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REVIEW AND SYNTHESIS

Neighbour tolerance, not suppression, provides competitive advantage to non-native plants

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Abstract

High competitive ability has often been invoked as a key determinant of invasion success and ecological impacts of non-native plants. Yet our understanding of the strategies that non-natives use to gain competitive dominance remains limited. Particularly, it remains unknown whether the two non-mutually exclusive competitive strategies, neighbour suppression and neighbour tolerance, are equally important for the competitive advantage of non-native plants. Here, we analyse data from 192 peer-reviewed studies on pairwise plant competition within a Bayesian multilevel meta-analytic framework and show that non-native plants outperform their native counterparts due to high tolerance of competition, as opposed to strong suppressive ability. Competitive tolerance ability of non-native plants was driven by neighbour's origin and was expressed in response to a heterospecific native but not heterospecific non-native neighbour. In contrast to natives, non-native species were not more suppressed by hetero- vs. conspecific neighbours, which was partially due to higher intensity of intraspecific competition among non-natives. Heterogeneity in the data was primarily associated with methodological differences among studies and not with phylogenetic relatedness among species. Altogether, our synthesis demonstrates that non-native plants are competitively distinct from native plants and challenges the common notion that neighbour suppression is the primary strategy for plant invasion success.

Keywords

Bayesian multilevel meta-analysis, competitive strategy, inter- vs. intraspecific competition, net neighbour effect, non-native invasive plants, pairwise competition, phylogenetic correction, statistical non-independence.

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INTRODUCTION

High competitive ability has often been invoked as a key determinant of invasion success and ecological impacts of non-native plants (Levine *et al.* 2003; Gioria & Osborne 2014). Yet our understanding of the strategies that non-natives use to gain competitive dominance remains limited. Non-native plants are often assumed to be good suppressors of their native counterparts via superior resource acquisition or allelopathic activity (i.e. express high competitive effects *sensu* Goldberg 1990; Ridenour & Callaway 2001; Vilà & Weiner 2004; Garcia-Serrano *et al.* 2007; Kueffer *et al.* 2007; Maron & Marler 2008; Kuebbing & Nuñez 2016; but see Daehler 2003; Dawson *et al.* 2012; Dostál 2011; Perkins & Hatfield 2014). However, theory suggests that neighbour confrontation is not always an optimal competitive strategy in plants (Goldberg 1990; Novoplansky 2009). Specifically, the ability to suppress neighbouring plants is likely to provide an advantage only at early stages of succession and in the presence of disturbance, whereas the ability to tolerate unfavourable conditions associated with the presence of neighbours (i.e. low competitive response *sensu* Goldberg 1990) would determine species composition in late-successional communities (Goldberg 1990; MacDougall & Turkington 2004). Indeed, high neighbour tolerance has been demonstrated for many non-native plant species invading undisturbed communities (MacDougall & Turkington 2004; Suding *et al.* 2004; Maron & Marler 2008; Callaway *et al.* 2011). Moreover, it has been shown that non-native plants have a potential to evolve towards increased neighbour tolerance (Huang *et al.* 2017). Similarly, increased competitive tolerance has been proposed as a mechanism of coexistence of native with highly abundant non-native plants (Goergen *et al.* 2011; Oduor 2013; Fletcher *et al.* 2016).

Neighbour suppression and neighbour tolerance are not mutually exclusive strategies, yet are often associated with different sets of traits, suggesting a potentially different adaptive value for non-native plants (Goldberg & Landa 1991; Keddy *et al.* 1994; Cahill *et al.* 2005; Baron *et al.* 2015). Specifically, suppressive ability is closely associated with size-related traits (Gaudet & Keddy 1988; Cahill *et al.* 2005; Violle *et al.* 2009; Wang *et al.* 2010) and allelopathic activity (Callaway & Aschehoug 2000; Hierro & Callaway 2003; Callaway & Ridenour 2004), and several hypotheses relate species invasion success precisely to those traits and predict directional selection on them in the new range (e.g. *the evolution of increased competitive ability hypothesis*; Blossey & Nötzold 1995; *the enemy release hypothesis*; Keane & Crawley 2002; *the novel weapons hypothesis*; Callaway & Ridenour 2004; Ridenour *et al.* 2008). Meanwhile, competitive tolerance appears to be highly

contingent upon the identity of the neighbouring plant and environmental context, and thus cannot be related to any fixed set of traits (Wang *et al*. 2010; Baron *et al*. 2015). Moreover, competitive tolerance can appear either in the form of stress tolerance (i.e. the ability to tolerate low resource levels or high concentrations of allelopathic chemicals) or as partial avoidance of competition via niche divergence. The role of the latter for invasion success has been articulated in such influential hypotheses as *Darwin's naturalisation hypothesis* (Darwin 1859; a.k.a. *the competition-relatedness hypothesis*; Cahill *et al*. 2008) and *the empty niche hypothesis* (Elton 1958; Stachowicz & Tilman 2005), which both predict that the ability of non-native species to effectively use underutilised resources allows them to establish and thrive in the novel range. Contrary to suppressive ability, possible selection towards increased competitive tolerance in non-native species has not been theoretically framed.

Which of the two competitive strategies prevails among non-native plants has not been rigorously tested. Empirical studies and syntheses on plant competition involving non-natives have primarily focused on competitive effects of native and non-native plants on each other, which only allows inference about competitive superiority (Vilà & Weiner 2004). However, combining data on competition between native and non-native plants with the vast evidence on competition among native and non-native plants permits the assessment of the importance of competitive suppression vs. tolerance for invasion success. Specifically, if non-native plants are inherently stronger suppressors than native plants, the performance of native and non-native plants will be reduced more by heterospecific non-native than heterospecific native neighbours. If non-natives are innately more tolerant to interspecific competition than natives, they will be affected by competition from heterospecifics less than native species. If non-natives intrinsically surpass natives at both competitive suppression and tolerance, reduced performance due to competition with a non-native will be observed in native but not in other non-native species. Alternatively, a competitive advantage of non-native plants might be driven by a distinct eco-evolutionary context in the novel range and thus will arise in the form of suppression, tolerance or both only relative to native species (Callaway & Aschehoug 2000; Callaway & Ridenour 2004; Ridenour *et al*. 2008).

The actual mechanisms and the magnitude of interspecific plant competition are highly variable across species (Weigelt *et al*. 2002), genotypes (Cahill *et al*. 2005; Bossdorf *et al*. 2009), environmental gradients (Grime 1973; Wilson & Keddy 1986; He *et al*. 2013) and over time (Connolly *et al*. 1990; Mangla *et al*. 2011), and depend on species establishment order (Goldberg *et al*. 2001; MacDougall & Turkington 2004) and coevolutionary history (Aarssen 1983). This implies that any generalisation on plant competition is prone to bias. The two major potential sources of bias are artefacts of experimental design and inherent data structure. The former bears a risk of artificially exaggerating the magnitude of the competitive effect of non-native species due to inappropriate choice of species or environmental conditions (Vilà & Weiner 2004; Passioura 2006; Dalling *et al*. 2013; Parepa & Bossdorf 2016). Meanwhile, the latter is associated with the presence of non-independence (i.e. correlative structures), which, if not accounted for, can lead to erroneous conclusions due to inflation of Type I error (Nakagawa & Santos 2012). Non-independence arises when multiple effect sizes are obtained from a single study, a common control is used for calculating multiple effect sizes, or some species are represented in the data more than once; phylogenetic relatedness among species is another possible source of non-independence (Olkin & Gleser 2009; Nakagawa & Santos 2012). Failing to acknowledge, for example, species- and study-level non-independence could result in a bias towards a most common species in the data set or experimental conditions of a study with the highest number of effect sizes. To our knowledge, non-independence has not been incorporated in previous syntheses on plant competition involving non-natives (e.g. Vilà & Weiner 2004; Kuebbing & Nuñez 2016).

