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LETTER

The potential for indirect effects between co-flowering plants via shared pollinators depends on resource abundance, accessibility and relatedness

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Abstract
Co-flowering plant species commonly share flower visitors, and thus have the potential to influence each other's pollination. In this study we analysed 750 quantitative plant–pollinator networks from 28 studies representing diverse biomes worldwide. We show that the potential for one plant species to influence another indirectly via shared pollinators was greater for plants whose resources were more abundant (higher floral unit number and nectar sugar content) and more accessible. The potential indirect influence was also stronger between phylogenetically closer plant species and was independent of plant geographic origin (native vs. non-native). The positive effect of nectar sugar content and phylogenetic proximity was much more accentuated for bees than for other groups. Consequently, the impact of these factors depends on the pollination mode of plants, e.g. bee or fly pollinated. Our findings may help predict which plant species have the greatest importance in the functioning of plant–pollination networks.

Keywords
Facilitation, floral traits, flower density, flower resources, indirect interactions, interspecific competition, morphological similarity, nectar, phylogenetic distance, plant–pollinator networks.

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INTRODUCTION

The impacts of loss or gain of particular species on the patterns of interaction networks shape community structure, functioning and stability (e.g. Rezende *et al.* 2007; Aizen *et al.* 2012; Lever *et al.* 2014). Within the same trophic level, species sharing more interaction partners may be more likely to influence each other through indirect effects (e.g. Morris *et al.*

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2004). Whether two species from different trophic levels interact or not may depend on temporal, morphological or chemical matching rules (e.g. Gibson *et al.* 2012; Eklöf *et al.* 2013; Rosas-Guerrero *et al.* 2014). It is, however, unclear whether such matching rules are consistent across different communities. Moreover, the potential for one species to indirectly influence another species from the same trophic level via shared interaction partners will depend not only on the presence, but also on the strength (i.e. frequency) of each interaction link (e.g. Müller *et al.* 1999; Morris *et al.* 2004).

For plant–pollinator networks, the potential for an indirect influence between co-flowering plant species may lead to facilitation, whereby the presence of one plant species increases the visitation of effective pollinators and conspecific pollen deposition for another, or to competition, whereby the presence of one plant species attracts effective pollinators away from another (Mitchell *et al.* 2009; Morales & Traveset 2009). A particular plant species may even facilitate pollination for some species whilst competing with others (e.g. Vilà *et al.* 2009). As visitation rate is often positively associated with fruit set (e.g. Vazquéz *et al.* 2005; Garibaldi *et al.* 2013), such alteration of influence strengths can have important short-term effect on plants' seed set and consequently long-term effects on plant population dynamics. However, management actions altering plant communities (e.g. removal of non-native plants for conservation purposes, Carvalheiro *et al.* 2008; or addition of floral resources to boost pollination services, Nicholls & Altieri 2013) are commonly applied without considering the potential effects on the remaining plants. Understanding which plant species characteristics define interaction patterns can help identify influential plant species for the whole community or for a particular species (e.g. an endangered species).

Using data from 750 quantitative plant–pollinator networks gathered from 28 studies in diverse biomes we identify how plant characteristics such as flower traits and resource abundance affect the ability of one plant species to influence (positively or negatively) the pollination of another, via shared pollinators.

Floral displays vary in shape, size, colour, height and scent, and can act as attraction signals or barriers for flower visitors (e.g. Campbell *et al.* 2012; Gibson *et al.* 2012; Junker *et al.* 2013). While convergent evolution can lead to trait similarity among co-flowering species (Rosas-Guerrero *et al.* 2014), in the absence of such selection pressure trait dissimilarity will tend to increase with time since divergence (Danieli-Silva *et al.* 2012). Thus, phylogenetic distance may be a proxy of similarity of certain floral traits. Therefore, we expect plant species' ability to influence another via shared pollinators to increase with greater similarity in flower traits, and to decline with increased phylogenetic distance (hypothesis 1).

Plants offering more resources are likely to be visited by more pollinators (e.g. Kunin 1997; Cartar 2009; Bartomeus 2013). We therefore expect greater resource availability (flower abundance or floral resource quality) of a plant species to result in greater influence on the pollination of co-flowering plant species (hypothesis 2).

Differences in floral resource accessibility between species may also play an important role on visitation patterns (e.g. Stang *et al.* 2006; Campbell *et al.* 2012). For plants with nec-

tar tubes, nectar accessibility may depend on the length of these, such that visitation of certain pollinator species are constrained if these are long (Stang *et al.* 2006; Campbell *et al.* 2012). Moreover, if the nectar available within a floral unit is distributed among several small flowers rather than concentrated in a single flower (i.e. higher nectar splitting; e.g. *Cirsium acaule*, Asteraceae vs. *Impatiens glandulifera*, Balsaminaceae), it could be energetically more expensive to harvest. We therefore expect more accessible flowers (short tubes with little nectar splitting within a floral unit) to have a higher influence on other plants via shared pollinators (hypothesis 3).

Finally, although some studies suggest that non-native flowers may have disproportionate effects on visitation patterns to co-flowering plants (e.g. Lopezaraiza-Mikel *et al.* 2007; Morales & Traveset 2009), they often focus on abundant non-native plants with attractive flowers (e.g. high nectar rewards and 'showy' flowers). It is, hence, unclear whether plant traits, abundance or even geographic origin *per se* are the reason for such strong effects. We expect that it is rather those attributes and not the origin *per se* which determine the observed influences on co-flowering plants (hypothesis 4, see also Williams *et al.* 2011; Kaiser-Bunbury *et al.* 2011).

