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Can invasive species replace native species as a resource for birds under climate change? A case study on bird-fruit interactions

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ABSTRACT

Wild fruits are an important food source for many north temperate-breeding landbirds during autumn migration and, in turn, birds provide the service of seed dispersal. Despite the importance of these autumn interactions, their potential to shift with climate change and species invasions remains poorly understood. As invasive fleshy-fruited shrubs spread across the Northeast USA and many landbird species pass through stopover sites later with warming temperatures, the potential for changes in bird-fruit interactions depends on the phenology and availability of native and invasive wild fruits, and bird preferences across the autumn season. We observed the fruiting phenology of 25 native and invasive fleshy-fruited wild plant species at Manomet, a migratory stopover site on the coast of Massachusetts, USA, during the autumn migration season (August to November) in 2014 and 2015. We also monitored fruit availability across Manomet in 2015. To determine whether fruit consumption reflected phenology and availability, we identified seeds from 469 fecal samples collected from songbirds captured during the 2014 and 2015 autumn banding seasons. We found that while invasive shrubs fruited later, on average, than native plants, and comprised a large proportion of the total available fruits in late-autumn, birds primarily consumed the fruits of native species throughout the autumn season. Our results demonstrate that native fruits are an important food resource for birds during the autumn migration season and are unlikely to be replaced by abundant fruits of late-season invasive species under climate change.

1. Introduction

During the autumn migration season, many north temperate-breeding landbirds consume fleshy fruits and disperse their seeds (Levey and del Rio, 2001; Snow, 1971; Stiles, 1980). This interaction is energetically critical for birds, which rely on fruits for fats and other nutrients to fuel migration (McWilliams et al., 2004), a process during which the majority of bird mortality takes place (Holmes, 2007). In turn, plants rely on birds for seed dispersal (Garcia et al., 2010; Snow, 1971), a service that drives plant establishment and long-term community dynamics (Howe and Miriti, 2004). Despite the importance of these autumn interactions, the potential that they will be altered by climate change remains poorly understood, particularly compared with an increasing knowledge of interactions in spring (Both et al., 2006; Gallinat et al., 2015; Kharouba et al., 2018). In addition, climate change has been shown to benefit invasive plants through shifts in other phenological events, including flowering, leaf-out, and leaf senescence (Fridley, 2012; Polgar et al., 2014; Willis et al., 2008), but it remains unclear to what extent climate change might further facilitate invasive plant success through changing bird-fruit interactions. Species-specific bird-fruit interactions are dependent on the likelihood that birds will encounter particular fruits in space and time (Carnicer et al., 2009; Thompson and Willson, 1979), and choose to consume particular fruits (Parrish, 1997). Therefore, to assess the potential for bird-fruit interactions to change with climate change and benefit invasive species, we must understand the patterns of autumn fruit phenology, availability, and birds' fruit preferences.

Plant and bird phenology are integral to frugivorous interactions (Burns, 2002); plant species ripen at different times across the summer and autumn (Gallinat et al., 2018a; Stiles, 1980), and bird species vary in their migration and stopover timing (Ellwood et al., 2015; Stegman et al., 2017). Climate change has already altered both fruit and bird phenology, with consequences for their synchrony and interactions (Gallinat et al., 2015): increasing temperatures are resulting in earlier fruit ripening for many plant species (Menzel et al., 2006; Rathcke and Lacey, 1985) but *later* autumn passage for many birds (Ellwood et al.,

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Fig. 1. Map of the field site at Manomet in Plymouth, MA. The inset shows the location of Manomet on the coast of Massachusetts. In the main figure, the blue line indicates the banding trail, which also served as the phenology walking trail in 2014 and 2015. White lines indicate mist nets. Yellow stars indicate locations where fruit abundance was monitored in 2015 (each star represents five 1 × 2 m subplots monitored weekly for fruit abundance). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2015; Van Buskirk et al., 2009; but see also Jenni and Kery (2003) for many species advancing autumn passage over time in Western Europe). At Manomet in coastal Massachusetts, USA, 13 bird species are delaying their autumn passage in warm years and one is advancing passage, with a range from −1.1 to +3.6 days/ºC (Ellwood et al., 2015). With many birds and plants exhibiting diverging phenological responses, birds could encounter fewer native fruits in late-autumn, creating an opportunity for invasive plants to have enhanced fruit dispersal due to lower competition for dispersers (Gallinat et al., 2015; Gosper et al., 2005). Evidence from herbarium specimens collected across New England show that invasive shrubs fruit, on average, 26 days later than native species, and their fruits persist longer into the winter (Gallinat et al., 2018b). This potential late-autumn and winter niche for invasive fleshy-fruited species would reflect established theory that invasive species benefit from occupying distinct early- or late-season phenological niches, often exacerbated by climate change (Wolkovich and Cleland, 2011). This theory has already been empirically demonstrated for plant vegetative and reproductive phenology in spring and autumn (Fridley, 2012; Polgar et al., 2014; Willis et al., 2008; Wolkovich and Cleland, 2014). A late-autumn fruiting niche for invasive plants would require that birds feed based on availability: as invasive species become more dominant in the landscape, birds must consume more of them. White and Stiles (1992) found some evidence to support this invasive niche hypothesis for fruiting; using fecal sampling, they found migratory birds in New Jersey consumed more invasive fruits when they became more available in late-autumn and winter.

To understand how landbirds will respond to available invasive fruits, we must understand their dietary plasticity and preference. At the individual and species level, landbirds vary in their diet specialization (Levey and del Rio, 2001). Most species can vary in their consumption of fruits and insects, as well as the plasticity with which they switch between these resources (Parrish, 1997; Thompson and Willson, 1979), obtaining higher levels of carbohydrates and lipids from fruits, and more proteins from insects (McWilliams and Karasov, 2001). Within their fruit consumption, some birds are documented specialists—such as the Myrtle Warbler (*Setophaga coronata coronata*), which consumes primarily Bayberry (*Myrica pensylvanica*) fruits (Place and Stiles, 1992)—while most species diversify their consumption across multiple fleshy-fruited species (Carnicer et al., 2009; Fuentes, 1995, p. 199; Parrish, 1997). Despite a breadth of research on the topic, there is little consensus about what drives birds' preferences for particular fruits (Levey and del Rio, 2001); however, there is growing evidence that fruit nutrition has a strong effect on what fruits birds consume, with birds showing preferences for fruits high in energy density, fat, and particular antioxidants (Bolser et al., 2013; Schaefer et al., 2003; Smith et al., 2007). Some studies have demonstrated bird preferences for the fruits of native species over invasive species (Smith et al., 2013; Whelan et al., 1991; but see LaFleur et al., 2007 for invasive fruit preferences), which may be due to the relatively low average nutritional quality of invasive fleshy fruits (Ingold and Craycraft, 1983; Smith et al., 2013; but see Greenberg and Walter, 2010 for no difference between native and invasive fruits), however bird preferences, particularly in the context of how invasive fleshy-fruited plants alter fruit phenology and availability, remain poorly understood.

