High Winter Temperatures Facilitate Invasion of *Tradescantia fluminensis* in the Apalachicola River Floodplain

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Abstract - Temperature impacts organisms at a finer scale than that represented by weather stations and climate models. I investigated whether the expansion of a non-native herbaceous plant species, *Tradescantia fluminensis* (Small-leaf Spiderwort), up the slopes of the Apalachicola River, FL, was related to topography and/or surface temperature. These slopes comprise the remaining range of *Torreya taxifolia* (Florida Torreya), one of the rarest tree species in North America, and reports raise the concern that the development of dense patches of Small-leaf Spiderwort can inhibit the establishment of native plants and tree seedlings. I measured vegetative growth over 1 year and surface-temperature minima during the winter of 2016–2017 at the upland boundaries of Small-leaf Spiderwort patches. Temperatures were colder at higher elevations and greater distances from the floodplain, but did not reach the lethal temperature of -4.2 °C. Ninety four percent of patches survived. They expanded upslope an average of 1.2 m/y, and could reach the closest Florida Torreya trees in 2 y. Temperature minima were >1.3 °C warmer than those at the weather station in nearby Wilma, FL. Historical records for Wilma indicate that two-thirds of winters reach sufficiently cold temperatures to kill Small-leaf Spiderwort, and cold temperatures in January 2018 did kill a small proportion of plants. The lack of sufficiently cold temperature since 2011 might account for the recent expansion of Small-leaf Spiderwort in the Apalachicola floodplain.

Introduction

Climate change is expected to cause range expansions of invasive species, including invasive plants in the southeastern US (Bradley et al. 2010). Cold winter temperatures limit the current and potential distribution of certain invasive plants, such as *Ligustrum sinense* Lour. (Chinese Privet) and *L. vulgare* L. (European Privet) (Bradley et al. 2010), and annual variation in minimum temperature accounts for variation in cover of the invasive *Azolla filiculoides* Lam. (Pacific Azolla) in a Spanish wetland (Espinar et al. 2015). At smaller time and spatial scales, dispersal of propagules limits invasion (Merow et al. 2011). However, climatic variables, including temperature, vary within a landscape at scales smaller than reflected in weather-station data and climate models, and these small-scale differences are important for organisms (Potter et al. 2013), suggesting that minimum temperature or other microclimate parameters may limit biological invasion at local scales. Understanding these limitations should improve prediction of areas at risk of invasion.

Temperature data from weather stations and climate models may not strongly correlate with field temperatures that are relevant to plant invasions. For example,

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a shallow-rooted herbaceous perennial would be affected by cold temperatures near the surface of the soil, but soil temperature is influenced by canopy- and litter-cover, soil moisture, wind, and humidity (Paul et al. 2004). Furthermore, microtopography significantly affects surface temperature (Sears et al. 2011).

I investigated the role of topography and temperature in limiting the local invasion of *Tradescantia fluminensis* Vell. (Commelinaceae) (Small-leaf Spiderwort) on slopes on the east bank of the Apalachicola River in northwestern Florida. These slopes are of primary conservation concern because they comprise the remaining range of one of the rarest trees in North America, *Torreya taxifolia* Arn. (Florida Torreya). This species is restricted to ravine slopes on the east side of the Apalachicola River in Liberty and Gadsden counties, FL, and Decatur County, GA (Schwartz et al. 2000). The Florida Torreya is listed as critically endangered A2ace on the IUCN Red List, and endangered on the US Endangered Species List (Spector et al. 2011, USFWS 2009). An estimated 500–600 trees remain in the wild (Spector et al. 2011), and this species has been assigned a recovery priority of 5 because of high threat and low recovery potential (USFWS 2009).

Small-leaf Spiderwort provides an excellent opportunity to investigate the role of microhabitat parameters on invasion, as invasive populations do not produce seeds and spread only by fragmentation and vegetative growth (see Study Species). The objectives of this study were to (1) explore whether the rapid expansion of Small-leaf Spiderwort in the floodplain could be accounted for by climate or inundation patterns; (2) document the present upslope limits of the distribution of Small-leaf Spiderwort, including proximity to Florida Torreya trees; and (3) quantify the rate at which these patches were spreading, by vegetative growth, into upland habitats. I also sought to determine factors that were associated with the survival or death, and fast vs. slow vegetative growth of the upland margins of these Small-leaf Spiderwort patches. In particular, I explored whether growth was halted, or patches killed, by winter-temperature minima, or topographic features expected to correlate with temperature minima or soil dryness (distance from the swamp forest, elevation above the swamp forest). I hypothesized that low temperature would kill patches of Small-leaf Spiderwort based on observations that it does not persist in areas with hard frosts (Stace 1991 cited in McMillan 1999). Growth-chamber experiments revealed Small-leaf Spiderwort is frost resistant to -4 °C over 8 h, with an LT_{50} (point of 50% damage) of -4.2 °C (Bannister 1986).

Understanding which parts of the upland adjacent to the floodplain are at risk of invasion will enable land managers to prioritize areas for treatment to control Small-leaf Spiderwort. Herbicide control of this invasive plant species is possible (Brown and Brown 2015; M.R. Jenkins, Florida Forest Service, pers. comm.; McCluggage 1998); suggestions for effective control in Florida are included in Seitz and Clark (2016). Manual control is effective for small colonies (Standish 2002); the shallow rooted-plants can be raked, but this technique necessitates removal of all fragments. Standish (2002) concluded that shading (for 17 months with 3 layers of cloth, reducing light to 2–5% of full sun) was the most effective Small-leaf Spiderwort control measure.

Study Area

I carried out this research on the east bank of the Apalachicola River floodplain and adjacent slopes in Apalachicola Bluffs and Ravines Preserve (ABRP) and Torreya State Park (TSP), Liberty and Gadsden counties, FL (Fig. 1). The lowlands

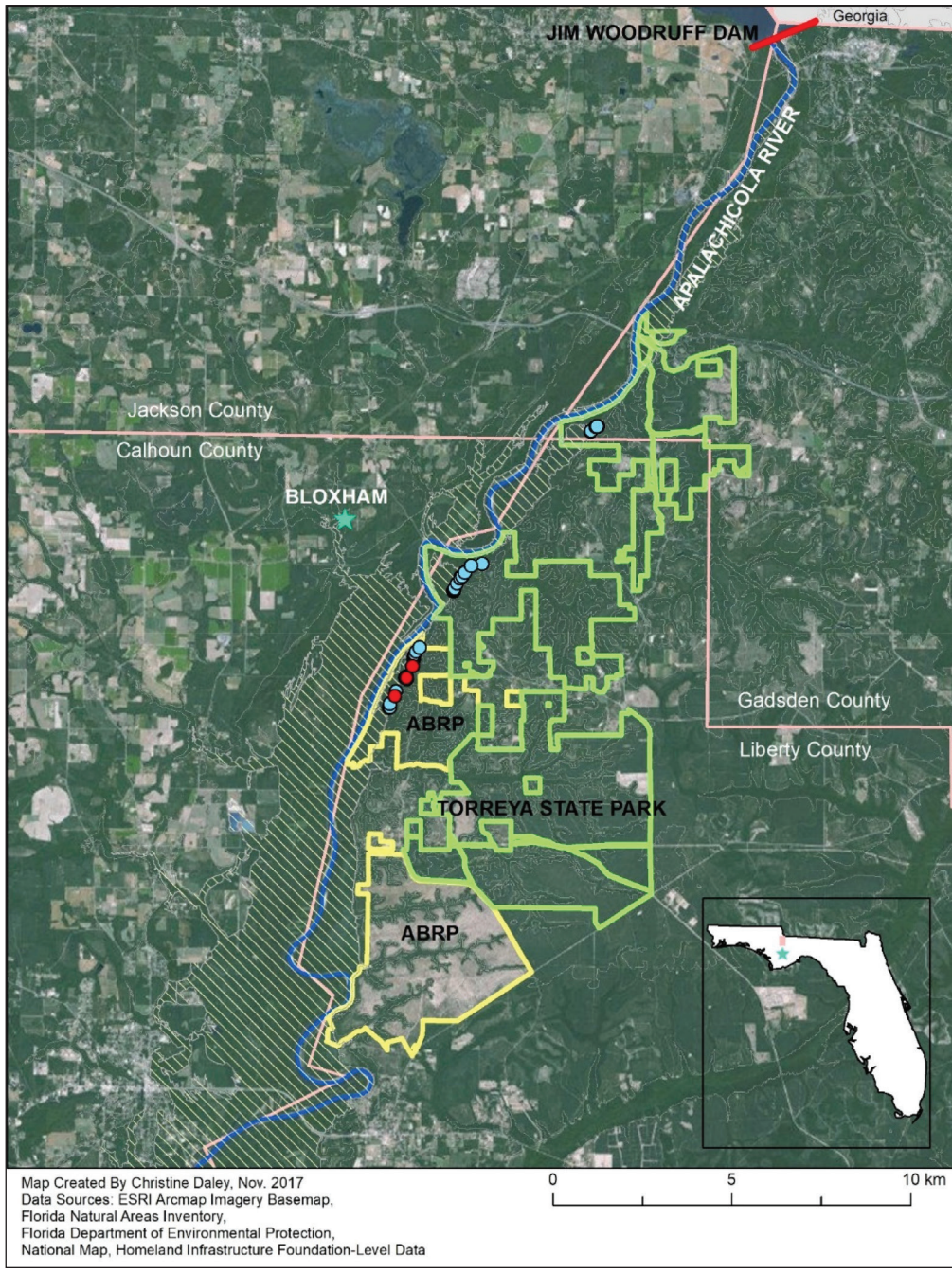

Figure 1.Map of study area. [Full caption on following page].

along this river, as well as the Apalachicola River itself, are hotspots of biodiversity (Blaustein 2008). This area harbors the largest floodplain forest in Florida, with about 60 tree species (Leitman et al. 1984). Most of the remaining Florida Torreya trees occur in TSP and ABRP. My study sites were along the upper reach of the Apalachicola River, below the Jim Woodruff Dam (30.44°N, 85.01°W) and north of Bristol, FL. Average air temperature at the closest weather station, Bloxham (elevation = 30.5 m; 30.5872°N, 84.9886°W), was 10.4 °C in January and 27.6 °C in July over the most recent 10 y (2007–2016) (data from http://www.ncdc.noaa.gov/cdo-web/search). There was an average of 35 d per year with a minimum temperature below 0 °C.

