Journal of
Plant Ecology

VOLUME 9, NUMBER 6,
PAGES 692–702

DECEMBER 2016

doi:10.1093/jpe/rtw020

Advance Access publication
31 March 2016

available online at
www.jpe.oxfordjournals.org

# Bird–plant interactions and vulnerability to biological invasions

*Adam D. Chupp* and Loretta L. Battaglia*

*Department of Plant Biology, Southern Illinois University, Life Sciences II, Mail Code 6509, Carbondale, IL 62901-6509, USA*
*Correspondence address. Department of Plant Biology, Southern Illinois University, Life Sciences II, Mail Code 6509, Carbondale, IL 62901-6509, USA. Tel: +1-251-460-6331; Fax: +1-251-414-8220; E-mail: adam.chupp@gmail.com

## Abstract

***Aims***
Species interactions regulate the invasiveness of non-native species and as declines of native tree species escalate, exotic tree species that offer supplementary resources to animal seed-dispersers should expand their distributions as they fill ecological roles. Our primary objective was to forecast impacts from an imminent biological invasion (laurel wilt disease) by quantifying resources provided by native (threatened) and exotic fruits (disease-resistant) and associated bird foraging preferences.

***Methods***
In the southeastern USA, we tested for redundancy among the resources provided by native and exotic fruits to overwintering birds. Comparisons between abundant subcanopy species *Persea borbonia* (native) and *Cinnamomum camphora* (exotic) were paramount considering the widespread disease-induced decline of *P. borbonia*, and the biological and phylogenetic similarities between these species. Across two winter survey periods, we quantified fruit removal and documented bird species using motion-activated cameras in the field. Physical and chemical fruit characteristics were also quantified.

***Important Findings***
Foraging bouts on both *P. borbonia* and *C. camphora* fruits were documented for four native bird species. There was no difference in selectivity between fruit types during Year 1 of our survey, but there was a significant preference for *C. camphora* fruit in Year 2; the change in preference was correlated with significantly lower temperatures in Year 2. While the pulp/seed ratio and moisture content differed, the nutritional content of fruit pulp (g/100 g) was similar between fruit types. Given the apparent redundancy among these native and exotic fruit resources, we forecast increases in the consumption and dispersal of exotic propagules following the widespread laurel wilt disease-induced decline of *P. borbonia* and other native fruit bearing members of Lauraceae. This empirically based prediction is among the first to document exotic forest pathogens as indirect threats to native bird–plant interactions and potential facilitators of exotic plant invasion.

***Keywords:*** bird frugivory, forest pests and pathogens, *Cinnamomum camphora*, laurel wilt disease, *Persea borbonia*

Received: 20 October 2015, Revised: 21 January 2016, Accepted: 19 March 2016

## INTRODUCTION

There are numerous examples of how exotic forest pests and pathogens have reduced the dominance of native tree species and changed the composition of forested habitats; dramatic declines of the American chestnut, American elm and American beech are well documented (e.g. Anagnostakis 1987; Dunn 1986; Houston *et al.* 1979). However, much less attention has been paid to higher trophic levels and the consequences mediated by the disruption of plant–animal interactions (Ellison *et al.* 2005; reviewed by Chupp and Battaglia 2014; Chupp *et al.* 2015; Lovett *et al.* 2006). Declines of herbivores, frugivores, and pollinators that depend on the resources provided by host tree species are a great concern. Disruptions of native plant–animal mutualisms can lead to coextinctions of native species and also create opportunities for exotic species to form beneficial relationships with indigenous species (Aslan *et al.* 2013; Gandhi and Herms 2010).

The importance of bird–plant mutualisms is widely recognized as the dispersal of plant propagules and the expansion of their distributions can depend entirely on their ability to attract frugivorous birds (reviewed by Richardson *et al.* 2000). Nearly 30% of invasive plants produce showy fruits (black, blue, or red) with propagules that are primarily bird-dispersed (Cronk and Fuller 1995; Richardson *et al.* 2000). Fruit preferences of birds are tied to increased nutritional rewards (Schaefer *et al.* 2003), dietary antioxidants (Schaefer *et al.* 2008) and fewer secondary compounds (Cipollini and Levey

1997). Recent evidence suggests that birds also prefer fruits rich in anthocyanins and polyphenols (antioxidants) during periods of oxidative stress (e.g. migration) (Bolser *et al.* 2013). In addition, birds preferentially forage on fruits according to sizes that are compatible with bill size and gape to facilitate shorter handling times; smaller fruits/seeds are consumed by a greater number of species (Jordano 1995).

Beyond the physical and chemical characteristics of fruits, birds may select their mutualistic partners in accordance with environmental parameters. Fruit removal is often correlated with the size of fruit crops and the identity and density of nearby fruit-bearing species (e.g. Carlo *et al.* 2007; Murray 1987; Ortiz-Pulido *et al.* 2007; Prasad and Sukumar 2010; Sargent 1990; Smith and McWilliams 2014). For example consumption of exotic plant fruits is relatively low in areas where bird-dispersed native plants are also abundant and have similar fruit characteristics (physical and chemical) and fruiting phenology as those exotic plants (Smith *et al.* 2013). In these situations, exotic species may fail to become invasive despite an abundance of fruit-consuming birds (Debussche and Isenmann 1990). However, when native and exotic fruits represent substitutable resources (Whelan *et al.* 1998), biological invasions that reduce the abundance of native fruits should encourage birds to subsidize more of their diet with exotic fruits. Knowledge of the resources provided by exotic and native fruits is vital for predicting shifts in bird preferences following the widespread mortality of a fruit-bearing species.

In the southeastern USA, an exotic ambrosia beetle (*Xyleborus glabratus* Eichoff) is vectoring a pathogenic fungus (*Raffalea lauricola* sp. nov. T.C. Harr. Fraedrich and Aghayeva), causing laurel wilt disease (LWD) in many native Lauraceae species (Fraedrich *et al.* 2008). Introduced to the USA in 2002 near Savannah, Georgia, LWD and its beetle vector have spread rapidly across South Carolina, Georgia and Florida (Fig. 1). The disease has more recently emerged in several counties in North Carolina, Louisiana, Texas, Alabama and Mississippi (Bates *et al.* 2015; Fig. 1). The fungus, which is introduced to host trees by the stem boring beetle, *X. glabratus*, spreads quickly through the xylem tissue and mortality of main stems can occur within only a few months of initial infection (Fraedrich *et al.* 2008; Mayfield 2008).

Although LWD has been identified in several Lauraceae species, the primary target is redbay (*Persea borbonia*), an abundant fruit-bearing tree found in the understory and subcanopy of many Atlantic and Gulf Coastal Plain habitats (Fraedrich *et al.* 2008; Van Deelen 1991); to date, it is estimated that >90% of all LWD infected trees are *P. borbonia* (JJ Riggins personal communication). On the Atlantic Coastal Plain, mortality rates within *P. borbonia* populations are as high as 97%, and the persistence of *P. borbonia* stump sprouts is doubtful as the fungal pathogen may be reintroduced by beetles and by dispersal through root systems (Evans *et al.* 2014; Fraedrich *et al.* 2015; Spiegel and Leege 2013). This same rate of widespread *P. borbonia* mortality will soon pervade all of the southeastern Coastal Plain, leaving behind very few or no mature fruit-bearing trees. The focal area of the current study (extreme southeast Mississippi) was not invaded by LWD at the time of study (2012 to 2014) but LWD infection rates and subsequent mortality of *P. borbonia* was increasing rapidly by January 2016. We estimate that by 2020, LWD will have eradicated >95% of fruit bearing *P. borbonia* in this

