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Avian use of introduced plants: Ornithologist records illuminate interspecific associations and research needs

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Abstract. Introduced species have the potential to impact processes central to the organization of ecological communities. Although hundreds of nonnative plant species have naturalized in the United States, only a small percentage of these have been studied in their new biotic communities. Their interactions with resident (native and introduced) bird species remain largely unexplored. As a group, citizen scientists such as ornithologists possess a wide range of experiences. They may offer insights into the prevalence and form of bird interactions with nonnative plants on a broad geographic scale. We surveyed 173 ornithologists from four U.S. states, asking them to report observations of bird interactions with nonnative plants. The primary goal of the survey was to obtain information useful in guiding future empirical research. In all, 1143 unique bird–plant interactions were reported, involving 99 plant taxa and 168 bird species. Forty-seven percent of reported interactions concerned potential dispersal (feeding on seeds or fruits). Remaining "habitat interactions" involved bird use of plants for nesting, perching, woodpecking, gleaning, and other activities. We utilized detrended correspondence analysis to ordinate birds with respect to the plants they reportedly utilize. Results illuminate the new guilds formed by these interactions. We assessed the existing level of knowledge about invasiveness of those plants reported most often in feeding interactions, identifying information gaps for biological invasions research priority. To exemplify the usefulness of citizen science data, we utilized survey results to guide field research on invasiveness in some of these plant species and observed both qualitatively and quantitatively strong agreement between survey reports and our empirical data. Questionnaire reports are therefore heuristically informative for the fields of both avian ecology and invasion biology.

Key words: *birds; citizen science; guilds; introduced plants; invasive species; mutualisms; ornithologists; questionnaire*.

Introduction

Biological invasions have received intense scrutiny in recent decades due to their potential to threaten biodiversity (Levine et al. 2003, Simberloff 2005). In spite of this attention, however, invasions continue to multiply and risk assessments remain the weakest component of invasion biology (Hulme 2003, Davis 2009). Efforts to predict and mitigate the broad ecosystem impacts of invasive species suffer from lack of general understanding regarding mechanisms and likely effects (Levine et al. 2003). As a group, species introductions carry the potential to alter ecosystem processes. This can occur through modifications of the abiotic environment (Strayer et al. 2006) or through formation of novel biotic interactions (Mitchell et al. 2006). And while such biotic interactions are generally considered negative for native species (e.g., competition, predation, parasitism), there may be other instances in which they are beneficial for natives (e.g., mutualisms, commensalisms, or functional replacement of extirpated species). One such group of species interactions is between introduced plants and resident birds.

The ecological relationship between introduced plant and native bird species is multifaceted (Fig. 1). Birds can utilize introduced plants as food sources, perch sites, and nest locations. Birds may influence invasions as facilitators through new mutualisms (Richardson et al. 2000, Widrlechner et al. 2004, Gosper et al. 2005) or as impediments through folivory, seed predation, and other mechanisms (Downs et al. 2000, Corlett 2005). Plant introductions may draw birds into areas previously unsuitable for them, such as urban zones (Chace and Walsh 2006), exposing the birds to unfamiliar risks. Nonnative plants may stimulate vertebrate behavioral changes, altered habitat use, and phenological shifts (Richardson et al. 2000, Catling 2005, Theel and Dibble 2008). Such plants may also ameliorate native species loss (e.g., *Tamarix* spp. as nest sites replacing lost native willow stands; Brown and Trosset 1989).

While the effect of plant introductions on native birds provokes bird conservation interest, nonnative birds also interact with introduced plants. Successful nonnative birds include generalists such as the European starling (*Sturnus vulgaris*) and house sparrow (*Passer domesticus*), which have naturalized on almost all

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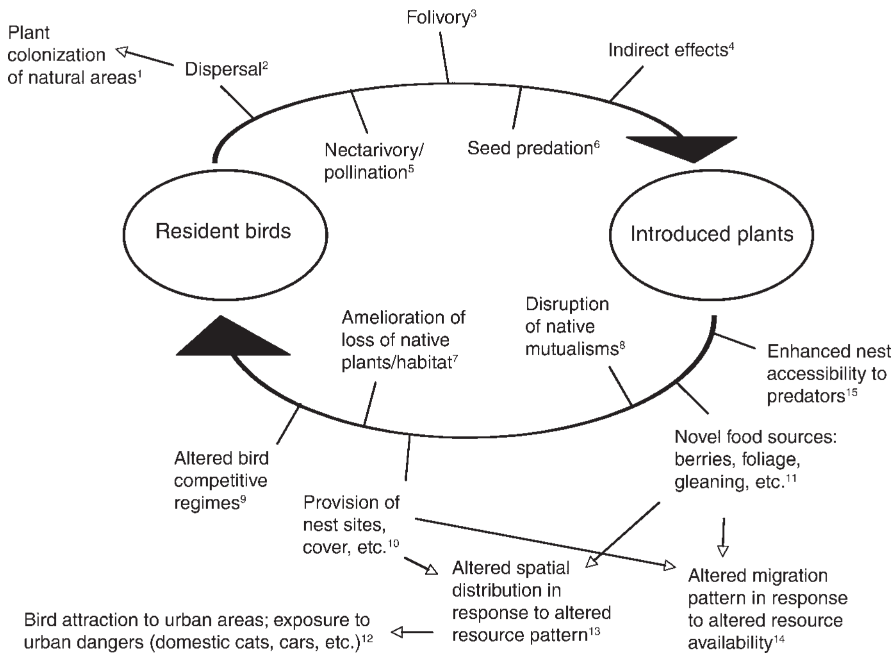

FIG. 1. Conceptual summary of the potential interactions between resident birds (native and exotic) and introduced plants. The short lines off the upper arrow represent avenues by which birds impact plants, while short lines off the lower arrow represent avenues by which plants impact birds. References provide examples of empirical studies illustrating each phenomenon: (1) Luken and Thieret 1996, Meyer and Florence 1996; (2) Smith 2000, Renne et al. 2002, Gosper 2004; (3) Downs et al. 2000; (4) Meehan et al. 2005; (5) Ford 1985, French et al. 2005; (6) Corlett 2005, Bartuszevige and Gorchov 2006; (7) Brown and Trosset 1989, Cook and Toft 2005; (8) Traveset and Richardson 2006; (9) Kawakami and Higuchi 2003, Remeš 2003; (10) Cristinacce et al. 2009; (11) Mitra and Sheldon 1993, LaFleur et al. 2007; (12) Chace and Walsh 2006; (13) Rey 1995, Shukuroglou and McCarthy 2006; (14) Terrill and Ohmart 1984, Renne et al. 2002; (15) Schmidt and Whelan 1999.

continents, perform well alongside human activities, and occur in high densities in urban zones (Rosenberg et al. 1987, Catterall et al. 1989, Case 1996, Duncan et al. 2003, Lever 2005). Nonnative birds come in contact with introduced plants in every urban context. These birds are likely to influence introduced plant dynamics through activities such as seed predation or dispersal (Huenneke 1998, LaFleur et al. 2007).

Employment of questionnaires to inform ecological research is increasing as citizen scientists become accepted partners in conservation-oriented research (Stansbury and Vivian-Smith 2003, White et al. 2005, Cooper 2007). While species interactions reported in questionnaires are unverifiable and must be interpreted conservatively, the method can access observations from large numbers of people, covering both temporal and geographical scales that cannot be monitored through traditional observational techniques (Lepcyzk 2005). Birds as a focal taxon are amenable to study via citizen science because they are highly detectable and occur throughout human-dominated areas. Bird conservation is of public interest and relevant to citizens' personal experiences (Daily et al. 2001, Lepcyzk 2005, Per et al. 2006, Cooper 2007). Moreover, ornithologists are a large and active group, which includes many experts with thousands of field hours. The United States Fish and Wildlife Service's National Survey of Fishing, Hunting and Wildlife-Related Recreation estimated that Americans spent $32 billion on recreational birdwatching in 2001 (Pullis La Rouche 2006). Despite variation in observer competence and effort, questionnaire data sets similar to ours have contained patterns confirming trends observed through careful scientific observation (Cannon et al. 2005, Lepcyzk 2005). Furthermore, professional organizations such as the Ornithological Societies of North America have expert members that in general are likely better trained and possibly more precise in reporting than might be expected among other groups of citizen scientists. Particularly when issued to such professional groups, questionnaires are therefore capable of providing useful information.

