

Higher establishment success in specialized parasitoids: support for the existence of trade-offs in the evolution of specialization

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Summary

1. Most animals do not feed on all the resources available to them, but the mechanisms behind the evolution of dietary specialization are still debated. A central but unanswered question is whether specialists generally gain fitness advantages on their resource compared to generalists, experiencing a trade-off between the ability to use a broad range of resources and the fitness reached on each single one.

2. Empirical tests so far suffered from difficulties in measuring fitness; they were restricted to few species, and results were equivocal. This lack of support for the importance of trade-offs gave rise to theories explaining the evolution of specialization without such trade-offs.

3. Using a large dataset of intentional biological control introductions of 254 species of parasitoids from 15 families to locations outside their native range, we show that establishment success, a measure of total fitness, is higher in specialized species. This result holds when controlling for possible confounding factors such as the number of introduced individuals (propagule pressure).

4. The outcome of this study provides robust evidence that dietary specialization implies fitness advantages in an entire species-rich taxon, indicating that trade-offs might be widely involved in the evolution of specialization.

Key-words: biological control, establishment success, evolution of specialization, fitness advantages, fitness trade-offs, host range, parasitoids

Introduction

Dietary specialization is a widespread life strategy in animals. Most species use only a small portion of all the potential food types available, thereby limiting their nutritional resources (Fox & Morrow 1981). However, the mechanisms underlying the evolution of dietary specialization are still the subject of debate. The major hypothesis for diet restriction assumes that optimizing resource use implies physiological and morphological adaptations (Futuyma & Moreno 1988; Jaenike 1990; Fry 1996; Forister *et al.* 2012). Because species have limited adaptive capacities (Bernays & Wicislo 1994; Kotler & Mitchell 1995; Bernays & Funk 1999; Henry, Roitberg & Gillespie 2008), adaptation cannot be achieved towards an unlimited number of resources. These intrinsic limits preclude investing in using different resources without suffering a cost in terms of optimal exploitation of each single one of them;

species that specialize and increase their performance on one food type thus should have a decreased performance on others. Because of this trade-off, the hypothesis assumes the existence of fitness advantages when a specialist species feeds on its elected resource.

Several studies question fitness trade-offs associated with different food types as an essential condition for natural selection to favour specialization; they argue that evolutionary pathways leading to specialization are driven by genetic dynamics not necessarily involving fitness trade-offs (reviewed in Forister *et al.* 2012). For instance, Fry (1996) showed that natural selection can favour specialization, if alleles that are positively selected on one host are less positively selected or neutral, but not necessarily deleterious, on another host. Kawecki (1998) demonstrated theoretically that, if there is genetic variation in host preference, an initially generalist parasite population can evolve towards specialized host races, each choosing one host species. He showed that the genetic lineage of a parasite that evolves host preference becomes more consistently exposed

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to selection for performance on its preferred host, causing it to coevolve faster in response to evolving host defences than does a generalist lineage distributed among several host species. This mechanism does not require genetic trade-offs in performance on different host species because the ability of the parasite to overcome the resistance of different host species is to a large degree genetically independent (Kawecki 1998).

According to the trade-off hypothesis, specialists should have on average higher fitness than generalists when feeding on one of their preferred food types, while hypotheses without trade-offs would predict on average no fitness difference between specialists and generalists. Experimental evidence for any of these hypotheses is, however, limited and equivocal; some studies demonstrated better performance of specialists over generalists on their respective food sources while others failed to do so (Jaenike 1990; Fry 1996; Scheirs, Jordaens & De Bruyn 2005; Agosta & Klemens 2009; Forister *et al.* 2012).

