the quadrat deemed bittersweet present.
Distance/location			
GAPCAT	20.2% of quadrats were located outside extended gap boundaries	Dichotomous	Quadrat location within (1) or outside (0) extended gap boundaries (Fig. 2).
HECTARES	0.443 (ha)	0.104–1.262	Gap area.
SLOPE	30.3%	0–66.5%	Ground slope at quadrat.
TRANSASP	0.916	0.000–1.996	Transformed aspect at quadrat, per Beers et al. 1966; designed to give a 45° aspect the highest value.
TRANSECT	Categorical	NA[1]	Prevailing location east, north, south, or west of gap center.
Canopy cover and light			
Gap light index (GLI)	0.12 (unitless)	0.01–0.32	Proportion of photosynthetically active radiation delivered to the hemispherical camera lens mounted 1.0 m above ground in 1998 and at 1.0 and 2.0 m above ground in 2001. For the 2.0-m 2001 observations, data is the arithmetic average of four readings. GLI was imputed via hemiphoto analysis: for 1998 data, program Hemiview (Delta T Devices 1998) was used to analyze imagery; for 2001, program Hemisfer (Schleppi 2007).
TOTALCOV	0.858 (proportion)	0.000–1.000	Tree cover expressed as a proportion: canopy cover of mid-story and overstory trees. Measured with a go/no-go densitometer at 17 points within 3.6 m of quadrat center. Based on 17 points in 1997 but was based on 5 points in 2003 and 2016. Differences in outcomes with the 17- *versus* 5-point systems were highly correlated ($r = 0.71$) and therefore both were judged satisfactory. The 1997 measured TOTALCOVER values were assigned to the 1997 and 1998 data vectors; the 2003 values were assigned to the 2001 and 2005 data vectors and the 2016 values were assigned to the 2016 vectors.

Table 1. Continued.

Variable	Mean (units)	Range or values	Explanation
Site quality			
SITE	0 (dry), 1 (wet) dichotomous	Six gaps were classified as xeric, five as mesic	Site quality classification, on the basis of available soil moisture at the macroscale. Xeric and subxeric sites were classified overall as xeric; mesic and submesic as mesic. On the basis of the suite of tree species present by gap; for example, *Quercus stellata* and *Quercus coccinea* would indicate a dry site; *Quercus rubra* and *Liriodendron tulipifera* would indicate a wet site (McNab et al. 2002). This categorical variable is strongly related to site index (McNab and Keyser 2019).
TEMP	13.4 °C	11.6–16.0	Soil temperatures taken at 15.0-cm depth at the same times and locations as the TDR measurements.
TDR	1,075.9 (resistance)	930.5–1,171.5	Time domain reflectometry (TDR). Campbell Scientific CS615 TDR was used to measure resistance (greater resistance = lower volumetric soil water content) at 15.0-cm depth in native soil 5.2 m from 43 quadrat centers (soil plots located outside quadrat boundaries) at three microsites 5 cm apart per plot at three times, 1 wk apart in the late 1998 growing season—for a total of nine measurements per quadrat.
TRENCH	1,073.2 (resistance)	950.0–1301.7	TDR soil measurements taken at 15.0-cm depth within 15.2-cm diameter × 15.2-cm-long polyvinyl chloride pipes located as per the TDRs above. Pipes were hammered flush with ground surface; these served as miniroot trenching devices. All vegetation was clipped and removed 1 mo before TDR measurements. Same TDR measurement protocol as for the TDR measurements above.
Microtopography, woody debris, and time			
DEBRIS	0.027 (proportion)	0.000–0.750	Proportion of the 13.5-m^2 quadrat surface area covered with hurricane-felled woody debris suspended above ground. Measured once in 1996 (TIME 0).
RTMOUND	0.015 (proportion)	0.000–0.500	Proportion of the 13.5-m^2 quadrat surface area covered with pit or mound habitat. Measured once in 1996 (TIME 0).
SUMALL	4,435.0/ha	0–25,980.0/ha	Total tree regeneration (< 2.54 cm diameter breast height) stems/ha.
WOOD	0.080	0.000–1.000	Proportion of the 13.5-m^2 quadrat surface area covered with hurricane-felled woody debris found prostrate on the ground. Measured once in 1996 (TIME 0).

[1] NA = not applicable.

Table 2. Gap disturbance history.

Number of gaps	Site quality	Early history	Harvest history	Postharvest residual basal area (%)
Three	Mesic	Subsistence agriculture in 1800s	No timber harvest since 1900	100.0
Two	Xeric	Subsistence agriculture in 1800s; abandoned 1900, reverted to hardwood/pine stand	No timber harvest since 1900	100.0
Two	Xeric	Subsistence agriculture in 1800s; abandoned 1900, reverted to hardwood/pine stand	Partial cut timber harvest leaving approximately 80% of basal area in 1940s	80.0
One	Xeric	Extensive grazing, not farmed for crops in 1800s and early 1900s	Partial cut timber harvest leaving approximately 40% of basal area in 1940s	40.0
Two	Mesic	Extensive grazing, not farmed for crops in 1800s and early 1900s	Partial cut timber harvest leaving approximately 40% of basal area in 1940s	40.0
One	Xeric	Extensive grazing, not farmed for crops in 1800s and early 1900s	Partial cut timber harvest leaving < 20% of basal area in 1940s	20.0

microsites having GLI as low as 0.7% in 2001 (TIME 5, 5 yr after initial inventory).

We investigated changes in soil moisture at 43 quadrats in one xeric, two submesic, and one mesic Opal gap. Soil moisture at 15-cm depth in forest soil was measured with time domain reflectometry (TDR) (response variable is resistance; higher resistance = lower moisture) along the gap axes from center into the unaffected forest at three times 1 wk apart in both native soil (TDR) and within root exclusion barriers (TRENCH) (Table 1). For the within-gap quadrats, measured soil moisture was greatest west and south of centers. For quadrats outside gaps, moisture was greatest east and west of centers (OLS, $P = 0.0001$ for GAPCAT × TRANSECT interaction). Findings were essentially the same for both the within *versus* outside root barrier locations (Fig. 4; only the outside root barrier locations are displayed for simplicity). We also investigated measured soil moisture *versus* slope and aspect and as expected, soil moisture increased as slope increased (OLS, *P*

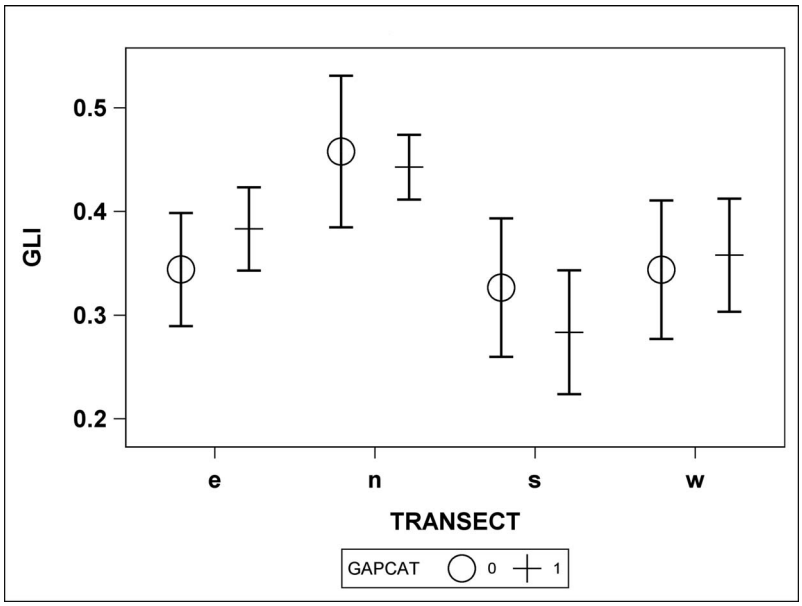

FIG. 3. Gap light index (GLI) by within *versus* outside gap (GAPCAT, 0 = outside gap 1 = inside gap) and direction east (e), north (n), south (s), and west (w) of gap center (TRANSECT) at 1.0 m above ground measured in 1998; with 95% confidence limits.

