

Implications of newly-formed seed-dispersal mutualisms between birds and introduced plants in northern California, USA

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Abstract I examined the role of bird dispersal in invasiveness of three non-native plant species in California, USA: *Triadica sebifera*, *Ligustrum lucidum*, and *Olea europaea*. I selected these species because their invasiveness in California is uncertain, but a survey of ornithologists highlighted them as likely bird-dispersed. I quantified bird frugivory of these plants, compared them with a native species (*Heteromeles arbutifolia*), and explored the management implications of dispersal mutualisms for these and other incipient invasive plants. Fruit removal by birds was sufficient to permit spread for all study species. Seed dispersers (rather than seed predators) and pulse feeders (flocking species with potential for long distance dispersal) performed most fruit removal for the non-native species, a pattern indicative of an effective dispersal regime. The number of fruiting trees per stand was a significant predictor of bird visitation. Founding population size may thus be important in management of invasive, bird-dispersed plants. Disperser-defined niches were relatively

narrow because a few disperser species performed the majority of fruit removal from study trees, but each fruit species was consumed by a variety of potential dispersers. This results in strong pairwise niche overlap between some plant species. Ordinated by bird use, study site-species combinations clustered more by geographic location than by plant species, emphasizing the opportunistic nature of bird foraging. None of the non-native focal plant species appears dispersal limited, and all have formed novel mutualisms in California. It is possible that these plants are now in lag phases preceding bird-mediated invasion. Consideration of bird dispersal when evaluating invasiveness is therefore an imperative.

Keywords Bird-mediated dispersal · Focal individual observations · Frugivory · Mutualisms · Niche · Risk assessment

Introduction

When plant species are introduced to new environments, their interactions with resident organisms may determine whether or not they become invasive (Richardson et al. 2000). Non-natives can be limited by competition with or herbivory by resident species (Cogni 2010; Corbin and D'Antonio 2004; Naeem et al. 2000). On the other hand, positive interactions such as mutualisms with dispersers, pollinators, or

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soil biota may permit invasion of new environments (Bascompte and Jordano 2007; Reinhart and Callaway 2006). Furthermore, such mutualisms are generally diffuse, with many mutualist species interacting with each plant species (Aslan and Rejmánek 2010; Bascompte and Jordano 2007; Jordano 1987b). For this reason, many introduced plants with fleshy fruits are able to develop effective dispersal interactions with resident fauna (e.g., Bartuszevige and Gorchov 2006; Drummond 2005; Gosper et al. 2005; Panetta and McKee 1997; Renne et al. 2002). Plant species unable to form novel dispersal mutualisms with new partners in their region of introduction may have greatly reduced potential for invasive spread (Gosper et al. 2005). Bird-mediated dispersal is therefore a trait that many rubrics associate with plant invasiveness (Pheloung et al. 1999; Pyšek and Richardson 2007; Rejmánek 2000; Rejmánek et al. 2005).

Mutualistic bird dispersal confers a number of advantages to the dispersed species. Bird-mediated dispersal removes seeds from the immediate neighborhood of the parent tree, possibly separating seeds and seedlings from natural enemies and often depositing them in suitable recruitment sites (Connell 1971; Gosper et al. 2005; Janzen 1970; Wenny 2001). Long-distance dispersal events may greatly increase the overall spread rate of a dispersed species (Nathan 2006). Seeds passing through bird guts receive mechanical and chemical treatments that sometimes promote germination (Gosper et al. 2005; Traveset 1998). Additionally, because their dispersal is assisted, fleshy-fruited seeds can often be larger than wind-dispersed seeds, enabling them to carry energy stores that enhance survival over a variety of environmental conditions (Leishman et al. 2000).

Among bird-dispersed plants, species cover a spectrum of mutualism efficiency: on one extreme, plants produce many more fruits than are removed by bird dispersers, while on the other, nearly all available fruits are removed (Herrera 1984; Renne et al. 2000). A number of factors may influence bird visitation to fruiting plants. Small fruits and seeds appear to be removed and dispersed more effectively than large fruits (Gosper et al. 2005; Rey et al. 1997). Bird-dispersed seeds are often contained in fruits that are bright or bicolored (Wheelwright and Janson 1985; Whelan and Willson 1994). Birds prefer accessible over inaccessible fruits (Whelan and Willson 1994) and select between trees based on fruit abundance,

preferring trees with large crop sizes (Korine et al. 2000; Sallabanks 1993). Nutritional quality may attract birds to fruits of certain species (Levey and Martínez del Río 2001). Overall density of fruits in the neighborhood also appears to promote increased bird foraging (Kwit et al. 2004; Sargent 1990).

In a questionnaire distributed to ornithologists in California, Washington, New York, and Florida, consumption by birds was reported for fruits of 17 non-native species that had not yet been explored in invasion biology literature for invasiveness in the relevant states (Aslan and Rejmánek 2010). This list pinpointed information gaps: if questionnaire respondents were correct and birds are using the plants, the plants have a ready-made dispersal mechanism and should be examined for habitat compatibility, reproductive potential, and growth rate. If no barriers to establishment exist, the plants may be “sleeper” species in the lag phase preceding invasion (Groves 1999).

I chose three of these species for empirical examination of bird-mediated dispersal in California. The selected plants, *Olea europaea*, *Ligustrum lucidum*, and *Triadica sebifera*, are all winter-fruiting but differ in fruit type, size, and color. They are commonly planted in urban and agricultural areas in California’s Sacramento Valley. Furthermore, all three are problematic, bird-dispersed invasives elsewhere in the world, in habitats similar to those found in the Californian study region. It is therefore likely that these species will establish in Californian habitats if a dispersal vector is present. However, none of the three species has yet shown more than localized spread in California. Since questionnaire results indicated that Californian birds do use the fruits of these plants, I hypothesized that the plants are in lag phases and likely to be incipient invaders, facilitated by birds, in the region.

I conducted an observational study to examine the degree to which birds have integrated the plants into the regional bird-plant community. I gathered parallel information for *Heteromeles arbutifolia*, which is the only widespread, simultaneously-fruiting native species that co-occurs with the study species in both urban and rural sites in the region. I asked two primary questions, within which were nested several secondary questions: (1) Do bird visitation and fruit removal indicate that birds have the potential to disperse study species sufficiently to enable spread

across the landscape? Specifically, (a) what proportion of fruits of each study species are removed by birds? (b) How much fruit foraging may be attributed to birds of different behavioral and feeding guilds? (2) What are the implications of bird use of these species for management of these and other incipient, bird-dispersed invaders? Specifically, (a) what characteristics of local site and fruiting stands contribute to bird visitation and fruit removal from non-native trees? (b) Is dispersal attributable to one or a few primary dispersers that could be considered in management for invasion by these species, or is it highly diffuse? (c) How much disperser-defined niche overlap exists between study species and the native species?