Whilst many plant species are efficiently pollinated by bees, other common flower visitors, including flies, butterflies and beetles, can also pollinate efficiently (e.g. Cutler *et al.* 2012; King *et al.* 2013; Tyler & Davis 2013). As different pollinator taxa may be adapted to plants with different flower traits (e.g. Junker *et al.* 2013), we expect the effects described above (hypotheses 1 to 4) to differ between pollinator groups.

Our study shows that, across communities worldwide, a species' potential to influence co-flowering plants via shared pollinators is independent of plant geographical origin, but depends on flower resources availability and accessibility, and is also related to phylogenetic proximity. The importance of these variables does, however, depend on the pollinator group.

MATERIALS AND METHODS

We gathered data from 28 independent studies across 14 countries, a study being defined as a dataset collected independently in a given habitat and locality (Table S1 in Supporting Information). Criteria used for the inclusion of a particular study are described in Appendix S1. Twenty studies were conducted in Europe, four in Africa, one in North America, one in South America and one in Australia (Fig. 1a). These studies covered a range of (semi) natural and managed habitats. Each study collected data on flower visitation of plant communities in multiple sites or time periods, leading to a total of 750 plant–pollinator quantitative networks involving 1524 plant species and 3100 pollinator species or morphospecies. Data for each network were gathered in a relatively small study area and during a restricted time period (see study details in Table S1 and Appendix S1) to minimise the number of impossible interactions due to spatial and temporal mismatch, i.e. in principle all pollinators detected in a network could interact with all plants.
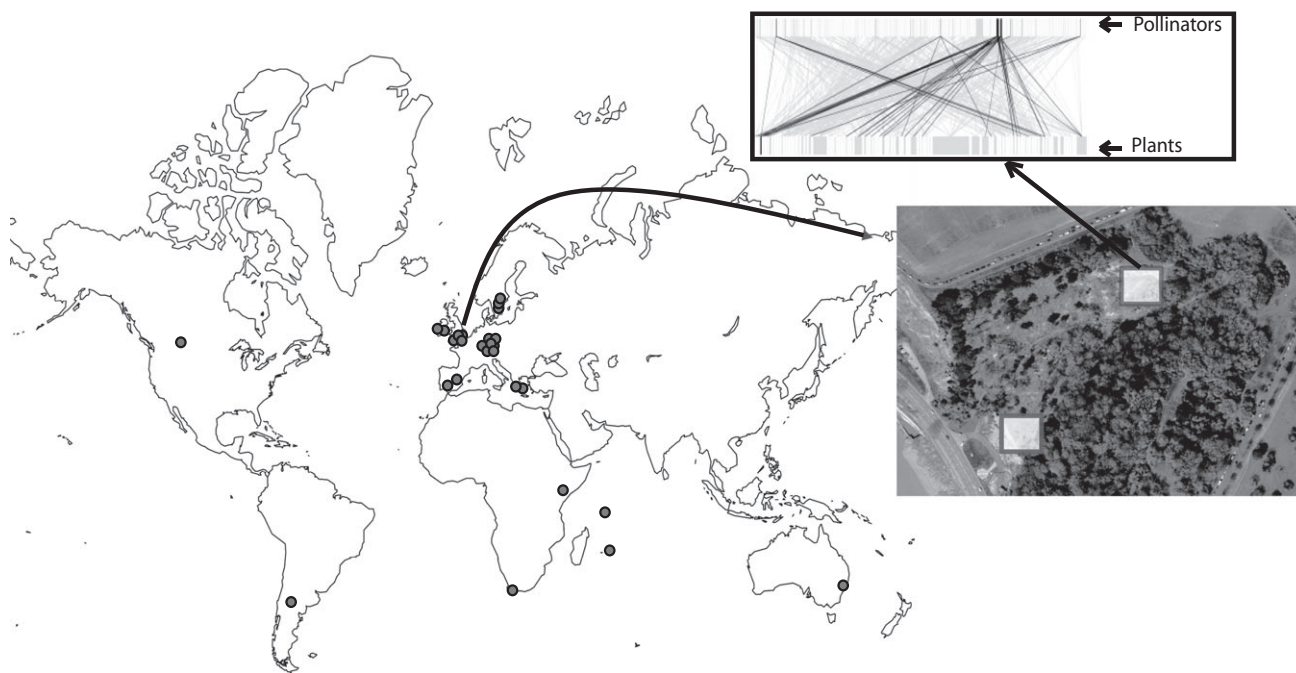
Figure 1 Locations of the 28 study regions. For each study there were several spatial and/or temporal replicates (details in Table S1) of plant–pollinator networks. Rectangles at the bottom of the network diagram represent different plant species; and rectangles on the top represent pollinator species. Rectangle size is proportional to the species abundance and visitation frequency, respectively.

We used flower visitation as a proxy for pollination. There are drawbacks to this approach, as some flower visitor species are inefficient pollinators (Castro *et al.* 2013; King *et al.* 2013). Nevertheless, visitation rate is often positively associated with fruit set (e.g. Vazquéz *et al.* 2005; Garibaldi *et al.* 2013), and hence is a reasonable proxy for the potential for pollination for many plant species.