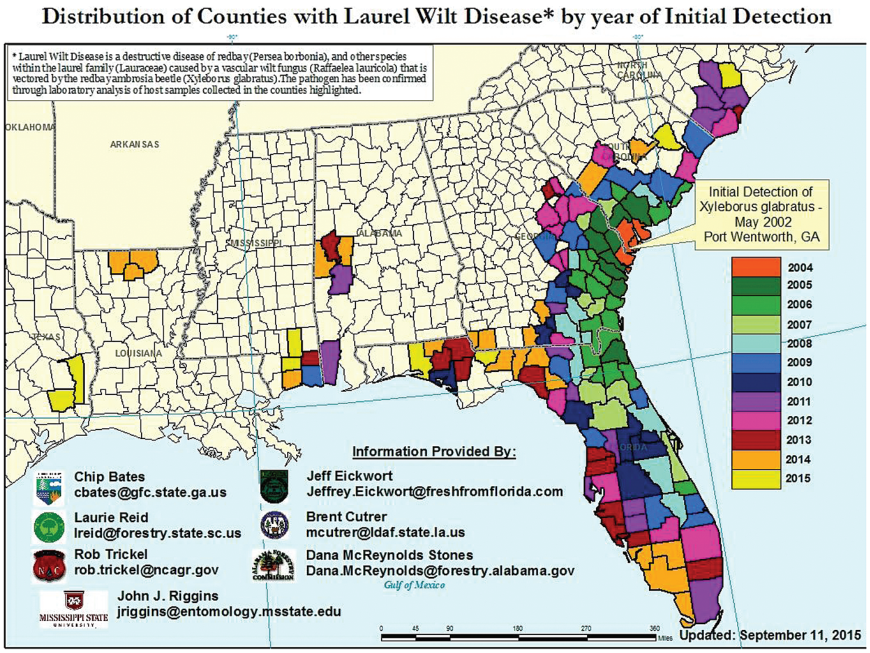

**Figure 1:** distribution of laurel wilt disease by county and year of initial detection (from Bates *et al.* 2015).

area. Conversely, the exotic *Cinnamomum camphora*, which is a closely related member of the Lauraceae (Chanderbali *et al.* 2001), has shown resistance to LWD. The few individuals which display signs of LWD infection show only minimal stem die-off (Smith *et al.* 2009a) whereas in other Lauraceae species, i.e. *Sassafras albidum*, the entire canopy succumbs to the disease (Smith *et al.* 2009b). Results from single point inoculation trials in the field and laboratory failed to produce LWD symptoms in *C. camphora* despite systemic colonization by *R. lauricola*; multiple point inoculations caused only localized branch dieback (Fraedrich *et al.* 2015).

*Cinnamomum camphora* is identified as an exotic invasive species in eight states of the southeastern USA, and its range is still expanding across this region. In Florida, *C. camphora* is naturalized in 27 counties but has been documented in nine others (USDA, NRCS 2014; Wunderlin and Hansen 2014). While it is often abundant in disturbed areas (e.g. roadsides and residential/commercial developments), including those of interest to the current study, large fruiting individuals are infrequently observed in relatively undisturbed forested habitats (A Chupp personal observation). Although preferences for *C. camphora* fruits have been observed in Asian and Australian bird species (Corlett 2005; Neilan *et al.* 2006), we found no documentation of North American bird preferences for the fruits of *C. camphora* or *P. borbonia*, only general accounts documenting the importance of *P. borbonia* fruits for wildlife (Brendemuehl 1990; Goodrum 1977).

In addition to *C. camphora*, *P. borbonia* also co-occurs with several other woody species including *Myrica cerifera* (native), and *Triadica sebifera* (exotic). All of these species have very similar fruiting phenologies and produce fruits that becomes ripe in late fall and are thus attractive to overwintering birds. However, similarities in fruit characteristics are greatest between *P. borbonia* and *C. camphora* which have similar size (5–10 mm), shape (round–oval), and color (dark blue–violet). In addition, individual trees of both species represent similar resource patches as equally sized trees produce a similar number of fruits (A Chupp personal observation). Based on these superficial characteristics, we hypothesized that the fruits of *P. borbonia* and *C. camphora* represent substitutable resources for overwintering birds. *Cinnamomum camphora* may be well-positioned to fill an ecological niche made available by widespread declines of *P. borbonia*.

Our primary objective was to compare interactions between frugivorous birds and native versus exotic plants prior to disturbance by LWD. Although individual bird species will differ in their preferences, our overarching hypothesis was that fruits of *P. borbonia* and *C. camphora* represent nearly substitutable resources (based on morphology and chemistry) and that fruit removal rates of *C. camphora* and *P. borbonia* by frugivorous bird species will be equivalent. Such findings would indicate that imminent LWD-induced declines of *P. borbonia* at our study site will favor increased interactions between frugivorous birds and *C. camphora*. Here, we report the first quantitative observations of bird frugivory on *P. borbonia* and *C. camphora* fruits in the southeastern USA and provide a forecast for the indirect effects of LWD on the consumption of native and exotic fruits.

## MATERIALS AND METHODS

### Study site

Bird frugivory was observed at Grand Bay National Estuarine Research Reserve (GBNERR) in Jackson County, Mississippi, USA. The study site corresponded to an area that was within 100 m of a 1.5 km stretch of Bayou Heron Road. The area included maritime forest, pine savanna and highly disturbed habitats (i.e. power line right-of-ways, parking lots and fire lanes). In this area, our focal species (*P. borbonia* and *C. camphora*) were common understory/subcanopy species. *Persea borbonia* was distributed throughout all habitat types whereas *C. camphora* was most often found along roadsides and other disturbed areas; *C. camphora* individuals were infrequently found in nonecotone zones of forested habitats. During transect surveys of the same forested habitats, *C. camphora* seedlings were rarely found, indicating that long distance dispersal is limited. Savannas consisted of a sparse slash pine overstory (*Pinus elliottii* Engelm.) and several native woody plants in the subcanopy and understory including *P. borbonia*, *M. cerifera*, *Ilex glabra* L., *Ilex vomitoria* Aiton, *C. camphora* and *T. sebifera*. We targeted bird species at GBNERR that are considered winter or permanent residents (Woodrey and Walker 2009), so observations were made during winter months (December–January). As such, we expected low day-to-day variability in local bird abundances relative to studies of birds along their fall migration route (Willson and Whelan 1993; Whelan and Willson 1994; Whelan *et al.* 1998).

### Artificial displays

During two winter seasons (December 2012–January 2013 and January 2014) we presented fruit of *P. borbonia* and *C. camphora* to free ranging birds on artificial infructescences. Similar displays have been successfully used to assess fruit choices of both captive and free-ranging migratory birds (Thompson and Willson 1978; Whelan and Willson 1994; Whelan *et al.* 1998). Fruit was collected from trees found in similar habitats adjacent to our study site. Each artificial infructescence consisted of a 1 cm diameter wooden dowel rod (30 cm in length) with 10 pieces of 16-gauge black wire (~8 cm in length) inserted perpendicularly through holes in the dowel rod (~2 cm between each hole). Wire pieces were inserted such that an equal portion of wire extended from each side of the dowel rod. Fruits were impaled on both ends of all 10 wires (20 fruits per infructescence). Fruits were only partially impaled so that they could be easily removed but also not fall off inadvertently. An artificial infructescence with fruits remaining is shown in Fig. 2.