Methods

Study species

Olea europaea

Originating in the Mediterranean basin, European olive (*Olea europaea* L., Oleaceae) was introduced to California in the late 1700s (Connell 2004). The tree is widespread in California today, mostly in orchards or windbreaks. Fruits are large drupes, deep purple to black at maturity, each containing a single seed with a very hard testa.

Olea europaea fruits are dispersed effectively by birds in the Mediterranean (Rey and Alcántara 2000) and in Australia, where *O. europaea* is invasive in natural areas (Spennemann and Allen 2000b). Abandoned *O. europaea* groves in Australia are now seed sources for naturalizing populations dispersed by birds; a lag phase of approximately 200 years occurred prior to the invasion (Besnard et al. 2007; Spennemann and Allen 2000a). Feral stands have dense, long-lived canopies under which heterospecific trees can rarely establish (Spennemann and Allen 2000a).

Triadica sebifera

Chinese tallow (*Triadica sebifera* (L.) Small or *Sapium sebiferum* (L.) Roxb., Euphorbiaceae) is native to eastern Asia and has been planted for the past 40 years in northern California as an ornamental landscaping tree. The species has become highly

invasive in the southeastern U.S., where it infests large floodplain, wetland, and low-lying forest areas, enriching soil and forming monocultures that displace native species (Bruce et al. 1997; Cameron and Spencer 1989; Jubinsky and Anderson 1996). Fourteen bird species in the invaded region have been shown to consume *T. sebifera* seeds (Renne et al. 2000). Fruits are capsules that dehisce with maturity to reveal 2–3 round seeds, each encased in a white, waxy aril.

Although *T. sebifera*'s moisture requirements exclude it from colonizing California's dry uplands, climate modeling predicts that the species will successfully establish in the state's highly-threatened riparian areas (Pattison and Mack 2008). Current spread into natural areas has been observed at a small number of riparian sites in northern California (Bower et al. 2009), but widespread and rapid invasion has not yet occurred. Since a substantial lag phase passed prior to invasion in the Southeast (Bruce et al. 1997), it is logical that the species may be exhibiting a similar delay before greater invasiveness in California (Bower et al. 2009).

Ligustrum lucidum

Glossy privet (*Ligustrum lucidum* W. T. Ait., Oleaceae), native to Asia, is a problematic invader in Florida, Japan, Australia, New Zealand, and Argentina (Aragón and Groom 2003; Dehgan 1998; Hashimoto et al. 2005; Panetta 2000) and an emerging invader in South Africa (Nel et al. 2004). Fruits are blue-black berries, smaller than those of the other study species, and borne in panicles with dozens to hundreds of fruits per infructescence. Individual tree fruit loads can be very large (e.g., 3 million fruits for an individual in moist conditions in Australia) (Swarbrick et al. 1999). While *L. lucidum* generally invades areas with abundant or elevated soil moisture (Hashimoto et al. 2007; Panetta 2000; Swarbrick et al. 1999) and is therefore probably limited in California to riparian zones, it can grow in a broad range of light, temperature, and soil conditions (Aragón and Groom 2003; Lichstein et al. 2004; Swarbrick et al. 1999). It dominates shrub and small tree strata in invaded regions (Panetta 2000). Soil fertility and understory light penetration were decreased and native sapling mortality increased where *L. lucidum* had invaded in Argentina

(Lichstein et al. 2004). The tree's dense, shallow root system depletes soil nutrients and water (Swarbrick et al. 1999).

Birds effectively disperse *L. lucidum* in its invaded regions. In Argentina, 11 resident bird species were observed eating *L. lucidum* fruits, with some birds acting as dispersers and others as seed predators (destroying seeds through crushing or other damage) (Montaldo 1993). In Australia, *L. lucidum* and its congener, *L. sinense*, represented three-quarters of the diet of native pied currawongs (*Strepera graculina*) during the fruiting season (Spennemann and Allen 2000b). Seventeen bird species were observed utilizing *L. lucidum* for various purposes in New South Wales, where the species has replaced extirpated native food sources (Ekert and Bucher 1999).

While *L. lucidum* has been observed spreading in certain localities in California (S. Mason, pers comm), its overall naturalized distribution and spread at the state level are unknown (DiTomaso and Healy 2007). The species is common in urban, irrigated areas throughout central and southern California, planted as a landscaping and hedge species.

Heteromeles arbutifolia

Toyon (*Heteromeles arbutifolia* Lindl., Rosaceae) is native to California and was utilized as a comparison species for all analyses. Although it differs from non-native study species in fruit color (red vs. purple, purple-black, and white) and growth form (tall shrub vs. short tree), it is the only native fleshy-fruited plant growing in all study sites and fruiting simultaneously with non-native study species. It grows as a shrub or small tree and is common in chaparral and mixed oak woodland communities (Hickman 1993). Fruits are round, bright-red pomes, borne in panicles of dozens to hundreds at the tips of branches; each plant can produce tens to hundreds of thousands of fruits per year (pers. obs.).

Study sites

I selected multiple, geographically distant study sites (treated as blocks in statistical analyses) for observations of each study species (Fig. 1). In all, six study sites were utilized in three counties (Butte, Yolo, and Sacramento). Because not all study species occurred in all study sites, each of the four plant species was

examined in at least three and not more than four of these sites (Fig. 1). Observations were conducted on a total of 12 stands of each species. I employed at least three stands per site-species combination, except for *O. europaea* in the Big Chico Creek Ecological Reserve, of which only two stands exist.

All study sites were located in the Sacramento River Valley of California, between 38°27'N and 39°53'N. The region is characterized by a mediterranean climate, receiving the large majority of its precipitation during the cool winter months. Agricultural fields, broken by urban pockets and remnant riparian corridors, dominate the valley. The abundance of agriculture provides ample food for wildlife and may be partially responsible for the high winter bird diversity (approximately 170 species) found in the region (Engilis 1995). Higher elevation regions at the valley's edges support chaparral and oak-grassland habitats.

Because two study species (*T. sebifera* and *L. lucidum*) are thus far largely restricted to urban zones where they have been planted, four of the six study sites were urban areas: Sacramento, Davis, Woodland, and Chico. Focal stands (3 or more reproductive individuals in close proximity) of study species were selected in urban parks and greenbelts.

