



Plant traits moderate pollen limitation of introduced and native plants: a phylogenetic meta-analysis of global scale

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Summary

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- The role of pollination in the success of invasive plants needs to be understood because invasives have substantial effects on species interactions and ecosystem functions. Previous research has shown both that reproduction of invasive plants is often pollen limited and that invasive plants can have high seed production, motivating the questions: How do invasive populations maintain reproductive success in spite of pollen limitation? What species traits moderate pollen limitation for invaders?
- We conducted a phylogenetic meta-analysis with 68 invasive, 50 introduced noninvasive and 1931 native plant populations, across 1249 species.
- We found that invasive populations with generalist pollination or pollinator dependence were less pollen limited than natives, but invasives and introduced noninvasives did not differ. Invasive species produced 3× fewer ovules/flower and > 250× more flowers per plant, compared with their native relatives. While these traits were negatively correlated, consistent with a tradeoff, this did not differ with invasion status.
- Invasive plants that produce many flowers and have floral generalisation are able to compensate for or avoid pollen limitation, potentially helping to explain the invaders' reproductive successes.

Introduction

A subset of introduced species becomes invasive (Mack *et al.*, 2000; Richardson *et al.*, 2000), spreading rapidly in its new range, often causing significant ecological, economic, and human harm (Simberloff *et al.*, 2013). Because most plant species spread via seeds and require pollination for seed production (Ollerton *et al.*, 2011), traits relating to pollination may determine whether introduced species become invasive and how rapidly they spread

(Richardson *et al.*, 2000). While species in the introduced range often leave behind pollinators, it is still unclear whether inadequate pollen receipt (pollen limitation) limits reproduction more in introduced than native populations, or if invasive populations have lower pollen limitation than introduced populations that fail to invade (Knight *et al.*, 2005). Comparisons between invasive species and their native or noninvasive relatives are therefore needed (Harmon-Threatt *et al.*, 2009; Burns *et al.*, 2011). Previous research has shown that at least some invasive species are significantly pollen limited (Parker, 1997; Larson *et al.*, 2002), making fewer seeds than they could with saturating pollen

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receipt. Yet these invaders are clearly reproducing and spreading, suggesting that features in addition to pollen limitation influence reproductive success. To date, it is unclear what traits associated with sexual reproduction allow invasive species to succeed despite pollen limitation or moderate the degree of pollen limitation (Fig. 1).

Most flowering plants are dependent, at least to some extent, on mutualistic animal pollinators for their reproductive success (Ollerton *et al.*, 2011). When plants are introduced to new habitats, the loss of their native pollinators may limit their reproduction (Richardson *et al.*, 2000). This factor may be especially problematic for introduced species with specialised floral structures that rely on specialist pollinators for their reproductive success. By contrast, introduced plants with generalised floral form and/or those that attract generalist pollinators may be more robust to the loss of their native pollinators, as generalist pollinators in the plant's introduced range may be effective pollinators. Indeed, invasive plants are more generalised with respect to their pollinators than native plants (Albrecht *et al.*, 2014; Vanbergen *et al.*, 2018). Furthermore, many introduced plants with generalised pollination systems become well integrated into the resident plant–pollinator network (Memmott & Waser, 2002; Vila *et al.*, 2009; Chung *et al.*, 2014), suggesting that the loss of their original pollinators does not necessarily reduce pollination success of these plants in their introduced ranges. Therefore, we predicted that pollen limitation would be greater for introduced specialists than for floral generalists (Fig. 1).

Whether or not introduced plants are successful will depend on the reproductive system of the species that is mediated by the plant's mating system and reliance on pollinators (Fig. 1). For self-incompatible species and those that lack autofertility (that is pollinator-dependent species), reproductive success depends on pollinator visitation, and pollen limitation is highest amongst plants with these reproductive strategies (Knight *et al.*, 2005; Rodger & Ellis, 2016). According to Baker's law, nonpollinator-dependent, self-compatible or autofertile (that is the ability to autonomously self-fertilise) plants may establish more readily following a long-distance dispersal event than self-incompatible species, because they are able to produce offspring in the absence of mates (Baker, 1955, 1967; Pannell *et al.*, 2015). Consistent with this factor, self-compatible and autofertile species are highly represented in introduced floras (Rambuda & Johnson, 2004), and more autofertile species have a greater introduced range (Van Kleunen & Johnson, 2007; Razanajatovo *et al.*, 2016).

Comparative studies also found that invasive species are highly autofertile compared with their native or noninvasive relatives (van Kleunen *et al.*, 2008; Harmon-Threatt *et al.*, 2009; Burns *et al.*, 2011). Therefore, we predicted that introduced pollinator-dependent plant species will be more pollen limited than those that are autofertile, and self-incompatible plants will be more pollen limited than self-compatible plants.

Often missing from studies of pollen limitation of invasive species is consideration of year of introduction of the introduced species. Plants introduced earlier support more pathogens and herbivores than those introduced more recently (Hawkes, 2007; Mitchell *et al.*, 2010). Similarly, plants introduced earlier have more associations with native pollinating insects than those introduced more recently (Pyšek *et al.*, 2011). Shortly after introduction, introduced species might have an advantage in attracting pollinators if they produce more flowers or offer greater rewards than natives (Brown *et al.*, 2002). As invasion proceeds, and invader populations increase in density, intraspecific competition for pollinator services could increase (Mustajärvi *et al.*, 2001) or autofertility could evolve (Barrett *et al.*, 2008), leading to increased or decreased pollen limitation, respectively. Alternatively, pollen quality could decline over time if deleterious mutations accumulate through high levels of genetic drift at the invasion front (that is 'expansion load'; Peischl *et al.*, 2013; Bock *et al.*, 2015). Therefore, we predicted that pollination success might change during the invasion process.

Invasive plants could maintain high fecundity, despite high pollen limitation, if they produce more ovules or package them more effectively than native species. Amongst flowering plants, the overproduction of ovules within flowers is a common adaptation to unpredictability in pollination and fertilisation success (Burd *et al.*, 2009). Burd *et al.* (2009) found that the number of ovules per flower correlated positively with the standard deviation in stigmatic pollen loads or seed number per fruit across 187 angiosperm species. These patterns are consistent with the hypothesis that ovule overproduction evolves when the variance in reproductive success at the floral level is high, as might occur when pollinator services are stochastic in space or time. Although we are not suggesting that selection acts directly to favor invasiveness, and many factors might influence the evolution of ovule packaging within flowers (for example pollinator availability (Burd, 1995), kin selection (Bawa, 2016)), the production of many ovules per flower might be associated with invasiveness. For example, if invasive plants have more ovules per flower

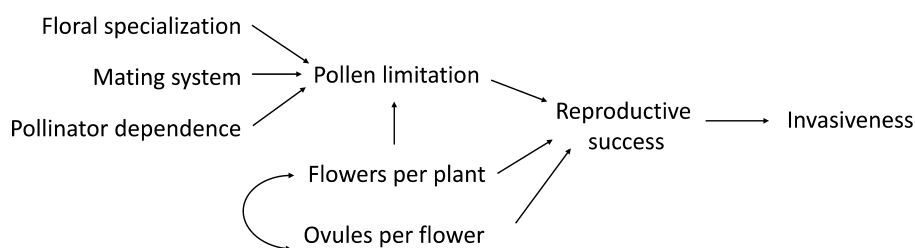


Fig. 1 Conceptual outline of some hypothesised relationships amongst species traits, reproductive success and invasiveness. Although relationships amongst traits and invasiveness are likely complex, this outline guides our analysis approach.

compared with noninvasive or native species, they might take advantage of rare high pollinator availability, resulting in high reproductive output in some years or locations. An alternative ovule packaging strategy of few ovules per flower could also be associated with invasiveness, for example if plants make more, cheaper flowers. Plants that experience high pollen limitation (at the flower level) might maintain their reproductive success by producing more flowers, which increases attractiveness to pollinators (that is floral display size, or the number of flowers open at a given point in time), and/or leads to longer flowering times and spreads the risk of reproduction over time. Here, we explored whether native, invasive and introduced noninvasive plants differed in their ovule packaging.