We distributed a questionnaire to ornithologists in four disjunct U.S. states, in an exploratory study laying the groundwork for our field research about bird-mediated dispersal of nonnative plants. The survey evaluated the ecological relationship between birds and nonnative plants at a national level, with emphasis on bird dispersal of seeds. Our primary goals for the questionnaire were: (1) to evaluate broadscale patterns of bird use of nonnative plants in the United States, examining the respective roles of fruit feeding (potential dispersal) interactions of interest to invasion biology,

TABLE 1. Questionnaire recipients from Ornithological Societies of North America (OSNA) and response rate by state.

State	OSNA members on original mailing list	No. bad addresses	No. assumed delivered	No. respondents	Response rate (%)
California	551	55	496	88	17.7
Florida	178	1	177	31	17.5
New York	205	16	189	25	13.2
Washington	154	13	141	29	20.6
Total	1088	85	1003	173	17.2

and habitat (non-dispersal) interactions of interest to avian ecology; (2) to visually examine the novel interaction webs and guilds formed by bird interactions with nonnative plants by ordinating bird species with respect to the plant species they utilize in questionnaire reports; and (3) to evaluate the extent to which reported interactions and observed patterns may be heuristic guides, identifying empirical research gaps useful for prioritization of more traditional academic research. To achieve this third goal, we briefly compared questionnaire results with our observation-based field data, which was guided by and displays agreement with questionnaire results.

Some aspects of bird interactions with nonnative plants have been examined previously. The implications and theoretical shape of novel interaction web development stemming from plant introductions have been evaluated in review papers (Reichard et al. 2001, Gosper et al. 2005). A questionnaire more limited than ours in both geographic and taxonomic scope was administered to Queensland, Australia, birdwatchers to explore bird-mediated dispersal patterns for 28 Queensland weeds (Stansbury and Vivian-Smith 2003). Additionally, species-driven studies have reported bird–plant interactions for a number of nonnative plants (e.g., Glyphis et al. 1981, Stansbury 1996, Renne et al. 2000). The present study, however, was the first use of a broadscale tool such as a questionnaire to examine bird habitat transformation by introduced plants across widely distributed U.S. regions.

METHODS

Questionnaires were mailed through the U.S. Postal Service in July, 2006, to 1003 ornithologists in four U.S. states: California (CA), Florida (FL), Washington (WA), and New York (NY). Ornithologist addresses were obtained from the Ornithological Societies of North America (OSNA), which manages the largest existing single mailing list of ornithologists from the focal states of this study. OSNA membership includes hobbyist birdwatchers, but is weighted toward professional ornithologists, academics, and wildlife managers as these are most likely to choose membership in ornithological societies. Since a large proportion of OSNA members have therefore been trained in data collection and reporting, it is likely that information gathered from OSNA members is more reliable than similar data collected from a more naïve group of citizen scientists might be.

We selected CA, FL, NY, and WA because they are geographically widely distributed, encompass a broad range of bird and plant species, and have active invasive plant councils or nonprofit organizations offering lists of invasive plant species. Additionally, there were at least 100 members of OSNA from each of the four states, providing a substantial number of questionnaire recipients from each region (Table 1). Furthermore, CA, FL, and NY are the three U.S. states with the highest numbers of naturalized plant species (Kartesz and Meacham 1999).

Questionnaires included four sections. In the first, we asked respondents to provide basic information about their birding habits and skill level, including the frequency with which they birdwatch, their bird and plant identification abilities, and the habitats and U.S. states in which they birdwatch (multiple selections permitted). The second section offered a list of nonnative plants and asked respondents to record birds that they had observed using those plants along with the nature of the interaction (e.g., frugivory, nesting, perching, roosting, and so forth). Since our primary focal interaction was bird-mediated seed dispersal, we confined our list to nonnative plants that are fleshy-fruited, woody species, and hence, habitually bird dispersed. The list varied by region to capture those bird-dispersed nonnative plants known to be of concern in each part of the country, but contained some plants in common across all regions (total number of species on the list ranged from 9 in WA to 15 in NY; Appendix A). We tailored these lists by region because we expected that plant identification skills would be lower on average than bird identification skills (given the population from which our sample was drawn) and wanted to raise the likelihood that respondents could identify most plants on the list they received. Notably, since the questionnaire was directed at ornithologists who, primarily, were recording only casual observations, it could not distinguish between rare and common interactions. Thus, a respondent's report of a given bird feeding on one of the target plants does not provide any hint of the relative importance of that plant in the bird's diet. Without assessment of interaction frequency, there is a danger that, because the questionnaire asked recipients to focus on nonnative plants, such interactions may have been overreported to some degree. This underscores the importance of conservative interpretation of questionnaire results, as well as comparison with empirical data.

The third section of the questionnaire presented a list of birds known to be partially frugivorous and asked respondents to report the items they had seen these birds eating. For this list, we selected a manageable number of birds (18) that would enable us to keep the total survey to a single sheet of paper in an effort to enhance response rate. The same list of birds was used in all regions (Appendix A). We selected common bird species so that they would be readily identifiable and likely to be encountered frequently by respondents; we expected that this would generate a substantial enough number of records per bird species to permit a range of potential analyses. The inevitable result of this decision was that the bird list contained some birds that are mainly eastern species and others that are mainly western species, in addition to some transcontinental species. Since many respondents reported observations from multiple states, however, individual surveys frequently contained reports relevant to the full bird list.

The fourth section of the questionnaire was a free-response box in which we asked respondents to record any other bird–plant interactions not reported elsewhere on the survey. Most respondents utilized this space, providing a list of birds and plants that was expanded well beyond that which we originally provided.

The final data set melds species that we included by name on the original survey and species offered by respondents in the free-response section. We expected that those species that we included on the original survey would appear in a larger number of reported interactions and that those interactions would be mentioned with greater frequency than for those species occurring only in the free-response section. At the same time, however, the original provided list included many of the most frugivorous birds that occur nationally; we therefore expected the list to contain those most likely to feed on nonnative plants. A higher occurrence of interactions with nonnative plants may be realistic for these birds and may promote greater frequency of responses involving them. We cannot separate those two causal possibilities, but feel that our use of purely descriptive analyses alleviates any bias that the mixed data set may cause. For clarity, however, we make available the lists of birds and plants that we included by name on the original survey (Appendix A).

To visually inspect the nature and composition of the new guilds (plant–bird interaction webs) formed by introduced plants, we performed ordination by detrended correspondence analysis (DCA; Lepš and Šmilauer 2003), using default options in CANOCO 4.5 (ter Braak and Šmilauer 2002). The first DCA ordinated bird species by frequency of use of plant species in feeding interactions, while the second DCA ordinated bird species by plant species used in habitat interactions. For accuracy and manageability, we included in these analyses only the subset of species that had each been reported ≥ 5 times as participating in the ordinated interactions. Therefore, the feeding DCA included 34 bird species and 36 plant species, while the habitat DCA utilized 38 bird species and 19 plant species. To assist with interpretation, we included as supplementary environmental data the dominant habitat in which each bird species is most likely to be found (habitats as described in Sibley 2000, 2003), as well as the typical association of that species with human activities. Habitat categories included woodland, brush, riparian, open, and edge. Categories describing association with humans included urban (frequently associated with humans), suburban (sometimes associated with humans), and nonurban (rarely associated with humans). Habitat categories are presented as centroids in the resulting ordination diagrams.

