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Native fruit traits may mediate dispersal competition between native and non-native plants

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Abstract

Seed disperser preferences may mediate the impact of invasive, non-native plant species on their new ecological communities. Significant seed disperser preference for invasives over native species could facilitate the spread of the invasives while impeding native plant dispersal. Such competition for dispersers could negatively impact the fitness of some native plants. Here, we review published literature to identify circumstances under which preference for non-native fruits occurs. The importance of fruit attraction is underscored by several studies demonstrating that invasive, fleshy-fruited plant species are particularly attractive to regional frugivores. A small set of studies directly compare frugivore preference for native vs. invasive species, and we find that different designs and goals within such studies frequently yield contrasting results. When similar native and non-native plant species have been compared, frugivores have tended to show preference for the non-natives. This preference appears to stem from enhanced feeding efficiency or accessibility associated with the non-native fruits. On the other hand, studies examining preference within existing suites of co-occurring species, with no attempt to maximize fruit similarity, show mixed results, with frugivores in most cases acting opportunistically or preferring native species. A simple, exploratory meta-analysis finds significant preference for native species when these studies are examined as a group. We illustrate the contrasting findings typical of these two approaches with results from two small-scale aviary experiments we conducted to determine preference by frugivorous bird species in northern California. In these case studies, native birds preferred the native fruit species as long as it was dissimilar from non-native fruits, while non-native European starlings preferred non-native fruit. However, native birds showed slight, non-significant preference for non-native fruit species when such fruits were selected for their physical resemblance to the native fruit species. Based on our review and case studies, we propose that fruit characteristics of native plant communities could dictate how well a non-native, fleshy-fruited plant species competes for dispersers with natives. Native bird preferences may be largely influenced by regional native fruits, such that birds are attracted to the colors, morphology, and infructescence structures characteristic of preferred native fruits. Non-native fruits exhibiting similar traits are likely to encounter bird communities predisposed to consume them. If those non-natives offer greater fruit abundance, energy content, or accessibility, they may outcompete native plants for dispersers.

Keywords

Catharus guttatus, feeding preference, frugivory, *Sturnus vulgaris, Turdus migratorius*

Introduction

Invasive non-native plant species may exert a range of impacts on native communities. They can alter resource availability (e.g., Yelenik et al. 2004), transform fire regimes (Brooks et al. 2004), promote erosion (D'Antonio and Meyerson 2002), or reduce local diversity through formation of monodominant stands (Hejda et al. 2009, Greene and Blossey 2011). Additionally, invasive plant species may directly compete with natives by sequestering necessary resources such as water (e.g., Enloe et al. 2004) or nutrients (Wardle et al. 1994).

Competition with invasive plants may further impact native communities by altering interactions between native species. Invaders can transform food web structure, for example, by outcompeting high-quality native food plants and thereby diminishing an herbivore's resources (Going and Dudley 2008). Similarly, competition with invasives can disrupt mutualistic interactions, as when a non-native species monopolizes pollination services, diminishing native plant reproduction (Brown et al. 2002, Muñoz and Cavieres 2008). A number of authors have suggested that such competition may also derail native seed dispersal relationships (Vilá and D'Antonio 1998, Renne et al. 2000, Richardson et al. 2000, Gosper 2004, Traveset and Richardson 2006). However, dispersal competition has rarely been directly measured. It is unknown whether such competition is a widespread or significant impact of biological invasions.

Among introduced species, fleshy-fruited plants adapted to animal-mediated seed dispersal are often considered high-risk for invasiveness (Rejmánek and Richardson 1996, Daehler et al. 2004, Richardson and Rejmánek 2011). Along with enabling rapid spatial spread, zoochorous dispersal may enhance seed germination (Panetta and McKee 1997, Verdú and Traveset 2004) and disproportionately deposit seeds in favorable microsites (Wenny 2001). Notable invasions mediated by regional frugivores have included the tropical, monotypic stand-forming invaders *Lantana camara* (Gosper and Vivian-Smith 2006) and *Miconia calvescens* (Meyer 1998), the temperate forest invader *Lonicera mackii* (Schierenbeck 2004, Bartuszevige and Gorchov 2006), and the riparian specialist *Triadica sebifera* (Renne et al. 2002). The importance of animal-mediated dispersal in biological invasions has been addressed in a number of review papers (Richardson et al. 2000, Reichard et al. 2001, Daehler 2003, Gosper et al. 2005, Buckley et al. 2006, Schupp 2011, Tsoar et al. 2011).

Animal-dispersed invasive plants can have the same community impacts as other invasives, forming monospecific thickets (Williams et al. 2006), altering nutrient regimes (Cameron and Spencer 1989), and reducing the quality of wildlife habitat (Schmidt and Whelan 1999). If such species also monopolize seed dispersal services and quantitatively reduce native seed dispersal, they are likely to exert a competitive impact on native fleshy-fruiting plants, which may experience reduced fitness if their seeds fail to disperse from the immediate parent neighborhood (Ridley 1930, Liu et al., in press). An important component of this scenario is seed disperser preference: if dispersers commonly prefer invasive fruits, a significant reduction in dispersal of native species is likely (Gosper et al. 2006). Of course, frugivores do not explicitly consider a food plant's origin in their selection. However, non-native species could be particularly attractive to dispersers if they are relatively robust, with brightly-colored fruits, or exhibit very large crop sizes, all characteristics that might result from anthropogenic selection for horticultural purposes or from absence of natural enemies in the zone of introduction. On the other hand, dispersers may be more likely to favor native fruit species if they have natal experience with the fruits typical of the region (Stamps and Davis 2006) or if they display neophobia toward novel food items (Marples and Kelly 1999, Greenberg and Mettke-Hofmann 2001). If these scenarios are the rule, native fleshy-fruiting species might outcompete introduced species for dispersal, or at least are unlikely to be negatively impacted by dispersal competition, limiting the broad importance of such competition in biological invasions.