To standardise measurements of flower abundance and visitation frequency across all species within and between studies, we defined a floral unit to be 1 cm^2 with at least one open flower. This definition uses the visitor's perspective, whereby the number of visitors that a floral unit can physically support is approximately constant across plant species. When the receptacle area (including stamen and nectaries; excluding petals) of a single flower was larger than 1 cm^2 we considered it to equate more than one floral unit (e.g. *Carpobrotus edulis*, Aizoaceae), where the number of floral units corresponded to the receptacle area in cm^2. We obtained information on size and clustering of flowers directly from data-holders or from floras, herbaria or scaled images of the species. Then, for each plant–pollinator network we calculated the potential of each plant species to influence all co-flowering plant species via shared pollinators using an index proposed by Müller *et al.* (1999); hereafter referred to as Müller's index (for details on the calculation and properties of Müller's index see Appendix S2). Müller's index is usually applied in ecological networks to quantify the potential for apparent competition via shared consumers between resource species in antagonistic interaction networks (see Morris *et al.* 2004; Carvalheiro *et al.* 2010), but it is well-suited for assessing the potential for any indirect influence (apparent competition or facilitation, see Tack *et al.* 2011), for example, between plants via shared pollinators. The index quantifies how much one ('acting') plant species contributes to the diets of pollinators visiting another ('target') species.

We ran all calculations based on the interactions made only by bees (28 studies, see Table S1), and repeated using only interactions made by flies (25 studies), only by beetles (11 studies) and only by butterflies and moths (18 studies).

Data analyses

Although Müller's index was calculated taking into account all plants in each network, not all plant pairs were included in subsequent analyses. First, we only included pairs for which we had information on flower abundance, floral colour, height, display, flower shape, nectar tube length and nectar splitting within a floral unit (see traits methods description below) and phylogeny for both acting and target plant. Second, all pairs in which the target plant did not receive any visits were excluded, as we could not assess the contribution of other plants to the diet of its pollinators. These selection criteria resulted in a total of 98108 records of plant pairs, corresponding to 564 plant species (see Table S1).

The four hypotheses presented in the introduction were tested with Generalised Linear Mixed Models using package lme4 (Bates *et al.* 2013) for R 3.0.1 (R Development Core Team 2014). To account for the hierarchical structure of the data, we included acting plant and target plant nested within

network nested within study as random terms. To deal with zero-inflation, we first analysed the probability of one plant influencing another by converting Müller's index to a binomial variable (0: no influence, i.e. plant pairs with no shared pollinators; 1: Müller's index > 0, i.e. plant pairs with shared pollinators) and analysed the probability of a species sharing insects with another plant using binomial error structure. In a second step we analysed the variation of Müller's index among species that shared flower pollinators by selecting only the plant pairs which had a Müller's index greater than zero. We log$_e$-transformed data to normalise residuals, and analysed the resulting data assuming Gaussian error structure. To analyse the probability of a plant influencing another with the Binomial model, we used all 98108 records of plant pairs. To analyse variability of Müller's Index among species that shared pollinators with the Gaussian model, we used 12587 records of plant pairs. However, nectar sugar content, a variable required to test our second and third hypotheses, was only available for a limited number of European and African plant species (164 of the total 564 plant species included in pairs selected for data analyses, see Table S1). Consequently, we repeated the analyses with the subset of plant pairs (hereafter 'reduced dataset') for which we had nectar sugar content data, considering the results for all four hypotheses. The reduced dataset consisted of 49694 records of pairs for the analyses of probability of sharing visitors (Binomial model) and to 6765 records of plant pairs when analysing the variability of Müller's index among species that shared pollinators (Gaussian model).

For both the Binomial and Gaussian approach, to identify the most parsimonious model, we used model selection based on the Bayesian Information Criterion (BIC), which is stricter on terms with limited explanatory power than the Akaike Information Criterion. The fixed terms included in the initial full model, relevant to the testing of each hypothesis, are described below, and all possible combinations of such terms were considered. Using simulated data (Fig. S1, S2), we found that interaction frequency (i.e. mean number of individual pollinators recorded per link) and plant richness have effects on Müller's index, particularly when interaction evenness (i.e. evenness of plant–pollinator interaction frequency) is high (Fig. S2). These relationships are therefore purely statistical inevitabilities. Moreover, it is possible that pollinators truly change their foraging pattern depending on the visitor density or on the diversity of resources (Lázaro & Totland 2010) present within a community, thereby affecting Müller's index. Consequently, in addition to the terms used for hypotheses testing (see below), we included in the models plant species richness, interaction frequency, interaction evenness of the respective plant–pollinator network, and any two-way interactions between them as terms. To test if mechanisms that regulate visitation differed across pollinator groups (bees; flies; beetles; butterflies and moths) we tested if the effect of each of the terms used to test the hypotheses (see below) varied significantly among pollinator groups, i.e. we tested for a significant interaction between each term and the factorial variable 'pollinator group'. To evaluate variability of the effects, we ran the most parsimonious models considering random slopes of each of the variables selected.

Effect of similarity in flower traits (hypothesis 1)

Four measures of flower trait similarity were considered in this study: flower shape (open vs. closed), floral display (flowers grouped into inflorescences vs. single flowers), flower height and colour. We used colour as perceived by humans, a measure that is readily available for all plants (for more details and discussion on the drawbacks of using this colour metric, see Appendix S3). We used phylogenetic distance between target and acting plant as a proxy for unmeasured traits that may be phylogenetically related. For further information on flower trait definitions, calculation of phylogenetic distance and correlations between variables see Appendix S3 and Figs. S3 and S4.