Most of the floodplain in the study area was cypress/tupelo floodplain swamp dominated by *Nyssa aquatica* L. (Water Tupelo) and *Taxodium distichum* (L.) Rich. (Baldcypress) (FNAI 2010). This swamp forest is typically inundated for 4–9 months each year, with water levels closely tracking river levels (Darst and Light 2008). Slightly higher, and inundated typically 2–4 months per year, is low, bottomland hardwood forest (type B, in Leitman et al. 1984) dominated by *Carya aquatica* (Michx. F.) Nutt. (Water Hickory), *Fraxinus pennsylvanica* Marsh. (Green Ash), *Quercus lyrata* Walt. (Overcup Oak), and *Q. laurifolia* Michx. (Diamond-leaf Oak). Above that is high bottomland hardwoods (type A, in Leitman et al. 1984) dominated by *Liquidambar styraciflua* L. (Sweetgum), *Celtis laevigata* Willd. (Hackberry), and *Q. nigra* L. (Water Oak). Above the floodplain were steep slopes, covered with forest characterized by *Fagus grandifolia* Ehrh. (American Beech), *Acer saccharum* ssp. *floridanum* (Chapm.) Desmarais (Florida Maple), *Q. alba* L. (White Oak), *Magnolia ashei* Weath. (Ashe's Magnolia), *M. grandiflora* L. (Southern Magnolia), *Pinus glabra* Walter (Spruce Pine), and *Q. shumardii* Buckley (Shumard's Oak) (FNAI 2010).

Small-leaf Spiderwort invasion in the Apalachicola floodplain

The first detection of a somewhat large patch of Small-leaf Spiderwort in the area that includes the remaining populations of Florida Torreya was by Annie Schmidt (Wildland Resources LLC, Bristol, FL) in May 2012 in the Apalachicola River floodplain Park Elbow area of TSP (Fig. 1). By November 2014, many extensive patches had been found, all restricted to the floodplain forest and floodplain

Figure 1 [preceeding page]. Map of the study areas along the east bank of the Apalachicola River, FL, with 20-m elevation contours. Blue dots indicate where iButtons were placed at the upslope limits of Small-leaf Spiderwort patches in 2 areas of Torreya State Park (boundary in green): the northern Aspalaga Tract and the central Park Elbow area, as well as in the Sweetwater West tract of The Nature Conservancy's Apalachicola Bluffs and Ravines Preserve (ABRP, boundaries in yellow). iButtons were also placed at Florida Torreya trees (red dots) that were particularly close to Small-leaf Spiderwort in ABRP. Diagonal striping marks areas below 16 m elevation on both sides of the Apalachicola River, which approximates the boundary of the floodplain in this reach. The Jim Woodruff Dam is shown at the north end of the map. Weather stations are marked with blue stars; note Wilma is to the south, shown on the Florida inset map. Greater spatial resolution for the Sweetwater West points is provided in Figure 5.

swamp areas, from TSP Park Elbow and Aspalaga Tract south to The Nature Conservancy (TNC) Sweetwater Tract. By the summer of 2015 these had expanded, and many more patches appeared throughout the floodplain (A. Schmidt, pers. comm.).

Small-leaf Spiderwort often forms dense patches of leafy stems within invaded areas in the Apalachicola floodplain, as it does in other areas where it has invaded (Kelly and Skipworth 1984, Standish et al. 2001). The current distribution of Small-leaf Spiderwort in this area appears to correspond to areas inundated during the highest water levels reached by the Apalachicola River during periods of high flow from the Jim Woodruff Dam. However, A. Schmidt (pers. comm.) observed patches of Small-leaf Spiderwort spreading vegetatively from the floodplain to slope forest in the Park Elbow area of TSP and the Sweetwater Tract of ABRP, including within 35 m of a Florida Torreya at the latter site.

Fluvial dynamics

Water level in the Apalachicola River and floodplain is driven primarily by discharge from the Jim Woodruff Dam (Fig. 1) on the Apalachicola River, which was completed in 1957 and is about 300 m south of that river's origin at the confluence of the Flint and Chattahoochee Rivers (Leitman et al. 1984, Smith et al. 2013). Typically, there is a major flood pulse in late winter or early spring, and a period of low flow in the fall (Smith et al. 2013).

I obtained data on dam discharge (Chattahoochee) and gage height at Blountstown (the point closest to the study area) from the US Geological Survey National Water Information System Web Interface (http://waterdata.usgs.gov/nwis). Gage height at Blountstown is available only from 12 October 2013, but correlates very strongly with gage height at Chattahoochee (Fig. 2), which is available from 10 October 2007.

Methods

Study species

Small-leaf Spiderwort is native to several provinces in northern Argentina, southeastern Brazil, southern Paraguay, and Uruguay (USDA 2017); these provinces span approximately 15–39° S latitude. This perennial herbaceous species has been planted as an ornamental groundcover in many countries and is now invasive in natural areas in New Zealand, Australia, Africa, southern Europe, and parts of the southern US (Butcher and Kelly 2011, Fowler et al. 2013, McMillan 1999, USDA 2017). It is listed as Category I (altering native plant communities) by the Florida Exotic Pest Plant Council. Although Small-leaf Spiderwort is a new invader to the east bank of the Apalachicola River, this species has been reported in several localities in north and central Florida, including Calhoun and Leon counties in the Panhandle (Seitz and Clark 2016). Godfrey and Wooten (1979:532) stated that it is sometimes very abundant, "to the virtual exclusion of native herbs," in bottomland and floodplain forests in north Florida.

This species has been well-studied in New Zealand forests, where it often forms a dense layer of up to 100% cover and 60 cm depth (Kelly and Skipworth 1984)

with up to 800 g m^{-2} dry biomass (Standish et al. 2001). New Zealand plots invaded by Small-leaf Spiderwort had lower species richness and abundance of native tree seedlings than uninvaded patches of the same forests (Kelly and Skipworth 1984, Standish et al. 2001). Schmitz et al. (1997) referred to a report of the species forming dense monocultures and apparently inhibiting native plants in North Florida hardwood forests, and Langeland et al. (2008) referred to an observation that Small-leaf Spiderwort smothers groundcover and tree seedlings in Florida. Competition experiments in Gainesville, FL, showed that Small-leaf Spiderwort reduced growth of the native *Oplismenus hirtellus* (L.) P. Beauv. (Bristle Basketgrass) (McMillan 1999). For this reason, there is concern that small individuals of the endangered endemic Florida Torreya will be negatively affected if dense patches of Small-leaf Spiderwort reach them.

Small-leaf Spiderwort has very small roots and grows best in moist soils with high nitrate concentration (Maule et al. 1995, Standish et al. 2001) and most poorly on rocky substrate (Smale and Gardner 1999 cited in Hill n.d.). Evidence that dry soil limits growth includes McMillan's (1999) observation that plants lost leaves during the April–July 1998 drought in mesic forest conditions in Gainesville, FL, but that plants regrew leaves and resumed growth when rains resumed.