Experimental tests of fitness advantages of specialization so far suffer from two major shortcomings. First, dietary specialization was investigated within single species or by comparing the performance of species pairs or of a small number of closely related species of varying degree of host specialization. In such experiments the effect of specialization cannot be distinguished from other differences among the investigated species that affect their fitness. Moreover, variation in average fitness among different species of specialists and generalists can lead to spurious effects (or mask real effects) when comparing only few species. Thus, it is difficult to assess in experiments with few species how general fitness advantages of specialization are. Second, experimental studies on fitness advantages of specialization were restricted to measures of fitness components such as body size, fecundity and survival rates, but did not investigate total fitness (e.g. per capita population growth rate), which is difficult to measure since it requires that study populations be followed over more than one generation. Effects on single fitness components, however, may or may not translate into effects on total fitness because other life-history traits may counterbalance their impact (Stephens, Sutherland & Freckleton 1999; Zaugg, Benrey & Bacher 2013). Comparative studies on trade-offs due to dietary specialization involving a large number of species did not study fitness advantages directly, but used population abundance or parasitism rate as an indirect indicator of host use efficiency, also with mixed results (Poulin 1998; Straub, Ives & Gratton 2011).

In the present study, we overcome these issues by testing for total fitness advantages of dietary specialization in 256 species of parasitic wasps, so-called parasitoids, from 16 families of the order Hymenoptera. Hymenopteran parasitoids are one of the major insect groups comprising more than 20 families and probably more than one million species (Godfray 1994; Bacher 2012). Their common characteristic is to parasitize other insect species by laying their eggs upon or inside the host's body, where hatching larvae

develop and eventually kill the host. Within parasitic hymenopterans, all degrees of diet breadth are found; however, narrow host ranges characterize most species (Godfray 1994). While generalist parasitoids parasitize many different host species, each individual wasp completes its entire development on one single host individual and thus comes into contact with only one host species during its larval life. Parasitic hymenopterans have been widely used to control insect pests; thus, there is detailed and reliable information about their biology and host range. Parasitoids used for classical biocontrol are introduced to locations outside their native range to an area infested with an exotic pest that is one of their natural hosts in an attempt to reduce its density (Bellows & Fisher 1999). Approximately one-third of the intentional parasitoid introductions have resulted in establishment (Stiling 1990).

A population can be considered as established if at least one individual leaves a persistent line of descendants (Leung, Drake & Lodge 2004). The success of establishment is determined by chance events, the level of adaptation of the parasitoids to the new environment (e.g. to habitat or climate), the fitness (among other factors determined by the level of adaptation to their host) and number of the individuals released (Lockwood, Cassey & Blackburn 2005). High release numbers will mitigate stochastic and Allee effects and eventually make an introduction programme more likely to succeed. In releases for biological control, availability of resources can be considered as not limiting establishment because the hosts are considered pests and thus occur in abundance in release areas.

The establishment probability P is a measure of the average total fitness of the individuals released, because individuals that produce on average more surviving offspring (i.e. fitter individuals) have a higher chance of leaving a persistent lineage. Total fitness is typically measured as *per capita* growth rate [$r = b$ (birth rate) $- d$ (death rate)] (Odum & Allee 1954), which is related to the probability that an individual will establish [$P = 1 - (d/b) = r/b$ when $b > d$, and zero otherwise] (Dennis 2002; Drake 2004). Thus, if specialization towards a few hosts generally is accompanied by fitness advantages, we expect parasitic wasps with narrow host ranges to have on average higher establishment success on any one of their hosts than wasps with broad host ranges on any host of theirs.

Biocontrol experiments are ideally suited to answer questions about the evolution of specialization, because (i) both specialists and generalists are forced to develop on a single, unlimited resource: the pest against which they are released, and (ii) the probability that a founder population will establish a persistent population is a measurement of the total fitness of the species on that host. Parasitoids are further an ideal group to study fitness advantages of dietary specialization because parasitoids develop on a single host individual. Thus, individuals of generalist and specialist parasitoid species both use only one food source during their entire larval life and do not mix diets or switch to alternative hosts. In other groups, such as phytophagous

insects, generalists may need to feed on more than one food source to ensure normal development (Waldbauer & Friedman 1991), and therefore, it is difficult in these groups to disentangle effects of trade-offs on fitness from effects due to lack of dietary mixing. We analyse data on releases that were carried out in a standardized way, for example, where the number of individuals released and the fate of the population was recorded, thus allowing us to compare a large number of species differing in their degree of specialization. To our knowledge, this is the most comprehensive test of the generality of fitness advantages due to dietary specialization for a large taxonomic group and the first test that measures total fitness.

