Received: 15 March 2024 | Revised: 12 June 2024 | Accepted: 20 June 2024

DOI: 10.1111/ele.14477

SYNTHESIS

ECOLOGY LETTERS WILEY

Meta-analytical evidence for frequency-dependent selection across the tree of life

Miguel Gómez-Llano[1] | **Ronald D. Bassar**[2] | **Erik I. Svensson**[3] | **Simon P. Tye**[4] | **Adam M. Siepielski**[4]

[1]Department of Environmental and Life Science, Karlstad University, Karlstad, Sweden

[2]Department of Biological Sciences, Auburn University, Auburn, Alabama, USA

[3]Department of Biology, Lund University, Lund, Sweden

[4]Department of Biological Sciences, University of Arkansas, Fayetteville, Arkansas, USA

Correspondence
Miguel Gómez-Llano, Department of Environmental and Life Science, Karlstad University, Karlstad, Sweden.
Email: miguel.gomez@kau.se

Funding information
Vetenskapsrådet, Grant/Award Number: 2020-03123; Division of Environmental Biology, Grant/Award Number: 1748945, 2100163 and 2306183

Editor: Stephan B. Munch

Abstract

Explaining the maintenance of genetic variation in fitness-related traits within populations is a fundamental challenge in ecology and evolutionary biology. Frequency-dependent selection (FDS) is one mechanism that can maintain such variation, especially when selection favours rare variants (negative FDS). However, our general knowledge about the occurrence of FDS, its strength and direction remain fragmented, limiting general inferences about this important evolutionary process. We systematically reviewed the published literature on FDS and assembled a database of 747 effect sizes from 101 studies to analyse the occurrence, strength, and direction of FDS, and the factors that could explain heterogeneity in FDS. Using a meta-analysis, we found that overall, FDS is more commonly negative, although not significantly when accounting for phylogeny. An analysis of absolute values of effect sizes, however, revealed the widespread occurrence of modest FDS. However, negative FDS was only significant in laboratory experiments and non-significant in mesocosms and field-based studies. Moreover, negative FDS was stronger in studies measuring fecundity and involving resource competition over studies using other fitness components or focused on other ecological interactions. Our study unveils key general patterns of FDS and points in future promising research directions that can help us understand a long-standing fundamental problem in evolutionary biology and its consequences for demography and ecological dynamics.

KEYWORDS
frequency-dependent selection, genetic variation, meta-analysis

INTRODUCTION

Darwin's picture of natural selection as a ubiquitous process '*daily and hourly scrutinising, through the world, every variation, even the slightest; rejecting that which is bad*' (Darwin, 1859) predicts a continuous process of erosion of genetic variation. Yet, field and laboratory studies have documented substantial genetic variation for most phenotypic traits (Bonnet et al., 2022; Houle, 1992; Mousseau & Roff, 1987), typically more than what could be expected based on de novo mutations (Barton & Keightley, 2002; Charlesworth, 2015; Mitchell-Olds et al., 2007) or mutation-selection balance (Ayala & Campbell, 1974; Sinervo & Lively, 1996). Consequently, explaining the maintenance of genetic variation in fitness-related traits remains a fundamental challenge.

Different mechanisms have been proposed to explain the maintenance of genetic variation, such as spatial or temporal variation in environmental heterogeneity (Hedrick, 1976), gene flow (Morrissey & de Kerckhove, 2009) and balancing selection (Levene, 1953). Frequency-dependent selection (FDS) is one of several forms of balancing selection (Ayala & Campbell, 1974; Sinervo & Lively, 1996) and arises when the fitness of a trait or genotype depends on its prevalence in the population (Ayala & Campbell, 1974; Fisher, 1930; Kojima, 1971; Lewontin, 1958). In negative frequency-dependent selection (NFDS), the relative fitness of a genotype or phenotype increases as it becomes *less* common; thereby rescuing rare genetic and phenotypic variants within a population (Fisher, 1930; Lewontin, 1958). In positive frequency-dependence (PFDS), the relative fitness of a genotype or phenotype increases as it becomes *more* common and, in the context of a metapopulation, can maintain variation among populations (Chouteau et al., 2016; Fisher, 1930; Frank, 1994). Importantly, similar mechanisms can lead to either positive or negative FDS. For example, female mate choice can favour rare (Potter et al., 2023) or common variants (Gordon et al., 2015). Overall, FDS challenges the assumption that fitness is a fixed property of a genotype or phenotype (Kojima, 1971), and can strongly shape microevolutionary trajectories (Le Rouzic et al., 2015; Nosil et al., 2018), increase evolutionary predictability (Chevin et al., 2022), and shape genetic and phenotypic diversity over time, thereby influencing extinction risk (Svensson & Connallon, 2019).

One of the main attributes that makes FDS, especially NFDS, an appealing mechanism for explaining standing genetic variation is its perceived generality, encompassing all domains of life and levels of selection, as well as its relevance linking ecology and evolution (Christie & McNickle, 2023). Despite a long history of research about how FDS affects a wide diversity of organisms, including viruses (Turner, 2005), bacteria (Rendueles et al., 2015; Rozen & Lenski, 2000), plants (Garrido et al., 2016; Mundt et al., 2008) and animals (Fitzpatrick et al., 2007; Sinervo & Lively, 1996), we lack an understanding about general patterns of FDS. This gap largely exists because different taxa experience different biotic interactions that invoke different selective regimes and agents, and past studies have used a variety of experimental settings and focused on different types of traits and/or biotic interactions.

To develop a synthetic understanding, and quantify the occurrence, overall strength and direction of FDS, we conducted a systematic literature review and phylogenetically informed meta-analysis of published studies of FDS. We analysed different moderators to explain heterogeneity in the strength and direction of FDS. Some of these moderators were methodological, and others were chosen based on their ecological and evolutionary relevance. Our study aims to quantify the strength and direction of FDS in different ecological contexts and identify critical knowledge gaps in existing literature. Our results show that NFDS can be a pervasive force maintaining genetic variation within populations and highlights different ecological contexts in which FDS appears more likely to act.

METHODS

Literature search

To conduct our systematic literature review, we used the Preferred Reporting Items for Systematic Review and Meta-Analysis in Ecology and Evo'ution (PRISMA-EcoEvo; O'Dea et al., 2021). Specifically, we used ISI Web of Knowledge (Web of Science Core Collection, KCI-Korean Journal Database, MEDLINE®, Russian Science Citation Index, SciELO Citation Index and Zoological Record) and PubMed on 21 September 2021 with the search terms *'freque* depende* select*'*. While these terms are exact, we note that these search terms may not necessarily uncover all studies representative of the broader scope of studies that have touched on ideas focused on aspects of FDS (*see below*). Indeed, we also suspect that to some extent studies focused on FDS do so because they have strong a priori reasons to expect it is occurring (e.g. based on elements of a species natural history, prior studies with a particular or closely related species, or theoretical reasons) rather than a uniformed reason to go out and study the phenomenon simply to investigate it. Similar issues have been identified in studies of spatial variation in selection, where, for example, it is unlikely that researchers randomly choose study populations and instead chose those where selection is expected to vary along an environmental gradient (Siepielski et al., 2013). Consequently, it is difficult to assess broadly the occurrence of FDS because of these potential biases. Our literature review was limited to studies published in English and yielded 2878 publications (ISI Web of Knowledge 1959 and PubMed 919); after removing duplicates and an initial title/abstract screening, we were left with 702 publications to be further evaluated. Following our exclusion criteria (see below), we had 121 publications and were able to extract information from 101 (Figure S1).