This species provides a simple model-system for invasion dynamics because, despite substantial flower production, its invasive populations spread only from vegetative growth and water dispersal of vegetative fragments, at least in Florida (D. Gorchov, pers. observ.; McMillan 1999) and New Zealand (Esler 1978 cited in

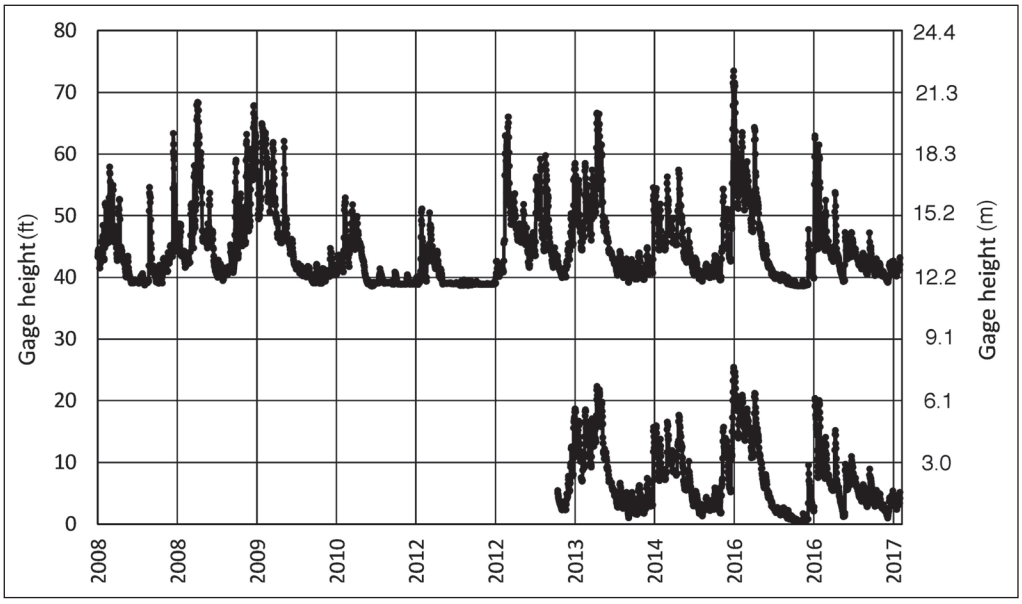

Figure 2. Gage height at Chattahoochee (upper trace) and Blountstown (lower trace) obtained from the US Geological Survey National Water Information System Web Interface (http://waterdata.usgs.gov/nwis). Blountstown is closer to the study area, but gage-height data are incomplete before 12 October 2013. Note the strong correlation in gage height between the 2 sites, and the lack of winter floods in 2010–2011 and 2011–2012.

Butcher and Kelly 2011, Esler 1988, Kelly and Skipworth 1984). McMillan (1999) speculates that Florida plants are sterile because the invasive populations are descendant from cultivars that are triploid in chromosome number. Plants of this species fragment easily and initiate new patches—even small fragments can root and establish new plants (Kelly and Skipworth 1984). Thus, within floodplains, new patches likely initiate from floodwater-dispersed fragments and subsequently grow vegetatively, whereas patches extend into uplands primarily by vegetative growth.

Vegetative growth of Small-leaf Spiderwort, however, is rapid when conditions are warm and wet. In New Zealand, horizontal shoots grew 0.2–0.3 cm per day in summer and 0.04–0.06 cm per day in winter (Maule et al. 1995), suggesting expansion of >60 cm/y is possible. This herb is shade tolerant, but growth is greater at high to moderate than at low levels of light (Kelly and Skipworth 1984, Maule et al. 1995).

Little is known about its invasion dynamics in upland areas. Based on the literature, Small-leaf Spiderwort can survive and spread in mesic habitats. For example, McMillan (1999) carried out experiments in dense populations in mesic hardwoods (hammocks) in and near Gainesville, FL. IFAS (2016) lists Small-leaf Spiderwort as invasive in North and Central Florida, specifying that it is known to occur in mesic uplands and floodplain wetlands in North Florida, and xeric uplands, mesic and wet flatwoods, and floodplain and basin wetlands in South Florida. However, the linear rate of vegetative spread is not known, nor is the dependence of this rate on temperature and topography.

Selection and mapping of study points

From February 2016 through August 2017, I documented the current upland limit of the distribution of Small-leaf Spiderwort in ABRP and TSP, quantified the rate of vegetative spread upslope, and related these parameters to topography and other field conditions. I walked the margin of the floodplain on the eastern side of the Apalachicola River in February–April 2016. Upon detection of Small-leaf Spiderwort patches that reached the swamp forest/slope boundary or extended to the slope, I marked a point at the upland edge of each patch with a stake flag and conduit (Figs. 1, 3). While core areas of these patches within the swamp forest often had 100% cover of Small-leaf Spiderwort, cover of this invasive near the marked points was much less, often about 10%. I added additional points in June, October, and December 2016. A. Schmidt georeferenced these points in the winter of 2016–2017 with a Trimble Geo 7X GPS receiver. I checked points quarterly to determine the extent of upslope growth (or occasionally retreat) of the Small-leaf Spiderwort patch. On 10 August 2017, I measured both the elevation of the initial point (above swamp-forest elevation) and the linear distance between the initial point and the swamp forest. On that date, I also located the upland limit of each surviving patch. I quantified upland vegetative-growth distance (hereafter, growth) as the distance between the original and final upland limits of the patch, measured perpendicular to the swamp edge. Annual vegetative growth is this distance multiplied by 12 and divided by the number of months between the first and last measurement.

Temperature

To record temperatures at these flagged points, as well as at trees of Florida Torreya closest to the invasion points, I used self-recording temperature data loggers (Thermochron iButton model DS1921G-F5 [hereafter, iButtons]; https://www.maximintegrated.com/en/products/comms/ibutton.html), which record to 0.5 °C accuracy. While iButtons have frequently been used in ecological studies, only 22% of studies used them to measure soil temperature (Terando et al. 2017). iButtons often overestimate daytime temperatures, particularly when not appropriately shielded from solar radiation, but they cause little bias in estimates of minimum temperatures, which usually occur at night (Terando et al. 2017). I programmed the iButtons to record temperature at 1-h intervals; at this frequency, each should have had sufficient memory to store data for 80 d. To prevent iButtons from being moved by small mammals or sheetflow, I put in a small (~3 cm x 3 cm) sleeve of fiberglass window screening that had been folded and stapled (Fig. 4), placed on the ground surface (soil or litter), and anchored to stake flags with a small wire each iButton. Fiberglass screening allowed water and heat to move in and out of sleeves more efficiently than did Coleman kerosene mantles and iButtons in the sleeves reached colder minima than those in mantles at the same location (Fig. 4). Nightly minimum temperatures recorded by iButtons in these sleeves were very similar but slightly lower than those logged by paired adjacent unenclosed iButtons placed on litter in an Ohio forest (regression of enclosed versus unenclosed nightly minima: $y = 1.08x - 1.65$, $R^2 = 0.89$, $n = 72$; 8 pairs x 9 consecutive nights 18–26 November 2017, at temperatures of -2.5

Figure 3. A Small-leaf Spiderwort patch at the edge of the floodplain. Orange flag and conduit in foreground mark upland edge of this patch. In the background is swamp forest with nearly complete cover of Small-leaf Spiderwort.

Figure 4. iButton in fiberglass mesh sleeve (gray) paired with another iButton in a Coleman kerosene-lantern mantle (white), both anchored to a stake flag marking the edge of a Small-leaf Spiderwort patch. Note the shoots of Small-leaf Spiderwort just above ground level, and the 5 anchoring pins surrounding the buttons to minimize small mammal access. Paired trials revealed that iButtons in fiberglass mesh sleeves reached lower nighttime temperatures than those in lantern mantles, so only those sleeves were used for this study.

to 6.5 °C, similar to the winter minima at the Florida study site). It is not clear whether the temperatures from enclosed or unenclosed iButtons more closely track the actual substrate temperature.

I placed landscape staples around each mesh sleeve to discourage access by small mammals (Fig. 4). Approximately once per month, I retrieved each ibutton, which I removed from the sleeve, wiped dry, placed in a 1-wire driver connected to a laptop computer to download data to a .csv file, and reset on a new mission. I calculated the daily minimum temperature for each site from these hourly records. Occasionally, iButtons failed to record, or terminated before recovery date, resulting in incomplete temperature records at some sites.

For all points that included iButton data for the coldest period (7–10 January 2017), I extracted the minimum detected temperature during the 2016–2017 winter. I obtained temperature data for the geographically closest weather station, at Bloxham, as well as the second closest, at Wilma (elevation = 15.2 m, 30.1694°N, 84.9344°W), from the Global Historical Climatology Network, accessed from http://www.ncdc.noaa.gov/cdo-web/search. Specifically, I used daily minimum temperature from 1 January 2005 through 30 April 2017, and extreme monthly minimum temperature for the same period.

To determine the relationship between temperatures measured with iButtons on the forest floor with temperatures at these nearby weather stations during the coldest events, I first determined the 15 coldest dates in the winter of 2016–2017 based on weather-station data. I then determined which points had daily minimum temperatures for at least 11 of these dates. Then, I correlated these minimum temperatures on these dates with temperatures on the same dates from Bloxham and Wilma, separately, for each point.

On 2 nights in January 2018, minimum temperatures were lower than in the winter of 2016–2017, providing an opportunity to further test the effects of cold on Small-leaf Spiderwort. On 19 January 2018, I checked 11 of the Small-leaf Spiderwort patches, and estimated the proportion of ramets <1 m from the marker that had been killed (wilted and dead) at each. Small-leaf Spiderwort has extremely small and shallow roots (Maule et al. 1995); thus, I infer that this tiny amount of tissue in the litter and humus layer associated with a dead ramet would not survive and generate new shoots. I used linear regression to test whether this mortality was dependent on elevation, distance from the swamp forest, or minimum temperature from the previous winter.

