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The ecological causes and consequences of hard and soft selection

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Abstract

Interactions between natural selection and population dynamics are central to both evolutionary-ecology and biological responses to anthropogenic change. Natural selection is often thought to incur a demographic cost that, at least temporarily, reduces population growth. However, hard and soft selection clarify that the influence of natural selection on population dynamics depends on the ecological context. Under hard selection, an individual's fitness is independent of the phenotypic composition of the population, and substantial population declines can occur when phenotypes are mismatched to the environment. In contrast, under soft selection, an individual's fitness is influenced by its phenotype relative to other interacting conspecifics, and selection generally influences which, but not how many, individuals survive and reproduce, resulting in little influence on population growth. Despite these important differences, the distinction between hard and soft selection is rarely considered in ecology. Here, we review and synthesize literature on hard and soft selection, explore their ecological causes and implications, and highlight their conservation relevance to climate change, inbreeding depression, outbreeding depression, and harvest. Overall, these concepts emphasize that natural selection and evolution may often have negligible or counterintuitive effects on population growth — underappreciated outcomes that have major implications in a rapidly changing world.

For Review Only

Hard selection is both density- and frequency-independent. For that reason, it is the mathematical geneticist's dream; for the same reason, it is the ecologist's nightmare".

- Bruce Wallace, 1975

"Don't compare me to the Almighty, compare me to the alternative."

- Political proverb

1. Introduction

The realization that evolution can occur on the same time scale as ecology has fueled renewed interest in clarifying the links between natural selection and population dynamics (Carroll *et al.* 2007; Hendry 2017). This endeavor is especially critical as rapid anthropogenic change threatens populations globally (Stockwell *et al.* 2003; Kinnison & Hairston 2007; Trisos *et al.* 2020). Natural selection is often thought to incur a demographic cost (*sensu* Haldane 1957) through either increased mortality or reduced fertility, which places an upper limit on the sustainable rates of adaptive evolution that a population can endure without going extinct (Bürger & Lynch 1995; Gomulkiewicz & Holt 1995; Orr & Unckless 2008). Indeed, this may often be the case for traits undergoing hard selection, where an individual's fitness (here referring to absolute fitness unless otherwise stated; Box 1) is dependent on the match between its *absolute* trait value and the environment and is independent of the phenotypic composition of the population (Wallace 1975; Box 1). For instance, individuals with lower thermal tolerances are more likely to perish as temperatures rise, independent of the thermal tolerances of others in the population. Rising temperatures can cause substantial population declines when many individuals are poorly matched to the thermal environment, and population persistence then depends on whether adaptive evolution can sufficiently reduce thermal mismatch (Killeen *et al.* 2017). The

For Review Only

expectation of population declines and recoveries during adaptation to novel stressors implicitly assumes hard selection (e.g., Carlson *et al.* 2014; Bell 2017).

In 1968, several researchers emphasized that natural selection might have little influence on population growth when, in contrast to hard selection, the fitness of an individual with a given phenotype is *dependent* on the phenotypic composition of the population (Maynard Smith 1968; Sved 1968; Wallace 1968), termed soft selection (Wallace 1968). To understand soft selection, it is helpful to picture the environment containing a limited number of ecological 'vacancies' (*sensu* Reznick 2016) that are critical for survival or reproduction (e.g., territories, mates, survivors of a given predation rate). Relative trait values determine which individuals fill those ecological vacancies. For example, if early arriving migratory birds are more likely to secure an essential breeding territory (i.e., the ecological vacancy), whether an individual's arrival time is sufficiently early to acquire a territory depends on the arrival times of other individuals in the population (Kokko 1999; Johansson & Jonzén 2012). In this scenario, the ratio of breeding territories to individuals competing for those territories determines the mean reproductive success of the population, and selection for early arrival time determines which, but not how many, individuals gain a territory (Day & Kokko 2015). In other words, in the context of soft selection, one individual's loss in failing to acquire an ecological vacancy is often another's gain (i.e., a zero-sum game). The key idea with soft selection is that an individual only needs to be more aggressive, sexier, different, less palatable, faster, etc. than its neighbors to give it an advantage in acquiring food, territories, mates, or pollinators, or avoiding harm from herbivores, parasites, or predators. Assuming equal selection strength, soft selection should generally have much lower influences on population dynamics than hard selection.

For Review Only

Consideration of hard and soft selection can alter predicted responses to anthropogenic change (e.g., Day & Kokko 2015). Importantly, these concepts highlight that natural selection and adaptive evolution can proceed with less influence on population growth than may often be expected. However, interactions between hard and soft selection can both increase or decrease extinction risk (Svensson & Connallon 2019), suggesting that their combined influence on population dynamics can be complex.

Despite important differences in how hard and soft selection influence, and are influenced by, population dynamics, these concepts have received infrequent attention in the evolutionary and ecological literature. Although many researchers assume selection is hard, soft selection might be the more common form of natural selection (Wallace 1991; Reznick 2016). Here, we review the theoretical and empirical literature on hard and soft selection. Although recent work has examined the evolutionary implications of hard and soft selection in meta-populations (e.g., Gallet *et al.* 2018), we focus on the local population scale and examine how hard and soft selection influence population dynamics. Further, we place these concepts in the wider context of eco-evolutionary dynamics and illustrate their relevance to a range of applied questions involving population responses to anthropogenic stressors.