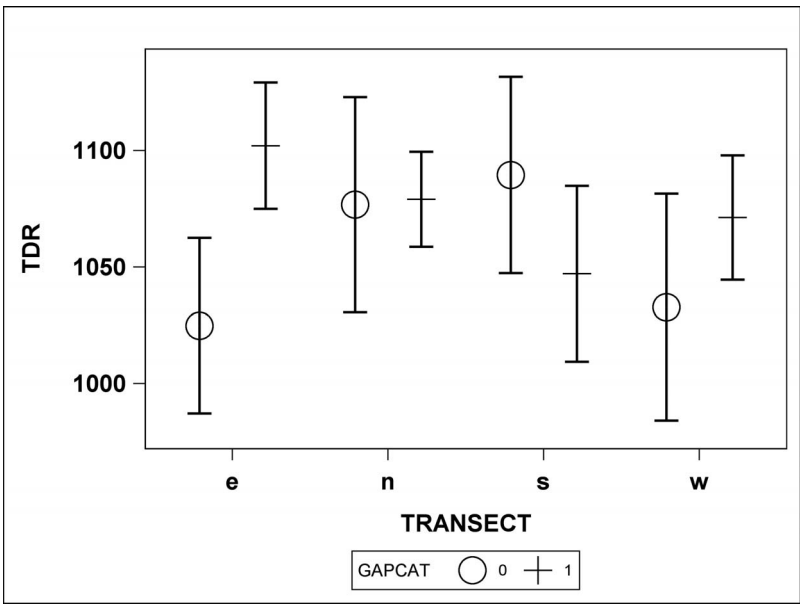

FIG. 4. Time domain reflectometry (TDR) resistance measured in native soil at 15-cm depth by within *versus* outside gap (GAPCAT, 0 = outside gap 1 = inside gap) and direction east (e), north (n), south (s), and west (w) of gap center (TRANSECT); higher TDR resistance = less available soil moisture; with 95% confidence limits.

= 0.0100) and on low-energy (north and east)-facing slopes (OLS, $P = 0.0012$). We therefore tested slope (SLOPE) and aspect (TRANSASP) in our presence model.

Next, we sought reasons for changes in soil moisture by location. We investigated the relationship between soil moisture *versus* solar radiation, and as Gray *et al*. (2002) and Kollmann and Grubb (1999) found, soil moisture declined as GLI increased (in 1998, OLS, $P = 0.0107$). Because soil temperature would likely vary by location and relate directly to soil moisture (Rosenberg *et al*. 1983), we examined changes in soil temperature at 15-cm depth using the soil moisture measurement location protocol. The relationship of soil temperature with soil moisture is complex and these two resources interact in varied ways; nonetheless, higher soil temperatures often result in lower available soil moisture near ground surface (Rosenberg *et al*. 1983). Soil temperature results mirrored soil moisture findings; for the within-gap sites, soil temperatures were greatest east and north of centers. At locations outside gaps, temperatures varied little by direction from centers (east *versus* west and north *versus* south). Outside-gap soil temperatures were moderated by heavy tree canopy cover in the unaffected forest (OLS, $P =$ 0.0006 for GAPCAT × TRANSECT interaction, Fig. 5).

We concluded that differences in growing-season available soil moisture by direction from center were largely driven by received solar radiation shaped by shade patterns cast by canopy trees at gap edge, and therefore bittersweet presence may be strongly related to location; in general, greater radiation received at ground level yielded drier soils. We first related bittersweet presence to linear distance from gap centers. Although presence was strongly related to linear distance from center to individual quadrats ($P <$ 0.0054 for all distance measures), we worried that bittersweet root spread may be affecting presence in adjacent quadrats. We therefore adopted categorical direction from center variables instead of distance-based measures in our presence model. We tested variables representing azimuth from center and locations pegged by east–west and north–south locations from center. We found that both approaches varied little *versus* a simple predominant direction from gap center, TRANSECT, which represented essentially clusters of quadrats located east, north, south, and west of gap center. We therefore adopted TRANSECT as our position-from-gap-center variable.

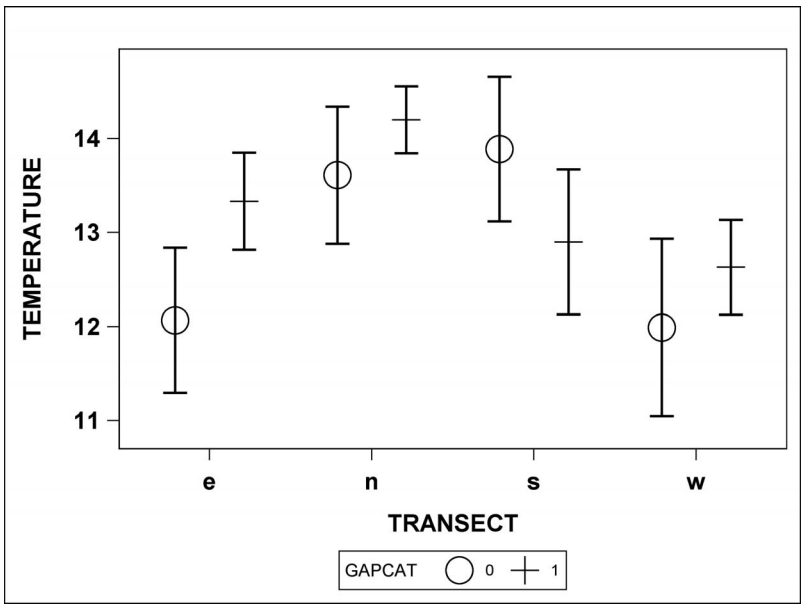

FIG. 5. Soil temperature (TEMPERATURE, °C) measured at 15-cm depth by within *versus* outside gap (GAPCAT, 0 = outside gap 1 = inside gap) and direction east (e), north (n), south (s), and west (w) of gap center (TRANSECT); with 95% confidence limits.

DATA ANALYSIS. *Hypothesis 1: Presence*. Data were pooled across all 11 gaps and 241 quadrats and analyzed with SAS PROC GLIMMIX (SAS Institute 2013) as random-intercept multilevel (quadrats within gaps, to account for clustering of data) repeated-measures (in time) logistic regression models. We used Zhang's (2017) coefficient of determination (penalized R^2 for generalized linear models) to compare the fits of bittersweet presence candidate models. The response variable was whether or not any bittersweet vegetation, including leaves and stems, was present within the quadrat cylinder. We evaluated TIME, GAPCAT, TRANSECT, SLOPE, TRANSASP, and SITE as potential presence model covariates (Table 1).