To assess the relative importance of competitive suppression and tolerance for non-native plants, we synthesised the extensive experimental evidence on pairwise plant competition within a Bayesian multilevel meta-analytic framework. Our data set comprised 3415 observations from 192 studies published between 1981–2017 and was representative of 471 plant species from 283 genera and 73 families. The use of the multilevel approach allowed us to account for non-independence while preserving original heterogeneity in the data and to explore the data using meta-regressions. We aimed to answer the following questions: (1) Do heterospecific non-native neighbours suppress native plants more than heterospecific native neighbours? (2) Are non-native plants more competitively tolerant than native plants? (3) Do native and non-native plants differ in the intensity of inter- vs. intraspecific competition? (4) Is the intensity of interspecific competition mediated by phylogenetic relatedness? (5) Are neighbour suppression and tolerance associated with any particular species traits, environmental conditions or attributes of study design? By addressing these questions, our study provides a comprehensive analysis of competitive strategies of vascular plants through the prism of biogeographical origin. Our study highlights differential competitive behaviour of non-native and native plant species and outlines future research directions on the mechanisms and the role of competition in promoting invasiveness and coexistence of plant species of different biogeographical origin.

MATERIAL AND METHODS

Literature search

We compiled a comprehensive database of peer-reviewed studies on pairwise plant competition in several steps. First, we searched ISI Web of Science Core Collection database for studies involving non-native species using the search combination: Topic = ((invasi* OR invad* OR alien OR exotic OR introduced OR non*native OR non*indigenous OR weed*) AND (compet* OR interference OR facilitat* OR interact*) AND (plant* OR tree* OR shrub* OR herb OR herbs OR forb* OR grass OR grasses OR graminoid* OR vine* OR liana* OR cact* OR sedge* OR fern*)) AND Research Area = (environment* NOT marine NOT agriculture). Next,

we conducted ISI Web of Science search of studies on competition among native species, explicitly excluding non-natives from the search combination: Topic = ((compet* OR interference OR facilitat* OR interact*) AND (plant* OR tree* OR shrub* OR herb OR herbs OR forb* OR grass OR grasses OR graminoid* OR vine* OR liana* OR cact* OR sedge* OR fern*) NOT (invasi* OR invad* OR alien OR exotic OR introduced OR non*native OR non*indigenous OR weed*)) AND Research Area = (environment* NOT marine NOT agriculture). We did not impose restrictions in terms of publication date and language on our searches. We carried out the two initial searches in September 2015 and updated our database on a weekly basis using the same search criteria via Web of Science alerts until December 2016. The two searches returned 27 854 publications. To select relevant studies, we first refined the results of the searches based on research area and journal title and then screened titles and abstracts of the remaining publications using a GUI screener included in the package *METAGEAR* (Lajeunesse 2016) in R v.3.3.1 (R Core Team 2016). The database was further supplemented with relevant publications cited in pre-selected studies and previous syntheses on plant interactions (Callaway 1995; Vilà & Weiner 2004; Bruno *et al*. 2005; Maestre *et al*. 2005; Lortie 2010; Bonanomi *et al*. 2011; Abella & Smith 2013; He *et al*. 2013; Iacarella *et al*. 2015; Kuebbing & Nuñez 2015).

Studies were included in our database if they met all the following criteria: (1) a manipulative study designed as an additive (including removal) or replacement series (see Appendix S2 for details on experimental designs of plant competition studies); (2) conducted in a field setting or under controlled conditions in terrestrial ecosystems excluding cropping systems; (3) a study system with two naturally co-occurring and taxonomically identified vascular plant species; (4) a target species deliberately planted into a natural or experimentally manipulated neighbour species community comprising at least one individual; (5) study design allowed for a full range of interaction mechanisms (i.e. studies looking only at allelopathy, root competition, etc. were not considered); (6) final total or aboveground biomass of a target species in a control and competition treatment measured via destructive harvesting and reported as either raw data or summary statistics. Out of 745 relevant studies, 192 studies published between 1981 and 2017 met our criteria and were used for statistical analyses (see Appendix S1).

Data collection

We extracted data using the following rules: (1) if both total and aboveground biomass were reported and/or measurements were taken repeatedly on the same sampling unit, results on total biomass and of the final measurement were included to avoid pseudoreplication (Gurevitch *et al*. 1992); (2) final biomass of each species in a competition treatment was considered an independent observation; (3) each unique combination of factors manipulated in a study was considered an independent observation (e.g. if a study looked at competition across multiple nutrient levels, we extracted data for each nutrient level). For each observation, we recorded final sample size, the mean and the standard deviation for the final biomass of a target species in a control and competition treatment. When the median and the range were reported, we used them to approximate the mean and the variance as in Hozo *et al*. (2005). Numeric data from figures were extracted using the software GetData Graph Digitizer (http://www.getdata-graph-digitizer.com). We checked and, if necessary, updated the names of plant species included in our data set and collected data on biogeographical origin and traits of plant species as well as on study details (see Data collection in Appendix S2 for more details). Our final data set contained 3415 observations, of which 1743 and 1672 corresponded to the additive and replacement series study design respectively. The data set included 471 species from 283 genera and 73 families.

To incorporate phylogenetic relatedness into our analyses and to test *the competition-relatedness hypothesis* (Cahill *et al*. 2008), we used a recently published molecular phylogeny of 32 223 land plant species (Zanne *et al*. 2014). The phylogeny was generated using a maximum likelihood approach based on data from seven gene regions (18S, 26S, ITS, matK, rbcL, atpB and trnLF) and calibrated using fossil data. The full phylogeny is available at the Dryad Digital Repository (https://doi.org/10.5061/dryad.63q27/). Out of 471 species represented in our data sets, 339 were included in the published phylogeny. We calculated pairwise phylogenetic distances among all species in the phylogeny using the function *'cophenetic.phylo'*, trimmed the published phylogeny to obtain phylogenies for target and neighbour species using the function *'drop.tip'*, and used the trimmed trees to calculate phylogenetic correlation matrices under the Brownian motion model of evolution using the function '*vcv.phylo'* in the package *ape* (Paradis *et al*. 2004) in R v.3.3.1 (R Core Team 2016).

Effect size calculation

We used the data from additive and replacement series experiments to calculate absolute net neighbour effects (ANNE) and relative net neighbour effects (RNNE) respectively. The ANNE was defined as the mean standardised difference between the final biomass of a species in the presence of a heterospecific neighbour vs. when grown in isolation. The RNNE was defined as the mean standardised difference between the final biomass of a species in the presence of a heterospecific vs. conspecific neighbour. ANNEs and RNNEs were quantified using Hedges' *d* effect size statistic. To assess the magnitude of competitive inequality within pairs of species, we calculated the absolute differences between reciprocal ANNEs ($N_{ANNE\ pairs}$ = 637). To assess the degree of competitive release when competing with hetero- vs. conspecifics, averaged across two species, we calculated the sums of reciprocal RNNEs ($N_{RNNE\ pairs}$ = 707; see *Effect size calculation* in Appendix S2 for more details). The four effect size statistics were analysed independently.

Statistical models

All statistical analyses were performed within a Bayesian multilevel modelling framework. The advantages of the Bayesian approach are that (1) all parameters are modelled with

uncertainty; (2) direct probability statements about quantities of interest can be made; (3) additional relevant information can be incorporated via priors (4) and importantly, complex data structures can be accommodated for (Sutton & Abrams 2001). To calculate the overall mean effects and assess heterogeneity, we initially developed two multilevel models, without and with phylogenetic correction; the latter can be written as:

$$EffectSize_i = \mu_i + a_{T_{k[i]}} + a_{N_{l[i]}} + s_{T_{k[i]}} + s_{N_{l[i]}} + q_{h[i]} + u_{j[i]} + e_i + m_i \quad (1)$$