2. The origins and definitions of hard and soft selection

Bruce Wallace introduced the concepts of hard and soft selection to explain why populations can persist despite apparent maladaptation (Wallace 1968). At that time, population genetic theory assumed that there is one optimal genotype for a given environment and the presence of any genetic variation should reduce mean fitness (i.e., hard selection). This prediction was at odds with the surprisingly high amounts of genetic variation being documented in contemporaneous

For Review Only

empirical studies (Harris 1966; Hubby & Lewontin 1966). Wallace suggested that this apparent paradox could be explained by viewing the problem through the lens of soft selection. If an individual is 'judged' relative to the other conspecifics with which it interacts instead of against a theoretical, ideal organism, high amounts of genetic variation can be withstood with minimal influence on population growth.

To help explain soft selection, Wallace presented a set of equations along with a hypothetical example of N bears competing for K caves in which to hibernate (i.e., ecological vacancies; Wallace 1991; Fig. 2a,b). Individuals must secure a cave to survive. Bears have either aggressive or submissive phenotypes, and aggressive bears always outcompete submissive bears for caves. The behavioral phenotype is determined by a single locus, and aggressive behavior is completely dominant (*AA* and *Aa*). The frequencies of submissive and aggressive bears prior to selection are thus q^2 and $1\text{-}q^2$, respectively. The strength of selection (s) is one minus the relative fitness of submissive bears. The influence of these competitive interactions on selection can be separated into three cases. First, selection does not act when there are fewer bears than caves because every bear can secure a cave independent of its behavioral phenotype (Case 1; Fig. 1A&B). Second, all submissive bears will die when there are enough aggressive bears to secure every cave (Case 2). Finally, the strength of selection depends on the proportion of submissive bears that acquire caves when the number of caves is limited but there are too few aggressive bears to fill every cave (Case 3).

Case 1: $s = 0 \quad for \quad K > N$

Case 2: $s = 1 \quad for \quad K < (1 - q^2)N$

Case 3: $s = 1 - \frac{K - (1-q^2)N}{q^2 N} \quad for \quad (1 - q^2)N < K \leq N$

For Review Only

An outcome of Wallace's soft selection equations is that the strength of selection increases with greater reproductive excess (i.e., $N > K$) and with higher frequency of the advantageous phenotype. As a result, Wallace defined soft selection as being density and frequency dependent (Wallace 1975). To better understand how this contrasts with hard selection, consider a population of snowshoe hares (*Lepus americanus*) in which predation risk depends on an individual's color match to the snowless background (e.g., Zimova *et al.* 2016). Assume that hares with brown coats are resistant to predation on snowless backgrounds (matched), while hares with white coats have a 50% risk of predation (mismatched). In this example, the relative fitness of the mismatched hares is constant (0.5), and is not influenced by reproductive excess or coat color frequencies (Fig. 1c,d; we relax this assumption in section 3). For this reason, Wallace defined hard selection as being frequency and density *independent* (Wallace 1975). Note that these simple depictions of hard and soft selection also highlight differences in their influences on population dynamics (Fig. 1; discussed in section 4).

Importantly, the type of frequency dependence Wallace referred to simply arises from the fact that phenotypes are judged against the phenotypes of others in the population and is more general than negative frequency-dependent selection (e.g., Gigord *et al.* 2001). The behavioral phenotypes of Wallace's bears are under directional selection because the aggressive bears are always at a competitive advantage, and negative frequency dependence never enters this example. The manner in which Wallace used frequency dependence appears to be a source of confusion surrounding hard and soft selection (Gromko 1976) and partly responsible for a proliferation of uses of these terms that, although providing critical insights for evolution, deviate from Wallace's initial concept to varying degrees (Box 2). Additionally, soft selection is

For Review Only

not density-dependent *per se*, but is rather dependent on the ratio of density to ecological vacancies (discussed in Section 3).

In an attempt to further clarify the topic while remaining consistent with Wallace's original concepts, we define soft selection as natural selection that occurs when the absolute fitness of an individual depends on its phenotype relative to that of other conspecifics with which it interacts. In contrast, hard selection is natural selection that occurs when the absolute fitness of an individual depends only on its *absolute* trait value and is independent of the phenotypic composition of the population. For both hard and soft selection, individual *relative* fitness always depends on the phenotypes of others in a statistical sense because it is a scaled measure (Box 1). The key distinction is that with soft selection there is a causal dependence of individual fitness on the phenotypes of others, whereas with hard selection there is no such causal dependence.

Soft selection can be readily generalized from Wallace's heuristic example of bears competing for caves to more complex scenarios. First, Wallace's model assumed truncation selection, but this is not necessary (Charlesworth 2013). Second, Wallace presented soft selection as directional, but soft selection can involve any mode of selection, including balancing and diversifying (e.g., Svanbäck & Bolnick 2007). Third, soft selection is equally valid for continuous and discrete traits and applies to quantitative as well as population genetic frameworks. For example, from a quantitative genetic perspective, soft selection occurs when genes expressed in one individual (e.g., predisposition to be aggressive) alter the fitness of another conspecific (i.e., indirect genetic effects; Fisher & McAdam 2019). A range of models touch on the various genetic and evolutionary possibilities outlined above, but often without explicit mention of soft selection (Maynard Smith 1968; Sved 1968; Clarke 1973; Smouse 1976; Anderson & Arnold 1983; Bürger & Gimelfarb 2004; Svensson & Connallon 2019; Engen *et al.*

For Review Only

2020). Hard and soft selection can also be generalized to much more diverse ecological scenarios.