Methods

DATA

We compiled a database on releases of parasitoids on one of their insect hosts from reports on classical biological control (McGugan & Coppel 1962; McLeod 1962; Anonymous 1971; Greathead 1971, 1976; Rao *et al.* 1971; Clausen 1978; Kelleher & Hulme 1981; Cock 1985; Cameron *et al.* 1989; Mason & Huber 2001). In the beginning of each biological control project using parasitoids, potential biocontrol agents are collected as immatures in their native range on the target pest species and reared to the adult stage for identification and further study (Bellows & Fisher 1999). This ensures that parasitoids used for classical biological control can complete their development on the target species that is a natural host in their native range. We excluded cases in which 'new associations' (Hokkanen & Pimentel 1989) were tested, that is, in which species were released on target pests that were not their natural hosts, if this was mentioned in the report. We only included cases where propagule pressure (the number of individuals released) was known and whether or not the introduction resulted in the establishment of a persistent population. Only individuals released before the establishment of the population were accounted for; any further releases of a species in locations where it was already established were not included so that the numbers released represent the minimal propagule pressures that led to establishment. Altogether we found data for 515 introductions for classical biological control comprising 254 species of parasitic wasps from 15 families. Establishment success was recorded as reported in the original publication. Data on diet specificity (the number of documented hosts of a parasitoid species, compiled from the primary literature) were taken from world databases on Chalcidoidea and Ichneumonoidea (Noyes 2001; Yu, Van Achterberg & Horstmann 2005). We checked all records for host synonyms, which were removed, and found a rate of synonymy <1%. Taxonomy of parasitoids and hosts is according to Taxapad (Noyes 2001; Yu, Van Achterberg & Horstmann 2005). Data are available as Supporting Information (Table S1).

GENERAL MODELLING APPROACH

Propagule pressure is a strong predictor of establishment success (Lockwood, Cassey & Blackburn 2005). The relationship between probability of establishment and propagule pressure can be modelled within the framework of generalized linear models by assuming the response variable as binomially distributed (established, not established) and specifying a complementary log-log link function, with log(propagule pressure) as an explanatory variable (detailed explanations below).

Diet specificity was included in the models as a fixed effect. Diet specificity was calculated as two separate indices: (i) the number of

documented host species (host number) and (ii) the smallest taxonomic unit comprising all documented hosts [taxonomic specificity: (i) species-, (ii) genus-, (iii) family-, (iv) order- or (v) class-specific]. The host number would better describe diet specificity if each new host would on average be equally difficult to parasitize while the taxonomic specificity would be more appropriate if hosts that are more distantly related are more difficult to parasitize. Both indices are correlated (Pearson's $r = 0.45$; $N = 251$; $P < 0.001$), although there is still some remaining variation. Various specificity indices have been suggested in the literature (e.g. Poulin, Krasnov & Moulliot 2011), incorporating the number of host species and their relatedness in different ways. However, we refrained from using more indices because the two we used capture the basic ideas of the two components of specificity and should thus be correlated with other specificity indices. Moreover, we currently do not have a convincing argument to favour one index over the other.

We also included the following confounding factors that might affect establishment success and which have been mentioned in previous studies: the differences in host taxonomy (represented as host order; Stiling 1990), the year of introduction (Hall & Ehler 1979), the degree of human-induced disturbance of the habitat at the release location [high (1): annual arable fields and pastures; intermediate (2): orchards, perennial plantations and ornamental trees; low (3): forest and wild vegetation; Hall & Ehler 1979; Stiling 1990; Gross 1991], parasitic lifestyle (Stiling 1990), that is, whether the species was an endo- or ectoparasitoid (larvae of the former develop inside the host's body, larvae of the latter feed externally on their hosts), body size of the adult wasps (measured as body length; Noyes 2001; Yu, Van Achterberg & Horstmann 2005) and the degree of climate preadaptation (Bacon *et al.* 2014), defined as the degree of overlap in the temperature spectrum between the species' native range and the release site (see below for details on climate matching).