To investigate the impact of invasive fleshy-fruited plants on bird-fruit interactions, we observed when native and invasive fruits were available, abundant, and consumed at Manomet, a migratory stopover site in coastal Massachusetts, USA, where biologists have been banding birds since 1969. Specifically, we addressed the following questions:

(1) *Phenology:* Do invasive species fruit later than native species?
(2) *Availability:* How do native and invasive fruits vary in availability

(phenology and abundance) throughout autumn the season?
(3) *Preference*: Does fruit consumption by birds follow patterns of fruit availability?

The answers to these questions are important for understanding how birds and fruit interact in autumn, the potential for these interactions to change with increased abundance of invasive plants, and the conservation management of fleshy-fruited plants and migratory birds.

2. Material and methods

2.1. Site description

All fruit phenology and abundance data and fecal sample data were collected at Manomet, a migratory stopover site for landbirds on the Atlantic coast, and a long-term bird banding site, located in Plymouth County, Massachusetts, USA (41° 50′N, 70° 30′W) (Fig. 1). The Manomet grounds constitute 7 ha of coastal forest habitat, dominated by brushy deciduous secondary growth, including abundant native and invasive woody understory plants. Dominant tree species include *Acer rubrum*, *Quercus alba, Prunus serotina*, and *Pinus rigida* (Lloyd-Evans and Atwood, 2004). The north and west edges of Manomet are abutted by shrubby wetlands, while the south and east sides are a steep, eroding coastal bluff. The habitat is largely unchanged over the past 50 years.

Standardized, passive bird banding has been in operation at Manomet from 1969 to present. Fifty nylon 12 × 2.6 m, 36 mm mesh nets are spread out along the Manomet banding trail (Fig. 1), and the location of the nets has not changed since 1969. All nets are opened (when weather conditions allow) from sunrise to sunset, 5 days per week in the spring (15 April–15 June) and autumn (15 August–15 November) migration seasons.

2.2. Phenology observations

We monitored fruiting phenology in autumn of 2014 (25 August–14 Nov) and 2015 (25 August–10 November). In each year, five individuals (when possible; see Table S1) were identified along the Manomet banding trail (Fig. 1) of each of the 25 most common fleshy-fruited plant species. We chose to focus on fleshy-fruited—and exclude dry-fruited—plants due to their tight ecological and evolutionary connections to animal (and specifically, bird) dispersal (Snow, 1971). The 25 plant species included 10 invasive species and 15 native species (Table S1); native or invasive classification was determined using the Invasive Plant Atlas of New England Current Species List (10 June 2017; https://www.eddmaps.org/ipane). Individuals were chosen using randomized starting locations along the trail, after which point the first individual seen of the species was identified, and labeled for future visits (researchers were careful not to bias sightings based on plant size or number of fruits present).

We revisited all labeled plants weekly, and recorded for each individual the phenological stage, including whether the plant had (1) at least one but < 50% ripe fruits, (2) ≥50% ripe fruits, or (3) ≥50% past ripe fruits (either removed or rotten). Characteristics used to determine ripeness varied by species, but included a combination of color, texture, and size for each species. When possible we used the USA National Phenology Network's Nature's Notebook (http://www.usanpn.org/natures_notebook) descriptions of ripe fruits (for 22 species, descriptions of ripe fruits for the exact species or another species in the same genus were available). One observer made all observations for consistency, with notes to track changes between visits.

Using the weekly observations, we calculated the following fruiting stage dates for each individual: first ripe fruit (the date on which ripe fruits were first observed), onset of peak fruiting (the first date on which ≥50% fruits were observed as ripe), end of peak fruiting (the last date on which ≥50% fruits were observed as ripe), and last ripe fruit (the last date on which any ripe fruits were observed).

2.3. Availability observations

We monitored fruit availability weekly in autumn of 2015 (9 August–10 November). We randomly selected 10 nets from the 50 nets at Manomet located along the banding trail (Fig. 1). At each net, we identified a sampling zone 12 m wide (the length of the net) and 12 m into the forest (starting one m from the net). We then randomized the location of ten 1 × 2 m subplots, placing five on either side of the net. Two nets were inaccessible on one side due to dense vegetation; these nets had only 5 subplots, for a total of 90 total subplots across Manomet. Each week, for 13 weeks, we recorded at each subplot which species had ripe fruits and how many fruits there were of each species, using the following categories: 1: 1–10; 2: 11–25; 3: 26–100; 4: 101–250; 5: 251–1000.

Our 13-week sampling window meant that we were not able to capture the full fruiting phenology windows for several species that began fruiting (and, in the case of *V. corymbosum* and *L. morrowii*, entered peak fruiting) before monitoring began, or that retained fruits after monitoring ended (e.g. *E. umbellata, L. vulgare, R. multiflora, B. thunbergii*, and others). In this study, for the purpose of focusing just on the autumn migration season, we recorded the last day of fruiting as the last day of monitoring for persistent species; however, it should be noted that many of these late-fruiting species have been shown to retain fruits into the winter and in some cases the following spring (Gallinat et al., 2018a,b; Greenberg and Walter, 2010; Stiles, 1980).