Results

The rapid expansion of Small-leaf Spiderwort in the Apalachicola River floodplain between 2013 and 2015 occurred in years that experienced a winter flood (gage height of >20 feet at Blountstown; Fig. 2). Such winter floods were common in the recent past, but did not occur in the winters of 2010–2011 and 2011–2012 (Fig. 2). Evidence that new patches are derived from water-dispersal of vegetative fragments includes my personal observation of live, unrooted fragments on the ground in this floodplain shortly after floodwaters receded in February 2016.

Of the 36 points marked at the upslope edge of Small-leaf Spiderwort patches in 2016, this species was no longer present at 2 points but survived at the other 34 by August 2017. For the inital points of the 34 surviving patches, the elevation relative to and distance from the swamp forest spanned from 0 m above and 0 m distant to 5.12 m above and 40 m away from the swamp forest (means = 1.1 m and 7.3 m, respectively; Fig. 5). One of the patches that died (Tra flu 1) was in the swamp

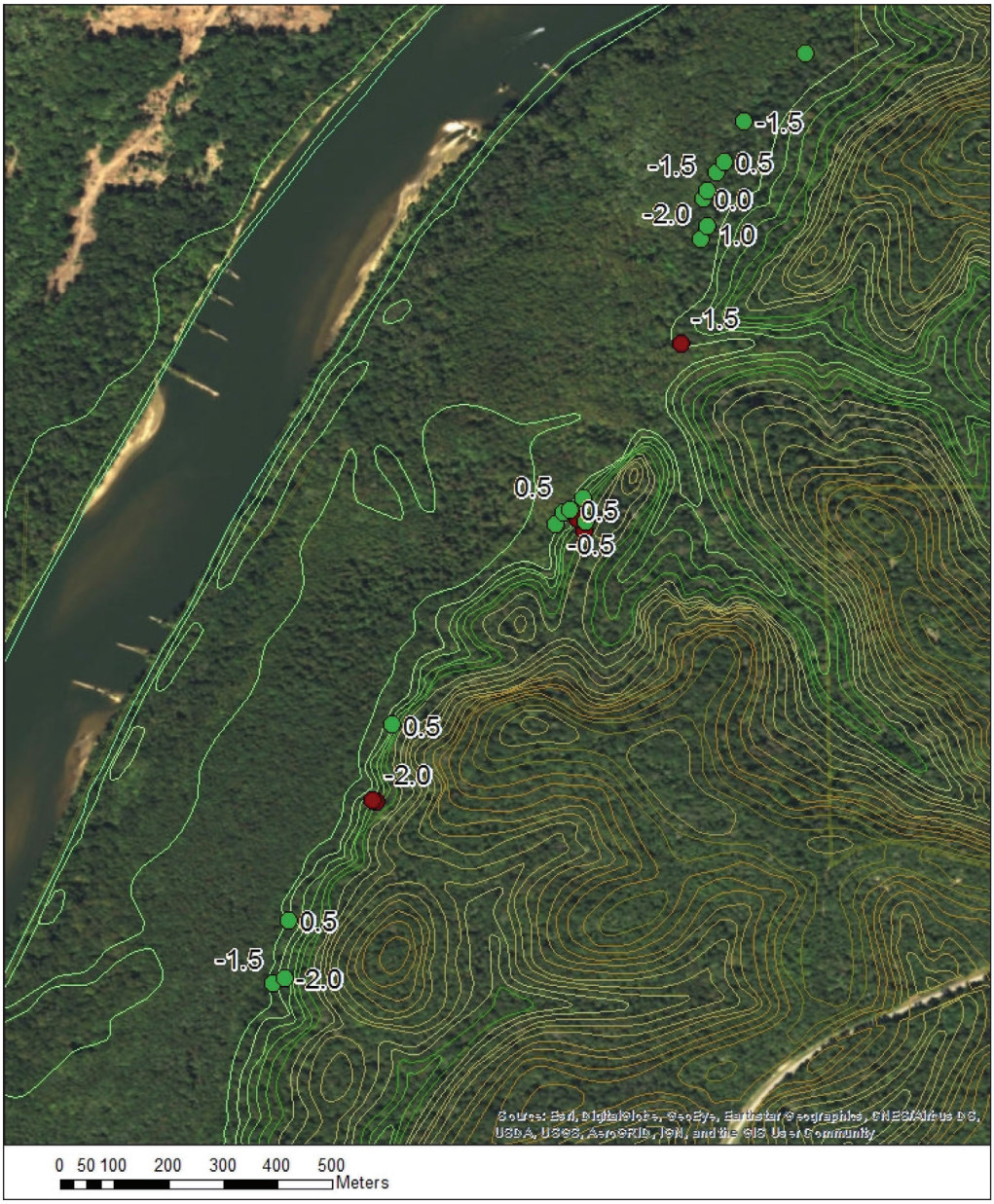

Figure 5. Minimum temperatures (°C) during the winter 2016–2017 for points at the upland edge of Small-leaf Spiderwort patches (green) and Florida Torreya trees (red) in the Sweetwater West Tract of Apalachicola Bluffs and Ravines Preserve, TNC.

forest, and mortality occurred after burial by sediment and litter in the 2016–2017 winter; the other (TNC 4) died between October 2016 and March 2017 and was at a moderate elevation (0.8 m) and distance fom the swamp forest (6 m).

For the surviving Small-leaf Spiderwort patches, vegetative expansion upslope over the study period varied from -1.5 m (a retreat, as the edge of the patch had retreated back toward the swamp) to 10.1 m, corresponding to a mean of 1.2 m per year (sd = 2.1, min–max = -0.1 to 12.2) (Table 1). Annual upslope growth of Small-leaf Spiderwort patches did not show a significant relationship with either relative elevation (regression $P = 0.50$, $R^2 = 0.01$, $n = 34$) or distance from the swamp forest ($P = 0.91$, $R^2 = 0.0004$).

Considering the available temperature records for 37 sites with iButtons, minima temperature recorded during the 2016/17 winter varied from -2 °C to 6 °C (mean = 1.5 °C, sd = 2.3 °C), compared to -5° C at Bloxham and -3.3° at Wilma. Ten of the marked points had iButton temperature records that spanned at least 11 of the 14 coldest days of the winter of 2016–2017 (Table 2). For each of these 10 points, the minimum daily temperatures on these cold dates correlated more strongly with Wilma than Bloxham, with $r \geq 0.8$ for 7 of these points (Table 1). Regressions of iButton minimum temperature with Wilma weather-station minima are shown for the site with highest correlation (TNC 7) and the site with the lowest (Tra flu 15) correlation (Fig. 6). The daily minimum temperature trace for TNC 7 closely tracked that for Wilma, from December 2016 to March 2017 (Fig. 7), but is consistently less cold on the coldest dates.

The coldest period during the winter (7–10 January) occurred when the river was at flood stage (evidenced by gage heights at Blountstown; Fig. 8), inundating the floodplain. Of the 36 marked points with iButtons in the floodplain and adjacent slope, 24 had complete records for 7–10 January 2017, including all 10 of the points with the most complete records (Table 2). Minimum temperatures for the 7–10 January 2017 period at these points varied from -2 °C to 10 °C (mean = 1.1 °C, sd = 2.9 °C), compared to -3.3 °C at Wilma. The points with the 2 highest temperatures during the 7–10 January cold spell, Tra flu 1 and Tra flu 15, were both in the swamp forest (relative elevation = 0 m), and therefore, submerged under floodwaters during most or all this period. Tra flu 15 was also 1 of the 10 Small-leaf Spiderwort points with a complete enough temperature record to explore the correlation with weather-station minima, and it had 1 of the 2 lowest correlations (Table 1). The point with the lowest correlation, TNC 4, was only 0.8 m above the swamp forest, and was also submerged during part of the flood.

Minimum temperatures recorded by iButtons at points in the floodplain and adjacent slope were negatively related to relative elevation ($y = -0.98x + 2.04$, $R^2 = 0.40$, $P = 0.0380$; Table 1); points at higher elevation experienced slightly colder minima. I detected a stronger negative relationship between minimum temperature and distance from the floodplain (Fig. 9); patches farther from the floodplain experienced colder minima. However, annual growth did not show a relationship with minimum temperature ($P = 0.68$, $R^2 = 0.01$; Table 1).

Table 1. Distance from the swamp forest and relative elevation above the swamp forest for points marking the initial upslope limit of Small-leaf Spiderwort patches in TSP (Tra flu) and TNC and for nearby Florida Torreya trees, annualized upslope growth of patches, minimum temperature (°C) during winter 2016–2017, proportion of ramets dead after January 2018 cold-weather event, and, for each of the 10 sites with the most complete iButton temperature records correlation coefficient of daily temperature with each of 2 closest weather stations, Bloxham and Wilma, for the coldest days. Correlation coefficients (r) ≥ 0.8 indicated by an asterisk (*). The variable most significantly related to minimum temperature was distance from the swamp forest, as illustrated in Figure 9.