Since releases of the same or closely related species can be expected to result in similar outcomes, such data cannot be considered as independent; also, outcomes of introductions to the same location will be correlated (Sol, Vilà & Kühn 2008). In order to correct for multiple introductions of the same species and taxonomical or geographical biases, we included in our analysis the taxonomy (species nested within family) and the biogeographic region of the introduction location (Afrotropic, Australasian, Indo-Malaysian, Nearctic, Neotropic, Oceanic, Palearctic) as random factors (Sol, Vilà & Kühn 2008). A preliminary analysis, including all fixed factors, revealed that variation in random effects is primarily located in the biogeography and in the taxonomy at the level of the species, with other taxonomic levels contributing five orders of magnitude less (see, for example, Table 2), indicating that establishment success in parasitoids is not clustered at higher taxonomic levels (Zuur *et al.* 2009). We still decided to keep the taxonomic structure 'species nested within family' for all analyses, but results were qualitatively unchanged when using only species and biogeographic region as random effects. When taxonomy is the best information available about phylogenetic relationships, controlling for phylogenetic clustering by random effects is equivalent to phylogenetic independent contrasts (Sol, Vilà & Kühn 2008).

We fitted generalized linear mixed effects models to release data using the function `glmer` (package `lme4`, version 0.999999-2; Bates, Maechler & Bolker 2013) in the software `R` (version 3.0.1; R Development Core Team 2013). We identified the factors determining establishment success in parasitic wasps in an information theoretic framework for model selection (Burnham & Anderson 2002; Richards 2008). We first fitted models with all possible combinations of explanatory variables (Table 1). We then ranked all models according to Akaike's Information Criterion corrected for finite sample sizes (AICc). To determine the explanatory variables that best explain variation in establishment success, we selected all models that conformed to two rules (Richards 2008). First, we

selected all models with a ΔAICc value ≤ 6 , that is, all models whose AICc value was at most 6 higher than the lowest AICc obtained. This threshold of $\Delta\text{AICc} \leq 6$ is much higher than the widely applied rule-of-thumb of selecting all models with a ΔAICc value ≤ 2 (Burnham & Anderson 2002), but it recently has been demonstrated that the most parsimonious model, defined as the one with the lowest expected Kullback–Leibler distance, which is a measure of the mean discrepancy between the model and the unknowable truth, may be missed otherwise (Richards 2005). As a second rule, we only selected a model if its AICc value was less than the AICc value of all the simpler models nested within it, in order to avoid selecting overly complex models (Richards 2008). The reasoning for this is that if an additional parameter provides little or no increase in model fit, then the more complex model with the additional parameter will have a ΔAICc value less or equal to 2 to the simpler model; thus, the more complex model fits the data equally well as the simpler model. However, in such cases, the more complex model with the additional parameter should not be considered for ecological inference, since nothing is explained by the additional complexity (Burnham & Anderson 2002; Richards 2008).

We then estimated the value of all model parameters by model averaging among the set of candidate models chosen by the above model selection procedure (package MUMIN, version 1.9.13; Barton 2013). This method weights parameter estimates of more credible models (i.e. with lower AICc) higher than those with lower credibility. A parameter can be considered as having a significant effect on establishment probability if its confidence interval does not include zero. Parameters that were not included in any model chosen by model selection can be considered as having no relevant explanatory power.

RELATIONSHIP BETWEEN PROBABILITY OF ESTABLISHMENT AND PROPAGULE PRESSURE

Starting from a model of establishment success suggested by Leung, Drake & Lodge (2004), we define the probability of an individual to leave a line of descendants that does not die out as P . If individuals each have the same probability of leaving a line of descendants, then the probability E that an introduction of N individuals will result in an established population is:

$$E(N) = 1 - (1 - P)^N \quad \text{eqn 1}$$

Equation 1 can be rewritten as:

$$E(N) = 1 - e^{-\alpha N} \quad \text{eqn 2}$$

where $\alpha = -\log(1 - P)$

However, the probability of an individual to leave a line of descendants can vary with the number of individuals released, for example, if Allee effects operate. To allow for this, we modify eqn 2 by adding a shape parameter, c (Leung, Drake & Lodge 2004):

Table 1. Model fit (ΔAICc) and parameter estimates for all credible models remaining after model selection explaining establishment success in parasitic wasps (fitted on 286 release events of 120 species)