Furthermore, per flower ovule packaging may tradeoff with flowers per plant (Friedmann & Barrett, 2011). For example, theory suggests that wind-pollinated species experience selection for the production of many, inexpensive flowers with few ovules per flower to capture stochastically available pollen (Friedmann & Barrett, 2011). Such life-history tradeoffs are generally expected, and a comparative study amongst 251 species of angiosperms found that flower size (a proxy for costs) trades off with flower number (Sargent *et al.*, 2007). Although costs might vary with ovule size and quality (Soloman, 1988; Ashman, 1992), and assuming that ovules are costly to produce (Burd, 1995), we expected a negative correlation between flowers per plant and ovules per flower (Fig. 1). We predicted that invasive populations might have a weaker tradeoff between flowers per plant and ovules per flower than natives, if invasive populations experience release from competition or otherwise experience less resource limitation.

Three types of comparisons are particularly relevant for understanding pollen limitation in introduced species (Pyšek & Richardson, 2007). Comparisons between native and invasive species address questions such as: are invasive plants better at attracting pollinator services, leading to lower pollen limitation? Comparisons between introduced species that have either become invasive or failed to invade (that is introduced 'noninvasive' species) address questions such as: why do some introduced species become invasive, having high reproductive success, while other introduced species are less successful? Finally, comparisons between native and introduced species (both invasive and noninvasive) address questions about the role of traits, such as flower number and mating system (Fig. 1) in pollen limitation for introduced species.

Here, we conducted a phylogenetic meta-analysis of a global dataset of pollen supplementation studies to address the following questions:

(1) How does the magnitude of pollen limitation differ for native, invasive and noninvasive introduced species? For example, if introduced species lose pollinator services upon introduction, then we expect introduced species to be more pollen limited than native species (Knight *et al.*, 2005). Moreover, if invaders are better at acquiring pollinator services than noninvasives, then we expect them to be less pollen limited than their noninvasive relatives. We also expect that these differences will depend on species traits, such as floral specialisation (generalist vs specialist), pollinator dependence (autofertile vs pollinator dependent), mating

system (that is self-compatibility vs self-incompatibility, *sensu* Charlesworth, 2006), flowers per plant and ovules per flower (Fig. 1), as well as year of introduction.

(2) Is invasiveness associated with ovule packaging patterns or flowers per plant? In other words, do invasive species produce more or fewer ovules per flower, compared with native or noninvasive relatives? Do invasive species have more flowers per plant than native or noninvasive relatives?

(3) Does flowers per plant correlate negatively with ovules per flower? Does the correlation between flowers per plant and ovules per flower differ amongst native, invasive and noninvasive species?

(4) What are the putative causal relationships amongst plant traits, pollen limitation and invasiveness?

Materials and Methods

Literature search and compilation of plant trait information

Our meta-analysis utilised a global database of pollen supplementation (the GloPL) with 2969 unique pollen supplementation experiments conducted on 1265 plant species across the globe (161 plant families, six continents; additional details available in Bennett *et al.*, 2018). We used all of the data in this database with adequate sample sizes (see details below) to address our questions. See the Results section for actual sample sizes. Pollen limitation effect sizes were based on several measures of reproductive output, including seed set, fruit set, seeds per flower, seeds per fruit and seeds per plant. Here, we present analyses on the pollen limitation (PL) effect size, following the list of priorities described in Bennett *et al.* (2018). For each data record within the GloPL database, the pollen limitation effect size (PL) was calculated as a log response ratio (Hedges *et al.*, 1999; Gurevitch *et al.*, 2001). PL was calculated by comparing reproductive output in pollen supplemented treatments (hand) with that in unsupplemented controls (natural), that is in flowers exposed to natural pollination:

$$PL = \log_e(\text{hand}) - \log_e(\text{natural}).$$

While this approach drops data with zero values for supplement or open treatments, such values represent only 2.4% of the database. Analyses with an alternative effect size, where a small constant was added to zero values before transformation, resulted in similar or stronger statistical outcomes, but are not shown here, making our presented results conservative. To summarise the data for these analyses, we calculated weighted mean pollen limitation across morphs or seasons, such that each population and year of study had a single mean estimate of the magnitude of pollen limitation, and an estimate of the pooled variance in the effect size for this estimate. Therefore there were multiple records ('populations') for some species, and species was included as a random effect in the models (see Data analysis in the Materials and Methods section, below). See Bennett *et al.* (2018) for additional details.

We classified populations in the GloPL database as either native or introduced, as designated by the original authors of the pollen supplementation studies; *c.* 6% of populations ($n = 125$)

were measured in the introduced range. We searched the primary literature, secondary literature, and publicly available databases of invasive species to further classify each introduced plant in our database as either invasive or noninvasive (see Supporting Information Notes S1 for list of references) and we considered species invasive if they spread rapidly in the introduced range. Because many of the native species in our dataset have not been introduced elsewhere, their potential invasive status is unknown (Pyšek & Richardson, 2007). Therefore, we use noninvasive to refer only to introduced species that have naturalised in the introduced range, but failed to become invasive (*sensu* Burns, 2004), rather than including 'noninvasive' native species in this category. We categorised a species as invasive when a source listed the species as invasive in the country where the pollen supplementation study was conducted. One species, *Lythrum salicaria*, was present in both native and introduced ranges in our data set. Flower number data corresponded to the native range, so this species was treated as only native in the flower number analysis. Based on our review of these sources (Notes S1), we further gathered information on the year of introduction of the species to the country where the pollen supplementation study was conducted ($n = 33$ studies). When a range of years was provided, we took the midpoint.

