Dynamics of an Unprecedented Outbreak

of Two Native Moth Species, *Cissusa spadix* and *Phoberia atomaris* (Lepidoptera: Noctuidae), on Oak Trees (*Quercus* spp.) in the Southeastern United States

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Outbreaks of native herbivorous insect species are often spectacular and extensive, and persist for a short term in forest ecosystems (Wallner 1987). Such outbreaks can be either cyclical, when they occur at regular time intervals, or acyclical, when they occur at irregular intervals (Wallner 1987). Forest insects known to outbreak, such as the southern pine beetle, *Dendroctonus frontalis* Zimmerman (Coleoptera: Curculionidae: Scolytinae), forest tent caterpillar, *Malacosoma disstria* Hübner (Lepidoptera: Lasiocampidae), western spruce budworm, *Christoneura occidentalis* Freeman (Lepidoptera: Tortricidae), and Pandora moth, *Coloradia pandora* (Blake) (Lepidoptera: Saturniidae), are well studied in terms of their life history, ecological and economic impacts, and management practices (Speer and Holmes 2004, Pye et al. 2005, Azuma and Overhulser 2008, Man and Rice 2010). The mountain pine beetle, which is the most prominent outbreak herbivore in North America, has caused millions of hectares of tree mortality in the past several years alone (Man 2012). As these species have "normative outbreaks," they are considered important natural disturbance agents that may retrigger forest succession (Mattson 1996, Raffa et al. 2008). In contrast to these outbreak insect species, herbivorous insects that historically do not outbreak are largely ignored because they have rarely caused significant forest damage. Hence, when outbreaks of such native "innocuous species" occur, they are impossible to predict, which allows little time for management activities. Nevertheless, the lack of treatment of native herbivore outbreaks may result in significant economic damage, alterations of ecological processes, and changes in biotic successional pathways.

Within the last 2–3 decades, there have been growing numbers of new emergent native pests on forest and shade trees in North America, with major implications for tree and forest health. Examples include the red oak borer, *Enaphalodes rufulus* (Haldeman) (Coleoptera: Cerambycidae), which caused widespread mortality of mature oak trees (*Quercus* spp.) in Arkansas during the 2000s (Stephen et al. 2001, Riggins et al. 2009); the Bruce spanworm, *Operophtera bruceata* (Hulst) (Lepidoptera: Geometridae), which defoliated thousands of hectares of hardwood timber in northern Canada during the last few years (http://www.emr.gov.yk.ca/forestry/pdf/forest_health5.pdf); the pine looper, *Phaeoura mexicanaria* (Grote), which defoliated ponderosa pine (*Pinus ponderosa* Laws.) in eastern Montana in the 1970s (Dewey et al. 1974); and the elm spanworm, *Ennomos subsignarius* Hübner (Lepidoptera:

Geometridae), which caused heavy defoliation on several urban tree species in Newfoundland (Ryall 2010). In many instances, repeated defoliation events by some of these species acted as predisposing factors that in turn led to outbreaks of bark beetles and, eventually, tree dieback and mortality (Dewey et al. 1974, Raffa et al. 2008).

As forest managers and researchers appear to be dealing with a greater incidence of novel outbreaks of native forest insects in North America, the two questions most frequently asked are why are these species suddenly increasing dramatically in numbers, and is this a new trend toward increases in pestiferous load on North American trees? The underlying causes of these insect outbreaks can be both abiotic (e.g., temperature and precipitation patterns) and biotic (e.g., host defensive chemicals, predators, and parasitoids), and whether the herbivores are released from environmental, bottom-up, and/or top-down factors (Dwyer et al. 2004, Raimondo et al. 2004). For example, in the case of red oak borer, drought, tree age, and overstocking of trees were identified as major factors that increased host susceptibility to insect outbreaks (Haavik et al. 2012). For the Bruce spanworm, it is hypothesized that warm and dry spring weather resulted in less larval mortality, and hence a greater number of adult moths (http://www.emr.gov.yk.ca/forestry/pdf/forest_health5.pdf). The mountain pine beetle outbreak, which spans thousands of hectares in western North America, is linked directly to warmer winter conditions resulting in greater larval survival, along with presence of overmature pine trees as suitable hosts on the landscape (Safranyik and Wilson 2006, Raffa et al. 2008). In fact, the mountain pine beetle has crossed the Rocky Mountain barrier from British Columbia into Alberta, and has come into contact with novel pine hosts in boreal Canada, causing concerns for other pine forests in eastern North America (Cullingham et al. 2011, de la Giroday et al. 2012). Overall, there appears to be an emerging consensus that certain native forest insect species may at least partially benefit from the current climatic changes in temperature and precipitation patterns, perhaps leading to new emergent threats to forest ecosystems (Ayres and Lombardero 2000, Bale et al. 2002).

In this study, we document a spectacular, unprecedented, and concurrent outbreak of two native moth species during 2010–2012 on oak trees in the southeastern U.S. One species is an innocuous one that had never been known to outbreak, and the second had rarely been known to outbreak. In April of 2010, noctuid caterpillars feeding in large numbers on oak trees in Clarke County in northeastern Georgia were first brought to the attention of co-authors KG, JP, and JM. During the following two weeks, a greater incidence of the noctuid caterpillar outbreak was discovered in northeastern Georgia. Using DNA barcoding, the species was identified as the black-dotted brown moth, *Cissusa spadix* (Cram.) (Lepidoptera: Noctuidae). Concurrently, an outbreak of common oak moth larvae, *Phoberia atomaris* (Hübner) (Lepidoptera: Noctuidae),

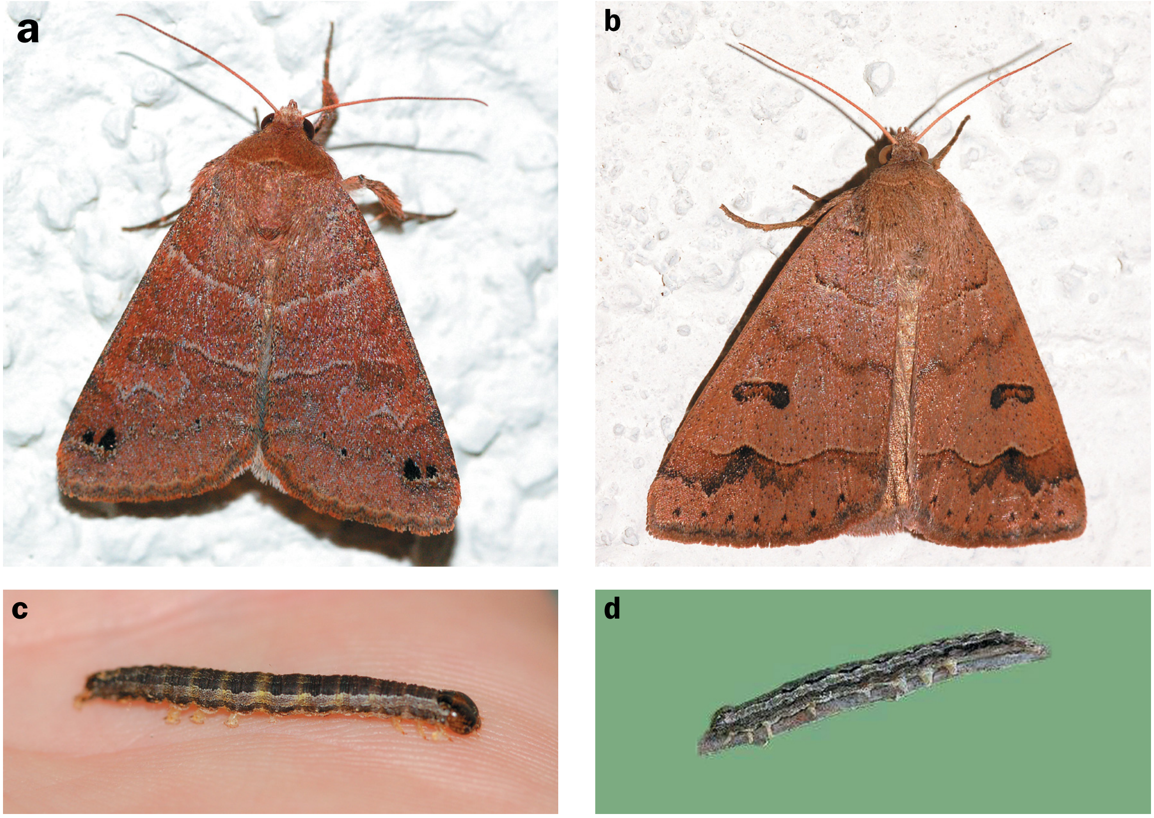


Fig. 1. (a) *C. spadix* adult, (b) *P. atomaris* adult, (c) *C. spadix* larva, and (d) *P. atomaris* larva. Photo credits to John Pickering, www.discoverlife.org (a, b, and c) and Tom Bentley (d).

