

Integrating ecological and evolutionary perspectives to predict the multi-generational fitness legacies of natural immigration

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Abstract

Natural dispersal between populations, and resulting immigration, influences population size and genetic diversity and is therefore a key process driving reciprocal interactions between ecological and evolutionary dynamics. Both ecological and evolutionary consequences of dispersal fundamentally depend on the relative fitnesses of immigrants and their various descendants manifested in the context of natural environments. Yet, despite this commonality, recent research advances in predicting immigrants' legacies remain substantially disconnected across disciplines. To bridge resulting divides, we synthesize empirical and theoretical work examining fitness consequences of inter-breeding across the full spectrum of genetic divergence from inbred lines to inter-specific hybridization. We demonstrate how common underlying processes can generate positive or negative fitness consequences of immigration depending on interacting genetic and environmental effects. Impacts of inter-breeding following natural dispersal among sub-populations could consequently vary dramatically, shaping eco-evolutionary outcomes. Yet, our systematic literature review reveals a striking paucity of empirical studies that quantify multi-generational fitness consequences of immigration in natural metapopulations, precluding general inferences on outcomes. Hence, to provide new impetus, we highlight key theoretical and empirical gaps, and outline how cutting-edge statistical and genomic tools could be combined with multi-generational field datasets to advance understanding of dispersal-mediated drivers and constraints on eco-evolutionary dynamics.

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ABSTRACT

Natural dispersal between populations, and resulting immigration, influences population size and genetic diversity and is therefore a key process driving reciprocal interactions between ecological and evolutionary dynamics. Both ecological and evolutionary consequences of dispersal fundamentally depend on the relative fitnesses of immigrants and their various descendants manifested in the context of natural environments. Yet, despite this commonality, recent research advances in predicting immigrants' legacies remain substantially disconnected across disciplines. To bridge resulting divides, we synthesize empirical and theoretical work examining fitness consequences of inter-breeding across the full spectrum of genetic divergence from inbred lines to inter-specific hybridization. We demonstrate how common underlying processes can generate positive or negative fitness consequences of immigration depending on interacting genetic and environmental effects. Impacts of inter-breeding following natural dispersal among sub-populations could consequently vary dramatically, shaping eco-evolutionary outcomes. Yet, our systematic literature review reveals a striking paucity of empirical studies that quantify multi-generational fitness consequences of immigration in natural metapopulations, precluding general inferences on outcomes. Hence, to provide new impetus, we highlight key theoretical and empirical gaps, and outline how cutting-edge statistical and genomic tools could be combined with multi-generational field datasets to advance understanding of dispersal-mediated drivers and constraints on eco-evolutionary dynamics.

INTRODUCTION

Dispersal of individuals among populations, and resulting immigration, fundamentally underpins key ecological and evolutionary processes that shape populations dynamics and persistence (Lenormand 2002, Lowe et al. 2017). Ecologists have traditionally aimed to understand short and long-term contributions of immigrants to demographic parameters, while evolutionary biologists aim to understand consequences of effective gene flow in mediating adaptive versus non-adaptive evolution and diversification. Yet, the key processes that link these two goals – the underlying causes and resulting magnitudes of fitness of immigrants and their descendants – remain considerably unexplored in both empirical and theoretical studies of metapopulations, and hence in precisely the context where eco-evolutionary implications of dispersal could be most substantial. Here, we synthesize theoretical and empirical knowledge from different disciplines, which provide a framework for advancing understanding of multigenerational fitness effects of immigration in wild metapopulation systems. These advances are fundamental to embedding dispersal, and resulting immigration, as a central driver of reciprocal eco-evolutionary dynamics, thereby facilitating understanding of biodiversity dynamics (Pelletier & Coltman 2018, Pelletier et al. 2009, Reznick et al. 2019, Sutherland et al. 2013).

Immigration can benefit populations by increasing local population size, thereby reducing Allee effects (Stephens & Sutherland 1999) or demographic stochasticity (e.g. Schaub et al. 2013, reviewed in Milon et al. 2019). Whenever immigrants recruit to the adult population and produce viable offspring, further profound short- and long-term impacts on populations can result. Descendants of immigrants can contribute to population growth rates (e.g. Åkesson et al 2016, Ranke et al. 2017) and in turn, larger population sizes can increase the efficiency of natural selection against deleterious alleles (Kimura 1962, Raynes et al.

2018), possibly facilitating evolutionary rescue (Bell 2017, Hoffmann et al. 2021, Stewart et al. 2017). Via introgression of new genetic variants, immigrants can also replenish local genetic variation, alleviating inbreeding and genetic drift load, and increasing individual and population fitness (Adams et al. 2011, Bell 2017, Millon et al. 2019, Stewart et al. 2017, Szucs et al. 2014, Tallmon et al. 2004). Yet, conversely, immigrants could reduce population fitness. For instance, introgression of locally maladaptive alleles, and disruptions of genomic coadaptations due to recombination between immigrant and local genomes (Dobzhansky 1950, Soule 1967; see also Kawecki & Ebert 2004), can counter-act local adaptation and generate migration load (Bolnick & Nosil 2007, García-Ramos & Kirkpatrick 1997, Lenormand 2002, Paul et al. 2011, Reid et al. 2021). Net eco-evolutionary impacts of immigration therefore depend on the balance between positive and negative fitness effects of imported genetic variants, and on resulting degrees and rates of introgression, which are contingent on the relative fitnesses of immigrants, residents, and their descendants, and on the frequency in which different descendant categories are naturally produced in populations (Ingvarsson & Whitlock 2000, Pfennig & Lachance 2022).

While the frequency and fitness of immigrants is compared to that of existing residents in some demographic studies of natural populations (Millon et al. 2019), explicit estimates for subsequent filial generations (including F_1 s, F_2 s and various backcrosses; Fig. 1) are typically lacking. Furthermore, hybrid offspring from immigrant-resident matings are often classified as residents in these comparisons, implying an assumption of equal fitness between residents and the descendants of immigrants. Yet, the fitness of hybrid filial generations will likely differ from that of residents, leading to under- or over-estimation of demographic and genetic contributions of immigrants. Moreover, the relative fitnesses of immigrants, residents and their various descendants (Fig. 1) are ultimately determined by the genetic architecture of fitness and its interactions with environmental conditions, which are shaped by the relative contributions of adaptive and non-adaptive mechanisms to the evolutionary history of population divergence (Barton 2001, Chevin et al. 2014, Dagilis et al. 2019, Lynch 1991, Lynch & Walsh 1998, Rundle & Whitlock 2001, Simon et al. 2018, Schneemann et al. 2020). Therefore, while comprehensive theory is fundamental to predicting the relative fitnesses of subsequent filial generations, empirical studies are essential to test predictions and to elucidate the prevalence and magnitude of effects in natural populations.

Fitness effects of crosses between individuals of different lineages or populations (i.e. outbreeding or outcrossing, terms used interchangeably hereafter) have long been documented and rationalized conceptually in agricultural and [incipient] speciation research (e.g. Crow 1948, Darwin 1876, Dobzhansky 1950, Lynch & Walsh 1998, Orr 1995; Fig. 2). These theoretical developments have also been successfully extended and applied to severely inbred natural populations within the context of ‘genetic rescue’ (Hoffmann et al. 2021, Ingvarsson 2001, Tallmon et al. 2004, Whiteley et al. 2015). However, such theory has rarely been exploited by evolutionary ecologists interested in the consequences of natural dispersal and resulting immigration and gene flow in fragmented populations of single species. Yet, crosses between inbred lines derived from individuals within single or weakly differentiated populations and crosses between isolated species represent two extreme ends of a continuum of genetic divergence where subdivided populations connected by natural dispersal are intermediate (Demuth & Wade 2005, Hughes & Vickery 1974, Simon et al. 2018; Fig. 2). This gap therefore likely simply reflects academic silos, where researchers working on demographic variation and eco-evolutionary dynamics in wild (meta)populations are not focusing explicitly on theory and principles that are central to speciation and agricultural or conservation research.

Hence, to bridge these divides and inspire new activity in evolutionary ecology, we synthesise key aspects of the current empirical and theoretical states of the art in line-cross theory, as primarily developed in the contexts of hybridization or speciation, that aim to rationalize and predict fitness outcomes resulting from complex genetic consequences of multigenerational introgression. We then provide a systematic literature review which highlights that, despite the increasing availability of applicable theory and multigenerational field datasets, fitness outcomes from interbreeding resulting from natural immigration in fragmented populations have still very rarely been explicitly or rigorously estimated. Finally, we highlight conceptual and empirical opportunities and challenges which, in conjunction with newly available methods, can now culminate in comprehensive overview of the consequences of outbreeding spanning the full biological range of divergence.

