

Invasive plants as novel food resources, the pollinators' perspective

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Biological invasions are one of the main drivers of global change and have negatively impacted all biomes and trophic levels (Hobbs 2000, Vilà et al. 2011). While most introduced species fail to establish, or establish small naturalized populations (hereafter exotic species), a few become invasive and rapidly increase in abundance and/or range (hereafter invasives or invaders; Pysek et al. 2004). It is these invader species that are most often linked to negative impacts on native / endemic communities. Although most interactions between invasive and native species at the same trophic level result in negative direct impacts (e.g. plant-plant competitive interactions, Vilà et al. 2011), when the invasive plant species can be used as a resource those interactions can also be positive for consumers such as native herbivores, predators or mutualists, at least for some species (Heleno et al. 2009, Bezemer et al. 2004). Entomophilous exotic plant species, for example, not only compete directly for space and light with other plants, but also offer resource opportunities for the native pollinator community (Stouffer et al. 2014). Most research on this topic to date has taken the plant perspective, focusing on how successful plant invaders integrate into the native plant-pollinator interaction networks (Vilà et al. 2009), and how this integration in turn impacts the native plant community (Morales and Traveset 2009). However, species specific responses of pollinators to the addition of exotic plants are rarely taken into account. This represent an important gap in our knowledge as pollinator foraging choices determine the structure of interactions within communities, which in turn have important implications for the community stability (Thébault and Fontain 2010) and functioning (Thomson et al. 2012). How different pollinators respond to the changed composition of floral species within the community that results from exotic plant invaders deserves more attention.

From the pollinators' point of view, exotic plants are novel food resources, and as such their relative abundance, attractiveness, rewards (i.e. nutritional value) and distinctiveness partly

38 determine their use by various pollinators (Carvalho et al. 2014). Although exotics as a
group are not preferred or avoided within their new communities (Williams et al. 2010), it
40 might be that particular exotic species are preferred by some pollinators while avoided by
others. The intrinsic preferences for different plant hosts is an important factor determining
42 host use. Hence, the direct benefits or costs of a novel resource use will differ among
pollinator species. Moreover, in a community context, the preferences of each pollinator
44 affect the other pollinators' choices, potentially leading to indirect effects. For example, some
pollinator species may obtain indirect benefits if the invasive plants distract other pollinators
46 from natives, reducing competition. Alternatively, pollinators may pay indirect costs if
competition is increased or if invasive plants reduce the availability of a preferred native
48 plant.

50 We review the evidence on direct and indirect benefits and costs of invasive plants on
pollinators and re-analyze Williams et al. (2010) dataset on pollinator specific preferences so
52 as to identify species that prefer some exotic plants over native plants and vice-versa. This
information is crucial to understanding the consequence for the pollinator community
54 because if only some pollinators take advantage of alien plants this can favour populations of
some pollinator species (winners) over others (losers). By using an approach that takes into
56 account both pollinator behavioral responses and interaction network structure, we can better
understand the invasion process, with important implications for conservation actions.

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Effects of plant invasions on pollinator populations and community structure.

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The impact of invasive plants interacting with native pollinators has received considerable
62 attention for its potential to disrupt native mutualisms (Traveset and Richardson 2006).
However, most work to date has focused solely on how invasive plant interactions with
64 native pollinators changes the pollination success of native plants. Interestingly, existing data
show that invasive plants can have positive, neutral, or negative effects on pollination of
66 native plants (Bjerknes et al. 2007). The contrasting results may reflect invasive plant density
(Muñoz and Cavieres 2008, Dietzsch et al. 2011), spatial aggregation (Cariveau and Norton
68 2009) or flower morphology and attractiveness (Morales and Traveset 2009, Carvalho et
al. 2014).