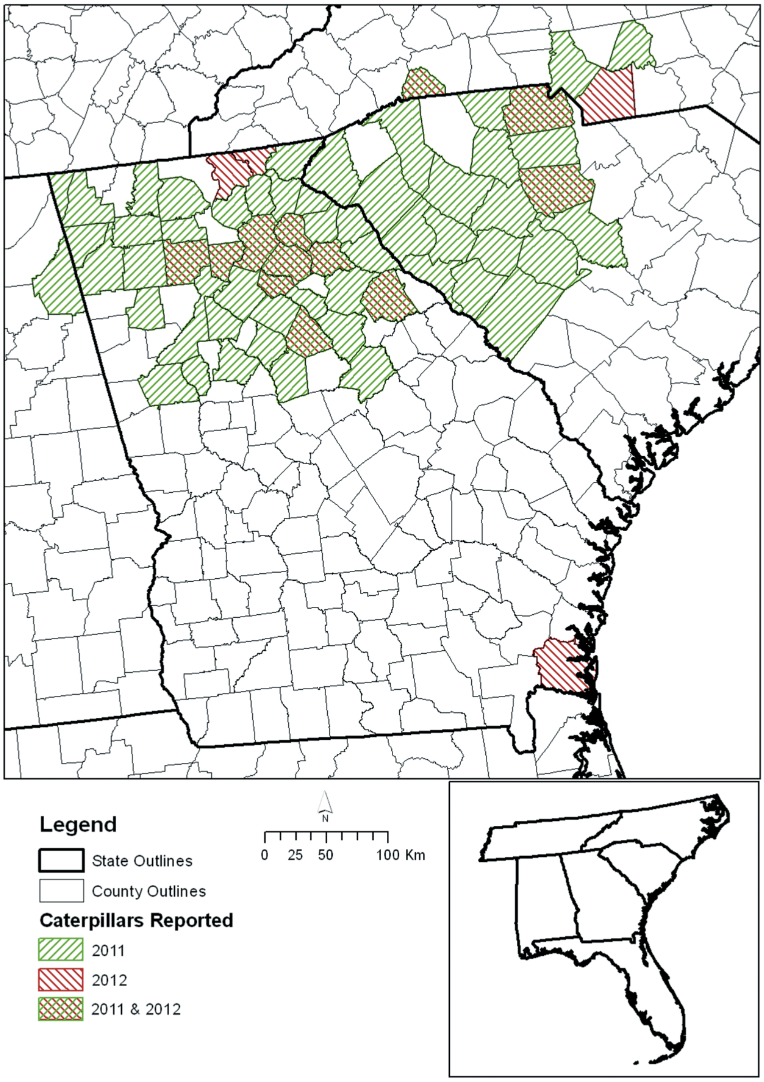


Fig. 2. Southeastern U.S. counties where spring oak defoliation was reported by citizen scientists in 2011 and 2012. One report was considered positive for a particular county.

was occurring in Georgia and South Carolina (≈13 counties) on oak trees (http://www.state.sc.us/forest/b050710.htm; C. Beckham, pers. comm.). In eastern North America, *C. spadix* and *P. atomaris* are mostly sympatric in distribution: both species occur from Ontario, Canada, and Maine south to Florida and west to Kansas and Texas in the U.S. (McFarland 1967, Muller 1973, Butler and Strazanac 2000, Covell 2005, Lafontaine and Schmidt 2010). While localized *P. atomaris* outbreaks have been well documented from Missouri (http://www.na.fs.fed.us/fhp/fhw/csfhw/jul02/jul02.pdf), Kentucky (http://pest.ca.uky.edu/EXT/BugID/BugEvents.shtml), and Ohio and West Virginia (http://www.na.fs.fed.us/fhp/pcond/2005/2005-na-pest-cond.pdf) on oak trees during the last decade, an outbreak of *C. spadix* has never been recorded anywhere in its geographic range.

This finding of two native species of noctuid moths in an outbreak phase on southern oaks is novel and unusual because *C. spadix* has never been known to outbreak anywhere in its entire range. Also, *C. spadix* caterpillars are morphologically similar to *P. atomaris* caterpillars (the adults are distinct) (Fig. 1), and they may have been mistaken for one another in the past (D. Wagner, pers. comm.). Although they are in different genera, *C. spadix* and *P. atomaris* have very similar life-history strategies, and during spring of 2010, they appeared to coexist and outbreak together in early spring on the same trees. Further, as region-wide outbreaks occurred in the urban-suburban-forest interphase, a large number of homeowners reported on their occurrence, allowing us to use citizen science for various biological observations.

At present, little is known about the natural history of *C. spadix* or *P. atomaris*. Here, we report novel observations about the biology of these little-known but important defoliators, including their life cycle and their predators and parasitoids. Since the outbreak was well documented by homeowners and landowners in the southeastern region, we used citizen science to determine the general distribution of the outbreak. We also conducted host choice and no-choice experiments during 2010–2012 to assess their host range among various southern oak species and other tree species commonly found on the same landscape. Finally, we offer a hypotheses to explain why these two native and usually rare defoliators may have suddenly reached outbreak levels for three years in a row. Identifying these rare and unpredictable outbreaks early in the event may be critical to limiting their effect on tree and forest ecosystem health. Moreover, if these outbreaks of herbivorous insects occur in urban and rural areas, defoliation events may have a wider impact on human communities, including loss of aesthetic value on property, nuisance to area residents, and economic loss if trees die from repeated outbreak events.

Distribution of Caterpillar Outbreak Using Citizen Science

In 2011, co-authors KG and JM issued a press release about the oak defoliator outbreak to address many questions related to the life cycle of the pests, management strategies, and citizens' concern for the health of oak trees (http://news.uga.edu/releases/article/outbreak-strange-moth-danger-trees/). As a result, during 2011–2012, over 300 citizens in western Alabama, northern Georgia, southwestern North Carolina, and western South Carolina either brought caterpillars for identification, sent e-mails, or left voice messages reporting the occurrence of caterpillars, high levels of oak defoliation, and observed predators on their properties. In total, early spring oak defoliation was reported in 68 counties in the southeastern U.S. (Fig. 2), indicating that it was a regionally distributed phenomenon. Oaks were the most commonly reported tree species being defoliated, but several other urban tree species, such as apple (*Malus* spp.), beech (*Fagus* spp.), cherry (*Prunus* spp.), chestnut (*Castanea* spp.), hickory (*Carya* spp.), pine (*Pinus* spp.), and sweetgum (*Liquidambar styraciflya* L.), were also reported. While we cannot be sure about the caterpillar species identifications of these