2.4. Fecal sampling

Bird banders at Manomet collected fecal samples in 2014 (15 August–13 November) and 2015 (18 August–9 November). The protocols used for collecting, storing, and sorting samples, and identifying seeds from samples were adapted from Parrish (1997). Clean cotton bags were used to transfer birds from mist nets back to the central banding lab for processing; birds remained in bags for up to 60 min. If while banding and processing the birds, bird banders noted that a fecal sample was deposited into the cotton bag, they collected it; they recorded the bird species, band number, date, and net number, and stored this information with the sample. In 2014, banders collected fecal samples from any landbird species (all passerines or near-passerines). However, in 2015 they avoided collecting samples from species for which the fecal samples from 2014 rarely contained seeds; this list included Black-capped Chicadees (*Poecile atricapillus*), and all sparrows and flycatchers. They also avoided collecting samples from Myrtle Warblers because their highly-specialized diet of *Myrica pensylvanica* was confirmed by samples collected in 2014.

Fecal samples were transferred weekly from cotton bags into plastic bags, and brought back to the laboratory at Boston University, where they were refrigerated until processing. For each sample, we used a dissecting microscope to record the presence or absence of seeds; where seeds were present, we also recorded any evidence of insects (typically partial insects, such as elytra, heads, or legs). All samples were checked for seeds and insects by two observers. For each sample with seeds, we removed all seeds and stored them in 70% isopropyl alcohol solution. All seeds from a sample were kept in the same vial with a code, which was associated separately with all other sample information (such as bird species and date collected) to avoid any bias in seed identification.

2.5. Seed identification

Seeds were identified using a reference collection of 48 species; in some cases, identification could only be done to the genus level, such as for *Rubus* and *Vaccinium* species. The reference collection contained seeds from ripe fruits, collected from plants identified on the grounds of Manomet throughout autumn of 2014. Reference samples for each species were collected from at least five fruits of at least 5 individuals, when possible, to capture variation among fruits and individuals.

Reference seed samples for each species were preserved using two methods: seeds were dried and stored, and seeds were also preserved in 70% isopropyl alcohol solution. During seed identification, the reference collection was also supplemented with an online guide to the seeds of fleshy-fruited bird-dispersed plants of Southern Michigan (http://seedguide.blogspot.com/). We used seed size, shape, surface patterns, and (in some cases, with caution) color to identify seeds under a dissecting microscope—in all cases, seeds were directly compared to the reference samples for identity confirmation. For each sample, we recorded the seed species and seed count for each species. We were unable to identify 8 samples (out of 195 total) in 2015. Since the number of seeds deposited does not indicate the number of fruits consumed across all plant species (e.g., one *Nyssa* seed represents one fruit, while dozens of *Vaccinium* seeds could be from one or several fruits), when a species was observed in a sample in any quantity we recorded it as present. In all analyses, therefore, the metric we use to indicate consumption frequency is the number of fecal samples in which a species was present, hereafter called "seed occurrence."

2.6. Data analysis

All data were analyzed using R statistical software v3.4.2 (R Core Team, 2018).

2.6.1. Fruit phenology

To identify the schedule of fruiting across all species, we calculated the average date (± SE) of each phenophase for each species in each year. We used Analysis of Variance (ANOVA) to determine whether fruiting phenology differed significantly among species, for each of the four fruiting stages in both years (a total of 8 tests). To gauge consistency in the timing of fruiting across species between years, we used Pearson product-moment correlations to compare the average date of each fruiting stage for each species between 2014 and 2015 (for a total of four models). We compared the average date of each fruiting stage between native and invasive species using a linear mixed effects (LME) model, including all observations with species included as a random effect and invasive or native as a fixed effect, and date of fruiting stage as the response variable. We used the 'lmer' command in *lme4* v1.1.13 (Bates et al., 2015) and the 'Anova' command in *car* v2.1.4 (Fox and Weisberg, 2011) to determine p-values for fixed effects. Given the rarity of data on species-specific fruiting times for this region, the novelty of using herbarium specimens to investigate fruiting phenology, and to place the two years of phenology data collected for this study into a broader temporal and geographic context, we compared the wild phenology records from this study to published dates gathered from herbarium specimens (Gallinat et al., 2018b). For the 20 species included in both data sets, we examined the correlation of each species' mean fruiting date in the herbarium records to onset of peak fruiting dates recorded in 2014 and 2015 at Manomet.

2.6.2. Fruit availability

We converted fruit abundance category data (see *availability observations*) to the mean value of each category (1: 5; 2: 18; 3: 63; 4: 175.5; 5: 625.5). We averaged the number of ripe fruits across subplots to get a weekly average value for each plant species at each net, and then averaged across nets to calculate, the density of fruits of each species (fruits per m^2) per week, and the proportion of total fruits belonging to each species.

2.6.3. Fruit consumption

To compare fruit consumption with fruit phenology, for each plant species in each year we calculated the percentage of total seed occurrences identified within the period when ripe fruits were observed (for instance, what percentage of the total seed occurrences of *Viburnum recognitum* in 2015 were deposited between the average first fruiting date and last fruiting date observed for *V. recognitum* in 2015?). To compare fruit consumption with fruit availability, we first combined seed occurrence data by week, corresponding with the weekly dates on which fruit availability was monitored. Then, to determine whether birds consume what is most available, we conducted χ^2 tests (one per week of observation in 2015) in which species seed occurrences were the observed values and the weekly proportions of available fruits belonging to each species were the expected distributions. Due to low overlap between species observed as available and those in fecal samples, we limited our analysis to weeks in which at least 2 species were common between the two data sets (7 of 13 weeks).

To determine the preferability of each plant species observed, we calculated season-wide proportions of total fruit availability and total seed occurrence belonging to each species. We then calculated Ivlev's Electivity Index (Ivlev, 1961) for each observed plant species using the 'ivlev' command in *selectapref* v0.1.0 (Richardson, 2017). Ivlev's Electivity is a foraging preference metric that compares how often a resource is encountered to how often it is consumed. The index ranges from −1 to 1, with −1 indicating avoidance of a resource, 0 indicating no preference (in other words, the resource is consumed in the same proportion in which it is available) and 1 indicating a strong preference.

We used simple linear regression to test whether the weekly proportion of total invasive fruits available could significantly predict the weekly proportion of total invasive seed occurrences across the season. To explore similarity in seed consumption by Gray Catbirds (*Dumetella carolinensis*) between 2014 and 2015, we used Pearson correlation to compare the number of seeds of each plant species between years.