There have been a few attempts in localized systems to determine whether competition for dispersers occurs. Gosper et al. (2006) examined vertebrate-mediated dispersal of native plant species growing with and without invasive *Chrysanthemoides monilifera*, but found no effect of the invasive on native dispersal. Lichstein et al. (2004) found that native tree sapling mortality was elevated by *Ligustrum lucidum* invasion, but found no evidence that the invasive created dispersal limitation for natives. Similarly, although Aslan (2011) demonstrated potential competition for dispersers through niche overlap between native and non-native species in California, the native plant species in that system received proportionally more dispersal than did any of the non-natives. It is therefore unclear whether or not competition for dispersers is a common impact of biological invasions, or, rather, an unfounded suggestion by ecologists.

Since preference may play a key role in such competition, we combined a literature review, exploratory meta-analysis, and two case study aviary experiments to address the question: Under what circumstances do seed dispersers demonstrate preference for non-native fruits? We began by examining a number of studies that have probed the causes of fleshy-fruited invasion and identified characteristics that appear to promote animal-mediated dispersal of the invasive species in question. These studies do not directly compare native and non-native seed dispersal, but shed light on factors that may be pivotal in seed disperser preference. Additionally, a limited number of studies have directly examined frugivore preference for native vs non-native fruits

(Table 1). These studies have fallen into two categories: a small set of experiments comparing disperser preference for native and non-native species selected for their similarity; and somewhat more numerous studies comparing disperser preference for native and non-native species in an existing suite of co-occurring species, with no attempt to control species similarity. We conducted a small-scale meta-analysis on comparative studies containing sufficient quantitative information to examine relative disperser preferences for non-native vs. native species. Implications of resulting preference data varied qualitatively depending on study category. We illustrate the contrasting outcomes of the two approaches by including here the results of two aviary case studies we conducted in which we compared bird preferences for native and non-native species when fruits were controlled for similarity and when they were not. In combination, our review and case studies suggest that the regional native fruit assemblage is likely to strongly influence frugivore preferences, and that the degree to

Table 1. Studies that have directly compared seed disperser preferences for native vs. non-native fruits. Effect size, used in meta-analysis calculation, is the natural log of the response ratio, calculated as the proportion of non-native fruit consumed to the proportion of native fruit consumed. Studies with insufficient quantitative data were not included in the meta-analysis, although their qualitative results are discussed in the review. *Superior feeding efficiency* reflects author interpretations within each study and may include factors such as larger fruit size, higher fruit energy or nutritional content, higher fruit flesh to seed ratio, larger infructescences, larger plants, and more accessible fruits. † *Approach* distinguishes between studies that deliberately matched surface fruit characteristics such as color and fruit type (= "matched") and studies that examined existing suites of fruits without controlling for similarity (= "unmatched").

Study	**Disperser**	**Effect size (lnRR)**	**Offers superior feeding efficiency**
Approach †: Unmatched			
Corlett 2005	Birds	Insufficient quantitative data	Non-native
Drummond 2005	Birds	-0.06	Native
Ferreras et al. 2008	Birds	Insufficient quantitative data	Native
Greenberg and Walter 2010	Birds	0.04	No clear superior
Jung 1992	Birds	0.14	No clear superior
Meisenburg 2007	Birds	-0.12	Not discussed
Montaldo 2000	Birds	-0.20	Not discussed
Rowles and O'Dowd 2009	Ants	-0.33	Non-native
Whelan and Willson 1994	Birds	-0.82	No clear superior
White and Stiles 1992	Birds	Insufficient quantitative data	Native
Williams and Karl 1996	Birds	Insufficient quantitative data	Native
Our experiment #1, this paper	Birds	-0.62	No clear superior
Approach †: Matched			
Greenberg et al. 2001	Birds	-0.14	Not discussed
Jones and Wheelwright 1987	Birds	-1.84	Native
LaFleur et al. 2007	Birds	0.95	Non-native
Sallabanks 1993a	Birds	Insufficient quantitative data	Non-native
Our experiment #2, this paper	Birds	0.42	Not explored

which an introduced species monopolizes dispersal services may depend on its superficial similarity to native species.

Plant trait focus: Disentangling causes of ongoing fleshy-fruited plant invasions

Many studies in invasion biology are intended to elucidate the causes of ongoing invasions by particular species. Among fleshy-fruited invaders, fruit attractiveness to frugivore dispersers is frequently examined. Characteristics such as color, fruit size, infructescence structure, nutritional content, and pulp to seed ratio are considered general determinants of fruit attractiveness to frugivores (Debussche and Isenmann 1989, Herrera 1998, Levey and Martínez del Rio 2001, Sallabanks 1993b, Whelan and Willson 1994), and these traits have also been implicated in frugivore mediation of invasions (Westcott and Fletcher 2011). Larger fruit size may enhance feeding efficiency but can constrain dispersal if native frugivore gape widths are exceeded. Frugivores in Hong Kong consumed exotic fruits that were on average larger and contained relatively lower seed mass than native species (Corlett 2005), presumably boosting feeding efficiency. Similarly, cassowaries (*Casuarius casuarius*) in Australia demonstrated disproportionately high consumption of large-fruited species (Bradford et al. 2008). By contrast, *Asparagus asparagoides* is more invasive than *A. declinatus* in Australia although both are non-native: not only does *A. asparagoides* have brighter and more accessible displays than *A. declinatus*, but the smaller fruit size of *A. asparagoides* facilitates a wider array of potential frugivores due to gape width limitations (Bass et al. 2006). Smaller fruit sizes similarly enabled a substantially expanded suite of potential dispersers of *Olea europaea* fruits in California (Aslan and Rejmánek, in press) and in the Mediterranean (Rey et al. 1997) and promoted black rat dispersal of various non-native seeds in Hawaii (Shiels 2011). Fruit composition is also important. *Acacia cyclops*, a bird-dispersed invader in South Africa, produces arils that are much more energy-rich than those produced by non-bird-dispersed congeners (Glyphis et al. 1981). Within a broad array of native and invasive fleshy-fruiting species from the island of Mahé, invasive species exhibit a wider range of nutrient content than is found among natives and include many species nutritionally superior to any native species, suggesting that fruit energy content may aid plant invasions on oceanic islands (Kueffer et al. 2009). By contrast, bird-dispersed non-native species in New Jersey were found to be disproportionately low in nutritional quality and, perhaps as a consequence, consumed largely after native fruiting species were no longer available (White and Stiles 1992). Both within and between fruiting species, total per-tree crop size was significantly and positively related to bird visitation rates in some studies (Sallabanks 1992, Deckers et al. 2007), although it had no effect in others (Renne et al. 2000, Cordeiro et al. 2004, Aslan 2011, Greenberg et al. 2001). Crop size may be key in plant invasiveness in South Africa, where the fruiting displays of invasive non-native species tended to be larger and more conspicuous than those of native species (Knight 1986).