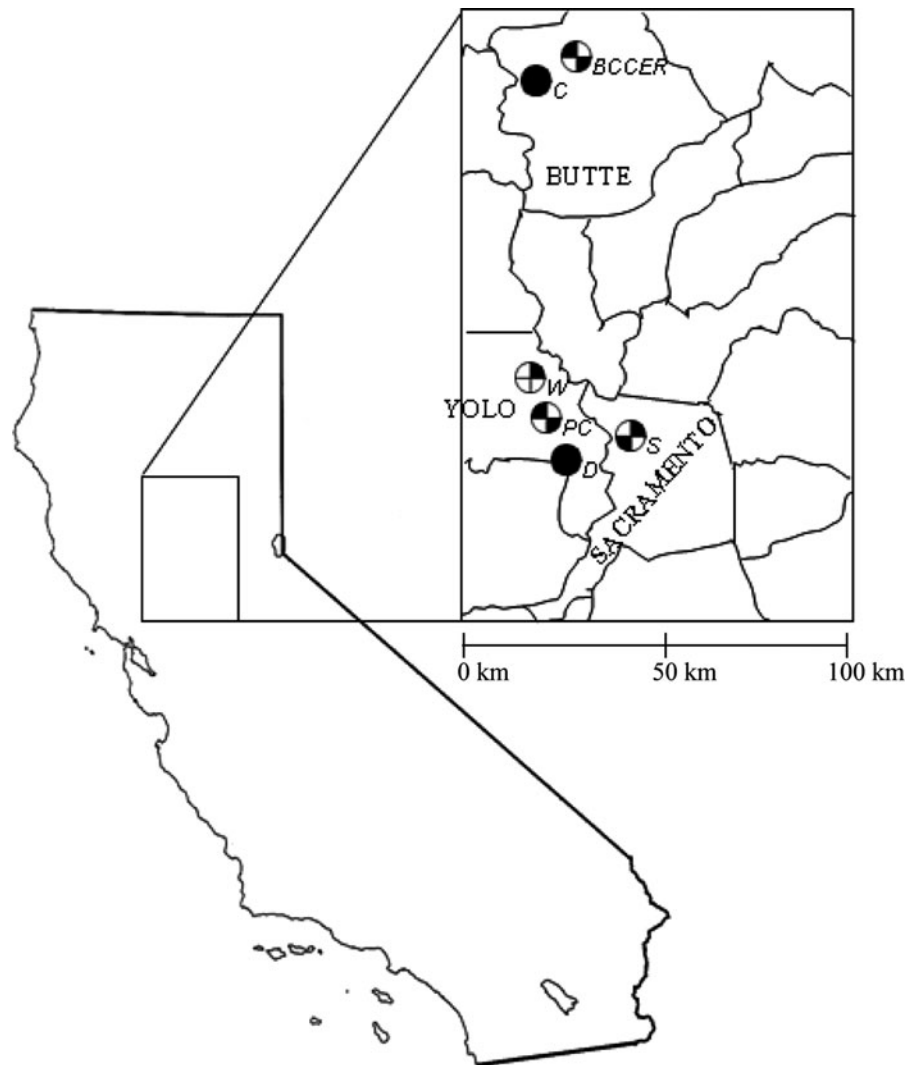
The two rural study sites had stands of *O. europaea* and *H. arbutifolia* (Fig. 1). The first of these was the Putah Creek riparian zone between the city of Davis and the coast range foothills. This site included fallow agricultural fields and chaparral sites adjacent to riparian vegetation. The second rural site was the Big Chico Creek Ecological Reserve (BCCER), located in the chaparral- and oak-dominated foothills of the northern Sierra Nevada, upstream from the city of Chico.

Bird removal and consumption of study species fruits

Fruit traps: mutualism efficiency (overall proportion of fruits removed)

To estimate the proportion of fruits removed by bird foragers, I placed fruit collection traps beneath study tree canopies. Traps were large buckets of heavy plastic, 38 cm in diameter, covered with concave Bird Block® netting with 1 cm² mesh size to prevent vertebrate entry (for *O. europaea*, since fruits are

Fig. 1 Map of study site-species combinations. Study sites were located in Butte, Yolo, and Sacramento Counties in the Sacramento River Valley, California. A total of 12 study stands, distributed among 3–4 sites, were used for each plant species. *Circles and italicized abbreviations* identify study sites on the map as follows: BCCER = Big Chico Creek Ecological Reserve; C = Chico; W = Woodland; PC = Putah Creek watershed; S = Sacramento; D = Davis. Each *circle* is divided into four segments and *shaded* to indicate which study species were present and utilized in that site. *Upper left quadrant* indicates *Heteromeles arbutifolia*; *upper right quadrant* indicates *Triadica sebifera*; *lower right quadrant* indicates *Olea europaea*; *lower left quadrant* indicates *Ligustrum lucidum*



larger, I instead used concave hardware cloth with 2 cm-width openings). Holes at the bottom of the buckets permitted rainwater to exit, but were covered with screen to keep seeds inside. Each trap was anchored with two pieces of 1.2 m rebar, driven 45 cm into the ground and connected to the trap with zip-ties. Two traps were placed on the ground under randomly-selected trees at each of four stands in two sites per study species, for a total of 32 sampled trees. In trap placement, the outer trap edge was aligned directly beneath the outer edge of the tree's canopy. Traps remained in place throughout the fruiting season until all ripe fruits had fallen or been removed from the tree by bird foragers. Traps were checked weekly to ensure that they remained in place and that their mesh covers were undisturbed.

To estimate the total fruit load of sampled trees, I measured the tree canopy diameter and counted the fruits in the canopy slice formed by a random 1-m arc of the tree's perimeter, then extrapolated over the full tree. I treated each tree canopy as a hollow cone, measuring the diameter of the inner, fruit-free region surrounding the tree's trunk and calculating the volume of the fruit-bearing canopy as the difference between the total canopy cone volume and that inner cone volume. Canopy height was measured with a clinometer. The sampled volume of the canopy was the proportion of the total fruit-carrying region that was directly above each trap. I used this proportion to generate an expected number of fruits in the region above each trap. The difference between that expected number and the count of fruits in the trap at the end of

the season was my estimate of the number of fruits removed by birds. This method addresses a daunting challenge: to estimate the proportion of fruit removed by birds in a tree producing hundreds of thousands of fruits. Since trees are non-uniform in fruit distribution and since wind, rain, and other factors can shift the angle of seed rain, error may be high for this or any other method of fruit fate assessment. By using two traps per tree (placed on opposite sides of the tree's trunk), I was able to calculate average estimated numbers of fruits removed for each tree and to examine standard error to evaluate the degree of agreement between the two trap results.

While almost all foraging on *H. arbutifolia*, *L. lucidum*, and *T. sebifera* fruits occurred in the trees themselves, a large proportion of the foraging observed on *O. europaea* took place on fallen fruits on the ground beneath trees. To explore the proportion of *O. europaea* fruits taken by birds, I therefore included a ground removal estimate, as follows: at the beginning of the fruiting season, I used 0.6 m rebar to mark a circle on the ground adjacent and equivalent in diameter to each *O. europaea* fruit trap. I cleared these circles of *O. europaea* seed remnants from previous seasons. At the end of the studied fruiting period, I counted the number of intact *O. europaea* seeds in that circle and compared that quantity with the number of fruits captured in the fruit trap. In all cases, a much smaller number of seeds was found in the circle than in the trap; the difference provided an estimate of the proportion of fruits that were removed by vertebrate foragers (either birds or ground-foraging mammals) after falling from the tree.