Those interactions (as specific bird–plant pairs) that were reported ≥ 5 separate times were of particular interest for follow-up evaluation and field work because multiple independent reports offer support for their accuracy. We examined all plant species involved in feeding (potential dispersal) interactions reported ≥ 5 times to determine which are considered invasive or of concern in the four target states, whether by state agencies or nonprofit invasive plant organizations. We considered these plants "high risk" because they both occur on these state lists and are likely to be bird dispersed. Furthermore, although the interactions data set included plants with a number of different fruit types, all of the plants on this "high-risk" list are fleshy-fruited, apparently preadapted to vertebrate dispersal, and therefore contain seeds that are theoretically likely to survive bird ingestion.

Once we had generated this list of high-risk plants, we conducted a literature search to ascertain which of them have been examined for invasiveness in the peer-reviewed scientific literature. We distinguished between invasiveness reports outside of the scientific literature (i.e., by nonprofit organizations and state agencies) and those in the peer-reviewed literature because it has been our experience that managers, concerned citizens, and others creating state lists have somewhat different criteria for designation of invasiveness than do field ecologists. Thus, a species appearing on a state list might occur there because an author of the list has observed it spreading, because anecdotal reports of such spreading have circulated within the local weed-response community, or even because the species is known to spread elsewhere and therefore appears risky to list authors. However, since there are generally fewer research scientists working in these areas than there are concerned citizens or managers, not all species of concern have been investigated for invasiveness using rigorous methodology. Species appearing on state lists but not in the peer-reviewed literature require scientific research to confirm their invasiveness and explore its extent. For our peer-reviewed literature search, we used the free internet-based search engine Google Scholar (Google 2008) in conjunction with BIOSIS Web of Science (Thomson Reuters 2008). The advantage to Google Scholar for this analysis is that it examines complete documents for search terms, which enabled us to locate papers with any mention at all of a given plant as invasive, whether or not the plant was important enough in the study to be included in the abstract. We identified information gaps where high-risk plants were absent in the peer-reviewed literature, indicating a need for research into their invasiveness in relevant states. Isolating these research gaps has helped to guide our ongoing empirical research by pinpointing three species that occur in our field sites and have not been explored in scientific literature for regional invasiveness: *Olea europaea*, *Ligustrum lucidum*, and *Triadica sebifera*. We targeted these species to investigate the role of birds in invasiveness facilitation in California. After systematic observation of bird visitation and feeding on these fruits during two fruiting seasons (winter 2007–2008 and winter 2008–2009), we have developed lists of the birds using these species in California and here compare the birds' frequencies on these lists with those reported using the plants in questionnaires. For this purpose, we used Kendall rank correlation coefficient (Kendall's tau).

For our analyses, we used Sibley (2000, 2003) and Kartesz and Meacham (1999) to examine the full list of reported birds and plants, eliminate from consideration those plants that are or may be native, and combine those common names that refer to the same species. Additionally, identity of exact species in some plant reports was uncertain, either because the survey respondent included only the common name or because a genus was provided for which there are multiple introduced species in the target states. Where this uncertainty could not be resolved with confidence (using Kartesz and Meacham 1999), we lumped such species into genera (e.g., *Berberis* spp., *Rubus* spp.).

Results

A total of 173 or 17% of respondents completed and returned the survey (Table 1). Fifty-one percent of responses were sent from California, 18% from Florida, 14% from New York, and 17% from Washington. As is to be expected given the professional leaning of OSNA membership, respondents largely considered their bird identification skills advanced (56%) or highly advanced (29%), with only 13% rating themselves intermediate and 2% beginner. Self-assessed plant identification skills were lower: 13% considered themselves beginners, 51% intermediate, 30% advanced, and 6% highly advanced. Most respondents reported watching birds with high frequency: 32% birdwatch daily and 25% a few times a week, while 17% birdwatch weekly, 10% biweekly, 10% monthly, and 6% rarely. Thirty-nine percent of respondents reported birdwatching in urban habitat, 68% in suburban habitat, 65% in riparian habitat, 46% in agricultural habitat, 39% in coastal habitat, and 69% in natural areas.

Broadscale interaction patterns

Survey responses referenced a total of 99 plant taxa and 168 bird species, with 1143 distinct bird–plant interactions. Of these interactions, 539 (47%) involved birds feeding on fruits or seeds of nonnative plants (potential dispersal mutualist pairs). These feeding interactions involved 139 bird species (83% of all reported birds) and 85 plant species (86%). Meanwhile, 604 "habitat interactions" described use of nonnative plants by birds in non-dispersal capacities of interest to avian ecology. Prominent among these were nonnative plants as cover and perch sites (35% of all habitat interactions) and nest sites (26%). Additional habitat interactions included unspecified foraging (15%), nectar feeding (11%), roosting (5%), woodpecking (3%), singing (2%), gleaning (2%), sapsucking (1%), sallying (<1%), and caching (<1%).

Participation by family in reported interactions was uneven for both birds and plants (Appendix B). For plants, family Rosaceae was strongly represented among all interactions (19% of all plant species). Among birds, high frequencies were observed for families Emberizidae (15% of all bird species), Parulidae (12%), Icteridae (11%), Ardeidae (10%), and Picidae (10%). Furthermore, there was a strong tendency overall for related birds to appear in the data set: among the 37 included avian families, all were represented by at least 10% of their North American (north of Mexico) members and 13 were represented by 50% or more of their members (Appendix B). Conversely, among plants, the percentages of families' total naturalized exotic species spanned a much larger range, from under 1% to 100% (Appendix B).

Ordination: interaction web depiction

Although the supplementary environmental data included (habitat and association with urban areas) were derived from a bird field guide (Sibley 2000, 2003) and based entirely on known bird habits, the plants in the feeding interactions DCA tracked expected ecological positions quite well. The first axis separated suburban and woodland areas from open and urban environments (Fig. 2a). Plants characteristic of thicker vegetation appear at the left side of the diagram, as would be expected (e.g., *Rubus* spp., *Rosa canina*), while plants that normally appear more commonly in open, agricultural, or heavily urban environments fell on the right side of the diagram (e.g., *Triadica sebifera*, *Olea europaea*, *Melia azedarach*). This agreement between expected and observed plant habitat, derived in the analysis entirely from bird associations, lends credence to the DCA's accuracy. This first axis of the feeding interactions DCA explained 15% of the total variation in the data set, while the second axis explained an additional 8% of the data set variation.

In the habitat interactions DCA, plants were similarly located as would be expected by known occurrence