Hypothesis 2: Cover. We identified the square meters of bittersweet cover per quadrat to a maximum height of 2.0 m as the response variable (Table 1). We analyzed cover using pooled quadrat data with analysis of variance and adopted a split-split plot design on the basis of three variables that stemmed from the rationale used to build our presence models: (a) location—within *versus* outside the gaps in the unaffected forest; (b) direction in relation to gap centers; and (c) time since disturbance. Data were analyzed with SAS PROC MIXED (SAS Institute 2013) through repeated-measures analysis at each of the six time periods.

Results. HYPOTHESIS 1: PRESENCE. We sought parsimony and so included only essential covariates tied directly to our location-based hypothesis plus time since disturbance and site quality in our final model. We found several ancillary variables to be strongly related to bittersweet presence. We considered adding some of these to our presence model but decided to pare our model back to essential regressors needed to test our hypothesis. We provide findings of bittersweet presence *versus* these ancillary variables, including tree canopy cover, woody debris, gap areal size, pit and mound habitat, and tree seedling competition, in the Appendix.

FINAL MODEL. Penalized R^2 increased from 0.12 (incorporating only time) to 0.23 for the "best" model (Tables 3 and 4). Area under the receiver operating characteristic curve increased slightly from 0.93 with time-only to 0.94 for the full-model best linear unbiased predictor (BLUP), which included both fixed effects and random intercept clustering effects. However, the area under the curve = 0.66 for time-only increased to 0.87 for the full model for fixed effects (non-BLUP). This suggests a "good" trade-off between specificity ?2

Table 3. Asiatic bittersweet (*Celastrus orbiculatus*) presence model parameter estimates for 11 hurricane-created gaps.

Effect	Transect	GAPCAT	SITE	Estimate	Standard error	d.f.	t	$P > \|t\|$
Intercept				−3.1581	1.0296	9	−3.07	0.0134
TIME				0.3467	0.0506	1,378	6.86	< 0.0001
TIME × TIME				−0.0103	0.0023	1,378	−4.47	< 0.0001
GAPCAT		0		−0.9303	0.4010	1,378	−2.32	0.0205
GAPCAT		1		0.0000				
SLOPE				0.0318	0.0131	1,378	2.42	0.0155
TRANSECT	e[1]			1.5662	0.8534	1,378	1.84	0.0667
TRANSECT	n			−0.3508	0.8781	1,378	−0.4	0.6896
TRANSECT	s			0.0951	0.7822	1,378	0.12	0.9033
TRANSECT	s			0.0000				
SITE			1	−5.1633	1.3167	1,378	−3.92	< 0.0001
SITE			2	0.0000				
TRANSECT × GAPCAT	e	0		2.3815	0.6089	1,378	3.91	< 0.0001
TRANSECT × GAPCAT	e	1		0.0000				
TRANSECT × GAPCAT	n	0		1.2280	0.6123	1,378	2.01	0.0451
TRANSECT × GAPCAT	n	1		0.0000				
TRANSECT × GAPCAT	s	0		−0.8030	0.6320	1,378	−1.27	0.2041
TRANSECT × GAPCAT	s	1		0.0000				
TRANSECT × GAPCAT	w	0		0.0000				
TRANSECT × GAPCAT	w	1		0.0000				
SLOPE × TRANSECT	e			−0.0772	0.0232	1,378	−3.32	0.0009
SLOPE × TRANSECT	n			0.0120	0.0223	1,378	0.54	0.5912
SLOPE × TRANSECT	s			−0.0048	0.0163	1,378	−0.29	0.7692
SLOPE × TRANSECT	w			0.0000				

[1] e = east, n = north, s = south, w = west.

and sensitivity. The odds ratio estimates (Table 5) demonstrated strong contributions for several covariates in the full model. For example, presence is predicted to increase nearly fivefold for microsites east of center outside gaps compared with east of center within gaps. The final model was: presence = f (TIME, GAPCAT, SITE, SLOPE, TRANSECT plus interactions) (Tables 3 and 4).

The predicted probability of bittersweet being present varied widely by time, site quality, and location. Bittersweet was more frequently found within gaps compared with outside gaps. Predicted presence ramped up sharply from the first measurement at TIME 0 on mesic sites to TIME = 9, then increased slowly to 0.65 within gaps and to 0.43 outside gaps at TIME 20 (Table 6). Bittersweet is clearly a mesic site species; probability of presence was predicted to increase to only slightly more than 0.00 outside and to 0.01 within gaps by TIME 20 in xeric sites. By

Table 4. Asiatic bittersweet (*Celastrus orbiculatus*) presence type III fixed effects for 11 hurricane-created gaps.

Effect	Numerator d.f.	Denominator d.f.	χ^2	F	$P > \chi^2$	$P > F$
TIME	1	1,378	47.03	47.03	< 0.0001	< 0.0001
TIME × TIME	1	1,378	19.97	19.97	< 0.0001	< 0.0001
GAPCAT	1	1,378	1.03	1.03	0.3095	0.3097
SLOPE	1	1,378	1.81	1.81	0.1787	0.1790
TRANSECT	3	1,378	12.69	4.23	0.0054	0.0055
SITE	1	1,378	15.38	15.38	< 0.0001	< 0.0001
TRANSECT × GAPCAT	3	1,378	26.49	8.83	< 0.0001	< 0.0001
SLOPE × TRANSECT	3	1,378	12.71	4.24	0.0053	0.0054

Response variable = PRESENCE. Parameter estimates and type III fixed effects for multilevel (quadrats within gaps) repeated-measures (over six TIME periods) logistic regressions parameterized with SAS PROC GLIMMIX (SAS 2013). Testing the presence hypothesis by covariate parameter values, $H_0 = 0.0$. Model parameterized at the individual quadrat level with $n = 241$ sample quadrats within 11 gaps. Variables (see Table 1): TIME = number of years since study installation in1996; GAPCAT= quadrat location, either within the gap (value = 1) or outside the gap in the unaffected forest = 0); SITE = site quality, 1 = xeric, 2 = mesic; SLOPE = percent slope; TRANSECT (east, north, south, or west of center).

Table 5. Presence model odds ratios (see Table 1 for variable definitions).