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In contrast, the effects of exotic or invasive species on the pollinator populations and
72 communities have received far less attention (Stout and Morales 2008). Because most plant-
pollinator systems are generalized (Waser et al. 1996), invasive plants are usually well
74 integrated in the plant–pollinator network of interactions (Vilà et al 2009). Hence, we might
expect overall effects on pollinators to mirror the changes (positive or negative) in floral
76 resources offered by the newly invaded community. If the entomophilous exotic or invasive
plants increase the resources present in the community, this should also allow the increase of
78 most pollinator populations (Tepedino et al. 2008). Stout and Morales (2008) cite indirect
evidence that some social pollinators (e.g., bumblebees) can be favoured by non-native mass
80 flowering crops (Westphal et al. 2003, Herrmann et al. 2007), which may be analogous to the
effect of abundant invasive species. However, the same authors note examples where exotic
82 plants are not used by native pollinators due to flower morphology or chemistry. Despite
Stout and Morales' (2008) call for more research on this topic, few additional studies have
84 been published since then.

86 Current evidence suggests that food resource availability may indeed regulate pollinator's
populations, at least those of bees (reviewed in, Roulston and Goodell 2011, Williams and
88 Kremen 2007, Crone 2013, but see Steffan-Dewenter and Schiele 2008 for potential
regulation by nesting resources). However, studies of the effect of exotic plants on
90 pollinators' population dynamics are extremely rare, particularly for non-invasive exotic
plants that establish small populations. Palladini and Maron (2014) provide one of the few
92 examples of effects of exotic plants (mainly *Euphorbia esula*) on the reproduction of a
solitary bee species (*Osmia lignaria*). For this species, the number of nests established and
94 offspring production per female was positively related to native plant abundance and
negatively related to exotic plant species. This may be because although *Osmia lignaria*
96 foraged on exotics for nectar, the species did not use *Euphorbia esula* exotic pollen to
provision nests. Thus, the specific ability to use the invader resources emerges as a key factor
98 affecting the potential impacts of the invader on pollinators. The only other evidence to date
for direct effects of invasive plants through resource augmentation is for bumblebees, whose
100 annual social life history allows demographic responses to be measured within a single
season. Within-season abundance can increase almost four times in sites invaded by the plant
102 *Lupinus polyphyllus*, compared to in non-invaded sites (Jakobsson and Padrón 2014). In
addition, the foraging season of *Bombus terrestris* in the United Kingdom can be extended

104 into winter through its use of exotic plants that fill a late season phenological niche (Stelzer et
al. 2010). Such within-season demographic responses are likely to have longer-term
106 population effects, although no study has quantified such effect to date.

108 A second group of studies provides indirect evidence that exotic plants affect
pollinators' by using community approaches to compare invaded with non-invaded sites.
110 These studies show a variety of pollinator responses, including increased abundance and
species richness in invaded sites (Lopezaraiza-mikel et al. 2007), lower abundance and
112 diversity of pollinators in invaded areas (Moron et al. 2009), or no difference in abundance
between invaded and non-invaded sites (Nienhuis et al. 2009). It is therefore not surprising
114 that a recent meta-analysis reported no changes in overall pollinator abundance in invaded
sites (Montero-castaño and Vilà 2012). However, the studies included in the meta-analysis
116 were not designed to infer population changes, and the result should be interpreted with
caution. Moreover, most of the examples concern abundant invasive plants. Plant abundance
118 can strongly influence pollinators decision to incorporate a new plant into its diet
(Valdovinos et al. 2010), and thus the results may differ when examining non-invasive exotic
120 plants. Likewise, given the wide array of pollinators ranging from birds and bats to bees and
hoverflies, it is unlikely to find a consistent overall response.

122

The importance of behaviour

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While exotic plants can represent new resource opportunities for native animals, evidence
126 suggests that only a minority of pollinator species can take advantage of these new
opportunities. For example, generalist bees more commonly forage on invasive exotic plants
128 than specialists (Lopezaraiza-Mikel et al., 2007; Tepedino et al., 2008; Padrón et al. 2009), or
that social bumblebees are more common in invaded sites than solitary bees (Nienhuis et al.
130 2009). Bartomeus et al. (2009), for example, report that bees were more often recorded on
native species than on the invader *Carpobrotus* aff. *acinaciformis*, except for the social
132 bumblebee *Bombus terrestris* and for most beetles, which visited *Carpobrotus* flowers almost
exclusively. Hence, pollinators can discriminate between native and exotic plants, and the
134 decision of exploiting one or another can vary across species. Analyzing the invasion process
as a novel resource availability for pollinators may give us a framework to predict which
136 pollinators can benefit from the invasion process.