To be included in the meta-analysis, publications needed to report estimates of fitness or a fitness component (e.g. survivorship, mating success) of at least one variant (phenotype or genotype) in at least two different frequencies. Thus, although informative, we excluded publications that only estimated fitness of either common and rare variants, but not these variants at different frequencies, such as studies of the Major Histocompatibility Complex (MHC; e.g. Peng et al., 2021). Further, studies comparing observed and expected frequency after a period of selection (such that deviations from a slope of 1.0 would reject the null hypothesis) were not included because they can suffer from regression to the mean (Barnett et al., 2005) and cannot be standardised with other measurements of FDS (i.e. instead of negative values, slopes between 0 and 1 reflect NFDS and slopes close to 1 reflect lack of FDS). We included studies that used models of organisms (e.g. pictures, dead or parts of individuals; Gordon et al., 2021; Janif et al., 2015) if it was clear in the publication that these were realistic models of different variants of a single existing species.

Effect size calculations

We calculated unbiased standardised' mean differences (Hedge's *g*) as our effect size (Borenstein, 2009). To do this, first we obtained the mean fitness of a variant at the higher frequency and the mean fitness at lower frequency, or the correlation coefficient of a relationship between fitness of a variant and its frequency from low to high. We then initially used these values to calculate Cohen's *d* (i.e. standardised difference between the means of the two groups). However, *d* can overestimate values with small samples. Thus, we transformed Cohen's *d* to Hedge's *g*, which has a correction that eliminates this bias (for details see Borenstein, 2009). Thus, positive values represent PFDS and negative values represent NFDS. In some studies, the effect of variant on fitness was quantified as, for example, a positive relationship between frequency and predation risk, indicating a decrease of fitness at higher frequencies. In these cases, we multiplied *g* by −1 so that all effect sizes were on the same scale. Study mean values, standard errors and correlation coefficients were either extracted from figures, using the package '*metaDigistise*' (Pick et al., 2019) or obtained directly from Tables or text.

Moderators

We recorded several moderators of interest that could explain heterogeneity in the data. We included study type (laboratory experiment, mesocosm, field experiment or field observations) as a methodological moderator. Among biological moderators, we included sex class, which was grouped into five categories: asexual, hermaphrodites, females, males or both (studies using males and females). Variant class was classified into one of seven categories: behavioural, colouration, ecotype, genotype, life history, morphological or pheromones. We further classified the fitness component measured: fecundity, sexual selection and viability. Finally, we classified the type of ecological interaction into five categories: resource competition, herbivory, parasitism, predation, reproductive interactions or other. The group 'other' includes studies that did not specify the type of interaction driving selection (see Table 1 for a data summary).

We included study type because, unless FDS is very strong, environmentally driven variation in selection can obscure patterns of FDS (Chevin et al., 2022). Given temporal and spatial variation in natural selection due to environmental conditions (Ehrlén & Valdés, 2020; Endler, 1986; Gómez-Llano et al., 2023; Hunter et al., 2018; Siepielski et al., 2017; Wade & Kalisz, 1990), we predicted FDS would be weaker in field studies than in laboratory-based experiments.

Biological characteristics of study organisms could also explain heterogeneity in FDS among studies. Some of these characteristics are specific to the studies, such as sex and variant class (e.g. phenotype or genotype), which can influence the strength and direction of FDS, but for which we do not have specific predictions. First, because both sex (Koskella & Lively, 2009) and sexual selection are often tightly associated with negative or positive FDS (Gordon et al., 2015; Hughes et al., 2013; Sinervo & Lively, 1996; Svensson et al., 2005), we tested the effect of sex class (asexual or sexual, and which sex). Then, we evaluated variant classes to investigate how different aspects of organisms may affect FDS among studies.

TABLE 1 Summary of records in our meta-analysis database.

	Studies	Effects	Species
(a) Kingdom			
Animalia	52	242	30
Bacteria	11	68	6
Chromista	1	3	1
Fungi	1	18	1
Plantae	35	414	29
Viruses	1	2	1
(b) Method			
Field experiments	31	326	24
Field observations	20	124	17
Laboratory	45	255	32
Mesocosms	8	42	7
(c) Sex			
Asexual	19	108	13
Both	17	80	13
Females	27	130	19
Hermaphrodites	28	369	23
Males	21	60	14
(d) Variant			
Behaviour	3	5	2
Colouration	35	161	21
Ecotype	2	8	2
Genotype	42	379	28
Life history	3	30	3
Morphology	14	150	13
Pheromone	2	14	2
(e) Fitness component			
Fecundity	25	180	24
Sexual	31	128	23
Viability	63	439	46
(f) Ecological interaction			
Competition	38	228	26
Herbivory	5	89	4
Other	8	54	9
Parasitism	5	161	3
Predation	7	19	6
Reproduction	43	196	31

Note: Numbers refer to the number of records (studies, effect sizes and species) in the different Kingdoms (a), study method (b), sex (c), variant (d), fintess component (e) and ecological interaction studied (f).

Previous meta-analyses of selection in natural populations have revealed substantial variation in the strength of selection among traits and fitness components (Hereford et al., 2004; Kingsolver et al., 2001), which could also affect FDS. For example, several meta-analyses have found that selection on survival is weaker than selection on fecundity and mating success (Hoekstra et al., 2001; Kingsolver et al., 2001; Siepielski et al., 2011). If this general finding exists for FDS, we expect fecundity and mating success to show stronger NFDS than viability. FDS also often operates on traits modulating intraspecific competitive interactions (Weeks & Hoffmann, 2008), including reproductive interactions (Hughes et al., 2013; Takahashi et al., 2010), and interspecific interac—ons, including predator–prey (Olendorf et al., 2006) and parasite–host interactions (Brunet & Mundt, 2000). We predicted that, if selection is stronger on fecundity and mating success (Hoekstra et al., 2001; Kingsolver et al., 2001; Siepielski et al., 2011, 2013), ecological interactions that more directly affect reproductive fitness (e.g. reproductive competition) would show stronger NFDS than ecological interactions that mainly affect viability (e.g. predation).

Statistical analysis

We tested for publication bias in two ways: small-study effects (i.e. larger effects in studies with smaller sample sizes) and time-lag bias (i.e. more significant results are more quickly to be published than less significant or negative results; *reviewed in* Nakagawa et al., 2022). These tests were done by fitting uni-moderator multilevel meta-analytic regressions including standard error or publication year for small-study effects and time-lag biases, respectively (Supplementary Analysis S1).

To investigate the overall strength and direction of FDS across studies, we fit two multilevel meta-analytic models (intercept only) using our measure of effect size as the response variable. The first model included study identity (study id) and species as random effects. Because most studies in our database had multiple effect sizes (mean ± SD: 7.3 ± 14.8), each effect size was not independent. Thus, to account for this non-independence, we included the individual effect size (observation) within study as random effects. Species was included as a random effect because if the same species was used in multiple studies the effect size are likely similar.

The second model also contained study id, species and observation as random effects, but unlike the previous model, it also included phylogeny as a random effect to account for non-independence due to phylogenetic relatedness between species. This last model has been the most recommended for meta-analysis in ecology and evolution (Cinar et al., 2022). The phylogeny was derived from the open Tree of Life database (https://tree.opentreeoflife.org/) and branch lengths wer' calculated using Grafen's method (Grafen, 1989) using the '*ape*' package (Paradis & Schliep, 2019).

While these two models allow us to investigate the mean strength and direction of FDS across studies, it is important to note that many of the individual studies reported PFDS and NFDS. To illustrate this, in Figures 1–3, we denote individual studies as statistically significant (i.e. if the effect size and the variance in the effect do not overlap zero) or not. While we are not advocating for (nor conduct) any kind of vote counting interpretation, we do highlight this mix of negative and positive effect sizes simply to emphasise that many individual studies reported varying signs of FDS (*see also* Hasik et al., 2023; Kingsolver et al., 2001). As a result, it is possible that this mix of signs could generate an average across studies of no detectable overall FDS, despite the individual studies. Estimating this overall effect across studies, is of course the point of our meta-analysis, but it does obscure detecting the overall strength of FDS.