PREDICTING MULTIGENERATIONAL OUTCOMES OF OUTCROSSING

Heterosis via non-additive genetic effects

Understanding and predicting the fitness outcomes of outcrossing has been a core ambition in biology since at least the 19th century, motivated by agriculture and artificial breeding reports of high yield of hybrid offspring (reviewed in Crow 1987). Specifically, when highly inbred lines derived from individuals within single or weakly differentiated populations are crossed, F_1 offspring commonly show “hybrid vigour” or “outbreeding enhancement”, where values of focal phenotypic traits exceed the mean across the parental lines, or even exceed the maximum parental value (Burke & Arnold 2001, Crow 1987, Lynch & Walsh 1998). These early findings fueled extensive study on “heterosis”, describing [positive or negative] deviations of offspring phenotypic value from the mid-parental phenotype expected under additive genetic effects (Burke & Arnold 2001, Lynch & Walsh 1998; Box 1, Fig. 3). This work has subsequently generated theoretical and empirical insights with consequences well beyond their applications to agriculture.

In wild populations, positive heterosis is commonly observed as the result of outbreeding with conspecifics that arrive or are artificially translocated to alleviate inbreeding depression in highly inbred populations (termed ‘genetic rescue’; Fig. 2; Derry et al. 2019, Frankham 2015, Hoffmann et al. 2021, Ingvarsson 2001, Whiteley et al. 2015). These beneficial effects have been shown to span multiple generations (Derry et al. 2019, Frankham 2016), leading to increased population growth (e.g. Åkesson et al. 2016) and rapid fixation of immigrant’s genetic variants (e.g. Adams et al. 2011). Here, heterosis primarily reflects genetic dominance (Box 1, Fig. 3A,C), via heterozygosity masking the consequences of deleterious recessive alleles or via overdominance (Charlesworth & Willi 2009, Crow 1948, Lamkey & Edwards 1999).

Meanwhile, at the other end of the spectrum of parental divergence, hybrid offspring of crosses between distantly related populations, including inter-(sub)species crosses, often show decreased fitness (termed negative heterosis or outbreeding depression; Lynch 1991, Rhymer & Simberloff 1996, Tallmon et al. 2004, Waser & Price 1989; Fig. 2). While hybrid inviability or sterility may imply reproductive isolation between lineages, these crosses often show imperfect isolation in the F_1 offspring or fitness reductions that are only apparent in later generations (e.g. F_2 and backcrosses). This may allow introgression of locally maladaptive variants that can lead to genetic or population extinction (Allendorf et al. 2004, Rhymer and Simberloff 1996). These consequences are often caused by negative effects of epistasis due to incompatibilities between highly diverged genomes (genetic, intrinsic or Dobzhansky-Muller incompatibility; Box 1, Fig. 3A,D) or by loss of within-lineage coadapted epistatic interactions (Demuth & Wade 2005, Dobzhansky 1950, Edmands & Deimler 2004, Orr 1995, Rundle & Whitlock 2001).

Despite such broad generalisations, it is now clear that fitness outcomes of interbreeding are far more complex. Crossing inbred lines can cause decreased fitness in hybrid offspring (Derry et al. 2019, Edmands 2007, Lynch 1991). Conversely, interspecific crosses may commonly generate beneficial effects, that even last to the F_2 generation (Brice 2021). Furthermore, such crosses can result in novel or transgressive phenotypes (i.e. outside of the limits of parental phenotypes, e.g. best-parent heterosis) for fitness and fitness-related traits in F_1 offspring (Atsumi et al. 2021, Grant & Grant 2010, Rieseberg et al. 1999). In turn, transgressive phenotypes have been linked to increased adaptive potential (Edelman & Mallet 2021), and increased ability of hybrids to colonize new environments (Pfennig et al. 2016, Rius & Darling 2014). Therefore, contrary to traditional expectations, crosses between either inbred lines or highly divergent lineages may result in either negative or positive effects.

This complexity in outcomes derives from two main facts. First, fitness consequences depend on more than just the degree of genetic divergence between parental lineages, but also on an axis of variation pertaining to the degree of ecological (i.e. adaptive) divergence between the parental lineages (Fig. 2). Here, fitness decreases with greater divergence between the parental environments as a consequence of genotype-environment mismatches, leading to extrinsic or ecologically dependent incompatibility even at the lower end of the spectrum of genetic divergence (Derry et al. 2019, Edmands & Deimler 2004, Rundle & Whitlock 2001, Thompson et al. 2022a,b). Second, both positive or negative heterosis can result from combinations of various genetic

effects, including dominance, under/overdominance and epistasis, as outlined by traditional line-cross theory (Box 1; Boeven et al. 2020, Fu et al. 2015, Guo et al. 2014, Kusterer et al. 2007, Lynch 1991, Lynch and Walsh 1998, Mather & Jinks 1982, Shapira et al. 2014). Fitness outcomes, therefore, may depend not on one of the genetic effects alone, but on a balance between the relative magnitude of them, resulting in outcomes that can be unique to individual crosses and contexts (e.g. Armbruster et al. 1997).

In fact, fitness outcomes vary across traits that differ in underlying genetic architecture, and change across filial generations, because of changes in the magnitude of the different genetic effects (Burke & Arnold 2001, Brice et al. 2021, Fox et al. 2004, Lamkey & Edwards 1999, Lynch 1991, Roff & Emerson 2006, Rundle & Whitlock 2001, Rius & Darling 2014, Zhang et al. 2021). For instance, fitness components are often more affected by outcrossing than other traits (Whitlock et al. 2013), in line with findings that dominance and epistasis are more common in life history than in morphological traits (Roff & Emerson 2006). In turn, fitness gains in F_1 offspring can be partially or entirely wiped out, or even reversed, in the F_2 or subsequent generations, due to reduced dominance and increased epistatic interactions across filial generations (Box 1, Fig. 3D). Similarly, gene-by-environment interactions may change the relative magnitudes of genetic effects across rearing environments experienced by the hybrid offspring (e.g. Fox et al. 2004). Finally, loss of beneficial epistatic interactions that commonly arise from adaptive ecological differentiation (e.g. Carroll et al. 2003) can outweigh benefits of increased heterozygosity even for highly inbred populations in an environment-dependent manner (Edmands 2007, Frankham et al. 2011; Fig. 2). Outcomes of outbreeding, therefore, are affected by current environmental conditions experienced by the hybrid offspring, and also by how the genetic architecture of traits have been shaped by past evolutionary responses of the parental lineages.

A recent model of speciation (Dagilis et al. 2019) further emphasizes the complexity in fitness outcomes of outbreeding and how the balance between positive and negative effects connects the extremes of the genetic and ecological divergence continuum. Specifically, in addition to negative epistatic interactions arising in hybrid offspring (i.e. Dobzhansky-Muller incompatibilities), and loss of positive epistatic interaction within lineages (i.e. breakdown of coadapted gene complexes), Dagilis et al. (2019) allowed outcrosses to result in positive epistasis and loss of negative epistasis. Under these conditions, the same genetic effects can explain both positive and negative heterosis along a continuum of genetic and ecological divergence, as the balance between positive and negative epistatic effects (i.e. the fitness of the hybrid offspring) changes across the divergence continuum. Interestingly, the net balance between effects is extremely variable in the early stages of lineage divergence, due to the relative influence of drift and selection on focal loci (Dagilis et al. 2019). This is exactly the parameter space that demes within fragmented wild populations typically occupy, highlighting the potential for genetic effects to generate complex and dynamic forms of both positive and negative heterosis following natural dispersal and outcrossing in metapopulation systems.

Indeed, manifestation of heterosis does not require crosses between highly diverged or inbred lines or demes, but can arise from crosses among demes that show genetic structuring (i.e. population level inbreeding) due to adaptive (i.e. ecological) divergence or independent random fixation of alleles via genetic drift fostered by restricted dispersal (Barton 2001, Chevin et al. 2014, Crow 1948, Fenster et al. 1997, Lamkey & Edwards 1999, Simon et al. 2018, Whitlock et al. 2000). This scenario likely comprises most wild populations, since local adaptation is common across natural systems (Hereford 2009, Leimu & Fischer 2008) and genetic structure not only occurs in populations with geographical separation, but also along clines or center-edge continuum of distribution ranges (García-Ramos & Kirkpatrick 1997, Koski et al. 2019, Kottler et al. 2021). These empirical and theoretical developments suggest that heterosis could be widespread or even ubiquitous in wild systems, raising key questions of what fitness outcomes can - and generally do - arise following crosses between populations with intermediate degrees of genetic differentiation (Fig. 2).