138 Incorporating any novel resource into the diet requires a series of conditions to be met. First,
the pollinator must recognize the novel resource as a host, second, the visitor must be able to
140 use this new resource and third, the resource must be profitable (i.e., a net benefit) for the
visitor to exploit it. Hence, exotic plant use depends on intrinsic traits of the plant and
142 pollinator. We cannot assume that for native pollinators exotic flowering species are always
fundamentally different than the native flowering species; nevertheless, plants presenting new
144 colors, shapes or chemical compounds may not be easily used by all pollinators in the
community (Stout and Morales 2008). Furthermore many pollinators have innate preferences
146 for certain colors and/or shapes (Gumbert 2000, Riffell et al. 2008), which may make novel
flowers less attractive than the natives which have coevolved in the community. Neophobic
148 responses also may make some pollinators unlikely to approach and explore novel food
opportunities (Forrest and Thomson 2009). However, some pollinators may learn how to
150 exploit new resources if their behaviour is flexible enough (Chittka et al. 2009, Forrest and
Thomson 2009). In particular, bees, which are the main pollinator group both in numbers and
152 in effectiveness (reviewed in Winfree et al. 2011), have a powerful neuronal system able to
learn new tasks (Chittka et al. 2009) and their behavior flexibility has been suggested to be
154 linked to their ability to persist in disturbed environments (Kevan and Menzel 2012).
However the role of learning abilities in incorporating new foraging plants is little explored
156 (Dukas and Real 1993) and most information comes from a handful of species (mostly
social).

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Even if the exotic plant is recognized as a potential host, pollinators might not be able to
160 exploit the new plant species if they are unable to handle its flowers (Parker 1997, Corbet et
al. 2001), or to digest its nectar (Adler and Irwin, 2005) or pollen (Sedivy et al. 2011,
162 Palladini and Maron 2014). Morphological matching between flowers and pollinators may
thus be important in determining pollinator visitation patterns (Gibson et al. 2012, Bartomeus
164 2013, Stang et al. 2009, see also Pearse et al. 2014 for antagonist insect-plant interactions).
Second, even in the cases where pollinators recognize and can use the novel resource, their
166 decision to include it in its diet will depend on its quality and abundance relative to others in
the community. The thresholds for switching to a resource based on its quality or abundance
168 have been show to be variable among different species in birds (Carnicer et al. 2008). Insect
pollinators switch between foraging plants depending on the resource availability (Inouye

170 1978, Chittka et al 1997). Like for birds, thresholds for switching are likely to be different for
different species, however, the experimental evidence that insect pollinators can discriminate
172 between different resources and learn to forage on the preferred one is limited to a handful of
bee species, and the switching strategies among species is mostly unknown.

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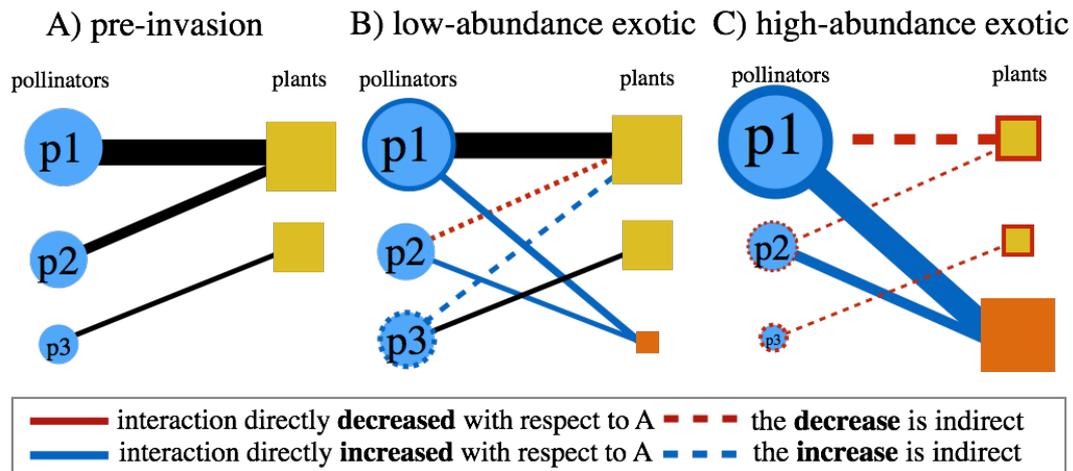
176 **The importance of the community context.**