We calculated flower height similarity as the absolute difference between the value for the target and acting plants. A maximum influence was expected when dissimilarity was zero. For categorical variables (flower colour, shape, display) we considered target and acting species as either similar or dissimilar.

Effect of flower resource availability (hypothesis 2)

We considered two measures of floral resources of the acting plant: floral unit abundance relative to the whole community (acting plant relative abundance), and reward availability per floral unit (acting plant nectar sugar content).

To calculate the acting plant relative abundance, the number of floral units of the acting plant was divided by total floral unit abundance of all species combined. Nectar sugar content values were available for 126 European species and 38 species from the Seychelles (Baude *et al.* in prep., Kaiser-Bunbury *et al.* in prep., see methods description in Appendix S4).

As resource availability of the target plant may also affect the extent to which this plant is influenced by any other plant, we also calculated the floral unit abundance of the target plant relative to the acting plant as the log$_e$ of the ratio between the values for the target and acting plants (target-acting plant floral abundance balance), and also the nectar sugar content of the target plant relative to the acting plant (target-acting sugar content balance) and included these variables as well as their interaction with the acting plant relative abundance and sugar content during model selection.

Effect of nectar accessibility (hypothesis 3)

We considered three measures of nectar accessibility of the acting plant: (1) nectar tube length (log$_e$-transformed to normalise residuals), where species with longer tube were considered to be less accessible than flowers with shorter tubes, (2) nectar splitting within floral units, where species with multiple flowers per floral unit (e.g. Asteraceae, Apiaceae, *Trifolium* spp.) were considered to require more energy to extract available resources from than species with the same amount of nectar concentrated in a single flower and (3) shape, where closed flowers were considered to have less accessible flower resources (nectar or pollen) than open flowers.

Nectar sugar content is higher in plants with closed flower shape (Fig. S4a), and is significantly related with nectar tube length (Fig. S4c). To test if the effect of resource accessibility depended on nectar sugar content we considered the two-way

interactions between these accessibility measures and nectar sugar content, as well as the interactions between nectar tube length and nectar splitting. Nectar tube length is significantly higher in plants with close flower shape than in plants with open flower shape (Fig. S4d) so we always tested the effect of one of these variables over and above the effect of the other. As accessibility of the target species can also play a role, we also considered the similarity between acting and target plant accessibility traits (calculated $\log_e$ ratio of target plant value and acting plant value) as variables during model selection.

Effect of plant geographic origin (hypothesis 4)

Plant geographic origin (native or non-native) of the acting plant was included as a variable in the model selection procedure. We considered all neophyte plants (i.e. those introduced to the studied country after 1500 AD) as non-native.

RESULTS

Resource availability and accessibility, as well as phylogenetic distance between plants, explained a significant part of the variability in the probability of one plant species sharing pollinators with another plant (Binomial models results in Table 1 for the full dataset, and in Table S3 for the reduced dataset which accounts for the effect of nectar sugar content). These variables also explained the variability in the influence strength of one plant on other plants in the community (Gaussian models results presented in Table 2 for the full dataset, and in Table S4 for the reduced dataset). The most parsimonious Gaussian model explained 22.2% of the total deviance of the data (model 1 of Table 2). Flower resource availability terms explained most of such deviance, followed by accessibility terms and phylogeny. Similarity in morphological traits only had a significant role in explaining the probability of plants sharing pollinators (Binomial model).

Effect of similarity in flower traits (hypothesis 1)

As expected, floral trait similarity (colour, shape, height) played an important role in explaining the probability of one plant species influencing another (Table 1, Table S3, Binomial model). However, floral trait similarity did not explain the

Table 1 Effect of floral traits, phylogenetic distance, floral abundance and geographic origin on the probability of one (acting) plant sharing pollinators with another (target) plant (Binomial model)

	Estimates for model 1				Best models		
Terms	Bees	Flies	Beetles	Butterflies	Model1	Model2	Model3
Group	0.62	−0.51	−1.70	−2.37	x	x	x
PD	−0.33	−0.33	−0.33	−0.33	x	x	x
PD*Group					-	x	x
ColourSim	−0.33	−0.04	−0.04	−0.60	x	x	x
ColourSim*Group					x	x	x
ShapeSim	−0.11	−0.11	−0.11	−0.11	x	x	x
HeightSim	0.15	−0.17	0.12	0.27	x	x	x
HeightSim*Group					x	x	x
ARF	0.49	0.60	0.27	0.51	x	x	x
ARF*Group					x	x	x
TAB	0.14	0.20	0.04	0.16	x	x	x
TAB*Group					x	x	x
ARF*TAB	-	-	-	-	-	-	x
TL	−0.14	−0.30	−0.19	−0.20	x	x	x
TL*Group					x	x	x
NS	−0.21	0.48	0.31	0.26	x	x	x
NS*Group					x	x	x
TL*NS	0.11	0.20	0.26	0.12	x	x	x
TL*NS*Group					x	x	x
Ashape	0.02	1.07	0.79	−0.29	x	x	x
Ashape*Group					x	x	x
PR	−0.05	−0.05	−0.05	−0.05	x	x	x
VD	0.01	0.01	0.01	0.01	x	x	x
IE	−3.15	−3.15	−3.15	−3.15	x	x	x
PR*VD	0.0006	0.0006	0.0006	0.0006	x	x	x
PR*IE	0.09	0.09	0.09	0.09	x	x	x
BIC					55578	55594	55605
ΔBIC					0	15	27