Comparison	Estimate	95% Confidence limits	
Unit change of TIME from mean	1.241	1.182	1.303
GAPCAT 0 *versus* 1	0.913	0.563	1.480
Unit change of SLOPE from mean for GAPCAT 0	0.986	0.951	1.022
Unit change of SLOPE from mean for GAPCAT 1	1.023	0.999	1.047
SITE 1 *versus* 2	0.006	< 0.001	0.084
TRANSECT e *versus* w	1.624	0.830	3.177
TRANSECT n *versus* w	1.930	0.972	3.833
TRANSECT s *versus* w	0.617	0.311	1.224
Unit change of SLOPE from mean for TRANSECT e	0.948	0.903	0.994
Unit change of SLOPE from mean for TRANSECT n	1.031	0.989	1.074
Unit change of SLOPE from mean for TRANSECT s	1.016	0.983	1.050
Unit change of SLOPE from mean for TRANSECT w	1.025	0.997	1.055
TRANSECT e × GAPCAT 0 *versus* 1	4.984	1.943	12.783
TRANSECT n × GAPCAT 0 *versus* 1	1.415	0.558	3.590
TRANSECT s × GAPCAT 0 *versus* 1	0.200	0.069	0.580
TRANSECT w × GAPCAT 0 *versus* 1	0.493	0.207	1.175

Odds ratio interpretation by example: bittersweet (*Celastrus orbiculatus*) is predicted to be present nearly five times (odds ratio = 4.984) more often outside gaps (GAPCAT = 0) compared with within gaps (GAPCAT = 1) where TRANSECT = e (east of gap center).

categorical variable TRANSECT, presence was greater west of gap centers for quadrats located within gaps. However, this relationship reversed for quadrats located outside gaps; presence was greater east of centers. (Fig. 6). Ultimately, changes in presence were a function of varied combinations of soil moisture and solar radiation; bittersweet is highly shade tolerant, but small increases in light in concert with high levels of soil moisture yielded increases in presence. This is supported by increases in presence outside of gaps east and north of gap centers. In these locations, GLI was relatively large compared with locations west of gap centers; heavy tree canopies outside gaps sheltered forest soils and helped maintain high levels of shallow (*i.e.*, at 10- to 15-cm depth) depth moisture. Moisture at greater depths may have been reduced because of increased transpiration from greater tree basal area outside gaps. Presence was strongly related to differences in topography, indexed by SLOPE (Fig. 7), but was not related to aspect (TRANSASP, $P = 0.47$). Presence was predicted to increase rapidly as slope increased north, south, and west of centers within gaps, but slope had little impact on presence outside gaps, other than east of centers where received radiation was highest of all locations (Fig. 3).

HYPOTHESIS 2. COVER. To test our second hypothesis that bittersweet cover would increase

Table 6. Proportion of sample quadrats with measured proportion bittersweet (*Celastrus orbiculatus*) presence and model-predicted presence with 95% percent confidence limits (CL) by years from first measurement in 1996 (TIME) and site quality (SITE).

		Outside gaps				Within gaps			
TIME	SITE	Proportion present	Predicted presence	Lower CL	Upper CL	Proportion present	Predicted presence	Lower CL	Upper CL
0	Xeric	0.0000	0.0003	0.0000	0.0022	0.0000	0.0006	0.0001	0.0051
1	Xeric	0.0000	0.0004	0.0000	0.0030	0.0000	0.0009	0.0001	0.0070
2	Xeric	0.0000	0.0005	0.0001	0.0041	0.0000	0.0012	0.0002	0.0094
5	Xeric	0.0000	0.0011	0.0001	0.0091	0.0103	0.0028	0.0004	0.0211
9	Xeric	0.0000	0.0025	0.0003	0.0203	0.0000	0.0063	0.0008	0.0465
20	Xeric	0.0000	0.0043	0.0005	0.0343	0.0238	0.0107	0.0014	0.0773
0	Mesic	0.1111	0.0421	0.0074	0.2066	0.1579	0.1003	0.0199	0.3803
1	Mesic	0.2222	0.0580	0.0105	0.2640	0.2421	0.1350	0.0280	0.4587
2	Mesic	0.2963	0.0779	0.0144	0.3274	0.2737	0.1764	0.0382	0.5355
5	Mesic	0.2143	0.1616	0.0327	0.5237	0.3192	0.3282	0.0834	0.7240
9	Mesic	0.5185	0.3028	0.0704	0.7135	0.5326	0.5240	0.1684	0.8568
20	Mesic	0.4615	0.4276	0.1138	0.8130	0.5807	0.6545	0.2554	0.9127

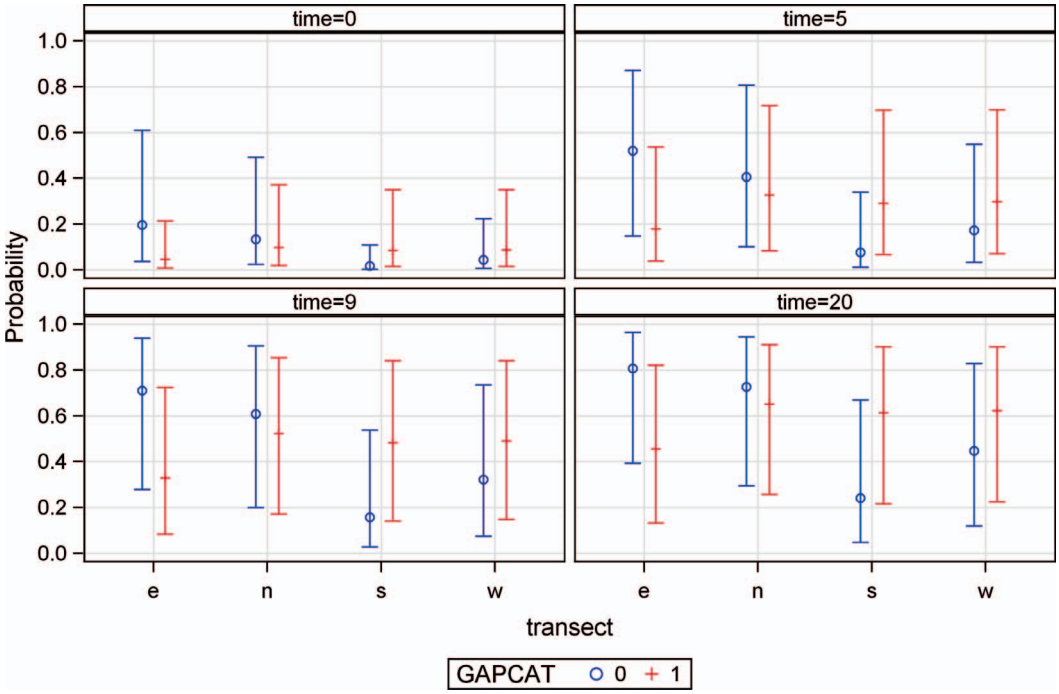

FIG. 6. Probability of bittersweet (*Celastrus orbiculatus*) being present *versus* location within *versus* outside gaps (GAPCAT, 0 = outside gap 1 = inside gap), direction east (e), north (n), south (s), and west (w) of gap center (TRANSECT) and years from first inventory in 1996 (TIME) in mesic sites; with 95% confidence limits.

within gaps compared with outside gaps in the unaffected forest, we analyzed cover data by location within *versus* outside gaps and by location north, east, south, or west of gap center and by time since first measurement. Because bittersweet was essentially found only in mesic sites and to simplify our model, we restricted our analysis of bittersweet cover to only the five mesic gaps. Bittersweet cover increased with time since hurricane disturbance. Cover was related to the interaction of GAPCAT and TRANSECT and was predicted to be higher east of gap center outside gaps and west of gap center within gaps (Tables 7 and 8, Fig. 8).