Propagule pressure	Diet specificity	Level of habitat disturbance	Parasitoid lifestyle	ΔAICc
0.104	-0.024	0.422	0.662	0
0.089	-0.025			0.34
	-0.025			1.31

AIC, Akaike Information Criterion.

$$E(N) = 1 - e^{(-\alpha N)^c} \quad \text{eqn 3}$$

The parameter c determines the extent to which individuals introduced at low (compared to high) propagule pressure are disproportionately more ($0 < c < 1$; due to, for example, heterogeneity in habitat suitability: R. Duncan, T.M. Blackburn, S. Rossinelli & S. Bacher, unpublished data) or less ($c > 1$; due to Allee effects: Leung, Drake & Lodge 2004) likely to establish.

Equation 3 can be rewritten as follows:

$$\log(-\log(1 - E(N))) = c \log \alpha + c \log N. \quad \text{eqn 4}$$

The term on the left hand side is the probability of an introduction of N individuals establishing, $E(N)$, under a complementary log-log transformation. The term on the right hand side is a linear equation of the form:

$$\beta_0 + \beta_1 \log N. \quad \text{eqn 5}$$

Thus, the relationship between probability of establishment and propagule pressure (eqn 3) can be modelled as a general linear model of the form shown in eqns 4 and 5 by modelling the response variable (whether an introduction established or not) as binomially distributed and specifying a complementary log-log link function, with $\log(N)$ as the predictor variable.

CLIMATE RANGE DEFINITION AND CLIMATE MATCHING

Parasitoid species distribution data were obtained on a per country basis (Noyes 2001; Yu, Van Achterberg & Horstmann 2005). To define the climatic range of each species, we referred to the World Map of Köppen–Geiger Climate Classification (Kottek *et al.* 2006), where each climatic zone is described as a combination of two variables, precipitation (in six ranked categories, from dry to wet) and temperature (in seven ranked categories, from hot to cold), plus a third variable designated as main climate (equatorial to polar in six categories; not used in our analysis). We recorded all temperature and precipitation categories that were found in the native distribution range of each parasitoid species. We defined the degree of preadaptation by calculating the rank-difference of the climatic category of the location where the species was introduced and the closest-matching climatic category in the native distribution of the species, separately for temperature and precipitation. A rank-difference of zero would indicate that the climate at the release location can be found in the native distribution range of the species and thus indicates preadaptation, whereas values larger than zero indicate increasing maladaptation. Because data for precipitation and temperature were highly correlated (Pearson $r = 0.24$, $P < 0.0001$, $N = 515$), we only used temperature in the models to avoid problems in model fitting through collinearity (Dormann *et al.* 2013).

Results

Parasitoids used in the analysis varied in their host use from being monospecific to using more than 200 different host species (Fig. 1). We first analysed a subset of 286 releases (comprising 120 species from 10 families) for which we had information on whether the release resulted in the establishment of a persistent population, the diet specificity of parasitic wasps and all covariates mentioned above that can potentially also affect establishment success. Diet specificity measured as the number of host species was consistently associated with the establishment success of parasitoid species in all 92 models with a high probability of being the best model describing the data

(i.e. models with ΔAICc values < 6 ; Table S2, Supporting information). Other factors that often occurred in the models were propagule pressure (in 52 models), the level of disturbance (48 models) and parasitoid lifestyle (45 models); other factors were only occasionally found in the best models. After the model selection procedure, only three models remained as candidates for further inference (Table 1); these three models contained only the diet specificity, propagule pressure, the degree of disturbance and the parasitoid lifestyle as explanatory variables. All other models were extensions of the three candidate models, but with worse fit to the data. Averaging over the three candidate models showed that the number of hosts used by wasp species was negatively associated with their probability of establishment (-0.024 ± 0.008 SE; 95% confidence interval: $-0.039, -0.009$). The number of individuals released (propagule pressure) was the only other factor that had a significant influence on establishment success (0.093 ± 0.045 SE; 95% confidence interval: $0.005, 0.182$); the level of disturbance (0.42 ± 0.22 SE; 95% confidence interval: $-0.022, 0.85$) and the parasitoid lifestyle (0.66 ± 0.40 SE; 95% confidence interval: $-0.12, 1.44$) had both confidence intervals overlapping zero and were thus excluded from further analysis. We then fitted models with all combinations of factors supported by the model selection procedure (dietary specialization, propagule pressure) to all cases for which we had information on propagule pressure and diet specificity (515 releases comprising 254 species from 15 families). The model including both factors was highly favoured over the model with only diet specificity or propagule pressure as explanatory variable ($\Delta\text{AICc} > 8.46$). Parameter estimates from model averaging remained almost the same as for the smaller data set, but with narrower confidence intervals (diet specificity: -0.023 ± 0.007 SE; 95% confidence interval: $-0.034, -0.009$; propagule pressure: 0.12 ± 0.03 SE; 95% confidence interval: $0.06, 0.18$). Thus, parasitic wasps with restricted diet have a higher probability of establishing a persistent population than species that feed on a larger range of resources.