All combinations of terms were tested, but only the terms included in the three best models are listed: colour similarity (ColourSim), shape similarity (ShapeSim), display similarity (DisplaySim), height similarity (HeightSim), phylogenetic distance (PD), acting plant floral abundance relative to the whole community (ARF), target-acting plant floral abundance balance (TAB), acting plant's nectar tube length (TL), acting plant's nectar splitting level (NS), acting plant's flower shape (Ashape, reference level: 'closed'), visitor density (VD), interaction evenness (IE), plant richness (PR). Reference level of the similarity factorial variables: 'similar'. 'x' indicates terms included in the models; '-' indicates that a term was not included in the model. Whenever an interaction with 'Group' is included in the best model, it is considered in the calculation of variable estimates.

strength of this influence, as none of the variables were selected in the most parsimonious BIC Gaussian model (Table 2, Table S4).

Phylogenetic distance was related to trait similarity, being higher in plants with dissimilar floral display and shape, but not colour (Fig. S3). Nevertheless, the probability of sharing pollinators (Table 1, all groups) and, for bees, the average influence of one plant species on other co-flowering species (Table 2, Fig. 2) declined with phylogenetic distance independently of the effect of explicit floral traits. This effect was highly variable across studies (Fig. S5a).

Effect of flower resource availability (hypothesis 2)

As expected, increasing flower abundance of a plant species (relative to the whole plant community) increased its probability of influencing other plant species (binomial model; Table 1), as well as the average strength of such influence (Gaussian model, Table 2). This positive relationship was nonlinear (logit-log$_e$, Fig S7), with a decelerating slope indicating that above a certain flower abundance threshold all plants have a similar chance of influencing co-flowering species. The effect of acting plant relative abundance was also dependent on the abundance of the target plant (i.e. target plant flower abundance relative to the acting plant had a significant effect, Fig. S6). When repeating the analyses with the reduced dataset, the positive influence of flower abundance was maintained (Table S3, S4).

As expected, for bees, plants with higher nectar sugar content had a significantly higher Müller's index (Table S4, Fig. 3). As with flower abundance, the effect was dependent on the nectar sugar content of the target plant (i.e. similarity of nectar sugar content between acting and target plant was significant) and was nonlinear with a decelerating slope indicating that after a certain threshold value of sugar, plants have similar chances of influencing co-flowering species (Table S4). A positive trend with nectar sugar content was also detected for some studies with other pollinator groups (Fig. S5c). However, the overall effect was much less accentuated for beetles, butterflies and moths and for flies, nectar sugar content was negatively related to the Müller's index (Fig. 3).

Effect of nectar accessibility (hypothesis 3)

Nectar tube length and shape were positively related to nectar sugar content (Fig.S4a, b). Therefore, the effect of nectar accessibility should only be evaluated when also taking into account the effect of nectar sugar content (i.e. analyses presented with the reduced dataset, Table S3 and S4). For all pollinator groups, plants with longer nectar tubes had a lower probability of sharing pollinators with other plants (Binomial model, Table S3). When sharing pollinators, plants with longer nectar tubes had less influence on other plants (Gaussian model, Fig. 4). This pattern held for bees, beetles, butterflies and moths. However, for flies no effect of nectar tube length on mean Müller's index was detected, and for bees a

Table 2 Effect of floral traits, phylogenetic distance, floral abundance and geographic origin on the average influence of one (acting) plant on another (target) plant (Gaussian model)

Terms	Deviance PDEF	Estimates for model 1				Best models		
		Bees	Flies	Beetles	Butterflies	Model1	Model2	Model3
Group	0.025	−2.67	−2.11	−2.10	−2.04	x	x	x
PD	0.028	−0.40	−0.14	0.04	−0.07	x	x	x
PD*Group	0.017					x	x	x
ShapeSim	-	-	-	-	-	-	-	x
ARF	0.619	0.38	0.41	0.35	0.10	x	x	x
ARF*Group	0.009					x	x	x
TAB	0.177	−0.23	−0.23	−0.23	−0.23	x	x	x
TAB*Group	-	-	-	-	-	-	x	x
TL	0.003	0.06	−0.24	−0.35	0.06	x	x	x
TL*Group	0.059					x	x	x
NS	0.003	−0.22	−0.22	−0.22	−0.22	x	x	x
TL*NS	0.005	0.11	0.11	0.11	0.11	x	x	x
PR	0.001	0.05	0.05	0.05	0.05	x	x	x
VD	0.013	0.004	0.004	0.004	0.004	x	x	x
IE	0.029	3.34	3.34	3.34	3.34	x	x	x
PR*VD	0.003	0.0004	0.0004	0.0004	0.0004	x	x	x
PR*IE	0.009	−0.12	−0.12	−0.12	−0.12	x	x	x
BIC						49327	49328	49329
ΔBIC						0	1	2