Animal behavior focus: Frugivore preferences for native vs. non-native fruits matched for similarity

The small number of experiments that have examined frugivore preferences for native vs. non-native fruits that are similar in surface characteristics such as color and structure (e.g., both with red berries) have more often found preference for non-native than for native fruiting species (Table 1). Authors have suggested that frugivores use fine-scale differences to distinguish between similar food items. In two out of three aviary choice tests among color-matched pairs, European starlings and American robins preferred non-native over native fruits (LaFleur et al. 2007); the authors speculated that causal factors might include nutritional content and smaller relative seed mass (LaFleur et al. 2007). Captive American robins preferred similar native species to non-native *Viburnum opulus*, evidently due to low palatability of the introduced species (Jones and Wheelwright 1987). In a comparison of frugivory of native and invasive hawthorn (*Crataegus* spp.), bird attraction to larger pomes, greater fruit loads, and greater pulp to seed ratio were found to underlie a preference for the invasive species (Sallabanks 1993a). All of these characteristics imply that frugivores obtained a higher reward from each visit to the preferred plant than was available by visiting the less preferred. By contrast, frugivore-mediated fruit removal rates in North Carolina did not differ between invasive *Celastrus orbiculatus* and native *Ilex opaca*, which produce similarly colored and sized fruits, nor did fruit density per patch influence frugivory of *C. orbiculatus* (Greenberg et al. 2001). In this case, the authors suggested that normal bird flocking behavior was responsible for the lack of influence of per-patch fruit density on fruit removal as well as uneven fruit removal rates over the course of the season (Greenberg et al. 2001): birds likely moved from patch to patch and consumed resources opportunistically as they encountered them, rather than honing in on high-quality focal plants.

Frugivore preferences within existing suites of fleshy-fruited species

When combinations of native and invasive species in existing plant communities have been examined for frugivore preference, most studies have detected lack of preference or preference for native fruits (Table 1). No significant preference for either native or non-native fruits was observed when fruit removal by birds of two non-native and five native tree species co-occurring in Argentina was examined (Montaldo 2000). Birds consumed both native and non-native fruits at rates proportional to their availability, implying opportunistic consumption (Montaldo 2000). Opportunism has likewise been apparent in systems where non-native species offer fleshy fruits during a different season than the normal native fruiting season (White and Stiles 1992, Gosper 2004, Corlett 2005, Ferreras et al. 2008, Greenberg and Walter 2010, White and Vivian-Smith 2011); thus, non-native species benefit by supplying a resource that is otherwise rare or unavailable. On the other hand, distinct preference structure was detected in a suite of co-occurring fleshy fruited plants in Maine, but no consistent factor underlying preference was detected: one non-native species and one native species experienced significant frugivore preference, while one non-native and one native species were less preferred (Drummond 2005). When offered paired choices between non-native *Adisia crenata* and a variety of native species, native birds in Florida almost unilaterally preferred native species, although the cause of such preferences were not elucidated (Meisenburg 2007). Preferences of native birds in a series of field and aviary experiments in Illinois varied by context, but under several conditions native *Phytolacca americana* was preferred above non-native *Eleagnus umbellata* and *Lonicera maackii* (Whelan and Willson 1994), leading the authors to suggest that making native fruits available to dispersers could enhance management of non-native species. In western Massachusetts, frugivorous birds utilized native fruits more than non-natives, and bird body condition was better in sites dominated by native species (Labbe 2011). By contrast, native birds in Pennsylvania achieved highest density and also elevated consumption of native fruits in areas of high invasive plant density (Gleditsch and Carlo 2011). Individual American robins displayed varying preference hierarchies when offered two non-native and one native fruit species that co-occurred in Wisconsin and varied in color and fruit type; bird body size appeared to influence choices more consistently than fruit characteristics (Jung 1992). The identity, origin, and native range of the frugivores themselves may also play a role. In diverse community of native and non-native fruits in New Zealand, endemic birds consumed far more native fruits than non-native fruits, while non-endemic and non-native birds acted more opportunistically and consumed both native and non-native fruits readily (Williams and Karl 1996). Notably, the sole preference study we found in which the disperser was an invertebrate showed results contrasting with the general trend in this category. Reward content relative to diaspore size was important for ant dispersal in Australia, where non-native ants preferentially dispersed small non-native seeds with large elaiosomes rather than larger native seeds (Rowles and O'Dowd 2009).

Meta-analysis: Frugivore preferences for native vs. non-native fruit

Because such a small number of studies have directly compared frugivore preferences for native vs. non-native fruits, a quantitative examination of combined study results has limited power. Therefore, although we conducted an exploratory meta-analysis to evaluate overall trends, we consider meta-analysis results preliminary and urge further study before general conclusions regarding frugivore preferences may be drawn.