In all credible models, variation in random effects was similarly distributed; we only show the random effects of the best model fitted to the entire data set (Table 2). There was considerable variation in establishment success among species but little variation among parasitoid families. Establishment success was higher than average in Australasia and the Palearctic region (Fig. 2).

Discussion

The negative relationship between diet breadth and establishment success suggests the existence of significant fitness trade-offs with diet breadth; these trade-offs appear to be widespread and generally involved in the evolution of dietary specialization in the hyper-diverse taxon of parasitic wasps. It might be that some of the generalist species included in our study actually are cryptic species com-

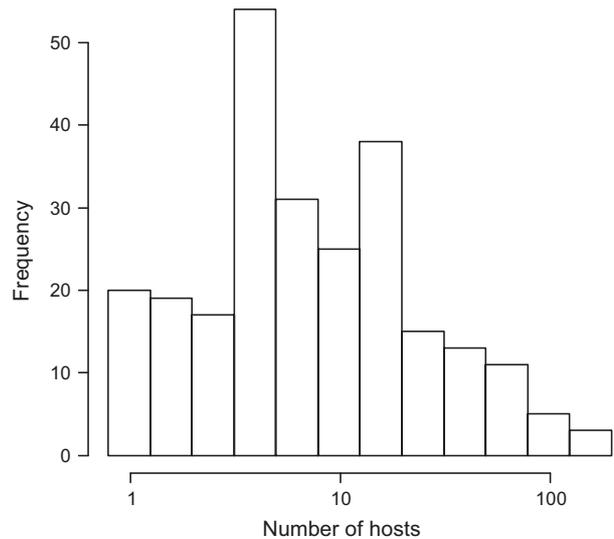


Fig. 1. Histogram of the distribution of the degree of dietary specialization for 254 parasitoid species used in the analysis. Note the log-scale of host range.

plexes consisting of multiple species with narrower host ranges. Erroneously assigning specialists as generalists in our study should either have no effect on the results (if there is no relationship between host range and establishment success) or even decrease the probability of finding fitness advantages when the specialists have higher establishment success, as supported by our results. Thus, the actual fitness advantages of specialists may even be higher than our data suggests. The same applies to erroneously assigning a generalist as a specialist, for example, when the full host range is only poorly known. This again would only increase variation in the response variable, but would not create a pattern as the one we report here. However, we do not expect that this happened frequently in our data because biocontrol agents are carefully studied for their host range before release (Van Driesche, Hoddle & Center 2008). The fact that we found a strong correlation between establishment success and dietary specialization despite possible uncertainty in the data is therefore a strong indication that this effect is real. The importance of host range as determinant of establishment success is also underlined by the fact that its effect was stronger than the effect of propagule pressure, which is usually the major determinant of establishment success (reviewed in Greathead 1986; Cassey *et al.* 2004). For example, in similarly designed comparative studies of correlates of establishment success in alien birds and mammals, the number of introduced individuals was always by far the most important factor, overriding the effect of species traits (Cassey *et al.* 2004; Sol *et al.* 2008).