Thus, to explicitly analyse the occurrence and strength of FDS we conducted an analysis of the absolute values of effect sizes. To accomplish this, we follow the 'analyse-then-transform' method suggested by Morrissey (2016a, 2016b) as it has shown to eliminate upward biases associated with using absolute values. Briefly, the estimates and variance obtained from the phylogenetic model of the mean effect sizes were transformed using a folded normal distribution (Morrissey, 2016a, 2016b). To estimate credible intervals around the mean absolute effect, we used a Bayesian approach using the package *brms* (Bürkner, 2018) and applied the posterior distribution to the folded normal distribution transformation (*see also* García-Roa et al., 2020).

We then fit individual multilevel meta-analytic regression models (i.e. meta-regressions) to explore the importance of the various moderators described earlier. Each model includes a different moderator, and all these moderators were treated as fixed effects. Because our phylogenetic model showed better fit to the data than the non-phylogenetic model (see below), the meta-regressions included study, observation, species and phylogeny as random effects. Analysis of the mean absolute effect sizes of all the moderators were performed following the methodology above and results reported in the Supplementary Information (Table S2). For the intercept only 'odels we present Cochran's Q as a measure of total absolute heterogeneity, and I^2 as a measure of the proportion of variance among effect sizes not attributable to sampling error, partitioned into its different components (Senior et al., 2016). Statistical analyses were performed using the package '*metafor*' (Viechtbauer, 2010) in R (R Development Core Team, 2018).

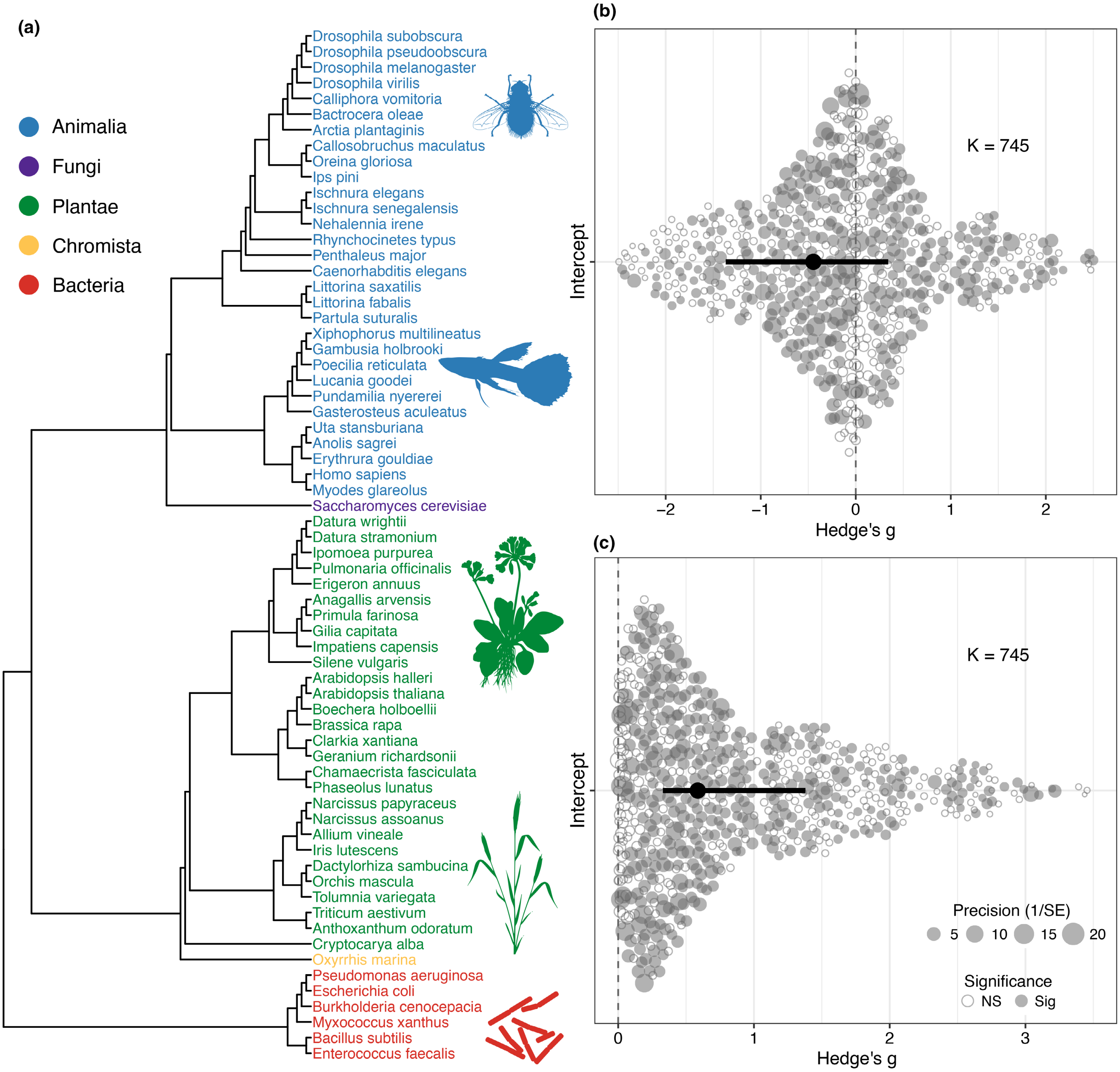

FIGURE 1 Phylogenetic tree of the species included in the database; lineages are colour coded (a). Overall, we found a non-significant NFDS trend when analysing the mean effect size (b) and moderate strength of FDS when analysing the mean absolute effects (c). Dots show individual effect sizes (Hedge's *g*), the value *k* shows the number of effect sizes. We evaluate significance of effect sizes when Hedge's g ± variance did not overlap 0. X-axes in (b) and (c) were truncated to improve visibility of the summary. Summary shows the mean and 95% confidence intervals (b) and credible intervals (c).

RESULTS

Overview of data set and publication bias

We obtained 747 effect sizes (*k*) from 101 different studies involving 67 species (Table 1). The data are represented mainly by plants and animals, followed by bacteria, fungi, chromista and viruses (which could not be accounted for in the phylogeny; Figure 1a). Most studies in our data set were laboratory-based or field-based experiments. Females and hermaphrodites were the dominant sex category. In addition, most studies focused on genotypes or colour, using viability or fecundity as a fitness component. Finally, reproductive and resource competition were the dominant species interactions. A summary of the records (number of studies, effect sizes and species) by kingdom and all moderators can be found in Table 1.

We found no evidence for a time-lag bias, but we found evidence for a modest small-study effect, with more extreme and negative effects associated with larger standard errors (Supplementary Analysis S1, Figure S1).