### Fruit analyses

We also collected fruits of both *P. borbonia* and *C. camphora* for chemical and morphological analyses; enough fruits were

**Figure 2:** motion-activated photo of *Dumetella carolinensis* just prior to its removal of a *Cinnamomum camphora* fruit from an artificial infructescence during the selectivity experiment.

collected to obtain at least 10 g of dried pulp from each species. We used fruit from five individual trees for each species (~100–150 fruits per species) with at least 20 fruits collected from each tree. The pulp and seeds of these fruits were separated and dried to a constant weight at 55°C. The fruit pulp of both species was separately milled and shipped to Alkemist labs in Costa Mesa, CA and Covance Laboratories in Madison, WI where it was analyzed for total polyphenols (as gallic acid UV-Vis spectrophotometry) and nutritional content (calories, fat, carbohydrate, protein and moisture). Each analysis was based on one composite sample per species of fruit, except for total polyphenols for which four subsamples were taken from our single composite and analyzed separately.

A composite sample approach was required because of the small size of fruits and the amount of pulp required to generate accurate measurements of chemical traits (i.e. we could not obtain enough fruits from individual trees to make those trees our sample units). As such, we are unable to report variation in nutritional content. Although interspecific and seasonal variation in the nutritional contents of fruits is well documented (e.g. Herrera 1982, 1987), we found no prior evidence of significant intraspecific variation in nutritional characteristics that could affect removal rates by frugivorous birds (but see Jordano 1989, Cipollini and Whigham 1994). In Edgewater, Maryland, USA, the mineral content of pulp and seeds of *Lindera benzoin* (closely related to *P. borbonia* and *C. camphora*) did not vary significantly and was not affected by experimental thinning. Fruit crops of *Pistacia lentiscus* (*n* = 6 individual trees) in southwestern Spain showed minimal variation in pulp nutrient content which had no effect on removal rates by avian seed dispersers (Jordano 1989). Given these findings and the substantial number of fruits we used to form our samples, we are confident that the composite samples collected for each species and results of subsequent analyses are good representations for the nutritional values of these fruits within the geographic area that was sampled.

Methods of nutritional analyses follow AOAC (2005) International official methods of analysis (ash, fat by acid hydrolysis, moisture and protein [2005]), the Code of Federal Regulations (calories and calories from fat), and the USDA (carbohydrates [1973]). Variability in estimates produced from these methods range from 3% to 5% relative standard deviation (Covance Laboratories personal communication). For a subset of fruits (51 *P. borbonia* fruits and 52 *C. camphora* fruits), the seed and pulp were weighed separately and the pulp:seed ratio was calculated for each species.

## Selectivity experiment

Artificial infructescences were displayed on two different "background" species (*M. cerifera* and *T. sebifera*) that are very common at GBNERR. Both of these species produce waxy, lipid-rich fruits that are unlike the fleshy fruits of *P. borbonia* and *C. camphora* which likely contain much higher concentrations of carbohydrates (Place and Stiles 1992; Baldwin *et al.* 2008). All ripen during winter months. In a previous study that used the same type of artificial infructescences, birds were more likely to select fruits when they were presented with a background of fruits that were nutritionally complementary (Whelan *et al.* 1998). We used nutritional complementarity as one criterion for selecting the background tree species mentioned above. We also considered fruit color when selecting background trees. Birds have excellent color vision and although bird foraging patterns are regulated by several factors (described above), fruit color and conspicuousness are key signals used during the selection process (Schmidt *et al.* 2004). Refinements of the cone and a system of oil droplets indicate that bird eyes can distinguish more hues than what human eyes are capable of seeing (Vorobyev *et al.* 1998). These optical enhancements should allow birds to identify much greater differences in what we perceive as similarly colored fruit, such as those displayed during this study (*P. borbonia* (blue hues) and *C. camphora* (violet hues). It should also be noted that while these fruits have darker hues, the fruits of our background species (*T. sebifera* and *M. cerifera*) have light gray-white colored fruits and should therefore increase the conspicuousness of displayed fruit to frugivorous birds. Across both years of our survey we used 66 different background trees (*M. cerifera*, *n* = 32; *T. sebifera*, *n* = 34). These trees were dispersed throughout our survey area and each tree contained an abundant fruit crop. All background trees were >20 m apart. Trees of each species were selected so that no fruit-bearing individuals of the other species were within 20 m.

The artificial infructescences were displayed for 3–5 days at a time, after which new background trees were selected. Displays placed on different individual trees were considered replicates (one display per tree). During survey periods, we always had an equal number of replicates on each background species. We began deploying 10 replicate displays at a time but later increased the sample size to 12. Each display contained an equal number of *P. borbonia* and *C. camphora* fruits, which were kept separate on opposite sides of the display. Artificial infructescences were attached to background tree branches with rubber bands. Because accessibility can impact the removal of fruits by captive and free-ranging birds (e.g. Whelan and Willson 1994), we were careful to place displays in positions where perches were available for birds to easily access both sides of the display. Displays were checked each day at sunset or just after (17:00–18:00 h). At this time, we recorded the number of fruits taken of each species and replaced all removed fruits.

### Fruit accessibility experiments

After determining the relative preferences of *P. borbonia* and *C. camphora* fruits when both are equally accessible, we used a behavioral titration approach to determine the strength of these preferences (after Moermond and Denslow 1983; Whelan and Willson 1994). In January 2014, we used a subset of background trees (*M. cerifera* and *T. sebifera*) that received high levels of bird activity during previous selectivity experiments. We placed fruit of the more preferred species in less accessible positions. These less accessible displays were hung vertically from the bottom of a perpendicular branch such that no perches were within 20 cm of the fruit on display. At the same time, displays containing fruit of the less preferred species were hung in a highly accessible position as described above. Therefore, two displays, each containing 20 fruit of one species, were simultaneously placed on each background tree. Displays were left in this arrangement for 2–3 days. We then repeated these trials but with the accessibility of species switched. Displays were checked at sunset as described above.

### Camera trapping

During 10 days of our survey in January 2014, we used a motion/heat activated camera to document fruit removal by bird species. The camera monitored displays during both selectivity and accessibility experiments. We chose to monitor displays on background trees that received the highest rates of fruit removal. The camera (NatureView HD 119438, Bushnell, Kansas, USA) was mounted on a tripod and placed 1–2 m from a display. We set the camera to take three pictures in rapid succession (3 s) followed by a 2 s delay before more pictures could be triggered. The camera was active from sunrise to sunset. Photos were used (i) to verify visitation by specific species, (ii) to determine the relative frequency that each species visited displays, and (iii) to document patterns of fruit removal and selectivity during individual foraging bouts. We considered a foraging bout to be any continuous series of photographs (not separated by more than 2 minu) capturing the same species. Within a given foraging bout, the number of fruits removed was determined by examining the first and last images of the series. In cases where these details were indiscernible, fruit preferences could not be calculated for these foraging bouts and were therefore discarded. Because individuals could not be identified in photographs, it is possible that some individuals were represented in more than one foraging bout.

### Statistical analyses

Relative preferences were quantified with Manly's $\alpha$ (Manly *et al.* 1972) which can be adapted for situations where food is depleted over the course of daily foraging bouts (Chesson 1983). Manly's $\alpha$ ranges from 0 to 1; $\alpha = 0$ when the food type is not represented in the diet and $\alpha = 1$ when it is the only food type in the diet (Chesson 1983). Results from the same background tree during 3–5 day periods were pooled and $\alpha$ was calculated from these summed data. Because fruit removal rates may be affected by temperature (e.g. Kwit *et al.* 2004), we examined winter temperatures across both years of our survey. Winter temperatures were calculated as mean daily temperature (average of daily high and low) for each day that our displays were active (obtained from NOAA NERR CDMO 2014). We compared mean daily temperatures between the 2 years of our selectivity experiments using an independent sample *t*-test.