Given that the same genetic effects shape the fitness of outcrossed offspring across the biological spectrum of genetic divergence, predictions regarding observed fitness outcomes of outcrossed offspring resulting from natural immigration can be formulated. For example, fitness consequences depend on the specific genetic architecture of a trait within a population and between the pair of populations, and can vary across life stages, sexes, and environments. Outcomes should consequently not be universal across traits, across life

stages, or between sexes, and should vary among different pairwise combinations of populations of the same species, or even when the same pairwise combination experiences different environments. Yet, dominance effects should be more pronounced as non-adaptive genetic divergence between demes increases, generating a positive relationship between hybrid fitness in the F_1 generation and pairwise genetic distance or divergence time between parental populations (Whitlock et al. 2000).

However, interactions with the environment may affect predicted outcomes. For instance, if dominance effects are environment-dependent, relative fitness for F_1 and F_2 offspring should vary across parental environments. If, instead, epistatic interactions are environment-dependent, F_1 and F_2 fitness should be similar across parental environments, but environment-dependent effects should emerge in reciprocal backcrosses (Dagilis et al. 2019, Rundle & Whitlock 2001). In the context of natural dispersal between spatially structured populations, backcrosses resulting from matings between F_1 and residents (i.e. B_1 or B_2) will most likely live in the environment of the parental population that composes most of their genome (i.e. P_1 or P_2 , respectively). Therefore, the fitness of these backcrosses should be higher than that of the F_2 in these respective environments, due to effects of both dominance and epistasis (Edmands & Deimler 2004, Rundle & Whitlock 2001).

Finally, since coadapted gene complexes may play a big role in local adaptation, epistasis may be stronger than dominance in cases of ecologically driven divergence. For instance, populations may adaptively evolve within-lineage positive epistatic effects that, if broken during outbreeding, reduce the fitness of the hybrid offspring. Consequently a negative relationship between hybrid fitness and genetic distance between parental populations. Under such genetic architecture, fitness gains via dominance in F_1 offspring may be outweighed by the loss of positive epistatic effects at larger genetic distances, leading to an optimal intermediate crossing distance between lineages (Lynch 1991, Price & Waser 1979; see also Fenster 1991). As beneficial dominance effects decrease, and negative between-lineage epistatic effects appear due to recombination, fitness declines for hybrids along the divergence continuum may become particularly severe for the F_2 offspring and further recombinant generations. These conclusions mirror those of simulations using line-cross theory, whereby fitness of F_1 and F_2 offspring in respect to the mid-parent value decline as epistasis becomes stronger than dominance (Lynch 1991).

Overall, these theoretical developments reveal the degree to which complex multigenerational fitness effects resulting from natural immigration could arise, and provide tractable routes to predicting and rationalising observed variation.

Heterosis via non-linear phenotypic effects

While heterosis has been widely viewed as emerging from non-additive genetic effects (Box 1, Figure 3), recent developments suggest that heterosis could alternatively result from non-linear phenotypic effects. Such outcomes can arise given a non-linear genotype-phenotype map, even when underlying genetic effects are purely additive and do not depend on the genetic background (Lynch & Walsh 1998, Fiévet et al. 2010, 2018) (Fig. 4A). The trait value for a heterozygous individual can then be closer to the value of one of the parents and deviate from the mid-parent value, fulfilling the broad definition of heterosis (Box 1). For instance, Wright’s model of physiological dominance proposes that the physiological activity of enzymes saturates, resulting in a non-linear relationship between enzyme concentration, i.e. the product of additive genetic effects between multiple loci, and the resultant metabolic flux or phenotype (as in Fig. 4A; see also Fiévet et al. 2010). Similarly, as individuals increase linearly in body size, other traits within the organisms may increase logarithmically (i.e. allometric traits). This non-linear increase in trait values with respect to body size changes has been shown to explain up to 75% of heterosis magnitude in two fitness-related traits in *Arabidopsis thaliana* (Vasseur et al. 2019).

The importance of non-linear relationships in determining heterosis may be far greater, and further highlight the importance of accounting for the ecological divergence between parental lineages when predicting fitness effects of the hybrid offspring (Fig. 2). This is because the relationship between phenotype and fitness is expected to be non-linear, due to effects of stabilizing selection as populations adapt to local conditions and

approach the optima (Phillips & Arnold 1989). Moreover, if local conditions vary spatially, adaptation to local conditions may result in patterns of local adaptation, whereby individuals from a focal population have higher fitness in their environment of origin than in a foreign environment (“home vs away”) or individuals from a local population present higher fitness than the ones from foreign populations (“local vs foreign”) (Kawecki & Ebert 2004). In these cases, the non-linearity of the adaptive landscapes and fitness trade-off between environment can lead to dominance reversals (see Connallon & Chenoweth 2019). As such, the shape of the adaptive landscape across environments and the degree of maladaptation presented by immigrant individuals may influence not just differences in fitness between residents and immigrants, but that of the hybrid filial generations (Fig. 2). Reciprocally, estimates of fitness across filial generations and parental environments can reveal the differences between optima in the adaptive landscape across the respective environmental conditions of subpopulations (Fig 4B-C).

These intuitions are highlighted by a series of theoretical studies using Fisher’s geometrical model (Barton 2001, Chevin et al. 2014, Simon et al. 2018, Schneemann et al. 2020), culminating in an extension of genetic effects coefficients (Box 1) that explicitly accounts for the degree of local adaptation (Schneemann et al. 2020). These studies consider a fitness function with additive phenotypic effects and stabilizing selection near the optimum in a fitness landscape which results in a non-linear relationship between the [multi-dimensional] phenotype and fitness. Variations of this model have been shown to make reasonable predictions of heterosis in F_1 and recombinant hybrids (Barton 2001, Chevin et al. 2014, Simon et al. 2018, Vasseur et al. 2019) and to match empirical data from inbred line-crosses (Simon et al. 2018).

Moreover, similarly to Dagilis et al. 2019 (previously discussed), these studies present conclusions that are highly relevant to the case of natural dispersal in spatially structured populations. Namely, that expectations for hybrid fitness depend on the relative influence of drift and selection during early stages of lineage diversification (Barton 2001, Chevin et al. 2014, Simon et al. 2018, Schneemann et al. 2020). Specifically, non-adaptive genetic divergence (e.g. with population-level inbreeding) leads to a net benefit of increased heterozygosity (Schneemann et al. 2020), which decays across generations from the maximum value in F_1 . With adaptive divergence, positive heterosis is also expected for the F_1 , but due to a net benefit of admixture via transgressive variation (Schneemann et al. 2020). In F_2 s and backcrosses, however, this benefit can be outweighed by a cost of recombination creating phenotypic variance around the optimum (i.e. segregational variance; Barton 2001, Chevin et al. 2014). When both selection and drift interact, such as in the case of stabilizing selection on phenotype with the evolution of cryptic genetic differentiation between populations (i.e. “system drift”), the intermediate phenotype of F_1 hybrids presents higher fitness than the mid-parent value, due to the curvature of the fitness landscape (Barton 2001). However, recombinants incur a cost of admixture due to the breakdown of coadapted gene complexes from the parental lines (Chevin et al. 2014, Schneemann et al. 2020). Predicted hybrid fitness from these models, therefore, also generally align to predictions of the traditional line-cross theory, and nuances are determined by the relative importance of adaptive and non-adaptive processes during the divergence of populations.

MULTIGENERATIONAL OUTCOMES OF OUTCROSSING IN NATURAL POPULATIONS

The theoretical possibilities reviewed above highlight the potentially complex set of fitness outcomes from outcrossing due to natural immigration across spatially structured populations. We therefore conducted a literature review, aiming to evaluate the degree to which key effects have actually been estimated in wild populations where immigrants naturally outbreed with resident individuals, and thereby synthesise the overall body of empirical knowledge. We used search terms on Web of Science aimed to find ecological studies that estimate the fitness of the offspring of natural immigrants, including studies that do not specifically interpret results within the heterosis framework, as well as more traditional heterosis-related search terms (Fig. 5). Due to the high number of results initially found, we filtered for studies within the Web of Science category of “ecology or evolutionary biology”, aiming to exclude studies on domesticated or agricultural lines, resulting in 12,862 studies after duplicate removal. We validated our search by comparing the results to a list of previously known studies by our research group, and triaged the results based on the series of criteria

presented in Table 1. The definition of criteria and the triage were done by DG in consultation with HJ and JMR.