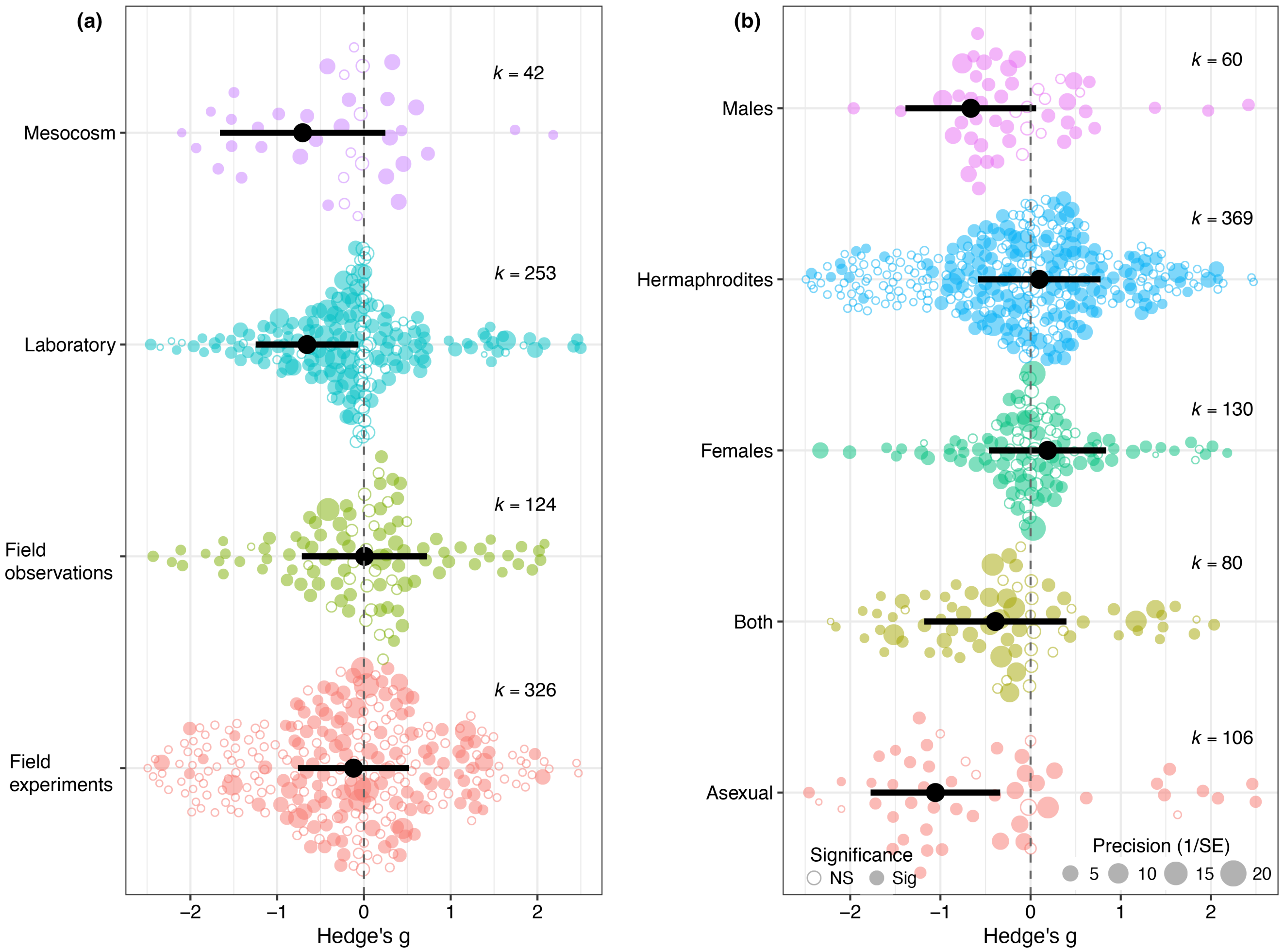

FIGURE 2 Effects of two moderators capturing different characteristics of the original studies: Study methodology (a) and sex class (b). We found that laboratory studies showed significant NFDS, a negative but non-significant FDS in mesocosms and field experimental studies, while field observational studies showed marginally positive although non-significant FDS (a). Except females and hermaphrodites, all the other groups showed NFDS, although the effect was only significant in asexual species. Dots show indiv'dual effect sizes (Hedge's *g*), the value *k* shows the number of effect sizes. We evaluate significance o' effect sizes when Hedge's g±variance did not overlap 0. The *x*-axes were truncated to improve visibility of the summary. Summary shows the mean effect size (large circle) and 95% confidence intervals (error bars).

Overall effects

Results from both phylogenetic and non-phylogenetic models showed overall NFDS, although the effect was only statistically significant in the non-phylogenetic model (Phylogenetic: estimate = −0.47, 95% CI = −1.23 to 0.52, $p = 0.21$; non-phylogenetic: estimate = −0.26, 95% CI = −0.51 to −0.01, $p = 0.036$; Figure 1b). Removing highly influential effect sizes in the phylogenetic mode’, identified by the Cook's distance (Supplementary Analysis S2), revealed marginally significant NFDS (estimate = −0.23, 95% CI = −0.48 to 0.01, $p = 0.063$), suggestive of widespread NFDS (Table S1). The model that incorporated phylogenetic relatedness between species showed better fit than the model without phylogeny (ΔAICc = 11.65) and was therefore used in all further analyses. The analysis of mean absolute effect sizes showed a moderate (Cohen, 2013) strength of FDS (mean = 0.59; 95% Credible Intervals = 0.33, 1.41; Figure 1c). In Table S2a, we report and contrast the results from the mean effects in both the phylogenetic and non-phylogenetic models as well as mean absolute effects.

We found substantial heterogeneity'in the data set (Cochran's $Q = 5603.92$, df = 744, $p < 0.001$). Differences between and within studies generally explained similar proportions of heterogeneity in effect sizes ($I^2_{\text{between}} = 31\%$, $I^2_{\text{within}} = 44\%$). Phylogenetic relatedness explained less but still considerable variation ($I^2_{\text{phylo}} = 19\%$), whereas differences between species explained little variation ($I^2_{\text{species}} = 0.6\%$). The total heterogeneity was large $I^2_{\text{total}} = 95\%$, indicating substantial variation among studies not attributable to sampling error, and falls well within the norm for meta-analyses in ecology and evolution (Senior et al., 2016).

Moderators

Laboratory-based experiments showed statistically significant NFDS, whereas mesocosm and field