We also gathered information on floral specialisation (generalist vs specialist floral phenotype), pollinator dependence (autofertile vs pollinator dependent), mating system (self-compatible, partially self-compatible vs self-incompatible), flowers per plant and ovules per flower. We categorised each species in our dataset as producing phenotypically generalised or specialised flowers based on five floral traits. For each species, character states within each of these five floral traits were evaluated and classified as being more generalised or more specialised. The traits were: (1) the type of reward offered (generalised (none, nectar, pollen) vs specialised (heat, oil, floral parts, scent, resin)); (2) accessibility of reward to pollinators (generalised (that is easily accessible) vs specialised (that is hard to access)); (3) floral tube length or corolla depth (generalised (< 10 mm) vs specialised (≥ 10 mm)); (4) flower shape (generalised (bell/funnel, brush, inconspicuous, open/dish) vs specialised (chamber, flag, gullet, keel, spurred)); and (5) flower symmetry (generalised (actinomorphic) vs specialised (zygomorphic)). Accessibility of reward was classified as 'hard' for trigger flowers, or when pollen is in poricidal anthers (buzz pollinated). Accessibility was considered 'easy' if flowers have no restriction to reward collection or pollinators do not need complex body structures or mechanisms to collect rewards. The cut-off of 10 mm for floral tube length was defined based on the literature (Bawa *et al.*, 1985; Ramirez, 1989), which states that flowers of species pollinated by small diverse insects generally are < 1 cm in length, characterising generalised pollination systems. Moreover, there is evidence that a size threshold where the majority of the proboscis length and nectar depths were below 10 mm size can explain the degree of generalisation in structuring pollination webs (Stang *et al.*, 2009). Therefore, corolla length larger than this would represent constraints to access the reward. Each plant species was coded as specialised if it was specialised in any of these categories and otherwise was considered generalised. Plants pollinated by abiotic vectors were categorised as

generalised, using the original information mentioned in the primary studies (if the species was biotic or abiotic pollinated). For rows with missing data we assigned abiotic or biotic based on family membership, namely predominantly wind-pollinated families such as graminoid monocots were classified as abiotic, the remaining cases were assigned as biotic. For a few cases, NA attribution was assigned (biotic vs abiotic: 93.6% (2846) original data, 5.6% (171) inferred based on family, 0.7% (23) NA).

Mating system was coded into three categories, self-compatible (SC), partially self-compatible (P), and self-incompatible (SI). When hand outcross and hand self-pollinations were conducted for a given species within a pollen supplementation study, we calculated the index of self-incompatibility (ISI) from the raw data as $1 - (\text{seed number}_{\text{hand self-pollination}} / \text{seed number}_{\text{hand outcross-pollination}})$. Based on this, species were coded as SI if $\text{ISI} \geq 0.8$, as P if $0.2 > \text{ISI} < 0.8$, and SC if $\text{ISI} \leq 0.2$ (as per Bawa, 1974) (available for 10% of populations). When data were unavailable to calculate ISI index, we recorded the self-incompatibility status of a species based on species descriptions within the original pollen supplementation publication or additional primary literature sources. Species described as partially SC or partially SI were coded as P. Dioecious, distylous, and tristylous species were recorded as SI; 3% of populations were unclassified in our dataset.

Autofertility (AF) is the ability to autonomously set seed in the absence of pollinator visitation. When both pollinator exclusion (that is bagged flowers) and hand pollination (that is outcrossed or supplemental pollination) treatments were conducted for a given species within the pollen supplementation publication, we calculated the autofertility ratio as: $\text{seed number}_{\text{bagged}} / \text{seed number}_{\text{hand outcross or supplemental pollination}}$. Based on this ratio, species were coded as autofertile (AF) if this ratio was ≥ 0.2 or pollinator dependent (PD) if this ratio was < 0.2 . Self-incompatible, dioecious, distylous and tristylous species were categorised as PD. When quantitative data was unavailable to calculate AF and PD, we scored this trait based on species descriptions within the original pollen supplementation publication or additional primary literature sources (Rodger & Ellis, 2016). When no such data were available the species was recorded as having unknown pollinator dependence (2% of populations).

For all species in our dataset, we searched the original pollen supplementation publications as well as additional primary literature for estimates of ovules per flower and mean flowers per plant. For species within plant families with a fixed ovule number, we recorded ovule number per flower for all species within this family as the fixed value. When ovule or flower number ranges were given in the literature, the midpoint ovule number and/or flower number was recorded for the species. When a minimum ovule or flower number was provided, we recorded this value as the ovule or flower number, respectively. Flower number is always reported as true flower number, not number of inflorescences, including for species with compact inflorescences, such as Asteraceae. When no other data were available (*c.* 12% of populations), ovules per flower were estimated using a regression approach based on species in the GloPL data set having both ovule and seed data. The regression equation was $(\log_{10}(\text{ovule number}) = 0.36741 + 0.9209 \times \log_{10}(\text{seed number}); R^2 = 0.93)$.

Data analysis

How does the magnitude of pollen limitation differ for native, invasive and noninvasive introduced species and do these patterns depend on species traits? To determine whether pollen limitation varied with introduction status (native, invasive and noninvasive) and species traits, we conducted phylogenetic meta-analyses on pollen limitation effect sizes. As in standard meta-analyses, effect sizes are weighted by the inverse of their variances (Koricheva & Gurevitch, 2013). This analysis also incorporates a variance–covariance error structure based on phylogenetic relationships, therefore taking nonindependence amongst species into account (Lajeunesse *et al.*, 2013). To incorporate phylogeny, we used the angiosperm supertree of Zanne *et al.* (2014), modified as described in Bennett *et al.* (2018), with a single tip per species. Species missing in the ‘Zanne phylogeny’ were added into the phylogeny using best available evidence ($n = 60$ species, *c.* 5% of species in the data set, see details in Bennett *et al.*, 2018).

For our phylogenetic meta-analysis, following methods described in Oduor *et al.* (2016), we modeled phylogeny as a variance–covariance matrix using the *vcv* function in the *APE* package (Paradis *et al.*, 2004) on the subsets of taxa described for each analysis. We used a mixed effects meta-analysis using the *rma.mv* function in the *METAFOR* package (Viechtbauer, 2010), with the Knapp Hartung adjustment (*knha* = TRUE) for more accurate type I error rates (Knapp & Hartung, 2003). Because some ($n = 13$ out of 2408) pooled variance estimates were zero, causing the model to fail to converge, a small constant (0.0001) was added to all of the variance estimates. Results were qualitatively similar, but more conservative, with the addition of a larger constant. Because variance can only be calculated for effect sizes with > 1 estimate, 58 pooled variance estimates were coded as NA. We included species as a random effect in all models and sample sizes for these analyses are reported at the population level. We examined profile plots of the likelihood surfaces, and likelihoods exhibited a clear peak at the maximum likelihood estimate. For most comparisons, model coefficients matched raw data in direction, and we mostly present raw data. However, when model coefficients differed in direction from raw data, we presented the phylogenetically corrected model coefficients.

We used introduction status (native, invasive, noninvasive) as a categorical predictor in separate models for each covariate including floral specialisation, pollinator dependence (AF, aut-*ofertile*; PD, pollinator dependent; UNK, unknown pollinator dependence), mating system (P, partially self-compatible; SC, self-compatible; SI, self-incompatible), and year of introduction. We included two-way interactions where appropriate (for example for introduction status \times floral specialisation). For significant interactions, we also conducted all possible comparisons amongst means within the interaction, using the Holm adjustment for multiple comparisons. For example, we expected an interaction between floral specialisation and invasive status. If there is a benefit to being a generalist upon introduction, then we expect invasive generalists to be less pollen limited than invasive specialists. If pollinator services are acquired over time for introduced species

– through adaptation, behavioral modification or the introduction of new pollinators – then we expect pollen limitation to be greater for more recent introductions (that is we predicted a positive slope with year of introduction).