$$\mu_i = b_0 + b_1 x_{1_i} \quad (2)$$

$$a_T \sim N(\mathbf{0}, \sigma^2_{a_T} \boldsymbol{A_T}) \quad (3)$$

$$a_N \sim N(\mathbf{0}, \sigma^2_{a_N} \boldsymbol{A_N}) \quad (4)$$

$$s_T \sim N(\mathbf{0}, \sigma^2_{s_T} \boldsymbol{I_T}) \quad (5)$$

$$s_N \sim N(\mathbf{0}, \sigma^2_{s_N} \boldsymbol{I_N}) \quad (6)$$

$$q \sim N(\mathbf{0}, \sigma^2_q \boldsymbol{I_{sdep}}) \quad (7)$$

$$u \sim N(\mathbf{0}, \sigma^2_u \boldsymbol{I_{study}}) \quad (8)$$

$$e \sim N(\mathbf{0}, \sigma^2_e \boldsymbol{I_{obs}}) \quad (9)$$

$$m \sim N(\mathbf{0}, \boldsymbol{M}) \quad (10)$$

where $EffectSize_i$ is the estimated effect size statistic for the ith observation ($i = 1, \ldots, N_{obs}$); μ_i is the overall mean for the ith observation; b_0 and b_1 are regression coefficients; x_{1_i} is the proportion of a target species in a competition treatment centred at 0.5 for the ith observation; $a_{T_{k[i]}}$ is the phylogenetic effect of the kth target species ($k = 1, \ldots, N_{target}$); $a_{N_{l[i]}}$ is the phylogenetic effect of the lth neighbour species ($l = 1, \ldots, N_{neighbour}$); $s_{T_{k[i]}}$ is the residual (i.e. not explained by phylogeny) effect of the kth target species; $s_{N_{l[i]}}$ is the residual effect of the lth neighbour species; $q_{h[i]}$ is the effect of the hth sampling dependency group (i.e. common control group) ($h = 1, \ldots, N_{sdep}$); $u_{j[i]}$ is the effect of the jth study ($j = 1, \ldots, N_{study}$); e_i is the residual effect of the ith observation; m_i is the measured sampling error associated with $EffectSize_i$; $\sigma^2_{a_T}$ is the phylogenetic variance at the target-species level; $\sigma^2_{a_N}$ is the phylogenetic variance at the neighbour-species level; $\sigma^2_{s_T}$ is the residual variance at the target-species level; $\sigma^2_{s_N}$ is the residual variance at the neighbour-species level; σ^2_q is the variance at the sampling-dependency-group level; σ^2_u is the study-level variance; σ^2_e is the residual variance; $\boldsymbol{A_T}$ is the N_{target} by N_{target} phylogenetic correlation matrix for target species; $\boldsymbol{A_N}$ is the $N_{neighbour}$ by $N_{neighbour}$ phylogenetic correlation matrix for neighbour species; $\boldsymbol{I_T}$ is a N_{target} by N_{target} identity matrix; $\boldsymbol{I_N}$ is a $N_{neighbour}$ by $N_{neighbour}$ identity matrix; $\boldsymbol{I_{sdep}}$ is a N_{sdep} by N_{sdep} identity matrix; $\boldsymbol{I_{study}}$ is a N_{study} by N_{study} identity matrix; $\boldsymbol{I_{obs}}$ is a N_{obs} by N_{obs} identity matrix; and $\boldsymbol{M}$ is a N_{obs} by N_{obs} diagonal matrix with sampling variances on the diagonal (see *Effect size calculation* in Appendix S2 for details on sampling variance calculation). The model without phylogenetic correction did not include the phylogenetic effects, a_T and a_N. We independently fitted the models without and with phylogenetic correction to the data on all ANNEs, all RNNEs, reciprocal ANNEs (a subset of the ANNE data set), reciprocal RNNEs (a subset of the RNNE data set), competitive inequality and competitive release. We analysed the data on reciprocal ANNEs and RNNEs because then the mean net outcome of pairwise competition could be assessed as the average across pairs of competing plant species, thus controlling for competitive inequality. In contrast, our full data sets contained multiple unpaired observations, which could potentially affect the estimates of the mean net neighbour effect of native on native and non-native on non-native plants. Data for analyses with phylogenetic correction were restricted to the species included in the published phylogeny (Zanne *et al.* 2014). To control for differences in the full and phylogeny-restricted data sets, we additionally performed analyses without phylogenetic correction on the phylogeny-restricted data sets.

To estimate the mean net neighbour effects for each of the four unique permutations of target and neighbour origins (i.e. native target and native neighbour; native target and non-native neighbour; non-native target and native neighbour and non-native target and non-native neighbour), we extended our two initial models by allowing the intercept, b_0, in eqn 2 to vary between the species origin permutations:

$$\mu_i = b_{0_{g[i]}} + b_1 x_{1_i} \quad (11)$$

where $b_{0_{g[i]}}$ is the regression intercept for the gth species origin permutation ($g = 1, 2, 3, 4$); and the other notations are as in eqn 2. To further explain heterogeneity that was captured at the study, species and observation levels, we iteratively augmented the initial models with additional predictors (e.g. study duration, global invasion status and N-fixing ability of species, etc.; see *Data Collection* in Appendix S2 for description of predictors and Table S1 in Appendix S5 for the full list of models). Continuous predictors were mean-centred and scaled prior to analyses to improve model fitting and facilitate across-model comparisons.

To test *the competition-relatedness hypothesis*, we independently assessed the relationship between the pair-averaged intensity of competition, competitive inequality and competitive release (response variable) and the target-neighbour phylogenetic distance (predictor) using an exponential function of the form $y = a(1 - e^{-bx})$. This non-linear function is rooted at 0, ranges from linear to asymptotic, and was previously shown to provide a good fit for the relationship between competition and phylogenetic relatedness (Godoy *et al.* 2014). When necessary, a response variable was centred around the minimum value prior to analyses to avoid negative values. We incorporated the exponential function into eqn 2 of our model with phylogenetic correction, allowing parameters a and b to vary depending on whether competing species were monocots or eudicots (Cahill *et al.* 2008):

$$EffectSize_i = \mu_i + a_{T_{k[i]}} + a_{N_{l[i]}} + s_{T_{k[i]}} + s_{N_{l[i]}} + q_{h[i]} + u_{j[i]} + e_i + m_i \quad (12)$$

$$\mu_i = a_{m[i]}(1 - e^{-b_{m[i]}x_{0_i}}) + b_1 x_{1_i} \quad (13)$$

where $EffectSize_i$ is the measured intensity of competition, competitive inequality, or competitive release; $a_{m[i]}$ and $b_{m[i]}$ are coefficients of the exponential function for the mth monocot/eudicot group ($m = 1$ when at least one species in a competing pair is a monocot; $m = 2$ when both species are eudicots); x_{0_i} is the phylogenetic distance between two species in the ith pair of reciprocal effects ($i = 1, \ldots, N_{pairs}$); and the other notations are as in eqns 1–2.

Computational implementation

Full Bayesian statistical inference was performed using the Hamiltonian Monte Carlo sampling algorithm implemented in the modelling software Stan (Carpenter *et al*. 2017). We used non-centred parametrisation for all grouping effects in our models, which allowed us to increase the sampling efficiency and directly estimate all variances (Betancourt & Girolami 2015; Stan Development Team 2016a). In all our models, the overall mean effects and predictors were given Normal(0, 5^2) priors and scale parameters σ^2 were given half-Normal(0, 5^2) priors, except for $\sigma^2_{a_N}$ and $\sigma^2_{a_T}$, which were modelled with Gamma(2, 2) priors. The parameters a and b in the relatedness-competition model (eqn 13) were given half-Normal(0, 5^2) and Gamma(2, 2) priors respectively. The chosen priors were weakly informative because they contained enough information to leave out unreasonable parameter values (i.e. regularise the extreme inferences that can be obtained using non-informative priors) while not restraining parameter estimation (Simpson *et al*. 2017). The inference regularisation allowed us to improve fitting and speed up convergence of the models with phylogenetic correction. For each model, we ran three chains with 20 000 iterations per chain, starting from default values. We used the first half of each chain as a warm-up and thinned the other half at the interval of 20, which resulted in a posterior sample of 1500 for each parameter. We used default settings for Stan, except for decreasing the initial step size from its default of 1 to 0.5 and increasing the target acceptance rate from 0.8 to 0.999 to avoid divergent transitions (Stan Development Team 2016a). To assess mixing, we visually examined traceplots and calculated autocorrelation in chains. We checked convergence with the potential scale reduction factor, $\hat{R}$, which is close to 1 at convergence (Gelman & Rubin 1992). All Bayesian analyses were performed in R v.3.3.1 (R Core Team 2016) using the package *rstan*, which provides an R interface to Stan (Stan Development Team 2016b). Stan code for all models is provided in Appendix S3.