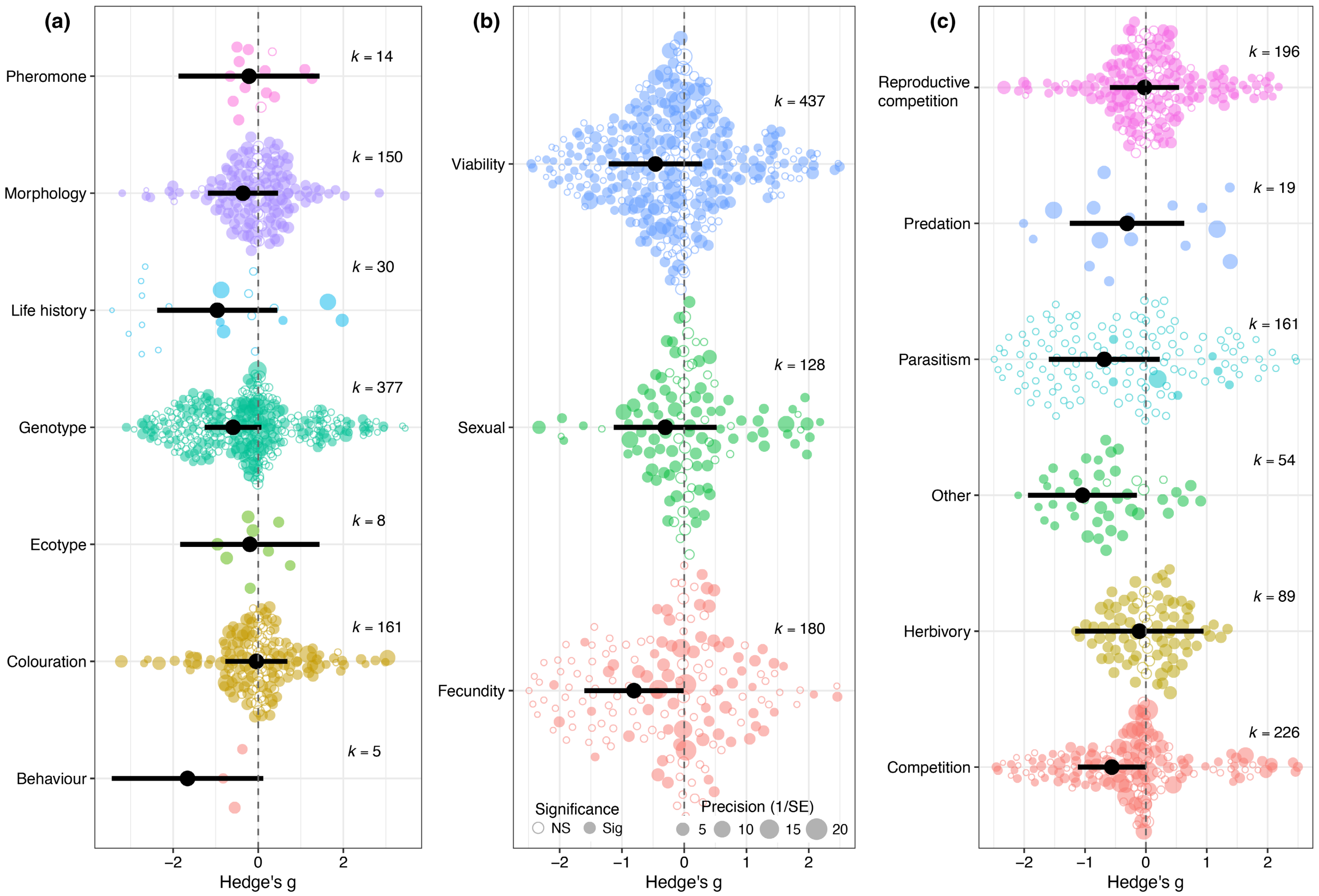

FIGURE 3 Effects of variant classes (a), fitness component (b) and ecological interaction (c) across studies. We found widespread NFDS, but not statistically significant, in either studies focusing on genotypes or phenotypes (a). We found statistically significant NFDS only in studies measuring fecundity (b). All ecological interactions show NFDS, although only competition and 'other' were statistically significant (c). Dots show individual effect sizes (Hedge's *g*), the value *k* shows the number of effect sizes. We evaluate significance of effect sizes when Hedge's g ± variance did not overlap 0. *X*-axes were truncated to improve visibility of the summary. Summary shows the mean effect size (large circle) and 95% confidenceintervals (error bars).

experiments studies, although overall negative, showed no statistically significant effects. Surprisingly, there was PFDS, although non-significant, for field observations (Figure 2a). Mean absolute effects were largest for mesocosm studies (mean = 0.9; 95% CI = 0.45, 1.95) and smallest for field experiments (mean = 0.48; 95% CI = 0.34, 1.13; Table S2b).

We found that females and hermaphrodites show positive, although, non-significant FDS. Studies grouping males and females ('both'), males and asexual species showed NFDS, although this was only statistically significant for asexual species (Figure 2b). Mean absolute effects varied from 1.1 (95% CI = 0.42, 1.98) in asexual to 0.45 (95% CI = 0.32, 0.97) in hermaphrodites (Table S2c).

We found evidence of widespread NFDS across all variant classes, although the effect was only marginal in genotype and behaviour, and non-significant for the other phenotypes (Figure 3a). Mean absolute effects ranged from 1.77 (95% CI = 0.76, 3.53) in behaviour to 0.49 in colouration (95% CI = 0.35, 1.06; Table S2d).

Among the different fitness components, we predicted that sexual and fecundity fitness components would be strongly affected by NFDS, while viability would not. We found partial support for this prediction (Figure 3b, Table S2e). There was evidence for statistically significant NFDS in studies measuring fecundity and appreciable but non-significant NFDS on sexual and viability fitness components (Figure 3b). Mean absolute effects were stronger in fecundity (mean = 0.89, 95% CI = 0.4, 1.95) than in sexual (mean = 0.63, 95% CI = 0.42, 1.55) and viability (mean = 0.63, 95% CI = 0.36, 1.55; Table S2e).

Finally, we predicted ecological interactions that more directly affect reproductive fitness (i.e. 'r"productive competition'), such as competition for mates, would be subject to stronger NFDS. Although we found an overall pattern of NFDS across all ecological interactions, only resource competition and non-specified interactions ('other') were statistically significant (Figure 3c). Mean absolute effects ranged from 1.05 in parasitism to 0.36 in reproductive competition (Table S2f).

DISCUSSION

FDS has been implicated as important for maintaining genetic variation (Ayala & Campbell, 1974; Sinervo & Calsbeek, 2006), sexual selection (Hughes et al., 2013), assortative mating and reproductive isolation (Otto et al., 2008; Udovic, 1980), the evolution of mimicry (Brower, 1960; Chouteau et al., 2016; Pfennig et al., 2001), and speciation and adaptive radiations (Dieckmann & Doebeli, 1999; Martin, 2016; Melián et al., 2010). The results from our meta-analysis indicate that, overall (e.g. across studies), FDS is more commonly negative, although not significantly when accounting for phylogeny. Despite this, it is important to emphasise that there was also considerable heterogeneity among studies that was not attributable to sampling error. Moreover, our analysis of the absolute effect sizes revealed the widespread occurrence of FDS (Table S2). The significant phylogenetic signal might either reflect that FDS is non-randomly distributed with respect to phylogeny, or alternatively, that researchers tend to pick certain taxonomic groups in a non-random fashion, choosing related species to those where FDS has already been detected or is a priori more likely to operate. Our results also indicate that both study characteristics and biological factors often influence the strength and direction of FDS in different study systems, populations, and species. In the following, we highlight the main results and discuss the implications of these findings in a broader context.

Methodological moderator

NFDS was significant in laboratory experiments, but weaker and non-significant in less controlled settings such as field studies. One possible explanation for this is that selection in general, including NFDS, is strongly affected by environmental variation, which is present in field studies but more controlled for in laboratory settings. Thus, weak mean effects in field studies is consistent with previous studies in natural populations, where natural and sexual selection are variable in space and time (Hereford et al., 2004; Hoekstra et al., 2001; Kingsolver et al., 2001; Siepielski et al., 2009, 2011, 2013) and often affected by underlying environmental conditions (Ehrlén & Valdés, 2020; Gómez-Llano et al., 2023; Hunter et al., 2018; Siepielski et al., 2017, 2022; Wade & Kalisz, 1990). Indeed, ascribing variation in selection to FDS versus a changing environment is difficult when both operate jointly (Chevin et al., 2022). Importantly, although mean effects were weak, absolute effects showed moderate to strong FDS (Table S2). Identifying sources of environmental variation that can expose or mask FDS and make it more difficult to quantify its strength and direction is an important area o further investigation.

Biological moderators

Sex and variant class generally showed evidence of NFDS, although this was only significant in asexual species. This suggests that NFDS is especially important, or easier to detect, in asexual species than in sexual species. Notably, however, asexual species were overrepresented in laboratory studies where NFDS was also detected. Therefore, these results might reflect a general bias of study systems. That is, is NFDS exceptionally strong in asexual species or is their overrepresentation in controlled laboratory studies driving this pattern?

To answer this, we used a meta-regression model with kingdom as moderator. This analysis showed that the three kingdoms that are asexual and have been studied exclusively in laboratories (chromista, fungi and bacteria) exhibit NFDS, but this was only statistically significant in fungi (Supplementary Analysis S3, Table S3). Moreover, absolute effects show stronger FDS in asexual species than in all the other groups (Table S2). Although our data do not allow us to make any more definitive conclusions, collectively these analyses suggest that NFDS is stronger in laboratory settings with no environmental confounding variables, rather than asexual species being under exceptionally strong NFDS. Alternatively, sexual species can generate novel genotypes faster due to recombination than asexual species, which are limited by mutations (Felsenstein, 1974; Muller, 1932, 1964). This will result in an increased evolutionary lag and longer persistence of low-fitness high-frequency genotypes in asexual species compared to sexual species. However, multiple asexual species, such as fungi and bacteria, have very short generation times and large effective population sizes, which can accelerate evolution and eliminate evolutionary lags relative to sexual species.