Foraging observations (focal individual and scan sampling)

Focal individual observations and scan sampling (modified from Farwig et al. 2006) were combined to quantify visitation and fruit removal by birds at 12 stands of each study species. Observations were conducted in two fruiting seasons: November 2007–March 2008, and November 2008–March 2009. For each observation period, the stand and time of day were selected at random with each stand observed on at least 3 separate occasions during the course of each season (and, each season, at least once each at sunrise and sunset). I continued to select stands for observation until no more fruits remained

on study trees. In all, 97.5 h of observations were conducted on *O. europaea*, 108 h on *L. lucidum*, 96 h on *T. sebifera*, and 105 h on *H. arbutifolia*.

Because most bird foraging occurs at dawn and dusk, observations were restricted to those periods. Exploratory visits to study stands at other times during the day found minimal or no bird activity. Sunrise observations began 15 min prior to sunrise, while sunset observations began 75 min prior to sunset. Each observation period lasted 90 min and was divided into nine 10-min periods. For the first minute of each period, an observer conducted scan sampling from a predetermined point, noting all bird species and the number of individuals of each species in the visible trees of the stand during that minute. For the remaining 9 min of each period, the observer conducted focal individual observations, selecting individuals haphazardly and following each selected individual with binoculars, counting the number of fruits swallowed, dropped, pecked, and taken in flight (meaning that the bird carried the fruit away in its beak and ingestion was not observed) until the individual flew away or until 120 s had elapsed. The observer recorded the total time that each individual was observed, then selected another individual. When possible, the observer selected a new species each time; if this was impossible, a new member of an observed species was selected.

When calculating rates of fruit removal, I combined counts of fruits swallowed and of fruits taken in flight to generate a total estimate of fruits dispersed per focal individual (after Renne et al. 2000). I calculated the rate of dispersal as the number of fruits dispersed per individual per minute per tree, averaged across all observations on that stand. A Type 1 ANOVA determined that Year was not a significant predictor of fruit removal, so I pooled the information from the two study years to generate final fruit dispersal rates for each species. Repeated observations of the same sample trees were treated as subsamples and averaged to estimate rates of fruit removal from those trees by each bird species.

To compare the dispersal importance of each bird species for each plant species, I calculated Flock Dispersal Importance (FDI) and Overall Dispersal Importance (ODI) after Renne et al. (2000) for all bird-plant species combinations. FDI is the product of the average per-individual fruit dispersal rate and the average number of individuals per species (i.e., flock

size) detected per tree during scan sampling; it provides an estimate of dispersal importance per foraging bout of a given bird species. ODI is the product of FDI and the number of observations in which that species was detected foraging in observed trees; it takes into account the number of flocks per species over the full study, distinguishing between common and rare interactions.

I distinguished two bird guilds defined by flocking and territorial behavior. “Pulse feeders” was the label I assigned to birds that visited fruiting plants in large foraging flocks, moving over the landscape between stands and visiting each for a brief portion of the fruiting season (resulting in a heavy but short-lived pulse of fruit removal). “Background feeders,” on the other hand, displayed resident territoriality and were present in stands in constant but low numbers throughout the fruiting season. Fruit-handling guilds included “dispersers” that swallowed fruits and likely defecated or regurgitated many of them whole and “seed predators” that destroyed most seeds during feeding or are known from physiological studies to destroy seeds after swallowing them. Since dispersal of fruits by predators occurs far less than does predation, I calculated FRI (Fruit Removal Importance) instead of FDI and ORI (Overall Removal Importance) instead of ODI for predators.

Implications for management

Stand description

A multiple linear regression with sequential (type I) tests, with plant species as a covariate, was used to determine which stand and site characteristics are predictive of bird visitation rates (averaged across all bird species) within each plant species. Data were log-transformed to meet MLR assumptions. Statistical analysis was performed in JMP version 5.0.1 (SAS Institute). Significance was accepted at $P \leq 0.05$. The following characteristics were measured: number of conspecifics in the stand, total stand area, distance to water, average height, basal diameter and dbh of stand trees, average distance between conspecifics in the stand, distance to the nearest road or path, estimated number of fruits per stand, and site-specific estimate of frugivore density (obtained through variable-plot distance sampling). Because the total number of samples was low (48) relative to the

variable list, we used coefficients of determination to guide model selection. Our final model included plant species as covariate and number of conspecific individuals, average plant height, and their interaction as independent variables.

To evaluate the effect of different sites (with, presumably, differing avian communities) on bird visitation rates, I conducted variable-plot distance sampling at all six study sites to estimate frugivorous bird densities. I conducted point counts at 70 random points per study site. Each point was separated from other points by at least 200 m. Point counts lasted 7 min. During each count, I recorded all birds seen and heard and measured the distance from the point to each bird using a Nikon laser rangefinder. Estimates of bird densities were then obtained using the program Distance (Thomas et al. 2010), which employs a likelihood function to account for missed detections. I used ANOVA to determine whether estimated frugivore densities were predictive of bird visitation.

Niche overlap analysis and ordination

Niche analyses and ordination enabled me to explore the form and function of study species membership in the regional bird-plant community. Quantification of niche breadth and overlap allows assessment of an organism’s functional specialization, as well as its relationships with related or functionally similar species (Hutchinson 1957; Whittaker et al. 1973). Such metrics are usually employed with reference to dietary or spatial requirements, although Grubb (1977) discussed the importance of dispersal and other aspects of regeneration in niche definition. I applied niche quantification methods in a new fashion by identifying avian frugivores as the niche-defining resource and basing niche calculations on that resource. Frugivore-defined niche breadth indicates whether these plants rely upon a few key mutualists (implied by low niche breadth values) versus dispersal by a broader range of species (i.e., greater evenness). Niche overlap measures the similarity in resource use (in this case, use of avian dispersers) displayed by focal species (Krebs 1999). Species with greater overlap likely compete more for avian dispersers than those with low overlap. Overlap quantification allowed me to consider the implications of widespread occurrence of these non-native

species in the ecological community. I then employed canonical correspondence analysis (CCA) to examine bird use of study plants over space, time, and broadscale habitat types. The resulting triplot offered a visual depiction of the frugivore-defined community position in the study area.

To perform niche and ordination analyses, I used ODI and ORI values for each bird-plant species combination. Levins's measure of niche breadth ($B = 1/\sum p_j^2$), where p_j = the proportion of individuals found in or using resource state j or, in this context, the proportion of each plant's total ODI/ORI that was attributable to each bird species, quantifies niche breadth in order to assess the degree to which each plant specializes on certain disperser species (after Krebs 1999). Levins's measure is standardized with the formula

$$B_A = \frac{B - 1}{n - 1}$$

where B_A = standardized niche breadth, B = Levins's measure of niche breadth, and n = the number of possible resource states. Here, I considered the number of possible resource states to be equal to the number of bird species observed dispersing fruits over the course of the study; a similar technique has been used to apply Levins's measure to assess mutualist-defined niche breadth in pollinator relationships (Kephart 1983). Application of this metric in this way assumes that all four of my focal plant species had access to the same number of potential disperser species (i.e., that the same total (across all sites) suite of potential frugivores was present for all plants). Although this assumption may be imperfect, I pooled fruit removal data for each plant species across its 12 study stands to generate the species-specific numbers used here. Data for each plant species are therefore derived from 3 to 4 different geographic sites and include sites where the different study species occur in close proximity to one another.