Flower number per plant might influence reproductive success either directly, by resulting in more total opportunities for reproduction, or indirectly, by increasing pollinator attraction and decreasing pollen limitation (Fig. 1). To determine whether flowers per plant influences pollen limitation, we used a phylogenetic meta-analysis with pollen limitation as the response variable, and flowers per plant (\log_e transformed), introduction status and their interaction as predictors. If greater floral display size increases attraction of pollinators, then we predict a negative correlation between flowers per plant and pollen limitation.

Is invasiveness associated with ovules per flower or flowers per plant? To determine whether ovules per flower and flower number correlated with introduction status, we conducted phylogenetic generalized least squares (PGLS) analysis on \log_e transformed variables, summarised at the species-level (Martins & Hansen, 1997). No variances were available for ovules per flower or flowers per plant, so meta-analysis is not appropriate. PGLS analysis includes phylogeny in the error structure of the model, therefore accounting for nonindependence in the data due to shared evolutionary history (Martins & Hansen, 1997). Phylogeny was modeled as a variance–covariance matrix based on a Brownian motion model of evolution using the *corBrownian* function in the *APE* package (Paradis *et al.*, 2004). This model was compared with a model without phylogeny in the error structure with a likelihood ratio test. Only species with complete data (that is no NAs) were analysed with this approach, altering sample sizes (reported in Results section). For example, analyses for effects of invasive category on ovules per flower included only those records with both of these variables, reducing the number of species included. We used a categorical variable with introduction status (native, invasive, noninvasive) as a predictor and *a priori* contrasts comparing native vs invasive species and invasive vs noninvasive species. We predicted that invasive species would have more flowers per plant than native species, potentially helping explain their rapid spread rates. We also predicted that invasive species would have more flowers per plant than noninvasive species, if differences in flowers per plant contributed to differences in invasiveness amongst introduced species. Although we had no directional expectations for ovules per flower, contrasts between native vs invasive and invasive vs noninvasive species might inform future hypotheses about ovule packaging and invasiveness.

Does flowers per plant correlate negatively with ovules per flower? We also conducted a PGLS to determine whether flower number per plant correlated with ovule number per flower, for the 212 species for which both flowers per plant and ovules per flower were available in our data set. Although many factors are expected to influence flower costs and flower production (Burd, 1998), if producing more ovules per flower results in higher flower production costs, then we predicted a negative correlation

between the number of ovules per flower and the number of flowers per plant. We used *phylosig* in the *PHYTOOLS* package (Revell, 2012) with 1000 replicates and Pagel's λ (Pagel, 1999) to describe the phylogenetic signal in the ovule number and flower number data. All analyses were conducted in R (v.3.3.3; R Core Team, 2017). Diagnostic plots were examined and model assumptions were well-met for all analyses presented here.

What are the putative causal relationships amongst plant traits, pollen limitation and invasiveness? To explore possible causal relationships amongst our variables, we used phylogenetic path analysis using *phylo_path* in the *PHYLOPATH* package (von Hardenberg & Gonzalez-Voyer, 2013; van der Bijl, 2018). We compared six plausible models (Fig. 2) including correlations between pollen limitation, invasiveness, and our modifier variables (Fig. 2). Our 'baseline' model included effects of modifier variables floral specialisation, pollinator dependence, and mating system on pollen limitation, an effect of pollen limitation on invasiveness, and a direct effect of flower number per plant on

invasiveness (Fig. 2). We compared this model with one with a direct effect of ovule number on invasiveness ('direct.ovule'). This model tests the hypotheses that few ovules per flower directly benefit invasive plants by reducing reproductive risk or larger numbers of ovules per flower benefit invaders through rare high quality pollination events. We also tested for an indirect effect of ovule number on invasiveness, via a correlation between ovules per flower and flowers per plant ('indirect.ovule', Fig. 2), to determine whether correlations between invasiveness and ovules per flower might be driven by a general life-history trade-off. Further, we compared these models to one with an indirect effect of flower number via pollen limitation ('indirect.flw'), because we hypothesised that plants with more flowers might attract more pollinator services and experience lower pollen limitation (Fig. 2). We also explored possible direct effects of key traits (floral specialisation, pollinator dependence, mating system) on invasiveness ('direct.traits' and 'direct.both', which also includes a direct effect of ovule number on invasiveness; Fig. 2). We used C-statistic information criterion corrected for small