Model evaluation and pairwise comparisons

To evaluate the predictive accuracy of our models, we performed approximate leave-one-out (LOO) cross-validations using Pareto smoothed importance sampling implemented in the package *loo* (Vehtari *et al*. 2016) in R v.3.3.1 (R Core Team 2016). The reliability of the method depends on the shape of the generalised Pareto distribution; we therefore assessed the values of the tail shape parameter k in each model to ensure that most values were between $-\infty$ and 0.7 (Vehtari *et al*. 2016). The results of the approximate LOO cross-validations were summarised with the LOO information criterion (LOOIC) and its standard error, both of which were as well estimated using the package *loo* (Vehtari *et al*. 2016) in R v.3.3.1 (R Core Team 2016). In addition, for our final models (i.e. models with the lowest LOOIC), we generated predicted values using the observed predictors' values (replicated data *sensu* Gelman *et al*. 2015) and graphically inspected discrepancies between observed and predicted values. An effect was considered significant if its 95% posterior credible interval did not contain zero. Similarly, two effects were considered significantly different if the 95% posterior credible interval of the difference between these effects (Δ) did not overlap with zero. Pairwise differences were not adjusted for multiple comparisons because the Bayesian multilevel approach, when applied in combination with appropriate, centred at no effect priors, provides highly conservative inference that does not require further correction for multiple comparisons (Gelman *et al*. 2012). Posterior distributions are reported as the posterior means and the 95% posterior credible intervals.

Quantifying heterogeneity

The reliability of the overall trend estimated by meta-analysis depends on the degree of consistency among individual studies (i.e. heterogeneity). Following the approach proposed by Nakagawa & Santos (2012), we quantified the total heterogeneity, σ^2_{tot}, as the sum of all variance components in a model; σ^2_{tot} in the model with phylogenetic correction was calculated as follows:

$$\sigma^2_{tot} = \sigma^2_{a_T} + \sigma^2_{a_N} + \sigma^2_{s_T} + \sigma^2_{s_N} + \sigma^2_q + \sigma^2_u + \sigma^2_e + \sigma^2_m \quad (14)$$

where σ^2_m is the total sampling variance; and the other notations are as above. The total sampling variance, σ^2_m, was estimated as follows:

$$\boldsymbol{P} = \boldsymbol{W} - \boldsymbol{W}\boldsymbol{X}(\boldsymbol{X}'\boldsymbol{W}\boldsymbol{X})^{-1}\boldsymbol{X}'\boldsymbol{W} \quad (15)$$

$$\sigma^2_m = \frac{k - p}{tr[\boldsymbol{P}]} \quad (16)$$

where $\boldsymbol{W}$ is a diagonal matrix with the inverse sampling variances on the diagonal; $\boldsymbol{X}$ is the design matrix; k is the number of observations; p is the number of columns in $\boldsymbol{X}$; and $tr[\boldsymbol{P}]$ is the trace of the $\boldsymbol{P}$ matrix. We calculated the relative amounts of heterogeneity captured by individual grouping effects as the ratio of the variance associated with a specific grouping effect to the total heterogeneity. Such approach to quantifying heterogeneity is an extension of the common practice of calculating the I^2 statistic (Higgins & Thompson 2002) to a multilevel meta-analytic setting (Nakagawa & Santos 2012). For example, the study-level heterogeneity, I^2_u, can be written as follows:

$$I_u^2 = \frac{\sigma_u^2}{\sigma_{tot}^2}. \quad (17)$$

Similarly, we quantified phylogenetic signals for target and neighbour species, H_T^2 and H_N^2, as the ratio of the phylogenetic variance for target and neighbour species respectively to the sum of all variance components in a model except for the total sampling variance, σ_m^2. Using the same notation, the two phylogenetic signals can be written as follows:

$$H_T^2 = \frac{\sigma_{a_T}^2}{\sigma_{a_T}^2 + \sigma_{a_N}^2 + \sigma_{s_T}^2 + \sigma_{s_N}^2 + \sigma_q^2 + \sigma_u^2 + \sigma_e^2} \quad (18)$$

$$H_N^2 = \frac{\sigma_{a_N}^2}{\sigma_{a_T}^2 + \sigma_{a_N}^2 + \sigma_{s_T}^2 + \sigma_{s_N}^2 + \sigma_q^2 + \sigma_u^2 + \sigma_e^2}. \quad (19)$$

The phylogenetic effects, H_T^2 or H_N^2, range between 0 and 1 and are equivalent to Pagel's λ (Pagel 1999) (discussed in Nakagawa & Santos 2012).

Publication bias

Publication bias occurs whenever the research that appears in the published literature is systematically unrepresentative of the population of completed studies (Rothstein *et al.* 2005). The most commonly addressed type of publication bias is when statistically significant results have a higher chance to be published than otherwise (i.e. the 'file drawer problem'; Rothstein *et al.* 2005). We tested for the presence of this type of bias in our data by exploring asymmetry in funnel plots. We visually inspected contour-enhanced funnel plots (Peters *et al.* 2008) of the posterior means of meta-analytic residuals (i.e. the sums of observation-level errors, e_i and sampling errors, m_i) of our final models against precisions (i.e. inverse of sampling errors, w_i) created with the package *meta* (Schwarzer 2007) in R v.3.3.1 (R Core Team 2016). In addition, we performed an Egger's regression analysis on the posterior means of meta-analytic residuals as described in Nakagawa & Santos (2012). The modified Egger's regression model can be written as follows:

$$\boldsymbol{o} \sim N(b_0 + b_1\sqrt{\boldsymbol{w}}, \sigma_o^2\boldsymbol{I}) \quad (20)$$

$$o_i = (e_i + m_i)\sqrt{w_i} \quad (21)$$

where b_0 and b_1 are regression coefficients; σ_o^2 is the residual regression variance; $\boldsymbol{I}$ is a N_{obs} by N_{obs} identity matrix; e_i is the observation-level (i.e. residual) error for the ith observation ($i = 1, \ldots, N_{obs}$); m_i is the sampling error associated with the ith effect size; w_i is the inverse of the sampling variance associated with the ith effect size. When the intercept, b_0, is significantly different from zero, one concludes that there is evidence for publication bias (Nakagawa & Santos 2012). Meta-analytic residuals were used instead of initially proposed effect size estimates because non-independence of effect sizes violated the assumptions of the original methods (Egger *et al.* 1997; Peters *et al.* 2008). We also tested for time-lag bias, which occurs when effect size correlates with publication date, by including the year of publication as a predictor in our initial models (Trikalinos & Ioannidis 2005).

RESULTS

Net neighbour effects

Overall, target plants were negatively affected by the presence of a heterospecific neighbour (overall mean ANNE: −1.06 [−1.25, −0.86]; overall mean reciprocal ANNE: −0.95 [−1.19, −0.72]). However, the magnitude of competitive suppression varied with biogeographical origin of a target and a neighbour species (Fig. 1). The results on all data were largely consistent with the results on reciprocal net neighbour effects (Fig. 1) and none of those were affected by phylogenetic correction (Fig. 2). Non-native neighbours were, on average, equally strong suppressors against heterospecific native and heterospecific non-native plants (Δ all ANNEs: 0.01 [−0.22, 0.25]; Δ reciprocal ANNEs: −0.02 [−0.26, 0.24]; Fig. 1a,c). Likewise, the mean absolute effect of native on native was comparable to that of native on non-native (Δ all ANNEs: −0.13 [−0.32, 0.07]; Δ reciprocal ANNEs: −0.22 [−0.46, 0.01]; Fig. 1a,c). The mean absolute effect of non-native on native was not different from the effect of native on native (Δ all ANNEs: −0.18 [−0.38, 0.01]; Δ reciprocal ANNEs: −0.07 [−0.27, 0.14]; Fig. 1a,c). At the same time, non-natives were significantly less affected by the presence of a heterospecific native than heterospecific non-native neighbour (Δ all ANNEs: 0.30 [0.07, 0.52]; Δ reciprocal ANNEs: 0.32 [0.09, 0.55]), whereas natives were more affected by the presence of a heterospecific non-native than vice versa (Δ all ANNEs: −0.31 [−0.53, −0.10]; Δ reciprocal ANNEs: −0.29 [−0.56, −0.06]; Fig. 1a,c).