3. The ecological causes of soft and hard selection

Although Wallace was focused on intraspecific competition for abiotic resources, soft selection can involve a range of interspecific biotic interactions (Chao *et al.* 2000; Start 2020). Returning to the example of coat coloration in snowshoe hares (Section 2; Fig.1), we previously assumed that predators simply cannot find well-matched hares (e.g., brown hares on brown backgrounds) and hence this was an example of hard selection. Another possibility is that predators preferentially target mismatched hares when they are frequent because the search times involved are minimal, but switch to taking better-matched hares when mismatched hares become less frequent because they have no option but to search for longer. This corresponds to soft selection because the fitness of a mismatched hare now depends on how well matched other hares in the population are.

Using a second heuristic example from Chao *et al.* (2000), if lions prey on the slowest and most peripheral zebras in a herd, the phenotypic composition of the zebra herd determines which, but not necessarily how many, zebras are captured. This example of zebras avoiding predation mirrors bears competing for caves: the initial zebra population size minus the number of predation events determines the number of ecological vacancies (i.e., survivors of a fixed predation rate), and the relative speed and jockeying behavior of zebras determine which individuals obtain those ecological vacancies. Generally, soft selection arising from interspecific interactions can be broken into two categories: 1) intraspecific competition for a limited biotic

For Review Only

resource and 2) avoidance of negative biotic interactions. For any species that benefits in an interspecific biotic interaction (e.g., predators, herbivores, parasites, and mutualists), soft selection can occur due to intraspecific competition for access to, or consumption of, the interacting species (e.g., prey, plants, hosts, and the other mutualist, respectively). On the other hand, for the species experiencing the negative interaction (e.g., prey, plants, and hosts), soft selection is based on the relative ability to avoid harmful interactions.

Interspecific competition adds another layer of complexity to soft selection. When individuals compete for resources with both conspecifics and heterospecifics, individual fitness may be determined by their phenotype relative to members of the entire *guild* rather than just their population (a related concept is that guilds and ecosystems involve zero-sum games for energy, see Van Valen 1973; Ernest *et al.* 2009). In these cases, the process of phenotypic selection not only influences the evolution of each species (e.g., character displacement; Grant & Grant 2006) but also their abundances (e.g., competitive exclusion; Violle *et al.* 2011). To avoid adding more complexity, we do not consider interspecific competition further in this manuscript.

Hard selection can also involve both abiotic factors and biotic interactions, and whether a given selective agent (i.e., factor that causes selection) results in hard or soft selection depends on if the absolute or relative trait value in the focal species determines success in the interaction. Using an example involving mutualists, insect pollinators often impose selection on various aspects of flower morphology (Galen 1989; Benitez-Vieyra *et al.* 2006), including flower size (Parachnowitsch & Kessler 2010). If the pollinators will only visit a flower that is above a certain size, irrespectively of the sizes of the other flowers in the population, they impose hard selection. If, on the other hand, pollinators will still visit flowers regardless of the range of flower sizes in the population but are more likely to visit the relatively larger flowers, they

For Review Only

impose soft selection. Generally, hard and soft selection should not be distinguished based on the agent of selection (e.g., pollinators selecting flowers), but rather on the importance of relative versus absolute trait values in determining fitness of the focal species (Box 3).

Soft selection is often equated with intraspecific competition (e.g., Charlesworth 2013), but intraspecific competition can also lead to hard selection. For example, under intraspecific competition for resources due to high density, traits influencing resource use efficiency (e.g., metabolic rates and digestive efficiency) are likely under hard selection because whether an individual can survive on a given food ration is independent of the resource use efficiency of conspecifics (Agrawal 2010). In contrast, traits influencing resource acquisition ability should be under soft selection (Agrawal 2010), because an individual need only be better at acquiring resources than its neighbors to survive under conditions of high intraspecific competition. In other words, both hard and soft selection can involve intraspecific competition and be density-dependent.

Additionally, soft selection is not density-dependent *per se*, but instead dependents on the ratio of density to ecological vacancies (i.e., reproductive excess). If the number of bears stays the same but a landslide buries half of the caves, the strength of soft selection will increase because the ratio of bears to caves increased (i.e., reproductive excess was greater). Likewise, if the number of zebras remains the same but the number of predation events increases, the strength of soft selection will be greater because the ratio of initial zebras to survivors of predation increased. More generally, the strength of soft selection depends on the per capita amount of resources when intraspecific competition is involved (Agrawal 2010; Ho & Agrawal 2012) and the per capita rate of negative interspecific interactions when avoidance of harmful interactions is involved. This suggests that soft selection will be more temporally dynamic than Wallace's

For Review Only

example of bears in caves: in addition to variation in density, resource availability can also fluctuate, and when biotic interactions are involved, the density of both species can vary and both species can evolve (Yoshida *et al.* 2003; Reznick 2016).