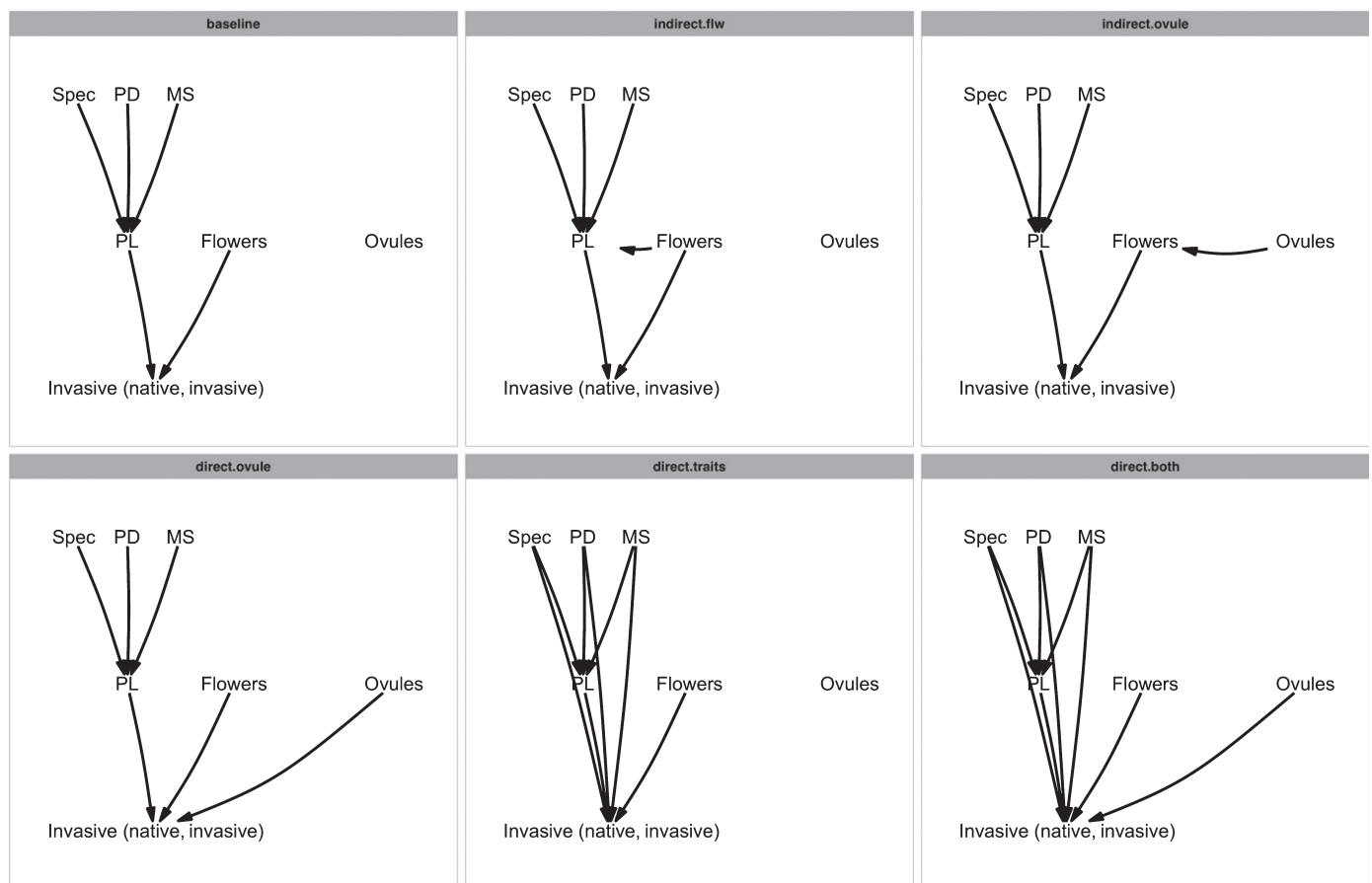


Fig. 2 Six hypothesised path models explored in phylogenetic path analysis with the following variables: floral specialisation (Spec, generalist, specialist), pollinator dependence (PD, autofertile, pollinator dependent), mating system (MS, self-compatible, self-incompatible), pollen limitation (PL), flowers per plant (Flowers), ovules per flower (Ovules), and Invasiveness (Invasive: native, invasive). The 'baseline' model contained direct effects of traits (Spec, PD, MS) on PL, PL on invasiveness and Flowers on invasiveness. The 'indirect.flw' model adds an indirect effect of Flowers on invasiveness via an effect on PL. The 'indirect.ovule' model adds an indirect effect of Ovules on invasiveness via an effect on Flowers. The 'direct.ovule' model adds a direct effect of Ovules on invasiveness. The 'direct.traits' model adds direct effects of traits (Spec, PD, MS) on PL and the 'direct.both' model includes direct effects of traits and Ovules on invasiveness.

sample sizes (CICc) to identify the best model(s) amongst this set. Because this analysis can only accept a binary response variable (not three categories), and because our sample of noninvasive species was relatively small ($n=18$ in this analysis), we compared only native and invasive species. Mating system was similarly simplified, and partially SC species ($n=31$) were dropped before analysis. Our final phylogenetic path analysis contained 159 species for which all of these variables were available.

Results

Invasive species were less pollen limited than native relatives for generalist and pollinator-dependent plants

Introduction status (PL estimates: native $n=2019$, invasive $n=71$, noninvasive $n=51$ populations) influenced pollen limitation (QM = 24.28, $df=2$, $P<0.0001$) in the phylogenetic meta-analysis. Invasive species were less pollen limited on average (phylogenetic meta-analysis model coefficient = 0.46 ± 3.75 SE) compared with their native relatives (PL = 0.58 ± 3.75 SE) (Holm adjusted multiple comparisons: t -value = -4.84 , $P<0.0001$). Native species did not differ from noninvasive species (t -value = -1.08 , $P=0.56$), and noninvasive species (PL = 0.38 ± 3.75 SE) did not differ from invasive species (t -value = -0.41 , $P=0.68$).

The relationship between introduction status and pollen limitation depended on floral specialisation and pollinator dependence. Floral specialisation interacted with introduction status to influence pollen limitation (QM = 19.13, $df=2$, $P<0.0001$). Within the native species, specialists were significantly more pollen limited than generalists ($t=-13.77$, $P<0.0001$); however, within the invasive species, there was no significant difference between generalists and specialists ($t=1.85$, $P=0.58$) (Fig. 3a). Within the generalists, invasive species were less pollen limited than natives ($t=-9.41$, $P<0.0001$). Specialist invasive species were no different in their pollen limitation from specialist native species ($t=1.69$, $P=0.73$), and invasive and noninvasive specialists did not differ ($t=-0.83$, $P=1.00$).

Introduction status interacted with pollinator dependence (Fig. 3b) to influence pollen limitation (QM = 65.10, $df=3$, $P<0.0001$). Within native species, as expected, autofertile species were less pollen limited than pollinator-dependent species ($t=103.52$, $P<0.0001$), but autofertile and pollinator-dependent species did not differ within the invasive species ($t=1.21$, $P=1.00$). Within the pollinator-dependent species, invasives were slightly less pollen limited compared with natives (invasive – native contrast estimate = -0.14 , $t=-5.30$, $P<0.0001$), although this phylogenetically corrected trend is not obvious in the raw means (Fig. 3b). Within the autofertile species, invasive species were more pollen limited than native species ($t=3.82$, $P=0.0023$) and invasive and noninvasive species did not differ ($t=-1.10$, $P=1.00$).

Plant mating system did not interact significantly with introduction status to influence pollen limitation (Fig. 3c; QM = 5.20, $df=4$, $P=0.27$), there was no main invasive status effect within