On average, native plants were more suppressed by hetero- than conspecific neighbours, whereas for non-native plants, the intensities of intra- and interspecific competition were nearly equal (Fig. 1b,d). In agreement with the results on the absolute effects, native plants were not more suppressed by heterospecific non-native than heterospecific native neighbours, as compared to conspecific neighbours (Δ all RNNEs: −0.12 [−0.52, 0.29]; Δ reciprocal RNNEs: −0.34 [−0.85, 0.17]; Fig. 1b,d). In the meantime, relative to interspecific competition, non-natives tended to compete more intensely with heterospecific non-native than heterospecific native neighbours, yet this was significant only when all data were analysed (Δ all RNNEs: −0.49 [−0.96, −0.04]; Δ reciprocal RNNEs: −0.34 [−0.85, 0.17]; Fig. 1b,d).

The slope associated with the proportion of a target species in the competition treatment was significantly positive across all models on the net neighbour effects.

Competitive inequality and competitive release

Overall, pairs of competing species differed in terms of their absolute effects on each other (overall mean competitive inequality: 1.23 [1.03, 1.45]); yet the magnitude of competitive inequality varied across the three origin-defined types of two-species combinations (Fig. 3a). Specifically, pairs of native species had, on average, more similar competitive abilities than non-native heterospecific pairs (Δ competitive inequality: 0.39 [0.02, 0.76]); meanwhile, competitive inequality across native–non-native pairs did not significantly differ from that of native (Δ competitive inequality: 0.21 [−0.02, 0.45]) and

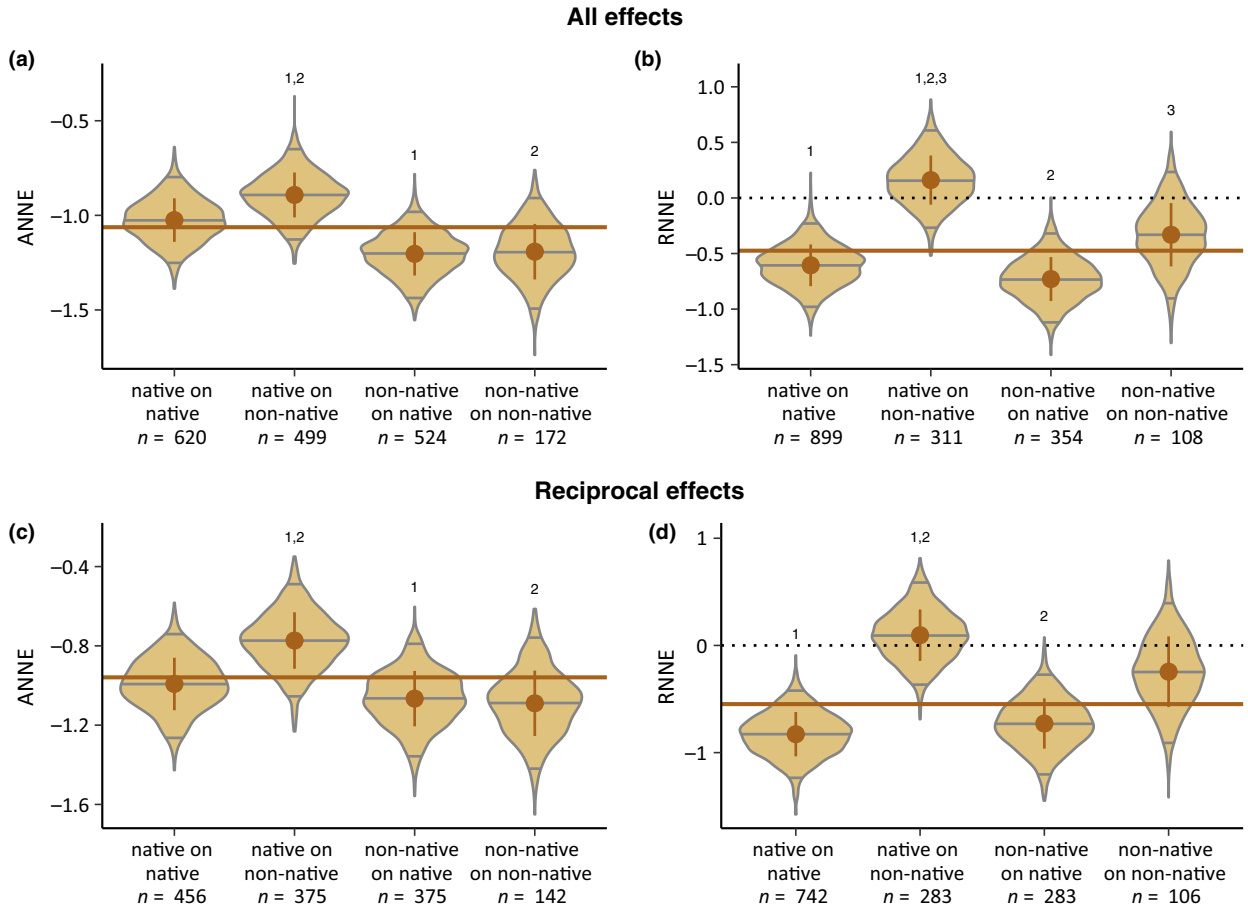

Figure 1 On average, non-native plants were less affected by competition from heterospecific native than heterospecific non-native (a, c) but not conspecific neighbours (b, d). Native plants were equally suppressed by heterospecific native and heterospecific non-native neighbours (a, c) and these effects were stronger than those of conspecific neighbours (b, d). Polygons are mirrored posterior kernel density plots, within-polygon horizontal lines from the bottom are 2.5, 50 and 97.5% posterior quantiles, within-polygon points are the posterior means and within-polygon vertical lines are the posterior standard deviations. Solid horizontal lines are the posterior mean estimates for the overall meta-analytic means. Indexes above the polygons indicate significant pairwise differences (95% credible interval does not include zero).

non-native pairs (Δ competitive inequality: −0.18 [−0.46, 0.13]; Fig. 3a). The magnitude of competitive release in inter- vs. intraspecific competition in native–non-native pairs was higher than in native pairs (Δ competitive release: 0.91 [0.05, 1.75]), but not different from that in non-native pairs (Δ competitive release: −0.15 [−0.99, 0.68]; Fig. 3b). Phylogenetic correction did not affect these results (Fig. 3c,d).

Sources of heterogeneity and model comparison

Without phylogenetic correction, unexplained heterogeneity constituted 85.6 [83.6, 87.7]% and 81.0 [77.1, 84.8]% of the total heterogeneity for ANNEs and 90.8 [89.7, 92.0]% and 91.2 [89.8, 92.6]% of the total heterogeneity for RNNEs in the data sets on all and reciprocal effects respectively. Significant amounts of heterogeneity were captured at all levels across all data sets, with the study and observation levels consistently being the most and the least important sources of heterogeneity respectively (Fig. 4a,b). In the ANNE data, the second largest amount of heterogeneity arose due to clustering at the sampling-dependency-group level (i.e. due to the use of common controls), followed by heterogeneity at the neighbour- and target-species levels. In the RNNE data, more heterogeneity was captured at the neighbour- and target-species than sampling-dependency-group level (Fig. 4a,b). Interestingly, when only reciprocal effects were analysed, the amounts of heterogeneity at the neighbour- and target-species levels were almost equal for both ANNEs and RNNEs (Fig. 4a,b). Heterogeneity patterns in the models with phylogenetic correction largely followed those in the models without phylogenetic correction (Fig. 4c,d). We detected significant yet very weak phylogenetic signals among neighbour species (all ANNEs: 0.08 [0.01, 0.23]; reciprocal ANNEs: 0.10 [0.01, 0.28]; all RNNEs: 0.15 [0.01, 0.40]; reciprocal RNNEs: 0.07 [0.001, 0.28]) and target species (all ANNEs: 0.05 [0.003, 0.15]; reciprocal ANNEs: 0.1 [0.005, 0.27]; all RNNEs: 0.07 [0.002, 0.20]; reciprocal RNNEs: 0.06 [0.001, 0.26]).