Among fitness components, we found significant NFDS for fecundity, and negative, but non-significant effects of sexual and viability selection. These results indicate that traits associated with fecundity should maintain more genetic variation, which corroborates an analysis of 842 estimates of genetic variation that found more genetic variation related to fecundity than to longevity (Houle, 1992). We also hypothesised that sexual selection would show NFDS given that both selection on fecundity and mating success are often stronger than viability selection (Hoekstra et al., 2001; Kingsolver et al., 2001; Siepielski et al., 2011). We found stronger FDS (absolute effects) in fecundity than sexual and viability selection, while FDS in sexual and viability selection had similar strengths (Table S2). However, we could also expect a stronger effect of fecundity than mating and viability if fecundity is a better proxy for total fitness. As in many studies of selection, it would be interesting to investigate whether more inclusive estimates of total fitness make it more or less likely to detect NFDS.

Interestingly, we found that FDS varied depending on ecological interaction. Specifically, FDS was more commonly negative in resource competition contexts and in non-specified interactions (i.e. other). The lack of NFDS in reproductive competition is surprising given that fecundity selection showed strong NFDS. This suggests that resource competition could be more important than reproductive competition, predation or parasitism in reducing female fecundity in a frequency-dependent way. One reason why there was no significant effect of NFDS for parasitism, herbivory and predation could be that these types of ecological interactions are primarily studied because of their effect on viability, and viability selection is generally weaker (Hoekstra et al., 2001; Kingsolver et al., 2001; Siepielski et al., 2011). However, although viability showed weaker FDS than fecundity (absolute effects), parasitism showed the strongest FDS (although usually non-significant, Figure 3c) of all ecological interactions and, interestingly, reproductive competition the weakest (Table S2). Moreover, non-significant NFDS in predation may be because strong PFDS (e.g. Chouteau et al., 2016) cancelling significant effects. If that was the case, we would find strong FDS (absolute effects). However, we found no especially strong FDS in predation, although confidence is low due to the small sample size. A key step towards validating our inferences would be to compare whether genetic variation underlying traits related to resource competition is greater than traits related to other ecological interactions, such as how additive genetic variation for fecundity is typically greater than additive genetic variation for longevity (Houle, 1992).

Limitations

We note that there were several aspects of FDS that we could not investigate in this meta-analysis due to lack of necessary data. First, we initially aimed to test the effect of population density on FDS. We expected FDS to be stronger at high densities and weaker at low densities because competitive interactions (Kilgour et al., 2018; Mueller, 1988), reproductive interactions (Gage, 1997), parasitism (Lessells, 1985) and predation (Bassar et al., 2013) often increase at higher densities (*reviewed in* Travis et al., 2023). However, we only found 13 studies including measurements of density and it was not clear what constitutes 'high density' relative to natural conditions.

Second, our results, and previous studies, suggest that environmental heterogeneity could potentially interact with FDS, and thereby make FDS less apparent in the wild than in the laboratory (Svensson et al., 2020; Takahashi et al., 2011). For example, in the polymorphic damselfly *Ischnura senegalensis*, the presence and frequency of different morphs is best explained by a combination of frequency-independent and FDS, such that strong frequency-independent selection could lead to the fixation of one morph, but weaker frequency-independent selection enables the maintenance of genetic polymorphisms through NFDS (Takahashi et al., 2011). Another study revealed that frequency-independent selection driven by temperature during the immature stage preceding sexual maturation can interfere or even counteract FDS during the adult stage in a congeneric damselfly (*I. elegans*; Svensson et al., 2020).

Unfortunately, although we would have liked to have quantified how environmental heterogeneity shapes FDS, studies measuring the effect of the abiotic environment on FDS were rare. In our data, eight studies were classified as other ecological interactions, which included studies that measured the effect of the abiotic environment and those that did not identify the agent of selection. Quantifying the strength and variability of FDS across years or among populations varying in environmental conditions can enable researchers to identify environmental effects on FDS, much like how it has allowed identifying how environmental factors shape natural selection in the wild (Caruso et al., 2017; Siepielski et al., 2017). Performing experiments to test these ideas would add to our understanding of how FDS operates and will be especially insightful in understanding how FDS can affect ecological dynamics.

Conclusions

FDS has long been heralded as a key evolutionary mechanism underlying the maintenance of genetic variation in populations. Our meta-analysis revealed several general features about the occurrence, strength, direction of FDS. We found widespread evidence for FDS across taxonomic groups, though often more so under certain methodological settings or for specific ecological interactions. While this broader result is largely consistent with theory, our findings that NFDS primarily operates on fecundity and in the context of resource competition increases our general understanding about which ecological contexts are most likely to be affected by this fundamental evolutionary process. At the same time, these results pose interesting questions about why NFDS may be less common in some ecological contexts and suggest, for example, FDS may be empirically difficult to detect in natural settings because environmental variation may mask its effect. Although considerable knowledge has been gained, FDS will likely continue to be a promising area of research. We hope this study will help direct future research efforts, stimulate new ideas for both empiricists and theoreticians, and provide researchers with a useful database to ask other key questions about FDS. We encourage ecologists and evolutionary biologists to delve deeper into understanding the evolutionary and ecological mechanisms driving FDS.

AUTHOR CONTRIBUTIONS

MG and AMS conceived the idea. MG did the literature search. MG, AMS, SPT did the initial screening of publications. MG extracted effect sizes, did the analysis and wrote the manuscript. All authors contribute conceptually and with editing.

ACKNOWLEDGEMENTS

We thank Stephen De Lisle and three anonymous reviewers for helpful and thoughtful comments on a previous version of this manuscript. AMS was financed by the National Science Foundation (NSF DEB 1748945 and 2306183), RDB by the National Science Foundation (NSF DEB 2100163) and EIS by the Swedish Research Council (VR grant: 2020–03123).

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14477.

DATA AVAILABILITY STATEMENT

Data and code supporting the results are available at https://githb.com/mgomezllano/FDS.

ORCID

Miguel Gómez-Llano https://orcid.org/0000-0003-2714-2925
Erik I. Svensson https://orcid.org/0000-0001-9006-016X
Adam M. Siepielski https://orcid.org/0000-0002-9864-743X

REFERENCES

Ayala, F.J. & Campbell, C.A. (1974) Frequency-dependent selection. *Annual Review of Ecology and Systematics*, 5, 115–138.

Barnett, A.G., van der Pols, J.C. & Dobson, A.J. (2005) Regression to the mean: what it is and how to deal with it. *International Journal of Epidemiology*, 34, 215–220.

Barton, N.H. & Keightley, P.D. (2002) Understanding quantitative genetic variation. *Nature Reviews Genetics*, 3, 11–21.

Bassar, R.D., Lopez-Sepulcre, A., Reznick, D.N. & Travis, J. (2013) Experimental evidence for density-dependent regulation and selection on Trinidadian guppy life histories. *The American Naturalist*, 181, 25–38.

Bonnet, T., Morrissey, M.B., De Villemereuil, P., Alberts, S.C., Arcese, P., Bailey, L.D. et al. (2022) Genetic variance in fitness indicates rapid contemporary adaptive evolution in wild animals. *Science*, 376, 1012–1016.

Borenstein, M. (2009) Effect sizes for continuous data. In: *The handbook of research synthesis and meta-analysis*. New York: Russell Sage Foundation, pp. 221–235.

Brower, J. (1960) Experimental studies of mimicry. IV. The reactions of starlings to different proportions of models and mimics. *The American Naturalist*, 94, 271–282.

Brunet, J. & Mundt, C.C. (2000) Disease, frequency-dependent selection, and genetic polymorphisms: experiments with stripe rust and wheat. *Evolution*, 54, 406–415.