3. Results

3.1. Fruit phenology

Species significantly differed in their fruiting times ($p < 0.001$ for all stages in all years). The earliest species to fruit included *Sambucus canadensis*, *Lonicera morrowii*, *Rubus* sp., and *Prunus serotina* (Table S1, Fig. 2); all of these species began ripening prior to the first phenology monitoring date (Aug 25), and began peak onset in August, in both years. The last species to fruit, reaching onset of peak fruiting from mid-October to mid-November, included *Rosa multiflora*, *Lonicera japonica*, and *Ligustrum vulgare*. We found fruiting to be highly consistent ($r > 0.75$ and $p < 0.001$ for all fruiting stages) from year to year (Fig. S1); that is, species were characteristically early-fruiting or late-fruiting.

The LME results show that in both 2014 and 2015, invasive species fruited significantly later than native species in nearly all phenophases (Table 1). The onset of peak fruiting occurred 25 days earlier (± 7.5 SE, $p = 0.0008$) for native species compared to invasive species in 2014, and 21 days earlier (± 7.4, $p = 0.004$) in 2015. End of peak fruiting differences between native and invasive species were similar to onset of peak differences, while first ripe fruit dates differed slightly less between the groups; native species initiated fruiting, on average, 17 days earlier (± 7.8, $p = 0.026$) than invasive species in 2014, and 16 days earlier (± 7.5, $p = 0.032$) in 2015. The date on which the last ripe fruit was observed (within the monitoring period) did not significantly differ between native and invasive species. Comparing phenology observations from herbarium specimens (mean fruiting dates) to field observations at Manomet (onset of peak fruiting dates), we found they were strongly and significantly correlated in both 2014 ($r = 0.81$, $p < 0.001$) and 2015 (0.79, $p < 0.001$); that is, the order of fruiting is very similar when determined using field monitoring and herbarium specimens, and the order of fruiting observed at Manomet from 2014 to 2015 is consistent with that across New England from the early 1800s to present.

3.2. Fruit availability

Fruit availability varied across the autumn migration season,

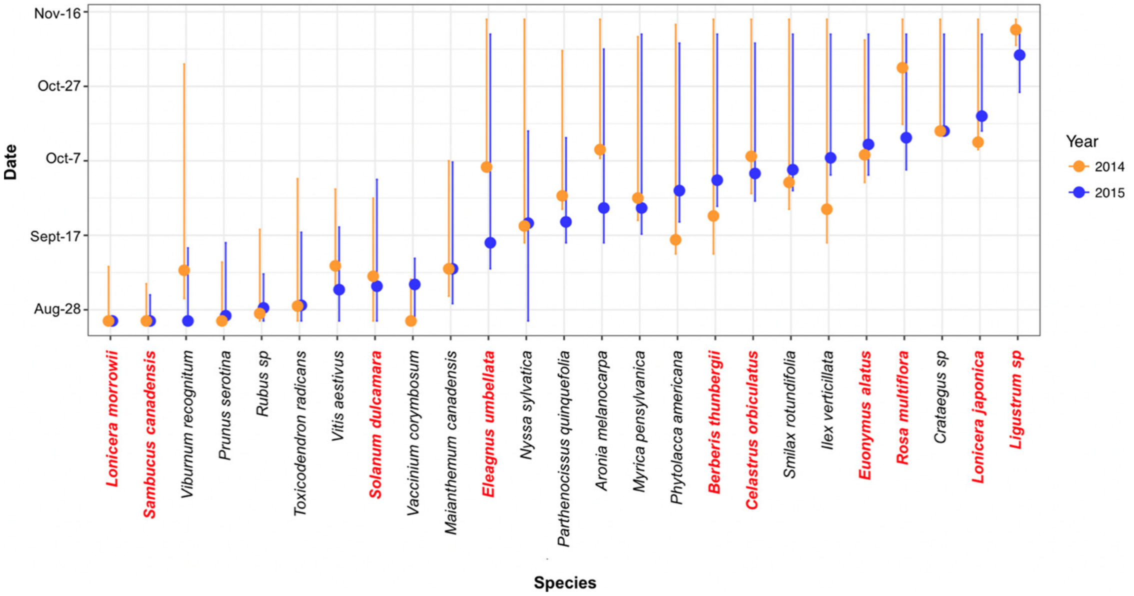

Fig. 2. Fruiting phenology for 25 species at Manomet in Plymouth, MA in 2014 and 2015. Points indicate the average onset of peak fruiting, and bars indicate the range from average first fruiting date to last fruiting date for each species. Invasive species are indicated in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Results from linear mixed effects models comparing the date of each fruiting stage (first ripe date, peak onset of fruiting, peak end of fruiting, and last ripe date) between native and invasive species. We present the difference between groups (intercept), degrees of freedom (df), standard error (SE), and P-value for all four fruiting stages in each year (negative values indicate earlier native than invasive phenology).

Year	Fruiting stage	Intercept	df	SE	P-value
2014	First Ripe	−17.39	24	7.80	**0.026**
	Peak Onset	−25.26	24	7.51	**0.001**
	Peak End	−25.23	23	9.95	**0.011**
	Last Ripe	−12.61	24	10.94	0.249
2015	First Ripe	−16.08	24	7.50	**0.032**
	Peak Onset	−21.06	23	7.39	**0.004**
	Peak End	−22.97	23	9.11	**0.012**
	Last Ripe	−18.56	24	10.87	0.088

declining consistently from early-October to mid-November when monitoring ended (Fig. 3). We observed ripe fleshy fruits of 18 species across the season (Fig. 3A). Species with the greatest availability early in the season included invasive *Lonicera morrowii* (83% of fruits available on 9 Aug), and native *Prunus serotina* (64% of fruits on 18 Aug, and 85% of fruits on 25 Aug), while native *Nyssa sylvatica* had the greatest availability mid-season (93% of fruits on 22 Sept). Species with greatest availability late in the season included *Euonymus alatus* (38% of fruits on 3 Nov), *Rosa multiflora* and *Ligustrum vulgare* (35% and 15%, respectively, of fruits on 10 Nov), all of which are invasive. While one species was dominant at any given time through most of August and September (*Lonicera morrowii*, then *Prunus serotina,* then *Nyssa sylvatica*), the end of the season was characterized by more equal abundances of several species, many of them invasive shrubs (*Berberis thunbergii, Ligustrum vulgare, Rosa multiflora,* and *Euonymus alatus,* but also the native species *Smilax rotundifolia*).