Meta-analysis methods

For our meta-analysis, we used the response ratio to compare effect sizes between studies (Rosenberg et al. 2000). This metric is calculated as:

$$\ln R = \ln \frac{\overline{X}^E}{\overline{X}^C}$$

where $\bar{X}^E$ is the weighted mean of the proportion of non-native fruits consumed and $\bar{X}^C$ is the weighted mean of the proportion of native fruits consumed. Using this metric, a negative mean effect size with a 95% bias-corrected confidence interval excluding zero indicates that native fruits are consumed significantly more than non-native fruits. A positive mean effect size with a 95% bias-corrected confidence interval excluding zero indicates that non-native fruits are consumed significantly more than native fruits. We used a random-effects model and generated confidence intervals using 5000 data randomizations (Rosenberg et al. 2000). To examine the influence of matching external fruit characteristics on experimental results, we conducted a categorical analysis in addition to the overall meta-analysis. Although meta-analysis weights effect sizes by the sample sizes and variances of the component studies, several of the studies we utilized omitted variance information from their results. Because the overall sample size of studies available to us was so low, we preferred to include as many studies as possible in the meta-analysis and therefore conducted an unweighted meta-analysis (after Johnson and Curtis 2001), in which variances for all component studies were set equal to 1. All meta-analysis calculations were performed in MetaWin 2.0 (Rosenberg et al. 2000).

Meta-analysis results

The overall meta-analysis detected no significant difference in frugivore consumption of native vs. non-native fruits (mean effect size = -0.21, 95% bias-corrected confidence interval -0.35 to 0.07, n = 12 studies). However, categorical analysis detected differences between studies examining matched vs. unmatched fruits. For studies in which fruits were matched by external characteristics, there was no significant difference in frugivore preference between native and non-native fruits, but a trend toward preference for non-native fruits was visible (mean effect size = 0.37, 95% bias-corrected confidence interval -0.16 to 0.91, n = 4 studies). For studies in which no attempt was made to match fruits, frugivores demonstrated significant preference for native fruits (mean effect size = -0.31, 95% bias-corrected confidence interval -0.37 to -0.03, n = 8 studies). Again, the number of studies available for each category was small enough that these meta-analysis calculations had low power and results should be treated with caution.

Case study: Bird preferences among fleshy-fruited species in northern California

We conducted two aviary feeding preference experiments using wild-caught birds and fleshy-fruited plants in northern California. Our results illustrate the importance of fruit similarity in experimental conclusions.

Field-based foraging observations on fleshy fruits in California demonstrated higher visitation and fruit consumption rates for native *Heteromeles arbutifolia* than for co-occurring non-natives *Olea europaea*, *Ligustrum lucidum*, and *Triadica sebifera* (Aslan 2011). To determine whether quantitative preference hierarchies were consistent with these observed foraging rates, we conducted aviary-based feeding trials, offering fruits of the four focal plant species to wild-caught individuals of two native bird species and one non-native bird species. In a separate study using a single native bird species, we examined preference hierarchies of birds offered native *H. arbutifolia* along with three non-native species selected for strong surface resemblance between their fruits and those of *H. arbutifolia*.

Case study methods

Preference hierarchy within an existing suite of fleshy-fruiting plants

The four non-native plants used in the first experiment are widely planted in the Sacramento Valley of California, co-occurring with the native species in many locations. *Olea europaea* L. (European olive, Oleaceae) produces racemes of large (ranging from 6–21 mm width), dark-purple drupes with high oil content and has become invasive in Australia (Spennemann and Allen 2000). *Ligustrum lucidum* W. T. Aiton (glossy privet, Oleaceae) invades natural areas in Australia and Argentina (Panetta 2000, Lichstein et al. 2004). Fruits are small (4–5 mm width) dark-purple berries produced in panicles with up to 3 million fruits per tree (Swarbrick et al. 1999). The plant's moisture requirements likely limit it to riparian areas in California. *Triadica sebifera* (L.) Small (Chinese tallow, Euphorbiaceae) produces round (7–8 mm width), white fruits in dehiscing capsules. Fruits consist of a seed with a hard coat surrounded by a waxy, lipid-rich aril. *Triadica sebifera* has become invasive in the southeastern United States (Bruce et al. 1997). In California, it is common in landscaping and spreads locally in a few riparian systems (Bower et al. 2009). These three non-native species were contrasted against the only simultaneously-fruiting and widespread native species: *H. arbutifolia* (toyon, Rosaceae). *Heteromeles arbutifolia* Lindl. (synonym *Photinia arbutifolia* Lindl.) produces red pomes (5–6 mm width) in panicles and is a largely upland, drought-adapted species. Nutritional analyses of the four plant species tested in this experiment show high similarity between *H. arbutifolia* and *L. lucidum*, which are both sugar-rich, and between *O. europaea* and *T. sebifera*, which are high in lipids (Supplementary table).

The bird species used in this experiment were selected to represent different functional guilds identified in field observations (Aslan 2011). American robins (*Turdus migratorius*) are native pulse feeders, feeding during winter in large flocks that move across the landscape and visit each fruiting stand in turn, removing most fruits there before moving on to a new feeding site. Hermit thrushes (*Catharus guttatus*) are native background feeders, present in each fruiting stand in low numbers throughout the season, with one or a few individuals exhibiting constant, low-level frugivory as long as fruits are present. European starlings (*Sturnus vulgaris*) are non-native pulse feeders that consumed non-native fruits far more than native fruits during field observations (Aslan 2011). Starlings were the top dispersers of *O. europaea* and *T. sebifera* in field observations; hermit thrushes were the top dispersers of *H. arbutifolia* and performed at least some dispersal for all four plant species; and robins were among the top four dispersers for all four plant species (Aslan 2011). Robin and starling flocks were larger than those of other species observed during field observations (Aslan 2011), so the preferences of these two species have high potential to impact seed dispersal dynamics. All three focal bird species are more heavily frugivorous in winter in California than at other times of the year, when they become more omnivorous as more diverse food sources become available.