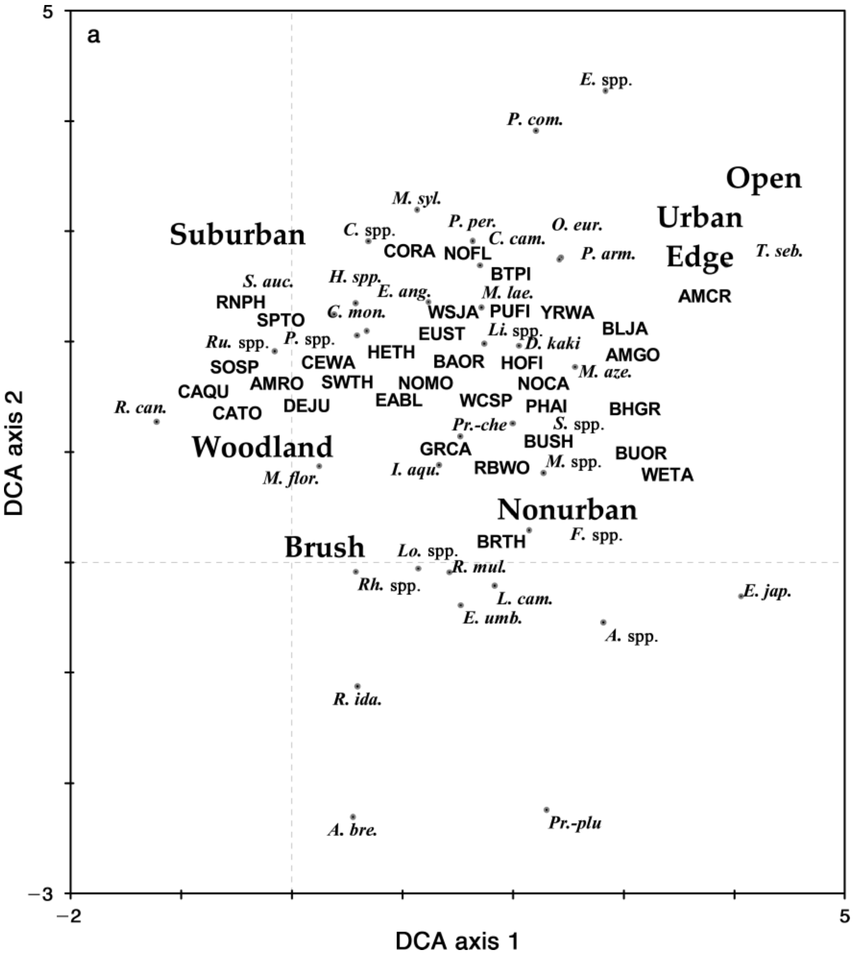

FIG. 2. Detrended correspondence analyses (DCA) presenting bird species ordinated with respect to the plant taxa they utilize. Only plant and bird taxa with five or more reports of interactions in survey responses are included in these analyses. (a) DCA of bird species ordinated with respect to plant taxa they utilize for fruit or seed feeding (potential dispersal interactions). (b) DCA of bird species ordinated with respect to plant taxa they utilize for habitat interactions. Bird abbreviations are: ALHU, Allen's Hummingbird; AMCR, American Crow; AMGO, American Goldfinch; AMRO, American Robin; ANHU, Anna's Hummingbird; BAOR, Baltimore Oriole; BCCH, Black-capped Chickadee; BEWR, Bewick's Wren; BHGR, Black-headed Grosbeak; BLJA, Blue Jay; BRBL, Brewer's Blackbird; BRTH, Brown Thrasher; BTPI, Band-tailed Pigeon; BUOR, Bullock's Oriole; BUSH, Bushtit; CAQU, California Quail; CATO, California Towhee; CEWA, Cedar Waxwing; CORA, Common Raven; DEJU, Dark-eyed Junco; EABL, Eastern Bluebird; EUST, European Starling; FOSP, Fox Sparrow; GCSP, Golden-crowned Sparrow; GRCA, Gray Catbird; HETH, Hermit Thrush; HOFI, House Finch; HOOR, Hooded Oriole; HOSP, House Sparrow; MODO, Mourning Dove; NOCA, Northern Cardinal; NOFL, Northern Flicker; NOMO, Northern Mockingbird; OATI, Oak Titmouse; OCWA, Orange-crowned Warbler; PHAI, Phainopepla; PUFI, Purple Finch; RBSA, Red-breasted Sapsucker; RBWO, Red-bellied Woodpecker; RCKI, Ruby-crowned Kinglet; RNPH, Ring-necked Pheasant; RTHU, Ruby-throated Hummingbird; RWBL, Red-winged Blackbird; SOSP, Song Sparrow; SPTO, Spotted Towhee; SWTH, Swainson's Thrush; TRBL, Tricolored Blackbird; WCSP, White-crowned Sparrow; WETA, Western Tanager; WSJA, Western Scrub-Jay; and YRWA, Yellow-rumped Warbler. Plant abbreviations are: *A.* spp., *Acacia* spp.; *A. bre*., *Ampelopsis brevipedunculata*; *C. rig*., *Callistemon rigidus*; *C. cam*., *Cinnamomum camphora*; *C.* spp., *Cotoneaster* spp.; *C. mon*., *Crataegus monogyna*; *D. kaki*, *Diospyros kaki*; *E. ang*., *Elaeagnus angustifolia*; *E. umb*., *Elaeagnus umbellata*; *E. jap*., *Eriobotrya japonica*; *E.* spp., *Eucalyptus* spp.; *F.* spp., *Ficus* spp.; *G. rob*., *Grevillea robusta*; *H.* spp., *Hedera* spp.; *I. aqu*., *Ilex aquifolium*; *L. cam*., *Lantana camara*; *Li.* spp., *Ligustrum* spp.; *Lo.* spp., *Lonicera* spp.; *M. flor*., *Malus floribunda*; *M. syl*., *Malus sylvestris*; *M. aze*., *Melia azedarach*; *M.* spp., *Morus* spp.; *M. lae*., *Myoporum laetum*; *O. eur*., *Olea europaea*; *P. und*., *Pittosporum undulatum*; *P. arm*., *Prunus armeniaca*; *Pr.-che*, *Prunus* spp. (cherry); *P. per*., *Prunus persica*; *Pr.-plu*, *Prunus* spp. (plum); *P.* spp., *Pyracantha* spp.; *P. com*., *Pyrus communis*; *Rh.* spp., *Rhamnus* spp.; *R. can*., *Rosa canina*; *R. mul*., *Rosa multiflora*; *R. ida*., *Rubus idaeus*; *Ru.* spp., *Rubus* spp.; *S.* spp., *Schinus* spp.; *S. auc*., *Sorbus aucuparia*; *T. seb*., *Triadica sebifera*.

patterns, although here the pattern was driven more strongly by association with humans. Thus, *Rubus* spp. and *Rosa canina* appear at the left of the diagram, associated with nonurban environments, while *Callistemon rigidus*, *Grevillea robusta*, and *Acacia* spp. appear on the right with urban environments. The first two habitat DCA axes cumulatively explained 34% of the variance in the data set and were considerably greater in length and eigenvalue than succeeding axes. The first axis had a length (the extent of species

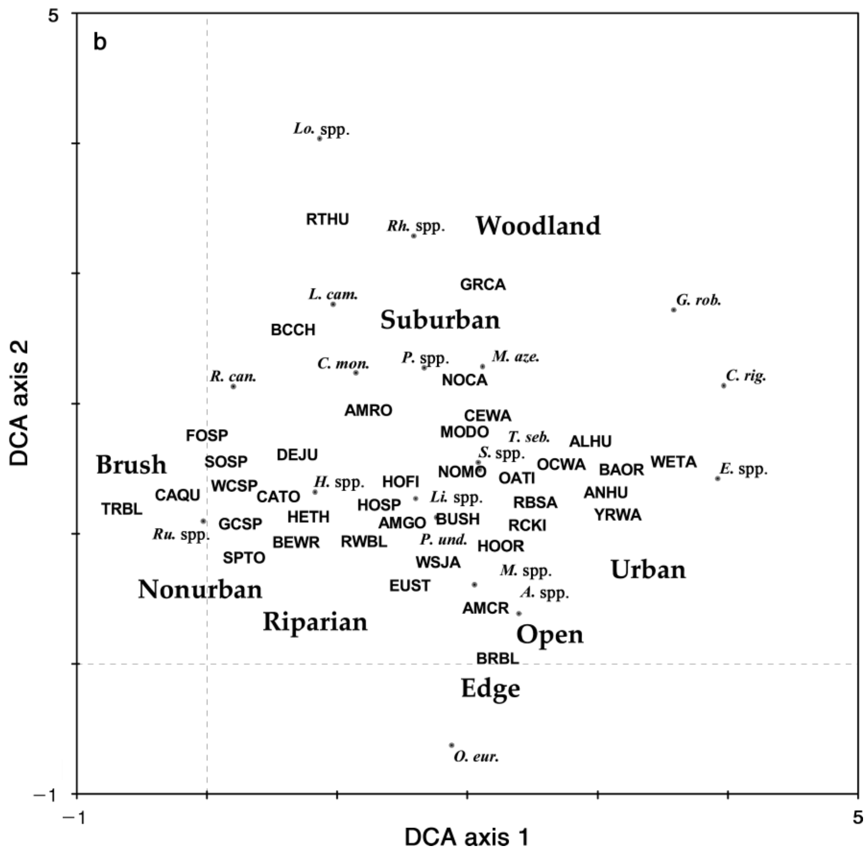

FIG. 2. Continued.

turnover) of 3.4 and explained 22% of the data set variance. This axis led from brush, riparian, and nonurban environments at its lowest scores to urban areas at its highest scores (Fig. 2b). The second axis had a length of 3.3 and explained a further 12% of the variance.