In addition to being determined by the same ecological factors, hard and soft selection might also operate on the same traits (Weis *et al.* 2015; Start 2020; i.e., slushy selection; Clutton-Brock & Pemberton 2004). In these cases, the hard and soft components of selection might act in opposing or concordant directions. In an experimental test of hard versus soft selection using *Brassica rapa*, Weis et al. (2015) measured fitness in monocultures and bicultures of early and late-emerging plants. Comparisons of fitness between monocultures of early and late emergence phenotypes revealed that early-emerging plants had higher fitness (i.e., hard selection), likely due to favorable weather conditions. Likewise, comparisons of fitness between early and late emergence phenotypes within mixed cultures showed that the competitive environment gave early-emerging plants an even greater advantage due to having a head start on growth (i.e., soft selection). Some researchers have suggested that hard and soft selection may often act on the same traits and are better viewed as a continuum rather than discrete categories (Ho & Agrawal 2012; Start 2020).

Furthermore, thresholds may be common where selection on a trait transitions from being primarily soft to predominantly hard as the mean phenotype increasingly deviates from an environmental optimum. For example, at warm but not extreme temperatures, individuals that cope better physiologically might be more competitive or better at avoiding negative biotic interactions than individuals with relatively poorer thermal performance (i.e., selection is predominantly soft). However, at extreme temperatures, individuals with lower thermal tolerance limits will be more likely to die for purely physiological reasons (Lutterschmidt & Hutchison

For Review Only

1997; i.e., selection becomes harder). Similarly, when the mean level of inbreeding in a population is low, individuals that are relatively more inbred than others might suffer from reduced competitive ability or lower relative ability to escape from predators, for example, but when the mean level of inbreeding is high, survival might plummet regardless of the competitive or predatory environment (Frankham 1995; e.g., Robinson *et al.* 2019).

4. The demographic costs of hard versus soft selection

Hard and soft selection provide a useful lens to understand how natural selection influences population dynamics. In this section, we discuss the influence of phenotypic selection on vital rates and population growth within the generation that selection occurs, and in the next section, we examine the demographic influences of evolutionary responses to selection. It is important to distinguish between *immediate* reductions in mean stage-specific vital rates owing to phenotypic selection versus *net* effects on mean fitness and, thus, population growth. Hard selection is always associated with a reduction in survival or reproductive success during the life-stage at which it occurs (compared to a population that is well adapted to those environmental conditions), whereas soft selection may have little or no influence on mean vital rates (compared to a population experiencing the same environmental conditions, but lacking phenotypic variation). For both types of selection, reductions in stage-specific vital rates may or may not result in a decrease in population growth.

To better clarify the immediate influences of hard and soft selection on vital rates, it is helpful to consider the fitness landscape of a trait undergoing directional selection. Under hard selection, mean survival (or fecundity) decreases when the mean trait value is further away from

For Review Only

an optimum phenotype for the environment (i.e., greater maladaptation; Fig. 2a). In contrast, under soft selection, changes in the mean trait value will influence the survival probability of a given trait value but may have little influence on mean survival (Fig. 2b; i.e., a zero-sum game).

In an empirical example that mirrors Wallace's illustration of bears competing for caves, the survival of aggressive and submissive strains of *Drosophila melanogaster* was compared under different densities and phenotype frequencies (Kilgour *et al.* 2018). Aggressiveness was found to be under negative frequency-dependent selection, with the strength of selection increasing under high density, competitive conditions (i.e., as the ratio of *Drosophila* to ecological vacancies increased). Survival of aggressive and submissive phenotypes only differed in mixed-phenotype treatments, suggesting selection was soft. Further, mean survival of experimental populations did not differ between uniform and mixed-phenotype treatments, or across mixed treatments with different phenotypic frequencies, suggesting that soft selection involved a zero-sum game.

However, soft selection can influence stage-specific vital rates when the phenotypic composition of a population not only influences *which* individuals obtain ecological vacancies, but also the *number* of ecological vacancies. For example, territorial defense can influence territory size, and thus the number of territories (López-Sepulcre & Kokko 2005). Some resources (e.g., food) need to be obtained throughout an organism's life span, and the number of ecological vacancies can be considered the number of individuals the resource-base (e.g., food-base) can support. Strong asymmetries in acquisition ability can create big winners that horde a disproportionate share of the resources (Weiner 1985; Weiner & Freckleton 2010; Yun & Agrawal 2014), which can reduce the total number of ecological vacancies and, hence, soft selection will reduce vital rates. However, when resources are extremely limited, such that equal

For Review Only

resource distribution among individuals would result in many or theoretically all individuals dying (Nicholson 1957; Miller 1967), competitive asymmetries may allow some individuals to hoard enough resources to survive, thus potentially increasing the mean survival. A similar process could also occur during interspecific avoidance. For example, asymmetries in palatability could create big losers that receive an unequal share of herbivore grazing, potentially increasing or decreasing mean survival. Overall, while hard selection will always result in a decrease in survival or fecundity, soft selection may either increase, decrease, or have no effect on stage-specific vital rates. These caveats to zero-sum games under soft selection do not change the general expectation that soft selection is less likely to depress vital rates than hard selection.

An experiment on emergence timing in *Brassica rapa* demonstrated that survival can be reduced by soft selection (Weis *et al.* 2015). Mortality was higher in mixed cultures of early and late-emerging plants compared to monocultures because the early-emerging plants gained a substantial competitive advantage for access to light which inhibited late-emerging plants from growing. However, despite differences in early life survival, the total reproductive output was similar in monocultures and bicultures (Weis 2015), suggesting that increased mortality due to soft selection was compensated for by increased reproductive output of the survivors, consistent with the law of constant yield in the plant literature (Weiner & Freckleton 2010). This experiment highlights that even when selection does reduce a vital rate, population growth can remain unaffected.