3.3. Fruit consumption

We collected a total of 970 fecal samples across two years (2014: n = 483, 2015: n = 487). Of those samples, 469 contained identifiable seeds (2014: n = 282, 2015: n = 187), and of the samples containing seeds all but five samples contained evidence of arthropods (n = 464). The majority of fecal samples were collected from Gray Catbirds (n = 317 total, 2014: n = 169, 2015: n = 148) followed by Myrtle Warblers in 2014 (n = 67) and, taken together, *Catharus* thrushes, which included Hermit Thrushes (*C. guttatus*), Swainson's Thrushes (*C. ustulatus*), Veeries (*C. fuscescens*), and Gray-cheeked Thrushes (*C. minimus*) (n = 54 total, 2014: n = 29, 2015: n = 25; Table S2). Most seeds found in fecal samples early in the season belonged to *Rubus* sp. and *Vaccinium* sp., followed by *Nyssa sylvatica* seeds in mid-autumn, and mostly *Parthenocissus quinquefolia* seeds as well as *Ilex verticillata, Myrica pensylvanica, Toxicodendron radicans,* and *Smilax rotundifolia* seeds at the end of the season (Fig. 3B), all of which are native species.

Combining fecal sample data across all bird species, the number of seeds consumed of each plant species was positively correlated between 2014 and 2015 ($r = 0.79$, $p < 0.001$, df = 12)—that is, birds ate the same kinds of fruits in each of these two years. Gray Catbirds consumed fruits from 14 plant species in 2014 and 15 plant species in 2015 (Table S2). *Catharus* thrushes, together, consumed fruits from 7 plant species in 2014 and 5 species in 2015. In 2014, when a large number of Myrtle Warblers were sampled, 61 of 62 fecal samples contained *Myrica pensylvanica* as the only seed type (Table S2).

The dates on which seeds were recovered from fecal samples fell predominantly within the time period that ripe fruits were observed (from average first ripe fruit date to last ripe fruit date) for that species in both years (Fig. 4; Table S1). However, in both years, seeds of some plant species were present in fecal samples before the fruits appeared to be ripe in our phenology observations (*e.g.*, *Myrica pensylvanica*, *Viburnum recognitum* and, in 2015, *Ilex verticillata*), or after the observed ripe period had ended (*e.g.*, *Rubus* sp., *Vaccinium* sp., *Toxicodendron radicans*).

In 2015 when fruit availability was measured, the number of seed occurrences in fecal samples in each week did not match the proportions of fruit availability in the same week, for all seven weeks tested ($p > 0.05$). For six of the thirteen weeks in which seed occurrence and fruit availability was observed (22 Sept, 29 Sept, 23 Oct, 29 Oct, 3 Nov, 10 Nov), we did not analyze similarities between seeds in fecal samples and fruit availability because fewer than two species overlapped between the two groups. In fact, most species commonly found in fecal samples were in fairly low relative abundance on the grounds of Manomet; the most commonly consumed seeds included *Rubus* sp., *Vaccinium* sp., *Nyssa sylvatica,* and *Parthenocissus quinquefolia*, whereas

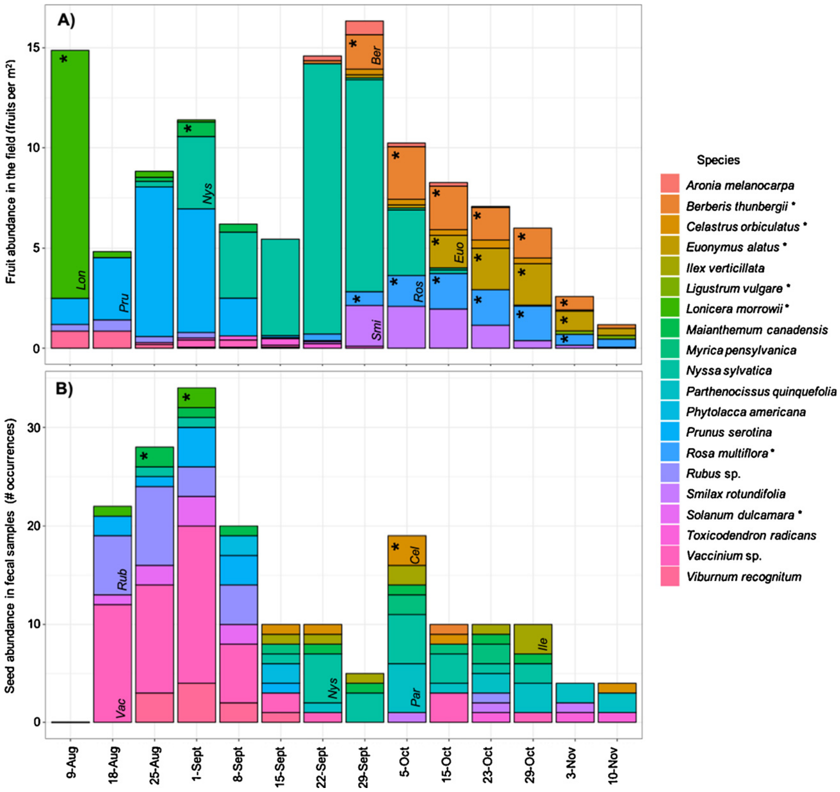

Fig. 3. Relative availability and consumption of wild fleshy-fruited species at Manomet in 2015. A) the proportion of fruits observed at Manomet in 2015 belonging to each species, from 9 August to 10 November. For each species, estimated fruit density (number of fruits per m^2) was averaged across subplots and then across nets, in each week. B) The number of seed occurrences in fecal samples at Manomet in 2015 belonging to each species, from 18 August to 10 November. A single seed occurrence indicates a species' presence in one sample, regardless of the number of seeds present. Seed occurrence data are presented as weekly sums, grouped by the median date of the sampling range, with weeks ranging from 18 August to 10 November. In both panels, species with the greatest availability are labeled with the first three letters of the genus, on the first date on which they appear in large proportions. Invasive species are denoted with an asterisk.