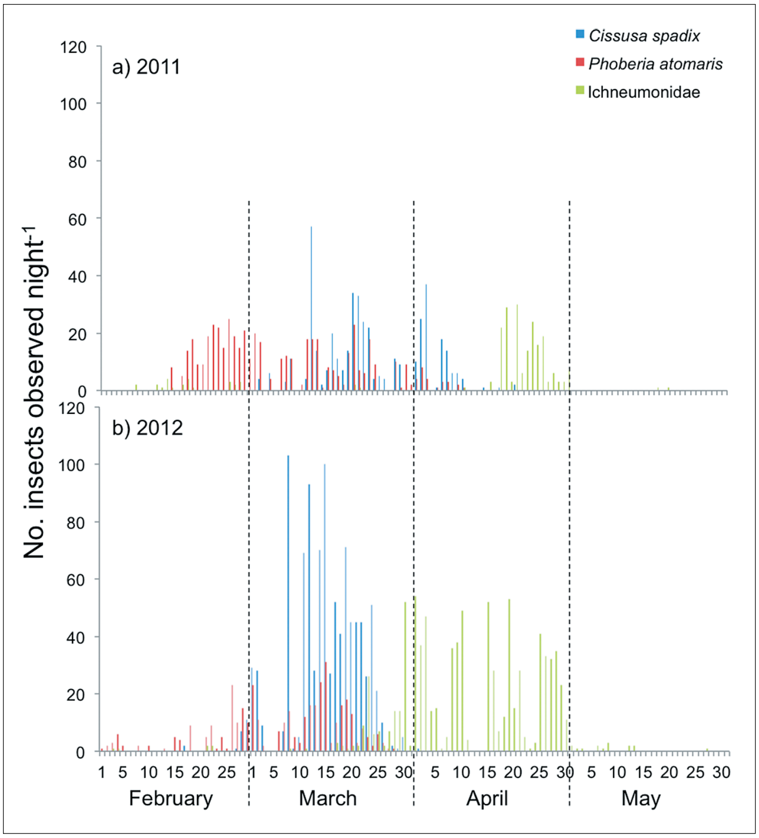


Fig. 3. Number of adult noctuid moths, *C. spadix* and *P. atomaris*, and ichneumonid parasitic wasps observed nightly at lights in early spring in 2011–2012 in Athens, Georgia.

reports, it was clear that the outbreak of lepidopteran defoliators on landscape trees in the southeastern U.S was widespread in the early spring of 2011–2012.

General Life Cycle of *C. spadix* and *P. atomaris*

In February 2010, co-author JP started photographing insects attracted to three porch lights at his house in Athens, GA, U.S. (33.89°N, 83.30°W) and uploading them to the Web for identification and analysis. This effort has grown to become Discover Life's *Mothing* project (www.discoverlife.org/moth), which currently monitors insect phenology and abundance at 10 sites in North America and one in Costa Rica. *Mothing*'s primary goal is to determine how climate, latitude, and other ecological factors affect generations of moths across sites and years. Each night, automated programs tabulate and graph the data and make them available by taxon, site, and date (see www.discoverlife.org/moth/report.html). Photographs of *C. spadix*, *P. atomaris*, and their natural enemies were taken every night (around midnight in 2011, at an hour before dawn in 2012) in February, March, April, and May during 2011 and 2012. During each year, we ran three 100-watt-equivalent bright white compact florescent bulbs nightly and a 15-watt 18″ black light on alternate nights.

The life cycle for both *C. spadix* and *P. atomaris* is one generation per year (Covell 2005). Adults of these two species are morphologically distinct: adults of both species are reddish-brown in color, but *C. spadix* has a 3-4.1 cm wingspan and forewings with two distinct black dots near wing tips (Fig. 1a), while *P. atomaris* has a 3.2-4.7 cm wingspan and forewings with a reniform spot in the middle part of the wing (Fig. 1b) (Covell 2005). Based on our observations, adults first appeared just before bud break on oak trees in early spring, and were seen flying high in the oak canopy at dusk. Adult *P. atomaris* were first observed in the *Mothing* data on 14 February 2011 and 1 February 2012, while adult *C. spadix* were first observed on 3 March 2011 and 17 February 2012. In both species, there was a general trend of adults appearing about 2–3 weeks earlier in 2012 than 2011. In 2011–2012, adults flew approximately a month before late instars appeared, with the peak *P. atomaris* flight up to two weeks earlier than *C. spadix* in both years. Overall, numbers of *C. spadix* nearly doubled from 2011 to 2012, while numbers of *P. atomaris* rose slightly during that time, resulting in an overall increase in the outbreak status of oak defoliators, especially *C. spadix* (Fig. 3).

After mating, female *P. atomaris* oviposit in bark fissures (Wagner et al. 2011). Oviposition location is unknown for *C. spadix*, though we hypothesize that females may be laying eggs close to tree buds. Eggs hatch and neonates appear just after bud break, when new oak leaves have opened. The number of instars is unknown, but *C. spadix* caterpillars can grow up

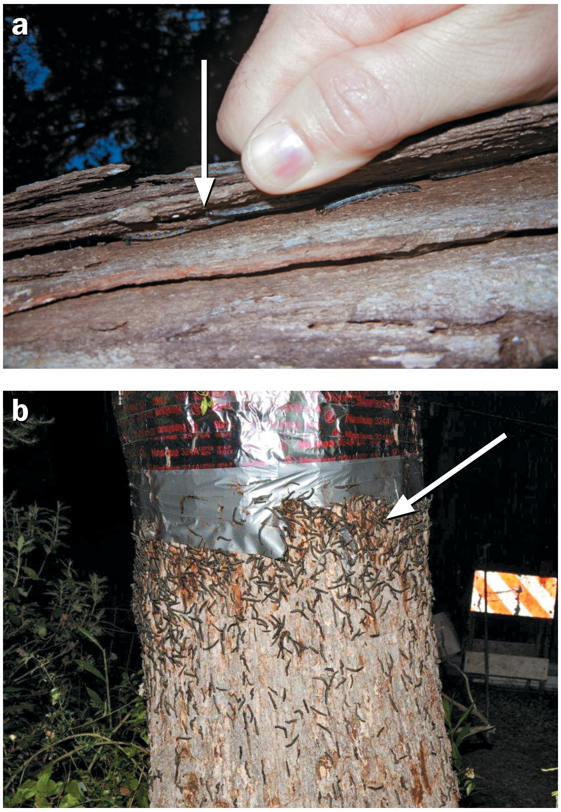


Fig. 4. (a) Caterpillars hiding under white oak bark. Caterpillars (identified by the arrow) spent most of the day in this position. (b) Shortly after dusk, caterpillars would ascend the tree trunk *en masse* to feed on canopy foliage. A barrier of plastic and duct tape, or burlap, shown in (b) can be an effective method to minimize larval ascension to canopy foliage. Photo credits to Brittany Barnes (a) and Douglas Hansen (b).

to 4.5 cm long (Wagner et al. 2011). Morphologically, caterpillars of *C. spadix* and *P. atomaris* are quite similar, with *P. atomaris* caterpillars having a slightly more pronounced white stripe along the lateral side (Figs. 1c, d). There does, however, appear to be a considerable amount of phenotypic variation in larval coloration.

Caterpillars were commonly seen hiding beneath white oak, *Quercus alba* L., bark during the day (Fig. 4a), a behavior not previously reported, as they are typically known to rest in leaf litter around host trees. Caterpillars of both species are strong climbers, and they can climb up and down the trees, depending upon the time of the day. After sunset, caterpillars ascend tree trunks *en masse* to free-feed on newly opened leaves (Fig 4b). Occasional larval activity was witnessed during the day, but caterpillars appeared to be primarily nocturnal. Feeding by caterpillars created a nuisance to homeowners due to the high volume of frass dropping from the trees; these droppings could be easily heard as a “drizzling” sound and seen on the ground. Furthermore, caterpillars were attracted to lights (especially porch, carport, or garage lights) and frequently found their way into homes. When handled, the caterpillars tended to vomit reddish-brown liquid that had a faint, yet pungent, odor. Wagner et al. (2011) reported that *P. atomaris* caterpillars play dead when alarmed, and writhe and snap their bodies when agitated. Both species can fold their heads under the abdomen when disturbed (Wagner et al. 2011).