To assess niche overlap among all pairs of study plants (a total of six comparisons), I utilized percentage overlap (Abrams 1980; Schoener 1970), which is calculated by the formula

$$P_{jk} = \left[\sum_{i=1}^n (\min p_{ij}, p_{ik}) \right] \cdot 100$$

where p_{jk} = percentage overlap between species j and k , p_{ij} = proportion disperser species i performed

of the total dispersal recorded for species j , p_{ik} = proportion disperser species i performed of the total dispersal recorded for species k , and n = total number of resource states. I utilized proportional comparisons instead of direct counts of fruits swallowed because the study fruits differ so substantially in size.

Ordination by CCA (Lepš and Šmilauer 2003) enabled me to visually examine niche separation and assess the influences of time, space, and plant species on the bird community's use of study fruits. These analyses were performed in CANOCO 4.5 (ter Braak and Šmilauer 2002) with default options. Broad habitat designations (urban, riparian, or chaparral) were included as nominal environmental variables for each site-study species combination. These environmental variables were tested for significance using 499 unconstrained Monte Carlo permutations. I treated individual stands as subsamples and unique site-plant species combinations as samples. To assess shifting bird communities over the winter, I separated early (through January) and late winter foraging data and compared the two resulting ordination diagrams. To minimize the effect of outliers, only those birds that visited at least two stands or for which ODI/ORI was ≥ 5.0 were included in this analysis. Habitat categories occur as centroids in the resulting triplots.

Results

Bird removal and consumption of study species fruits

Fruit traps: estimated proportion of fruits removed by birds

Averaged across sampled trees, the proportion of fruits removed by birds from native *H. arbutifolia* was 0.94 ± 0.02 SE. For *L. lucidum* the estimated proportion of fruits removed was 0.77 ± 0.13 SE, and for *T. sebifera*, the proportion was 0.24 ± 0.15 SE. For *O. europaea*, the proportion removed before fruit fell from trees was 0.27 ± 0.12 SE. The ground removal assessment estimated that the proportion of *O. europaea* fruits removed directly from the ground after falling from the tree was 0.45 ± 0.04 . Applying the tree removal proportions to all fruit loads in the study stands, I calculated an average total number of

fruits removed by birds per tree for each study species (Table 1).

For each study tree, the two seed traps were in strong agreement. The largest standard error of the mean of any trap pair was 0.05, and the majority of standard errors were less than 0.01.

Foraging observations (focal individual and scan sampling)

In all, 15 bird species consumed *T. sebifera* fruits, 13 species consumed *L. lucidum* fruits, 13 species consumed *O. europaea* fruits, and 10 species consumed native *H. arbutifolia* fruits (Online Resource 1). For non-native plants, pulse feeders and potential dispersers took disproportionately more fruits than background feeders or seed predators; that is, pulse and disperser species were a minority of visitors but responsible for a majority of frugivory. Potential dispersers took 96.3% of *T. sebifera* fruits while seed predators took 3.7%. Pulse feeders took 73.6% of *T. sebifera* fruits. However, of the bird species that took fruits from *T. sebifera*, just 27% were pulse feeders (Table 2). For *L. lucidum*, potential dispersers took 67.1% of fruits and pulse feeders took 53.7%. Meanwhile, pulse feeders accounted for just 23% and dispersers 62% of bird species that took fruits from *L. lucidum* (Table 2). For *O. europaea*, potential dispersers took 96.5% of fruits and pulse feeders 75.9%. Pulse feeders accounted for only 46% and dispersers 69% of the species taking *O. europaea* fruits (Table 2).

For the native *H. arbutifolia*, by contrast, pulse feeders took only 48.6% of fruits, slightly less than

background feeders, which took 51.4%. By handling guild, results were more similar to those encountered for non-native plants: dispersers took 94.7% of *H. arbutifolia* fruits. Pulse feeders accounted for 30% and dispersers for 60% of all species that took fruits from *H. arbutifolia* (Table 2).

Implications for management

Stand description

The number of conspecific plant individuals per study stand was significantly and positively related to the rate of bird visitation ($F_{(1,37)} = 20.31$; $P < 0.0001$). Frugivorous bird densities, estimated through variable-plot distance sampling, were not significantly related to bird visitation, nor were any other stand characteristics.

Niche measurements and ordination

Niche breadths were fairly consistent across all study species. *Olea europaea* exhibited the smallest niche breadth ($B_A = 0.04$), followed by *T. sebifera* ($B_A = 0.09$). Niche breadth was largest for *H. arbutifolia* ($B_A = 0.12$), but *L. lucidum* was a close second ($B_A = 0.11$).

Percentage overlap placed the plant species into two groups defined by actual disperser suite similarity (Table 3). Similarity emerged for *H. arbutifolia* and *L. lucidum* ($p_{jk} = 41.18\%$) and for *O. europaea* and *T. sebifera* ($p_{jk} = 61.06\%$). Although they belong to the same family, *O. europaea* and *L. lucidum* displayed little similarity ($p_{jk} = 4.99\%$).

Table 1 Total estimated numbers of seeds removed by birds from study stand trees

Study species	Prop. fruits removed	Avg. est. no. fruits per tree (fruit load)	Avg. est. no. seeds removed per tree	Minimum no. seeds removed from a sampled tree
<i>Heteromeles arbutifolia</i>	0.94 ± 0.02	105,983 ± 48,842	298,872 ± 137,733	11,118
<i>Ligustrum lucidum</i>	0.77 ± 0.13	712,820 ± 211,124	1,097,742 ± 325,130	38,610
<i>Triadica sebifera</i>	0.24 ± 0.15	38,462 ± 8,800	9,230 ± 2,112	7,666
<i>Olea europaea</i>	0.27 ± 0.12	10,642 ± 3,686	2,873 ± 1,619	1,486

Proportions of fruit removed were estimated by ground-anchored fruit collection traps placed beneath sample trees. Fruit loads were estimated for representative trees in each stand and then averaged across all stands of each study species. Numbers of fruits were multiplied by average number of seeds per fruit to obtain total estimated number of seeds removed. Numbers are means ± 1 standard error

Table 2 Summary of estimated removal of study species fruits by birds of different behavioral guilds