There are at least three reasons why an immediate reduction in a vital rate due to selection may not translate into a decrease in population growth. First, selection simply may not be strong enough to appreciably influence population growth. Second, the vital rate that selection affects may have a limited influence on population growth (Mills 2013). For example, inbreeding

For Review Only

in bighorn sheep (*Ovis canadensis*) reduced adult female fecundity, but matrix-projections suggested that this had little effect on population growth (Johnson *et al.* 2011). Third, as discussed in the example of *Brassica rapa*, selective mortality or reduced fertility is often partially or entirely compensated for by increased fitness in a later life stage, which we refer to as compensatory selection.

To further explain compensatory selection, assume a simple ceiling model of density dependence where K individuals survive to adulthood due to a fixed number of territories and reproductive excess occurs because more juveniles are born each year than there are territories ($N_{juveniles} > K$). Hard selection acting on a juvenile phenotype reduces their numbers to $N_{survivors}$. If $N_{survivors} > K$, selection has only eaten into the reproductive excess, and there is no effect on population growth. In other words, selection is fully compensatory. On the other hand, if $N_{survivors} < K$, selective mortalities are additive and a population decline will occur (Fig. 1D). Selection can also be compensatory under more complex models of density dependence (Ratikainen *et al.* 2007; Reed *et al.* 2015), and, in some cases, compensation could even increase population growth (e.g., Abrams 2009; McIntire & Juliano 2018).

A study on great tits (*Parus major*) provided empirical evidence for compensatory hard selection. Directional selection for earlier egg-laying in great tits is more intense in warmer springs when phenological mismatch with caterpillar prey is substantial (Husby *et al.* 2009). This is likely due, in a large part, to hard selection because the fledglings of mothers that miss resource peaks will starve regardless of the hatching timing of other families. Selective mortality of fledglings in mistimed nests reduced local competition and increased post-fledging survival, resulting in no effect on population growth (Reed *et al.* 2013a) even though the mean number of fledglings was lower (Reed *et al.* 2013b). Compensatory selection also likely occurred in a

For Review Only

population of pink salmon (*Oncorhychus gorbuscha*) that has undergone a rapid evolutionary change in adult migration timing (Kovach *et al.* 2012, 2013b). The near elimination of late migratory phenotypes aligned with the second-highest stream temperatures on record (Kovach *et al.* 2012), suggesting hard selection due to thermal mismatch. However, shifts in migration timing did not influence population growth (Kovach *et al.* 2013a), possibly because density-dependent reproductive success compensated for reduced adult survival (Fukushima *et al.* 1998).

Hard and soft selection can also interact to influence population growth (Svensson & Connallon 2019), and soft selection can either increase or decrease the demographic cost of subsequent or concurrent hard selection on the same, or a correlated, trait. Using body size as an example, soft selection can favor larger individuals that have a competitive advantage for resources (e.g., territories; Johnsson *et al.* 1999), and subsequent hard selection may favor larger body size in colder conditions and smaller body size in warmer conditions for physiological reasons (Gardner *et al.* 2011; Sheridan & Bickford 2011; but see Siepielski *et al.* 2019). If hard and soft selection act on body size in the same direction, soft selection helps to improve the match between the mean body size and the optimal body size, reducing the strength of hard selection and thus its influence on vital rates and population growth (Fig. 3a). Soft selection may instead oppose subsequent hard selection on body size, which would lead to a greater decline in survival or reproduction (Fig. 3b).

5. The demographic implications of evolution under hard and soft selection

We have thus far examined the influence of phenotypic selection on population growth, but hard and soft selection can also have unique influences on how the evolution of heritable traits affects

For Review Only

population dynamics. Although hard selection can reduce population growth in the generation that selection occurs, it is expected to increase mean fitness in subsequent generations (Fisher 1930). In cases where the environment changes abruptly or gradually across generations, adaptive evolution via hard selection can sometimes avert extinctions (i.e., evolutionary rescue; Hufbauer *et al.* 2015; Bell 2017). For example, yeast (*Saccharomyces cerevisiae*) exposed to mostly lethal salinity initially experienced a rapid decline, but as salt-tolerant phenotypes increased in frequency population declines were often reversed within several generations (Bell & Gonzalez 2009). With continuous environmental change, evolutionary trait shifts are expected to lag behind a moving environmental optimum (Lynch & Lande 1993; Bürger & Lynch 1995), leading to sustained hard selection. The inability of adaptive evolution to keep pace with environmental change can threaten long-term population viability (Quintero & Wiens 2013; Radchuk *et al.* 2019).

However, adaptive evolution can sometimes have negligible effects on population growth or abundance. Soft selection involving a zero-sum game allows for rapid trait evolution over multiple generations with minimal influence on population dynamics (e.g., Fisher & McAdam 2019), and thus high rates of sustainable evolution (e.g., Maynard Smith 1968; Sved 1968). The population size may also remain stable under evolution via hard selection when selective reductions in vital rates are compensated for. This is a type of cryptic eco-evolutionary dynamics (Kinnison *et al.* 2015) because although natural selection appears to not influence population growth, evolution in response to hard selection is preventing or limiting maladaptation that might otherwise result in a population decline (e.g., Reed *et al.* 2013b).