At the end of the last instar, caterpillars showed strong dispersal behavior, presumably to find suitable places to pupate. Caterpillars in the pre-pupal stage stopped feeding and became less active. Pupation occurred in the soil and duff layer, although we have observed caterpillars pupating in non-traditional places, such as loosely woven carpets in homes and under planters and small rocks in gardens. For example, co-author KG had at least 50 *C. spadix* emerge from carpet in her home in 2012, suggesting that pupation substrate may not be an issue in terms of survival. After April, the insect is in a pupal stage until adult emergence the following spring.

Host No-Choice and Choice Experiments on Caterpillars

With the exception of oaks, little was known about the host preferences of these caterpillars when the outbreak first started in 2010. Hence, we conducted host no-choice and choice feeding bioassays for three years (2010–2012) to determine the range of host species in these southern landscapes. In 2010, we collected mature larvae by hand from white oak tree trunks at the University of Georgia Whitehall Forest, Athens, GA (33.88°N, 83.36°W). Based on observations of caterpillar morphology (David Wagner, pers. comm.) and pupal rearing (JP, pers. obs.), the outbreaking caterpillar was identified as *C. spadix*, though there was a chance that this collection also included *P. atomaris*. We immediately placed larvae into jars containing twigs and tissue for habitat and maintained them at 24°C in 13.5 light: 10.5 dark conditions. We fed caterpillars young white oak leaves for 24 h, and then starved them for 48 h before beginning the assay. We placed two fresh, fully expanded green leaves of six different tree species [white oak, red oak (*Quercus rubra* L.), red maple (*Acer rubrum* L.), tulip poplar (*Liriodendron tulipifera* L.), sweetgum, and loblolly pine (*Pinus taeda* L.)] into each of eight dishes (n=8 per species). A moist Kimwipe was included in each dish. We then added a single healthy and active larva to each dish and allowed them to feed for 12 h. We kept dishes at the same temperature and light regimen as caterpillars, and recorded the percent of leaf area eaten at hours 0.5, 1, 6, and 12 (Lehman 2012). Percentage of leaf area consumed was arcsin transformed prior to statistical analyses, as the amounts were seldom in the mid-range (Sokal and Rohlf 1995).

In 2011, we collected late instar *C. spadix* and *P. atomaris* from the ground, from mature white oak stems, and from lights in the wooded backyard of co-author KG’s residence in Athens, GA, U.S. (33.90°N, 83.31°W) between 1900 and 2200 hours on 25 April 2011 (for no-choice and choice assays) and on 2 and 5 April 2012 (for choice and no-choice assays, respectively). We captured caterpillars by hand and placed them into plastic containers containing paper towels to provide structure and habitat. Before bioassays, we maintained caterpillars in 13 light: 11 dark conditions at 22°C without food. We initiated host no-choice and choice feeding assays 24 h following larval capture, using only apparently healthy and vigorous caterpillars in assays.

As based on the citizen science data in 2011, in which multiple hosts were reported for these noctuid caterpillars, we tested 16 putative host species obtained from various locations in Athens, GA (Table 1). We collected foliage one day after caterpillars were collected during each year. We clipped a foliage-bearing branch at least 60 cm long from each putative host, placed it into water, and transported it to the University of Georgia Whitehall Experimental Forest Greenhouse in Athens. We used foliage from leaf plastochron index (LPI, Larson and Isebrands 1971) 1-5 in assays, where LPI 0 represents the first fully-expanded leaf closest to the apical terminal with a lamina length of ≥3 cm. We measured leaf area using a leaf area meter (Model LI-3100, LI-COR Biosciences, Lincoln, NE) on all leaves used in assays prior to and immediately following assays.

For the 2011 host no-choice feeding assays, we placed three caterpillars into each of five Petri dishes (150 × 20 cm) per tree species. In 2012 we focused only on oak trees, and placed one larva into each of 14 Petri dishes per tree species (Table 1). We placed one piece of moistened Whatman filter paper on the bottom of each dish, wrapped leaf petioles in moist cotton, and placed them into a dish with the caterpillars. We held dishes in a growth chamber at 13 light: 11 dark with a 27:15 °C temperature regime and 65% relative humidity. These conditions were approximately equivalent to field conditions at the time of assay initiation. We removed caterpillars either after 48 h (in 2011) or 72 h (in 2012), and recorded larval survival and final leaf area.

Host choice feeding assays used four oak species

Table 1. Relationship of leaf area with fresh and dry weight for 16 putative host species (n = 20 leaves per species) found in northeastern Georgia, USA. All hosts were used in host no-choice assays, while only *Quercus* spp. were used in choice assays. All relationships were linear in the form y = *ax* + *b*. Data were analyzed using simple linear regression (Proc Reg, SAS Inc., Cary, NC).

Scientific name	Common name	Year in assay	GPS location	Wt. (g)	a	b	R^2	$F_{1,19}$	P
Acer palmatum Thunberg	Japanese maple	2011	33°54′N, 83°18′W	Fresh	69.26	1.26	0.9909	1967.53	<0.001
				Dry	228.78	1.73	0.9820	983.89	<0.001
Acer rubrum L.	Red maple	2010, 2011	33°55′N, 83°22′W	Fresh	49.09	7.21	0.9173	199.63	<0.001
				Dry	106.00	9.36	0.8477	100.17	<0.001
Cornus florida L.	Flowering dogwood	2011	33°55′N, 83°21′W	Fresh	67.77	3.61	0.9174	199.90	<0.001
				Dry	182.00	4.61	0.8712	121.72	<0.001
Fagus grandifolia Ehrhart	American beech	2011	33°53′N, 83°21′W	Fresh	155.15	3.91	0.9924	2339.83	<0.001
				Dry	401.66	3.41	0.9840	1106.71	<0.001
Liquidambar styraciflua L.	Sweetgum[a]	2010, 2011	33°55′N, 83°21′W	Fresh	55.52	6.25	0.9332	237.67	<0.001
				Dry	211.68	9.44	0.9488	315.29	<0.001
Liriodendron tulipifera L.	Tulip poplar	2010, 2011	33°55′N, 83°22′W	Fresh	71.55	3.43	0.9398	280.95	<0.001
				Dry	243.75	9.74	0.9794	857.05	<0.001
Magnolia grandiflora L.	Southern magnolia	2011	33°55′N, 83°22′W	Fresh	34.48	-4.27	0.8422	96.09	<0.001
				Dry	203.95	-6.39	0.7380	50.69	<0.001
Pinus palustris Miller	Longleaf pine	2011	33°56′N, 83°22′W	Fresh	9.14	-0.85	0.8927	149.74	<0.001
				Dry	19.48	-0.89	0.8622	112.62	<0.001
Pinus taeda L.	Loblolly pine	2010, 2011	33°56′N, 83°22′W	Fresh	9.87	-0.02	0.9463	317.37	<0.001
				Dry	19.93	0.09	0.9156	195.15	<0.001
Platanus occidentalis L.	American sycamore	2011	33°53′N, 83°21′W	Fresh	51.42	-1.47	0.8719	122.52	<0.001
				Dry	209.39	-8.17	0.8995	161.14	<0.001
Quercus alba L.	Eastern white oak	2010, 2011, 2012	33°55′N, 83°21′W	Fresh	73.93	4.18	0.9708	597.53	<0.001
				Dry	244.93	2.66	0.9483	330.04	<0.001
Quercus falcata Michaux	Southern red oak	2011, 2012	33°55′N, 83°21′W	Fresh	48.84	3.15	0.9698	577.47	<0.001
				Dry	123.58	3.54	0.9607	439.85	<0.001
Quercus macrocarpa Michaux	Bur oak	2011, 2012	33°56′N, 83°22′W	Fresh	39.16	7.47	0.9734	659.48	<0.001
				Dry	125.52	10.26	0.9587	417.71	<0.001
Quercus nigra L.	Water oak	2011, 2012	33°55′N, 83°21′W	Fresh	51.17	0.28	0.9120	186.66	<0.001
				Dry	128.50	0.24	0.9193	205.05	<0.001
Quercus rubra L.	Red oak[b]	2010	33°53′N, 83°21′W						
Quercus stellata Wangenh.	Post oak[b]	2012	33°57′N, 83°22′W						
Tilia heterophylla Ventenat	White basswood	2011	33°55′N, 83°21′W	Fresh	65.23	6.33	0.9753	712.21	<0.001
				Dry	179.25	9.60	0.9481	328.87	<0.001