Ten robins were captured with mist nets in Butte County, CA, in December, 2007. Nineteen starlings were captured with walk-in traps in Marin County, CA, in November, 2008. Seven hermit thrushes were captured with mist nets in Butte and Yolo Counties, CA, in January, 2009. All birds were returned to open-air cages at the University of California, Davis. Cages measured 2.4 m tall, 1.5 m wide, and 3.8 m long. A single bird was housed in each cage and opaque green shade cloth was attached to walls between cages to prevent birds from observing and mimicking one another. Cages were roofed with metal sheeting to shelter birds from precipitation but were open at either end to allow natural sunlight and airflow/temperature. Birds were kept in cages for 10 days following capture to enable them to adapt to cage conditions. During this period, birds were provided *ad libitum* a maintenance diet with a banana/soy protein base (Denslow et al. 1987), supplemented with mealworms (10 per bird per day). Roudybush crumble maintenance diet (Roudybush, Inc., Woodland, CA) and moistened Eukanuba Small Bites Puppy Chow (Iams Co., Dayton, OH) were also made available to all birds, although these appeared to be consumed only rarely. Maintenance food was refreshed twice daily. Experimental treatments started on the 11th day of captivity; throughout the experimental period, the same maintenance diet was returned to the cages each day after experimental trials were completed (approximately 2 hours after sunrise) and remained available to birds for the remainder of the day. Birds were provided with water *ad libitum* at all times during captivity. Birds were weighed twice per week for the duration of the experiment to ensure that they were maintaining body weight; body weights decreased on average 10% during the first week of the experiment before stabilizing for the remainder of the captivity period.

For choice tests, experimental fruits were hung from weighted fishing line attached to cage ceilings. Fresh infructescences were collected from plants during the morning of each trial and were suspended from fishing line by looping the line around the infructescence stems. A separate line was used for each plant species so that the infructescences were presented to birds in a row across one end of the cage, separated from one another by approximately 30 cm. A long perch was hung in front of the row of fruits, allowing the bird easy access to all fruits. The fishing line allowed infructescences to bounce naturally as the bird foraged, mimicking branch movement in the wild. Whole infructescences were used so that the appearance, relative abundance, and arrangement of fruits reflected those encountered in the field. There was no attempt to artificially enhance similarity between plant species by controlling for fruit size or per-infructescence fruit abundance. Size differences between fruits are so great that any attempt to equalize mass, for example, would require a given trial to utilize a very small number of *O. europaea* fruits relative to the number of *L. lucidum* fruits, skewing food item abundance dramatically. Whole infructescence use resulted in *L. lucidum* being the most numerous fruit offered, while *O. europaea* was usually offered in the greatest mass. Statistical analyses took into account initial availability of each fruit species per trial. At the end of each trial, fruits of all four species remained in all bird cages, demonstrating that quantities initially provided were sufficient to allow birds to make choices throughout the duration of each trial.

Choice trials were conducted as follows: Each phase of choice trials lasted six days. Just before daybreak on each day, one ripe (containing only fruits visibly as bright in color as any available on regional source trees) infructescence of each of the four study species was placed in each cage. Birds had fasted overnight. Infructescences were hung in random order from the fishing lines so that the arrangement differed from day to day. All birds were offered all fruits each day. All fruits were counted prior to their placement in the cages. Birds were allowed to forage freely for two hours. Birds showed evidence of hunger during this time, since most birds foraged, but not starvation (on some days, a minority of birds did not forage during the two-hour period). At the end of this period, all infructescences were removed and maintenance food replaced in cages. The final numbers of fruits per infructescence were counted to determine how many fruits had been removed. Cage floors were inspected and any whole fruits that had been dropped or had fallen from infructescences were collected so that actual numbers of fruits consumed could be calculated. Samples of fruits of each species were then weighed so that approximate masses of fruits available and consumed could be estimated. The same fruit species were offered on each of the six days, and these days were considered subsamples for statistical calculations. This minimized the effect of weather and other factors that may have caused variation in birds' daily feeding behavior.

During the second experimental phase, the fruit species most preferred by each bird species was withheld in order to determine preference hierarchy among remaining fruit species (to force some birds to choose between species they had previously ignored). Again, results from each day within this phase were considered subsamples for calculation of within-phase preference. Because robins and hermit thrushes preferred the native *H. arbutifolia* during phase 1, a third experimental phase included the native fruit once again in the experimental array so that birds had all four options. This was to ensure that preferences for the native in phase 1 were not due simply to familiarity with the native fruit, since it is more widespread in northern California than are the target non-natives, which are still clustered around urban and agricultural areas. Because birds had consumed non-native fruits during phase 2, when no natives were available, we hypothesized that neophobia or any similarly transient cause of preference would be purged by phase 2. Phase 3 thus elucidated the robustness of the initial preference for the native fruiting species, determining whether birds maintained that preference even after demonstrated familiarity with non-native fruits.

Preference hierarchy among plants selected for resemblance

In the second experiment, seven hermit thrushes (captured and maintained following the same methods and facilities described above) were offered fruits of four species selected for their resemblance to one another in the surface characteristics of fruit color, shape, and size: native *H. arbutifolia* and non-natives *Cotoneaster pannosus*, *Photinia x fraseri*, and *Pyracantha angustifolia*. All three of these non-native species are in the family Rosaceae and produce panicles of small red pomes. *Cotoneaster pannosus* is considered a potentially invasive species in California due to its invasiveness elsewhere and observed spreading in natural areas (Bossard et al. 2000). *Pyracantha angustifolia* is invasive in Argentina (Tecco et al. 2006) in environmental conditions similar to those found in parts of California. No instances of invasion by *Photinia x fraseri* in any environment have been recorded. Infructescences of these species were offered side by side for a single experimental phase of ten days, and fruit availability and consumption were tracked following the same protocol as described above for the first experiment.

Statistical analyses

Number of fruits consumed is more relevant to seed dispersal than is mass consumed since the number of fruits translates directly to the number of seeds that could be dispersed. For simplicity, therefore, figures and tables include only results by number. All statistical tests were performed for mass as well, but results did not differ qualitatively from results by number.