Plant species	FG	HG	ODI/ORI
<i>Triadica sebifera</i>	Pulse	Dispersers	29.41 ± 7.38
	Background	Dispersers	9.05 ± 1.92
	Pulse	Seed predators	None
	Background	Seed predators	1.48 ± 0.38
<i>Ligustrum lucidum</i>	Pulse	Dispersers	275.94 ± 48.86
	Background	Dispersers	68.44 ± 8.73
	Pulse	Seed predators	None
	Background	Seed predators	169.17 ± 20.74
<i>Olea europaea</i>	Pulse	Dispersers	116.61 ± 34.86
	Background	Dispersers	34.33 ± 11.59
	Pulse	Seed predators	2.10 ± 0.00
	Background	Seed predators	3.37 ± 1.19
<i>Heteromeles arbutifolia</i>	Pulse	Dispersers	98.57 ± 19.56
	Background	Dispersers	93.4 ± 11.48
	Pulse	Seed predators	None
	Background	Seed predators	10.81 ± 5.54

FG = feeding guild. HG = handling guild. Total ODI/ORI = overall dispersal importance (for dispersers) and overall removal importance (for seed predators). Total ODI/ORI = \sum (the average number of fruits removed per minute per tree × the number of observations in which the bird species was present in observed trees), summed across all bird species in these guilds. Per-species ODI, number of observations, and average flock size are available in Online Resource 1

CCA triplots ordinated each site-plant combination (as samples) with respect to the bird ODI values specific to that combination (Fig. 2a, b). For data collected during the first half of each winter, environmental variables were not significant. The triplot for fruit removal during early winter demonstrated samples clustering more by site than by plant type (Fig. 2a). Thus, samples from Chico, Putah Creek, and the BCCER tended to cluster in the upper and left portions of the triplot, associated with riparian and chaparral birds including hermit thrushes, purple finches, and spotted towhees (Fig. 2a). Most samples

from Davis, Sacramento, and Woodland clustered in the lower center of the triplot, associated with urban birds including house finches, European starlings, American crows, and yellow-rumped warblers. The

Table 3 Niche overlap values calculated for study species pairs using percentage overlap

Species A	Species B	Percentage overlap (%)
Heteromeles	Olea	4.41
Heteromeles	Triadica	23.04
Heteromeles	Ligustrum	41.18
Ligustrum	Olea	4.99
Ligustrum	Triadica	21.64
Olea	Triadica	61.06

Only genus names are provided; species are *Heteromeles arbutifolia*, *Olea europaea*, *Triadica sebifera*, and *Ligustrum lucidum*

Fig. 2 Triplots presenting results of canonical correspondence analysis. Samples are indicated with *large black circles* and are ordinated with respect to their use by avian foragers (*small gray triangles*), with habitats as nominal environmental variables (centroids as *large black triangles*). *Sample label code letters* indicate plant species (H = *Heteromeles arbutifolia*; O = *Olea europaea*; T = *Triadica sebifera*; L = *Ligustrum lucidum*). *Sample label code numbers* indicate study site (1 = Davis; 2 = Sacramento; 3 = Woodland; 4 = Chico; 5 = Putah Creek; 6 = Big Chico Creek Ecological Reserve). Only bird species that consumed at least two samples or had total ODI/ORI >5 were included in these analyses. **a** CCA of samples ordinated by avian use during early winter (November–January). **b** CCA of samples ordinated by avian use during late winter (February–March). Bird abbreviations: AMCR = American crow; AMRO = American robin; CAQU = California quail; CEWA = cedar waxwing; DEJU = dark-eyed junco; EUST = European starling; GCSP = golden-crowned sparrow; HETH = hermit thrush; HOFI = house finch; NOFL = northern flicker; NOMO = northern mockingbird; NUWO = Nuttall's woodpecker; PUF1 = purple finch; SPTO = spotted towhee; WCSP = white-crowned sparrow; WEBL = western bluebird; WITU = wild turkey; WSJA = western scrub-jay; YRWA = yellow-rumped warbler

first axis of the ordination explained 10.6% of the variation and the second axis 8.1%.

The late winter ordination reflected the same tendency for samples to cluster more by site than by plant species (Fig. 2b). Here, the environmental variable “chaparral” was significant ($P = 0.002$). Samples from sites with a high percentage of chaparral habitat, including the BCCER and Putah Creek, clustered at the right end of the x-axis, associated with chaparral birds including wild turkeys, California quail, and purple finch. Remaining samples clustered on the left end of the x-axis, associated with urban and riparian birds including American robins, American crows, house finches, and

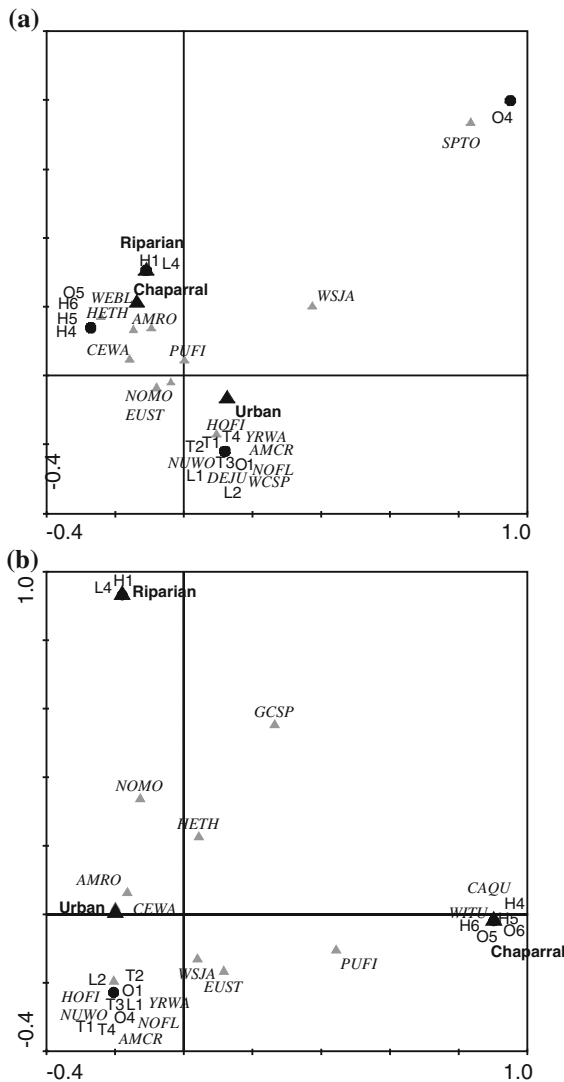
Nuttall’s woodpeckers. The first axis of this ordination explained 25.4% of the variation and the second axis 4.3%.

Discussion

Primary question 1: do bird visitation and fruit removal indicate that birds have the potential to disperse study species sufficiently to enable spread across the landscape?

In spite of considerable variation among them, fruits of all three non-native plant species were removed by birds at rates that, given the large fruit load per individual, could easily facilitate spread through the landscape (i.e., thousands of fruits taken per plant over the course of the season). The fruits of native *H. arbutifolia* were removed at the highest rate. This is consistent with observations from an ecological community in Argentina where native fruits were taken by frugivorous birds at higher rates than non-native fruits (Montaldo 2000), although contrasting results were found in North Carolina (Greenberg and Walter 2010). Winter-fruiting non-natives in my study region compete for frugivores primarily with *H. arbutifolia* and each other. Evidently, *H. arbutifolia* is a strong competitor for dispersers. However, where *H. arbutifolia* is absent (such as urban settings where it is uncommon in landscaping), non-native species monopolize cold-weather bird frugivory and bird-mediated dispersal.