All combinations of terms were tested, but only the terms included in the three best models are listed: shape similarity (ShapeSim), phylogenetic distance (PD), acting plant floral abundance relative to the whole community (ARF), target-acting plant floral abundance balance (TAB), acting plant's nectar tube length (TL) and nectar splitting level (NS), visitor density (VD), interaction evenness (IE), plant richness (PR). Reference level of the similarity factorial variables: 'similar'. 'x' indicates terms included in the models; '-' indicates that a term was not included in the model. Total deviance explained: 22.2% (17.9% by random terms and 4.3% by fixed terms). PDEF-proportion of the fixed variance explained by each variable. See Table S5 to check all models with ΔBIC <3.
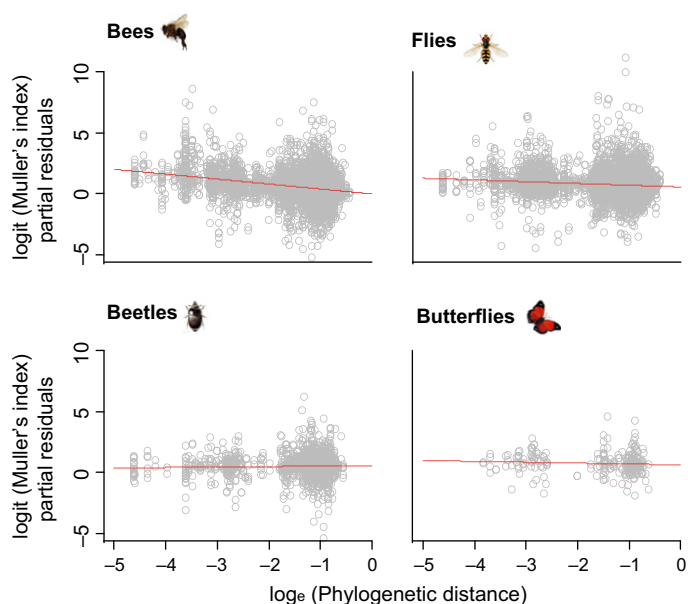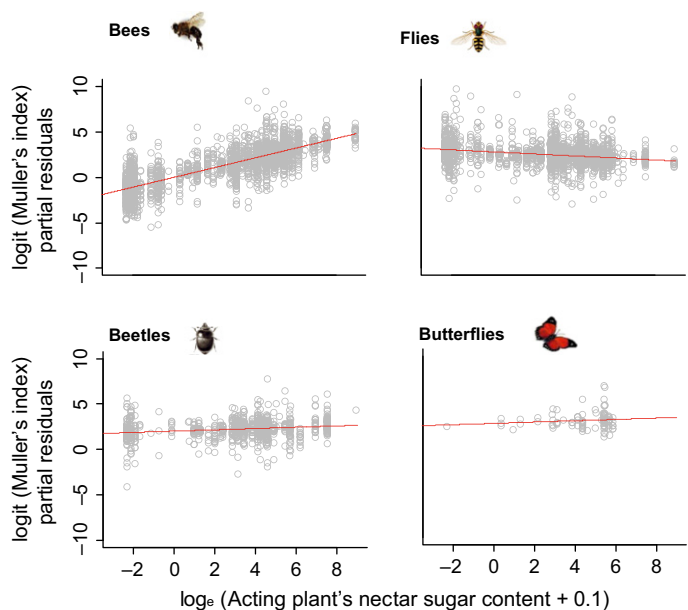
Figure 2 Effect of phylogenetic distance on the influence that a plant species has on another via shared pollinators (Müller's index, Gaussian model, Table 2). Dots represent partial residuals (i.e. residuals after removing the variation explained by other variables). Müller's index based on the bee visits significantly declined with phylogenetic distance between plants. Regression line is presented in red.

negative effect was only found when nectar splitting level (i.e. number of flowers per flower unit) was low (Fig. 4). When nectar splitting was high, nectar tube length actually had a

Figure 3 Effect of nectar sugar content on the influence that a plant species has on another via shared pollinators (Müller's index, Gaussian model, Table S4). Dots represent partial residuals (i.e. residuals after removing the variation explained by other variables). Regression line is presented in red. Nectar sugar content of the acting plant had a positive effect on Müller's index for bees and a negative effect for flies.

positive effect for bees. This was caused by the fact that plants with higher levels of nectar splitting had less influence on other plants, particularly for plants with short nectar tube (significant interaction between nectar splitting level and nectar tube length, Table S4: Gaussian model). Similarity in accessibility traits between acting and target plant did not explain the variability in Müller's index.

Effect of plant geographic origin (hypothesis 4)

Acting plant origin was not included in the most parsimonious models (Tables 1 and 2, Table S3 and S4), and so no significant differences were detected between the influence of native and non-native plants on the visitation of other plants.

DISCUSSION

Determining the potential for one plant to influence another via shared pollinators is an important step towards predicting the impacts of changes in the abundance of specific plant species on plant–pollinator networks. Knowing which species are likely to have a high influence (potentially facilitating some plants and competing with others) can help prioritise efforts to manage invasive species or protect species of conservation concern.

By analysing 750 quantitative plant–pollinator networks from five continents, we show that resource availability and accessibility, as well as phylogeny, play an important role in defining the potential for one plant species to influence another via shared pollinators. Changes in the strength of such influences will benefit some plant species and negatively affect others, potentially influencing fruit set. Thus, if plant populations are seed limited, such influences may translate to changes in population sizes. For particular purposes of applied ecology, such as the choice of plants to boost ecosystem services within agricultural fields (e.g. Wratten et al. 2012), or to evaluate potential negative impacts on specific protected species (Carvalheiro et al. 2008), it would be important to be able to predict under which circumstances these indirect influences lead to competition or facilitation. This requires experimental tests and further detailed analyses that evaluate changes in visitation or fruit set of focal plants when exposed to different floral abundances of acting plants (e.g. Lopezaraiza-Mikel et al. 2007). Moreover, the unexplained variation in our models suggests that additional factors not considered in this study may also play an important role. Nevertheless, the findings discussed below can help identify which species within a plant community are most likely to impact the pollination patterns.

