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Integration of alien plants into a native flower–pollinator visitation web

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Introduced alien species influence many ecosystem services, including pollination of plants by animals. We extend the scope of recent 'single species' studies by analysing how alien plant species integrate themselves into a native flower visitation web. Historical records for a community in central USA show that 456 plant species received visits from 1429 insect and 1 hummingbird species, yielding 15 265 unique interactions. Aliens comprised 12.3% of all plant species, whereas only a few insects were alien. On average, the flowers of alien plants were visited by significantly fewer animal species than those of native plants. Most of these visitors were generalists, visiting many other plant species. The web of interactions between flowers and visitors was less richly connected for alien plants than for natives; nonetheless, aliens were well integrated into the native web. Because most visitors appear to be pollinators, this integration implies possible competitive and facilitative interactions between native and alien plants, mediated through animal visitors to flowers.

Keywords: connectance; food web; generalization; introduced species; pollination

1. INTRODUCTION

Most higher plants rely on animals to pollinate their flowers. The resulting plant–animal mutualism constitutes a critical 'free service' in all natural terrestrial ecosystems and in many agroecosystems (Costanza *et al.* 1997). Unfortunately this ecosystem service is under increasing pressure from human activities (Kearns *et al.* 1998).

Pollination systems face three major anthropogenic impacts. The first stems from changing land use, including fragmentation of natural habitats, which directly affects population biology of plants and animals and thereby their interactions, including pollination (e.g. Schulke & Waser 2001; Steffan-Dewenter *et al.* 2001). A second impact stems from elevated atmospheric carbon dioxide, which can alter flower production and longevity (e.g. Osborne *et al.* 1997; Rusterholz & Erhardt 1998), and which drives climate change that may disrupt the seasonal timing of flowering and of animal activity (e.g. Price & Waser 1998). The third major impact, on which we focus here, derives from the intentional and unintentional introduction of alien plants and pollinators into natural ecosystems.

Recent studies have begun to explore how native plant–pollinator interactions are affected by alien pollinators, in particular honeybees, *Apis mellifera*, and bumble-bees, *Bombus* spp. (e.g. Kwak 1987; Paton 1993; Dafni & Shmida 1996; Hingston & McQuillan 1998) and by alien plants (Brown & Mitchell 2001; Chittka & Schürkens 2001). To date, such studies have adopted a 'single species' approach, focusing on one or a few plant or animal species, and in some cases employing the powerful tool of experimentation. This approach is fundamental, but an important further step is to broaden the focus to the level of entire communities.

Here, we adopt this broader focus. We analyse data from a study published in the early twentieth century, which provides records of flower visitation for an entire North American plant–pollinator community, including several hundred plant species, a sizeable fraction of which are alien to the area. These records allowed us to construct a 'flower visitation web' akin to a food web, and to address the following questions: (i) are flowers of native and alien plants visited by equal numbers of animal species and is the number of visitors to an alien influenced by the taxonomic affinity of that plant to the native flora?; (ii) are similar percentages of visitors to native and alien plants classified as 'abundant' species and are they actually likely to pollinate the flowers?; (iii) are the visitors to flowers of native and alien plant species equally likely to have generalized floral diets?; (iv) what fraction of all animal species visits alien plants and do these animals visit aliens in proportion to their representation in the overall flora?; (v) does the connectance of the flower visitation web differ for native and alien plant communities?; and (vi) are alien flower visitors more or less generalized in floral diet than native insects?

2. METHODS

In a self-published monograph, Robertson (1929) listed 1429 animal species visiting flowers of 456 plant species that grew in a small area in southwestern Illinois, USA. Marlin & LaBerge (2001) describe Robertson's methods. Of the plants, 56 species were introduced aliens growing either in forest, prairie and other natural and semi-natural habitats, or as cultivars (and in a few cases crops) growing near human habitation. In addition, Robertson judged which visitors were pollinators, based on contact with sexual parts of flowers; and assessed a subset of visitors qualitatively as 'abundant' or 'rare'. He also provided first and last flowering dates for each plant species.

We transformed Robertson's list of flowers and visitors into a computerized database, including information on pollinator status, qualitative abundance and flowering phenology. It was then possible to construct a connectance web depicting which

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visitors were observed at which flowers, but lacking information on relative abundances of animals and flowers and relative frequencies of their interactions (for contrast see Memmott (1999)). We used non-parametric statistics to analyse attributes of plants, animals, and their interactions, as most data failed to conform to the assumptions of parametric tests.