Discussion. The site quality variation among the hurricane-formed gaps provided an opportunity in our study to examine watershed-scale variation of moisture regimes as an experimental factor, which differs from many well-designed gap studies where site variation is minimized, such as the study of gap size reported by Shure et al. (2006). The combination of site quality variation with the long-term observations has resulted in findings of Asiatic bittersweet dynamics that to our knowledge have not been studied or reported elsewhere. Newly available light resources after hurricane-created gaps almost certainly facilitated the rapid expansion of bittersweet. Because bittersweet is shade tolerant (Ellsworth *et al*. 2004; Leicht-Young *et al*. 2007), any reductions in canopy cover would have provided sufficient increases in photosynthetic active radiation to fuel increases in both presence and cover. Our finding of bittersweet being present in extremely low light levels concurs with that of Leight-Young *et al*. (2007); available light was only weakly related to bittersweet mortality in their study.

Several investigators have found that wind disturbance accelerates the spread of invasive plants, and the rate of spread in some ecosystems is of particular concern. For example, Bellingham *et al*. (2005) reported the rapid spread of the invasive alien tree *Pittosporum undulatum* after a hurricane in Jamaica; *Pittosporum* advanced from not being present on any vegetation plots before the hurricane to being present on 69% of plots by 16 yr after the hurricane. Our predicted rate of

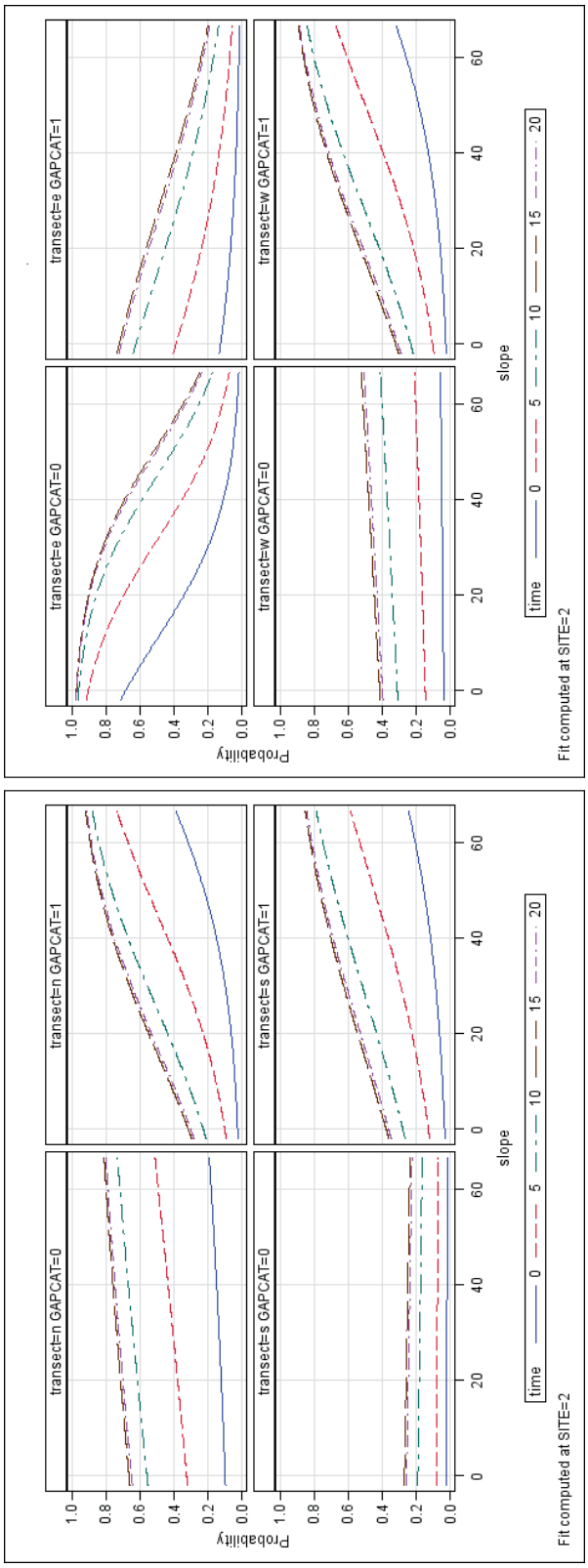

FIG. 7. Probability of bittersweet (*Celastrus orbiculatus*) being present *versus* percent slope, location within *versus* outside gaps (GAPCAT, 0 = outside gap 1 = inside gap), direction east (e), north (n), south (s), and west (w) of gap center (TRANSECT), and years from first inventory in 1996 (TIME).

Table 7. Bittersweet (*Celastrus orbiculatus*) cover-split-split plot model type III effect estimates for 11 hurricane-created gaps.

Effect	Numerator d.f.	Denominator d.f.	*F*	$P > F$
GAPCAT	1	4	0.00	0.9709
TRANSECT	3	21	2.03	0.1402
GAPCAT × TRANSECT	3	21	3.06	0.0504
TIME	5	143	9.72	<.0001
GAPCAT × TIME	5	143	0.17	0.9717
TRANSECT × TIME	15	143	1.05	0.4120
GAPCAT × TRANSECT × TIME	15	143	1.29	0.2139

increase in bittersweet presence somewhat mirrored that of Bellingham's observed rate of *Pittosporum* spread: by 20 yr after initial inventory, the predicted probability of bittersweet presence within mesic gaps in our study had increased to approximately 0.64 (Table 6).

Bittersweet's advances in presence with time in the current study mirrored those of other investigators (Fike and Niering 1999; Silveri *et al*. 2001). However, the rate of presence increase declined substantially between TIME 9 and TIME 20 in our study. As Daniels and Larson (2019) and Khaniya and Shrestha (2020) found with multiple invasive species, bittersweet spread in our study slowed because of increasing tree canopy cover (Appendix) that reduced available light. Our results concurred with those of other investigators: The probability of finding bittersweet increased within wind-created forest gaps compared with outside gaps (McNab and Loftis 2002).

Several investigators have reported that bittersweet is more frequently found on mesic than on xeric sites (McNab and Loftis 2002; Leicht-Young *et al*. 2007). This concurs with our findings that bittersweet is found essentially only in mesic sites. Bittersweet presence was found to be highly sensitive to changes in soil moisture as represented by the macrosite variable SITE. Leicht-Young *et al*. (2007) reported that bittersweet survivorship peaked at volumetric water content of approximately 0.60 and survivorship was predicted to decline in higher moisture levels. However, Berg (1998) found bittersweet present at soil water content > 0.75 within a subset of this study's quadrats; he found no asymptote for this relationship. Bittersweet was seldom observed on xeric sites in our study, regardless of the values of other environmental variables.

In our study, greater bittersweet presence in specific combinations of location variables GAPCAT and TRANSECT was likely driven primarily by differences in received light and available soil moisture. We suggest that these findings related directly to shade cast by canopy trees at gap edge; locations west and south of center within gaps received more shade during times of peak solar radiation loads, and so presence was less compared with locations east and north of centers within gaps. Several investigators have reported similar results, including Gray et al. (2002). Additionally, other than on locations east of gap centers where steeper slopes exacerbated moisture loss, presence

Table 8. Bittersweet (*Celastrus orbiculatus*) cover-split-split plot model least-squares means for 11 hurricane-created gaps.