Treating the days within each experimental phase as subsamples, we calculated mean numbers available and consumed of each fruit species by each bird. We used these averages to calculate the selection index (w_i) of each fruit species by individual bird: $w_i = o_i/p_i$, where o_i = the proportion of species *i* in the diet, and p_i = the proportion of species *i* available in the environment (Krebs 1999). Selection index values exceeding 1.0 indicate preference for a food item since it has been consumed more than is proportional to its availability. We compared selection indices for each fruit species by bird species, separated by experimental phase, using standard least squares analysis of variance with individual bird as a blocking factor. To satisfy model assumptions, selection index values were square-root transformed prior to the performance of the ANOVA. Results were back-transformed for data presentation in figures. For each significant ANOVA model, a Tukey HSD means comparison was used to detect significant differences among fruit species. For all tests, significance was accepted at $p \leq 0.05$. Statistical analyses were performed in JMP 5.0.1 (SAS Institute, 2002).

Results of the case study

For the first experiment, analysis of variance revealed significant feeding preferences by selection index for all bird species in all experimental phases (Table 2, Figure 1). Robins preferred native *H. arbutifolia* to other test fruits when the native was available. When *H. arbutifolia* was withheld, they preferred *O. europaea* (Figure 1a). On average, starlings preferred *O. europaea* to other experimental fruit species. When *O. europaea* was withheld, starlings avoided *T. sebifera* but preferred *L. lucidum* and *H. arbutifolia* equally (Figure 1b). Hermit thrushes preferred *H. arbutifolia* to other fruits (both first and third experimental phases). When the native was withheld, they preferred *O. europaea* to other fruits with *L. lucidum* as a close second (Figure 1c). *Triadica sebifera* was consumed least by all birds during all phases (Figure 1).

During the second experiment, when experimental fruits were selected for their similarity, hermit thrush selection indices displayed little preference structure (Table 3). Analysis of variance results showed no overall significant difference in feeding preference among the four red-fruited species (Figure 2; a = 0.05), although raw numbers demonstrated greater consumption of all three non-native fruits than of the native *H. arbutifolia*.

Table 2. Results of analyses of variance comparing fruit species selection indices (w_i) separated by bird species and by experimental phase. Individual birds were treated as blocks for analysis. Data were square-root transformed to meet assumptions of homogeneity of variance.

Bird species	Experimental phase	Source	DF	F ratio	Prob > F
American robin (*Turdus migratorius*)	1	Fruit	3	26.82	<0.0001
		Bird (Block)	9	0.4035	0.9222
	2	Fruit	2	13.68	0.0002
		Bird (Block)	9	0.6943	0.7058
	3	Fruit	3	55.07	<0.0001
		Bird (Block)	9	0.6974	0.7055
European starling (*Sturnus vulgaris*)	1	Fruit	3	13.68	<0.0001
		Bird (Block)	18	0.4404	0.9711
	2	Fruit	2	7.95	0.0014
		Bird (Block)	18	0.6810	0.8064
Hermit thrush (*Catharus guttatus*)	1	Fruit	3	33.82	<0.0001
		Bird (Block)	6	0.6470	0.6921
	2	Fruit	2	4.35	0.0380
		Bird (Block)	6	0.4374	0.8403
	3	Fruit	3	9.97	0.0004
		Bird (Block)	6	0.0911	0.9965