[a] N = 19 in 2011

[b] Foliage was not collected for fresh/dry weight analyses.

Table 2. Larval *C. spadix* and *P. atomaris* feeding preferences on tree hosts in northeastern Georgia, USA, in 2010. We recorded the percent leaf area consumed by caterpillars over 12 h in a no-choice assay. Means sharing a letter are not significantly different as determined by the two sample t-test ($\alpha = 0.05$).

Tree species	% Defoliation ± SE
Red oak	9.6 ± 5.0a
White oak	6.9 ± 3.1ab
Red maple	1.3 ± 0.8b
Tulip poplar	0.0c
Sweetgum	0.0c
Loblolly pine	0.0c

in 2011: white oak, southern red oak (*Quercus falcata* Michaux), bur oak (*Quercus macrocarpa* Michaux), and water oak (*Quercus nigra* L.). In 2012, we added post oak (*Quercus stellata* Wangenh.) (Table 1). Twenty (in 2011) or 60 (in 2012) Petri dishes (150 × 20 cm) were assembled identically to those in the no-choice assays, with the exception that instead of whole leaves, we placed two circular leaf discs (each 23 mm diam.) from each tree species into each dish. We placed both discs from each host side by side, equidistant from other host disc groups. We then placed one larva in the middle of the dish, and held all dishes in a growth chamber under identical conditions as the host no-choice assays. We removed caterpillars from assays either after 36 h (in 2011) or 24 h (in 2012), and recorded larval survival and the remaining leaf area.

Many feeding assays record leaf area consumption rather than leaf mass consumption (Oliveira de Freitas Bueno et al. 2010, Perez et al. 2010). To test the validity of this approach, we measured fresh leaf area and mass of 20 additional leaves from each tree species. We dried leaves in an oven at 60°C for 5 d, after which we recorded leaf dry mass. These data allowed us to test the relationship between fresh leaf area, fresh leaf mass, and dry leaf mass for each tree species using simple linear regression (Proc Reg, SAS Institute, Cary, NC). Since fresh leaf area and leaf mass were highly correlated in all tree species, with r^2 values ranging from 0.738 to >0.992 (Table 1), we report fresh leaf area consumed hereafter. We tested leaf area consumption data from host no-choice assays for normality using Proc Univariate tests (SAS Institute, Cary, NC) and square root transformed the data to achieve normality. In the host no-choice experiments, we analyzed leaf area consumption data using a one-way analysis of variance (Proc Glm, SAS Institute, Cary, NC) with the Tukey t-test to separate means, with an α level of 0.05 considered significant. When no feeding occurred in a Petri dish in the choice assays, we eliminated these dishes from further analyses. We tested leaf area consumption data from choice assays for normality using Proc Univariate (SAS Institute, Cary, NC). Because standard statistical transformations did not achieve normality with these data, we also used logistic regression (Proc Logistic, SAS Institute, Cary, NC) with a binary logit model to examine the probability that a larva would consume each of the four *Quercus* spp. hosts in the choice arena. We then conducted mean separations on rank data among the tree species used in the choice assays. We conducted analyses separately for each sampling year (2011 and 2012).

Caterpillars of *C. spadix* and *P. atomaris* are very similar, making field identification difficult. A subset of four caterpillars from those collected in 2011 was sent to the Canadian Centre for DNA Barcoding, University of Guelph, Canada for DNA identification using the standard mtDNA *Cytochrome Oxidase I* (*COI*) gene. We found that two caterpillars were *C. spadix* and two were *P. atomaris*. Hereafter, we refer to the collective group of *C. spadix* and *P. atomaris* caterpillars simply as "caterpillars." For the 2011 collections, we were logistically unable to determine the identification of each assay specimen; however, rearings suggest that most larvae were *C. spadix*. We identified every larva (n=129) from our laboratory assays in 2012 to determine whether the two moth species may be partitioning the oak resource. First, we sequenced a 670 bp portion of *COI* from ten adults of each moth species, using the standard DNA barcoding primers LepF1 and LepR1 (Hebert et al. 2004). DNA was extracted from the head of each moth using Qiagen's Puregene kit (Qiagen, Valencia, CA), and PCR was conducted using standard conditions. DNA was

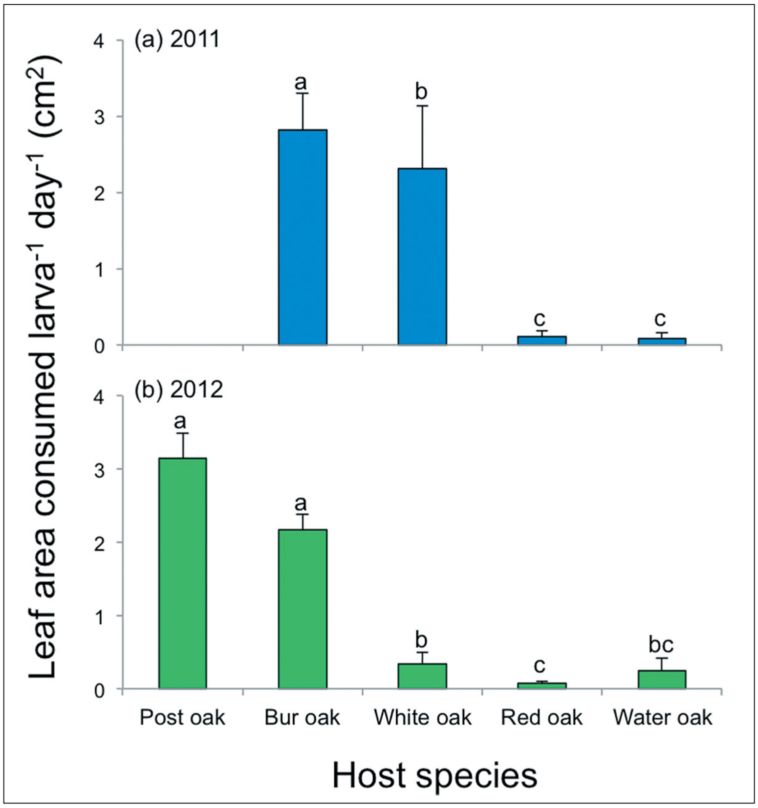


Fig. 5. Larval *C. spadix* and *P. atomaris* feeding on tree species in northeastern Georgia, USA. In 2011, mixed *C. spadix* and *P. atomaris* larvae fed for 48 h in no-choice petri dish assays on 15 different putative hosts (a). In 2012, *C. spadix* larvae fed for 72 h and we focused on putative oak species only (b). Post oak was not used in 2011. Within each year, means sharing a letter are not significantly different as determined by the Tukey test ($\alpha = 0.05$).

sequenced using Big Dye v3.1 (Applied Biosystems, Carlsbad, CA) and run out at the Georgia Genomics Facility at the University of Georgia, Athens. We verified base calls of the chromatograms using Sequencher (Gene Codes, Ann Arbor, MI). Using nucleotide sites with fixed differences between species, we identified restriction enzymes that cut this *COI* fragment in one species but not the other. Two representative sequences from each species have been deposited in Genbank (Accession numbers KC012712-KC012715).