Effect of similarity in flower traits

Our results confirm previous findings suggesting that species with more similar flower traits share more pollinators (Binomial model). Despite the fundamental differences between colour vision in insects and humans (e.g. Bennett et al. 1994), we found significant effects of colour as perceived by humans (see also Gibson et al. 2012; Eklöf et al. 2013). Although colour
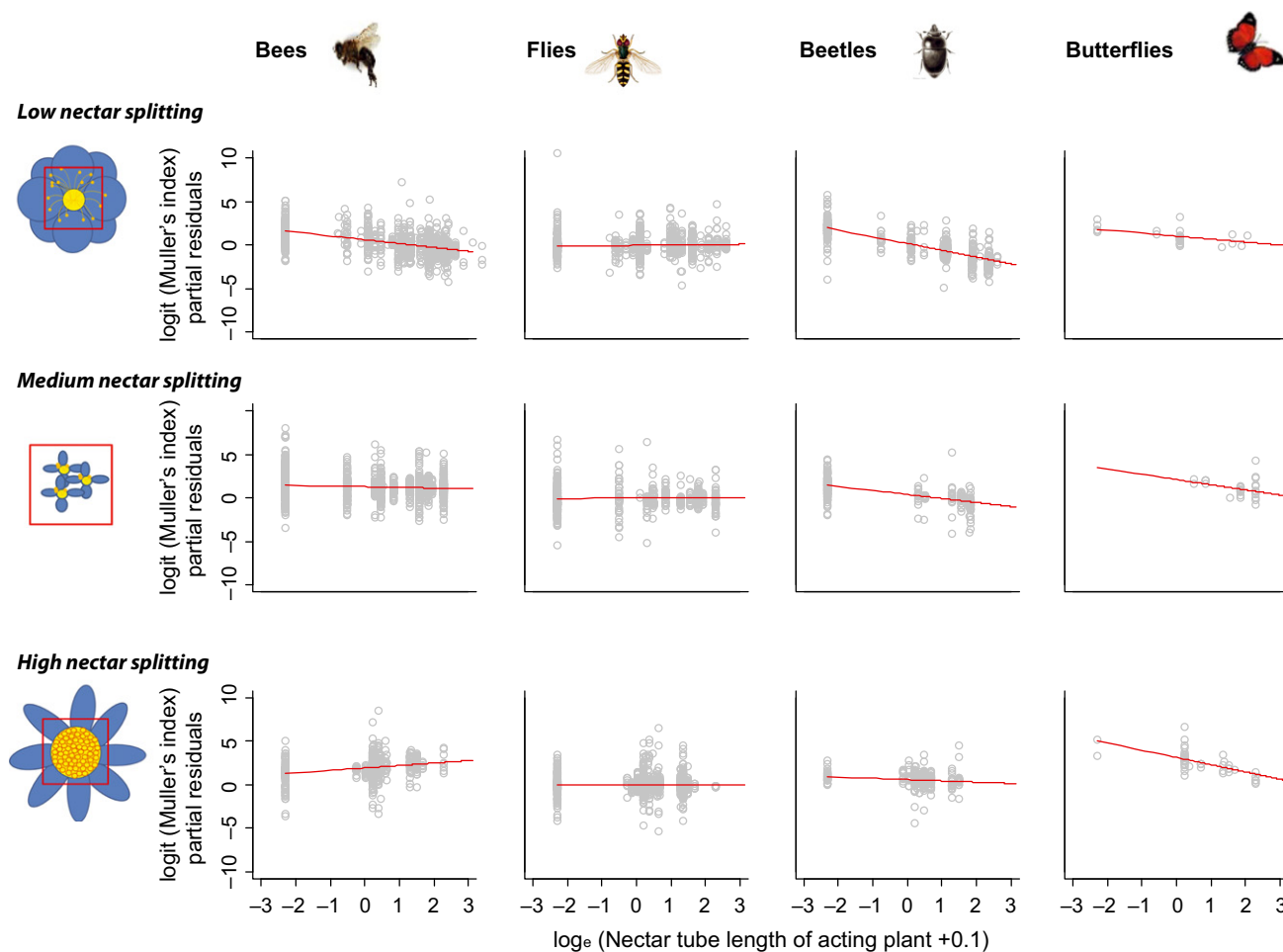
Figure 4 Effect of nectar tube depth and level of nectar splitting within floral unit on the influence that a plant species has on another via shared pollinators (Müller's index, Gaussian model, Table S4), after removing the effect of nectar sugar content. Müller's index decreased with acting plant's nectar splitting level and with nectar tube length for all pollinators groups except for flies. For bees and beetles the effect of tube length was most accentuated when splitting was low. Dots represent partial residuals (i.e. residuals after removing the variation explained by other variables). Regression line is presented in red. Graphs showing the results obtained with the full dataset (without considering the effect of nectar sugar content) are presented in Fig. S8.

as perceived by humans and UV reflectance can be correlated, it is likely that including a more precise colour measurement would increase the explanatory power of our models.