We found 111 studies (0.86% of 12,862) on natural populations with at least one estimate of fitness or a fitness-related trait for both within and between population crosses for at least one generation (criteria 1-5; Supplementary Table S1). These studies exclusively focused on animals or plants (Fig. 6), encompassing 89 different species. Focal fitness metrics and traits varied across studies, but commonly included: germination, biomass, number of flowers, fruits and seeds produced and seed mass in plants; and number and size of offspring produced (e.g. clutch and egg size) and developmental time in animals. For both plants and animals, survival across different life stages and metrics of cumulative fitness were also common.

Over a third of the 111 studies (39.6%, N=44) presented crosses between populations for which the degree of connectivity was unclear (Fig. 7), whether due to a lack of knowledge regarding dispersal in the focal populations, lack of mention of it within the paper, or because the information presented was not sufficient for a categorization considering our specified criteria (Table 1, criteria 6). Another large proportion of studies (45%, N=50) included heterosis estimates for hybrid offspring resulting from introduction (N=1) or artificial crosses (N=49) between populations further than the distance of natural dispersal, such as crosses between populations separated by several hundreds of kilometers, and even populations from different continents. More than half of these studies (N=29) only estimated heterosis at this level of connectivity, while the others (N=21) combined estimates across different levels of connectivity (category “both” in Fig. 7). Among the remaining 17 studies (15%), which we could classify as only studying populations that are, or possibly are, interconnected by natural dispersal, only three reported fitness estimates for hybrid offspring resulting from interbreeding due to natural immigration (Fig. 7).

In two of the three studies conducted under the context of natural dispersal (Marr et al. 2002, Martinig et al. 2020), estimates were for the hybrid offspring between residents and natural immigrants, whereby long-term fitness and parentage data (18-29 years) allowed the categorization of individuals into resident or immigrant, and their offspring into the relevant filial generations. While Marr and collaborators (2002) explicitly aimed to estimate the fitness consequences of outcrossing following natural dispersal into an island population of song sparrows (*Melospiza melodia*), Martinig and collaborators (2020) aimed to investigate sex-specific fitness consequences of dispersal in the North American red squirrels (*Tamiasciurus hudsonicus*).

In the song sparrows, male immigrants showed lower reproductive performance than residents, but no difference in survival. Among comparisons of reproductive performance and survival including hybrid filial generations, no difference was found for hybrid F₁s versus average immigrant-resident, hybrid F₁s versus F₂s, and hybrid F₂s versus average F₁-immigrant-resident (Marr et al. 2002). However, F₁s produced between 27.1% (females) to 30.2% (males) more offspring than the average between immigrant and residents, and about 2 (females) to 3 times (males) more offspring than F₂s. F₂ males also showed decreased survival in comparison to F₁s in both juvenile (46%) and adult (35.1%) stages. These heterotic effects are likely biologically significant, and the lack of strong statistical evidence for these differences possibly resulted from low power due to a small number of immigrants (14 females and 4 males vs. >100 residents). In turn, male immigrants of North American red squirrels had longer lifespans and produced more offspring than residents, while female immigrants had reduced lifetime reproductive success (Martinig et al. 2020). In addition, researchers found that both immigrant males and females produced daughters with lower lifetime reproductive success than resident males and females, respectively. However, no further comparisons or specifications of filial generations were presented, nor a distinction was made between offspring of immigrant-immigrant versus immigrant-resident crosses.

The third study (Bull & Sunnucks 2014) investigated the fitness of hybrid offspring along a contact zone between two races of a velvet worm (*Euperipatoides rowelli*), aiming to investigate the maintenance of morphological differentiation between the races. Using body coloration patterns and haplotypes to classify individuals and embryos as either of the races or as hybrids, researchers found no evidence for a difference in embryo-to-adult survival across categories. However, hybrids represented a single category for which genetic

admixture proportions deviated 15% in either direction from the pure parental races and, therefore, likely included different filial generations.

The remaining studies classified as using populations that were or likely to be connected by natural dispersal (N=14) conducted experimental crosses to obtain hybrid offspring. Most of these studies estimated fitness under artificial or semi-natural conditions (Fig. 7), with ten studies (71.4% of 14) investigating fitness within a single environmental condition, and only five estimating fitness for at least one component under at least one of the native parental environments. None of the studies using experimental crosses explicitly considered sex differences in F_1 heterosis, likely due to focusing on hermaphroditic [plant] species or pre-sexual maturation life stages in animals. Moreover, only five of the 14 studies (35.7%) considered filial generations beyond the F_1 , including estimates for F_2 (N=2), F_3 (N=1) or backcrosses (N=3). These observations do not appreciably change when considering all of the 111 studies, with 70.3% (N=78) of the studies including only estimates for the F_1 offspring, 70.3% including estimates for a single environmental condition, and only one study (Matsubayashi et al. 2011) that quantified male- and female-specific traits.

Among the studies using experimental crosses that included populations that are or likely are connected by natural dispersal (i.e. categories “Connected” and “Both” on Fig. 7), a mixture of evidence for positive, negative, or no heterosis was found. Heterosis often varied within studies, among traits or pairwise population combinations, and even among replicate crosses of the same populations. In some cases, such differences resulted from rearing environment (Ostevik et al. 2016) or maternal population of origin (Barnard-Kubow et al. 2016, Barnard-Kubow & Galloway 2017), demonstrating that outcomes may depend on environmental and on maternal effects, cytoplasmatic-nuclear genome interactions (Burton et al. 2006), or sex-chromosomal effects (Saavedra & Amat 2005). Some studies also found a relationship between heterosis and the genetic (Barker et al. 2019, Barnard-Kubow et al. 2016, Barnard-Kubow & Galloway 2017), geographical (Barnard-Kubow et al. 2016) or environmental distance (Pickup et al. 2013) between parental populations, or the size and the genetic diversity within populations (Pickup et al. 2013, Willi et al. 2007). Genetic or geographical distance (Barnard-Kubow et al. 2016, Barnard-Kubow & Galloway 2017, Willi & Van Buskirk 2005) and genetic diversity (Barker et al. 2019, Pickup et al. 2013, Willi & Van Buskirk 2005, Willi et al. 2007), however, were also reported to not affect heterosis in other studies or in different traits, environments, or filial generations within the same study. As an interesting example, fitness of hybrid offspring of the herb *Campanulastrum americanum* showed no relationship with genetic distance estimated from nuclear markers, but decreased with the genetic distance estimated from the predominantly maternally inherited chloroplast markers (Barnard-Kubow et al. 2016, Barnard-Kubow & Galloway 2017; but see Barnard-Kubow et al. 2017). Even further, maternal population of origin reversed the direction of heterosis within both F_1 and backcrosses of reciprocal crosses for some traits and population combinations (Barnard-Kubow et al. 2016). Therefore, cytoplasmatic-nuclear interactions may not just affect heterosis levels per se, but also the correlation between heterosis and genetic distance.

Unfortunately, our review also revealed that explicitly quantifying and contrasting conditions under which heterosis is positive, negative, or absent across studies is constrained by forms of analyses and data reporting. Papers commonly presented a single statistical estimate for crosses between several populations, sometimes of different connectivity levels. Moreover, criteria for determination of heterosis varied enormously across studies, ranging from statistical comparisons between mean values of hybrid F_1 and mean parental values, to more elaborate calculations involving the average offspring values of within and between population crosses (Supplementary Table S2). Finally, these studies also often implement methodological priorities that may introduce errors or biases within the context of our research agenda. For example, many study designs used a substantial number of offspring (e.g. >20) from a small number of parents (e.g. <5 parent pairs), rather than using offspring generated from more parental combinations. Also common was the use of multiple sires or pollen mixtures (sometimes from different source populations) for fertilization, with the aim of reducing the probability of unsuccessful crosses. Further, unsuccessful crosses were sometimes replaced, to ensure estimation of fruit or flower productivity in the offspring. Although these tactics are justified under alternative research contexts, key information regarding differences across families, pairwise population combinations, degrees of connectivity, or environmental characteristics is lost. Conclusions are also

muddled by averaging of positive and negative outcomes within individual generations or pairwise population combinations. Furthermore, eliminating unsuccessful crosses from the data, or removing or confounding individual level variation via use of single or mixed sires, restricts proper variance and error estimations in the statistical analyses, and prevent documentation of cases in which outcrossing does not result in viable offspring. Therefore, estimates and conclusions about heterotic effects from these studies may not provide adequate evidence for heterotic effects within the context of eco-evolutionary consequences of dispersal in wild populations.