The genotyping assay to infer the species identity of each individual caterpillar consisted of amplifying *COI* with the above barcoding primers, and then a double digest of the amplicon with the enzymes *BsiHKAI* and *EarI* (New England Biolabs, Ipswich, MA). *BsiHKAI* digests only *P. atomaris* and results in 290 bp and 380 bp fragments, and *EarI* digests only *C. spadix* and results in 220 bp and 450 bp fragments. In this way, we expect the *COI* PCR product of every individual to be cut, as long as it was one of these two species. In short, to 7 µL of PCR product we added 5 µL of *EarI*, 1 µL of *BsiHKAI*, as well as additional MgCl2 and NaCl to bring their final concentrations to 10 mM and 50 mM, respectively. We incubated the digest at 37°C for 20 h, which is the optimal temperature for *EarI*, and then for 2 h at 65°C, which is optimal for *BsiHKAI*. The digested PCR product was run on an agarose gel and the fragments were visualized and scored. We confirmed that this assay distinguished these species by assaying an additional 24 adults of each species. Caterpillars from the 2012 feeding assays were genotyped in this same way. There were a few caterpillars for which we could not successfully extract and amplify DNA; however, of those that did amplify, there was no caterpillar that was not one of the two focal species based on this method.

Although overall defoliation amounts in the 2010 no-choice assay were low (generally <10%), caterpillars showed a clear preference for red oak (*Quercus rubra* L.) and white oak (F = 4.66, df = 5, 42, *P* = 0.0018; Table 2). Caterpillars fed over 7 times less on red maple than on red oak (Table 2). Caterpillars did not consume tulip poplar, sweetgum, or loblolly pine (Table 2).

In the 2011 no-choice feeding trials, caterpillars did not consume American beech (*Fagus grandifolia* Ehrh.), American sycamore (*Platanus occidentalis* L.), longleaf pine (*Pinus palustris* Miller), Southern magnolia (*Magnolia grandiflora* L.), white basswood (*Tilia heterophylla* Ventenat), red maple, tulip poplar, or sweetgum (Fig. 4). Caterpillars fed minimally (i.e. <2 total mm^2 of leaf tissue consumed) on Japanese maple (*Acer palmatum* Thunberg) and loblolly pine. Noctuid caterpillars consumed over twice as much white, red, or bur oak than water oak, and consumed water oak over four times more than dogwood (*Cornus florida* L.) (F = 14.12; df = 14, 60; *P* < 0.001; Fig. 5). Hence, through our 2010 and 2011 no-choice assays, we found that oak trees were the main host for *C. spadix* and *P. atomaris*.

In the 2012 no-choice feeding trials, 94% of caterpillars were *C. spadix*, as only four caterpillars were *P. atomaris* (three caterpillars in red oak dishes; one in a water oak dish). We were unable to obtain DNA information for one larva. *Cissusa spadix* caterpillars consumed over three times more bur oak than any other oak species in 2012 (F = 15.94; df = 4, 58; *P* < 0.001; Fig. 5). Post, white, and red oak were consumed at approximately 30% the rate of bur oak, and water oak was consumed only about 10% the rate of bur oak (Fig. 5).

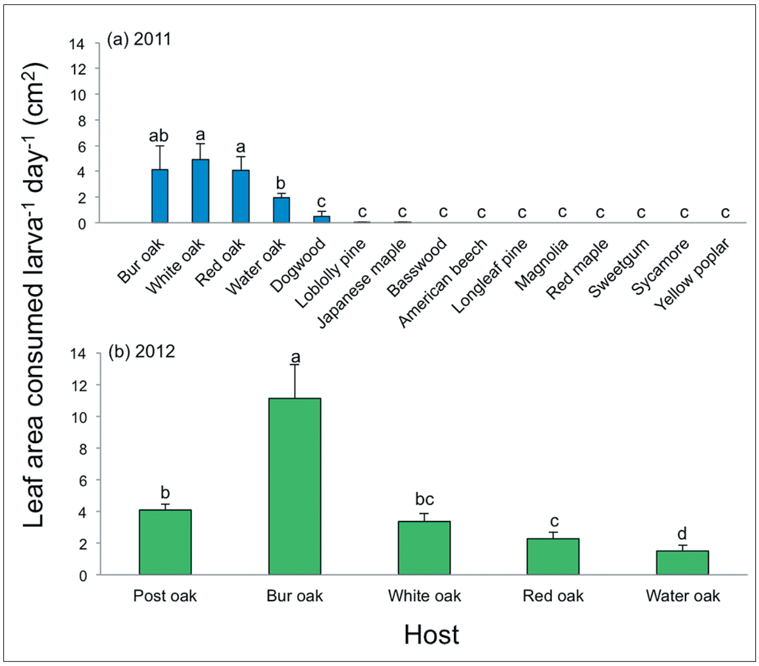


Fig. 6. Larval *C. spadix* and *P. atomaris* feeding on oak hosts in northeastern Georgia, USA. In 2011, mixed *C. spadix* and *P. atomaris* larvae fed for 36 h in petri dish assays, with four hosts available concurrently (a). In 2012, *C. spadix* larvae fed for 24 h with five hosts available concurrently (b). Post oak was not used in 2011. Within each year, means sharing a letter are not significantly different as determined by the Tukey test (α = 0.05).

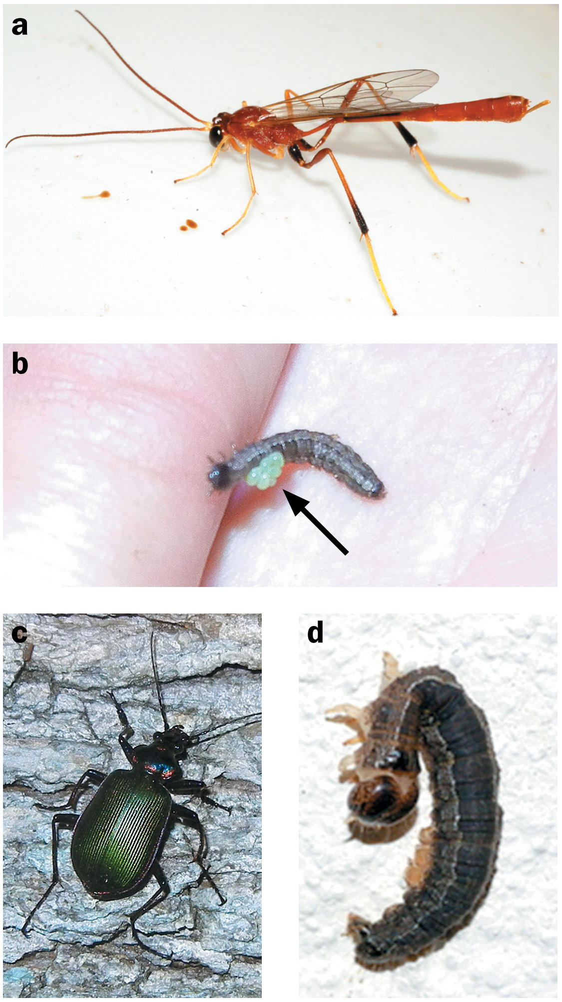
In the 2011 choice feeding trials, caterpillars showed clear feeding preferences ($\chi^2 = 21.612$; df = 3; *P* < 0.001), with bur oak being the most preferred, followed closely by white oak, and with red and water oak minimally consumed (Fig. 6). White and bur oak leaf consumption rates were >20 times greater than red or water oak. We were unable to obtain DNA from six caterpillars in the 2012 choice feeding trails; all other caterpillars were *C. spadix*. Feeding preference differed among oak hosts for *C. spadix* ($\chi^2 = 75.257$; df = 4; *P* < 0.001). Post and bur oak were the most preferred species by *C. spadix*, as larvae consumed over six and four times more foliage than white, red, or water oak (Fig. 6).