Site	Distance (m)	Relative elevation (m)	Growth (m/y)	Min temp	% dead 2018	Bloxham r	Wilma r
Bloxham	-	-	-	-5.0	-	1.00	-
Wilma	-	-	-	-3.3	-	0.85*	1.00
Tra flu 1	0.0	0.0	-	5.5	-	-	
Tra flu 4	4.2	2.3	-0.1	1.5	-	-	-
Tra flu 5	3.3	1.1	0.7	2.5	-	-	-
Tra flu 6	5.0	1.3	0.4	4.0	-	-	-
Tra flu 7	5.6	1.3	0.4	3.0	-	-	-
Tra flu 9	2.8	0.5	1.1	-	-	-	-
Tra flu 10	40.0	0.8	1.1	-0.5	-	-	-
Tra flu 11	0.0	0.0	0.7	3.5	-	-	-
Tra flu 12	0.0	0.0	0.6	4.0	-	0.72	0.80*
Tra flu 14	0.0	0.0	0.9	4.5	-	-	-
Tra flu 15	0.0	0.0	2.0	5.0	-	0.35	0.33
Tra flu 16	8.1	0.3	1.0	2.0	-	0.70	0.86*
Tra flu 17	10.5	3.5	0.3	1.0	-	-	-
Tra flu 19	2.5	0.7	1.7	-	-	-	-
TNC 1	1.6	0.4	0.8	-	-	-	-
TNC 2	0.0	0.0	2.6	-1.5	0	0.68	0.86*
TNC 3	15.0	1.4	0.9	-2.0	25	0.64	0.84*
TNC 4	6.0	0.8	-	0.5	-	-0.02	0.43
TNC 5	4.8	1.0	0.0	-0.5	0	0.70	0.85*
TNC 6	6.7	1.6	0.1	0.5	0	0.75	0.86*
TNC 7	4.7	1.1	0.1	-0.5	5	0.78	0.94*
TNC 8	2.7	1.0	0.0	-	0	-	-
TNC 9	4.2	0.2	2.7	1.0	-	-	-
TNC 10	7.2	2.1	1.4	0.0	-	-	-
TNC 11	9.3	2.3	0.7	-1.5	-	-	-
TNC 12	8.1	2.1	1.2	-	-	-	-
TNC 15	1.5	0.3	0.2	0.5	5	0.35	0.68
TNC 16	4.2	0.4	0.5	-	25	-	-
TNC 17	8.2	0.8	2.4	-	10	-	-
TNC 18	3.8	1.3	1.1	-	0	-	-
TNC 20	18.2	2.7	0.6	0.5	-	-	-
TNC 21	10.2	1.4	0.4	-1.5	-	-	-
TNC 22	12.0	1.0	12.2	-2.0	-	-	-
TNC 23	37.8	5.1	0.3	-	15	-	-
Torreya 1000	8.3	2.9	-	-	-	-	-
Torreya 1002	4.0	0.9	-	-2.0	-	-	-
Torreya 1007	51.2	7.3	-	-	-	-	
Torreya 1008	24.3	3.7	-	-	-	-	-
Torreya 1096	32.0	2.2	-	-1.5	-	-	

Table 2. Minimum temperatures (°C) on the coldest days of the 2016–2017 winter from 2 weather stations (Bloxham, Wilma) and from iButtons at the 10 Small-leaf Spiderwort locations with the most complete records. The last column is the minimum of the listed temperatures at the point. Regressions of temperatures at points with the highest (TNC 7) and lowest (Tra flu 15) associations with Wilma temperatures are graphed in Fig. 6.

	Date															
Location	11/20	11/21	11/22	11/27	12/9	12/10	12/30	12/31	1/7	1/8	1/9	1/10	1/30	3/15	3/16	Minimum
Bloxham	0.0	-2.2	-1.1	0.0	-0.6	-1.7	-1.7	-1.7	-1.1	-3.9	-5.0	-1.1	-1.1	-1.7	-2.2	-5.0
Wilma	0.0	-1.7	-0.6	1.7	0.0	-1.7	0.0	0.0	-0.6	-3.3	-3.3	0.6	1.1	0.6	-1.7	-3.3
Tra flu12	6.5	4.5	6.0	7.0	-	-	7.5	7.5	7.0	4.5	4.0	6.5	6.5	6.0	4.0	4.0
Tra flu 15	7.0	5.0	5.5	7.5	-	-	8.5	8.5	12.5	6.5	5.5	7.5	-	6.0	6.0	5.0
Tra flu 16	5.0	3.0	4.5	6.5	-	-	6.0	5.5	3.5	2.0	2.5	4.5	6.5	4.0	2.0	2.0
TNC 2	-	-	-	-	3.5	1.0	4.0	4.0	0.5	-1.5	-1.0	2.5	5.5	5.0	3.5	-1.5
TNC 3	-	-	-	-	2.5	0.5	3.5	3.0	0.5	-2.0	-1.0	2.5	5.0	5.5	3.5	-2.0
TNC 4	-	-	-	-	2.5	0.5	6.0	5.5	4.5	4.0	5.5	7.0	6.5	6.0	3.5	0.5
TNC 5	-	-	-	-	4.0	2.5	4.5	5.0	1.0	-0.5	-0.5	4.0	4.5	6.5	3.5	-0.5
TNC 6	-	-	-	-	5.0	2.5	5.5	5.5	2.5	0.5	0.5	4.0	4.5	5.5	4.0	0.5
TNC 7	-	-	-	-	4.0	1.5	3.5	3.5	1.5	-0.5	0.0	4.5	3.5	4.5	1.5	-0.5
TNC 15	-	-	-	-	3.0	0.5	3.5	3.0	2.5	1.5	2.5	5.0	6.0	6.5	4.5	0.5

Given the difference of 1.3 °C between the minimum at the Wilma weather station and the coldest of the marked points in and near the Apalachicola River floodplain, and the LT_{50} of -4.2 °C reported for Small-leaf Spiderwort (Bannister 1986), I estimate that a Wilma weather station temperature of -5.5 °C or lower sustained over 8 h would be necessary for temperatures to be cold enough in the floodplain to kill half of the Small-leaf Spiderwort ramets. Winter (November–March) minimum temperatures at Wilma varied from -7.8 °C to -2.8 °C from 2005–2006 to 2016–2017 (mean = -5.5 °C, sd = 1.7, n = 12). Winter minima were -5.5 °C or lower in Wilma in 8 of the past 10 winters (Fig. 10). However, hourly data were not available, so it is not clear in which winters such cold temperatures were maintained for >8 hours.

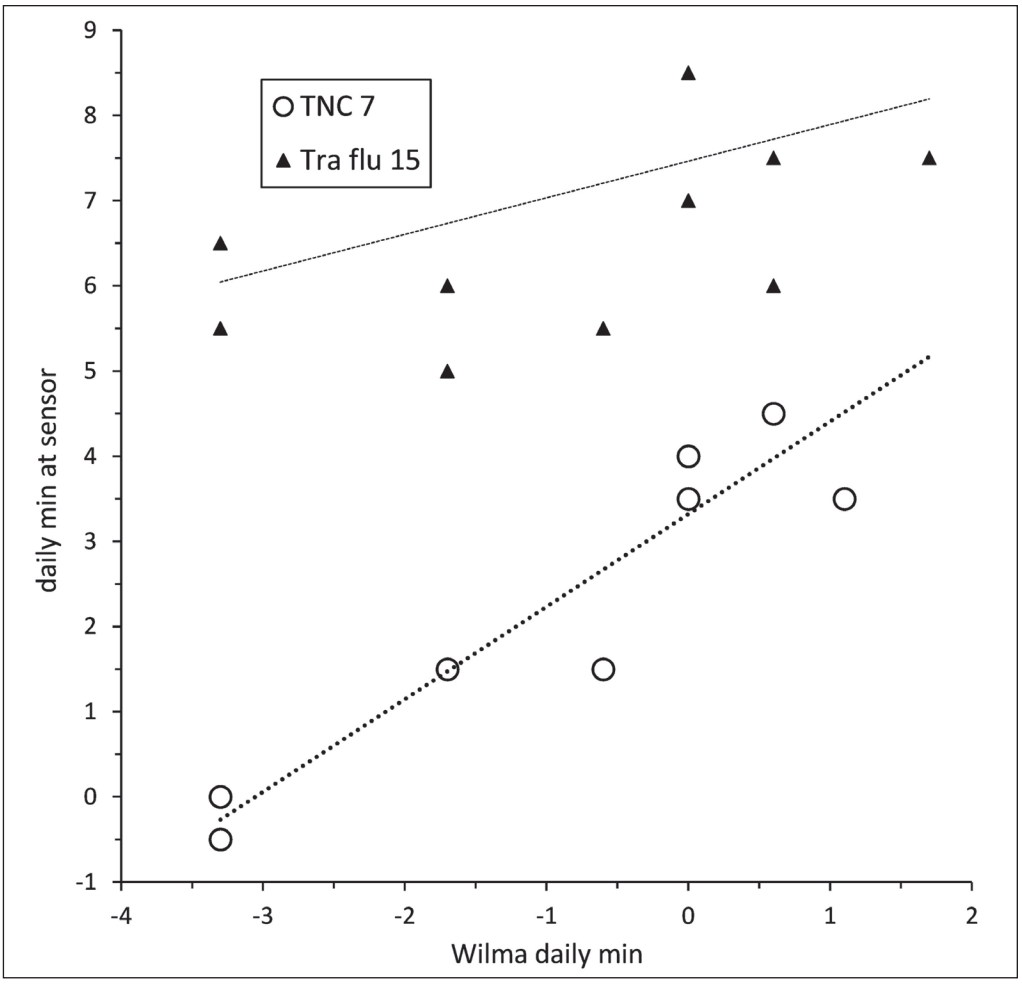

Figure 6. Minimum temperatures at Wilma weather station and 2 flagged points at the edge of the Small-leaf Spiderwort invasion, for 11 of the 15 coldest dates in the winter of 2016–2017. TNC 7 was the site with the highest correlation with Wilma, and Tra flu 15 was the site with the lowest (See Table 1). Linear regression equation for TNC 7: $y = 1.0875x + 3.3205$, $R^2 = 0.89$; for TNC 4: $y = 0.4296x + 7.4638$, $R^2 = 0.11$.