In addition to influencing population growth, evolution under hard and soft selection may influence the number of individuals the environment can support. For example, hard selection

For Review Only

can increase the carrying capacity through the evolution of greater resource use efficiency (Kinnison & Hairston 2007). Under soft selection, evolution can sometimes alter the number of ecological vacancies, which is demonstrated by research on the evolution of warning coloration (i.e., aposematism). Predators learn to avoid the most common aposematic warning signals (Chouteau *et al.* 2016), and the individual fitness of prey depends on how common its warning phenotype is in the population (i.e., positive frequency-dependent selection; for a review of why warning signals may still be polymorphic, see Briolat *et al.* 2019). Locations with predominantly one warning pattern experience decreased predation rates (Mallet 1999; Chouteau *et al.* 2016), suggesting that as a single warning pattern becomes more frequent in a population the number of ecological vacancies increase. Another, perhaps common, way in which evolution under soft selection can increase the number of ecological vacancies is through diversifying selection to use a greater range of resources in competitive environments (Bolnick 2004; Svanbäck & Bolnick 2007).

Much research on the influence of evolution on demography has focused on life-history traits. Life-history theory predicts trade-offs between faster intrinsic growth rates and better competitive abilities, and the optimal strategy can vary with density (e.g., r-K selection; Reznick *et al.* 2002). Although hard and soft selection can both occur at any density (see Section 3), the hard-soft continuum may roughly map to the r-K continuum. Using offspring quantity versus size as an example, at lower densities, the absolute number of offspring matters more for parental fitness (r or hard selection), while at high densities the relative offspring size, which determines resource acquisition ability, matters more to parental fitness (Sæther *et al.* 2016; K or soft selection). Fluctuations in density can cause variation in the optimal number and size of offspring (Sæther *et al.* 2016), which can alter patterns of evolution and population dynamics.

For Review Only

For example, oscillations in r-K selection promoted stable population cycles in side-blotched lizards *(Uta stansburiana*; Sinervo *et al.* 2000).

As hard and soft selection may often act on the same traits (Laffafian *et al.* 2010), considering how their interactions influence evolution and population dynamics is especially critical. Soft selection can either aid or inhibit the scope for evolutionary responses to hard selection to track the optimum phenotype for the environment (Fig. 3; Johansson *et al.* 2015; Svensson & Connallon 2019), as demonstrated by research on sexual selection (Kokko & Brooks 2003). Sexual selection is usually soft because the relative phenotype (e.g., display) of individuals of the non-limiting sex determines who secures mates of the limiting sex (the ecological vacancies). Sexual selection can act in the opposing direction to selection that is driven by other factors (Andersson 1994), thus preventing the mean phenotype of the population from reaching a fitness optimum for the environment and reducing population growth. For example, male ornaments that attract females, or armaments that deter other males, might also increase vulnerability to predation (Hernandez-Jimenez & Rios-Cardenas 2012) and parasitism (Moore & Wilson 2002). In contrast, both hard and soft selection should often act in the same direction to reduce the frequency of unconditionally deleterious alleles that contribute to inbreeding depression (i.e., purifying selection). Consistent with this prediction, experimental populations of flour beetle (*Tribolium castaneum*) that evolved with high levels of sexual selection subsequently had lower extinction risk under periods of high inbreeding compared to populations that evolved with low sexual selection (Lumley *et al.* 2015). The extent to which interactions between hard and soft selection influence evolution and population dynamics likely varies considerably across traits and taxa.

6. Hard and soft selection in conservation contexts

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Climate Change

Climate change is expected to become a leading driver of extinction in the near future (Urban 2015; Trios 2020), and a major concern is that adaptive responses to climate change will be insufficient (Quintero & Wiens 2013; Radchuk *et al.* 2019). However, soft selection and compensatory selection might buffer against population declines driven by poor phenotypic matches with changing climatic conditions. For some climate-influenced traits, soft selection may often work in the same direction as, and thus reduce the demographic influences of, hard selection (Fig. 3a), which might be the case for thermal adaptation. Sexually-selected traits are often condition-dependent (Kotiaho *et al.* 2001), and individuals better matched to the changing thermal environment should have higher conditions and gain reproductive advantages, in turn improving thermal adaptation (García-Roa *et al.* 2020). Experiments comparing populations that evolved with weak versus strong sexual selection demonstrate that soft (sexual) selection can increase persistence probability at high temperatures (Plesnar-Bielak *et al.* 2012; Parrett & Knell 2018). However, large temperature increases will drive populations toward extinction regardless of buffering from soft selection (e.g., Parrett & Knell 2018).

Compensatory selection can also buffer against climate-driven extinction, which could partly explain why evidence for population impacts of climate-induced phenological mismatch has remained elusive despite being predicted by the match-mismatch hypothesis (Cushing 1969; Visser & Gienapp 2019). For example, cavity-nesting birds are typically regulated by competition for nest sites and food (Newton 1998), and climate-driven hard selection acting on phenology expressed before density regulation can have a limited impact on population growth, provided that climate change is not too extreme (Reed *et al.* 2013a, b). These examples have a common theme: soft selection and compensatory selection may buffer against climate-driven

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population declines to a point, but large changes in climate may nevertheless lead to extinction (Trisos *et al.* 2020).