3. RESULTS

(a) *The web*

The complete web consists of 15 265 unique interactions between 1429 flower-visiting animal species and 456 plant species. The visitors were insects with the exception of a single hummingbird, the ruby-throated, *Archilochus colubris* (Trochilidae). Six insect orders were observed: Hymenoptera (684 species, 8956 records), Diptera (466 species, 4165 records), Lepidoptera (97 species, 1397 records), Coleoptera (154 species, 576 records), Hemiptera (26 species, 134 records) and Neuroptera (one species, two records).

Fifty-six plant species, or 12.3% of all species, were weedy or cultivated aliens; their flowers were visited by 560 animal species, forming 1341 unique interactions. In comparison 400 plant species were natives, visited by 1381 animal species to form 13 924 unique interactions.

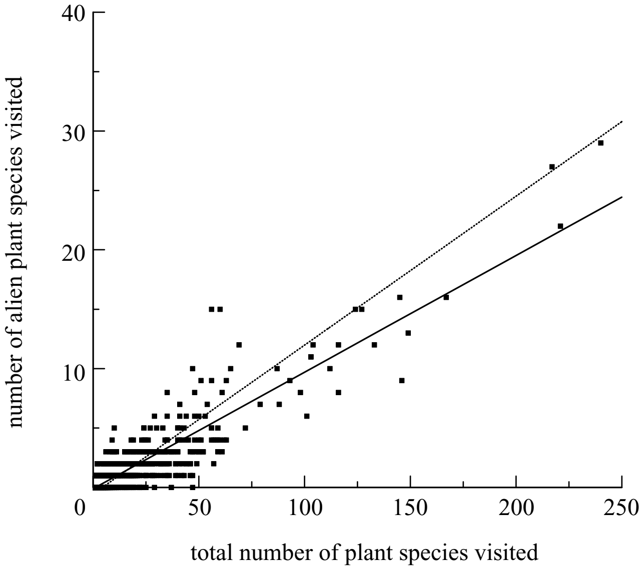

Figure 1. Relationship between total number of plant species included in the floral diet of an animal, and number of alien species visited. The solid line shows the actual relationship, with a slope of 0.098; the dotted line shows the predicted relationship if animals were to visit alien plants according to their proportional representation of 0.123 in the flora.

(b) *The plants' perspective: diversity and other aspects of visitors to flowers*

Flowers of native plants were visited on average by more animal species (mean = 34.0 visitor species per plant species, median = 18, range = 1–302) than flowers of alien plants (mean = 24.0, median = 10.5 range = 1–296; Mann–Whitney *U*-test = 8670, $p < 0.05$). This was true even though native plants had a flowering period on average only about half as long (mean = 59.9 days, median = 54) as that of alien plants (mean = 125.3, median = 126; $U = 2211$, $p < 0.005$), which would tend to expose natives to a smaller fraction of all potential flower visitors. The number of animal species visiting an alien plant species was positively related to the degree of taxonomic affinity of that species to the native flora. Thus, aliens which belong to plant families that contributed a large proportion of the native flora tended to have more visitors (Spearman's correlation coefficient between rank of family abundance in the flora and rank of visitor number = 0.538, d.f. = 55, $p < 0.005$). This relationship also held for native plants (Spearman's correlation coefficient = 0.232, d.f. = 399, $p < 0.01$). Similar percentages of all animal species visiting native plants (17.1%) and alien plants (14.1%) were classified by Robertson as being 'frequent' or 'abundant'. Moreover, there were no apparent differences in the percentages of all visitors which actually carried out pollination: Robertson recorded 81% of visitors to native plants as foraging legitimately for nectar or pollen and contacting sexual parts of flowers, in comparison to 79% of visitors to alien plants.

(c) *The flower visitors' perspective: aspects of floral diets*

The broader the floral diet of a given animal species, i.e. the more generalized its use of plant species, the more aliens it tended to include in the diet (figure 1). However, animals including alien plant species in their diets were not equally represented across the range of possible diet breadths depicted in figure 1. Instead, visitors to alien plants tended to have exceptionally broad diets: on average they were about fivefold more generalized (mean = 21.7 distinct plant species visited per animal species, median = 12, range = 1–240) than those never observed at aliens (mean = 3.6, median = 2, range = 1–47; $U = 79\,222$, $p < 0.0001$).