Pollinator-plant interactions do not occur in isolation, but form part of a complex network of
178 interactions (Bascompte and Jordano 2007). For example, competitive exclusion between
pollinator species can drive foraging behavior patterns (Jhonson and Hubell 1995). Invasive
180 plant species can modify the native network structure not only by creating new interactions
with native pollinators but also by modifying the existing plant-pollinator interactions among
182 the native species (Bartomeus et al. 2008, Albrecht et al. 2014). Such changes are especially
likely when invaders are abundant and provide accessible resources (i.e. nectar and pollen),
184 thus potentially interacting with a large proportion of the resident pollinator species (Albrecht
et al. 2014). In any case, modifications to pairwise interactions can have cascading effects
186 throughout the community. For example, dynamic pollination network models have been
used to show that removal of well-established invasive plants negatively affected the
188 persistence of pollinator interactions through the network (Valdovinos et al. 2009,
Carvalho et al. 2008). Detailed empirical studies, also show that co-flowering neighboring
190 invasive species affect pollinator choices (Cariveau and Norton 2009, Waters et al. 2014).

192 The behavioural switching (also called interaction rewiring) between resources has been
recently studied at the community level using network theory. There is increased evidence
194 that pollinators can rewire their community-wide interactions depending on the context
(Kaiser-Bunbury et al. 2010), such as the addition of a plant invasion. Jakobson and Padrón
196 (2014) speculate that the attraction of bumblebees to the invasive plant *Lupinus polyphyllus*,
reduced competition for the native plants, allowing an increase of solitary bee visits to
198 natives. Similarly, Montero-Castaño (2014) showed that monopolization of the invasive
species *Hedysarum coronarium* by honeybees allowed other bee species to establish
200 interactions with natives that are not realized when the honeybee is present. Context
dependent rewiring is supported by findings that despite for consistent species-specific
202 preferences for certain flowers across communities, there is also important variation and
flexibility in preferences among different contexts (Fründ et al. 2010). Hence, both direct

204 effects and indirect effects on pollinators are expected after a plant invasion, and those can
 only be understood in a community-wide framework.

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208 Figure 1. Simplified plant-pollinator networks before the invasion process (A) in two
 distinctive scenarios: (B) The exotic plant (orange square) adds a novel resource without
 210 affecting the rest of the community, and (C) a superabundant invasive plant (orange square)
 adds an abundant novel resource, while reducing native plants resource availability. In the
 212 schemes we can see the interactions established in each case (lines connecting pollinators and
 plants). The color of links depicts whether their frequency is increased (blue) or decreased
 214 (red) with respect to A. The changes in size of the plants or pollinators depict the winners
 (blue border) and losers (red border) of the invasion process. When the effect is indirect is
 216 noted with dashed lines. See text for further explanation.

218 In Figure 1, we illustrate a simplified plant-pollinator network with two distinctive scenarios.
 In the first one (Fig. 1.B), we add an entomophilous exotic plant that does not reduce the
 220 abundances of other plants. Pollinator species able to use this plant (identified as p1 and p2)
 will establish new links with this exotic plant (blue links). Species p1 will have more food
 222 resources and can potentially increase its population over time (bigger blue circle denotes
 population size increase) whereas species p2 will experience a neutral effect because it
 224 changes from foraging on natives to foraging on the exotic. These are the direct (often neutral
 or positive) effects of the exotic plant on pollinators. Other pollinators may not be able or
 226 may not choose to visit the new invasive plant (p3), but as the competition for their preferred
 resources is changed, they may receive indirect benefits (p3). Experiments removing
 228 dominant pollinators have shown that a relaxed competition for resources may lead to diet

expansion of some species (Brosi et al 2013), supporting our example with species p3.