Bürkner, P.-C. (2018) Advanced Bayesian multilevel modeling with the R package brms. *The R Journal*, 10, 395.

Caruso, C.M., Martin, R.A., Sletvold, N., Morrissey, M.B., Wade, M.J., Augustine, K.E. et al. (2017) What are the environmental determinants of phenotypic selection? A meta-analysis of experimental studies. *The American Naturalist*, 190, 363–376.

Charlesworth, B. (2015) Causes of natural variation in fitness: evidence from studies of *drosophila* populations. *Proceedings. National Academy of Sciences. United States of America*, 112, 1662–1669.

Chevin, L.-M., Gompert, Z. & Nosil, P. (2022) Frequency dependence and the predictability of evolution in a changing environment. *Evolution Letters*, 6, 21–33.

Chouteau, M., Arias, M. & Joron, M. (2016) Warning signals are under positive frequency-dependent selection in nature. *Proceedings. National Academy of Sciences. United States of America*, 113, 2164–2169.

Christie, M.R. & McNickle, G.G. (2023) Negative frequency dependent selection unites ecology and evolution. *Ecology and Evolution*, 13, e10327.

Cinar, O., Nakagawa, S. & Viechtbauer, W. (2022) Phylogenetic multilevel meta-analysis: a simulation study on the importance of modelling the phylogeny. *Methods in Ecology and Evolution*, 13, 383–395.

Cohen, J. (2013) *Statistical power analysis for the behavioral sciences*. New York: Routledge.

Darwin, C. (1859) *On the origin of species*. London: John Murray.

Dieckmann, U. & Doebeli, M. (1999) On the origin of species by sympatric speciation. *Nature*, 400, 354–357.

Ehrlén, J. & Valdés, A. (2020) Climate drives among-year variation in natural selection on flowering time. *Ecology Letters*, 23, 653–662.

Endler, J.A. (1986) *Natural selection in the wild*. Princeton: Princeton University Press.

Felsenstein, J. (1974) The evolutionary advantage of recombination. *Genetics*, 78, 737–756.

Fisher, R.A. (1930) *Genetical theory of natural selection*. Oxford, UK: Clarendon Press.

Fitzpatrick, M.J., Feder, E., Rowe, L. & Sokolowski, M.B. (2007) Maintaining a behaviour polymorphism by frequency-dependent selection on a single gene. *Nature*, 447, 210–212.

Frank, S.A. (1994) Spatial polymorphism of bacteriocins and other allelopathic traits. *Evolutionary Ecology*, 8, 369–386.

Gage, M.J.G. (1997) Continuous variation in reproductive strategy as an adaptive response to population density in the moth Plodia interpunctella. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 261, 25–30.

García-Roa, R., Garcia-Gonzalez, F., Noble, D.W. & Carazo, P. (2020) Temperature as a modulator of sexual selection. *Biological Reviews*, 95, 1607–1629.

Garrido, E., Llamas-Guzmán, L.P. & Fornoni, J. (2016) The effect of frequency-dependent selection on resistance and tolerance to herbivory. *Journal of Evolutionary Biology*, 29, 483–489.

Gómez-Llano, M., McPeek, M.A. & Siepielski, A.M. (2023) Environmental variation shapes and links parasitism to sexual selection. *Ecology and Evolution*, 37, 585–600.

Gordon, S.P., Burdfield-Steel, E., Kirvesoja, J. & Mappes, J. (2021) Safety in numbers: how color morph frequency affects predation risk in an aposematic moth. *The American Naturalist*, 198, 128–141.

Gordon, S.P., Kokko, H., Rojas, B., Nokelainen, O. & Mappes, J. (2015) Colour polymorphism torn apart by opposing positive frequency-dependent selection, yet maintained in space. *Journal of Animal Ecology*, 84, 1555–1564.

Grafen, A. (1989) The phylogenetic regression. *Philosophical Transactions of the Royal Society of London. B, Biological Sciences*, 326, 119–157.

Hasik, A.Z., De Angeli Dutra, D., Doherty, J., Duffy, M.A., Poulin, R. & Siepielski, A.M. (2023) Resetting our expectations for parasites and their effects on species interactions: a meta-analysis. *Ecology Letters*, 26, 184–199.

Hedrick, P.W. (1976) Genetic variation in a heterogeneous environment. II. Temporal heterogeneity and directional selection. *Genetics*, 84, 145–157.

Hereford, J., Hansen, T.F. & Houle, D. (2004) Comparing strengths of directional selection: how strong is strong? *Evolution*, 58, 2133–2143.

Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hoang, A., Hill, C.E. et al. (2001) Strength and tempo of directional selection in the wild. *Proceedings. National Academy of Sciences. United States of America*, 98, 9157–9160.

Houle, D. (1992) Comparing evolvability and variability of quantitative traits. *Genetics*, 130, 195–204.

Hughes, K.A., Houde, A.E., Price, A.C. & Rodd, F.H. (2013) Mating advantage for rare males in wild guppy populations. *Nature*, 503, 108–110.

Hunter, D.C., Pemberton, J.M., Pilkington, J.G. & Morrissey, M.B. (2018) Quantification and decomposition of environment-selection relationships. *Evolution*, 72, 851–866.

Janif, Z.J., Brooks, R.C. & Dixson, B.J. (2015) A'e preferences for Women's hair color frequency-dependent? *Adaptive Human Behavior and Physiology*, 1, 54–71.

Kilgour, R.J., McAdam, A.G., Betini, G.S. & Norris, D.R. (2018) Experimental evidence that density mediates negative frequency-dependent selection on aggression. *Journal of Animal Ecology*, 87, 1091–1101.

Kingsolver, J.G., Hoekstra, H.E., Hoekstra, J.M., Berrigan, D., Vignieri, S.N., Hill, C.E. et al. (2001) The strength of phenotypic selection in natural populations. *The American Naturalist*, 157, 245–261.

Kojima, K.-I. (1971) Is there a constant fitness value for a given genotype? No! *Evolution*, 25, 281–285.

Koskella, B. & Lively, C.M. (2009) Evidence for negative frequency-dependent selection during experimental coevolution of a freshwater snail and a sterilizing trematode. *Evolution*, 63, 2213–2221.

Le Rouzic, A., Hansen, T.F., Gosden, T.P. & Svensson, E.I. (2015) Evolutionary time-series analysis reveals the signature of frequency-dependent selection on a female mating polymorphism. *The American Naturalist*, 185, E182–E196.

Lessells, C.M. (1985) Parasitoid foraging: should parasitism be density dependent? *Journal of Animal Ecology*, 54, 27–41.

Levene, H. (1953) Genetic equilibrium when more than one ecological niche is available. *The American Naturalist*, 87, 331–333.

Lewontin, R.C. (1958) A general method for investigating the equilibrium of gene frequency in a population. *Genetics*, 43, 419.

Martin, C.H. (2016) Context dependence in complex adaptive landscapes: frequency and trait-dependent selection surfaces within an adaptive radiation of Caribbean pupfishes. *Evolution*, 70, 1265–1282.

Melián, C.J., Alonso, D., Vázquez, D.P., Regetz, J. & Allesina, S. (2010) Frequency-dependent selection predicts patterns of radiations and biodiversity. *PLoS Computational Biology*, 6, e1000892.

Mitchell-Olds, T., Willis, J.H. & Goldstein, D.B. (2007) Which evolutionary processes influence natural genetic variation for phenotypic traits? *Nature Reviews Genetics*, 8, 845–856.

Morrissey, M.B. (2016a) Meta-analysis of magnitudes, differences and variation in evolutionary parameters. *Journal of Evolutionary Biology*, 29, 1882–1904.