Soft selection will not always reduce extinction risk (Fig. 3), and research on phenology also demonstrates that hard and soft selection can act in opposing directions and interact in complex ways (Johansson & Jonzén 2012; Johansson *et al.* 2014; Day & Kokko 2015). For example, soft selection may favor early migration to gain territories that counteracts hard selection to match resource peaks (Kokko 1999; Svensson & Connallon 2019). This highlights that soft selection might either increase or decrease vulnerability to climate-driven extinction (Svensson & Connallon 2019), similar to how phenotypic plasticity can both aid or counter adaptation to climate change (Reed *et al.* 2011). In a counterintuitive example (Day & Kokko 2015), mismatched migration timing to advancing resource peaks can result in increased mortality due to hard selection, thus driving population declines. The population declines, in turn, reduce the strength of soft selection for early arrival to secure better territories. Thus, although hard and soft selection are now acting in the same direction, increasing mismatch can potentially cause the total strength of selection (the sum of the hard and soft components) to decrease. This can create a feedback loop that increases extinction risk: soft selection due to intraspecific competition weakens as the population becomes smaller, which reduces adaptation and contributes to further population declines via hard selection. Thus, as populations decline due to environmental mismatch, not only will the efficacy of selection decrease due to the increased influence of genetic drift (Lanfear *et al.* 2014), but the strength of selection may sometimes also decrease. In general, understanding hard selection, soft selection, and their interactions is important for anticipating likely impacts of climate change on evolutionary adaptation (Aitken *et al.* 2008), population performance (Beckerman *et al.* 2003; Benton *et al.*

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2006), range shift dynamics (Best *et al.* 2007; Cotto *et al.* 2017), and altered interspecific interactions (Cahill *et al.* 2013).

Small populations and the extinction vortex

Small, isolated populations face increased extinction risk due to interactions between demographic effects and inbreeding depression (i.e., extinction vortex; Soulé & Mills 1998). Note that inbreeding depression is the reduction in fitness of inbred *individuals* (Charlesworth & Willis 2009; Box 1) and does not require that mean fitness decreases. For example, inbreeding depression due to soft selection can involve a zero-sum game (Wallace 1975). Evolution in response to soft selection can reduce the frequency of deleterious alleles that would otherwise drive population declines through hard selection (e.g., Whitlock & Agrawal 2009; López-Cortegano *et al.* 2016), thus weakening the extinction vortex (Lumley *et al.* 2015). Soft selection could help explain why some small, inbred populations manage to persist (e.g., Benazzo *et al.* 2017; Grossen *et al.* 2020).

Consideration of soft selection could potentially improve the predicted influences of inbreeding depression in population viability analyses (PVAs). The magnitude of inbreeding depression can have strong influences on predicted extinction probability (O'Grady *et al.* 2006), and common PVAs frameworks implicitly assume that inbreeding depression is due to hard selection against deleterious alleles (e.g., Lacy 1993). However, if a portion of inbreeding depression is due to soft selection (e.g., Schmitt & Ehrhardt 1990; or hard selection is compensatory), these PVA frameworks will likely overestimate the effect of inbreeding depression on extinction risk. Accounting for the influences of soft selection and compensatory selection in PVAs would be highly informative but challenging. In any case, soft selection

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highlights the importance of accounting for multiple estimates of inbreeding depression in population viability analyses.

A promising conservation strategy to alleviate the detrimental effects of inbreeding in small populations is to translocate individuals to assist gene flow, which can increase population growth and, ultimately, persistence probability (i.e., genetic rescue; Whiteley *et al.* 2015; Bell *et al.* 2019). Similar to evolutionary rescue, the expectation of increased population growth with genetic rescue assumes that hard selection had a large contribution to inbreeding depression. There is little doubt that inbreeding can cause population declines (Bozzuto *et al.* 2019) and genetic rescue can reverse these declines (Madsen *et al.* 1999; Johnson *et al.* 2010). However, measuring increased fitness in intraspecific hybrids compared to non-admixed residents (a common measure of genetic rescue; Robinson *et al.* 2020) does not guarantee that population growth increased, just as measuring inbreeding depression does not necessarily indicate a population decline. Overall, consideration of soft selection and compensatory selection can influence both theoretical and empirical investigation of inbreeding depression and genetic rescue.

Hybridization, outbreeding depression, and captive breeding

Outbreeding depression (i.e., a decrease in individual fitness owing to the genetic admixture of divergent genomes) from human-induced hybridization, through either release of captive-bred individuals into the wild and introduction of species into their nonnative range, has been of significant concern for decades (e.g., Rhymer & Simberloff 1996; Allendorf *et al.* 2001). Consistent with inbreeding depression, outbreeding depression will not lead to decreased population growth if selection against hybrids is soft, and even when hard, ecologically strong

For Review Only

but compensatory selection does not necessitate a population decline when reproductive excess is high. Conversely, a lack of population decline does not suggest that outbreeding depression is negligible. Indeed, soft selection and compensatory selection offer a clear resolution to population persistence and stability despite human-induced outbreeding depression (e.g., Kovach *et al.* 2015). Few studies have attempted to directly quantify the effects of outbreeding depression on population dynamics (but see Sylvester *et al.* 2019; Willoughby & Christie 2019), and we are not aware of any that have considered soft selection.