Effect	TRANSECT	GAPCAT	Estimate	Standard error	d.f.	*t*	$P > \|t\|$
GAPCAT × TRANSECT	East	0	1.5350	0.3301	21	4.65	0.0001
GAPCAT × TRANSECT	North	0	0.1906	0.4154	21	0.46	0.6510
GAPCAT × TRANSECT	South	0	0.1584	0.3598	21	0.44	0.6643
GAPCAT × TRANSECT	West	0	0.6616	0.3218	21	2.06	0.0524
GAPCAT × TRANSECT	East	1	0.3422	0.3218	21	1.06	0.2997
GAPCAT × TRANSECT	North	1	0.4778	0.3218	21	1.48	0.1525
GAPCAT × TRANSECT	South	1	0.5539	0.3218	21	1.72	0.0999
GAPCAT × TRANSECT	West	1	1.2090	0.3218	21	3.76	0.0012

Response variable = COVER (square meters of bittersweet stem or leaf cover per quadrat); SAS PROC MIXED type III analysis results. Variables: GAPCAT ((0 = outside gap, 1 = within gap), TRANSECT (directions from center), and TIME (years from first measurement in 1996).

SAS PROC MIXED least-squares means of GAPCAT–TRANSECT interactions.

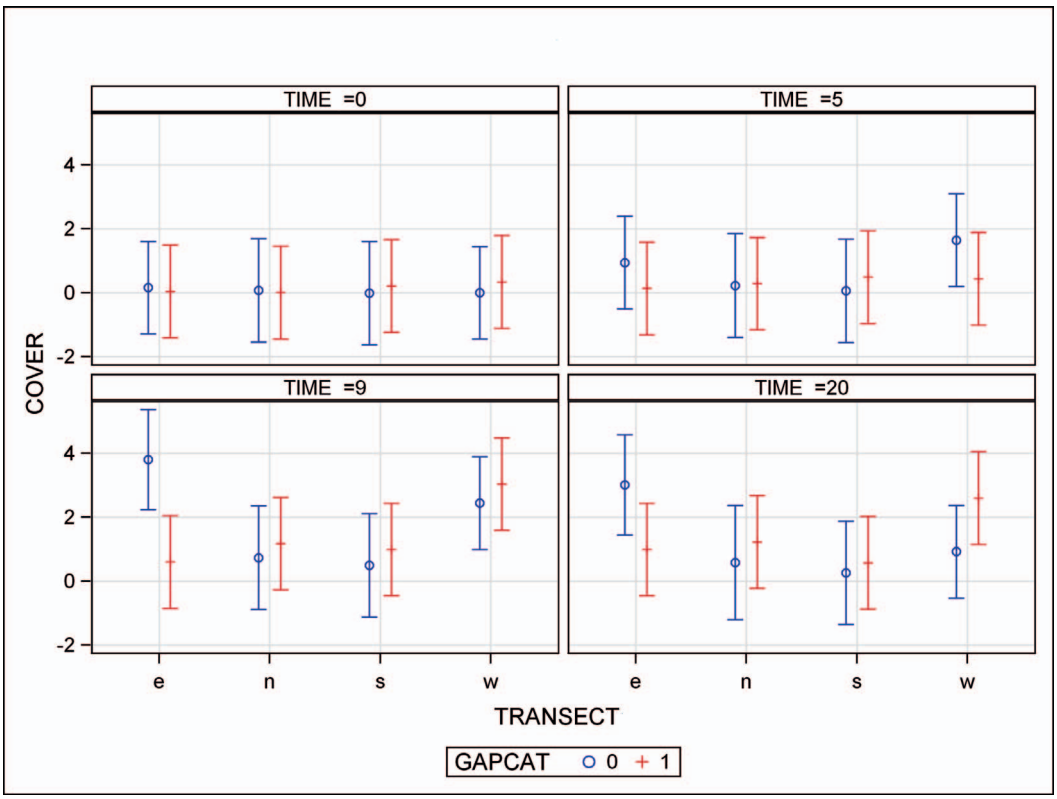

FIG. 8. Predicted bittersweet (*Celastrus orbiculatus*) square meters of cover per quadrat *versus* location within or outside gaps (GAPCAT, 0 = outside gap 1 = inside gap) and direction east (e), north (n), south (s), and west (w) of gap center (TRANSECT), and years from first inventory in 1996 (TIME) in mesic sites.

was greater on steep slopes that offered macrosite protection and reduced soil moisture losses (Fig. 7) (Rosenberg *et al*.1983). Our results concurred with those of McNab and Loftis (2002), who found low probability of bittersweet presence on xeric sites. In summary, Asiatic bittersweet is clearly a mesic-site species.

Our bittersweet cover model predictions mirrored those of other investigators, including Daniels and Larson (2019), who found increases in invasive shrub and liana cover with time and gap creation. As with our presence model, our cover model findings support gap partitioning by direction from center; cover increased west of centers within gaps, but we found no definitive differences in cover north or south of centers. Increases in cover slowed by TIME 9; we again attribute this to progressively increasing tree canopy cover. Our study confirms the role that gap partitioning (Sipe and Bazzaz 1995) plays in bittersweet distribution. Our findings agree with those of Van Couwenberghe *et al*. (2010) and Lu *et al*. (2018), who reported clear trends in tree species gap partitioning by location within gaps. Although Lu *et al*. (2018) reported a trend in tree species responses on the basis of location, their research extended only from gap centers to the edge of the gap. However, in our study partitioning extended beyond gap edges into the unaffected forest and bittersweet presence outside gaps varied greatly by location from gap centers.

This study had limitations. First, we had no data on bittersweet seed production in and around the 11 experimental gaps. Seed production and distribution by birds and small mammals may have been responsible for shaping some of our presence and cover findings (Greenberg *et al*. 2001). However, several bittersweet investigations (*e.g*., McNab and Loftis 2000, Silveri *et al*. 2001) relating presence and other attributes to environmental factors did not include seed distribution information, suggesting that important findings can be gleaned from research that lacks detailed seed data. Next, our response variables, presence and

cover, were observed solely within virtual cylinders from ground level to 2.0 m in height. Clearly, a fast-growing twining liana is not restricted to 2.0 m in height. However, despite these shortcomings, we suggest that our findings of presence and cover provide land managers with valid information to help inform their land management plans, especially over long time periods.

Summary of Findings, Conclusions, and Management Implications. Our research supports gap partitioning of bittersweet presence and cover. Presence and cover were found to be greater within *versus* outside gaps and in microsites with greater available soil moisture, specifically where canopy trees provided maximum shading during times of peak solar radiation loads. Increases in presence were particularly noted west and south of gap centers within gaps, and cover was found to be greatest west of centers within gaps. Gap partitioning influences extended beyond gap edges into the unaffected forest. In these outside-gap microsites with heavy tree canopy cover, bittersweet presence was particularly great east and north of centers and cover was greatest east of centers. We found bittersweet to be highly shade tolerant and a pervasive competitor of mesic sites, but it was rarely found in xeric sites. Presence and cover increased rapidly for the first 10 yr after hurricane disturbance; rates of increase then slowed to 20 yr posthurricane as forest canopy cover increased with time.