Additional predictors only slightly improved the models (Table S1 in Appendix S5). Globally invasive plant species were significantly stronger suppressors than globally non-invasive species (Δ from the overall mean effect: −0.33 [−0.60,

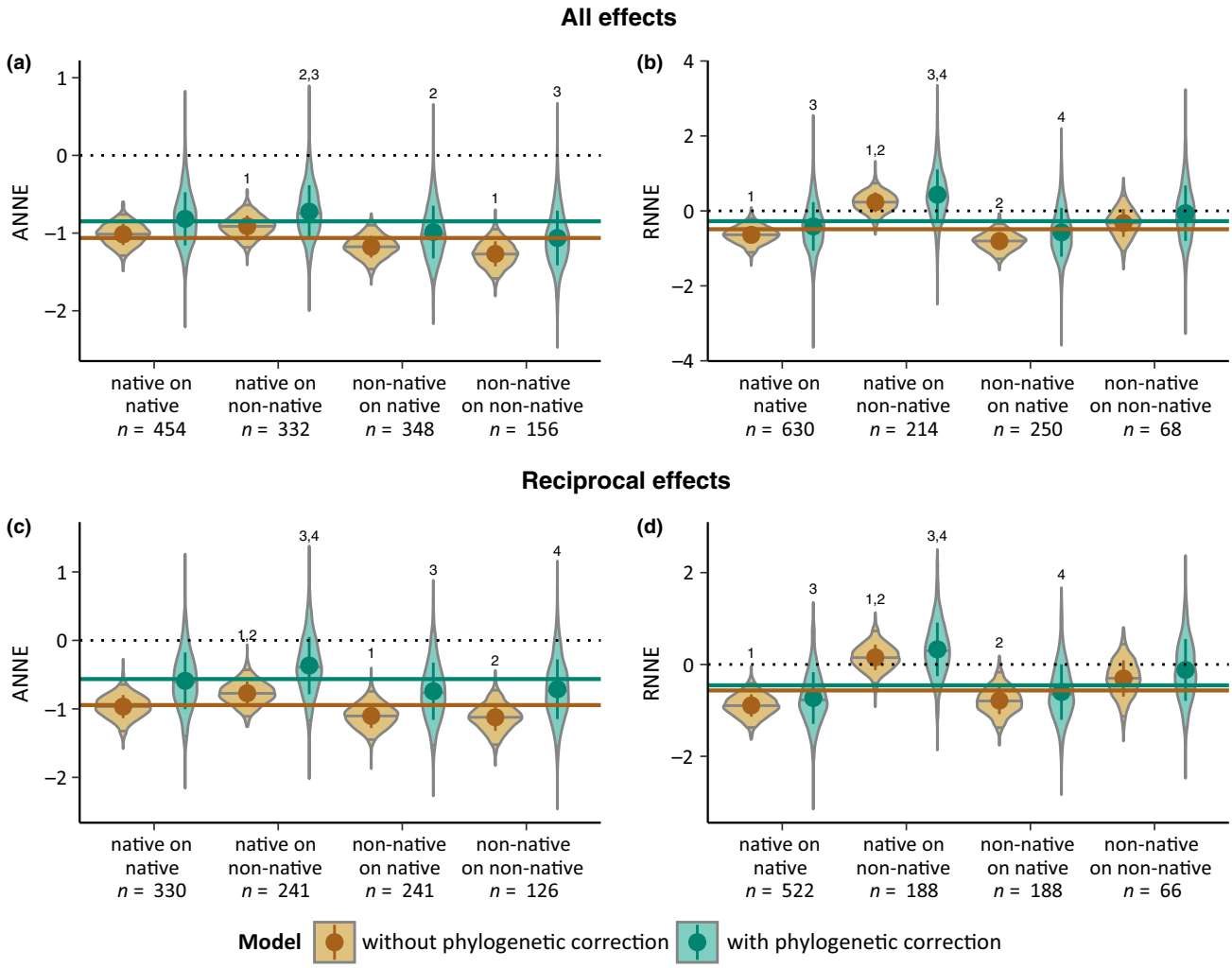

Figure 2 Phylogenetic correction did not change the overall conclusions of the meta-analyses: non-native plants were less affected by heterospecific native than heterospecific non-native (a, c) but not conspecific neighbours (b, d), whereas native plants were equally suppressed by heterospecific native and non-native neighbours (a, c) and the magnitude of heterospecific suppression was higher than of conspecific suppression (b, d). Note that the results are for the species included in the phylogeny (Zanne *et al.* 2014). Other details are as in Fig. 1.

−0.06]); however, this pattern disappeared after we accounted for local invasion status. N-fixers were more affected by heterospecific competition than non-N-fixers (−0.35 [−0.67, −0.02]), regardless of whether a neighbour was an N-fixer or not. Trees exhibited significantly weaker competitive effects in comparison to other life habit types (0.51 [0.09; 0.95]). In addition, neighbour effects tended to be more negative in tropics than on average (−1.78 [−3.24, −0.27]) and as the duration of experiment increased (regression slope: −0.11 [−0.23, 0.01]). Experimental setting and the presence of soil microbiota did not have consistent effects on ANNEs. Relative to conspecific neighbours, heterospecific perennials, especially trees, were less suppressive than other life forms (perennial: 0.49 [0.03, 0.94]; tree: 1.00 [0.28, 1.77]). In water-stressful environments, heterospecific neighbours, particularly those with the CAM photosynthetic pathway type, tended to have positive effects compared to conspecific neighbours (desert habitat: 3.98 [0.93, 6.99]; CAM photosynthesis: 8.71 [2.71, 14.91]). Other predictors did not have consistent effect on RNNEs. Overall, both our initial and extended models had high predictive accuracy (Fig. S1 in Appendix S4).

The competition-relatedness hypothesis

We were not able to provide support for *the competition-relatedness hypothesis*. The exponential curves reached the plateau almost immediately, indicating lack of the relationship of phylogenetic distance with the intensity of competition (Fig. S2a, b in Appendix S4), competitive inequality (Fig. S2c) and competitive release (Fig. S2d).

Publication bias

We detected a significant funnel plot asymmetry towards highly negative effects sizes with small precisions (Fig. S3 in Appendix S4). Year of publication did not explain any