While the number of host species was strongly correlated with establishment success, a simple taxonomic index of dietary specialization (species-, genus-, family-, order-, class-specific) did not explain establishment in parasitoids. We interpret this as indication that an index of host speci-

ficity based on taxonomic (=phylogenetic) distance of hosts does not properly capture the adaptations necessary to utilize different host species. By contrast, in a study on aphid parasitoids by Straub, Ives & Gratton (2011), a phylogenetic index was better correlated with parasitism rates (used as fitness proxy) than the number of host species. It appears that in our case simply the number of hosts is a strong predictor of establishment success. There are other indices available using different ways of incorporating the number of host species and their degree of relatedness into the calculation of specificity indices (reviewed in Poulin *et al.* 2011). However, the two indices we use capture the basic ideas of the two components of specificity (number of hosts, degree of relatedness) and thus will be correlated with other specificity indices, as they are already correlated with each other ($r = 0.45$). Moreover, we currently do not have a convincing theoretical argument to favour one index over the other, and which one would be a better proxy for dietary specialization might depend on the con-

Table 2. Distribution of random effects of the best model fitted to the entire data set of 515 releases of 254 species of 15 families to seven biogeographic regions. All credible models had a similar distribution of variance in their random effects (not shown)

Random effect	Variance	Standard deviation
Species, nested within families	1.33	1.15
Family	1.2 e-12	1.1 e-6
Biogeographic region	0.46	0.68

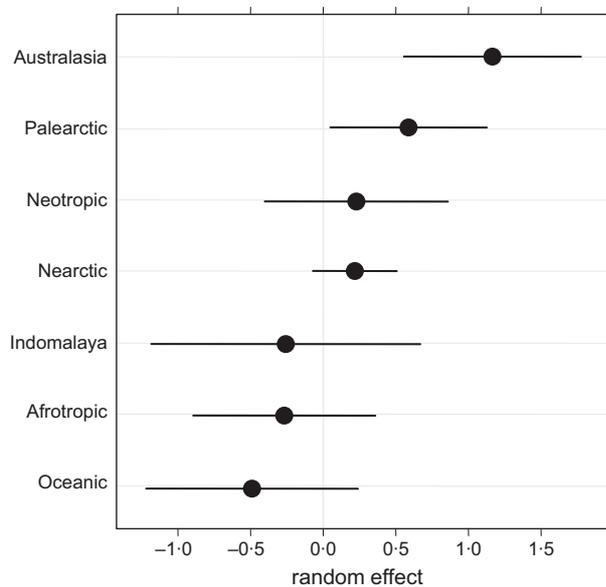


Fig. 2. A caterpillar plot of the conditional means and their associated 95 % prediction intervals for the random effects across biogeographic regions for the best model of establishment success as function of diet specificity and propagule pressure fitted to all data ($N = 515$). The prediction intervals for Australasia and the Palearctic do not overlap zero, indicating significantly higher establishment success than average and also justifying the inclusion of a biogeographic random effect in this model.

text. For example, closely related phytophagous insects often differ in their host plant use and thus might use different plant-derived secondary compounds to defend themselves against enemies (Bernays & Graham 1988). Adapting to these different compounds might be more difficult than coping with a more distant host feeding on the same host plant and thus using more similar compounds (Kester & Barbosa 1991). In such a situation, simply the number of hosts would better capture the degree of specialization than the phylogenetic distance. Finally, other indices of specificity are not needed to support our main argument because we already show a strong effect of specificity on establishment success by simply using the number of host species reported in the literature.

While our study shows that specialists have fitness advantages over generalists, this applies only to situations where both specialists and generalists have access to only one host and this host is abundant, like, for example, in intentional releases for classical biocontrol. This is not to say that the specialist lifestyle is generally superior to the generalist. Generalists profit in situations where hosts are rare or unpredictable, and they can switch to alternative hosts; specialists do not have this option. In fact, in invasion ecology, it has been shown that alien generalists usually establish better when released to places outside their natural range (e.g. birds: Sol *et al.* 2005; mammals: Sol *et al.* 2008). This has been explained by the fact that generalists can better cope with novel environments and the probability is higher for generalists to find their ecological niche. Most alien insects are actually transported and released accidentally (Hulme *et al.* 2008; Bacon, Bacher & Aebi 2012), and it can be expected that generalists establish better than specialists under these conditions. Indeed, work from Hawaii indicates that most self-introduced natural enemies of pests are generalists that attack a range of non-target species in addition to the pest of interest (Kaufman & Wright 2009).