Because $\alpha$ is calculated as a proportion of fruits removed, we performed arcsine square root transformations to meet assumptions of homoscedasticity and normality. For the results of our selectivity experiments, a two-way analysis of variance (ANOVA) was used to compare differences in $\alpha$ across years and types of background trees. One-sample *t*-tests were used to examine significant effects more closely; within each treatment we tested if $\alpha$ significantly differed from 0.5 ($\alpha = 0.5$ = no preference). The direction of significant differences indicated whether the fruits of *P. borbonia* or *C. camphora* were preferred ($\alpha < 0.5$ = preference for *C. camphora*, $\alpha > 0.5$ = preference for *P. borbonia*). Results from Wilcoxon Signed Rank tests were used if departures from normality were still detected after the data were transformed. A two-way ANOVA was also used to assess the effect of fruit accessibility and tree background on $\alpha$. Again, any significant effects were further analyzed with one-sample *t*-tests.

Manly's $\alpha$ was also calculated for individual foraging bouts that were captured on camera. In many cases, birds removed only one species of fruit during an individual foraging bout. As such, $\alpha$ values were often either 0 or 1 depending on whether the bird selected *P. borbonia* or *C. camphora*. In some cases, birds selected both types of fruit or did not remove any fruit at all. Contingency tables (2 × 3) and Pearson's chi-squared tests were used to determine if the number of foraging bouts observed differed among the following foraging bout types: (i) no removal of either fruit,

(ii) removal of both fruit types, and (iii) removal of just one species of fruit. One contingency table was constructed for each of the three experimental treatment types (equal accessibility, *P. borbonia* less accessible, and *C. camphora* less accessible). A Pearson's chi-squared test was also used to determine if the frequency of foraging bouts observed differed between cases when just *P. borbonia* was removed versus those in which only *C. camphora* was removed. Within each experimental treatment, Wilcoxon Signed Rank tests were used to examine if $\alpha$ significantly deviated from 0.5 for each species in which five or more foraging bouts were observed.

Differences in pulp and seed dry weight and pulp:seed ratio between species were examined using *t*-tests. Statistical differences in total polyphenols between species were not examined because subsamples obtained from the same composite sample were not independent of one another. All statistical tests and data transformations were conducted using SAS 9.3 statistical software (SAS Institute Inc. 2011).

# RESULTS

## Fruit analyses

Percent total polyphenol was more than three time higher for *C. camphora* than *P. borbonia* (Table 1). The pulp of individual *C. camphora* fruits was significantly heavier than that of *P. borbonia* ($t$ = 11.07, $P < 0.001$) whereas *C. camphora* seeds were significantly lighter ($t$ = 13.03, $P < 0.001$). The pulp:seed ratio was higher for *C. camphora* (0.995) compared to *P. borbonia* (0.337) ($t$ = 29.15, $P < 0.001$).

## Selectivity experiments

In December and January of 2012/2013 (Year 1), 3480 *P. borbonia* and *C. camphora* fruits (1740 of each species) were presented on displays. Displays were hung in 50 different background trees (25 *M. cerifera* trees and 25 *T. sebifera* trees). Across 16 days, birds removed 15.4% of fruits that were displayed, 249 *P. borbonia* fruits and 286 *C. camphora* fruits (Table 2). In January of 2014 (Year 2), 2280 total fruits (1140 of each species) were displayed on 22 different background trees (11 of each species). Birds removed 29.1% of fruits that were displayed, 237 *P. borbonia* and 427 *C. camphora* fruits (Table 2). Manly's $\alpha$ differed between years (ANOVA: $F_{1,43}$ = 5.95, $P$ = 0.019) but did not differ between background tree species (ANOVA: $F_{1,43}$ = 2.65, $P$ = 0.112). Manly's $\alpha$ did not significantly differ from 0.5 (i.e. no preference) in Year 1 of our survey ($t$ = 0.18, $P$ = 0.86) but it did differ from 0.5 in Year 2 ($t$ = −4.42, $P < 0.001$), when more *C. camphora* fruits were consumed. Manly's $\alpha$ calculated for *P. borbonia* was 0.31 ± 0.04 (mean ± SE) and therefore *C. camphora* fruits were more preferred ($\alpha = 0.69 \pm 0.04$) in Year 2. During the periods in which selectivity experiments were active, mean daily temperature was significantly higher in Year 1 (13.1 ± 1.0°C) compared to Year 2 (6.7 ± 1.8°C) ($t$ = 3.16, $P$ = 0.006) (Fig. 3). The 30-year average (1981–2010) mean daily temperature for the same active days at this site (days of the month in which experiments were active) is 10.0 ± 0.2°C (NOAA NCEI 2015).

**Table 1:** chemical properties of pulp and mass of *Cinnamomum camphora* and *Persea borbonia* fruits

| | *C. camphora* | *P. borbonia* |
|---|---|---|
| Calories (Cal/100 g) | 476 | 566 |
| Calories from fat (Cal/100 g) | 239 | 340 |
| Fat (g/100 g) | 26.6 | 37.8 |
| Carbohydrates (g/100 g) | 52.8 | 49.8 |
| Protein (g/100 g) | 6.42 | 6.62 |
| Moisture (g/100 g) | 5.02 | 1.77 |
| Total polyphenols (%) | 1.76 ± 0.37 | 0.54 ± 0.08 |
| Pulp dry weight (g) | $0.114 \pm 0.002^{a}$ | $0.074 \pm 0.003^{b}$ |
| Seed dry weight (g) | $0.115 \pm 0.002^{a}$ | $0.230 \pm 0.009^{b}$ |
| Pulp:seed ratio | $0.995 \pm 0.018^{a}$ | $0.337 \pm 0.014^{b}$ |

Total polyphenols, dry weights, and pulp:seed ratio are shown as mean ± standard error. Significant differences between fruits of each species ($P < 0.05$) are indicated with different letters.

## Fruit accessibility experiments

In January 2014, displays were placed in 10 different background trees (6 *T. sebifera* and 4 *M. cerifera*). Twenty different trials were conducted over a 14-day period: 10 trials where *C. camphora* fruits were highly accessible and *P. borbonia* fruits were less accessible, and 10 trials where fruit accessibility was switched. We presented a total of 860 fruits of each species, and birds removed 545 fruits of *P. borbonia* and 671 fruits of *C. camphora* (Table 2). Background tree type and fruit accessibility had no effect on $\alpha$ (respectively, ANOVA: $F_{1,16}$ = 2.87, $P$ = 0.110; $F_{1,16}$ = 0.02, $P$ = 0.89). However, a *t*-test revealed that $\alpha$ (0.40 ± 0.04) significantly deviated from 0.5 ($t$ = −2.32, $P$ = 0.032), indicating a preference for *C. camphora* fruits during these trials.