This study's results dovetailed with previous findings that gap-creating disturbances accelerated the spread of bittersweet. In mesic eastern USA ecosystems that support bittersweet colonization, forest managers can expect increases in bittersweet presence and cover when timber is harvested. Additional research of the interaction of received light and soil moisture over long time periods would help inform land managers of the risks of bittersweet invasion as a function of varied reductions in forest canopy cover.

Literature Cited

Abe, T., N. Tanaka, and Y. Shimizu. 2020. Outstanding performance of an invasive alien tree *Bischofia javanica* relative to native tree species and implications for management of insular primary forests. Peer J 8: e9573.

Albright, T. P., D. P. Anderson, N. S. Keuler, S. M. Pearson, and M. G. Turner. 2009. The spatial legacy of introduction: *Celastrus orbiculatus* in the southern Appalachians, USA. Journal of Applied Ecology 46: 1229–1238.

Beck, D. E. 1988. Clearcutting and other regeneration options for upland hardwoods, pp. 44–54. *In* Proceedings, 16th annual hardwood symposium of the Hardwood Research Council, Cashiers, NC.

Beers, T. W., P. E. Dress, and L. C. Wensel. 1966. Aspect transformation in site productivity research. Journal of Forestry 64: 691–692.

Bellingham, P. J., E. Tanner, and J. R. Healey. 2005. Hurricane disturbance accelerates invasion by the alien tree *Pittosporum undulatum* in Jamaican montane rain forests. Journal of Vegetation Science 16: 675–684.

Berg, E. C. 2002. Hurricane effects on forest understory vegetation in the southern Appalachians. Ph.D. dissertation. Clemson University, Clemson, SC. 112 pp.

Berg, E.C. 2004. Survivorship and growth of oak regeneration in wind-created gaps, pp. 143–149. *In* M. A. Spetich, ed. Upland oak ecology symposium: History, current conditions, and sustainability. General Technical Report SRS-73. United States Department of Agriculture, Forest Service, Southern Research Station, Asheville, NC.

Brown, N. 1996. A gradient of seedling growth from the centre of a tropical rain forest canopy gap. Forest Ecology and Management 82: 239–244.

Clinton, B. D. and C. R. Baker. 2000. Catastrophic windthrow in the southern Appalachians: Characteristics of pits and mounds and initial vegetation responses. Forest Ecology and Management 126: 51–60.

Coomes, D. A. and P. J. Grubb. 2000. Impacts of root competition in forests and woodlands: A theoretical framework and review of experiments. Ecological Monographs 70: 171–207.

Crowley, S. L., S. Hinchliffe, and R. A. McDonald. 2017. Conflict in invasive species management. Frontiers in Ecology and the Environment 15: 133–141.

Daniels, M. K. And E. R. Larson. 2019. Effects of forest windstorm disturbance on invasive plants in protected areas of southern Illinois, USA. Journal of Ecology 108: 199–211.

Delta T Devices. 1998. Program Hemiview. Hemispherical photo analysis software.

Ellsworth, J. W., R. A. Harrington, and J. H. Fownes. 2004. Survival, growth and gas exchange of *Celastrus orbiculatus* seedlings in sun and shade. American Midland Naturalist 151: 233–240.

Fahey, R. T. and K. J. Puettmann. 2008. Patterns in spatial extent of gap influence on understory plant communities. Forest Ecology and Management 255: 2801–2810.

Fike, J. and W. A. Niering. 1999. Four decades of old field vegetation and the role of *Celastrus orbiculatus* in the northeastern United States. Journal of Vegetation Science 10: 483–492.

Gray, A. N., T. A. Spies, and M. J. Easter. 2002. Microclimatic and soil moisture responses to gap formation in coastal Douglas-fir forests. Canadian Journal of Forest Research 32: 332–343.

GRAYSON, S. F., D. S. BUCKLEY, J. G. HENNING, C. J. SCHWEITZER, K. W. GOTTSCHALK, AND D. L. LOFTIS. 2012. Understory light regimes following silvicultural treatments in central hardwood forests in Kentucky, USA. Forest Ecology and Management 279: 66–76.

GREENBERG, C. H. AND W. H. MCNAB. 1998. Forest disturbance in hurricane-related downbursts in the Appalachian Mountains of North Carolina. Forest Ecology and Management 104: 179–191.

GREENBERG, C. H., L. M. SMITH, AND D. J. LEVEY. 2001. Fruit fate, seed germination and growth of an invasive vine—An experimental test of 'sit and wait' strategy. Biological Invasions 3: 363–372.

HORTON, J. L. AND J. S. FRANCIS. 2014. Using dendroecology to examine the effect of Oriental bittersweet (*Celastrus orbiculatus*) invasion on tulip poplar (*Liriodendron tulipifera*) growth. American Midland Naturalist 172: 25–36.

HORVITZ, C. C., J. B. PASCARELLA, J. B. MCMANN, S. FREEDMAN, A. FREEDMAN, AND R. H. HOFSTETTER. 1998. Functional roles of invasive non-indigenous plants in hurricane-affected subtropical hardwood forests. Ecological Applications 8: 947–974.

JOHNSON, P. S., S. R. SHIFLEY, R. ROGERS, D. C. DEY, AND J. M. KABRICK. 2019. The Ecology and Silviculture of Oaks, 3rd ed. CABI Publishing, New York, NY. 643 pp.

KENT, M. AND P. COKER. 1995. Vegetation Description and Analysis: A Practical Approach. John Wiley and Sons, New York, NY. 384 pp.

KHANIYA, L. AND B. B. SHRESTHA. 2020. Forest regrowth reduces richness and abundance of invasive alien plant species in community managed *Shorea robusta* forests of central Nepal. Journal of Ecology and Environment 44: 12.

KOLLMANN, J. AND P. J. GRUBB. 1999. Recruitment of fleshy-fruited species under different shrub species: Control by under-canopy environment. Ecological Research 14: 9–21.

LADWIG, L. M. AND S. J. MEINERS, 2009. Impacts of temperate lianas on tree growth in young deciduous forests. Forest Ecology and Management 259: 195–200.

LARSON, D. L., L. PHILLIPS-MAO, G. QUIRAM, L. SHARPE, R. Stark., S. Sugita, and A. Weiler. 2011. A framework for sustainable invasive species management: Environmental, social, and economic objectives. Journal of Environmental Management 92: 14–22.

LEICHT-YOUNG, S. A., A. M. LATIMER, AND J. A. SILANDER. 2011. Lianas escape self-thinning: Experimental evidence of positive density dependence in temperate lianas *Celastrus orbiculatus* and *C. scandens*. Perspectives in Plant Ecology, Evolution and Systematics 13: 163–172.

LEICHT-YOUNG, S. A., J. A. SILANDER, AND A. M. LATIMER. 2007. Comparative performance of invasive and native *Celastrus* species across environmental gradients. Oecologia 154: 273–282.

LOFTIS, D. L. 1991. A shelterwood method for regenerating red oak in the southern Appalachians. Forest Science 36: 917–929.

LU, D. D., G. G. WANG, Q. YAN, T. GAO, AND J. ZHU. 2018. Effects of gap size and within-gap position on seedling growth and biomass allocation: Is the gap partitioning hypothesis applicable to the temperate secondary forest ecosystems in Northeast China? Forest Ecology and Management 429: 351–362.