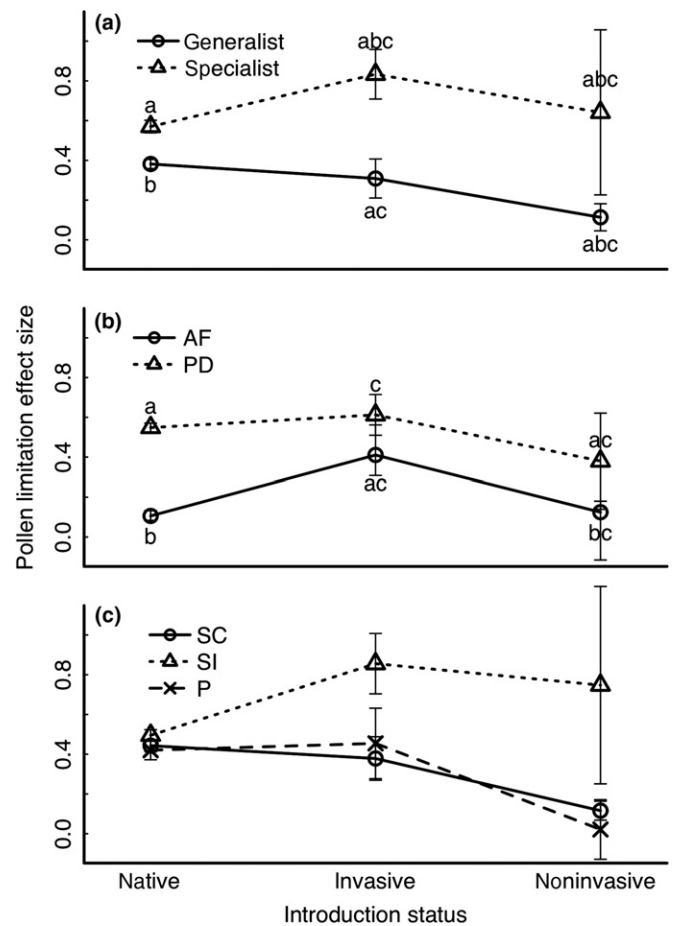


Fig. 3 Pollen limitation for species that differ in their introduction status and (a) floral strategy (g, generalist or s, specialist; sample sizes: native-g = 1148, native-s = 871, invasive-g = 33, invasive-s = 38, noninvasive-g = 38, noninvasive-s = 13), (b) pollinator dependence (autofertile (AF) or pollinator dependent (PD); sample sizes: native AF = 383, native PD = 1580, invasive AF = 17, invasive PD = 53, noninvasive AF = 25, noninvasive PD = 25; populations with unknown pollinator dependence are not shown), or (c) mating system (SC, self-compatible; SI, self-incompatible; P, partially self-compatible; sample sizes: native P = 338, native SC = 854, native SI = 772, invasive P = 17, invasive SC = 27, invasive SI = 27, noninvasive P = 4, noninvasive SC = 34, noninvasive SI = 12) (means \pm 1 SE). Shared letters indicate means that are not different in a phylogenetic meta-analysis, with Holm correction for multiple comparisons across all possible comparisons, except for (c), where the interaction was not significant and therefore this comparison was not conducted. Note that analyses are phylogenetically corrected and raw means are graphed.

this model (QM = 3.54, $df=2$, $P=0.17$), and there was a main effect of mating system on pollen limitation (QM = 13.11, $df=2$, $P=0.0014$). As expected, SI species were more pollen limited on average than SC species ($t=-2.24$, $P=0.05$).

There was a significant interaction between invasive status and the year of introduction for introduced species on pollen limitation (QM = 6.24, $df=1$, $P=0.013$). However, neither invasive nor noninvasive populations individually had a significant relationship between year of introduction and pollen limitation (Table S1); both slopes were nonsignificantly negative and noninvasives had a slightly steeper slope (Table S1). Therefore pollen

limitation decreased weakly with time since introduction at a slightly faster rate for noninvasive species than for invasive species.

There was an interaction between flowers per plant and introduction status on pollen limitation ($QM = 47.03$, $df = 2$, $P < 0.0001$) in a phylogenetic meta-analysis. However, none of the individual slopes were significantly different from zero for native (slope = 0.01, $P = 0.66$), invasive (slope = -0.02, $P = 0.60$), or noninvasive (slope = -0.03, $P = 0.34$) species. Therefore, while natives with more flowers had weakly greater pollen limitation, introduced species with more flowers had weakly lower pollen limitation, as expected. There was a significant main effect of flowers per plant on pollen limitation with a greater number of flowers leading to lower pollen limitation as expected (slope = -0.15, $SE = 0.04$, $QM = 15.44$, $df = 1$, $P < 0.0001$).

Invasive species produced fewer ovules per flower and more flowers than native relatives

There was strong phylogenetic signal in the number of ovules per flower ($\lambda = 0.98$, $P < 0.0001$) for the 716 species that could be included in this analysis. The PGLS model of ovule number per flower had a higher likelihood (log likelihood = -1333.73, $AIC = 2675.45$) than a generalised least squares (GLS) model (log-likelihood = -1588.92, $AIC = 3185.83$) ($\chi^2 = 510.38$, $P < 0.0001$), therefore we retained phylogeny in the analysis. Introduction status was associated with differences in ovule number per flower (Table 1), and native species had $> 3\times$ more ovules per flower on average, compared with invasive species (Fig. 4a; Table 1). Invasive species did not differ from their noninvasive relatives (Table 1).

There was a statistically significant ($P = 0.016$), but weak ($\lambda = 0.14$), phylogenetic signal on flower number per plant for the 282 species that could be included in this analysis. The PGLS analysis on flower number per plant has a lower likelihood (log-likelihood = -692.51, $AIC = 1393.03$) than an alternative model without phylogeny in the error structure (log-likelihood = -674.13, $AIC = 1356.27$) ($\chi^2 = 36.76$, $P < 0.0001$). Therefore, we focused on the GLS model without phylogeny. Invasive species produced over $250\times$ more flowers per plant on average than native species (Table 2; Fig. 4b). Invasive species,

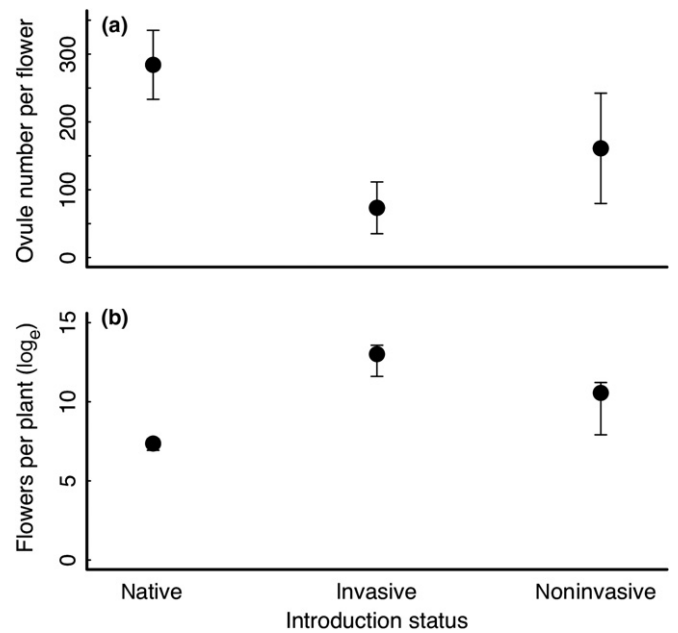


Fig. 4 (a) Ovule number per flower (Table 1, $n = 671$ native, 22 invasive, 23 noninvasive species) and (b) flower number per plant (note the log_e scale; Table 2, $n = 238$ native, 25 invasive, 19 noninvasive species) for species with different introduction status (means ± 1 SE).

however, did not differ from their noninvasive introduced relatives in flowers per plant (Table 2).

Flowers per plant correlated negatively with ovules per flower

There was a significant negative correlation between ovules per flower and flowers per plant (Fig. 5; slope = -0.09, $SE = 0.40$, $n = 212$) but no interaction with introduction status ($n = 212$ populations, Table 3). The model without phylogeny (log-likelihood = -497.96, $AIC = 1009.93$) was significantly more likely than the model with phylogeny (log-likelihood = -504.42, $AIC = 1022.85$) ($\chi^2 = 12.92$, $P < 0.0001$). The relationship between flowers per plant and ovules per flower did, however, depend significantly on the interaction with mating system (Table S2), and the slope of this relationship was negative for all mating systems but weakest for SC species (Fig. S1). The

Table 1 Results of a phylogenetic generalized least squares analysis of ovule number per flower as a function of introduction status.

	Num DF	Den DF	F-ra- tio	P- value
Introduction status (native, invasive, noninvasive)	2	713	3.22	0.041
Contrasts	Estimate	SE	t-value	P-value
Native vs invasive	-0.16	0.06	-2.53	0.012
Invasive vs noninvasive	-0.16	0.10	-1.60	0.11

A priori contrasts compared native with invasive species and invasive with noninvasive species. Effects that are significant ($P < 0.05$) are bolded.