## Camera trapping

During both selectivity and accessibility experiments, we recorded a total of 1139 photographs of the following bird species: gray catbird (*Dumetella carolinensis*), American robin (*Turdus migratorius*), hermit thrush (*Catharus guttatus*), brown thrasher (*Toxostoma rufum* L.), and eastern towhee (*Pipilo erythrophthalmus* L.). *Turdus migratorius* was represented in the greatest number of photos (44%), followed by *D. carolinensis* (36%) and *C. guttatus* (14%). From these photos, we identified a total of 59 individual foraging bouts that allowed for an accurate count of fruit removed. The number of foraging bouts was greatest for *D. carolinensis* (31) (shown in Fig. 2), followed by *T. migratorius* (18) and *C. guttatus* (9). No foraging bouts were recorded for *P. erythrophthalmus* (Table 3). During accessibility experiments, there were significantly more foraging bouts where only one fruit type was removed compared to those in which both types of fruit were removed and cases where no fruit was removed. However, there was

**Table 2:** results of selectivity and accessibility experiments

| | Selectivity experiments | | Accessibility experiments | |
|---|---|---|---|---|
| | Year 1 | Year 2 | *Persea borbonia* less accessible | *Cinnamomum camphora* less accessible |
| Fruits presented | | | | |
| *P. borbonia* | 1740 | 1140 | 360 | 500 |
| *C. camphora* | 1740 | 1140 | 360 | 500 |
| Fruits removed | | | | |
| *P. borbonia* | 249 (14%) | 237 (21%) | 300 (83%) | 245 (49%) |
| *C. camphora* | 286 (16%) | 427 (37%) | 348 (97%) | 323 (65%) |
| Mean $\alpha$ | $0.51 \pm 0.06$ | $0.31 \pm 0.04$** | $0.41 \pm 0.05$* | $0.40 \pm 0.07$* |

Selectivity experiments were conducted in December 2012–January 2013 (Year 1) and January 2014 (Year 2). Accessibility experiments were completed in January 2014. No fruit preference occurred when $\alpha = 0.50$; $\alpha < 0.50$ indicated a preference for *C. camphora* fruit and $\alpha > 0.50$ suggested a preference for *P. borbonia* fruit. Significant preference indicated with *$P < 0.05$, **$P < 0.001$.

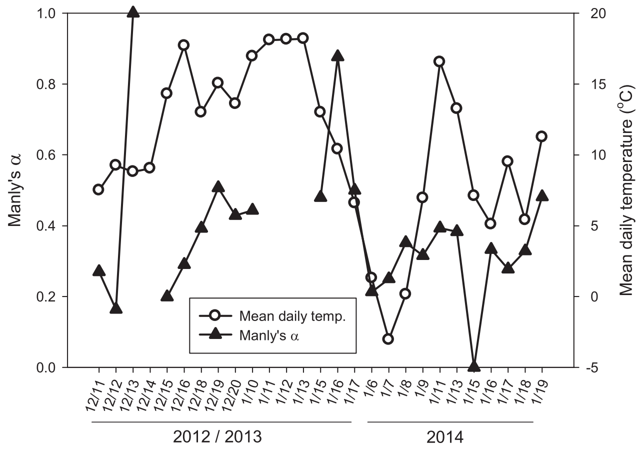

**Figure 3:** Mean daily temperatures (°C) and Manly's $\alpha$ as calculated from each day of the selectivity experiements. No fruit preference occurred when $\alpha = 0.50$; $\alpha < 0.50$ indicates a preference for *Cinnamomum camphora* fruit and $\alpha > 0.50$ suggests a preference for *P. borbonia* fruit. The first survey year (2012/2013) is shown on the left and the second year (2014) is on the right.

no difference in the number of foraging bouts in which *P. borbonia* or *C. camphora* were preferred ($\chi^2 < 3.84$, $P > 0.05$).

Across the three experimental types, there were five cases where five or more foraging bouts by the same species were captured in photos. The most foraging bouts were recorded for *D. carolinensis*, which had five or more bouts in each of the three experimental types. In the experiments in which *P. borbonia* fruit was less accessible, photos also captured at least five bouts by *T. migratorius* and *C. guttatus* (Table 3). In each case where at least five bouts were recorded ($n = 5$), $\alpha$ values calculated from the individual foraging bouts did not significantly differ from 0.5 ($P > 0.05$), indicating no evidence of fruit type preference.

## DISCUSSION

Results from both field trials and laboratory analyses indicate that the fruits of *P. borbonia* (native) and *C. camphora* (exotic) represent nearly substitutable resources for over-wintering birds; we observed similar rates of removal in the field and similar fruit characteristics (physical and chemical) in the laboratory. The results of our experiments represent the aggregated preferences of at least four over-wintering bird species (*D. carolinensis*, *T. migratorius*, *C. guttatus* and *T. rufum*). One or more foraging bouts were photographed for each of these species. Photographs of *D. carolinensis*, *T. migratorius* and *C. guttatus* documented removal of both *P. borbonia* and *C. camphora* fruits by each species across multiple foraging bouts. These generalist frugivores are known to forage on the fruit of many woody species including non-native species *Lonicera maackii* Rupr., *Lonicera morrowii* A. Gray and *T. sebifera* (Bartuszevige and Gorchov 2006; Gleditsch and Carlo 2011; Renne *et al.* 2002). Observations showed that these bird species removed and dispersed viable seeds thus increasing the invasiveness of these exotic plant species (Bartuszevige and Gorchov 2006; Gleditsch and Carlo 2011; McCay *et al.* 2009; Renne *et al.* 2002). Here, our results suggest that the same native birds may also be aiding the long-distance dispersal of *C. camphora*. While studies from Asia and Australia show that birds may quickly regurgitate or defecate *C. camphora* seeds, experiments with South African bird species suggested long seed retention times (10–55 min) which did not significantly vary among species (Firth 1981; Jordaan *et al.* 2011; Li 2004). In addition, passage through guts of South African bird species removed pulp from *C. camphora* seeds and increased germination rates (Jordaan *et al.* 2011). The manual removal of pulp also dramatically increased germination rates in *C. camphora* (Jordaan *et al.* 2011; Panetta 2001). The pulp of *C. camphora* decomposes slowly and the majority of seeds lose viability prior to pulp decomposition (1% viable after 12 months), thus indicating that frugivory is necessary for recruitment of this species which may rely little on seedbanks (Panetta 2001). Based on the these observations, it is apparent that some generalist birds have formed mutualisms with the exotic *C. camphora*, benefiting from the resources found in *C. camphora* fruit pulp and dispersing viable seeds. Although we lack the data to make a similar assertion on the Gulf Coastal Plain, the regular and consistent removal of *C. camphora* fruits by at least four

**Table 3:** observations collected from photos across three experimental types for each bird species

| | | | Fruit removed | | |
|---|---|---|---|---|---|
| Species | Photos | Foraging bouts | *Persea borbonia* | *Cinnamomum camphora* | Manly's $\alpha$ |
| Selectivity experiment | | | | | |
| *Turdus migratorius* | 23 | 2 | 2 | 1 | 0.50 ± 0.50 |
| *Dumetella carolinensis* | 107 | 12 | 8 | 17 | 0.36 ± 0.13 |
| *Catharus guttatus* | 41 | 1 | 1 | 0 | 1 |
| Accessibility experiment (*P. borbonia* less accessible) | | | | | |
| *T. migratorius* | 440 | 15 | 12 | 41 | 0.37 ± 0.12 |
| *D. carolinensis* | 201 | 7 | 8 | 5 | 0.64 ± 0.18 |
| *C. guttatus* | 105 | 5 | 7 | 3 | 0.69 ± 0.20 |
| *Toxostoma rufum* | 53 | 1 | 0 | 1 | 0 |
| Accessibility experiment (*C. camphora* less accessible) | | | | | |
| *T. migratorius* | 26 | 1 | 1 | 0 | 1 |
| *D. carolinensis* | 117 | 12 | 21 | 4 | 0.72 ± 0.13 |
| *C. guttatus* | 19 | 3 | 1 | 6 | 0.03 ± 0.03 |
| *T. rufum* | 4 | 0 | 0 | 0 | NA |
| *Pipilo erythrophthalmus* | 3 | 0 | 0 | 0 | NA |
| Total | 1139 | 59 | 61 | 78 | 0.53 ± 0.11 |

Manly's $\alpha$ was averaged (± standard error) across foraging bouts for each species within each experimental type.

native generalist birds during our surveys is indicative of similar relationships.