Information gaps

A total of 22 habitat interactions (Table 2) and 50 feeding interactions (Table 3) received $\geq$5 reports (where an interaction was defined as a bird–plant pair). In all, 17 of the plant species involved in these feeding (potential dispersal) interactions are considered problematic in the target states by nonprofit organizations (generally, state-specific invasive plant councils; Table 4). Only five species are listed as invasive by state government agencies, while 10 are considered invasive in peer-reviewed scientific literature (Table 4). One species, firethorn (*Pyracantha* spp.) has no record of invasiveness in the target states.

Seven of these plants are considered invasive by either nonprofit organizations or state agencies without evidence in peer-reviewed literature that their invasiveness has been examined. These species are: mulberry (*Morus* spp.), mountain ash (*Sorbus aucuparia*), European olive (*Olea europaea*), holly (*Ilex aquifolium*), *Cotoneaster* spp., cherry (*Prunus* spp.), and crab apple (*Malus floribunda*). Five additional species are considered invasive in some states based on peer-reviewed literature, but by only non-peer-reviewed sources elsewhere: privet (*Ligustrum* spp.), hawthorn (*Crataegus monogyna*), blackberry (*Rubus* spp.), Chinese tallow (*Triadica sebifera*), and ivy (*Hedera* spp.).

Agreement between survey results and field observations

In qualitative terms, 16 of the bird species reported in surveys as feeding on *O. europaea* fruits occurred in our study region; of these, we observed 11 species feeding on *O. europaea* fruits and a further three species visiting the trees for indeterminate purposes. For *L. lucidum*, 20 of the bird species reported in surveys as feeding on fruit occurred in our study region. We observed 14 of these consuming *L. lucidum* fruit, and observed indeterminate tree use by an additional three species. For *T. sebifera*, 17 of the bird species reported in surveys as feeding on fruit occurred in the study region. We observed nine of these eating the fruits and recorded indeterminate tree use by an additional three species (Table 5). For each of these three plant species, then, we have confirmed visitation by at least 70% of the birds occurring in our study region and reported in surveys as feeding on fruits. For these three tree species we also evaluated the

TABLE 2. Pairwise bird–plant habitat interactions receiving at least five separate reports.

Bird species†	Plant	No. reports
Song Sparrow (*Melospiza melodia*)	blackberry (*Rubus* spp.)	25
Spotted Towhee (*Pipilo maculatus*)	blackberry (*Rubus* spp.)	21
California Towhee (*Pipilo crissalis*)	blackberry (*Rubus* spp.)	14
White-crowned Sparrow (*Zonotrichia leucophrys*)	blackberry (*Rubus* spp.)	14
Golden-crowned Sparrow (*Zonotrichia atricapilla*)	blackberry (*Rubus* spp.)	11
California Quail (*Callipepla californica*)	blackberry (*Rubus* spp.)	10
Fox Sparrow (*Passerella iliaca*)	blackberry (*Rubus* spp.)	9
Northern Mockingbird (*Mimus polyglottos*)	peppertree (*Schinus* spp.)	9
Yellow-rumped Warbler (*Dendroica coronata*)	*Eucalyptus* spp.	9
American Robin (*Turdus migratorius*)	hawthorn (*Crataegus monogyna*)	7
Dark-eyed Junco (*Junco hyemalis*)	blackberry (*Rubus* spp.)	7
Tricolored Blackbird (*Agelaius tricolor*)	blackberry (*Rubus* spp.)	7
House Finch (*Carpodacus mexicanus*)	blackberry (*Rubus* spp.)	6
Northern Mockingbird (*Mimus polyglottos*)	firethorn (*Pyracantha* spp.)	6
Northern Mockingbird (*Mimus polyglottos*)	privet (*Ligustrum* spp.)	6
American Robin (*Turdus migratorius*)	blackberry (*Rubus* spp.)	6
Mourning Dove (*Zenaida macroura*)	peppertree (*Schinus* spp.)	5
Red-breasted Sapsucker (*Sphyrapicus ruber*)	peppertree (*Schinus* spp.)	5
Yellow-rumped Warbler (*Dendroica coronata*)	*Acacia* spp.	5
Bushtit (*Psaltriparus minimus*)	*Acacia* spp.	5
Cedar Waxwing (*Bombycilla cedrorum*)	hawthorn (*Crataegus monogyna*)	5
House Finch (*Carpodacus mexicanus*)	*Acacia* spp.	5

† Scientific nomenclature follows Sibley (2000, 2003).

agreement between the frequency of individual bird species in the reports and in our field data. Because the observations in the two data sets were collected quite differently (i.e., chance records with no quantification of frequency vs. systematic, quantitative field methods), we examined their agreement based both on number of observation periods in which bird species appeared and on total number of individual visitors from each bird species. Rank correlation (Kendall's tau) was positive and clearly significant for both comparisons ($P < 0.05$; Table 6).

DISCUSSION

Survey results permitted examination of broadscale interaction patterns, resulting guilds, and information gaps relevant to plant invasiveness. The use of a social science tool to access information gathered by ornithologists, as trained and expert citizen scientists, gave our analysis extensive geographical and temporal reach. This enabled us to probe the general implications of nonnative plant interactions with resident birds, with relevance for widely dispersed U.S. ecosystems. Our results identified new plant–animal associations arising from nonnative plant introductions and capable of impacting all involved species. Further research in this area can be both motivated and steered by these results.

Reported interactions fell into two categories: mutualistic seed or fruit feeding (potential dispersal), and commensalistic habitat interactions in which birds utilized introduced plants for various life functions. These differ in their ecological implications and render survey results of interest to both invasion biology and avian ecology.

Feeding interactions

Almost half of reported interactions were feeding interactions and a large majority of all species in the data set were involved in at least one feeding interaction. When interactions involve seed or fruit feeding, particularly for fleshy-fruited plants, plant dispersal is a potential outcome. Because birds may thereby promote invasions, fleshy-fruited plants are often considered of high environmental risk as ornamental, agricultural, or horticultural introductions (Rejmánek and Richardson 1996, Daehler et al. 2004, Aronson et al. 2007). When even rare long-distance dispersal events occur in dispersal kernel analyses, greatly increased spatial spread rates are expected and may be critical to invasion success (Kot et al. 1996, Richardson and Pyšek 2008). Results of concern can include spread of the plant beyond urban areas (e.g., Borgmann and Rodewald 2005) and new satellite plant populations that may be undetected because they are outside the monitoring area. Of conservation concern is the potential that bird dispersal may funnel the nonnative plant species into protected areas by way of corridors or landscape patches attractive to birds (Tewksbury et al. 2002, With 2002). Habitat corridors creating connectivity between patches and allowing migration are generally considered beneficial or even essential for conservation (Damschen et al. 2006). However, such corridors may be at risk of colonization by bird-dispersed invasive species (Buckley et al. 2006). If corridors draw frugivorous birds at the same rate as other mobile species, these habitat strips may accumulate bird-dispersed nonnatives at a faster rate than the surrounding matrix (even if that matrix is highly human modified) and may proceed to facilitate

TABLE 3. Pairwise bird–plant feeding interactions receiving at least five reports.