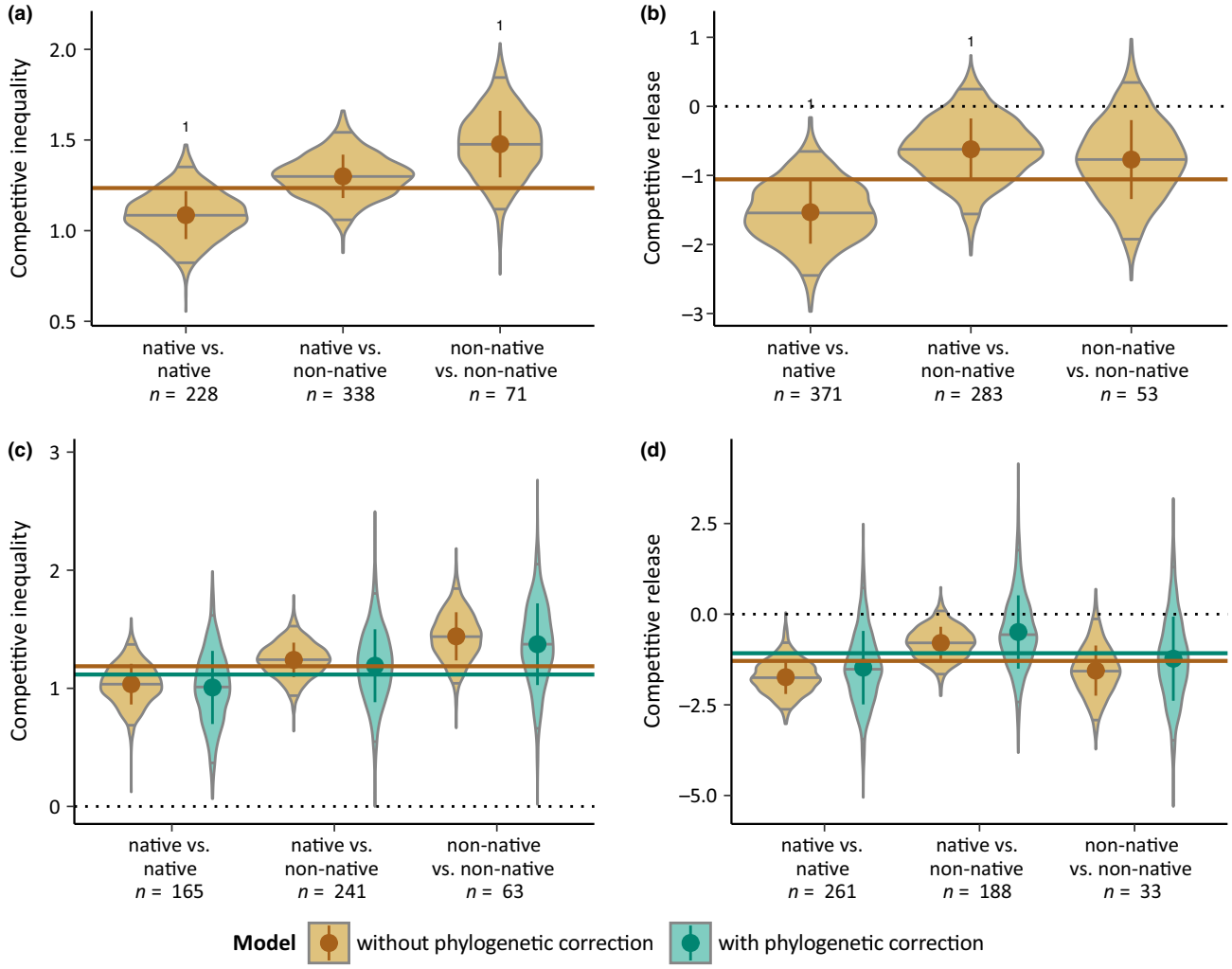

Figure 3 Averaged across species pairs, paired natives were less different in terms of their effect on each other than paired non-natives but not than paired native and non-native species (a). Native–non-native species pairs experienced greater degree of competitive release in inter- vs. intraspecific competition than native but not non-native species pairs (b). Phylogenetic correction did not affect the results of pairwise comparisons (c, d). Note that the results in (c, d) are for the species included in the phylogeny (Zanne *et al.* 2014). Other details are as in Fig. 1.

heterogeneity in the data, pointing to the absence of time-lag bias (model 13 in Table S1).

DISCUSSION

Net neighbour effects

Our synthesis showed that in a heterospecific competitive setting, non-native plants tend to outperform native plants, hence agreeing with the findings of previous meta-analyses (Vilà & Weiner 2004; Kuebbing & Nuñez 2016). However, contrary to the predominant view of non-natives as strong competitive suppressors (Levine *et al.* 2003; Kuebbing & Nuñez 2016), we showed that competitive advantage of non-native plants is primarily due to their low responsiveness (i.e. high tolerance) to the presence of a native neighbour and not because the degree of suppression they impose on natives is higher than that among natives (Fig. 1a,c). The observed discrepancy with earlier syntheses (Vilà & Weiner 2004; Kuebbing & Nuñez 2016) could be due to methodological differences, particularly differences in study inclusion criteria and statistical approach. For example, we considered only results of manipulative studies that were presented as individual plant biomass (as opposed to combining data from manipulative and observational studies on multiple traits). Furthermore, we used the Bayesian multilevel modelling approach, which imposes shrinkage on estimated group-level parameters and, in combination with zero-centred priors, provides highly conservative inference (Gelman *et al.* 2015).

Importantly, competitive tolerance of non-natives was evident in relation to heterospecific native but not heterospecific non-native plants, suggesting that this strategy is more likely to be driven by the distinct eco-evolutionary context in the introduced range rather than by the inherent ability of non-natives to withstand competition (Fig. 1a,c). This result is in agreement with several empirical studies that showed low responsiveness of non-native plants to the presence of natives

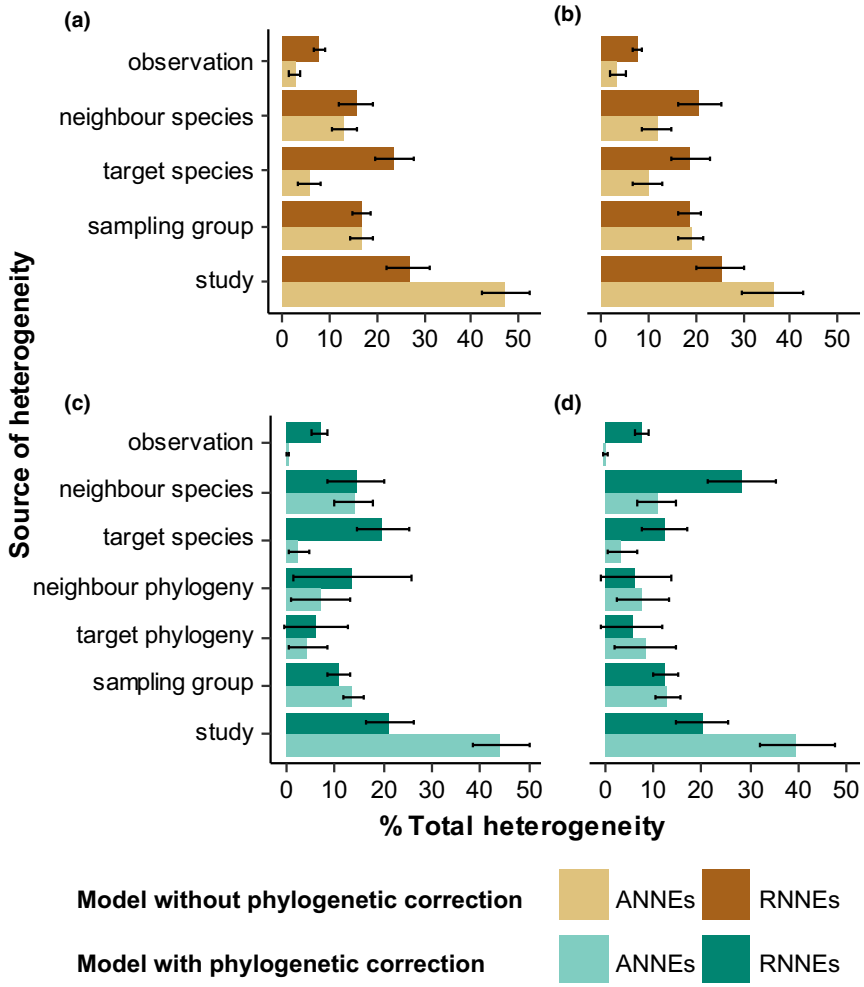

Figure 4 Distribution of unexplained heterogeneity among different levels in multilevel meta-analyses on pairwise plant competition. Bars are the posterior means and whiskers are the posterior standard deviations.

(Bakker & Wilson 2001; Suding *et al*. 2004; Maron & Marler 2008; French 2012; Mason *et al*. 2012) and extends the earlier finding that non-native plants experience lower level of interspecific competitive suppression in the introduced relative to native range (Callaway *et al*. 2011; Sun *et al*. 2014). Several non-mutually inclusive mechanisms could potentially lead to high tolerance of non-natives in regard to native heterospecifics. As one plausible explanation, non-natives might have evolved in highly competitive environments, which provided them with an advantage when introduced to environments with lower intensity of interspecific competition than at home. This is in line with *the evolutionary imbalance hypothesis*, which relies on the assumption that species from different parts of the world differ in their efficiency in converting resources into offspring for a given type of environment (Fridley & Sax 2014). Alternatively, non-native species might possess traits that allow them to fill in an 'empty' niche and thus partially avoid competition with natives. For example, Suding *et al*. (2004) experimentally demonstrated that *Centaurea diffusa* attained neighbour tolerance via its ability to effectively use phosphorus, which was not a limiting resource for natives. Importantly, under such circumstances, competitive tolerance of non-native plants can be overridden by forcing them to compete with other species for the same resource (Suding *et al*. 2004; Pearson *et al*. 2017). Lastly, heterospecific neighbour tolerance of non-natives could be at least to a certain extent the product of coevolution with native plant species, geared towards long-term persistence in the new range (Huang *et al*. 2017).