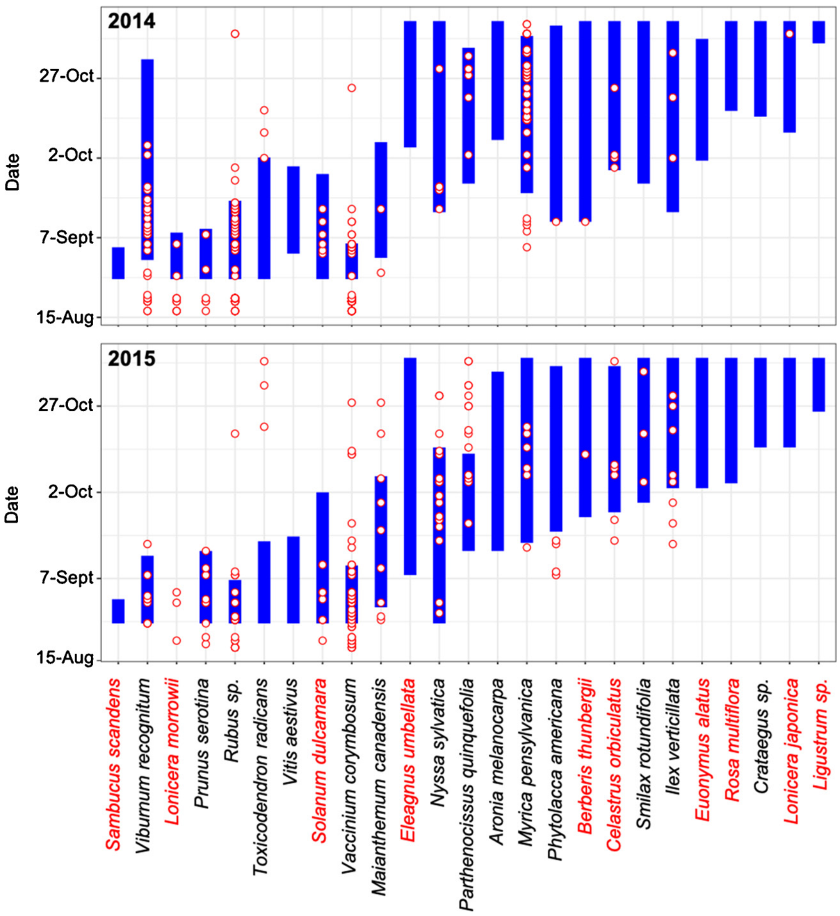

Fig. 4. The phenology of fruiting at Manomet overlaid with the dates on which seeds were deposited in fecal samples, in 2014 and 2015. Phenology bars (blue) range from mean first ripe fruit to mean last ripe fruit, averaged from observations of up to five individuals of each species (see Table S1 for sample sizes); red circles indicate a single seed occurrence (i.e. one fecal sample with at least one seed of the plant species present). Invasive species are indicated in red. See Table S1 for percentages of seeds overlapping with field phenological measurements. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Ivlev's Electivity Index for wild fruits at Manomet, Plymouth, MA. The index was calculated using the proportion of total fruits available and the proportion of total seed occurrences belonging to each species, across the autumn season. An index value of −1 indicates strong avoidance, 0 indicates random consumption, and 1 indicates strong preference. Invasive species are denoted with an asterisk.

Species	Ivlev's Electivity
Aronia melanocarpa	−1
*Euonymus alatus**	−1
*Ligustrum vulgare**	−1
*Rosa multiflora**	−1
*Berberis thunbergii**	−0.89
*Lonicera morrowii**	−0.75
Smilax rotundifolia	−0.61
Prunus serotina	−0.48
Nyssa sylvatica	−0.48
Toxicodendron radicans	0.33
*Celastrus orbiculatus**	0.47
Viburnum recognitum	0.51
Maianthemum canadensis	0.62
Rubus sp.	0.80
Myrica pensylvanica	0.85
Vaccinium sp.	0.95
Ilex verticillata	1
Parthenocissus quinquefolia	1
Phytolacca americana	1
*Solanum dulcamara**	1

the most abundant fruits on site included *Lonicera morrowii*, *Prunus serotina*, *Nyssa sylvatica*, and *Euonymus alatus*.

Quantification of the avoidance of and preference for different fruits, using Ivlev's Electivity Index for all species present in the wild and/or identified in fecal samples, shows that five of the eight fruits with low preference (index value < 0) were invasive species, including *Euonymus alatus, Rosa multiflora,* and *Berberis thunbergii*, and two were tree species (*Nyssa sylvatica* and *Prunus serotina*) which produced the largest quantities of fruits over the season (Table 2, Fig. 3). Highly preferred fruits (index value > 0) predominantly included native shrubs with moderate to little observed fruit availability over the 2015 autumn season, such as *Viburnum recognitum*, *Rubus* sp., and *Vaccinium* sp.

The total proportion of available fruits that were invasive did not significantly predict the total proportion of seeds occurrences that were invasive from week to week ($R^2 = 0.002$, $p = 0.88$, $df = 11$). Invasive fruit availability had two peaks, one in early-autumn and another in late-autumn, whereas native fruit availability was highest mid-autumn; however, most of the fruits consumed at the end of the season continued to be native fruits (Fig. 3).

4. Discussion

By synthesizing observations of fruit phenology, fruit availability, and fruit consumption by birds, we aimed to understand whether diverging effects of climate change on plants and birds might alter bird-fruit interactions, to the benefit of invasive plants. We found that, at a busy stopover site in coastal Massachusetts, USA, invasive plants, on average, fruited later in the year than native species, and comprised the majority of fruits available in the late-autumn. As many bird species are documented to be migrating later through this stopover site with warming temperatures (Ellwood et al., 2015; Stegman et al., 2017), it is likely that these birds will more frequently encounter abundant invasive fleshy fruits. However, we found that birds preferentially consumed native fleshy fruits rather than invasive fruits throughout the autumn season. Autumn bird-fruit dynamics represent a critical interaction in an under-studied season (Gallinat et al., 2015); each element of this study—phenology, availability, and preference—adds to our basic understanding of the role of invasive plants in temperate ecosystems, while interactions among the elements indicate that migratory birds are unlikely to switch from native to invasive fruits as an autumn resource.