Bird species†	Plant	No. reports
American Robin (*Turdus migratorius*)	firethorn (*Pyracantha* spp.)	38
Cedar Waxwing (*Bombycilla cedrorum*)	firethorn (*Pyracantha* spp.)	32
Northern Mockingbird (*Mimus polyglottis*)	firethorn (*Pyracantha* spp.)	23
American Robin (*Turdus migratorius*)	peppertree (*Schinus* spp.)	22
American Robin (*Turdus migratorius*)	mulberry (*Morus* spp.)	20
Cedar Waxwing (*Bombycilla cedrorum*)	privet (*Ligustrum* spp.)	20
American Robin (*Turdus migratorius*)	blackberry (*Rubus* spp.)	18
American Robin (*Turdus migratorius*)	hawthorn (*Crataegus monogyna*)	17
Northern Mockingbird (*Mimus polyglottis*)	peppertree (*Schinus* spp.)	16
Cedar Waxwing (*Bombycilla cedrorum*)	hawthorn (*Crataegus monogyna*)	15
Cedar Waxwing (*Bombycilla cedrorum*)	mulberry (*Morus* spp.)	14
Cedar Waxwing (*Bombycilla cedrorum*)	peppertree (*Schinus* spp.)	14
European Starling (*Sturnus vulgaris*)	mulberry (*Morus* spp.)	13
American Robin (*Turdus migratorius*)	mountain ash (*Sorbus aucuparia*)	12
Cedar Waxwing (*Bombycilla cedrorum*)	mountain ash (*Sorbus aucuparia*)	12
Yellow-rumped Warbler (*Dendroica coronata*)	peppertree (*Schinus* spp.)	12
American Crow (*Corvus brachyrhynchos*)	Chinese tallow (*Triadica sebifera*)	11
European Starling (*Sturnus vulgaris*)	European olive (*Olea europaea*)	11
American Robin (*Turdus migratorius*)	ivy (*Hedera* spp.)	11
American Robin (*Turdus migratorius*)	privet (*Ligustrum* spp.)	11
Northern Mockingbird (*Mimus polyglottis*)	blackberry (*Rubus* spp.)	10
Gray Catbird (*Dumetella carolinensis*)	peppertree (*Schinus* spp.)	10
Cedar Waxwing (*Bombycilla cedrorum*)	*Cotoneaster* spp.	9
American Robin (*Turdus migratorius*)	holly (*Ilex aquifolium*)	9
Cedar Waxwing (*Bombycilla cedrorum*)	holly (*Ilex aquifolium*)	9
Northern Mockingbird (*Mimus polyglottis*)	mulberry (*Morus* spp.)	9
Spotted Towhee (*Pipilo maculatus*)	blackberry (*Rubus* spp.)	8
American Robin (*Turdus migratorius*)	cherry (*Prunus* sp.)	8
American Robin (*Turdus migratorius*)	honeysuckle (*Lonicera* spp.)	8
Gray Catbird (*Dumetella carolinensis*)	mulberry (*Morus* spp.)	8
Northern Mockingbird (*Mimus polyglottis*)	privet (*Ligustrum* spp.)	8
American Robin (*Turdus migratorius*)	*Cotoneaster* spp.	7
American Robin (*Turdus migratorius*)	crab apple (*Malus floribunda*)	7
American Robin (*Turdus migratorius*)	European olive (*Olea europaea*)	7
Northern Mockingbird (*Mimus polyglottis*)	European olive (*Olea europaea*)	7
Hermit Thrush (*Catharus guttatus*)	firethorn (*Pyracantha* spp.)	7
European Starling (*Sturnus vulgaris*)	ivy (*Hedera* spp.)	7
Song Sparrow (*Melospiza melodia*)	blackberry (*Rubus* spp.)	6
Northern Mockingbird (*Mimus polyglottis*)	holly (*Ilex aquifolium*)	6
Northern Mockingbird (*Mimus polyglottis*)	multiflora rose (*Rosa multiflora*)	6
Cedar Waxwing (*Bombycilla cedrorum*)	blackberry (*Rubus* spp.)	5
Swainson's Thrush (*Catharus ustulatus*)	blackberry (*Rubus* spp.)	5
Western Scrub-Jay (*Aphelocoma californica*)	blackberry (*Rubus* spp.)	5
Cedar Waxwing (*Bombycilla cedrorum*)	crab apple (*Malus floribunda*)	5
Northern Mockingbird (*Mimus polyglottis*)	fig (*Ficus* spp.)	5
Cedar Waxwing (*Bombycilla cedrorum*)	honeysuckle (*Lonicera* spp.)	5
Gray Catbird (*Dumetella carolinensis*)	honeysuckle (*Lonicera* spp.)	5
Northern Mockingbird (*Mimus polyglottis*)	lantana (*Lantana camara*)	5
Western Tanager (*Piranga ludoviciana*)	mulberry (*Morus* spp.)	5
House Finch (*Carpodacus mexicanus*)	peppertree (*Schinus* spp.)	5

Note: These interactions involve feeding on fruits or seeds and therefore carry the potential for nonnative plant dispersal.
† Scientific nomenclature follows Sibley (2000, 2003).

invasion of the mostly intact habitat patches to which the corridors lead. Bolstering this theory, bird dispersal of a native plant species between habitat patches was substantially promoted by the presence of corridors (Levey et al. 2005). Riparian areas serve as a prime example of this risk, since many urban areas are located along river systems. Forested riverbanks stretching away from the city or town may encourage birds to move from the nonnative plant-dominated town along the stream to rural, natural, or even protected areas up- or downstream. Empirical studies exploring the role of corridors in facilitation of invasions have yielded mixed results: Damschen et al. (2006) showed no promotion of exotic species in general in corridors, while Hutchinson and Vankat (1998) demonstrated enhanced movement of a bird-dispersed exotic species in the presence of corridors.

In other cases, bird consumption of fruits or seeds does not lead to successful dispersal. Some birds that swallow seeds function as seed predators, perhaps because the bird's digestive tract kills swallowed seeds (Norconk et al. 1998, Conway et al. 2002*a*). In other seed predation scenarios, birds extract soft seed embryos from their seed coats, consuming only these highly destructible embryos and killing them in the process (Banko et al. 2002). Other birds eat the fruit flesh from around a target plant's seeds without transporting the

TABLE 4. The 18 plant species involved in feeding interactions reported five or more times.

Species	CA	FL	NY	WA	Source
Pyracantha spp.	···	···	···	···	
Schinus spp.	O, L	A, O, L	···	···	Nilsen and Muller (1980), Randall (2000*b*), Ewe and Sternberg (2002), FWC (2004), Zedler and Kercher (2004), Cal-IPC (2006), FLEPPC (2009)
Ligustrum spp.	O	O, L	O, L	···	Luken and Thieret (1997), Hunter and Mattice (2002), Wilcox and Beck (2007), FLEPPC (2009), BBG,† FBP,‡ IPCNYS,§ NEWFS¶
Crataegus monogyna	···	···	O, L	O	Hunter and Mattice (2002), WISC (2006), NEWFS¶
Morus spp.	···	···	O	···	BBG†
Rubus spp.	O, L	···	O	L	Cal-IPC (2006), Caplan and Yeakley (2006), Williams et al. (2006), BBG,† IPCNYS,§ NEWFS¶
Sorbus aucuparia	···	···	···	O	WISC (2006)
Cotoneaster spp.	O	···	···	···	Cal-IPC (2006)
Prunus spp.	···	···	O	···	IPCNYS§
Triadica sebifera	O#	A, O, L	···	···	Franklin et al. (1999), Conway et al. (2002*b*), FWC (2004), Rogers and Siemann (2004), Cal-IPC (2006), FLEPPC (2009)
Ilex aquifolium	O	···	A, O	A, O	Cal-IPC (2006), WISC (2006), Jones and Halpern (2007), NEWFS¶
Olea europaea‖	O	···	···	···	FBP‡
Lonicera spp.	L	O, L	O, L	···	Luken and Thieret (1997), Gordon (1998), Hunter and Mattice (2002), Vellend (2002), Schierenbeck (2004), FLEPPC (2009), BBG,† NEWFS¶
Malus floribunda	···	···	O	···	Wesley (1998), BBG†
Hedera spp.	O, L	···	O	A, O, L	Yost et al. (1991), Dlugosch (2005), Cal-IPC (2006), Clarke et al. (2006), WISC (2006), Rice (2008), WSNWCB (2008), NEWFS¶
Rosa multiflora	···	···	O, L	···	Hunter and Mattice (2002), BBG,† IPCNYS§
Ficus spp.	O, L	O, L	···	···	Gordon (1998), Randall (2000*a*), Cal-IPC (2006), FLEPPC (2009)
Lantana camara	···	O, L	···	···	Gordon (1998), FLEPPC (2009)

Notes: We explored these species by state (CA, California; FL, Florida; NY, New York; and WA, Washington) to determine whether they are considered invasive by nonprofit organizations (O), governmental/state agencies (A), or in the peer-reviewed literature (L). Ellipses (···) indicate that no data are available.