Despite the apparent redundancy in the characteristics of *P. borbonia* and *C. camphora* fruit, nutritional differences on a per fruit basis may affect preferences of energetically stressed birds and the relative dispersal rates of these species. Exotic species that have relatively smaller seeds and offer more pulp sugar per fruit than indigenous species may have greater invasion potential (Gosper and Vivian-Smith 2010). Although the removal rate of non-native *C. camphora* fruit was generally similar to that of indigenous *P. borbonia* fruit, removal rates of *C. camphora* fruits showed a significant increase during the second year of our selectivity experiments. This experimental period, where these fruits were clearly preferred over those of *P. borbonia*, coincided with significantly lower mean daily temperatures relative to the first year of our survey; compared to 30-year averages for the same dates, mean daily temperatures were on average 3.1°C higher during the first year of our survey and 3.3°C lower during the second year. Because low temperatures increase the energy demands of birds (Calder and King 1974) and reduce the abundance of insects upon which they feed (Thompson and Willson 1979), lower temperatures should increase dependence on fruit as a resource subsidy. A 9-year study of *M. cerifera* in South Carolina showed that mean time to fruit removal by birds was positively correlated with mean winter temperature (Kwit *et al.* 2004); likewise the percentage of fruit removed nearly doubled in the second, colder year of our survey. Birds may choose those fruits with the highest nutritional rewards, especially in periods of extreme energetic demand (e.g. cold temperatures and/or during migration). We suspect that the greater nutritional rewards offered by individual *C. camphora* fruits led to greater consumption during the coldest period of our survey. While fruits of each species contained similar nutritional contents per unit mass, individual *C. camphora* fruits had considerably larger pulp:seed ratios than *P. borbonia* fruits. On average, each *C. camphora* fruit contained 40 mg more dry pulp than *P. borbonia* fruits (Table 1). We also note that moisture content (per unit mass) was nearly three times higher in the pulp of *C. camphora* fruits and could also be an attractive quality during times when other sources of water are less available.

There are other chemical constituents of fruit that may increase preferences depending on metabolic demands. The fruit pulp of *C. camphora* contained more than three times the amount of total polyphenols compared to *P. borbonia* (Table 1). Studies have shown that temperate frugivorous birds prefer diets that are supplemented with polyphenols and other classes of antioxidant compounds such as anthocyanins, carotenoids and flavonoids (Bolser *et al.* 2013; Cantoni *et al.* 2008; Schaefer *et al.* 2008; Senar *et al.* 2010). In addition to polyphenols, it is likely that the fruits of *C. camphora* are enriched with these and other antioxidant compounds. The oils produced in the tissues of *C. camphora* have been used as healing agents in Asian cultures for centuries (Lawless 2013). Recent work using the cells of mice and human lung tissue has provided scientific evidence of the anti-inflammatory and antioxidant effects of *C. camphora* extracts (Hu *et al.* 2011; Lee *et al.* 2006). Interestingly, the seed oil of *C. camphora* contains extremely high levels of medium-chain triacylglycerol, which is very stable to oxidative reduction (Hu *et al.* 2011). While cellular level analyses have not been conducted on the tissues of birds, we suspect that these chemical characteristics of *C. camphora* fruit make it an attractive dietary supplement for frugivorous birds, especially during periods of elevated oxidative stress (e.g. during migration and extreme cold).

In some situations, frugivorous birds may become dependent on the resources provided by the fruits of *C. camphora* and other exotic plant species. In northern New South Wales, Australia, the fruits of *C. camphora* are the principal dietary component of several native bird species. Date *et al.* (1996) concluded that the presence of *C. camphora* was important for buffering these fauna against the effects of widespread habitat destruction. In Pennsylvania USA, greater local abundance of native bird species was due to the presence of exotic fruiting *Lonicera* spp. (Gleditsch and Carlo 2011). There are numerous studies that have shown how novel exotic plant species can provide beneficial ecological functions for native birds (Jones and Bock 2005; Impey *et al.* 2002). Examples such as these have ignited a growing interest and considerable debate over the value of non-native species and the novel interactions they form with native species (Hallett *et al.* 2013). Despite concern over the proliferation of exotics and their effects on native species, there has been a shift toward thinking about the services exotic species provide, especially in cases where restoration is not economically feasible (Hobbs *et al.* 2009). In situations where a key or dominant native is inevitably in decline, understanding how exotic species may provide functional redundancy is especially important; resources provided by exotic species could prevent the co-extinction/extirpation of other native species. We argue that while the decline of *P. borbonia* fruits due to LWD may not threaten the survival of generalist frugivorous, *C. camphora* fruits offer a substantial resource that may become increasingly necessary for maintaining healthy populations of overwintering birds. Increased consumption and dispersal of exotic *C. camphora* fruits/seeds due to impacts from an exotic pathogen would be a novel example of exotic-exotic facilitation mediated by bird frugivory (e.g. Simberloff and VonHolle 1999).

The empirical observations reported here highlight the potential for invasive pests/pathogens to facilitate other biological invasions. We expect the initial biological invasion (LWD) to ultimately facilitate an increase in the invasion potential of an exotic plant (*C. camphora*) whose propagules are now being more readily consumed and dispersed. In addition to providing timely ecological data prior to the arrival of LWD, we have also provided the first quantitative accounts of interactions between several native bird species and both *P. borbonia* and *C. camphora*. While our results suggest that current relationships between native bird species and *C. camphora* may cause increases in the dispersal of this exotic species and therefore competition with native plants, we encourage consideration for the potential benefits these fruits are simultaneously providing to overwintering birds, especially as fruits of *P. borbonia* become increasingly scarce due to LWD. Finally, we urge conservation biologists/ecologists, land managers and administrators to consider the potential indirect effects of exotic forest pests and pathogens that are mediated by frugivory and seed dispersal.

## FUNDING

This research was conducted in the National Estuarine Reserve System under an award from the Estuarine Reserves Division, Office of Ocean and Coastal Resource Management, National Ocean Service, National Oceanic and Atmospheric Administration (Award #NA11NOS4200080).

## ACKNOWLEDGEMENTS

We thank Will Underwood and Mark Woodrey for their logistical assistance at Grand Bay National Estuarine Research Reserve. We also thank Chris Whelan for productive discussions concerning methodological approaches and Charlie Kwit for helpful suggestions on a previous version of this manuscript.

*Conflict of interest statement*. None declared.

## REFERENCES

Anagnostakis SL (1987) Chestnut blight: the classical problem of an introduced pathogen. *Mycologia* **79**:23–37.

Aslan CE, Zavaleta ES, Tershy B, Croll D (2013) Mutualism disruption threatens global plant biodiversity: a systematic review. *PLOS ONE* **8**: e66993.

Association of Analytical Communities (AOAC) (2005) *Official Methods of Analysis*, 18th edn. Gaithersburg, MD: AOAC International.

Baldwin MJ, Barrow WC Jr, Jeske C, *et al.* (2008) Metabolizable energy in Chinese tallow fruit for yellow-rumped warblers, northern cardinals, and American robins. *Wilson J Ornithol* **120**:525–30.

Bartuszevige AM, Gorchov DL (2006) Avian seed dispersal of an invasive shrub. *Biol Invasions* **8**:1013–22.

Bates C, Eickwort J, Reid L, *et al*. (2015) Distribution of counties with Laurel Wilt Disease by year of Initial Detection (map). http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/stelprd3856318.pdf (5 January 2016, date last accessed).

Bolser JA, Alan RR, Smith AD, *et al.* (2013) Birds select fruits with more anthocyanins and phenolic compounds during autumn migration. *Wilson J Ornithol* **125**:97–108.