4.1. Fruit phenology

We found that fleshy-fruited species differed in their fruiting phenology across the autumn season—that is, individuals of a species tended to fruit in the same window of time, and fruiting times were strongly correlated between years. This was true for all four fruiting stages monitored (first fruit, onset of peak fruiting, end of peak fruiting, and last fruit). And for all fruiting stages except last fruiting date (likely because of end-of-season data limitations), we found that invasive plants fruited significantly later than native species. For instance, the onset of peak fruiting was 25 days later for invasive species than native species in 2014, and 21 days later in 2015. As these invasive species come predominantly from Europe and East Asia where the growing season is longer and more predictable, they have a stronger response to climate change, including earlier spring flowering and leaf out, and later and more extended leaf senescence and fruiting in the autumn (Fridley, 2012; Zohner and Renner, 2017). The results from our field observations are extremely similar to, and provide validation for, the results of an herbarium-based study of fruiting phenology with 20 of the same species, in which invasive species fruited, on average, 26 days later than native species (Gallinat et al., 2018b). In turn, the herbarium records provide a long-term context for our observations of fruiting phenology in the field from 2014 to 2015, indicating those observations are robust beyond the two years observed.

Theoretically, fleshy-fruited plants experience a trade-off between ripening when potential dispersers are most abundant and when other plants are fruiting in order to attract more dispersers to the area, and fruiting before or after other species to avoid competition for dispersers (Skeate, 1987; Stiles, 1980; Thompson and Willson, 1979). Many invasive fleshy-fruited plants appear to use a strategy of avoiding competition for dispersers, fruiting before (in the case of *Lonicera morrowii*) or, in most cases after, most native plants have completed fruiting. An important next step for understanding and predicting the spread of invasive plants is to test for more direct evidence of the winter niche (see 4.4).

4.2. Fruit availability

Our fruit availability observations, collected in 2015, build on the result that invasive plants fruited later than native plants by demonstrating that invasive fruits become increasingly available throughout autumn, and represent the majority of fleshy fruits available in late-autumn. Over the course of the season, we found fruit availability was highly variable, and peaks in overall fruit abundance were driven by short-term availability of two high-volume native fleshy-fruited tree species, *Nyssa sylvatica* and *Prunus serotina.* The availability of fruits declined steadily from early-October to mid-November, during which time the most available fruits were those of invasive shrubs *Rosa multiflora, Eleagnus alatus, Ligustrum vulgare,* and *Berberis thunbergii*, as well as the native vine *Smilax rotundifolia*. A late-season increase in these invasive fruits is reflected in other studies of late-autumn fruiting (Greenberg and Walter, 2010; Stiles, 1980; White and Stiles, 1992). The general patterns of fruit availability among native and invasive species that we found are likely applicable to most temperate forests of eastern North America with a mix of native and invasive fleshy-fruited species. However, we caution that we do not expect the specific abundance estimates that we calculated would be true of all years at Manomet, or of nearby sites, because of the wide spatial variation in species availability and seed production, and the potential for interannual variation in fruit yields (Jordano, 1987; though variation in seed production is relatively low for frugivore-dispersed plants compared to other means of dispersal, see: Herrera et al., 1998).

4.3. *Fruit consumption*

The results of our bird fecal analysis show that many birds at Manomet consumed a variety of fruits, typically accompanied by insects. Furthermore, we found that fruit consumption did not reflect fruit availability; and critically, as invasive fruits became more widely available in late-autumn, birds continued to consume the fruits of native plants. Together, these findings demonstrate that many birds have diverse omnivorous diets, and prefer native fruits to invasive fruits.

Previous studies have shown that many landbird species are generalist omnivores (Fuentes, 1995; Parrish, 1997; Thompson and Willson, 1979), switching between invertebrates and a variety of fruiting species throughout the autumn season. We found support for this claim, particularly for Gray Catbirds and *Catharus* thrushes, from which the majority of our samples were collected. The large number of Gray Catbird fecal samples in this data set is reflective of the bird community at Manomet, where Gray Catbirds represented more than 25% of mist-net captures in 2015. Our interaction results mirrored those of Davidar and Morton (1986) in which Gray Catbirds and *Catharus* sp. were shown to consume many taxa including native *Parthenocissus quinquefolia, Nyssa sylvatica, Viburnum* sp., and *Phytolacca americana*. We also found additional support for a highly-specialized relationship between Myrtle Warblers and *Myrica pensylvanica* fruits (Place and Stiles, 1992). Incidentally, in all but five of the 469 fecal samples that contained seeds, we also found evidence of arthropods. Many birds are known to include invertebrates as a substantial part of their autumn diets (Fuentes, 1995), and the consumption of invertebrates on migratory stopover is linked to faster individual gains in mass (Parrish, 1997). With declines in invertebrate biomass associated with the spread of invasive plant species, (Heleno et al., 2009; Tallamy, 2004), combined with other documented declines of insects worldwide (Dirzo et al., 2014; Habel et al., 2019; Hallmann et al., 2017; Sánchez-Bayo and Wyckhuys, 2019), fruits could become an increasingly important autumn food resource for omnivorous landbirds with high dietary plasticity, such as Gray Catbirds.

Our fruit preference results showed that fruit availability was not reflected in fruit consumption. In particular, birds primarily consumed the fruits of native species throughout the autumn season, despite the increasing relative abundance of invasive fruits in late-autumn, echoing previous studies that have shown birds prefer native fruits (Smith et al., 2013; Whelan et al., 1991; but see LaFleur et al., 2007). At Manomet, it appears that if native fruits are still available on site, even if they are present in low abundance (e.g. *I. verticillata, S. rotundifolia*), or are no longer ripe in the sampling area (e.g. *P. quinquefolia*, *V. corymbosum*), they will be selected over invasive species (though due to the species bias in our fecal sampling results, the application of this finding beyond Gray Catbirds requires further study). Preferences for native fruits may be due to nutritional differences between native and invasive fruits (Ingold and Craycraft, 1983; Smith et al., 2013; but see Greenberg and Walter, 2010 for no difference). Presumably, shifts in nutritional quality could have drastic effects for birds during migration; however, negative effects of invasive fruit consumption on bird body condition are not well-demonstrated (Nelson et al., 2017). A recent study of Gray Catbird stopover ecology showed that individuals in habitats dominated by native shrubs gained mass and had higher immune function, compared to individuals in habitats dominated by exotic shrubs, which actually lost mass during stopover (Oguchi et al., 2017). The agreement of our findings with previous results—including the avoidance of invasive fruits, and particular species of fruit consumed by Gray Catbirds and *Catharus* thrushes—along with the strong correlation we found in the number of seeds consumed of each plant species between 2014 and 2015, suggests that the two years observed in this study are representative of broader patterns. While we might expect the consumption of specific fruits to vary with strong interannual differences in fruit availability (Herrera, 1984), the dynamic of invasive species dominating fruit availability in the late-autumn while birds continue to consume native fruits is supported by this study and prior work by other researchers (Gosper et al., 2005; Greenberg and Walter, 2010; Smith et al., 2013).