Morrissey, M.B. (2016b) Rejoinder: further considerations for meta-analysis of transformed quantities such as absolute values. *Journal of Evolutionary Biology*, 29, 1922–1931.

Morrissey, M.B. & de Kerckhove, D.T. (2009) The maintenance of genetic variation due to asymmetric gene flow in dendritic metapopulations. *The American Naturalist*, 174, 875–889.

Mousseau, T.A. & Roff, D.A. (1987) Natural selection and the heritability of fitness components. *Heredity*, 59, 181–197.

Mueller, L.D. (1988) Evolution of competitive ability in drosophila by density-dependent natural selection. *Proceedings. National Academy of Sciences. United States of America*, 85, 4383–4386.

Muller, H.J. (1932) Some genetic aspects of sex. *The American Naturalist*, 66, 118–138.

Muller, H.J. (1964) The relation of recombination to mutational advance. *Mutation Research, Fundamental and Molecular Mechanisms of Mutagenesis*, 1, 2–9.

Mundt, C.C., Brunet, J. & Sackett, K.E. (2008) Impact of density and disease on frequency-dependent selection and genetic polymorphism: experiments with stripe rust and wheat. *Evolutionary Ecology*, 22, 637–657.

Nakagawa, S., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W., Parker, T.H. et al. (2022) Methods for testing publication bias in ecological and evolutionary meta-analyses. *Methods in Ecology and Evolution*, 13, 4–21.

Nosil, P., Villoutreix, R., de Carvalho, C.F., Farkas, T.E., Soria-Carrasco, V., Feder, J.L. et al. (2018) Natural selection and the predictability of evolution in *Timema* stick insects. *Science*, 359, 765–770.

O'Dea, R.E., Lagisz, M., Jennions, M.D., Koricheva, J., Noble, D.W.A., Parker, T.H. et al. (2021) Preferred reporting items for systematic reviews and meta-analyses in ecology and evolutionary biology: a PRISMA extension. *Biological Reviews*, 96, 1695–1722.

Olendorf, R., Rodd, F.H., Punzalan, D., Houde, A.E., Hurt, C., Reznick, D.N. et al. (2006) Frequency-dependent survival in natural guppy populations. *Nature*, 441, 633–636.

Otto, S.P., Servedio, M.R. & Nuismer, S.L. (2008) Frequency-dependent selection and the evolution of assortative mating. *Genetics*, 179, 2091–2112.

Paradis, E. & Schliep, K. (2019) Ape 5.0: an environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528.

Peng, F., Ballare, K.M., Hollis Woodard, S., den Haan, S. & Bolnick, D.I. (2021) What evolutionary processes maintain MHC IIβ diversity within and among populations of stickleback? *Molecular Ecology*, 30, 1659–1671.

Pfennig, D.W., Harcombe, W.R. & Pfennig, K.S. (2001) Frequency-dependent Batesian mimicry. *Nature*, 410, 323.

Pick, J.L., Nakagawa, S. & Noble, D.W.A. (2019) Reproducible, flexible and high-throughput data extraction from primary literature: the METADIGITISE R package. *Methods in Ecology and Evolution*, 10, 426–431.

Potter, T., Arendt, J., Bassar, R.D., Watson, B., Bentzen, P., Travis, J. et al. (2023) Female preference for rare males is maintained by indirect selection in Trinidadian guppies. *Science*, 380, 309–312.

R Development Core Team. (2018) R: A language and environment for statistical computing.

Rendueles, O., Amherd, M. & Velicer, G.J. (2015) Positively frequency-dependent interference competition maintains diversity and pervades a natural population of cooperative microbes. *Current Biology*, 25, 1673–1681.

Rozen, D.E. & Lenski, R.E. (2000) Long-term experimental evolution in *Escherichia coli*. VIII. Dynamics of a balanced polymorphism. *The American Naturalist*, 155, 24–35.

Senior, A.M., Gosby, A.K., Lu, J., Simpson, S.J. & Raubenheimer, D. (2016) Meta-analysis of variance: an illustration comparing the effects of two dietary interventions on variability in weight. *Evolution, Medicine, and Public Health*, 2016, 244–255.

Siepielski, A.M., DiBattista, J.D. & Car'son, S.M. (2009) It's about time: the temporal dynamics of phenotypic selection in the wild. *Ecology Letters*, 12, 1261–1276.

Siepielski, A.M., DiBattista, J.D., Evans, J.A. & Carlson, S.M. (2011) Differences in the temporal dynamics of phenotypic selection among fitness components in the wild. *Proceedings of the Royal Society B*, 278, 1572–1580.

Siepielski, A.M., Gómez-Llano, M. & McPeek, M.A. (2022) Environmental conditions during development affect sexual selection through trait-fitness relationships. *The American Naturalist*, 199, 34–50.

Siepielski, A.M., Gotanda, K.M., Morrissey, M.B., Diamond, S.E., DiBattista, J.D. & Carlson, S.M. (2013) The spatial patterns of directional phenotypic selection. *Ecology Letters*, 16, 1382–1392.

Siepielski, A.M., Morrissey, M.B., Buoro, M., Carlson, S.M., Caruso, C.M., Clegg, S.M. et al. (2017) Precipitation drives global variation in natural selection. *Science*, 355, 959–962.

Sinervo, B. & Calsbeek, R. (2006) The developmental, physiological, neural, and genetical causes and consequences of frequency-dependent selection in the wild. *Annual Review of Ecology, Evolution, and Systematics*, 37, 581–610.

Sinervo, B. & Lively, C.M. (1996) The rock–paper–scissors game and the evolution of alternative male strategies. *Nature*, 380, 240–243.

Svensson, E.I., Abbott, J. & Härdling, R. (2005) Female polymorphism, frequency dependence, and rapid evolutionary dynamics in natural populations. *The American Naturalist*, 165, 567–576.

Svensson, E.I. & Connallon, T. (2019) How frequency-dependent selection affects population fitness, maladaptation and evolutionary rescue. *Evolutionary Applications*, 12, 1243–1258.

Svensson, E.I., Willink, B., Duryea, M.C. & Lancaster, L.T. (2020) Temperature drives pre-reproductive selection and shapes the biogeography of a female polymorphism. *Ecology Letters*, 23, 149–159.

Takahashi, Y., Morita, S., Yoshimura, J. & Watanabe, M. (2011) A geographic cline induced by negative frequency-dependent selection. *BMC Evolutionary Biology*, 11, 256.

Takahashi, Y., Yoshimura, J., Morita, S. & Watanabe, M. (2010) Negative frequency-dependent selection in female color polymorphism of a damselfly. *Evolution*, 64, 3620–3628.

Travis, J., Bassar, R.D., Coulson, T., Reznick, D. & Walsh, M. (2023) Density-dependent selection. *Annual Review of Ecology, Evolution, and Systematics*, 54, 85–105.

Turner, P.E. (2005) Parasitism between co-infecting bacteriophages. *Advances in Ecological Research*, 37, 309–332.

Udovic, D. (1980) Frequency-dependent selection, disruptive selection, and the evolution of reproductive isolation. *The American Naturalist*, 116, 621–641.

Viechtbauer, W. (2010) Conducting meta-analyses in R with the metafor package. *Journal of Statistical Software*, 36, 1–48.

Wade, M.J. & Kalisz, S. (1990) The causes of natural selection. *Evolution*, 44, 1947–1955.

Weeks, A.R. & Hoffmann, A.A. (2008) Frequency-dependent selection maintains clonal diversity in an asexual organism. *Proceedings. National Academy of Sciences. United States of America*, 05, 17872–17877.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Gómez-Llano, M., Bassar, R.D., Svensson, E.I., Tye, S.P. & Siepielski, A.M. (2024) Meta-analytical evidence for frequency-dependent selection across the tree of life. *Ecology Letters*, 27, e14477. Available from: https://doi.org/10.1111/ele.14477