Natural Enemies of the Caterpillars

A large number of natural enemies of caterpillars, including parasitoids and predators, were observed during 2010–2012. We also established new host records for an ichneumonid and eulophid parasitoid wasp on *C. spadix*. Several adult parasitic wasps (Hymenoptera: Ichneumonidae) (Fig. 7a) were captured at night lights at the same time as caterpillars for the bioassays. These wasps were associated with outbreaks of *C. spadix* (Fig. 3), and their adult phenology patterns were recorded at the same time and manner as adult moths. Ichneumonid wasp counts were nearly three times higher in 2012 than 2011 (Fig. 3), mirroring population sizes of adult moths. We reared approximately 20 *C. spadix* caterpillars to pupae in 2010 and 2011. One *Aphanistes crepuscularis* Hopper (Hymenoptera: Ichneumonidae) was reared from the caterpillars collected in 2010. *Aphanistes crepuscularis* is a koinobiont endoparasitoid, ovipositing into live caterpillars and emerging from the pupa (David Wahl, pers. comm.). These wasps were commonly seen in swarms at lights after dark in areas where outbreaks of the caterpillars were occurring. Another ichneumonid, an *Ophion* spp., was also captured at lights and appeared similar to *A. crepuscularis*; however, we do not know if this species was parasitizing either of the caterpillar species.

On 25 April 2011, we captured a caterpillar with a bluish-green egg clutch attached to its back (Fig. 7b). We placed the caterpillar into a glass vial and held it in ambient conditions in the Forest Entomology laboratory at the Warnell School of Forestry and Natural Resources, University of Georgia, Athens. We do not know when the egg clutch was laid on the caterpillar, but after five days, the eggs hatched and we observed white vermiform larvae on the carcass of the caterpillar. The parasitoid larvae spun loose cocoons on the caterpillar cadaver six days after hatching, and adult parasitic wasps emerged five days later. The parasitic wasps were identified as *Euplectrus* sp. near *catocalae* Howard (Hymenoptera: Eulophidae) (Michael Gates, pers. comm.). Little is known about these tiny parasitic wasps, and this taxonomic group is in need of revision, making exact species identification impossible, but *E. catocalae* has been reported parasitizing Nantucket pine tip moth, *Rhyacionia frustrana* (Comstock) (Lepidoptera: Tortricidae) (Freeman and Berisford 1979), which is common in the southeastern U.S.

Fig. 7. (a) *Aphanistes crepuscularis* found in association with noctuid moth outbreaks from 2010 to 2012 in Athens, GA, USA. Hundreds of wasps were found around lights at night. (b) Larva found with parasitic wasp egg mass (identified by arrow). This egg mass was reared in the laboratory to adults of *Euplectrus* sp. nr. *catocalae*. (c) *Calosoma scrutator* adults were observed on tree trunks and near lights during the outbreak. (d) Many caterpillars exhibited symptoms of nucleopolyhedrosis virus (NPV). Photo credits to John Pickering, www.discoverlife.org (a, d) and Brittany Barnes (b, c).



We often observed *Calosoma scrutator* Fabricius (Coleoptera: Carabidae), commonly known as the fiery caterpillar hunter (Fig. 7c), on trees and near lights where caterpillars were present. *Calosoma scrutator* predatory beetles were photographed by JP in 2011 and 2012, and were observed on trees by KG in 2010, and DC, FL, JM, and KG in 2012. We found this beetle climbing trees and consuming caterpillars at night. Observations of *C. scrutator* during the *Mothing* project occurred shortly after occurrences of adult *C. spadix* and *P. atomaris* declined, which coincided with periods during which moth caterpillars would have been active. One citizen noted an abundance of *C. scrutator* on trees infested with caterpillars, while two others noticed black ants feeding on caterpillars.

We observed multiple caterpillars with symptoms of nucleopolyhedrovirus (NPV) infection (Fig. 7d). These symptoms included the characteristic upside-down V-shape (Andreadis and Weseloh 1990) as the mushy and shriveled bodies of caterpillars were attached to the bole of trees. Signs of NPV infection appeared to be more prevalent in 2012 than in former years of sampling, though we did not quantify this.

Squirrels were the most common vertebrate predators that citizens observed feeding on caterpillars; a local county extension agent (G. Sheppard, pers. comm.) and DC confirmed this observation. A large number of citizens called about the “stripping bark caterpillars,” as squirrels pulled strips of bark off tree trunks to capture and consume the caterpillars hiding beneath the bark (Fig. 8). Citizens noted several other vertebrate predators of the caterpillars, including wild birds, ducks, chickens, and fish (if caterpillars fell into ponds).

Discussion

We documented two little-known lepidopteran species which were previously either not known or rarely known to undergo spectacular outbreaks in southern oak stands. Larval *C. spadix* and *P. atomaris* fed on oak species in the Piedmont region of the southeastern U.S. each spring during 2010–2012, causing economic and aesthetic damage in urban and rural areas. Concurrent outbreaks of multiple lepidopteran species are relatively rare and/or not well documented (Torres 1992, Roland and Embree 1995, Walker and Welter 2001). For a multi-species herbivore outbreak to occur on the same host, several variables must be in alignment. First and foremost, the host must be susceptible, whether weakened by drought, disease, or some other factor. Second, phenology of the herbivores needs to be similar, without one species suppressing the other. Third, the herbivores must either adequately partition the host resource spatially or temporally so that both insect species can increase their populations, or the herbivores must not have any competition for host resources. Fourth, the host and herbivore must be in synchrony. Finally, natural enemies must be avoided long enough for herbivore populations to increase, thus initiating the outbreak. In many cases, one or more of these variables may occur in concert, but seldom do all happen concurrently; hence the rarity of multi-species outbreaks on the same host.

The specific factors that induce forest herbivore outbreaks are unknown, although several are believed to be responsible. Weather events are known to have a significant influence on insect populations, including the synchronization of multiple lepidopteran populations (Torres 1992, Myers 1998, Raimondo et al. 2004). Prolonged drought can lead to concentrated foliar nutrients, subsequently increasing tree palatability to herbivores (Mattson and Haack 1987). Drought can also deplete starch reserves in tree roots, thereby increasing susceptibility to herbivores the following spring (Dunn et al. 1987). In fact, drought preceded an outbreak of at least 12 species of Lepidoptera in Panama (Van Bael et al. 2004). Most of the southeastern U.S., including northern Georgia and the Piedmont region of South Carolina, has been under drought conditions since 2000 (http://www.droughtmonitor.unl.edu/archive.html), and it is possible that many trees are in susceptible (or overly palatable) stages, encouraging insect outbreaks to occur. Drought can also suppress natural enemies, especially fungal pathogens (Mattson and Haack 1987).