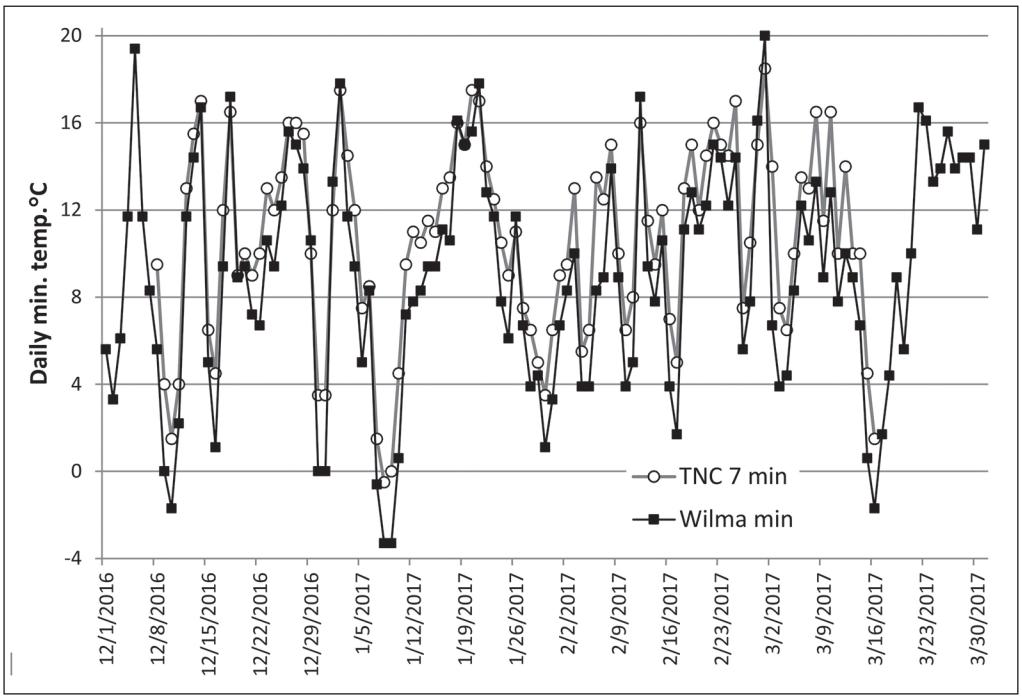

Figure 7. Daily minimum temperature at Wilma weather station and iButton placed at marker TNC 7 along edge of Small-leaf Spiderwort invasion in Apalachicola River floodplain. For the 10 coldest dates during the period with iButton records (8 December 2016–16 March 2017), the correlation between temperatures in the 2 sites is shown in Figure 6.

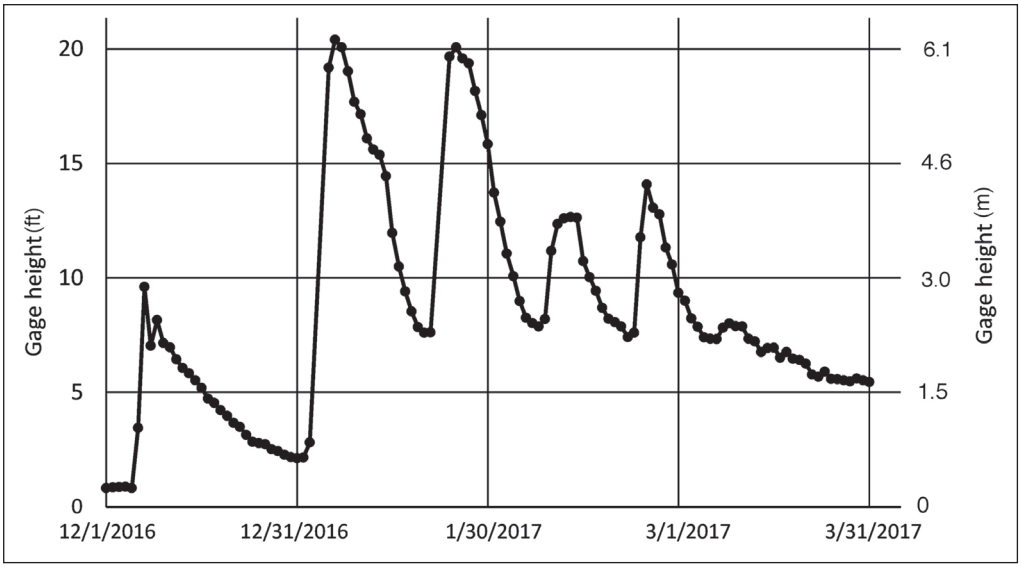

Figure 8. Gage height at Blountstown from 1 December 2016 through 31 March 2017, showing flood stage (5.18 m [17 ft]) during the coldest period (8–9 January 2017) that winter. Downloaded from https://nwis.waterdata.usgs.gov/fl/nwis/uv/?site_no=02358700&agency_cd=USGS&amp on 12 December 2017.

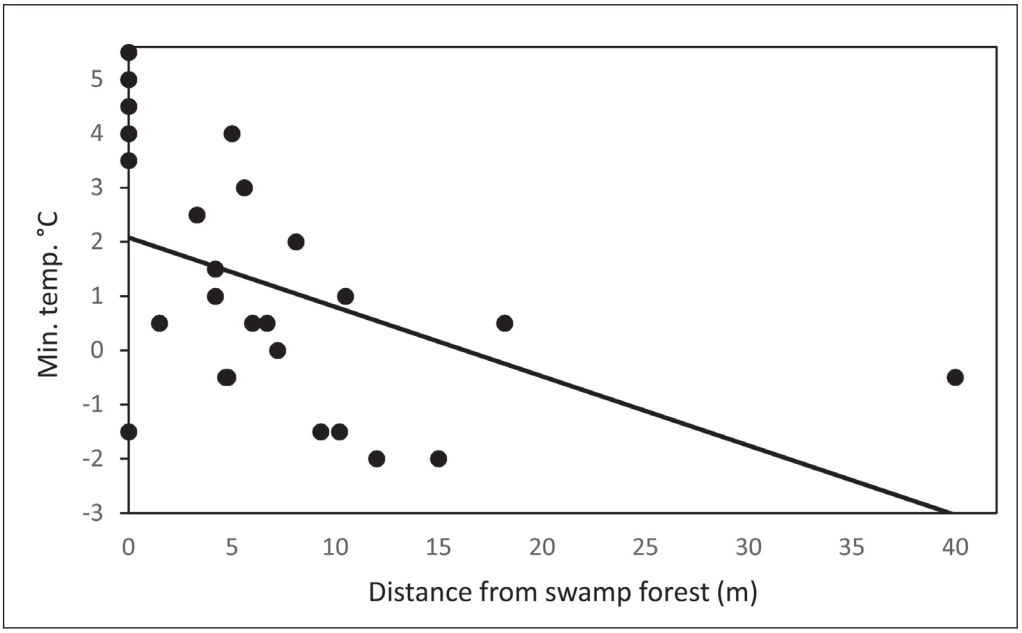

Figure 9. Minimum temperature during 2016–2017 winter as recorded by iButtons regressed on distance from the swamp forest. Distance to the swamp forest was the shortest distance between the initial upslope boundary and the level ground of the swamp forest. Regression equation $y = -0.12x + 1.88$, $R^2 = 0.22$, $P = 0.0128$. Data in Table 1.