Brendemuehl RH (1990) *Persea borbonia* (L.) Spreng. Redbay. In Burns RM, Honkala LH (eds). *Silvics of North America, Vol. II, Hardwoods, Agricultural Handbook 654*. Washington, DC: US Government Printing Office, 503–6.

Calder WA, King JR (1974) Thermal and caloric relations of birds. In Farner DS, King JR (eds). *Avian Biology*, Vol. **14**. New York, NY: Academic Press, 259–413.

Cantoni C, Schaefer HM, Peters A (2008) Fruit for health: the effect of flavonoids on humoral immune response and food selection in a frugivorous bird. *Funct Ecol* **22**:649–54.

Carlo TA, Aukema JE, Morales JM (2007) Plant–frugivore interactions as spatially explicit networks: integrating frugivore foraging with fruiting plant spatial patterns. In Dennis AJ, Green RJ, Schupp EW (eds). *Seed Dispersal: Theory and Its Application in a Changing World*. Wallingford, UK: Cabi, 369–90.

Chanderbali AS, Van der Werff H, Renner SS (2001) Phylogeny and historical biogeography of Lauraceae: evidence from the chloroplast and nuclear genomes. *Ann Mo Bot Gard* **88**:104–34.

Chesson J (1983) The estimation and analysis of preference and its relationship to foraging models. *Ecology* **64**:1297–304.

Chupp AD, Battaglia LL (2014) Potential for host-shifting in *Papilio palamedes* following invasion of laurel wilt disease. *Biol Invasions* **16**:2639–51.

Chupp AD, Battaglia LL, Schauber EM, *et al*. (2015) Orchid-pollinator interactions and potential vulnerability to biological invasion. *AoB Plants* **7** plv099.

Cipollini ML, Levey DJ (1997) Secondary metabolites of fleshy vertebrate-dispersed fruits: adaptive hypotheses and implications for seed dispersal. *Am Nat* **150**:346–72.

Cipollini ML, Whigham DF (1994) Sexual dimorphism and cost of reproduction in the dioecious shrub *Lindera benzoin* (Lauraceae). *Am J Bot* **81**:65–75.

Corlett RT (2005) Interactions between birds, fruit bats and exotic plants in urban Hong Kong, South China. *Urban Ecosyst* **8**:275–83.

Cronk QCB, Fuller JL (1995) *Plant Invaders: The Threat to Natural Ecosystems*. London, UK: Chapman and Hall.

Date EM, Recher HF, Ford HA, *et al*. (1996) The conservation and ecology of rainforest pigeons in north-eastern New South Wales. *Pacific Conserv Biol* **2**:299–308.

Debussche M, Isenmann P (1990) Introduced and cultivated fleshy-fruited plants: consequences of a mutualistic Mediterranean plant-bird system. In Di Castri F, Hansen AJ, Debussche M (eds). *Biological Invasions in Europe and the Mediterranean Basin*. Dordrecht, the Netherlands: Kluwer Academic Publishers, 399–416.

Dunn CP (1986) Shrub layer response to death of *Ulmus americana* in southeastern Wisconsin lowland forests. *Bull Torrey Bot Club* **113**:142–8.

Ellison AM, Bank MS, Clinton BD, *et al*. (2005) Loss of foundation species: consequences for the structure and dynamics of forested ecosystems. *Front Ecol Environ* **3**:479–86.

Evans JP, Scheffers BR, Hess M (2014) Effect of laurel wilt invasion on redbay populations in a maritime forest community. *Biol Invasions* **16**:1581–88.

Firth DJ (1981) Camphor laurel (*Cinnamomum camphora*): a new weed in north-eastern New South Wales. *Aust Weeds* **1**:26–8.

Fraedrich SW, Harrington TC, Best GS (2015) *Xyleborus glabratus* attacks and systemic colonization by *Raffaelea lauricola* associated with dieback of *Cinnamomum camphora* in the southeastern United States. *Forest Pathol* **45**:60–70.

Fraedrich SW, Harrington TC, Rabaglia RJ, *et al*. (2008) A fungal symbiont of the redbay ambrosia beetle causes a lethal wilt in redbay and other Lauraceae in the southeastern United States. *Plant Dis* **92**:215–24.

Gandhi KJK, Herms DA (2010) Direct and indirect effects of alien insect herbivores on ecological processes and interactions in forests of eastern North America. *Biol Invasions* **12**:389–405.

Gleditsch JM, Carlo TA (2011) Fruit quantity of invasive shrubs predicts the abundance of common native avian frugivores in central Pennsylvania. *Divers Distrib* **17**:244–53.

Goodrum PD (1977) Redbay/*Persea borbonia* (L.) Spreng. In southern fruit-producing, woody plants used by wildlife. *General Technical Report SO-16*. USDA Forest Service, 65.

Gosper CR, Vivian-Smith G (2010) Fruit traits of vertebrate-dispersed alien plants: smaller seeds and more pulp sugar than indigenous species. *Biol Invasions* **12**:2153–63.

Hallett LM, Standish RJ, Hulvey KB, *et al*. (2013) Towards a conceptual framework for novel ecosystems. In Hobbs RJ, Higgs ES, Hall CM (eds). *Novel Ecosystems: Intervening in the New Ecological World Order*. Chichester, UK: Wiley-Blackwell, 16–28.

Herrera CM (1982) Seasonal variation in the quality of fruits and diffuse coevolution between plants and avian disersers. *Ecology* **63**:773–85.

Herrera CM (1987) Vertebrate-dispersed plants of the Iberian Peninsula: a study of fruit characteristics. *Ecol Monograph* **57**:305–31.

Hobbs RJ, Higgs E, Harris JA (2009) Novel ecosystems: implications for conservation and restoration. *Trends Ecol Evol* **24**:599–605.

Houston DR, Parker EJ, Lonsdale D (1979) Beech bark disease: patterns of spread and development of the initiating agent *Cryptoccus fagisuga*. *Can J Forest Res* **18**:38–42.

Hu J-N, Zhang B, Zhu X-M, *et al*. (2011) Characterization of medium-chain triacylglycerol (MCT)-enriched seed oil from *Cinnamomum camphora* (Lauraceae) and its oxidative stability. *J Agric Food Chem* **59**:4771–8.

Impey AJ, Cote IM, Jones CG (2002) Population recovery of the threatened endemic Rodriques fody (*Foudia flavicans*) (Aves, Ploceidae) following reforestation. *Biol Conserv* **107**:299–305.

Jones ZF, Bock CE (2005) The Botteri's Sparrow and exotic Arizona grasslands: an ecological trap or habitat regained? *Condor* **107**:731–41.

Jordaan LA, Johnson SD, Downs CT (2011) The role of avian frugivores in germination of seeds of fleshy-fruited invasive alien plants. *Biol Invasions* **13**:1917–30.

Jordano P (1989) Pre-dispersal biology of *Pistacia lentiscus* (Anacardiaceae): cumulative effects on seed removal by birds. *Oikos* **55**:375–86.

Jordano P (1995) Angiosperm fleshy fruits and seed dispersers: a comparative analysis of adaptation and constraints in plant–animal interactions. *Am Nat* **145**:163–91.

Kwit C, Levey DJ, Greenberg CH, *et al*. (2004) Cold temperature increases winter fruit removal rate of a bird-dispersed shrub. *Oecologia* **139**:30–4.

Lawless J (2013) *The Encyclopedia of Essential Oils: The Complete Guide to the Use of Aromatic Oils in Aromatherapy, Herbalism, Health and Well-being*. Berkeley, CA: Conari Press.