Not only did the birds we sampled not consume fruits in the proportions that they were available at Manomet, but many of the fruits they consumed were not present in our abundance estimates at all, or were present in extremely low abundances, such as *Vaccinium* sp. and *Rubus* sp. in early-autumn, and *Parthenocissus quinquefolia* and *Ilex verticillata* in late-autumn, leading to high electivity values for these plants. However, we note that these species were all present on site, and were monitored for fruiting phenology, so we either did not capture the full range of fruit availability at Manomet, or some seeds were consumed in other locations (particularly in the case of *Vaccinium* sp. which may have been consumed from off-site cranberry bogs or blueberry crops). Future studies of fruiting phenology should consider sampling over larger areas than were sampled in our study; though we caution that for a community of birds in which species, and even individuals, likely forage over different areas, identifying an ideal representative sampling breadth for fruit availability is challenging. Recorded seed passage times are typically under one hour (LaFleur et al., 2009; Walsberg, 1975), and a study of stopover habitat use in an urban landscape showed individuals used between approximately 1–16 ha of area over several days (Seewagen et al., 2010). Therefore, we do expect that the majority of the seeds we identified were consumed at Manomet or nearby, but recommend the species-specific electivity values in this study be used with caution. In considering whether our availability observations are likely representative of habitat just beyond the grounds of Manomet, we can borrow support from our phenology observations, which show that of the species with ripe fruits in late-autumn, most were invasive. Therefore, we suspect that beyond the grounds of Manomet, the broad patterns of availability between native and invasive fruits that we observed are consistent. More studies using geolocation to track the stopover behavior of migratory songbirds will improve our understanding of stopover foraging ecology and allow us to better link fruit availability with fruit consumption.

The likelihood that some birds consumed the flesh of fruits without consuming the seeds, regurgitated seeds, or digested seeds, further limits our ability to use fecal sampling to definitively determine what birds are *not* eating. Large-seeded plants such as *Nyssa sylvatica* and *Prunus serotina* appeared in the fecal samples of larger-gaped birds (from which most samples were collected) such as Gray Catbirds, American Robins (*Turdus migratorius*), and *Catharus* thrushes, enabling our methods to detect the interaction; however, we did not detect when smaller-gaped birds, including Black-capped Chickadees and Tufted Titmice (*Baeolophus bicolor*), consumed the fruity flesh from these species without consuming seeds (Trevor Lloyd-Evans, *pers obs*).

4.4. *Future directions—the winter niche and sampling methods*

It remains unknown whether invasive fruits are consumed at Manomet in greater proportions in late-autumn and winter after native fruits and insects are no longer available. Several studies have found that invasive species have more persistent fruits than native species (Drummond, 2005; Gallinat et al., 2018b; White and Stiles, 1992) and others suggest that winter resident birds are the primary consumers and dispersers of invasive fruits (Gosper et al., 2005; Skeate, 1987; White and Stiles, 1992). As invasive fleshy-fruited plants are linked to increased abundances of some landbirds (Gleditsch and Carlo, 2011; Leston and Rodewald, 2006), the spread of invasive species and abundant winter fruit resources may be one reason that many birds overwintering in the northern hemisphere have expanded their winter ranges northward (La Sorte and Thompson, 2007). The removal of invasive fruits in winter increases with colder temperatures (Kwit et al., 2004), which further indicates that invasive fruits may serve as a novel food resource in winter. Future studies should further investigate links between invasive plants and expanding winter ranges of birds. To better understand the winter fruiting niche for invasive fruiting plants, next steps include identifying the primary species dispersing invasive seeds in winter, and measuring the dispersal and germination success of seeds deposited in winter.

The use of two methods for monitoring fruiting in the same year, at the same location, provides an opportunity for comparison. The phenology transect allowed us to monitor species present in both high and low abundance at Manomet and could be fairly easily incorporated into existing protocols at banding stations with multiple observers. However, the phenology method did not provide information on fruit abundance, which will be important for any researchers interested in what fruits are locally available (and which are *most* available) to birds. Our fruit availability method did capture fruit abundance but, compared to the phenology transect, was more time consuming and destructive to the plant community around the banding nets. In this study, fruit availability data did not capture many species that birds were eating, while fruit phenology data *did* typically overlap with seeds found in fecal samples. Therefore, at sites with high spatial heterogeneity like Manomet, researchers interested in monitoring fruits to determine what birds may be eating may receive equally valuable information from fruit phenology transects, while expending less effort and resources, than from intensive availability monitoring.

5. Conclusions

Taken together, our results show that the fruits consumed by migratory birds, particularly Gray Catbirds, at a stopover site in coastal MA reflect both fruit phenology and bird dietary preference. We found that plants had distinct fruiting times across the autumn season that were consistent from year to year, and birds primarily consumed fruits during times when ripe fruits were observed. Invasive plants fruited significantly later than native plants in the period observed, and these patterns were reflected in ripe fruit availability; as the overall volume of fruits, and availability of native fruits declined from early-October to mid-November, the availability of invasive fleshy fruits increased. However, these patterns were not reflected in fecal samples collected from birds at Manomet; most of the species sampled showed strong evidence of generalist feeding and dietary switching, and preferred to consume native species that were present in low abundance or were no longer ripe, rather than the abundant invasive ripe fruits on site. These results show the importance of native fruits as a nutritional resource for birds in autumn, and point to a winter niche for invasive fruits in deciduous forest communities.

Data Accessibility

All raw data from this project will be archived on Open Science Framework.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2019.108268.

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