Overall, 39% of flower visitor species included alien plants in their floral diets. If these animals visited alien plants in proportion to their representation in the flora as a whole, then on average 12.3% of their visits (i.e. 56 out of 456) would have been to aliens. If so, the relationship between the total number of plant species visited and the number of alien plants visited (figure 1) would have had a slope of 0.123. The actual slope, however, is 0.098, significantly less than 0.123 ($t = 24.8$, d.f. = 1,428, $p < 0.0001$). From figure 1 it is apparent that three highly generalized flower visitors are outliers from the main distribution. To ensure that these species did not unduly influence the slope, the analysis was repeated without their data: the slope changed to 0.092, which remains significantly different from the predicted value of 0.123 ($t = 30.6$, d.f. = 1,426, $p = 0.0001$). Overall, 79% of all species of flower visitor had floral diets in which alien species were underrepresented.

Of the total of 1429 flower-visiting insect species, 420 were observed visiting only a single plant species. Of these, 44 (or 10.5%) were observed visiting only an alien plant species. Given that 12.3% of the flora is alien, this result indicates no special tendency for alien plants to attract fewer or more specialists than native plants. Moreover, it is likely that some of these insects recorded at a single plant species were recorded in very low numbers and their 'specialization' is due to small sample size rather than a genuine behaviour.

The six different groups of flower visitors were found to different degrees on flowers of alien plants. Thus 41.4% of Hymenoptera species, 33.8% of Diptera species, 53.6% of Lepidoptera species, 31.2% of Coleoptera species, 26.9% of Hemiptera species, plus the single hummingbird species (100%) and the single Neuroptera species (100%) were observed visiting alien plants.

(d) *Web connectance*

Food-web connectance of the whole community, i.e. the fraction of all possible plant–visitor links actually observed, was 0.0234, compared with 0.0252 and 0.0428, respectively, for native and alien plant subsets of the community. However, these values cannot be compared directly, because connectance declines in flower-visitation webs as the number of species increases (Jordano 1987). Therefore, we compared connectance for the 56 species of the alien plant community to connectance of random picks without replacement of 56 species from the entire community. Randomization was repeated 600 times to yield a mean connectance of 0.0509 (range = 0.0383–0.0666), which is 1.2-fold greater than the actual connectance of 0.0428 for alien plants (exact two-tailed probability from randomization test, $p = 0.023$). Thus fewer of the potential links between plants and flower visitors were realized in the alien plant subset of the community than on average in the native subset.

(e) *Alien flower visitors*

Only a few of the 1429 species of flower visitor were identifiable as being alien to the site in southwestern Illinois. These are the honeybee *A. mellifera* (Apidae, Hymenoptera), the cabbage white butterfly *Pieris rapae* (Papilionidae, Lepidoptera), the wasp *Vespula germanica* (Vespidae, Hymenoptera), the blowfly *Lucilia sericata* (Calliphoridae, Diptera) and the syrphid fly *Eristalis tenax* (Syrphidae, Diptera). *Apis mellifera* visited 217 plant species, 12.4% of which were alien, which closely approximates the percentage of aliens (12.3%) in the overall flora. *Pieris rapae* visited 60 plant species, 25% of which were alien. *Lucilia sericata* visited 25 plant species, 12% of which were alien. *Vespula germanica* visited 24 natives and no aliens. *Eristalis tenax* visited 35 plant species, 11% of which were alien. All of these insects were in the top 12% of the most generalized flower visitors, and *A. mellifera* surely qualifies as a 'super-generalist'.

4. DISCUSSION

The ancestral habitats of southwestern Illinois were prairie mixed with some riparian forest. By 1895–1916, when Charles Robertson collected data on pollination, and *ca.* 75 years after European colonization, the landscape was already substantially transformed into small farms, orchards and hedgerows (Marlin & LaBerge 2001), and as discussed here *ca.* 12% of insect-visited flowering plant species were aliens. Almost a century after Robertson's study, the same area appears to support a somewhat higher percentage of alien plants. The Illinois Plant Information Network (ILPIN) (Iverson *et al.* 1999) lists 129 aliens among 817 species recorded for Macoupin County, Illinois, or 15.8% (graminoids excluded). We cannot be certain that these two estimates represent similar sampling efforts across habitats, or that the comparison of a larger area sampled in the ILPIN data compared with Robertson (note the larger total number of plants) introduces no bias. But the simplest interpretation is that Robertson's data represent an interim point in biotic transition towards increasing representation of aliens.