Lee HJ, Hyuna EA, Yoon WJ, *et al*. (2006) In vitro anti-inflammatory and antioxidative effects of *Cinnamomum camphora* extracts. *J Ethnopharmacol* **103**:208–16.

Li X-H (2004) Avian seed dispersal of the camphor tree (*Cinnamomum camphora*). In *Workshop on Seed Dispersal and Frugivory in Asia*. Xishuangbanna, Yunnan, China: Xishuangbanna Tropical Botanical Garden, CAS, pp. 12–13.

Lovett GM, Canham CD, Arthur MA, *et al*. (2006) Forest ecosystem responses to exotic pests and pathogens in eastern North America. *BioScience* **56**:395–405.

Manly BFJ, Miller P, Cook LM (1972) Analysis of a selective predation experiment. *Am Nat* **106**:719–36.

Mayfield AE III (2008) Laurel wilt. In *Forest and Shade Tree Pests*, leaflet number 13. Tallahassee, FL: Florida Department of Agriculture and Consumer Services, Division of Forestry.

McCay TS, McCay DH, Czajka JL (2009) Deposition of exotic bird-dispersed seeds into three habitats of a fragmented landscape in the northeastern United States. *Plant Ecol* **203**:59–67.

Moermond TC, Denslow JS (1983) Fruit choice in neotropical birds: effects of fruit type and accessibility on selectivity. *J Anim Ecol* **52**:407–20.

Murray KG (1987) Selection for optimal fruit-crop size in bird-dispersed plants. *Am Nat* **129**:18–31.

National Oceanic Atmospheric Administration, National Centers for Environmental Information (NOAA NCEI) (2015) *Pascagoula 3 NE, MS, US Station Normals of Temperature, Precipitation, and Heating and Cooling Degree (1981–2010)*. http://www.ncdc.noaa.gov/cdo-web/datasets/NORMAL_DLY/stations/GHCND:USC00226718/detail (25 June 2015, date last accessed).

National Oceanic Atmospheric Administration, National Estuarine Research Reserve, Centralized Data Management Office (NOAA NERR CDMO) (2014) *Grand Bay National Estuarine Research Reserve, Crooked Bayou Meteorological Station*. http://cdmo.baruch.sc.edu/get/export.cfm (19 February 2014, date last accessed).

Neilan W, Catterall CP, Kanowski J, *et al.* (2006) Do frugivorous birds assist rainforest succession in weed dominated oldfield regrowth of subtropical Australia? *Biol Conserv* **129**:393–407.

Ortiz-Pulido R, Albores-Barajas YV, Diaz SA (2007) Fruit removal efficiency and success: influence of crop size in a neotropical treelet. *Vegetatio* **189**:147–54.

Panetta FD (2001) Seedling emergence and seed longevity of the tree weeds *Celtis sinensis* and *Cinnamomum camphora*. *Weed Res* **41**:83–95.

Place AR, Stiles EW (1992) Living off the wax of the land: bayberries and yellow-rumped warblers. *Auk* **109**:334–45.

Prasad S, Sukumar R (2010) Context-dependency of a complex fruit-frugivore mutualism: temporal variation in crop size and neighborhood effects. *Oikos* **119**:514–23.

Renne IJ, Barrow WC Jr, Johnson-Randall LA, *et al.* (2002) Generalized avian dispersal syndrome contributes to Chinese tallow tree (*Sapium sebiferum*, Euphorbiaceae) invasiveness. *Divers Distrib* **8**:285–95.

Richardson DM, Allsopp N, D'Antonio CM, *et al.* (2000) Plant invasions the role of mutualisms. *Biol Rev* **75**:65–93.

Sargent (1990) Neighborhood effects on fruit removal by birds: a field experiment with *Viburnum dentatum* (Caprifoliaceae). *Ecology* **71**:1289–98.

SAS Institute Inc. 2011. *SAS Version 9.3*. Cary, NC: SAS Institute.

Schaefer HM, McGraw K, Cantoni C (2008) Birds use fruit colour as honest signal of dietary antioxidant rewards. *Funct Ecol* **22**:303–10.

Schmidt V, Schaefer HM, Winkler H (2004) Conspicuousness, not colour as foraging cue in plant-animal signaling. *Oikos* **106**:551–7.

Schaefer HM, Schmidt V, Winkler H (2003) Testing the defence trade-off hypothesis: how contents of nutrients and secondary compounds affect fruit removal. *Oikos* **102**:318–28.

Senar JC, Møller AP, Ruiz I, *et al.* (2010) Specific appetite for carotenoids in a colorful bird. *PLOS ONE* **5**: e10716.

Simberloff D, VonHolle B (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biol Invasions* **1**:21–32.

Smith AD, McWilliams SR (2014) Fruit removal rate depends on neighborhood fruit density, frugivore abundance, and spatial context. *Oecologia* **174**:931–42.

Smith JA, Dreaden TJ, Mayfield AE III, *et al.* (2009b) First report of laurel wilt disease caused by *Raffaelea lauricola* on sassafras in Florida and South Carolina. *Plant Dis* **93**:1079.

Smith JA, Mount L, Mayfield AE III, *et al.* (2009a) First report of laurel wilt disease caused by *Raffaelea lauricola* on camphor in Florida and Georgia. *Plant Dis* **93**:198.

Smith SB, DeSandro SA, Pagano T (2013) The value of native and invasive fruit-bearing shrubs for migrating songbirds. *Northeast Nat* **20**:171–84.

Spiegel KS, Leege LM (2013) Impacts of laurel wilt disease on redbay (*Persea borbonia* (L.) Spreng.) population structure and forest communities in the coastal plain of Georgia, USA. *Biol Invasions* **15**:2467–87.

Thompson JN, Willson MF (1978) Disturbance and the dispersal of fleshy fruits. *Science* **200**:1161–3.

Thompson JN, Willson MF (1979) Evolution of temperate fruit/bird interactions: phenological strategies. *Evolution* **33**:973–82.

USDA (1973) *Energy Value of Foods*. Agriculture Handbook No. 74, 2–11.

USDA, Natural Resource Conservation Service (NRCS) (2014) *The Plants Database, Plant Profile: Cinnamomum campohra*. National Plant Data Team. http://plants.usda.gov/core/profile?symbol=CICA (12 May 2014, data last accessed).

Van Deelen TR (1991) Persea borbonia. Fire Effects Information System [Online]. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory (Producer). http://www.fs.fed.us/database/feis/ (23 August 2015, date last accessed).

Vorobyev M, Osorio D, Bennett ATD, *et al.* (1998) Tetrachromacy, oil droplets and bird plumage colours. *J Comp Physiol A* **183**:621–33.

Whelan CJ, Schmidt KA, Steele BB, *et al.* (1998) Are bird-consumed fruits complementary resources? *Oikos* **83**:195–205.

Whelan CJ, Willson MF (1994) Fruit choice in North American migrant birds: aviary and field experiments. *Oikos* **71**:137–51.

Willson MF, Whelan C J (1993) Variation of dispersal phenology in a bird-dispersed shrub, *Conzus drummondii*. *Ecology* **63**:151–72.

Woodrey MS, Walker J (2009) *Selected Birds of the Grand Bay National Estuarine Research Reserve and Vicinity*. Moss Point, MS: Grand Bay National Estuarine Research Reserve.

Wunderlin RP, Hansen BF (2014) *Atlas of Florida Vascular Plants*.Tampa, FL: Institute for Systematic Botany/Florida Center for Community Design and Research, University of South Florida. http://florida.plantatlas.usf.edu/Plant.aspx?id=442 (12 May 2014, date last accessed).