Opportunities and challenges

Overall, our literature review indicates a strong interest in the consequences of population outcrossing across ecology and evolutionary biology. Yet, explicit and robust empirical estimates of heterosis in the context of natural dispersal within metapopulations are apparently remarkably lacking. The few broadly relevant studies are still mainly inspired by traditional research agendas of agriculture, conservation genetics and speciation fields. Consequently, they tend to focus on highly inbred and/or highly differentiated populations, or do not attempt to characterize the connectivity level across populations studied. Crosses between isolated populations provide valuable information on the genetic architecture of population differentiation and on possible ecological and evolutionary consequences within contexts such as genetic rescue or biological invasion. However, natural dispersal and interbreeding between these populations are unlikely, unless these populations come under secondary contact.

Although many study systems have been used to quantify demographic consequences of dispersal in natural populations (e.g. see Millon et al. 2019), most such study systems were notable for their absence from the list of retained studies that fulfilled our current criteria (Table 1). This may be because quantifying multi-generational fitness in wild populations is certainly challenging. For instance, 18 years of fieldwork still resulted in a small sample size for natural immigrants in song sparrows (Marr et al. 2002), constraining the strength of evidence for heterosis. However, the increasing number and length of available individual-based field studies should soon make such analyses feasible in at least some systems (e.g. reviewed in Clutton-Brock & Sheldon 2010). Our search found several studies contrasting fitness of immigrants and residents but that did not investigate the fitness of descendant generations, even if some fitness metrics include aspects of offspring fitness (e.g. number of fledglings in birds). The existence of such studies implies that failure to explicitly quantify and compare target individuals is not entirely due lack of data, but at least partly reflect that such ambitions are not currently on the radars of many population and evolutionary ecologists.

Logistical considerations are certainly prohibitive for some taxa. For example, invertebrates and other small sized taxonomic phyla are traditionally studied under artificial conditions, often using laboratory stock populations, due to the difficulties marking and identifying individuals in their natural environments. As a consequence, future estimates of heterosis in natural populations cannot rely on strategies such as long-term individuals-based studies, which typically involve vertebrates (but see “new methods” below). For other taxa, however, traditional approaches may simply require reconsideration. Ease of manipulation may present such a cost-effective approach in comparison to field-based parentage analyses in plants, that experimental crosses are often the method of choice. Alternatively, these choices may represent a historical oversight that is only now being corrected (see e.g. Ellstrand 2014).

The preponderance of experimental crossing approaches, however, may be another symptom of the disconnect between research silos. Indeed, we found that studies often presented methodological priorities that greatly limit inferences about demographic and evolutionary outcomes of outbreeding within the context of dispersal and resulting immigration in natural populations. For example, lack of knowledge regarding the origin of parental individuals may result in categories of parental and filial generations that include a mixed set of ancestries. Consequently, both means and variances within the categories compared are affected, rendering results difficult to interpret. Additionally, by not investigating the natural occurrence of interbreeding between populations, we lack information on the frequency with which different types of individuals are produced within a population. It then becomes difficult to predict the ultimate eco-evolutionary consequences of genetic effects manifested through outcrosses. For instance, even if F_2 descendants of immigrants have very

low fitness, any impact would be trivial if F_2 s are rarely conceived in the first place. F_2 s could be rare, even in the case of high fitness of F_1 s, if F_1 s rarely mate due to non-random mating within and among immigrant lineages, or if F_1 s are themselves rare and/or temporally segregated.

Note, however, that even our proposed research agenda may lead to variable recommendations regarding experimental approaches. In principle, the ability to manipulate breeding presents several advantages, such as a larger sample size across categories. In addition, artificial or semi-artificial experimental setting provide easier means to rear offspring under several environmental conditions and, for some taxa, the ability to rear different generations under the same environmental conditions. As maternal effects might be significant, experimental crossing also gives the opportunity for the systematic incorporation of such effects in the experimental design. Moreover, combining crosses between residents and immigrants from different sources into a global effect of outcrossing may be preferable in certain contexts. Logistically, it may be impossible to categorize immigrants into their exact population of origin and, even when possible, low source-specific immigration rates likely would prevent disentangling the heterotic effects across pairwise population combinations or filial generations. More importantly, when attempting to understand the eco-evolutionary consequences of immigration within the perspective of a focus population, the average effect of different population crosses may better represent the relevant outcome to the eco-evolutionary dynamics of that population. Therefore, methods and statistical considerations will depend on several logistic opportunities and limitations of the individual taxa/populations under study. In any case, methods applied must involve proper characterization and reporting of statistical expectations and errors.

New directions

Our theoretical review highlights that fitness outcomes from natural dispersal between demes can be complex. Unraveling such complexity will require natural studies reporting fitness comparisons beyond that of the parental generation of residents and immigrants, and relative frequencies of filial generations in the wild. These studies must also report proper error estimates. These conditions inevitably require methodological considerations pertaining sources of biases and inaccuracies, as discussed in the section above, but will allow for future synthesis studies.

Future studies should also aim to estimate fitness of hybrid offspring under natural conditions as well as possible environment-specific effects, which have so far seldom been considered. Environmental conditions may influence not only the genetic architecture of traits but also their fitness consequences. As the magnitude of genetic effects change across filial generations, environmental effects may influence filial generations differently. For example, even if F_1 hybrids consistently show positive heterosis, negative heterosis may be environment-dependent in recombinant filial generations, due to loss of locally adapted beneficial epistatic interactions. Consequently, selection against hybrid individuals, introgression rates and effective gene flow will differ across demes and pairs of demes in a metapopulation, likely influencing isolation-by-ecology patterns of population differentiation and the evolution of habitat-matching dispersal. Non-random gene flow, in turn, can have significant cascading consequences to the eco-evolutionary dynamics of natural populations (Edelaar & Bolnick 2012).

Estimates of sex-specific effects are also fundamental to the understanding of eco-evolutionary dynamics of populations. Some studies reported that the direction of the cross between populations or the sex of the immigrant individual affected the fitness outcome for the hybrid offspring, suggesting that not only the sex of the offspring needs to be considered, but also the sex of the parents with different origins. Since sexes can present different degrees of local adaptation (Svensson et al. 2018), and populations may experience different degrees of intersexual conflict (de Lisle et al. 2018), outcomes of outbreeding that depend on the sex of the immigrant may be ubiquitous, and drive the evolution of sex-biased dispersal. In fact, sex differences in the propensity and distance of dispersal are common in animals (e.g. Trochet et al. 2016) and in plants, where male gamete dispersal can occur at higher rates and for longer distances than seed dispersal (reviewed in Ellstrand 2014). Sex-specific dispersal, in turn, may further influence the dynamics of sexual conflict and sex differences in local adaptation. For instance, it can impact the evolution of uniparental inheritance via maternal or paternal effects (Revardel et al. 2010) or the evolution of parental care (Trochet et al.

2016). Sex-biased introgression due to sex-specific differences in fitness or sex-biased dispersal can further influence the evolution of uniparental gene expression (Raunsgard et al. 2018), and change dynamics of nuclear-cytoplasmatic conflict and the degree of sexual dimorphism which alter intrapopulation levels of sexual conflict (Runemark et al. 2018).

New methods

As genomic techniques are increasingly accessible, several methods can contribute to the estimation of fitness and characterization of filial generations in wild populations. For example, field-based pedigrees are commonly used in studies of birds and mammals (e.g. Marr et al. 2002, Martinig et al. 2020), and offer a promising perspective for other taxa (e.g. plants, Ellstrand 214). Alternatively, parental line genotyping has been used to identify admixed offspring (e.g. Bull & Sunnucks 2014), and even further discriminate among filial generations (e.g. Fitzpatrick et al. 2016), allowing for fitness comparisons in systems where individual-based datasets are impractical. More recently, new statistical tools have been developed that enable accurate genetic assignment of individuals into demes within genetically structured metapopulation systems (e.g. Kuismin et al. 2020). In combination with other field-based data, classification of individuals into immigrant, residents, and several filial generations is possible (e.g. Saatoglu et al. 2021). Therefore, these methods have the potential to enormously contribute to the feasibility of heterosis studies in natural populations. Furthermore, these methods can be combined with traditional experimental approaches such as controlled crosses and reciprocal transplants, significantly enriching the understanding of ancestry of individuals in cross-sectional studies.

Genomic tools may allow further advancements of the field by enabling field studies to assign continuous hybrid categorizations without explicit knowledge of filial generation categories (e.g. Aase et al. 2022). For instance, longevity and reproductive success were shown to positively correlate with Buerkle’s hybrid index (Buerkle 2005) in the bighorn sheep (*Ovis canadensis* ; Miller et al. 2012). In turn, although “pure” non-local individuals of the perennial plant *Arenaria grandiflora* had higher fitness than “pure” locals, admixed individuals with higher proportions of locally-sourced genetic composition presented the highest fitness, suggesting a complex, non-linear, relationship between fitness and Buerkle’s hybrid index (Zavodna et al. 2015). Moreover, genomic methods have been widely used to estimate relationships between fitness and heterozygosity in inbreeding depression studies. Notably, heterozygosity and Buerkle’s hybrid indexes parallel the concepts of hybridization and source indexes introduced by the line-cross theory (Box 1). Therefore, theoretical developments elucidating the relationship between these indexes are crucial, and will open new avenues of research by allowing the application of line-cross theory, as well as its extensions incorporating estimates of local adaptation (Schneemann et al. 2020), to the study of wild populations.