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In the second scenario (Fig 1. C), the exotic plant is an abundant invader that also reduces

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native plant abundance by direct competition (e.g. for space). In this scenario, only a few

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pollinators (p1) may benefit, while all others will experience increased competition for resources (p2, p3). This is an oversimplification, and of course the net benefit for pollinators

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will depend not only on the number of visits, but on the quality of those visits (e.g. reward

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uptake, nutritional content of the exotic species, etc.). Moreover, some species will require a variety of pollen sources to complete larvae development (Roulston and Cane 2000)

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highlighting the importance of maintaining plant diversity. The magnitude of the indirect and direct effects will depend also on the time-scale at which it is evaluated, with functional

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responses and local switching occurring faster than numerical responses (i.e. population growth). Moreover, the relative phenological timing of plants and bees can modify their

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mutual influence. All in all, the net costs and benefits are likely to depend on many factors,

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but this framework supports the scarce information presented above, where some social

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generalized species tend to increase their abundance after invasion by highly attractive species, but other pollinators have mixed responses.

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Case study: bee preferences in California

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Can we predict which pollinators will be winners or losers of the invasion process?

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Measuring population responses or fecundity is a daunting task, especially at the community level; however, we can gain indirect evidence by looking at pollinator preferences. Within a

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plant community, pollinators do not prefer exotic plants as a group (Williams et al. 2010) or even prefer natives (Chrobock et al. 2013), but individual pollinator preferences have not

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been explored yet. Preference is defined as using a resource more than expected given its abundance. Conversely, avoidance occurs when a resource is underused relative to its

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abundance. The null model of no preferences is the case when pollinators visit flowers in proportion to their abundance in the community. Deviations from this null model can help us

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identify pollinator species that prefer exotic species (hence receiving a potential direct benefit) and species that avoid the exotics (hence, receiving negative, neutral or positive

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indirect effects in some cases). We recognize that we cannot infer direct fitness

consequences, or predict indirect effects from a static network. Ours, nonetheless, is the first

262 attempt to identify direct effects and serve as a proxy for identifying pollinator winners after
the invasion process. Most importantly, this way we can emphasize that pollinators differ in
264 their behavior, acknowledging that the effects on specific pollinators cannot be generalized.
Furthermore, in the future, we can explore what determines pollinator preferences. Are they
266 driven by plant traits, such as abundance or morphology, by pollinator traits, or a
combination of both?

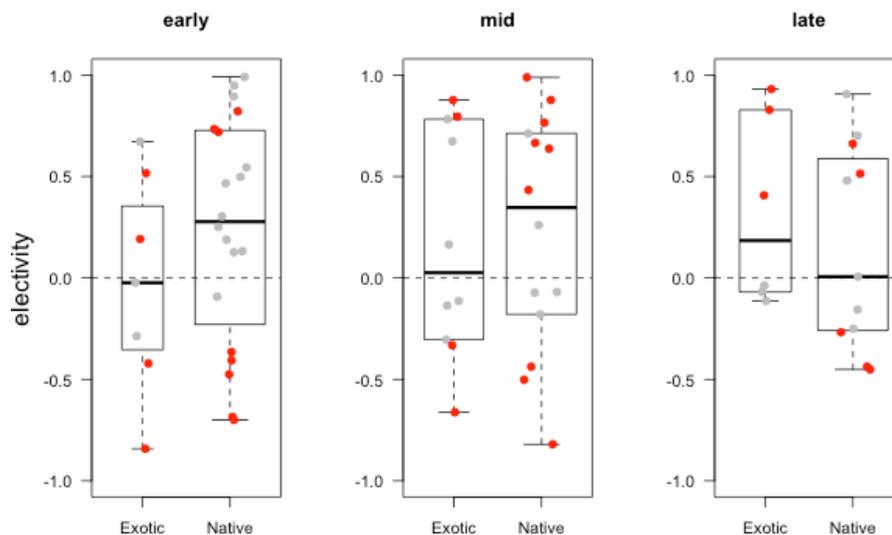
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To explore this preference-based proxy, we used the same dataset used in Williams et al.
270 (2010). For simplicity we show here only 7 sites from semi-natural habitats in California.
This system is especially suitable to test our questions, because it contains several exotic
272 plants, ranging from abundant invaders to naturalized exotic plants, as well as a variety of
pollinator species. We calculated preferences pooling all sites, but we separate our analysis in
274 three sampling periods (early, mid and late season). We treated periods separately because
plant turnover was substantial over the season and otherwise might have masked the
276 preference relationships.