Despite its importance in defining the probability of sharing pollinators (Binomial model), trait similarity was not important in determining the potential of one plant species to influence another plant via shared pollinators (Gaussian model). This suggests that visitation frequency (rather than pollinator identity) is mostly regulated by other factors. However, since increasing phylogenetic distance decreased the potential of one plant species to influence another, our results suggest that further phylogenetically related traits not considered here could be important in defining visitation of these pollinator groups. Such traits may include odours (Junker *et al.* 2010), UV reflectance (Campbell *et al.* 2010) and chemical composition of nectar or pollen (Petanidou *et al.* 2006; Hoover *et al.* 2012). As these traits are poorly documented, phylogenetic proximity could be a good proxy for trait similarity and, consequently be used to

assess the influence of co-flowering plants on each other's pollination.

Effect of flower resource availability

As expected, flower abundance was crucial to explain variance in Müller's index. This could be a simple result of chance, a pollinator randomly selecting flowers being more likely to land on the most abundant plant species. Alternatively, pollinators may actually prefer to forage on the abundant plants, but above a certain flower abundance threshold all plants species may have a similar chance of being visited. Comparisons between the observed slope and the slope expected from abundance-biases would be required to determine if pollinators indeed prefer more abundant plants. The nonlinear positive pattern found for nectar sugar content suggests that above a certain sugar level, pollinators tend to forage equally on plants. The positive relation between Müller's index and flower resource availability can also help explain the highly

nested pattern characteristic of pollinator networks (Joppa *et al.* 2010): more rewarding plants are more likely to be visited by rarer (and less connected) pollinators as well as by the most common pollinators, hence sharing pollinators with less abundant (and less connected) plant species.

While overall flower abundance had a positive effect across pollinator groups, the effect of nectar sugar content was highly variable (Fig. 4, Fig. S5b,c). The ability for sugar intake might be limited for certain visitor species, thereby preferring plants with specific sugar concentrations (e.g. Nardone *et al.* 2013), or rather select for nectar volume or amino acid content (Petanidou *et al.* 2006). Therefore, the effect of floral resources may depend on the specific requirements of the species composing each pollinator community. Moreover, different pollinator taxa employ different techniques to ingest nectar, and hence their ability to cope with nectar viscosity (which typically increases with nectar sugar content) also differs. Lepidopterans suck nectar through their proboscis, generating a pressure gradient, which makes them more sensitive to viscosity than other pollinator taxa (Kim *et al.* 2011). This may explain the less accentuated effect of nectar sugar content on butterfly visitation, relative to bees, whose tongues are well-suited to deal with viscous nectar (Kim *et al.* 2011). A possible explanation for the detected negative effect of nectar sugar content for flies is that they may avoid nectar-rich plant species to avoid competition with other pollinator groups. Indeed, the negative effect of nectar sugar content was slightly more accentuated in networks with higher bee richness, where chances of competition between flies and bees were greater (Fig. S7). In addition, although sugar intake is an important source of energy for many pollinators (Gilbert 1981; Kevan & Baker 1983), pollen is the most important source of protein for flies (Branquart & Hemptinne 2000) and bees (e.g. Ueira-Vieira *et al.* 2013). Further studies involving detailed measures of pollen availability could help disentangle the relative importance of nectar and pollen.

Effect of nectar accessibility

Nectar tube length may predict the minimal proboscis length of the nectar-feeding visitors (e.g. Stang *et al.* 2006). Some species are able to overcome such limitations, for example by nectar robbing through corolla perforation (Castro *et al.* 2013) or by being small enough to crawl inside wide nectar tubes. Nevertheless, if for most species there is a threshold defining the effect of tube length, then visitors to longer tubed plants should be a subset of those visiting shorter tubed plants; the latter having a higher influence on the former than vice versa. Indeed, in most cases the influence of plants declined with increasing nectar tube length (Fig. 4). The fact that for flies the effect of nectar tube was not significant, reinforces the hypothesis that fly visitation is less constrained by nectar supply. The accentuated and consistent effect found for beetles (Fig. S5d) likely results from the short tongue typical from this group. For plants with shorter nectar tubes and with equal resource availability, the potential for an indirect influence via shared bees was lower when nectar splitting was higher, possibly due to the high energy demands of this pollinator group, which require particularly efficient foraging.

Effect of plant geographic origin

The ability of one plant to indirectly influence the pollination of another was unaffected by plant origin (see also Williams *et al.* 2011). Previous studies have found plant origin (native vs. non-native) to define pollinator visitation patterns (Morales & Traveset 2009). However, these studies often focus on abundant non-native plants with attractive flowers (e.g. *Impatiens glandulifera* which provides exceptionally high amounts of nectar). In fact, after accounting for abundance and selected flower traits, the overall effect size of plant geographical origin becomes less accentuated (Morales & Traveset 2009) and some studies show that natives may be more visited than invasive plants (Chrobock *et al.* 2013). Thus, the causal effect is not plant origin *per se* but their qualitative and quantitative traits.

CONCLUDING REMARKS

Maintaining the intricate network of mutualistic interactions between plants and pollinators is fundamental for the preservation of biodiversity. Changes in the local abundance of plant species due to land-use change (Tamis *et al.* 2005), farming practices (Carvalheiro *et al.* 2012), or conservation actions (Carvalheiro *et al.* 2008), can alter such interaction patterns and thus affect pollination of local plant communities. Some plants may benefit from facilitation, while others may suffer from competition for pollinators, potentially disturbing the dynamics of plant populations within such communities. Based on a large number of studies across the World, our study shows that information on phylogenetic distance, floral resource abundance and accessibility regulate the potential for indirect effects between co-flowering plant species. These findings can help identify plant species that are most influential for local plant communities.

STATEMENT OF AUTHORSHIP

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