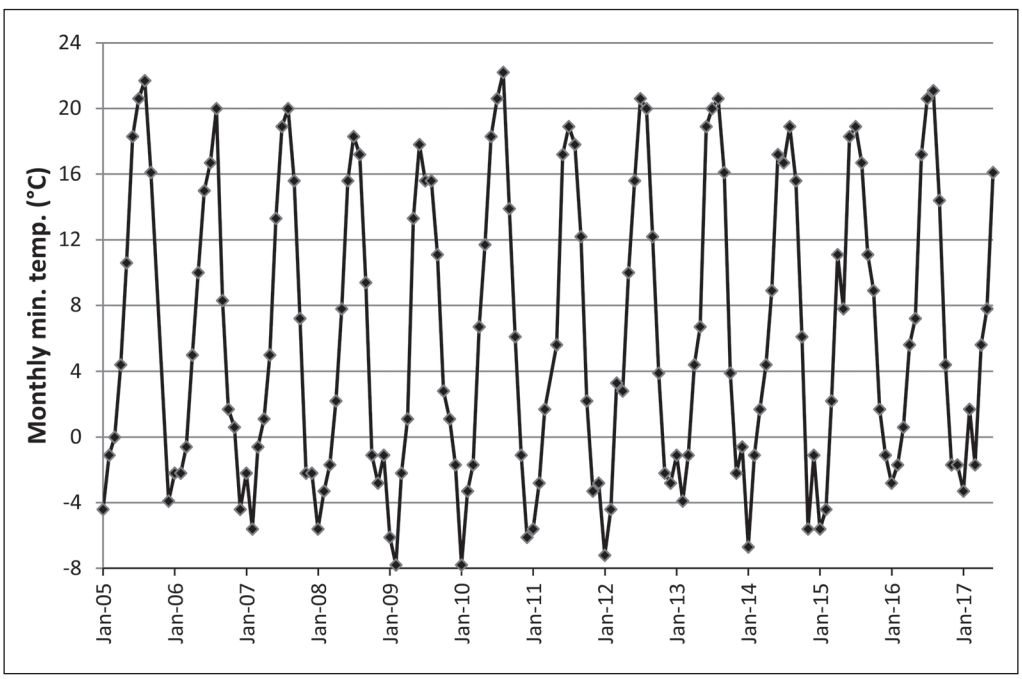

Figure 10. Monthly extreme minimum each month at the Wilma weather station from January 2005 through June 2017.

Florida Torreya trees

To assess the potential for Small-leaf Spiderwort to impact trees of the endangered Florida Torreya, I noted the locations and sizes of trees closest to invasive patches and the temperature minima at these points. Five Florida Torreya trees occurred on slopes near Small-leaf Spiderwort patches; the closest was only 2.7 m from Small-leaf Spiderwort by March 2017. These trees varied from 0.9 m relative elevation and 4 m from the swamp forest to 7.3 m elevation and 51.2 m from the swamp forest. All trees were small, varying from 0.7 m to 3.0 m (mean = 1.3 m) in height and 1 cm to 5 cm (mean = 2.8 cm) in basal diameter. Of the 24 points with complete iButton temperature records during the 7–10 January cold spell, 2 were at the base of Florida Torreya trees, and these had minima of -1.5 °C and -2.0 °C (Table 1, Fig. 5).

Effect of cold temperature events in January 2018

On 4 January 2018, the minimum temperature at Wilma was -5.6 °C, and on 18 January 2018 it was -6.7 °C—much colder than the -3.3 °C minimum from the previous winter. This temperature was sufficient to kill some Small-leaf Spiderwort, with dead ramets apparent in some slope patches but minimal mortality within the swamp forest. I checked 11 of the marked points, and mortality <1 m from the marker was 0–25% (median = 5%, mean = 8%). The proportion of dead Small-leaf Spiderwort was not related to elevation (R^2 = 0.04, P = 0.53), and, although mortality tended to be greater farther from the swamp forest, the regression was not significant (R^2 = 0.20, P = 0.17). Mortality was highest (25%) at the point that had reached the coldest temperatures the previous winter (TNC 3; -2.0 °C), but because only 6 of the 11 points were ones with temperature data from the previous winter, the regression was inconclusive ($y = -5.68x + 2.52$, R^2 = 0.36, P = 0.21).

Discussion

The appearance and rapid expansion of Small-leaf Spiderwort in the floodplain of the Apalachicola River from spring 2013 through summer 2015 was likely due to winter floods dispersing vegetative fragments. Floods occur during most winters, and Small-leaf Spiderwort is now abundant in numerous places in the floodplain; thus, we can anticipate annual establishment of new patches within the floodplain nearly every year. A few of these patches will likely disappear, however, due to deposition of sediment and debris, as was observed at some marked points in this study. Eradication of Small-leaf Spiderwort from the entire floodplain would be onerous, but any attempt should start with the most upstream patches and proceed downstream, since there is little risk of propagules moving against the current to recolonize upstream patches.

Outside of the floodplain, invasion of Small-leaf Spiderwort is generally limited to vegetative growth of established patches because of the absence of seed production and dispersal. This study showed that the average rate of extension upslope is 1.2 m/y, a distance greater than the 0.6–0.7 m/y reported in a forested site on the South Island of New Zealand (Maule et al. 1995). This expansion rate indicates

that periodic inspections of the boundary between the floodplain and the slope, and manual removal or targeted herbicide application on Small-leaf Spiderwort patches on slopes, will likely be needed to prevent invasion of slopes and other upland areas.

Small-leaf Spiderwort has extremely shallow roots; thus, I hypothesized that it would be killed if the soil-surface temperature reached -4.2 °C, the LT_{50} reported by Bannister (1986). During the winter of 2016–2017, soil-surface temperatures at the upslope boundary of this Small-leaf Spiderwort invasion got no colder -2.0 °C, and there was no evidence that cold temperatures killed any patches.

I can, however, predict the frequency of soil-surface temperatures reaching -4.2 °C, based on the strong correlation between temperatures documented by iButtons in the study area and those at nearby weather stations during the coldest nights of winter 2016–2017. Small-leaf Spiderwort patches experienced minima that were ≥1.3 °C warmer than the Wilma weather station; thus, I predict that minima of ≤-5.5 °C at Wilma would result in mortality of Small-leaf Spiderwort on the slopes of the Apalachicola River floodplain, although the temperature might need to stay that low for 8 h. Temperatures this low have occurred during 8 of the past 12 winters, suggesting that, in most years, there should be mortality of Small-leaf Spiderwort where it is not beneath floodwaters. Temperatures <-5.5 °C did occur at Wilma on 4 and 18 January 2018, and following these events (19 January) was the first time I observed ramets of Small-leaf Spiderwort killed by freezing. However, only about 8% of ramets near marked points were killed, likely because the cold temperatures were not sustained for 8 h. Although I did not have iButtons in the field in 2018, there was a trend for greater mortality at points that had colder minima the previous winter, supporting the inference that sites that get colder (e.g., due to topography) have higher mortality. Patches of Small-leaf Spiderwort should be monitored immediately after more sustained cold events (e.g., 8 h at ≤-5.5 °C at Wilma) to determine which patches are completely killed and whether this correlates with elevation or distance from the swamp forest.

My finding that minimum temperatures were lower at points higher in relative elevation and farther from the swamp forest (Fig. 9) indicates that the patches farthest from the floodplain will be killed more frequently when cold temperatures do occur. At the lowest elevations within the swamp forest, patches will typically be below floodwaters during cold periods (Fig. 8) and therefore insulated from lethal cold, although sediment and debris deposition will kill some patches in these areas. Thus, within the floodplain, the spatial pattern of invasion should be dynamic, whereas the upslope invasion will be slow and perhaps reversed during the coldest winters. Following the cold events of January 2018, there was a trend for greater mortality at points more distant from the swamp forest. However, during the winter of 2016–2017 there was no evidence that vegetative growth was slower at these cooler, higher-elevation points on the slopes. Other factors that could explain differences in growth among patches include edaphic factors (given McMillan's [1999] observation that growth halts when soil dries) and light (e.g., treefall gaps) (Kelly and Skipworth 1984).

Some of the Small-leaf Spiderwort patches were close to individual Florida Torreya trees—as close as 2.7 m in 1 case. With its average linear growth of 1.2 m/y,

Small-leaf Spiderwort should reach this tree in about 2 y and other Florida Torreya trees trees in the near future, raising concerns about competitive impacts, based on the small size of these trees and documented effects of Small-leaf Spiderwort on native tree seedlings in New Zealand (Kelly and Skipworth 1984, Standish et al. 2001). The Small-leaf Spiderwort patches close to these Florida Torreya trees would be among the most likely to be killed by cold events, given they occur at the highest elevations and greatest distances from the swamp forest of the invaded space. However, the modest mortality resulting from the January 2018 cold event suggests that managers cannot rely on these events to prevent Small-leaf Spiderwort from impacting this endangered tree. Simple raking and removal of Small-leaf Spiderwort ramets within 5 m of Florida Torreya trees every 4 y should suffice to prevent encroachment. More broadly, management should focus on the riparian areas along streams that dissect the slopes and enter the floodplain, as their low-elevation and hydric conditions indicate they will rarely be cold or dry enough to halt Small-leaf Spiderwort growth.

The stronger correlation of floodplain and slope soil-surface temperatures with the Wilma weather station than with the closer Bloxham station cannot be explained by similarity in topographic position. Bloxham is actually closer to the floodplain of the Apalachicola River than is Wilma (1.1 km vs. 5.5 km)..

The fact that the rapid expansion of Small-leaf Spiderwort in the Apalachicola floodplain began in the spring of 2012 might be explained by lack of extreme cold events since that time; the minimum at Wilma has not dropped to ≤-7 °C since the winter of 2011–2012 (Fig. 10). I hypothesize that the cold minimum temperatures in the winters of 2008–2009 through 2011–2012 were sufficient to kill many ramets, impeding any invasion. The lack of winter floods in 2010–2011 and 2011–2012 (Fig. 2) likely prevented water dispersal of fragments within the floodplain and also resulted in a greater exposed area that was not insulated by floodwaters from the cold temperatures.