Native and non-native plants were clearly distinguished from one another in terms of their response to inter- vs. intraspecific competition. Differential response to inter- vs. intraspecific competition has been repeatedly documented and interpreted as evidence for the prevalent role of competitive hierarchy (here defined in terms of the relative ability to suppress) compared to niche differentiation in structuring native plant communities (Willson *et al*. 1987; Argyres & Schmitt 1992; Goldberg & Barton 1992). Specifically, weak competitors are expected to perform better in the presence of con- than heterospecifics, whereas strong competitors often do better when surrounded by hetero- relative to conspecifics (Stoll & Prati 2001; Lambers *et al*. 2004). However, this pattern did not fully hold for native vs. non-native species in our study. Although we found that natives were less suppressed by hetero-

than conspecifics, the origin of a heterospecific neighbour was of no importance (Fig. 1b,d). Moreover, the effect of a heterospecific neighbour on non-natives was not consistently smaller than that of a conspecific neighbour, as would be expected if non-natives were strong suppressors (Fig. 1b,d). Nevertheless, when averaged across competitors, native–non-native pairs were to a larger degree released from competition in a hetero- vs. conspecific setting than native species pairs, supporting our previous statement that non-natives are competitively tolerant in regard to heterospecific natives (Fig. 3b).

Notably, the distinction between native and non-native species in terms of the magnitude of competitive release in inter- vs. intraspecific competition was due to their differential response to both hetero- and conspecifics. As collectively suggested by our results, non-natives were, on average, more affected by intraspecific competition than native species (note that we were not able to directly measure the intensity of interspecific competition because of the limitations of the experimental designs of individual plant competition studies). This is inconsistent with a recent study by Müller *et al.* (2016), who showed that biogeographical origin does not explain the intensity of competition with conspecifics. However, other lines of evidence suggest possible reasons for the observed difference. For example, the relative reduction in biomass in intraspecific competition might positively correlate with plant's biomass in isolation (Freckleton & Watkinson 2001). This pattern might hold in our data as we found that within native–non-native species pairs, biomass of individual non-native plants was, on average, greater than that of native plants (0.92 [0.00, 1.87]). Moreover, it has been shown that there is a trade-off between intra- and interspecific competitive ability at least in some non-native plant species (Lankau & Strauss 2007; Lankau 2009) and that non-native species may evolve towards increased intensity of intraspecific competition (Huang & Peng 2016), which could be as well reflected in our data.

On average, non-natives were less equivalent in terms of their competitive effects on each other than native species; meanwhile, at odds to our expectation, pairs of native and non-native species did not significantly differ in their competitive inequality neither from non-native, nor from native species pairs (Fig. 3a,c). Given the fact that the native ranges of competing non-natives always overlapped, strong reciprocal suppression among non-natives could be attributed to higher intensity of interspecific competition in their home vs. introduced range, as discussed previously. Alternatively, competition between non-native species could be exacerbated upon embedding them into a new ecological context, but this requires additional testing. Strong competition among non-natives can potentially affect the structure and dynamics of invaded plant communities, leading to increased biotic resistance to future invasions compared to uninvaded communities. For example, soil nutrient and moisture pre-emption in non-native-dominated communities have been shown to hamper establishment of other non-native plants (Berube & Myers 1982; Davies *et al.* 2010). Similarly, non-native species can be more effective than natives in preventing previously dominant invasive species from re-establishment (Davies *et al.* 2015). Our understanding of plant species competition and coexistence in invaded communities will be greatly enhanced by further research on multiple non-native species.

Heterogeneity

Heterogeneity in our data was mainly concentrated at the study level, indicating much higher similarity of effect sizes within than between studies (Fig. 4). This heterogeneity remained largely unexplained since none of the predictors at the study level showed a consistent effect. The use of a common control for calculating effect sizes was the second most important source of heterogeneity, followed by species-specific effects (Fig. 4). At the species level, we showed that N-fixers were less tolerant to competition, but not necessarily less suppressive of their neighbours than non-N-fixers. The latter, however, should not be considered in conflict with the extensive evidence on the facilitative role of N-fixers (Gómez-Aparicio *et al.* 2008). The spatial and temporal scale captured by our data was too small for detecting facilitation (Bruno *et al.* 2003). Moreover, soils used in competition experiments might have been initially rich in nitrogen, which could negatively affect competitive ability of N-fixers or mitigate their positive effect on neighbours (Harpole & Tilman 2007). Phylogenetic relatedness among neighbour and target species explained only little heterogeneity in the data, and correcting for it did not affect the overall results (Figs. 2, 3). Furthermore, in agreement with previous studies (Cahill *et al.* 2008; Dostál 2011; Fritschie *et al.* 2014; Godoy *et al.* 2014; Feng & van Kleunen 2016), we were unable to provide support for *the relatedness-competition hypothesis*. As previously suggested, lack of the relationship between phylogenetic relatedness and plant competition and coexistence might be because phylogeny does not precisely capture average fitness differences and stabilising niche differences among species (Godoy *et al.* 2014). Notably, the amount of heterogeneity remaining after accounting for all the known correlative structures (i.e. residual heterogeneity) was negligible, or put another way, variation in the data occurred at the levels higher than individual observation. The presence of multiple crossed dependencies within our data once again highlights the high context-dependent nature of the process of plant competition. We therefore highly encourage the use of a multilevel approach in future syntheses on plant competition and invasion.

Publication bias

We detected a significant negative asymmetry in funnel plots, suggesting that our inference could be potentially biased towards negative effect sizes (Fig. S3). We were not surprised by this as the bias in reporting and interpretation of the results towards significant negative effects has long been recognised among studies on species competition and invasion (Connell 1983; Warren *et al.* 2017). However, in contrast to the high sensitivity to extreme values of the methods used for detecting publication bias (the significance of the Egger's regression intercept was driven by roughly 6 and 3% of the ANNE and RNNE data respectively), our analyses were robust to potential outliers (Fig. S1). Moreover, our data were not systematically biased towards one origin group, which

suggests that origin-level comparisons are largely unaffected by publication bias. More importantly, we stress that the results of this study are representative of the short-term outcomes of competition in two-species systems under not necessarily realistic conditions and therefore might not scale up to community-level patterns (see Duralia & Reader 1993; Dormann & Roxburgh 2005; Engel & Weltzin 2008; Martorell & Freckleton 2014 for further discussion). Moreover, we used individual plant biomass as a proxy for fitness, yet biomass and fitness are not always positively correlated (e.g. Colautti & Barrett 2013). When possible, future studies on the role of origin in plant competition should incorporate indirect effects that arise in systems with three and more species and assess the outcome of competition directly in terms of fitness.

Concluding remarks

Our study demonstrated that non-native plants are competitively different from their heterospecific native counterparts in several ways. Specifically, we showed that, contrary to what is commonly believed, neighbour tolerance and not neighbour suppression allows non-natives to outperform native plants in a two-species setting. Interestingly, even though non-natives were less affected by heterospecific natives than vice versa, their overall performance when surrounded by natives was often not enhanced in comparison to that in the presence of conspecifics. We also showed that both inter- and intraspecific competition tended to be more intense among non-natives that among natives. Collectively, our results suggest that reduced intensity of interspecific competition in the introduced compared to native range plays an important role in the success of non-native plant species.

It remains unknown to what degree competitive tolerance of non-natives is driven by their distinct eco-evolutionary history and to what degree it is a product of rapid evolution in the introduced range. If competitive tolerance has high adaptive potential in the novel range, we might expect to see its increase in non-native plants over time (e.g. Huang *et al.* 2017). Similarly, we are limited in our knowledge on how native plants evolve in response to competition from non-native neighbours (Strauss *et al.* 2006). A handful of studies showed than native plants can develop tolerance towards their novel counterparts (e.g. Callaway *et al.* 2005; Lau 2006), and this could to a certain extent explain why native plants responded similarly to native and non-native neighbours in our study. Future studies that experimentally manipulate both competition and selection would greatly improve our understanding of the role of competition in plant invasions.

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AUTHORSHIP

MG and KFW conceived and designed the study. MG collected data, performed statistical analyses and wrote the first draft of the manuscript. KFW obtained funding and contributed to revisions.

DATA ACCESSIBILITY STATEMENT

Data available from the Figshare digital repository (https://doi.org/10.6084/m9.figshare.5868699).

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