Finally, because selection removes variation from the population, fitness estimates may be positively biased, resulting in apparent positive heterosis, due to the loss of less fit offspring before estimates are recorded. Consequently, fitness observed in further generations will result from a biased sample of the previous generations’ genotypes (e.g. see Thompson et al. 2022a). The application of line-cross theory in studies of wild populations, therefore, requires that future theoretical developments incorporate changes in allele frequencies across generations as to account for the effects of selection when estimating the expected fitness of hybrid offspring.

CONCLUSION

Our theoretical review highlights that short- and longer-term impacts of natural immigration on local population demography and evolutionary dynamics will depend on the relative fitness and frequencies of existing natives, F_1 s, F_2 s and various potential backcrosses that emerge across generations. In turn, these fitnesses will depend on underlying genetic effects, their interaction with the environment, as well as the relative contribution of adaptive and non-adaptive mechanisms to the evolutionary history of population differentiation. Quantifying the relative fitness of parents and filial generations in principle allows estimation of multiple components of dominance and epistasis impacting fitness, with the potential to reveal underlying genetic architectures of fitness and of population differentiation, or even complement population genetic and local adaptation studies aiming to understand the role of adaptive and non-adaptive divergence. By corollary,

quantifying such multi-generational effects, and hence resulting time-courses and manifestations of realized migration rates and effective gene flow, is necessary to predict population and micro-evolutionary dynamics in spatially structured populations. Our literature review indicates this resource remains almost entirely untapped within the context of natural dispersal and resulting immigration in wild populations and yet, spatial structure has the potential to generate a multitude of hybrid fitness effects across demes in a metapopulation. Therefore, studies of hybrid offspring at the metapopulation level may not only prove some of the most interesting and rich fields of research, but will be of fundamental importance to understanding eco-evolutionary dynamics in a world where fragmentation of populations is an ever-growing threat to biodiversity.

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TEXT BOX

Box 1. Hybrid genetic effects Definition of heterosis Within recent ecological and evolutionary studies, the term “heterosis” has been used to describe the increased fitness of hybrid offspring relative to their parents. Following Lynch’s (1991) notations, where p_m and p_f indicate the expected fraction of P_1 alleles in the sire and dam, respectively, the expected fitness of the hybrid offspring is given by:

TABLE

Table 1. Criteria used during the triage process of papers in the literature review.

| Criteria | Accept | Reject |
|------------|---|--|
| 1. Fitness | - At least one individual-level estimate of a fitness component or fitness-related trait, including life history and morphology | - Yield in agricultural context - Population metrics of fitness such as introgression rate or population growth |

| | | |
|--------------------------------|--|---|
| 2. Crosses and generations | - At least one hybrid filial generation for interpopulation crosses AND at least one parental or filial generation for within population crosses | - Only estimates for within parental populations crosses - Only estimates for hybrid offspring |
| 3. Environment | - Native environment of at least one of the parental populations - New or semi-natural environment such as common gardens or mesocosms - Laboratory or greenhouse | |
| 4. Individuals and populations | - Wild parental populations - Parental populations maintained in laboratory for a maximum of 3 generations prior to intra/inter-population crossing - Ecotypes and ecomorphs representing populations with locally adapted variants | - Subspecies or chromosomal races - Admixed populations due to several introduction events (e.g. multiple biological invasions) - Laboratory or commercial stocks, or domesticated, iso/inbred or mutant lines - Severely inbred populations as indicated by protracted isolation with decline due to inbreeding depression, vulnerability status or risk of extinction - Ecotypes and ecomorphs representing polymorphisms within a single fully breeding population |

| | | |
|----------------------------------|---|--|
| 5. Methods for obtaining hybrids | - Natural interbreeding between naturally dispersing individuals, translocated or reintroduced individuals - Experimental crossing | - Inference of admixture from mean d^2 indices |
| 6. Connectivity | - Explicitly stated that individuals disperse between populations - Geographically separated populations stated as presenting “low genetic differentiation” - Populations where the study implies possible connectivity | - Explicitly stated that individuals do not disperse between populations - High genetic differentiation between geographically separated populations - Populations where the study implies little or no possible connectivity - Unclear degree of connectivity either due to no mention or insufficient information for classification |

FIGURE LEGENDS

Figure 1. Pedigree illustration of parental lines (P_1 and P_2) and initial filial generations, where F_1 results from crossing the two parental lines, and F_2 results from crossing F_1 s. Backcrosses, B_1 and B_2 , result from crossing F_1 with the parental lines P_1 and P_2 , respectively.

Figure 2. Expectations for the fitness of hybrid F_1 offspring depend on ecological and genetic distances between parental lineages. To the left, outcrossing of inbred lines commonly leads to high fitness due to increased heterozygosity (known as ‘genetic rescue’ in conservation genetics). As ecological distance between parental lines increases, benefits of outcrossing are outweighed by negative effects of ecological incompatibility. To the right, hybrid F_1 from interspecific crosses commonly show low fitness due to genetic incompatibilities between highly divergent genomes. In between these extremes, indicated by the vertical dotted lines, the relative balance between positive and negative outcomes of both genetic and ecological divergence generates a rich spectrum of possible fitness consequences to the hybrid offspring of matings between natural immigrants and residents arising within metapopulation systems.

Figure 3. Different relative magnitudes of genetic effects can lead to positive or negative increments on trait or fitness values across filial generations, as demonstrated by imputing into the line-cross theory equation (A) arbitrary values for the magnitudes of genetic effects (C-E, top-right corner). The average trait value between parental lines (P_{mid}) indicates the expected trait value for the F_1 given purely additive (α_1) genetic effects, as in C. With additive and positive dominance (δ_1) effects (as in D), trait values for all filial generations

are larger than P_m , therefore showing positive mid- and/or best-parent heterosis. Positive heterosis is also observed for F_1 and B_1 when additive-by-dominance epistasis ($\alpha_1\delta_1$) is present in addition to additive and dominance effects (as in E). In this case, however, F_2 and B_2 show negative heterosis due to the loss of positive epistatic benefits, as indicated by the coefficients for source and hybridity indexes (B) for these filial generations (see Box 1 for details). Trait value expectations are indicated for in environment 1. Note that the y-axes in plots (C-E) are in the same scale, since the F_2 (square) is taken as reference (μ_0).

Figure 4. Non-linear genotype-phenotype maps can lead to heterosis. A) even if genetic effects are additive, i.e. gene product (x-axis) for the heterozygote (Aa) equals the mean of the recessive (aa) and dominant (AA) homozygotes, the phenotypic trait value (Y) for the heterozygote can deviate from the mean expectation (\bar{Y}). This conclusion can be extended to the case of concave adaptive landscapes where fitness is a non-linear function of the genotype/phenotype. In the context of local adaptation in spatially-structured populations (B-C), individuals in populations P_1 (circle) and P_2 (square) (presenting either 100% $P_1 = 0\%$ P_2 alleles or 0% $P_1 = 100\%$ P_2 alleles) are at the optima for the different adaptive landscapes corresponding to their respective local environments (yellow for P_1 and blue for P_2). When P_1 and P_2 interbreed (50% P_1 alleles), the fitness for the resulting F_1 deviates from the mean fitness of parental populations (P_{mid}) in either environment, as a consequence of the non-linearity of the fitness landscape. In both examples, populations match “home-vs-away” and “local-vs-foreign” criteria for patterns of local adaptation, but fitness decreases more abruptly in the adaptive landscapes of B than of C, representing more contrasting selective pressures between environments as the optima are further apart. Consequently, while scenario C leads to positive heterosis, hybrid offspring in B show outbreeding depression.

Figure 5 . Representation of literature review work pipeline. The flow diagram (left) depicts each stage of the process with the total number of studies advancing to the next stage displayed over the respective box. The Venn diagrams (right) show the numbers of papers found per keywords searched (colour codes) for two different stages of the process: total papers triaged (upper; $N=12,862$), and studies selected as containing fitness or fitness-related estimates of offspring from intra- and inter-population crosses (lower; $N=111$). Although a large total number of studies was found, the Venn diagrams indicate little overlap between results produced by keywords chosen to find ecological studies versus keywords representing more commonly used terms within traditional heterosis literature. See text and table 1 for details.