† Brooklyn Botanical Garden ⟨http://www.bbg.org⟩

‡ Friends of Bidwell Park ⟨http://www.friendsofbidwellpark.org/invasivetable.html⟩

§ Invasive Plant Council of New York State ⟨http://www.ipcnys.org⟩

¶ New England Wild Flower Society ⟨http://www.newfs.org/docs/docs/invalt2.pdf⟩

No invasiveness exploration in literature, but Pattison and Mack (2008) predict that *T. sebifera* may invade Californian riparian zones, and Hrusa et al. (2002) observe *T. sebifera* naturalization.

‖ *Olea europaea* is highly invasive in mediterranean Australia (Spennemann and Allen 2000).

seeds; these birds may function as seed predators by discouraging later dispersal of the chewed or scraped fruits (e.g., Yellow-rumped Warblers on *Triadica sebifera*; Conway et al. 2002*a*; C. E. Aslan, *personal observation*). Accurate understanding of seed dispersal by birds is necessary for assessment of the invasion risk posed by newly introduced, fleshy-fruited plants (Aronson et al. 2007).

At the same time, the formation of new feeding mutualisms may affect the ecology of resident birds. In the foothills of California's Sierra Nevada and coastal ranges, for example, the only native plant offering a substantial amount of fleshy fruits during most of the winter is toyon (*Heteromeles arbutifola*). The introduction of a host of ornamental and horticultural species to urban areas in the region, however, has resulted in many nonnative species fruiting locally at any given time of the year. Now, while *H. arbutifolia* is in fruit, so are privet (*Ligustrum* spp.), European olive (*Olea europaea*), Chinese tallow (*Triadica sebifera*), firethorn (*Pyracantha angustifolia*), heavenly bamboo (*Nandina domestica*), and others. How might this change affect bird phenology (e.g., migration patterns and breeding behavior transitions) and spatial distribution (e.g., attraction of birds into urban areas with associated dangers)?

Habitat interactions

Slightly more than half of all reported interactions were habitat interactions. As with feeding interactions, bird use of introduced plants for habitat creates new species assemblages (Wilson and Belcher 1989) and unpredictable changes in bird ecology (Witmer 1996, Reichard et al. 2001). Plant communities dominated by introduced plants may exhibit altered structural characteristics, which in turn alter local bird assemblages (Beachy and Robinson 2009). Introduced plants providing avian habitat may attract birds into urban zones. This may connect patches of native habitat, as when urban areas occur along rivers. On the other hand, urban zones represent additional dangers, including altered disease regimes and enhanced risk of domestic cat predation, car collisions, and window strikes (Chace and Walsh 2006).

From an avian conservation standpoint, plant introductions under some circumstances have offered essential structural or resource replacement for extirpated native plants, either at local points such as urban landscaping (Rosenberg et al. 1987), or regionally such as throughout a riparian region (Brown and Trosset 1989). These introductions have permitted persistence of

TABLE 5. Bird species reported in surveys as feeding on fruits of three introduced species, and whether confirmed by our California field observations.

Bird species	*Triadica sebifera*		*Ligustrum lucidum*		*Olea europaea*	
	Reported	Confirmed	Reported	Confirmed	Reported	Confirmed
American Crow	+	C	+	C	+	P
American Goldfinch	+	P	+	P	–	P
American Robin	+	C	+	C	+	C
Baltimore Oriole	–	N	–	N	+	N
Band-tailed Pigeon	–	N	–	N	+	N
Bewick's Wren	–	N	+	N	–	N
Brewer's Blackbird	–	N	–	N	+	P
Bushtit	–	C	+	C	–	C
Cedar Waxwing	+	C	+	C	+	C
Dark-eyed Junco	–	C	+	C	+	C
Downy Woodpecker	+	N	–	N	–	N
European Starling	–	C	+	C	+	C
Hairy Woodpecker	+	N	–	N	–	N
Hermit Thrush	+	C	+	C	–	C
House Finch	+	C	+	C	+	C
House Sparrow	–	P	+	C	–	N
Lesser Goldfinch	+	P	–	P	–	P
Northern Flicker	+	C	+	C	+	C
Northern Mockingbird	+	C	+	C	+	C
Nuttall's Woodpecker	+	C	–	C	–	P
Oak Titmouse	–	N	+	P	–	C
Orange-crowned Warbler	–	N	+	P	–	N
Pine Siskin	+	N	–	N	–	N
Purple Finch	+	P	+	C	+	P
Red-breasted Sapsucker	–	C	+	N	–	N
Red-winged Blackbird	+	N	–	N	–	N
Savannah Sparrow	–	N	–	N	+	N
Swainson's Thrush	–	N	+	N	–	N
Western Scrub-Jay	–	C	+	C	+	C
White-crowned Sparrow	–	C	–	C	+	C
Wild Turkey	–	N	–	N	+	C
Yellow-billed Magpie	+	N	–	N	–	P
Yellow-rumped Warbler	+	C	+	C	+	C

Notes: For the bird species reports: +, reported; –, not reported. For the plant species, records refer to number of survey responses, and observation hours refer to our California study: Chinese tallow *Triadica sebifera* (45 records, 101.5 h observation); glossy privet *Ligustrum lucidum* (70 records, 114 h observation); European olive *Olea europaea* (50 records, 104.5 h observation). Abbreviations are: C, confirmed fruit feeding; P, presence in observed stands and possible feeding on fruits; N, no visitation observed. Only birds that occur in the observation area during winter (when fruits are ripe) are included.

certain bird species in various locations (Brown and Trosset 1989, Cook and Toft 2005).

Participation in interactions by plant and bird families

Plant family Rosaceae has by far the most representatives (number of taxa) in our data set. There are at least five types of fleshy fruits in Rosaceae: achenetum (*Rosa*), drupe (*Prunus*), drupetum (*Rubus*), polyprenous drupe (*Cotoneaster*, *Crataegus*, *Pyracantha*), and pome (*Malus*, *Sorbus*) (Potter et al. 2007). New introductions of Rosaceae species may therefore be likely to have fleshy fruits and interact with resident birds. At the same

TABLE 6. Results of rank correlation (Kendall's tau corrected for ties) comparing frequencies of bird species reported in questionnaires as feeding on fruits of three target plant species with frequencies of the same bird species recorded feeding on these fruits in California field observations.