Our analysis provides insights into the position of alien plants, and their possible impact on natives, at this interim point. The insights are unique to date in representing an extensive plant–flower visitor web, which samples all species and interactions rather than a chosen subset (e.g. only common species or interactions). These virtues counterbalance deficiencies inherent in the historical data source, prime among them a lack of quantitative information on relative abundances of plants, animals and their interactions, and the lumping by Robertson of records across habitats and years of study.

What does this analysis indicate about the role of pollination in the integration of alien plants into native communities, and about the effect of the aliens on native plants and pollinators? In what follows we focus on these two topics, which seem especially timely given increasing invasion of plants, and anthropogenic threats to pollination interactions (Kearns *et al.* 1998).

(a) *The role of pollination in the integration of alien plants*

The 56 alien plants present in 1895–1916 could not rely on their ancestral pollinators. Indeed, honeybees and the few other alien insects recorded by Robertson may have formed part of the ancestral visitor fauna to some of the alien plants. But the alien plant species greatly outnumber these alien insects, making it unlikely that these were the sole ancestral pollinators. In fact these alien plants probably represent the common condition: they apparently have persisted by attracting native pollinators. In general, alien plants are well served by generalist pollinators and pollinator limitation does not appear to be a major barrier to the spread of introduced plants (Richardson *et al.* 2000). This interpretation requires that many plants are generalized in their use of pollinators. Evidence for generalization and opportunism in plant–pollinator interactions is widespread (e.g. Waser *et al.* 1996; Memmott 1999). In the community analysed here, over one-third of native flower visitors included alien plant species in their floral diets. The use of aliens did vary across the five insect orders, perhaps reflecting ordinal-level differences in degree of generalization and opportunism; the use of aliens by hummingbirds, which often are generalists, is in keeping with this. Indeed, visitors to aliens tended to include the most generalized of flower visitors, so that overall the visitors to alien plants averaged much broader floral diets than visitors to native plants. This was true even though some native insects were observed only on aliens, and the fraction of such floral specialists on aliens was in proportion to the fractional representation of the alien plants in the entire flora. Furthermore, the alien plants attracted visitors that were abundant, and that were of use to them in pollinating flowers, about as frequently as did native plants.

Not all is roses for alien plants, however. Our analysis shows on average that they attracted fewer species of flower visitors than natives. In fact, aliens might have been