The host community in the release environment should not affect the results of our study because the target host, that is, the pest insect which is an accepted host of the parasitoids, occurs at such high abundance at the release sites compared to native hosts that the parasitoids will rarely parasitize other species. This should be valid during the first phase of the invasion, until the populations established. At later phases, when the parasitoids have decreased the abundance of the pest, they might also parasitize native hosts that are in their host range. However, biocontrol agents normally need to be specific enough not to harm native species in order to get permission for their release. There have been a few cases of attacks of non-target species, but these are rare (Van Driesche, Hoddle & Center 2008). Thus, the native communities should not affect our results.

We did not identify factors other than propagule pressure and dietary specificity as drivers of establishment success in parasitoids as biocontrol agents. This is in contrast to previous studies (Hall & Ehler 1979; Greathead 1986; Stiling 1990; Gross 1991) that found evidence for one or more of

the confounding factors we included in our analysis (see Material & Methods). Interestingly, the only study investigating the relationship between dietary specificity and establishment success in parasitoids did not find a significant effect (Stiling 1990: $P = 0.075$, $N = 586$). However, previous studies on establishment rates of parasitoids for biocontrol did not control for propagule pressure and/or relatedness of species, generally used simplified statistical tests, and often did not include more than one variable at a time in their models. Our analysis shows that many factors previously thought to be important apparently do not explain establishment success when analysed within an appropriate statistical framework.

These results have direct implications for the practice of biological control. First, they confirm that the higher the number of individuals released the higher the probability that the biocontrol agents will establish. Second, and very importantly, specialized parasitoids have higher probabilities to establish than generalists. This finding underlines the importance of proper host specificity testing before release. Host specificity tests are currently standard practice in weed biocontrol, but are less common in biocontrol using parasitoids as agents (Van Driesche, Hoddle & Center 2008).

Fitness advantages in specialists are either general drivers of specialization or a general consequence of the adaptation of specialized species to their hosts. In parasites, lineages specialized on few hosts can adapt faster to host defences than generalist lineages distributed among several host species, because the former are more consistently exposed to selection for performance on their preferred host (Kawecki 1998). For the same reason, generalist populations are also more prone to fitness reductions due to accumulation of mutations that are deleterious in some habitats but neutral in others (Kawecki 1998). Thus, even in case the initial behavioural choice to specialize is not linked to fitness advantages (i.e. when preference and performance are initially uncoupled; e.g. Fry 1996) rapid evolution due to strong natural selection (i.e. adaptation) in specialized parasitoids must have created the trade-offs that we found are generally associated with specialization in parasitic wasps. Trade-offs might follow specialization instead of driving it, but are invariably linked to fitness advantages that specialization provides, and likely account for the persistence of the widespread high degree of specialization observed among parasitic wasp species.

Most of the studies on fitness advantages of specialization so far have been done on phytophagous insects (Bernays & Graham 1988; Futuyama & Moreno 1988; Jaenike 1990); however, no convincing support for the existence of trade-offs in the evolution of specialization so far has emerged in this group (Forister *et al.* 2012). Despite the large degree of host specialization that can be found in phytophagous insects, it might be difficult to demonstrate trade-offs associated with dietary specialization. Host plant choice in phytophagous insects supposedly is determined to a large extent by their attempt to escape their natural

enemies (Bernays & Graham 1988; Forister *et al.* 2012); in this case, a herbivore's diet would reflect a specialization towards enemies and therefore not necessarily implicate an adaptation to the plant as food resource. Thus, phytophagous insects that specialize on a certain plant species to escape enemies might not gain a nutritional advantage on that plant compared to generalists. Further investigations in this group should take account of the tri-trophic niche herbivores occupy (Price *et al.* 1980; Singer & Stireman 2005; Forister *et al.* 2012) and consider that natural enemies can significantly influence their preys' food choice. Trade-offs are probably easier to detect in groups higher up in their trophic position, for example parasitoids or predators, which are generally less exposed to natural selection from their own enemies; in such groups, diet specialization will be more likely directly linked to fitness benefits due to nutritional advantages.

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Data accessibility

Data: uploaded as online supporting information.

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Table S1. Data on parasitoid releases.

Table S2. List of credible models.