278 First we re-evaluated that pollinators do not prefer exotic plants as a group within a
quantitative framework, where expected (E) visitation values are calculated based on plant
280 mean abundance across sites, and observed (O) visitation values are the sums of pollinator
visitation to each plant across sites. Chi statistics were used for each of the three tests (i.e. one
282 per season) to assess if there is an overall preference. The Pearson residuals of the Chi tests
($(O-E)/\sqrt{E}$) estimate the magnitude of preference or avoidance for a given plant based on
284 deviation from expected values and its significance was assessed by building Bonferroni
confidence intervals (see Neu et al. 1974 and Byers and Steinhorst 1984). In order to test for
286 differences between exotics and natives we compared the *Electivity* values of exotic and
native plants using linear models. *Electivity* values ($(E'-O')/E'+O'$, where E' and O' are the
288 proportional expected and observed values, Ivlev 1964) are bound between -1 and +1, easier
to interpret and highly correlated with Pearson residuals. R code to calculate these indexes
290 can be found at (<https://gist.github.com/ibartomeus/cdddca21d5dbff26a25e>).

292 We show that when pooling visits for all pollinator species, some plants are preferred over
others (Chi square test p-values for early, mid and late seasons < 0.001; *Electivity* values
294 range from -0.84 to 0.82 indicating we find both over-preferred plants and under-preferred

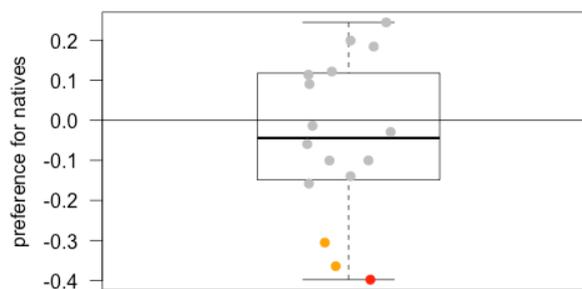
plants; Fig. 2). In accordance with the results reported in Williams et al. (2010), pooled
296 pollinators showed no preferences for exotic plants in any season (Fig. 2; early season: $F_{1,25} =$
1.29, p-value: 0.27; mid season: $F_{1,22} = 0.06$, p-value: 0.81; late season: $F_{1,15} = 0.46$, p-value:
298 0.51), but this general trend does not contradict the fact that specific native or exotic plants
are indeed preferred (in red in Fig. 2).
300



302 Figure 2: Boxplots of the *electivity* indices per plant species separated by plant origin (exotic,
native) and season (early, mid, late). Each plant value is plotted in the background in grey
304 when preference is not significant and in red when significant (significance based on Chi
square Pearson residuals test). Positive values indicate plants that are preferred and negative
306 values those that are avoided.

308 Second, we shift the focus of our analysis to analyze pollinator species-specific preferences.
We excluded pollinator species with less than 20 visits recorded per season in order to
310 prevent confounding rarity with specialization (Blüthgen 2010). We end up with 16 pollinator
species, some of them present in several seasons, making 22 pollinator-season combinations.
312 Again, each of the 22 pollinator-season combination was evaluated using Chi square tests and
electivity values were compared between exotic and native plants for each pollinator species
314 using mixed models with season as random effect. All pollinators showed significant
preferences for certain plant species (chi square p-values < 0.05). When analyzed individually
316 most pollinators do not show a consistent preference for exotic or native plants, with the
exception of three species (Fig. 3; all species p-values > 0.1, except *Bombus melanopygus* =