Published data from other regions allows comparison of the mutualism efficiency observed here with that occurring in the native landscape for *O. europaea* and in invaded regions for *L. lucidum* and *T. sebifera*. In Spanish shrublands, birds took 94% of available *O. europaea* fruits during a low-fruiting year and 52% during a high-fruiting year (Jordano 1987a). In Argentina, an estimated 60% of *L. lucidum* fruits were taken by birds (Montaldo 2000). In invaded regions of South Carolina, birds removed 40% of the available *T. sebifera* crop (Renne et al. 2000). Since the value obtained here for *L. lucidum* exceeds published reports, I conclude that this species likely receives sufficient dispersal in California to permit its spread. The fruit removal value that I obtained for *O. europaea* was 50% below the lower value observed in Spain. This may result largely from the large fruit



sizes of *O. europaea* planted in landscaping and hedgerows in California (sampled fruits from my study stand averaged 15.09 mm in width) as compared with the smaller fruits typical of wild *O. europaea* in Spanish shrublands (width averaging 8 mm) (Jordano 1987a). Because gape width constrains bird frugivory of large fruits (Wheelwright 1985), the total number of species capable of handling larger-fruited *O. europaea* is likely to be smaller than those utilizing smaller-fruited *O. europaea*. Notably, the ground removal assessment I performed for *O. europaea* after noticing a high rate of bird foraging from the ground beneath trees suggested that more fruits are likely removed from the ground than directly from trees. The fruit handling behavior (frequently selecting and then dropping fruits that were too large) associated with ground removal provides further support for the hypothesis that fruit size may be largely responsible for the low rate of in-tree feeding. If ground removal and tree removal are combined, the proportion of total fruits removed for *O. europaea* is well within the range observed in Spain.

For *T. sebifera*, I observed 40% lower fruit removal than was reported for South Carolina. This may stem from *T. sebifera*'s unusual fruit (white in color, waxy rather than fleshy) and lack of winter foliage combined with the notably high variety of fruiting species in the Sacramento Valley in the winter. As a major agricultural region, the Sacramento Valley has an abundance of both food crops and fruiting landscaping species throughout the winter, offering birds a wide array of options that may appear more attractive than *T. sebifera*. At least some successful dispersal of *T. sebifera* occurs, however, as indicated by volunteer seedlings that have been found in several watersheds (pers. obs.). Furthermore, water-mediated dispersal can facilitate population growth and spread around new reproductive individuals in riparian areas (Bower et al. 2009). Therefore, while this species may receive a lower incidence of bird-mediated dispersal than the other two study species, it does not appear that dispersal limitation is sufficient to block its invasion of riparian areas.

By guild, the large majority of fruit removal for all three non-native study species was done by potential dispersers and pulse feeders. This pattern is conducive to long-distance dispersal events. Most swallowed fruits will endure disperser handling and gut passage without being destroyed. The prevalence of pulse

feeding relative to background feeding has implications for dispersal distance. Pulse feeders move over the landscape in large flocks, visiting each stand in turn and consuming most of the fruits before moving to another food patch (pers. obs.). They generally roost elsewhere, traveling to the day's target stand to feed in the mornings and evenings. Background feeders, on the other hand, exhibit territorial behavior and are present in each stand throughout the day (pers. obs.); most likely roost in or near the stand, defending their territory from conspecifics. Because pulse feeders move much greater distances between roosts and feeding sites than do background feeders, those fruits consumed by pulse feeders are more likely to experience long-distance dispersal than are those consumed by background feeders. For each stand in each season, I observed a low and fairly constant level of frugivory by background feeders until pulse feeders arrived. Pulse feeders then removed fruits at a high rate for a brief period (a few days). After the pulse feeders departed, the remaining fruits (generally less than 20%) were taken at the low background feeding rate once more until the fruits were exhausted or the frugivory season passed.

The non-native European starling (*Sturnus vulgaris*) had the highest overall dispersal importance (ODI) for *T. sebifera* and *O. europaea*. Starlings are among the most adaptable birds on the planet, establishing successfully on six continents and maintaining large flocks in many habitats. It is unsurprising that they incorporate *T. sebifera* (unusual among study region fruits in color and texture) and *O. europaea* (unique in size) into their diets. Correspondingly, the relatively lower incidence of consumption of these fruits by native birds may be attributable to unfamiliarity (for *T. sebifera*) or size constraints (for *O. europaea*). Starlings are notably associated with disturbed habitats: they were abundant in urban and agricultural areas in this study, but during the non-nesting season are rare in more natural areas (BCCER and parts of the Putah Creek watershed). Spread by starlings of *T. sebifera* and *O. europaea* into natural areas is therefore likely uncommon at present.

Flock dispersal importance (FDI) allows direct quantitative comparison of the bird dispersal observed here with that recorded for *T. sebifera* in the southeastern U.S. (Renne et al. 2000). The suite of birds present in the Southeast differs somewhat

from those found in my study region, and those birds responsible for the highest rates of fruit removal in the Southeast do not occur in the Sacramento Valley (i.e., boat-tailed grackle, *Quiscalus major*, and fish crow, *Corvus ossifragus*). However, after eliminating from consideration birds that do not occur in both sites, the species with the top three FDI values in the Southeast are identical to those with the top three FDI values in this study: *S. vulgaris*, *Turdus migratorius* (American robin), and *Colaptes auratus* (northern flicker). Since *T. sebifera* has become a major environmental problem in the Southeast, its use by several of the same birds bolsters its likelihood of becoming invasive in California.

Primary question 2: what are the implications of bird use of these species for management of these and other incipient, bird-dispersed invaders?

Stand characteristics

Although a number of stand characteristics were measured to test the effect of localized site traits on bird visitation, only the number of conspecifics in the stand was significant: within each species, the total number of plants offering the same fruit resource appears to be a strong attractant to birds. This result is supported by recent modeling of the role of patch size in invasive species control when long-distance dispersal events are regular occurrences (Minor and Gardner 2011). My conclusion that number of fruiting trees is important also complements previous data showing that the total number of fruits in the neighborhood is significantly and positively related to greater levels of bird foraging on exotic species (Sargent 1990). The importance of large stands has management implications: non-native fruiting trees planted in large groups are more likely to be visited by avian dispersers than are single trees or mixed-species plantings. Managers seeking to eliminate problematic plants should consider the number of trees per stand and be aware that larger stands may be more responsible for long-distance, bird-mediated dispersal than are smaller stands.