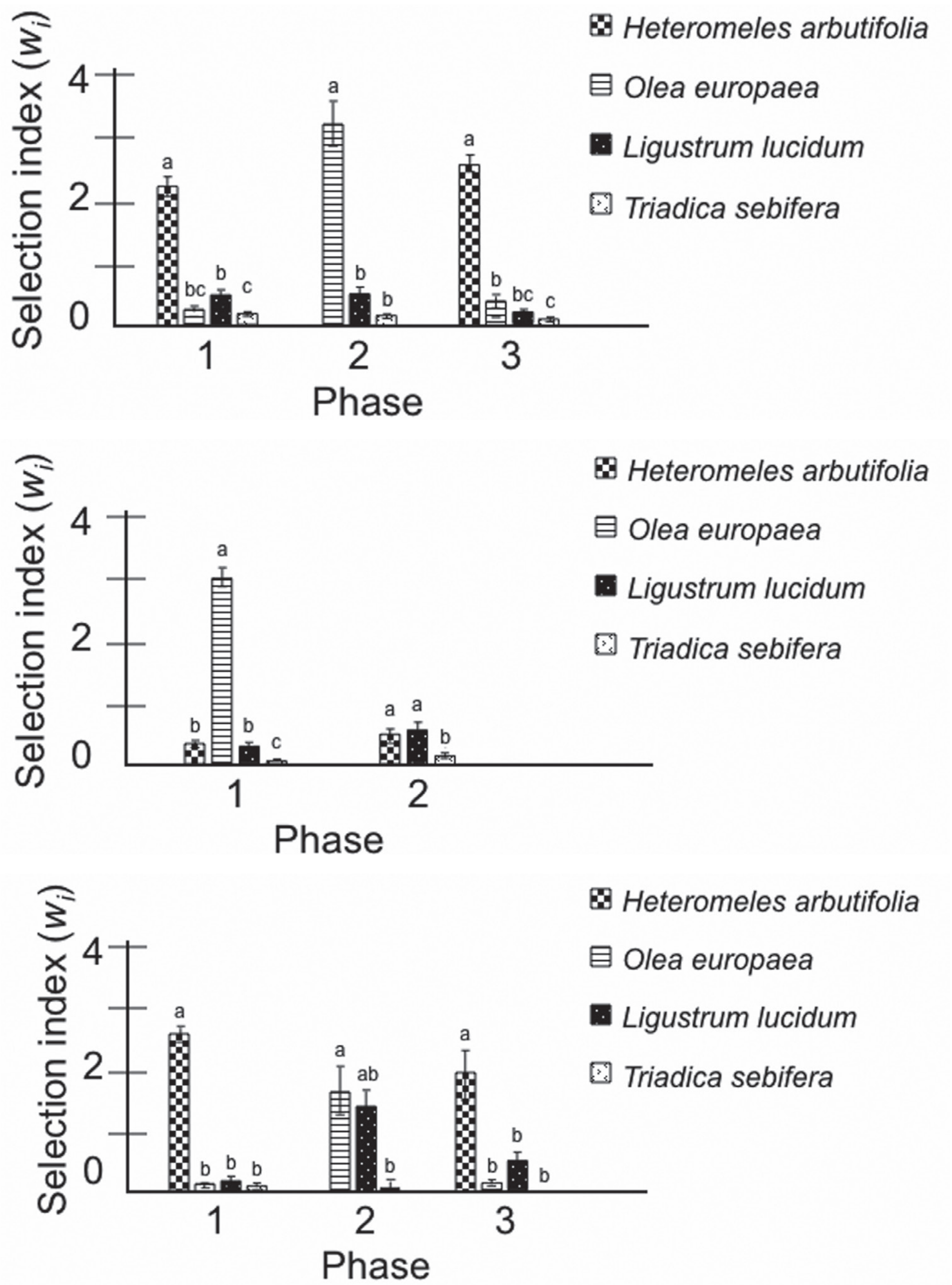

Figure 1. Mean (± SE) selection indices (w_i) by bird species and by experimental phase. Selection index values >1.0 indicate a preferred food item (consumed at a rate exceeding its availability). Analyses of variance with individual birds designated as blocks compared preferences within each experimental phase. Means within each ANOVA were compared using Tukey HSD means separation. Within each experimental phase, bars not designated by the same letter are significantly different at a = 0.05. **a** American robins (*Turdus migratorius*) **b** European starlings (*Sturnus vulgaris*) **c** Hermit thrushes (*Catharus guttatus*)

Table 3. Selection indices (w_i) for similarity experiment using red fruit and testing preferences of hermit thrushes (*Catharus guttatus*). Selection index values greater than 1.0 indicate preference by hermit thrush individuals for a food item, and these values are underlined. Values are presented for number of fruits as selection indices ± SE.

Bird	*Pyracantha angustifolia*	*Cotoneaster pannosus*	*Photinia x fraseri*	*Heteromeles arbutifolia*
A	0.12 ± 0.21	0.36 ± 0.31	<u>2.51</u> ± 0.37	0.50 ± 0.32
B	0.26 ± 0.32	<u>1.30</u> ± 0.57	<u>1.32</u> ± 0.44	0.87 ± 0.48
C	<u>1.94</u> ± 0.70	0.98 ± 0.54	0.47 ± 0.36	0.82 ± 0.49
D	<u>1.12</u> ± 1.23	0.97 ± 1.06	0.80 ± 0.88	<u>1.21</u> ± 1.33
E	<u>2.95</u> ± 0.73	0.21 ± 0.26	0.96 ± 0.41	0.26 ± 0.29
F	0.50 ± 0.36	0.40 ± 0.28	<u>2.33</u> ± 0.32	0.36 ± 0.23
G	0.40 ± 0.39	0.93 ± 0.52	<u>1.60</u> ± 0.40	0.66 ± 0.43

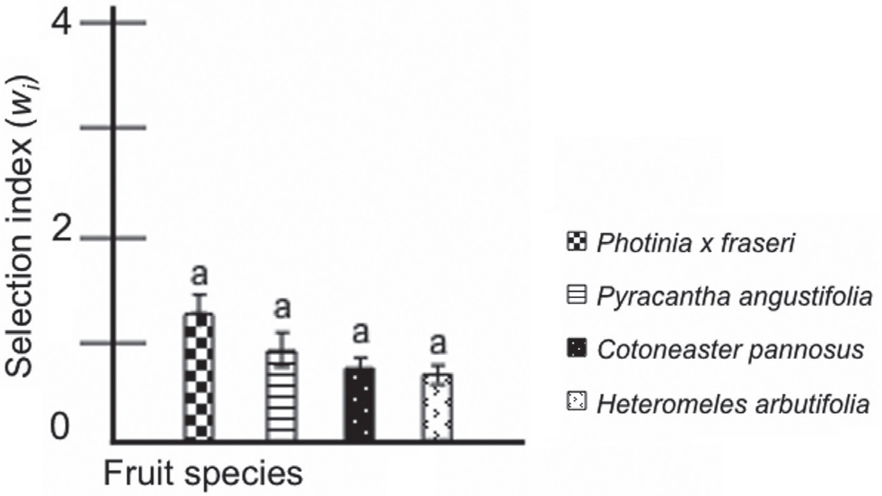

Figure 2. Hermit thrush (*Catharus guttatus*) fruit similarity experiment selection indices by fruit species. Mean selection indices were compared using analysis of variance, with individual bird as block. Means within each ANOVA were compared using Tukey HSD means separation. Within each experimental phase, bars not designated by the same letter are significantly different at a = 0.05.

Discussion

If native frugivores prefer introduced fruiting species in a given region, seed dispersal services are likely to be monopolized to some degree by the non-native plant species and withheld from native plants. Although the number of studies that have explored such dispersal competition is quite low, our review and meta-analysis of their results and our case study experiments indicate that native fruit characteristics may play an important role in determining frugivore preference. When frugivore preference is evaluated in the context of the full existing suite of fleshy-fruited plants, with no attempt to artificially enhance similarity between species, frugivores tend to prefer native fruits. However, when non-natives that are similar to natives in surface appearance have been examined, frugivores have shown an inclination, often slight, to prefer the non-native fruits. In published literature, preference for non-natives appeared to result from larger crop sizes, higher per-fruit energy content, or larger fruits relative to seed mass, implying that such species are preferred because the reward is likely greater for a given frugivore visit. Thus, frugivores in these studies seem to demonstrate general attraction to certain characteristics typical of native fruits (such as color or shape), and it is within sets of species sharing these characteristics that more subtle preferences favoring non-native species appear.