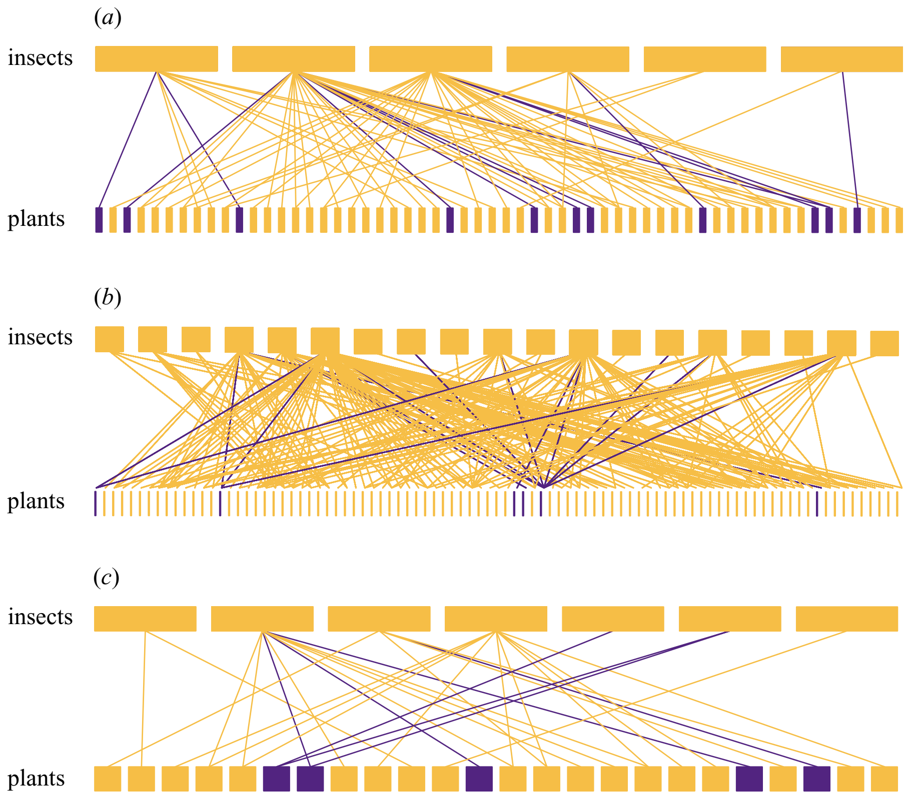

Figure 2. Three portions of the overall plant–flower visitor web, showing those interactions involving: (*a*) Anthophoridae (*sensu stricto*, Hymenoptera); (*b*) Sarcophagidae (Diptera); and (*c*) Sphingidae (Lepidoptera). Alien plant species and their interactions are shown in blue, and natives in yellow. Species names are omitted because they would be too small to be legible in some cases, and are not essential to visualize the integration of alien plants into the native web.

expected to have far more visitors than natives, because they flowered for twice as long on average. But an alternative interpretation, with different implications, is that successful aliens were those that fortuitously possessed a long flowering season, which allowed them to winnow out a sufficient number of native visitors to ensure adequate pollination and seedling recruitment. Those alien plants with taxonomic affinity to natives fared best, perhaps because their floral phenotypes resembled those of natives, and insects visiting the natives also included the related aliens. Native insects that visited alien plants also tended to include fewer alien species in their diets than predicted, based on the proportional representation of aliens in the flora. One possible explanation is that many of the alien plants were rare, which might lead many flower-visiting insects to ignore them.

In short, the attraction of native insects by alien plants is not absolutely equivalent to attraction by native plants. Indeed, the connectance of the part of the web including aliens was significantly lower than that for the web as a whole. Thus, a smaller proportion of potential interactions between plants and pollinators is realized for the alien web, in comparison to the native web. The visitors to alien plants were unusually generalized, but these generalists did not connect aliens as richly as they apparently did the native plants. One explanation is that most alien species had more limited habitat distributions than natives, and so experienced fewer connections with other aliens than did natives with natives. A second explanation is that alien plants were not a random sub-sample of the plants in the complete web. To investigate this, we assigned a life form to each plant (annual, annual–biennial or perennial) and asked whether these classes comprised equal proportions in the alien and the native web. Our analysis revealed that annuals accounted for a much greater proportion of the alien web (29% versus 13%).

To determine whether this bias towards annuals was leading to a lower connectance value in the alien web, we repeated our randomization tests, comparing the connectance of the 16 species of the alien annual community, to that of random picks, without replacement, of 16 species from the entire 67 species of the annual community. Randomization was repeated 600 times, yielding a mean connectance of 0.0941 (range = 0.0757–0.1188), which is not significantly different from the actual connectance of 0.951 for the alien annual plants (exact two-tailed probability from randomization test, $p = 0.57$). Thus, the higher number of annual plants in the alien web appears to be one of the reasons why the alien web is less well connected than the native web. However, it remains unclear whether annuals produce fewer rewards in their flowers or whether some other attribute such as habitat distribution is causing this result.

(b) *The effect of the aliens on native plants and pollinators*

Although alien plants and natives do not appear identical in flower visitation, the aliens were well integrated into the native web of flower visitors less than 100 years after European colonization. There was no evidence that aliens formed a distinct compartment or subweb within the overall web (compare with the evidence for compartments in

Dicks *et al.* (2002)). Although it is not feasible to depict the entire web of 15 265 individual links graphically, figure 2 provides a visual impression of the integration of alien plants by three representative insect families.

The integration of alien plants into the native web implies the possibility of interaction with native plants mediated through the services of animal visitors, including floral larcenists (*sensu* Irwin *et al.* 2001) and pollinators. Many of the interactions may be competitive, in which aliens harm pollination of natives or increase larceny to them (Free 1968; Waser 1983; Chittka & Schürkens 2001; Irwin *et al.* 2001). Other interactions could be mutually beneficial. Aliens and natives flowering concurrently sometimes facilitate each others' attraction of pollinators (Rathcke 1983), whereas those flowering in different seasons may indirectly act as mutualists by jointly maintaining pollinator populations at high levels (Waser & Real 1979). Dandelion, *Taraxacum officinale* Agg., is one example of an alien plant in many areas which sometimes 'feeds' insects such as bees that are critical pollinators of natives at other times in the season (Petanidou & Ellis 1996). Continued exploration of such competitive and facilitative interactions between alien plant species and natives is an important goal for the future.

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