The influence of temperature on insect phenology is well documented, as warmer temperatures were correlated with earlier emergence of 44 species of moths in Ireland (O'Neill et al. 2012), earlier flight periods of Odonata in the Netherlands (Dingemanse and Kalkman 2008), and earlier first appearance of certain Diptera species in the United Kingdom (Graham-Taylor et al. 2009). We observed a shift in moth phenology during our study: first observations and peak activity of adult *C. spadix* and *P. atomaris* were recorded two weeks earlier in 2012 than 2011 (Fig. 3). Much of the southeastern U.S. experienced an unseasonably warm winter in 2012 compared to previous years. For example, the mean temperature from 1 December 2010 through 31 January 2011 was 3.9 °C, while the mean temperature from 1 December 2011 through 31 January 2012 was 9.3 °C. The higher winter temperatures in 2011 compared to 2012 may contribute to the earlier adult observations. Alternately, short periods of relatively high heat, a phenomenon common in the southeastern U.S., especially during 2012, may have contributed to the advanced phenology of these moth species in these years (Müller and Obermaier 2012).

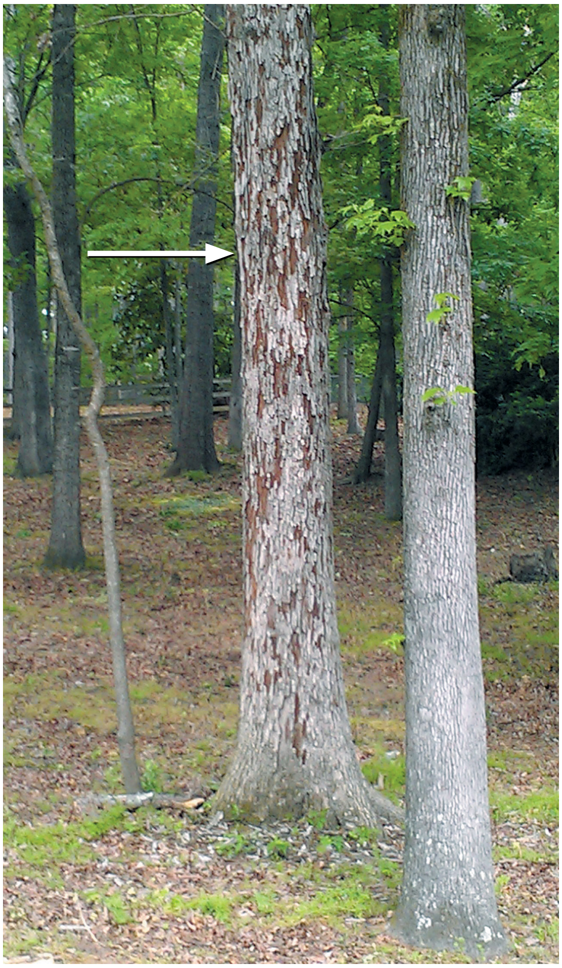


Fig. 8. White oak bark stripped by squirrels searching for *Cissusa spadix* and *Phoberis atomaris* caterpillars in Athens, Georgia (indicated by arrow). Photo credit to David Coyle.

Relatively little was known regarding the life history of *C. spadix* or *P. atomaris*, compared to other outbreak-prone forest Lepidoptera such as the elm spanworm or Bruce spanworm. According to Wagner (2005), caterpillars of *C. spadix*, *C. indiscreta* (Edwards), *P. atomaris*, and *P. orthosioides* (Guenée) all inhabit the same ecological niche, and are all extremely difficult to discern. These caterpillars seem to have a relatively narrow host range compared to other outbreak-prone, forest-dwelling Lepidoptera. For example, the elm spanworm feeds on at least 25 different woody hosts (Ciesla 1964, Fedde 1964, Ryall 2010), and both gypsy moth and forest tent caterpillar have notoriously large host ranges (Elkinton and Liebhold 1990, Meeker 1997). We found that caterpillars consumed white, southern red, bur, post, and water oak in our study, and citizens reported that they consumed pin oak (*Quercus palustris* Münchh.), willow oak (*Quercus phellos* L.), and blackjack oak (*Quercus marilandica* Münchh.), although these hosts were not confirmed. Our study provides new host associations for both *C. spadix* and *P. atomaris*, whose larval host plants were previously known only as oak trees (Covell 2005, Wagner 2005). In fact, previous outbreaks attributed to *P. atomaris* may have actually been *C. spadix* (D. Wagner, pers. comm.). We now have a better understanding of the ecology of these little-known herbivores, and this information may be useful in determining the cause of future spring defoliation on oaks.

These caterpillars seem to have a diverse suite of natural enemies, including a number of parasitoids and predators. *Cissusa spadix* is a new host record for both *A. crepuscularis* and *E. catocalae*; however, the extent to which these organisms can affect caterpillar population levels is unknown. *Calosoma* spp. are voracious predators on many caterpillar species, including Noctuidae, and adults are capable of consuming between 75 and 315 caterpillars during their lifetime (Burgess and Collins 1917, Young 2008). Gray squirrels are not known as primary consumers of caterpillars (Spritzer 2002), while birds are documented larval predators during outbreaks (Torres 1992, Van Bael et al. 2004). While the vertebrate predators we observed are omnivores, and likely used larvae as a supplement to their diet, the insect predators and parasitoids may have experienced an increase in population levels due to the abundance of a food source. We did not investigate the impacts of these natural enemies on other defoliators, but other herbivore species may have been affected (Follett and Duan 2000).

Defoliation events not only reduce the aesthetic value of trees, particularly those in urban settings, but can lead to weakened trees with increased susceptibility to future defoliation events and colonization by other insects, such as bark and woodboring insects (Rieske and Dillaway 2008). Mattson et al. (1988) indicated that spring defoliators may have much less impact than mid-season or late-season defoliators, as defoliation events later in the season result in diminished accumulation of energy reserves before the dormant season. Several citizens reported delayed leaf-out of oak trees, smaller leaves, and even mortality after those same trees had been heavily defoliated in previous years. The most frequent question we received from the citizens was whether or not their oak trees would die from defoliation events. We hypothesize that these caterpillars are likely inciting factors, and if there is repeated defoliation over several years, tree growth will at least be reduced (depending upon the intensity of feeding). Trees did reflush their foliage after the defoliation event, but it remains to be seen if oak trees die after undergoing several defoliation events during spring.

These early spring caterpillars became household pests during outbreak levels, as they seem adept at getting inside homes through cracks underneath doors and around windows (personal observations). Reports of caterpillars in homes, carports, or garages were made by >45 citizens in northern Georgia in spring 2011. Several homeowners used broad-spectrum insecticides, while most people employed mechanical control methods (e.g., collecting caterpillars with a vacuum) or manual removal of the caterpillars. In the unlikely event that these moth species maintain outbreak population levels in 2013, or return to outbreak levels in the future, home and landowners have several management options. Burlap bands attached to tree trunks can prevent caterpillars from crawling to the canopy at night time (Liebhold et al. 1986, Liang et al. 1998, Butler and Strazanac 2000) (Fig. 4b). Tree trunks of mature trees can be sprayed with Safari® 20 SG (active ingredient = dinotefuran), currently the only pesticide approved for trunk application. Canopies of smaller trees can be treated with foliar sprays of horticultural oil or insecticidal soap, or with approved pesticides containing active ingredients such as imidacloprid, bifenthrin, or permethrin. Future populations may be monitored by estimating defoliation on lower branches, a technique used successfully for elm spanworm, as lower branch defoliation was highly correlated with mean tree defoliation (Fry et al. 2008).

In summary, the oak caterpillar outbreak of 2010-2012 was an unexpected phenomenon from which we obtained new ecological knowledge about these emerging pests of urban and forest trees in the southeastern U.S. This outbreak likely occurred due to increased susceptibility of trees from repeated drought years, in concert with warmer than usual winters. Future research regarding factors such as climate change (Couture and Lindroth 2012, Jamieson et al. 2012) and bottom-up (host trees) and top-down (parasitoids and predators) effects on *C. spadix* and *P. atomaris* populations (Forkner et al. 2008) may be necessary to complete a management strategy for these insects. Determining relative performance and fitness implications from different hosts, as well as what long-term damage results from multiple larval defoliation events, may also be priorities for future researchers.

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