Winter temperatures are expected to rise in many parts of the US over the next century due to high greenhouse-gas concentrations in the atmosphere, with expectations for range expansion of many invasive plant species (Bradley et al. 2010). For the Florida Panhandle, climate models indicate that under a high-emissions scenario, mean winter temperature in 2041–2070 will be 2.5–2.8 °C (4.5–5 °F) higher than during 1971–2000, with a decrease in the number of days below 0 °C (32 °F) (Kunkel et al. 2013). This projected warming suggests that the potential for cold winter-temperature events to reverse the invasion of Small-leaf Spiderwort and other cold-sensitive plants will be reduced.

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Literature Cited

Bannister, P. 1986. Winter frost-resistance of leaves of some plants growing in Dunedin, New Zealand, in winter 1985. New Zealand Journal of Botany 24:505–507.

Blaustein, R.J. 2008. Biodiversity hotspot: The Florida Panhandle. BioScience 58:784–790.

Bradley, B.A., D.S. Wilcove, and M. Oppenheimer. 2010. Climate change increases risk of plant invasion in the Eastern United States. Biological Invasions 12:1855–1872.

Brown, K., and D. Brown. 2015. Control to eradication of *Tradescantia fluminensis* on Stephens Island (Takapourewa): The importance of systematic and persistent effort. DOC Research and Development Series 346. Department of Conservation, Wellington. 11 pp. Available online at http://www.doc.govt.nz/Documents/science–and–technical/drds346entire.pdf. Accessed 28 January 2016.

Butcher, E.R., and D. Kelly 2011. Physical and anthropogenic factors predict distribution of the invasive weed *Tradescantia fluminensis*. Austral Ecology 36:621–627.

Darst, M.R., and H.M. Light. 2008. Drier forest composition associated with hydrologic change in the Apalachicola River floodplain, Florida. US Geological Survey Scientific Investigations Report 2008-5062. US Government Printing Office, Washington, DC. 81 pp.

Esler, A.E. 1988. The naturalization of plants in urban Auckland, New Zealand 5. Success of the alien species. New Zealand Journal of Botany 26:565–584.

Espinar, J.L., R. Díaz-Delgado, M.A. Bravo-Utrera, and M. Vilà. 2015. Linking *Azolla filiculoides* invasion to increased winter temperatures in the Doñana marshland (SW Spain). Aquatic Invasions 10:17–24.

Florida Natural Areas Inventory (FNAI). 2010. Guide to the natural communities of Florida, 2010 Edition. Available online at www.fnai.org. Accessed 23 October 2017.

Fowler, S.V., R. Barreto, S. Dodd, D.M. Macedo, Q. Paynter, J.H. Pedrosa-Macedo, O.L. Pereira, P. Peterson, L. Smith, N. Waipara, C.J. Winks, and G. Forrester. 2013. *Tradescantia fluminensis*, an exotic weed affecting native forest regeneration in New Zealand: Ecological surveys, safety tests, and releases of four biocontrol agents from Brazil. Biological Control 64:323–329.

Godfrey, R.K., and J.W. Wooten. 1979. Aquatic and Wetland Plants of Southeastern United States. Monocotyledons. The University of Georgia Press, Athens, GA. 712 pp.

Hill, R. n.d. Notes on the ecology of *Tradescantia fluminensis* and a biological control program for its management. Richard Hill and Associates, Private Bag 4704, Christchurch. Available online at https://www.landcareresearch.co.nz/__data/assets/pdf_file/0003/39207/tradescantia_pest_status.pdf. Accessed 30 June 2015.

Institute of Food and Agricultural Sciences (IFAS), University of Florida. 2016. Conclusions from the IFAS Assessment of Non-native Plants in Florida's Natural Areas. *Tradescantia fluminensis.* Available online at http://assessment.ifas.ufl.edu/assessments/tradescantia_fluminensis/. Accessed 4 May 2016.

Kelly, D., and J.P. Skipworth. 1984. *Tradescantia fluminensis* in a Manawatu (New Zealand) forest. 1. Growth and effects on regeneration. New Zealand Journal of Botany 22:393–397.

Kunkel, K.E, L.E. Stevens, S.E. Stevens, L. Sun, E. Janssen, D. Wuebbles, C.E. Konrad II, C.M. Fuhrman, B.D. Keim, M.C. Kruk, A. Billet, H. Needham, M. Schafer, and J.G. Dobson. 2013. Regional Climate Trends and Scenarios for the US National Climate Assessment. Part 2. Climate of the Southeast US, NOAA Technical Report NESDIS 142-2, Washington, DC. 94 pp.

Langeland, K.A., H.M. Cherry, C.M. McCormick, and K.A. Craddock Burks. 2008. Identification and biology of nonnative plants in Florida's natural areas. SP 257. University of Florida Institute of Food and Agricultural Sciences, Gainesville, FL. 165 pp.

Leitman, H.M., J.E. Sohm, and M.A. Franklin. 1984. Wetland hydrology and tree distribution of the Apalachicola River flood plain, Florida. US Geological Survey Water-Supply Paper 2196-A, Alexandria, VA. 52 pp.

Maule, H.G., M. Andrew, J.D. Morton, A.V. Jones, and G.T. Daly. 1995. Sun–shade acclimation and nitrogen nutrition of *Tradescantia fluminensis,* a problem weed in New Zealand native forest remnants. New Zealand Journal of Ecology 19:35–46.

McCluggage, T. 1998. Herbicide trials on *Tradescantia fluminensis*. Conservation Advisory Science Notes 180. Department of Conservation. Available online at http://www.conservation.gen.nz/documents/science–and–technical/casn180.pdf. Accessed 28 January 2016.

McMillan, B.A. 1999. *Tradescantia fluminensis*: An exotic invasive species in Florida's mesic hardwood forests. M.Sc. Thesis. University of Florida, Gainesville, FL. 101 pp.

Merow, C., N. LaFleur, J.A. Silander Jr., A.M. Wilson, and M. Rubega. 2011. Developing dynamic mechanistic species distribution models: Predicting bird-mediated spread of invasive plants across northeastern North America. American Naturalist 178:30–43.

Paul, K.I., P.J. Polglase, P.J. Smethurst, A.M. O'Connell, C.J. Carlyle, P.K. Khanna. 2004. Soil temperature under forests: A simple model for predicting soil temperature under a range of forest types. Agricultural and Forest Meteorology 121:167–182.

Potter, K.A, H.A. Woods, and S. Pincebourde. 2013. Microclimate challenges in global change biology. Global Change Biology 19:2932–2939.

Schmitz, D.C., D. Simberloff, R.H. Hofstetter, W. Haller, and D. Sutton. 1997. The ecological impact of nonindigenous plants. Pp. 39–61, *In* D. Simberloff, D.C. Schmitz, and T.C. Brown (Eds.) Strangers in Paradise: Impact and Management of Nonindigenous Species in Florida. Island Press, Washington, DC. 467 pp.

Schwartz, M.W., S.M. Hermann, and P.J. van Mantgem. 2000. Estimating the magnitude of decline of the Florida Torreya (*Torreya taxifolia* Arn.). Biological Conservation 95:77–84.

Sears M.W., E. Raskin, and M.J. Angilletta Jr. 2011. The world is not flat: Defining relevant thermal landscapes in the context of climate change. Integrative and Comparative Biology 51:666–675.

Seitz, J.C., and M.W. Clark. 2016. Identification, biology, and control of Small-leaf Spiderwort (*Tradescantia fluminensis*): A widely introduced invasive plant. Document SL428. Department of Soil and Water Science, UF/IFAS Extention. Available online at https://edis.ifas.ufl.edu/ss652. Accessed 3 May 2018.

Smith, M.C., J.A. Stallins, J.T. Maxwell, and C. Van Dyke. 2013. Hydrological shifts and tree-growth responses to river modification along the Apalachicola River, Florida. Physical Geography 34:491–511.

Spector, T., R. Determann, and M. Gardner. 2011. *Torreya taxifolia*. The IUCN Red List of Threatened Species 2011: e.T30968A9585489. Available online at http://dx.doi.org/10.2305/IUCN.UK.2011–2.RLTS.T30968A9585489.en. Accessed 21 February 2016.

Standish, R.J. 2002. Experimenting with methods to control *Tradescantia fluminensis,* an invasive weed of native forest remnants in New Zealand. New Zealand Journal of Ecology 26:161–170.

Standish, R.J., A.W. Robertson, and P.A. Williams. 2001. The impact of an invasive weed, *Tradescantia fluminensis*, on native forest regeneration. Journal of Applied Ecology 38:1253–1263.

Terando, A.J., E. Youngsteadt, E.K. Meineke, and S.G. Prado. 2017. Ad hoc instrumentation methods in ecological studies produce highly biased temperature measurements. Ecology and Evolution 7:9890–9904.

US Department of Agriculture (USDA). 2017. ARS, National Genetic Resources Program. Germplasm Resources Information Network–(GRIN) [Online Database]. National Germplasm Resources. Laboratory, Beltsville, MD. Available online at http:/ /www.arsgrin.gov/. Accessed 23 October 2017.

US Fish and Wildlife Service (USFWS). 2009 *Torreya taxifolia* Florida torreya 5-Year review: Summary and evaluation. 25 pp. Available online at https://ecos.fws.gov/docs/five_year_review/doc3258.pdf. Accessed 25 January 2016.