MARTIN, P. H, C. D. CANHAM, AND P. L. MARKS. 2009. Why forests appear resistant to exotic plant invasions: Intentional introductions, stand dynamics, and the role of shade tolerance. Frontiers in Ecology and the Environment 7: 142–149.

MCNAB, W. H. 1993. A topographic index to quantify the effect of mesoscale landform on site productivity. Canadian Journal of Forest Research 23: 1100–1107.

MCNAB, W. H. AND T. L. KEYSER. 2020. A vegetative index of stand productivity based on tree inventory for predicting oak site index in the Central Hardwood Region. Canadian Journal of Forest Research 50: 750–763.

MCNAB, W. H. AND D. L. LOFTIS. 2002. Probability of occurrence and habitat features for oriental bittersweet in an oak forest in the southern Appalachian Mountains, USA. Forest Ecology and Management 155: 45–54.

MCNAB, W. H., C. H. GREENBERG, AND E. C. BERG. 2004. Landscape distribution and characteristics of large hurricane-related canopy gaps in a southern Appalachian watershed. Forest Ecology and Management 198: 435–447.

MCNAB, W. H., T. W. LLOYD, AND D. L. LOFTIS. 2002. Preliminary evaluation of methods for classifying forest site productivity on species composition in western North Carolina, pp. 10–18. *In* Proceedings, southern mensurationists' conference; November 4–6, 2001, Chattanooga, TN. Arkansas Forest Resources Center, Monticello, AR.

MORRISSEY, R. C., D. F. JACOBS, A. S. DAVIS, AND R. A. RATHFON. 2010. Survival and competitiveness of *Quercus rubra* regeneration associated with planting stocktype and harvest opening intensity. New Forests 40: 273–287.

PATTERSON, D. T. 1974. The ecology of oriental bittersweet, *Celastrus orbiculatus*, a weedy introduced ornamental vine. Ph.D. dissertation. Duke University, Durham, NC. 252 pp.

REBBECK, J. 2012. Fire management and woody invasive plants in oak ecosystems, pp. 142–155. *In* D. C. Dey, M. C. Stambaugh, S. L. Clark, L. Stacy, and C. J. Schweitzer, eds. Proceedings, 4th fire in eastern oak forests conference; May 17–19, 2011, Springfield, MO. General Technical Report NRS-P-102. United States Department of Agriculture, Forest Service, Northern Research Station, Newtown Square, PA.

ROSENBERG, N. J., B. L. BLAD, AND S. B. VERMA. 1983. Microclimate: The Biological Environment. John Wiley and Sons, New York, NY. 495 pp.

RUNKLE, J. R. 1985. Disturbance regimes in temperate forests, pp. 17–33. *In* S. A. Pickett and P. S. White, eds. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, NY.

RUNKLE, J. R. 1992. Guidelines and sample protocol for sampling forest gaps. General Technical Report PNW-GTR-283. United States Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR. 44 pp.

SAS Institute. 2013. The Statistical Analysis System, Version 9.4. Cary, NC.

Schleppi, P. 2007. Hemisfer. Hemispherical photography analysis software program. Available online at http://www.schleppi.ch/hemisfer/.

Shimwell, D. 1971. The Description and Classification of Vegetation. Sidgwick and Jackson, London, UK. 322 pp.

Shure, D. J., D. L. Phillips, and P. E. Bostick. 2006. Gap size and succession in cutover southern Appalachian forests: An 18 year study of vegetation dynamics. Plant Ecology 185: 299–318.

Silveri, A., P. W. Dunwiddie, and H. Michaels. 2001. Logging and edaphic factors in the invasion of an Asian woody vine in a mesic North American forest. Biological Invasions 3: 379–389.

Sipe, T. W. and F. A. Bazzaz. 1995. Gap partitioning among maples (*Acer*) in central new England: Survival and growth. Ecology 76: 1587–1602.

Van Couwenberghe, R., C. Collet, E. Lacombe, J. Pierrat, and J. Gégout. 2010. Gap partitioning among temperate tree species across a regional soil gradient in windstorm-disturbed forests. Forest Ecology and Management 260: 146–154.

Van Der Meer, P. J., P. Dignan, and A. G. Saveneh. 1999. Effect of gap size on seedling establishment, growth and survival at three years in mountain ash (*Eucalyptus regnans* F. Muell.) forest in Victoria, Australia. Forest Ecology and Management 117: 33–42.

Webster, C. R., M. A Jenkins, and S. Jose. 2006. Woody invaders and the challenges they pose to forest ecosystems in the eastern United States. Journal of Forestry 104: 366–374.

Yetter, T. C. and J. R. Runkle. 1986. Height growth rates of canopy tree species in southern Appalachian gaps. Castanea 51: 157–167.

Zhang, D. 2017. A coefficient of determination for generalized linear models. American Statistician 71: 310–316.

Appendix

Bittersweet presence responses to variables (Table 1) not included in the final model. We analyzed the relationship of presence with covariates frequently included in gap-based research and often of interest to land managers, including gap areal size, tree canopy cover, hurricane-related pit and mound habitat, and coarse woody debris felled within and outside gaps. We also tested bittersweet's sensitivity to tree seedling competition. In a simple model of presence $= f$ (TIME, TIME^2, TOTALCOV), presence declined with increasing TOTALCOV through time ($P = 0.06$). TOTALCOV averaged 0.77 in gaps and 0.96 in the unaffected forest outside gaps at TIME 0. By TIME 9, TOTALCOV had increased to 0.86 within gaps and remained unchanged from TIME 0 outside gaps. At TIME 20, TOTALCOV had increased to 0.97 within gaps and to 0.99 outside gaps. A novel result was the relationship of presence with hurricane-created woody debris; presence was predicted to increase with woody debris suspended above ground (DEBRIS, $P = 0.02$) or resting fully on the ground (WOOD, $P = 0.01$) when coupled with only time and time squared in presence models. Presence was not related to total gap hectares ($P = 0.43$ or root mound habitat (RTMOUND, $P = 0.89$). Bittersweet presence declined with increasing tree seedling density (SUMALL, $P = 0.0052$ when SUMALL was included in the final presence model), particularly within gaps ($P = 0.0082$ for the SUMALL $\times$ GAPCAT interaction) regardless of TRANSECT.

There are many possible reasons why bittersweet presence increased with hurricane-created woody debris, for example, microsite facilitation of bittersweet establishment by debris shading, or structure for bird perching. Experimental studies that manipulate coarse woody debris cover would yield better determination of the effects of debris on bittersweet colonization. Unlike the findings of Daniels and Larson (2019), we did not observe increases in cover with gap areal size. We attribute this to the large size (all gaps were > 0.1 ha) of our gaps. Presence was not related to locations on wind-created pits and mounds, in agreement with Clinton and Baker (2000). Because only a small fraction of gap areas was covered with pits and mounds, any statistical relationship would have been improbable. Contrary to Leicht-Young *et al.* (2011), we found that bittersweet was sensitive to plant competition; presence declined with increasing tree regeneration density. This was particularly true within gaps; the additional light within gaps fostered higher tree seedling densities, which therefore yielded reduced bittersweet presence compared with microsites with lower seedling densities found outside gaps.

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