Table 2 Results of a generalized least squares analysis of flower number as a function of introduction status.

	Num DF	Den DF	F-ra- tio	P-value
Introduction status (native, invasive, noninvasive)	2	279	18.96	< 0.0001
Contrasts	Estimate	SE	t-value	P-value
Native vs invasive	-1.71	0.29	-5.86	< 0.0001
Invasive vs noninvasive	-0.40	0.44	-0.90	0.37

A priori contrasts compared native with introduced species and invasive with noninvasive species. Effects that are significant ($P < 0.05$) are bolded.

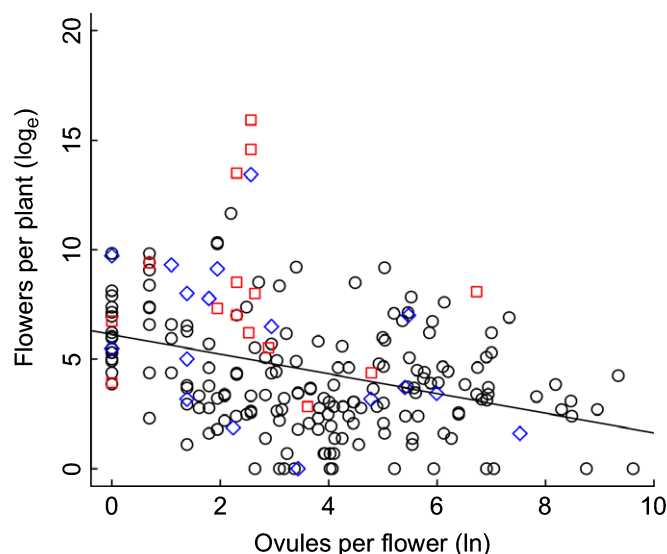


Fig. 5 Species mean flowers per plant and ovules per flower ($n = 212$) (black circles, native; red squares, invasive; blue diamonds, noninvasive; Table 3). Note \log_e scale on both axes.

Table 3 Results of a generalized least squares analysis of flower number per plants as a function of ovule number per flower, introduction status and an ovule number by introduction status interaction.

	Denom DF	Num DF	F- value	P-value
Ovule number	206	1	34.83	< 0.0001
Introduction status (native, invasive, noninvasive)	206	2	15.04	< 0.0001
Ovule \times Introduction status	206	2	1.12	0.33

Effects that are significant ($P < 0.05$) are bolded.

relationship between flowers per plant and ovules per flower did not depend on floral specialisation or pollinator dependence (Table S2).

More flowers per plant and lower pollen limitation correlated directly with invasiveness, but ovules per flower did not

The best model, with the lowest CICc, was the baseline model (Table S3), which included effects of pollen limitation and flowers per plant on invasiveness, and indirect effects of plant traits (floral specialisation, pollinator dependence, and mating system) on invasiveness, via their effects on pollen limitation (Fig. 6a). More specialised, pollinator-dependent, and SI species were all more pollen limited, and plants with lower pollen limitation were more invasive (Fig. 6a). Furthermore, plants with more flowers per plant were more invasive (Fig. 6a). An alternative model with an indirect effect of ovules per flower on invasiveness via a correlation with flower number per plant could not be rejected and was within two CICc of the best model (Table S3) with a negative correlation between flowers per plant and ovule number that was close to 0 (Fig. 6b, $\text{coef} = -0.002$, $\text{SE} = 0.095$).

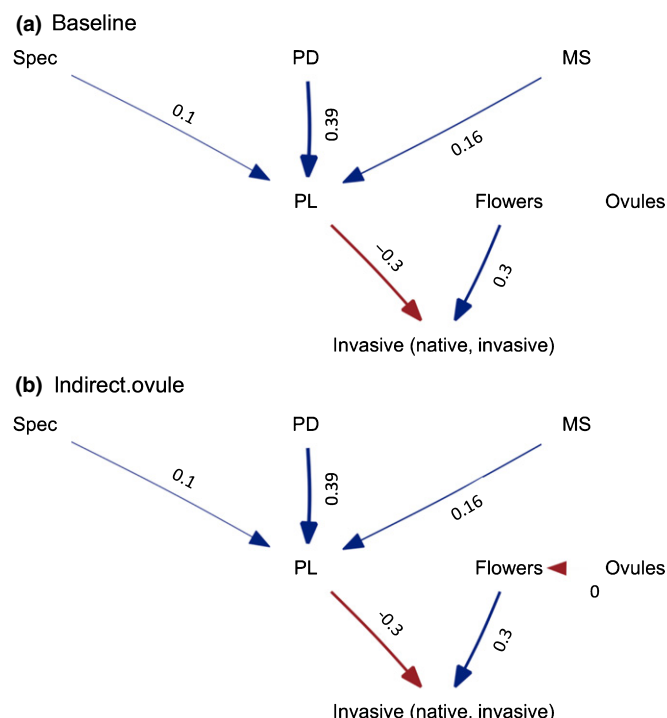


Fig. 6 (a) The best model amongst six phylogenetic path models explored (Fig. 2) with floral specialisation (Spec, g, generalist; s, specialist), pollinator dependence (PD; AF, autofertile; PD, pollinator dependent), and self-incompatibility (MS, mating system; SC, self-compatible; SI, self-incompatible) leading to greater pollen limitation (PL). Invasive populations have lower pollen limitation and more flowers per plant than native populations. (b) The alternative model with an indirect effect of ovules per flower on invasiveness via flowers per plant could not be rejected and was within 2 CICc of the best model (Supporting Information Table S3). Positive correlations are indicated with blue arrows and negative correlations with red arrows.

Discussion

Previous syntheses of pollen limitation in introduced species suggested that invasive species are often pollen limited, raising the question of how they can produce abundant seed in the face of this potential reproductive limitation (Burns *et al.*, 2011). Because reproduction depends on flower production, plant traits and successful pollination, we explored these factors in this larger, global data set (161 families and six continents). Here, we examine how plant traits, such as floral specialisation, pollinator dependence and mating system influence patterns of pollen limitation for invasive species. Overall, invasives were less pollen limited than natives, especially when they had generalist pollination systems. The relationship between invasiveness and pollen limitation was contingent on plant traits, with invasive species that were floral specialists, SI or autofertile exhibiting equivalent or higher pollen limitation than natives, while floral generalist and pollinator-dependent invasives were less pollen limited than natives. Our analysis of reproductive strategies points to greater flowers per plant as a possible avenue for invaders to compensate for pollen limitation, when it occurs. Differences between invasive and noninvasive species were minimal in our current analysis; however, relatively small sample sizes for this comparison suggest cautiously interpreting this result.