318 0.05, *Dialictus incompletum* = 0.07 and *Halictus ligatus* = 0.03), all of them preferring
exotics over natives. However, some pollinators of the 16 analyzed do prefer only one or
320 more native plants (4 species: *Evyllaesus sp*, *Osmia nemoris*, *Ceratina arizonensis*, *Calliopsis*
fracta), others prefer only one or more exotic plants (7 species: *Synhalonia actuosa*,
322 *Synhalonia frater*, *Bombus vosnesenskii*, *Halictus ligatus*, *Halictus tripartitus*, *Megachile*
apicalis, *Bombus californicus*) and some prefer a mix of exotic and natives (4 species:
324 *Bombus melanopygus*, *Ashmeadiella aridula*, *Dialictus incompletum*, *Dialictus*
tegulariforme). The differential preferences regarding the exotic status create the basis for
326 expecting winners and losers after an invasion process (see Fig. 1).



328 Figure 3. Boxplot of the effect sizes (i.e. model estimates) indicating the difference between
electivity to exotics and to natives for each pollinator species. Positive values indicate overall
330 preferences for natives, and negative values to exotics. Data points for each pollinator species
are indicated in grey when not significant, in orange when $p < 0.1$ and in red when $p < 0.05$.

332

In conclusion, although the overall pattern is no preference for exotic plants, some particular
334 exotic (and native) plants are overall preferred. Similarly, most pollinators do not have
overall preferences for exotics, but a few species do favor them. Those are social species,
336 usually common and sometimes even considered species typical of disturbed areas (e.g.
Halictus ligatus, *Dialictus incompletum*). Interestingly, even within the species with no
338 overall preference for exotics, we identify pollinators that prefer particular exotic plants.
These pollinators are more likely to be positively affected by the invasion process, the others
340 negatively affected, as their preferred resources will potentially diminish through
displacement by invasive plant species.

342

Relevance for conservation

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We highlighted that pollinator species vary in response to plant invasions, including
346 pollinators use, preference, and in some cases population dynamic consequences. Assessing
the winners and losers in front of the rapid rate of invasive species introductions is crucial for
348 understanding the responses of species groups performing important ecosystem functions,
like pollination (Ollerton et al. 2011, Klein et al. 2007). There has been a recent awareness of
350 pollinator declines globally (Potts et al. 2010, Gonzalez-Varo et al. 2013). However,
biological invasions, especially by plant species, have received little attention as a threat (but
352 see Stout and Morales 2008, and Morales et al. 2013 for effects of animal invasions). We
already know that not all pollinators are equally affected by global change, a few are winners
354 and many are losers (Bartomeus et al. 2013). Interestingly, among the winner pollinators we
found species that are able to use flowering crops and tolerate new human-modified habitats
356 (Bartomeus and Winfree 2013). Gaining information about which species are able also to
exploit new exotic plants will be a way forward to understand which species will be flexible
358 enough to survive in novel ecosystems, often dominated by exotic plants. In a changing
world, species able to adapt their foraging strategies to use new resources may be the better
360 suited to survive. For example, bumble bees that use the widespread plant invader *I.*
glandulifera in the EU are thriving, while endangered bumble bee species do not use it
362 (Kleijn and Raemaker 2008).

364 If we are going to manage emerging novel ecosystems, we need to incorporate pollinator
specific responses to different global change drivers, including plant invasions. Some bumble
366 bees and other trophic generalist bees can benefit from exotic plant invasions, as shown by
the fact that those can use and even prefer to forage on new exotic plants. This behavioral
368 flexibility may be the key to persisting in a changing world, and maintaining an important
ecosystem function. More research is needed on the degree that plant invasions negatively
370 affect those species in comparison with other disturbances that are occurring simultaneously.
We need to implement better population monitoring programs at the community level (so
372 indirect responses can be accounted for), but overall, understanding better which role play the
pollinator behavior flexibility and cognitive capabilities in the process of adapting to novel
374 environments is a promising line of research.

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