Plant species	No. bird species (n)	Kendall's tau	P
Triadica sebifera			
No. field observation periods	17	0.551	0.002
No. visits per bird species	17	0.479	0.007
Ligustrum lucidum			
No. field observation periods	20	0.342	0.035
No. visits per bird species	20	0.469	0.004
Olea europaea			
No. field observation periods	16	0.439	0.018
No. visits per bird species	16	0.407	0.028

Note: We compared questionnaire frequencies both with the number of field observation periods in which each bird species appeared and with the total number of visits by each bird species.

time, though, Rosaceae species are often well known and showy, and even sometimes edible for humans. Because of this, Rosaceae species may be more recognizable by questionnaire respondents than are other plants, which could lead to overreporting of Rosaceae in our data set. In spite of this potential problem, our data set contained many families (48) with three or fewer taxa with which birds were observed to interact, demonstrating the key point that bird attraction is widespread among plant families, but, in general, more common in families with many fleshy fruiting taxa.

Among birds, a different pattern emerges. A few families are best represented (Emberizidae, Parulidae, Icteridae), but there are a full 14 families with more than five representatives in our data set. This exemplifies the diffuse nature of bird–plant mutualisms in general (Richardson et al. 2000): birds opportunistically take advantage of nonnative plants. Possibilities are so plentiful that pairwise interactions after new introductions are unpredictable.

Examination of interaction-based, recently formed species assemblages

Examining the DCA ordination based on feeding interactions (Fig. 2a), several bird species cluster near the center of the two-dimensional ordination space (e.g., American Robin, Cedar Waxwing, Northern Mockingbird, Western Scrub-Jay, European Starling, House Finch). This probably reflects these generalists' ability to thrive in varying habitats and to unite a wide suite of fleshy-fruited plants in an interaction web (through diffuse mutualisms; Herrera 1985). The feeding DCA also clustered urban areas with open and edge environments, uniting birds and plants associated with agricultural areas, occasional drought stress, and structurally simple landscaping: these include such species as *Olea europaea*, *Triadica sebifera*, *Prunus armeniacus*, American Crow, Northern Flicker, Common Raven, and American Goldfinch. Opposite these relationships, woodland, brush, and nonurban areas included plants known for naturalizing in riparian zones (e.g., *Ficus* spp., *Lonicera* spp.), large trees typical of woodlands (e.g., *Malus floribunda*, *Prunus* spp.), and birds preferring dense vegetation (e.g., Brown Thrasher, Gray Catbird, Bushtit, Swainson's Thrush, Red-bellied Woodpecker). Intermediate in cover provision was "suburban" environment, with birds able to move successfully between human-dominated and natural areas (e.g., Ring-necked Pheasant, Spotted Towhee, Hermit Thrush, European Starling) and fast-growing plants that take advantage of this transition zone (e.g., *Crataegus monogyna*, *Elaeagnus angustifolia*, *Ligustrum lucidum*).

In the habitat interaction DCA, birds and plants were distributed along two axes more distinctly. This relationship may partially result from the smaller number of plants that was utilized in the habitat DCA analysis; there was less intermingling of conflicting influences. The first axis separates species by their association with humans (nonurban at the lowest values, through the transitional suburban category, to urban at the highest values). Toward the left appear *Rubus* spp., *Hedera* spp., and most sparrows. Opposite these are species abundant in urban zones, such as *Eucalyptus* spp., *Callistemon rigidus*, and associated hummingbird and warbler species. The second axis separates species by stricter environmental categories, with species attracted to woodlands at the top of the ordination space (such as Gray Catbird, Black-capped Chickadee, *Rhamnus* spp., and *Crataegus monogyna*), and by attraction to open and edge environments at the bottom (including American Crow, European Starling, *Acacia* spp., and *Olea europaea*).

Many of the same bird and plant species appeared in both the feeding and the habitat DCAs, but sometimes in very different positions. Such differences are in agreement with the long recognized distinctiveness of foraging, nesting, and resting bird "communities" or guilds (Pikula 1962, Emlen 1977, Hino 1985). The habitat DCA, for example, combines most sparrows with plants that provide cover for perching and roosting (brushy, nonurban, and riparian habitat). Many of the same species were drawn to suburban and woodland environments in the feeding DCA, reflecting birds' ability to use different plants for different purposes. Logically, we expect that most birds are able to use most plants for basic habitat needs such as perching. Habitat interactions, therefore, are likely to separate naturally by the environments in which birds find themselves a majority of the time. Feeding interactions, however, are likely to be more subject to bird preference, size, competing food sources, etc. They may therefore draw birds at certain seasons or times of day into different habitats; birds may move considerable distances to feed during the day, but return to a more-or-less regular site to roost at night, for example. These feeding movements may thus result in species assemblage patterns driven less by obvious abiotic factors than are habitat interactions.

Notably, some bird species that appeared to cluster in urban environments in the habitat DCA are likely tracking the availability of artificial bird feeders. Local abundances of some such species are known to be influenced by bird feeder availability (e.g., hummingbirds, goldfinches, sparrows, finches; Marzluff 1997, Wethington and Russell 2003, Fuller et al. 2008, Robb et al. 2008). While the birds appear to be utilizing the nonnative plants in urban environments for perching, roosting, nesting, and other habitat interactions, their role in these associations may be maintained by and dependent upon the continued presence of bird feeders offering reliable food sources. Since birds obviously require both suitable food and habitat sources, a decrease in the number of these artificial feeders could result in relocation of some birds outside of urban areas unless alternative urban food sources are available.

Guidance for empirical research: information gaps

The primary goal of this questionnaire was to stimulate and guide follow-up empirical research. Survey analyses identified seven plant taxa (*Morus* spp., *Sorbus aucuparia*, *Cotoneaster* spp., *Prunus* spp., *Ilex aquifolium*, *Olea europaea*, *Malus floribunda*) of particular biological invasion concern: our data set suggests that they are likely dispersed by birds, and they are considered invasive in our target states by nonprofit organizations or governmental agencies (i.e., spreading has been observed), but their invasiveness has neither been confirmed nor denied by peer-reviewed research (Table 4). These species are potential incipient invaders and should be prioritized for research. If bird dispersal of these plants indeed occurs and offers a reliable long-distance dispersal mechanism, the rate of spread may be rapid (Bullock et al. 2002) and invasiveness is of real concern. Rigorous scientific study appears lacking in these cases, perhaps by chance or because spread is relatively new. Are these species potential "sleeper" species, likely to become invasive in the future (Bomford 2003)? If not, what factors will keep them from invading?

In addition to the seven taxa listed in the previous paragraph, another five species are considered invasive by non-peer-reviewed sources in more states than by peer-reviewed sources (*Ligustrum* spp., *Crataegus monogyna*, *Rubus* spp., *Triadica sebifera*, *Hedera* spp.; Table 4). We recommend further research into the geographical distribution and spread of these species, as well, in order to more fully assess their invasive potential in different U.S. regions.

We have initiated this process by using our survey results to foster our selection of a subset of these information gap species (*Ligustrum lucidum*, *Olea europaea*, *Triadica sebifera*) for intensive field observation follow-up in California. The qualitative and quantitative agreement we have found between our field observations of birds using these trees and the bird lists developed from survey reports supports our use of the questionnaire data set to target our field research. Furthermore, it exemplifies applicability of survey data such as ours to ecological questions.

We emphasize that, given the professional nature of the mailing list source, the survey respondents in this data set had generally above-average expertise and experience in birdwatching. This almost certainly bolstered the level of agreement between the observations of these citizen scientists and our own field research. Other citizen scientist groups may have provided less trustworthy information, either because they are untrained in recording and reporting or because of lower familiarity with study species. Whenever social science methods such as questionnaires are utilized, the expertise level among respondents must be assessed and considered in results interpretation. Nevertheless, with an appropriate level of conservatism, such data sets drawn from a number of sources can have high heuristic value.

Interactions between birds and nonnative plants have clear conservation and management implications, but remain poorly understood at all spatial scales. There is a strong need for additional studies addressing both general and species-specific aspects of this phenomenon, particularly when results have direct application for invasion prevention or impact mediation.

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APPENDIX A

List of species included by name on original surveys (*Ecological Archives* A020-036-A1).

APPENDIX B

Bird and plant families participating in reported interactions, with number of species per family involved (*Ecological Archives* A020-036-A2).