Figure 6. Proportion of studies on major plant and animal groups for which estimates of fitness or fitness-related traits for both within and between population crosses were found in the literature review. In the outer pie, percentages are shown for groups that appeared in 5% (i.e. $N > 5$) or more studies out of the total number of studies using animals ($N=32$) or plants ($N=79$).

Figure 7. The literature review indicates a paucity of estimates of fitness consequences of interbreeding between natives and immigrants of populations connected by dispersal in natural environmental conditions. Studies found included population crosses across different levels of connectivity, with some (total number of studies presented above the bars) containing crosses between populations connected (“Connected” bars) or not connected (“Not connected”) by natural dispersal, some including crosses at both connectivity levels (“Both”), and some for which connectivity was not possible to be categorized (“Unclear”). For each connectivity category, left bar indicates approach used to obtain crosses between populations. “Introduction” indicates the translocation of individuals from a different population, or [re-]introduction of individuals from different populations into an uninhabited site. Right bars indicate the type of environment in which at least one fitness component or fitness-related trait was estimated for filial generations obtained via experimental crosses: “parental” indicates at least one of the parental environments, “semi-natural” indicates mesocosms, common gardens, or environments not occupied by the parental populations, and “artificial” indicates laboratory or greenhouse. Percentages shown are in reference to the total number of studies within each connectivity category using experimental crosses (left) or using experimental crosses and estimating fitness exclusively in artificial or semi-natural environments (right).