Notably, this result suggests management strategies that conflict with Moody and Mack's (1988) recommendation that satellite populations of invasive species should be prioritized for removal in order to

reduce overall spread rate. Behavior and preference of the dispersing agent may thus generate different long-distance dispersal dynamics for bird-dispersed species than arise for non-bird-dispersed species.

The bird-plant community: frugivore specialization and overlap

The majority of fruit consumption for each non-native plant species is performed by a limited number of bird species (pulse feeders with the largest flocks), as evidenced by small niche breadths. However, these mutualisms should still be considered diffuse since many birds perform at least some consumption and likely some dispersal for each plant. As the ordination plots emphasize, birds evidently utilize these species opportunistically, clustering more by habitat than by plant type: that is, they forage in accessible and local trees rather than displaying strong, landscape-scale attraction toward particular species. The key management implication of this pattern is that birds are likely to increasingly utilize non-native plants as they spread across the landscape due to elevated encounter rate. As visitation to such plants increases, bird-mediated spread rates are likely to grow in turn.

Introduction of non-native, bird-dispersed plants has the potential to impact native plants through competition for dispersers (Traveset and Richardson 2006). When the introduced species are still limited in their distribution as in the case of these study species, however, it is difficult to directly measure this competition: disperser populations are unlikely to be limiting, and the native and non-native plants are largely separated geographically. I quantified niche overlap to assess the likelihood that such competition will arise. Greatest niche overlap occurred between *O. europaea* and *T. sebifera* and between *H. arbutifolia* and *L. lucidum*. Among the non-native case study plants, *L. lucidum* therefore appears to have the greatest potential to compete with *H. arbutifolia*. The two species likely share many of the same dispersers and both exhibit high dispersal efficiency. As *L. lucidum* arrives in riparian areas, it will likely emerge from its lag phase through its demonstrated mutualisms with native birds. Greater densities of *L. lucidum* could reduce dispersal of *H. arbutifolia*.

Comparing early and late winter fruit consumption, the most notable difference is a strong shift in some of the most important disperser species from

chaparral-dominated to urban sites. American robins, cedar waxwings, northern mockingbirds, and hermit thrushes all occurred more in chaparral-based observations during the first half of the winter, and were more likely to appear in urban sites during the second half of the winter. All of these native birds visit *H. arbutifolia* early in the season and often strip those plants of fruit before foraging on heterospecific fruits from the same site (pers. obs.). Half of sampled *H. arbutifolia* plants were in chaparral habitats; this probably accounts for the early-season association of these birds with those habitats. Later in the season, as natural area fruits become exhausted, the birds move across the landscape in response to food availability in other sites. It is during this late-season foraging that native birds are most likely attracted to urban environments where a variety of non-native fruits are consistently present; birds thus may exhibit altered movement patterns as a result of non-native plant availability.

Since fruit availability is maximal at the beginning of winter, before any stands have been heavily depleted, it may be due simply to a sampling effect that a larger number of bird species coexists at any given site during this period than later in the season (because plants can support a greater number of individual birds). A similar pattern was observed when seasonal shifts in bird populations were directly examined in Pennsylvania: both diversity and densities declined in late winter, and the authors attributed the pattern to depleted food resources contributing to higher mortality and movement of birds to artificial feeders (Rollfinke and Yahner 1990).

Implications for riparian habitats

Since habitats invaded by *T. sebifera* and *L. lucidum* elsewhere in the world are wetter than upland California, human unassisted spread for both species in this region should be limited to riparian areas. While this eliminates a large proportion of the landscape, conservation concern remains substantial. Riparian areas are highly endangered in California, with less than 10% of the original riparian forest remaining in the study region (Hunter et al. 1999). At the same time, riparian areas with intact plant communities are critical habitat for a number of species, including special status and threatened taxa such as the valley elderberry longhorn beetle and

Swainson's hawk (Brode and Bury 1984; Lang et al. 1989; RHJV 2004). Furthermore, remnant forest patches throughout the study region are often concentrated along waterways. As birds are likely to utilize these corridors for cover, nesting, and foraging, bird-mediated dispersal of non-native species may concentrate in riparian habitats. The rates of seed removal for *T. sebifera* and *L. lucidum* suggest that dispersal may be common, indicating a high likelihood of incipient invasion of riparian areas by these species. Long-distance bird-mediated dispersal into riparian zones may create far-flung foci of new populations (Moody and Mack 1988), around which gravity- and water-assisted dispersal can lead to local population growth and spread.

Conclusion

While the observations reported here were confined to three non-native plant species, results are relevant to the broader realm of bird-dispersed introduced species. Study species fruits differed greatly in type and appearance, yet all were visited and consumed in abundance by birds. Ornithologist reports thus correctly identified non-native plants that have formed mutualisms with native species (Aslan and Rejmánek 2010). The bird guilds removing the greatest numbers of fruits from all three non-native species were dispersers and pulse feeders, providing a ready mechanism for dispersal to natural areas. Since this was true for such contrasting species, the inclusion of bird-mediated dispersal as a blanket risk factor in many invasiveness prediction rubrics appears valid.

Ordination results highlight the opportunistic nature of bird feeding on both native and non-native fruits: rather than tracking specific fruit types over the landscape, birds appeared to visit multiple fruiting species in each locale. There were no detectable barriers that might impede dispersal of new non-natives introduced into the community.

The significance of number of fruiting individuals as a driver of bird visitation indicates that birds use broad-scale assessments of the landscape to make foraging decisions. That is, rather than distinguishing among patches by actual density of fruits, birds are attracted to the trees themselves. This is logical when considering the importance to dispersal of large flocks (pulse feeders) flying from roost to feeding

sites; it seems reasonable that a bird in flight uses broad-scale instead of fine-scale cues to direct its landing. Managers may reduce bird dispersal of unwanted species by removing clustered individuals. Since native fruits were removed at particularly high rates in this study and share many avian foragers with *L. lucidum* in particular, planting of native fruiting species, as has been suggested elsewhere (Gosper et al. 2005; Gosper and Vivian-Smith 2009), might be another management technique that could reduce spread of non-native seeds by creating competition for dispersers. However, this strategy requires more direct study: it is also conceivable that increasing the density of native fruiting trees at a given site will lead to an increase in the total concentration of frugivorous birds at that site, and that those birds will then consume and disperse at an enhanced rate all fruiting species, native and non-native, in the site.

All three non-native species studied here have been assimilated into local bird diets and demonstrate evidence of effective dispersal regimes in the study area. The results of these observations therefore support the hypothesis that these species may be in lag phases and possess the necessary components for future invasion in the region. Research examining germination and actual seedling performance in Californian habitats for each of these species would clarify whether barriers at other life stages might impede invasion. For *T. sebifera*, these barriers have been examined and none appeared operational alongside waterways (Bower et al. 2009); in combination, that study and the results presented here present strong evidence that *T. sebifera* is a likely incipient invader in California. Similar barrier examination should now be undertaken for *O. europaea* and *L. lucidum*.

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