This current larger data set provides a more nuanced look at pollen limitation than our previous comparison (Burns *et al.*, 2011). In our previous analysis, pollen limitation was higher for invasive than noninvasive species, but only when failing to account for autofertility (Burns *et al.*, 2011), hinting that interactions with species traits should be taken into account. In our current analysis, new advances in phylogenetic comparative methods, such as phylogenetic meta-analysis and phylogenetic path analysis, suggest that when controlling for differences in species traits and phylogeny, invaders are generally less pollen limited than their native relatives (Fig. 6). However, this contrast is only significant within generalist and pollinator-dependent plants (Fig. 3), suggesting that it is contingent on species traits. This result is also not obvious from looking at raw means uncorrected for phylogeny, further suggesting that controlling for phylogeny is essential to understanding these trends.

Invasive species were less pollen limited than native relatives for generalist and pollinator-dependent plants

Plant traits influenced pollen limitation as expected for most traits (Knight *et al.*, 2005). In our global analysis, invasive floral generalists were less pollen limited than native generalists. Although we did not measure pollination services directly, this is consistent with invasive generalist populations acquiring more or higher quality pollinator services than native generalists. More flowers per plant for invasives than natives (Fig. 4b) could make them more attractive to pollinators, but several other factors that affect pollinator services such as reward quality, population density, and enemy escape may also differ between invasives and natives (Keane & Crawley, 2002; Pyšek *et al.*, 2011). As expected, native species that rely on pollinators were more pollen limited than autofertile natives. Unexpectedly, amongst the autofertile species, invasives were more pollen limited than natives and amongst invasive species autofertile and pollinator-dependent species did not differ. This could be the result of only 17 invasive species in the autofertile category, including the autofertile but reportedly strongly pollen limited *Alliaria petiolata* (PL = 0.25, 0.97). Alternatively, it could also be a result of differences in pollen quality. For example, invasive species that reproduce autonomously ('Baker's law'; Baker, 1955) might receive poorer quality pollen than natives. Finally, loss of autofertility could be occurring in the invaded range, such that invasive populations of plants like *Alliaria petiolata* might be misclassified as autofertile. However, evidence for this is lacking and high levels of selfing have been shown in both native and invasive ranges (Durka *et al.*, 2005). There was no indication that year of introduction significantly influenced pollen limitation within invasive or noninvasive species.

Invasive species produced fewer ovules per flower and more flowers per plant than native relatives

Assuming that ovules are costly to produce (Burd, 1995), our data suggests that invasive species may make more, less-costly,

flowers, potentially leading to greater overall reproduction, even in the face of limited or stochastic pollinator services. Although flower number per plant is not equivalent to fecundity, more flowers per plant in invasive species is consistent with comparative studies of fecundity based on invasion status (Leger & Rice, 2003). Demographic comparisons have found that invasive species have higher fecundity than their noninvasive relatives *in situ* in the introduced range (Burns *et al.*, 2013) and in the native range, when controlling for differences in plant size (Jelbert *et al.*, 2015). In our data set, *Cytisus scoparius* (Parker, 1997; Muir & Vamossi, 2015) and *Lonicera japonica* (Larson *et al.*, 2002) are highly invasive species that are pollen limited, have few ovules per flower, and produce large numbers of flowers per plant. *Cytisus scoparius* has a mean pollen limitation effect size of 1.10, or a c. 33% reduction in fruit or seed set in open vs supplemented flowers (range < 0–2.95), has 14 ovules per flower, and can produce c. 3000 flowers per plant. *Lonicera japonica* has a pollen limitation effect size of 1.51, or about a 22% reduction in fruit or seed set, has 12–13 ovules per flower, and can produce c. 500 flowers per plant. Producing more, cheaper flowers may allow plants to re-allocate resources from nonpollinated flowers into future reproduction, a potentially advantageous strategy when pollinator services are unpredictable (Thomson, 1989). For example, enemy escape in invaders could free resources for such reallocation (Keane & Crawley, 2002). Producing more flowers could also make invasive species better competitors for pollinators than native species (for example due to larger displays). Consistent with this, we found that generalist invasives experience lower pollen limitation than generalist natives, suggesting that they might be receiving more or better quality pollinator services (Vanbergen *et al.*, 2018), and many invasive species do receive adequate pollinator services (Thompson & Knight, 2018). However, we did not detect a significant negative indirect effect path of flower number on PL, so do not have evidence that increased flower number reduces pollen limitation through increased attraction of pollinators.

Flowers per plant correlated negatively with ovules per flower

Life-history tradeoffs may shape the reproductive strategies we describe (Lande, 1982; Stearns, 1989; Salguero-Gomez *et al.*, 2016). Consistent with tradeoffs between floral costs and flowers per plant (Sargent *et al.*, 2007), we found a consistently negative relationship between ovules per flower and the number of flowers per plant. Flower production costs are likely a function of more than ovule number, including ovule size, pollen production and quality of pollinator rewards, such as nectar production (Thomson, 1989). Per ovule costs might also fluctuate with ovule packaging strategy (Thomson, 1989). Nonetheless, ovule number may be an important component of flower cost. The shape of this tradeoff also did not differ substantially with introduction status or other covariates. However, our sample size was only 212 species for this analysis, and future studies might find these tradeoffs to be contingent on invasiveness or other covariates.

More flowers per plant and lower pollen limitation correlated directly with invasiveness, but ovules per flower did not correlate with invasiveness

Phylogenetic path analysis suggested that any correlation between ovules per flower and invasiveness is likely driven by the correlation between ovules per flower and flowers per plant. More invasive species in our data set had more flowers per plant and lower pollen limitation and direct effects of these variables were the best predictors of invasiveness. Furthermore, floral specialisation, pollinator dependence and self-incompatibility increased pollen limitation, as expected (Knight *et al.*, 2005).

Conclusions

Our global phylogenetic meta-analysis of pollen limitation suggests that, counter to the expectation from mutualism breakdown in invaded ranges, invasive plants are on average less pollen limited than natives. Plant traits such as floral specialisation and pollinator dependence modified the pollen limitation experienced by both native and introduced species, but sometimes in different ways. In addition, larger numbers of flowers were associated with invasiveness. Other global comparisons have also suggested that invasive species have a limited set of reproductive strategies, for example, high net reproductive rates and iteroparity (Salguero-Gomez *et al.*, 2016; Salguero-Gomez, 2017). Invasive plants that produce many flowers and have floral generalisation are able to avoid or compensate for pollen limitation, potentially helping explain the reproductive success of invasive plants.

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Author contributions

TLA, TMK and JAS designed the study. JMB conducted data checking. JHB conducted the analyses. JHB and JAS wrote the first draft of the manuscript. JHB, JMB, JL, JX, GA-G, MB,

LAB, WD, AGE, LF, JGR, JCV, MW, T-LA, TMK and JAS contributed to data collection, writing and revision. JHB and JAS contributed equally to this work.

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Supporting Information

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Fig. S1 The number of flowers per plant correlated negatively with the number of ovules per flower, for all mating systems (partially self-compatible (P), self-compatible (SC), self-incompatible (SI)).

Notes S1 References cited for classification of introduced species as invasive or noninvasive and time since introduction.

Table S1 Tests for interactions and slopes for models with year since introduction as a predictor and pollen limitation as a response variable.

Table S2 Results of analyses of flower number per plants as a function of ovule number per flower, and several covariates.

Table S3 Model output comparing six hypothesised path models (Fig. 2).

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