FIGURE 1

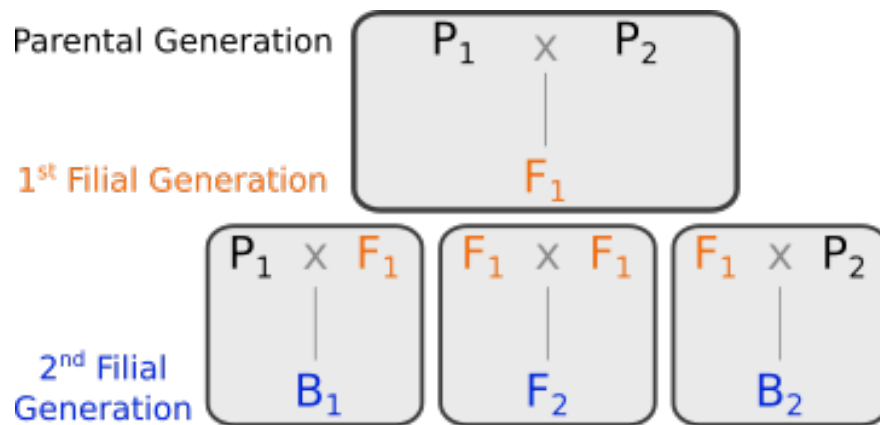


FIGURE 2

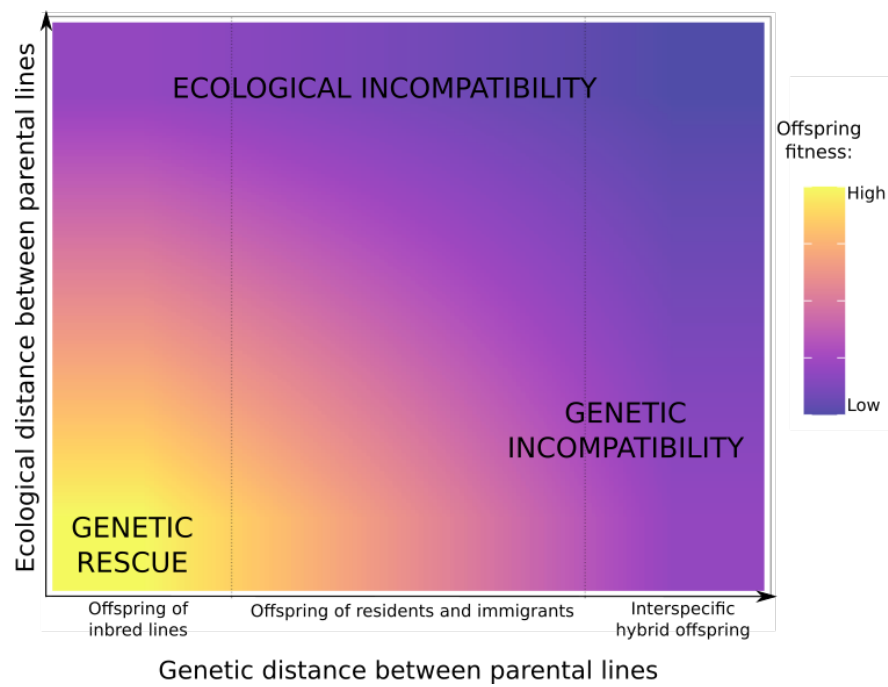


FIGURE 3

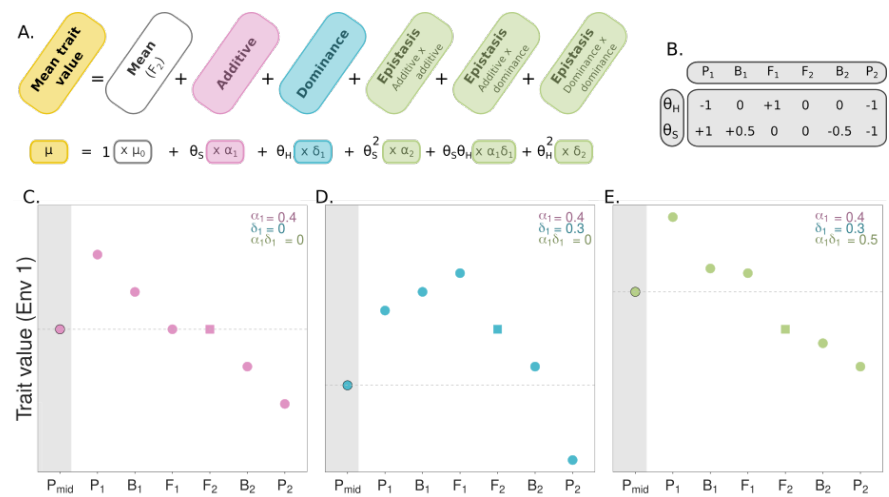


FIGURE 4

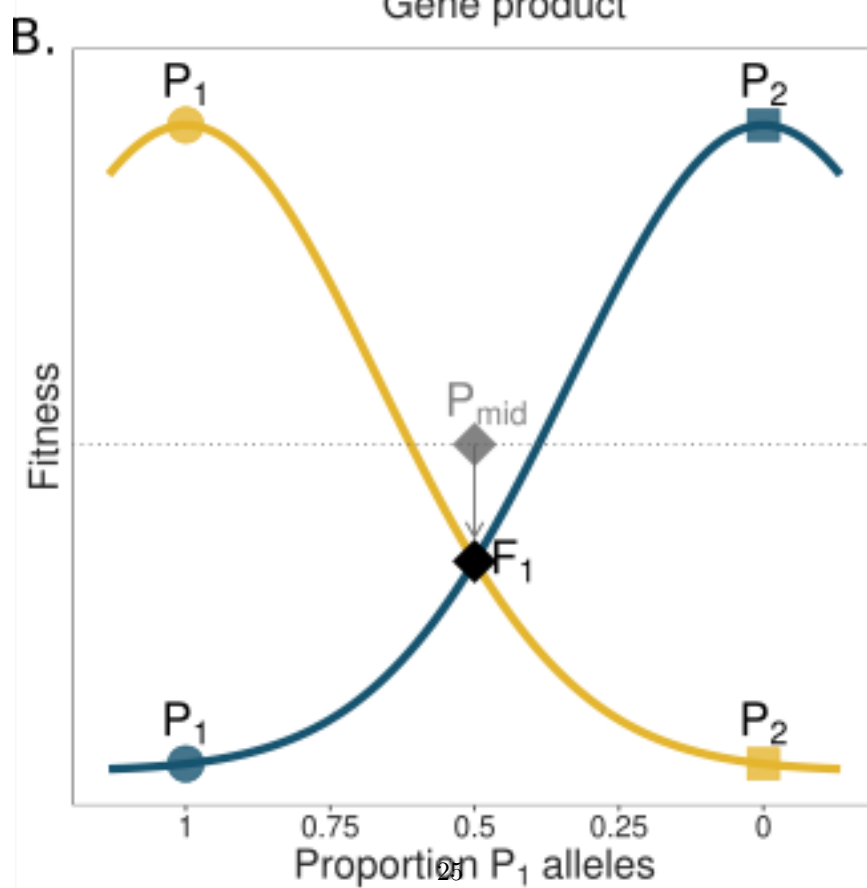
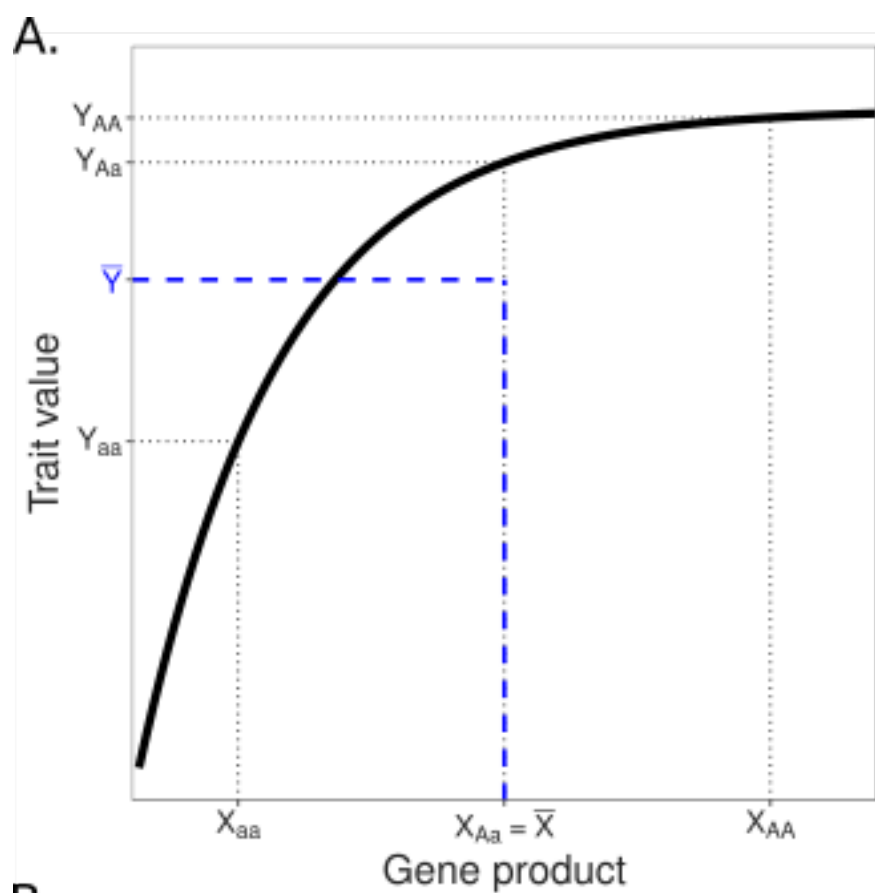


FIGURE 5

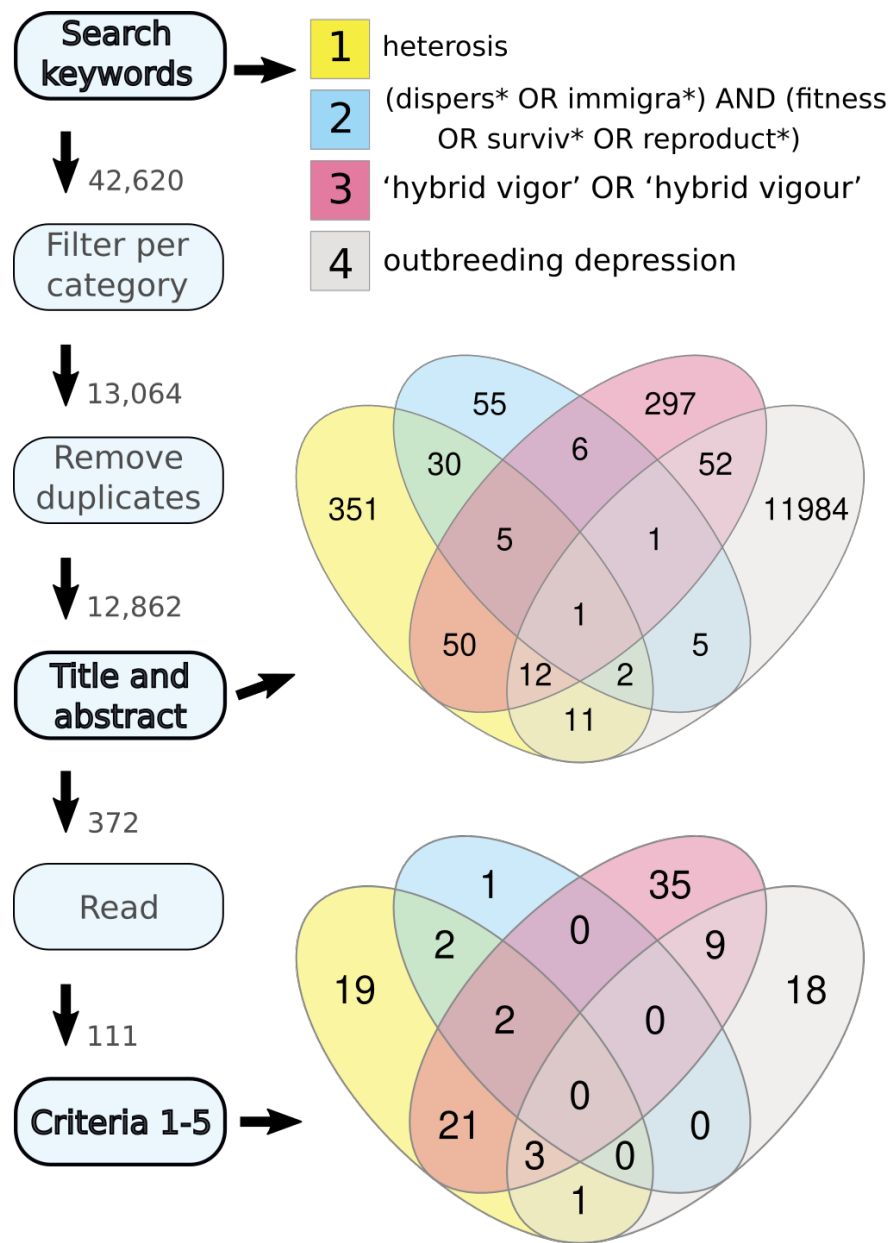


FIGURE 6

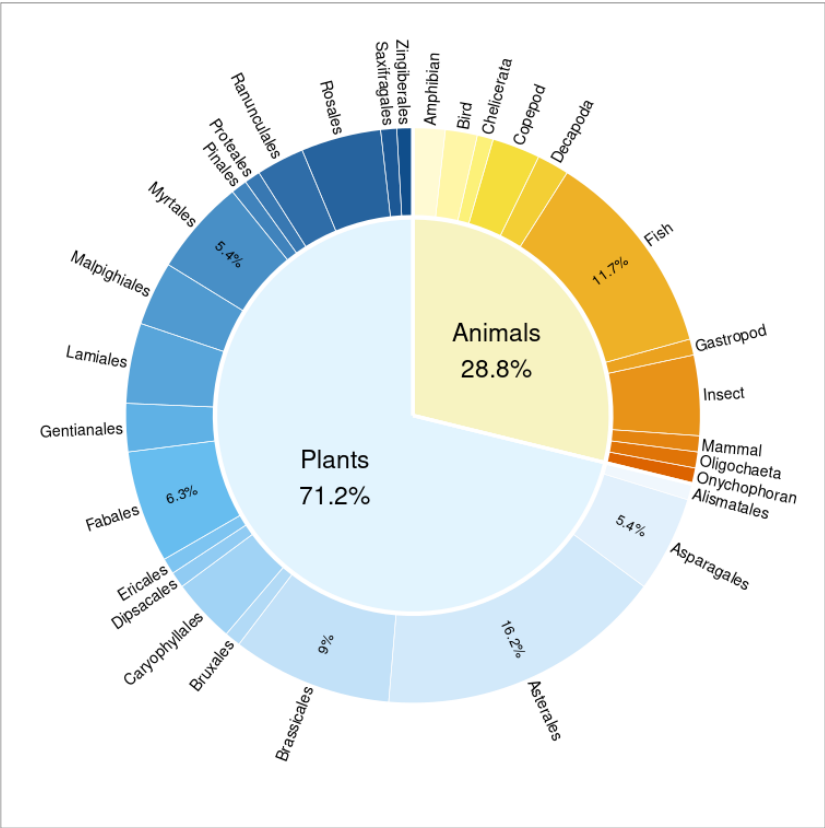


FIGURE 7