In our case study experiments, for example, both native bird species preferred the native red berry even above *Ligustrum lucidum* with its very large crop sizes of dark purple berries, although the two are extremely similar nutritionally. When the native fruit was contrasted against non-native, red-berried species offered to hermit thrushes, however, this strong preference for the native fruit disappeared. Birds that had displayed highly significant preference for native fruits displayed no significant preference structure when similar fruits were introduced. The non-native bird species, on the other hand, showed no preference at any time for the native species. The native bird fauna appears to maintain a robust preference for red-berried species, which could be the result of loose coevolution between the birds and fruits in the area: since the most available native fruit during the winter season is red, a preference for that color among native birds is unsurprising. When non-native species producing red berries are introduced to this system, they are likely preadapted to ready winter seed dispersal. As long as they produce larger or more accessible crops, they may draw dispersers away from the native species. By contrast, fruits of different color or structure from the native appear less preferred, likely because they lack such preadaptation. Under this scenario, native fruit characteristics appear to play a key role in determining whether native and non-native fruits will compete for dispersers. Introduced species sharing these characteristics (red berries) are most likely to exert a competitive impact. An important consideration is that bird adaptation to prefer a given native fruit may arise because that native fruit is a particularly suitable food source, for example contributing to higher bird fitness by offering high nutritional value. Decline in such fruit species through a competitive effect may therefore impact native bird populations.

Non-native frugivores may also affect seed dispersal. Such species have enhanced the dispersal of native species in some systems (Foster and Robinson 2007), while in others they facilitate invasions by non-native species (Mandon-Dalger et al. 2004). In our case study experiments, European starlings preferred non-native *Olea europaea* fruits, and they were dominant visitors to all three target non-native species in field observations (Aslan 2011). The preference hierarchy and foraging pattern displayed by starlings differed considerably from those observed in native bird species. Since introduced birds and native plants do not share an evolutionary history, it is unsurprising that they lack the tight linkage imposed by bird feeding preferences. It appears logical that the pattern we observed would also be found in other systems, although the preferences of non-native frugivores have been explored in only a handful of studies (e.g., Williams 2006, LaFleur et al. 2007, Kawakami et al. 2009). We thus qualify that the importance of native fruit characteristics, as discussed above, seems likely to diminish if a substantial portion of the local frugivore fauna is introduced.

Conclusion

The review, meta-analysis, and aviary experiments examined here suggest that frugivores are most likely to favor non-native fruits if they resemble preferred native fruits, at least on the surface. In several instances, frugivores have shown preference for non-native species that are selected to resemble native species in fruit color or type. When such introduced species offer a larger number of fruits per plant or relatively higher quantity of digestible material per fruit, they appear to attract more frugivory than the natives and thus have the potential to display a competitive edge over native fleshy fruits. When non-native species differ from natives in superficial characteristics such as fruit color or type, studies show a tendency for frugivores to prefer native species or at least to feed opportunistically. This pattern implies that non-native fruits are most likely to encounter preferential frugivory and thus to compete for dispersers with native fruits if they resemble those native fruits and offer enhanced feeding efficiency. When these conditions are met, competition for dispersers and eventual decline in the dispersal of native species may occur following fleshy-fruiting plant introductions.

If it is indeed widespread across geographies, such competition has implications both before and after plant introductions. When new plants are considered for a region, as horticultural, agricultural, or landscaping introductions, they may be most likely to encounter frequent dispersal and to exert competitive impact if they resemble preferred native plants and overlap with natives in fruiting phenology. Along with other known invasive impacts of such species, dispersal competition should be considered a potential additional impact of their introduction, and should be taken into account. Control of such species in favor of the native should be considered.

To date, the number of studies directly addressing seed disperser preference for native vs. non-native fruits is very low, and study designs differ considerably. A greater number of such studies will be necessary in order to evaluate with confidence how widespread these patterns may be. In addition, we recommend use of standardized methodologies (such as those described in Manly et al. 2002) that include comparisons of both similar and dissimilar fruits, in order to account for the role of native fruit characteristics in preference development. To our knowledge, no studies of exotic vs. native preference among two important groups of tropical dispersal agents, bats and primates, nor of frugivorous predators (D'hondt et al. 2011) have so far been conducted. Expansion of the taxonomic scope of the literature to include these and other groups, including further exploration of invertebrate dispersers, would be beneficial. Once the sample size of available studies has grown, a more robust meta-analysis may be useful to pinpoint more precisely the conditions under which seed dispersers favor non-native fruits.

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Supplementary table. Nutrient content of the four focal fruit species. Values are for fruit pulp, the fruit portion assimilated in most cases by frugivorous birds, which usually defecate or regurgitate seeds. Nutrient content analyses were conducted by a commercial food analysis company (National Food Laboratories, Inc., Livermore, CA).

Nutritional component	***Heteromeles arbutifolia***	***Olea europaea***	***Ligustrum lucidum***	***Triadica sebifera***
Fructose (%)	0.62	0.11	2.77	<0.25
Glucose (%)	5.06	1.06	5.80	<0.25
Lactose (%)	<0.25	<0.25	<0.25	<0.25
Maltose (%)	<0.25	<0.25	<0.25	<0.25
Sucrose (%)	<0.25	<0.25	0.63	2.27
Total Sugars (%)	5.88	1.67	9.71	2.27
Ash (%)	1.14	2.28	1.84	2.33
Calories (cal/100g)	134.07	346.21	95.07	1038.46
Carbohydrates (%)	33.28	22.04	25.75	3.16
Moisture (%)	64.91	45.78	72.24	28.01
Protein (%)	0.67	2.18	0.17	<0.25
Total Fat (%)	<0.25	27.71	<0.25	66.5