Oftentimes, outbreeding depression should be due to both hard and soft selection. This is likely the case for Pacific salmon, where captive-bred (i.e., hatchery-produced) individuals and their hybrids tend to have markedly reduced fitness in the wild due to rapid adaptation to the captive rearing environment (Araki *et al.* 2008; Christie *et al.* 2014). Reduction in fitness is likely cumulative over many traits, but it generally appears to result from reduced marine survival (Jonsson *et al.* 2003) and reproductive success during spawning (Thériault *et al.* 2011). The latter is due, at least in part, to soft selection. Experimental studies have demonstrated that, compared to wild-born fish, hatchery-born females are competitively inferior at acquiring and defending breeding sites, and males have a substantially lower ability to obtain mates (Fleming & Gross 1993; Neff *et al.* 2015). However, competitive disadvantages of hatchery-born fish were generally weaker at low densities (Fleming & Gross 1993), and hatchery-born fish readily breed in the absence of wild-fish (Fleming & Gross 1992). Therefore, low abundance of wild-born fish can increase the reproductive success of hatchery-born fish, thereby producing offspring with reduced marine survival. Even if reduced marine survival is only partially due to hard selection (e.g., O'Sullivan *et al.* 2020), increased production of hybrids could exacerbate population declines, the exact opposite of the desired outcome of captive breeding programs.

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Harvest

Strategic harvest of reproductive excess is at the core of sustainable fisheries and wildlife management (e.g., Boyce *et al.* 1999). While theoretically and empirically justified when viewed solely in the light of population abundance, the harvest of population excesses can decrease the efficacy of soft selection on traits mediating success in intraspecific competition and reduce the buffering capacity afforded by compensatory selection (Young 2003). Furthermore, harvest often acts as a selective force (Allendorf & Hard 2009), especially on traits that are subject to strong sexual selection (e.g., body size, horn size). In a population harvested exactly at maximum sustainable yield, and hence kept at population sizes below which there is strong intraspecific competition for a limiting resource (e.g., breeding territories), the strength of soft selection will likely be reduced and hence these traits might be more vulnerable to the effects of genetic drift. At best, this might create situations where natural selection cannot act to shift populations toward fitness peaks that are desired by humans (e.g. larger body sizes). At worst, harvest could act to increase the phenotypic maladaptation that many populations of conservation concern already face (Waples *et al.* 2008), which might prove increasingly worrisome as populations are subject to novel or more acute selective pressures under global change. In either scenario, it is clear that consideration of soft selection is fundamental in predicting the ecological and evolutionary implications of harvest.

7. Conclusion

Hard and soft selection are neglected topics of broad relevance for uniting ecology and evolution (Lowe *et al.* 2017). Hard and soft selection are connected to demography in fundamentally

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different ways (Wallace 1975; Reznick 2016), and their interactions can have a variety of influences on population dynamics (Svensson & Connallon 2019). Research that has considered hard and soft selection has revealed unexpected influences of natural selection on population growth (e.g., Sinervo *et al.* 2000; Day & Kokko 2015). Interactions between hard and soft selection may also be a common contributor to feedbacks between ecology and evolution (Kokko & López-Sepulcre 2007; Ferriere & Legendre 2013), for example, because hard selection is more likely to influence density, density can alter the strength of soft selection, and soft selection then influences the strength of subsequent hard selection (e.g., Day & Kokko 2015). As the links between natural selection and population dynamics are central to evolutionary-ecology (Hendry 2017), consideration of hard and soft selection may also influence theoretical and empirical evaluation of eco-evolutionary dynamics in communities and ecosystems. However, many aspects of hard and soft selection remain poorly understood, and further research on these topics is needed.

As more studies on hard and soft selection accumulate, we can better address a range of questions, such as: Is soft selection generally stronger or weaker than hard selection? How do the influences of hard and soft selection vary across traits, taxa, and types of interspecific interactions? How often and under what conditions does soft selection work in the same versus opposing direction as hard selection? Do hard and soft selection have differing or cascading influences on meta-populations, communities, and ecosystems? How often and to what extent does selection influence population growth and extinction risk? How common are thresholds where selection changes from primarily soft to primarily hard? Is anthropogenic change 'hardening' selection as populations become increasingly maladapted and reach critical thresholds? Theoretical work has provided critical insight into some of these topics. Empirical

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research on hard and soft selection presents a more substantial challenge, particularly in wild populations, but insights from empirical studies will be valuable to test theory and aid conservation efforts.

Consideration of these topics can alter predicted extinction risks, a core issue in conservation biology. Encouragingly, assessments of population viability that ignore soft selection and compensatory processes may be overly dire because natural selection and adaptive evolution can proceed with little influence on population growth. However, soft selection can sometimes increase extinction risk (Svensson & Connallon 2019), further emphasizing the need to incorporate these concepts into population viability analyses. Additionally, similar to adaptive phenotypic plasticity (Simmonds *et al.* 2020), soft selection and compensatory selection may buffer against population declines (Reed *et al.* 2013a; Parrett & Knell 2018), but only up to a point in which mismatch to the environment becomes too severe for persistence (Frankham 1995; Trisos *et al.* 2020). Unfortunately, humans are reducing the density of many populations, sometimes intentionally (e.g., harvest), which will often decrease buffering from soft selection and compensatory processes and, in turn, increase extinction risk. Overall, hard and soft selection highlight the need to explicitly consider how the ecological context in which natural selection occurs influences contemporary evolution and its demographic consequences in a changing world.

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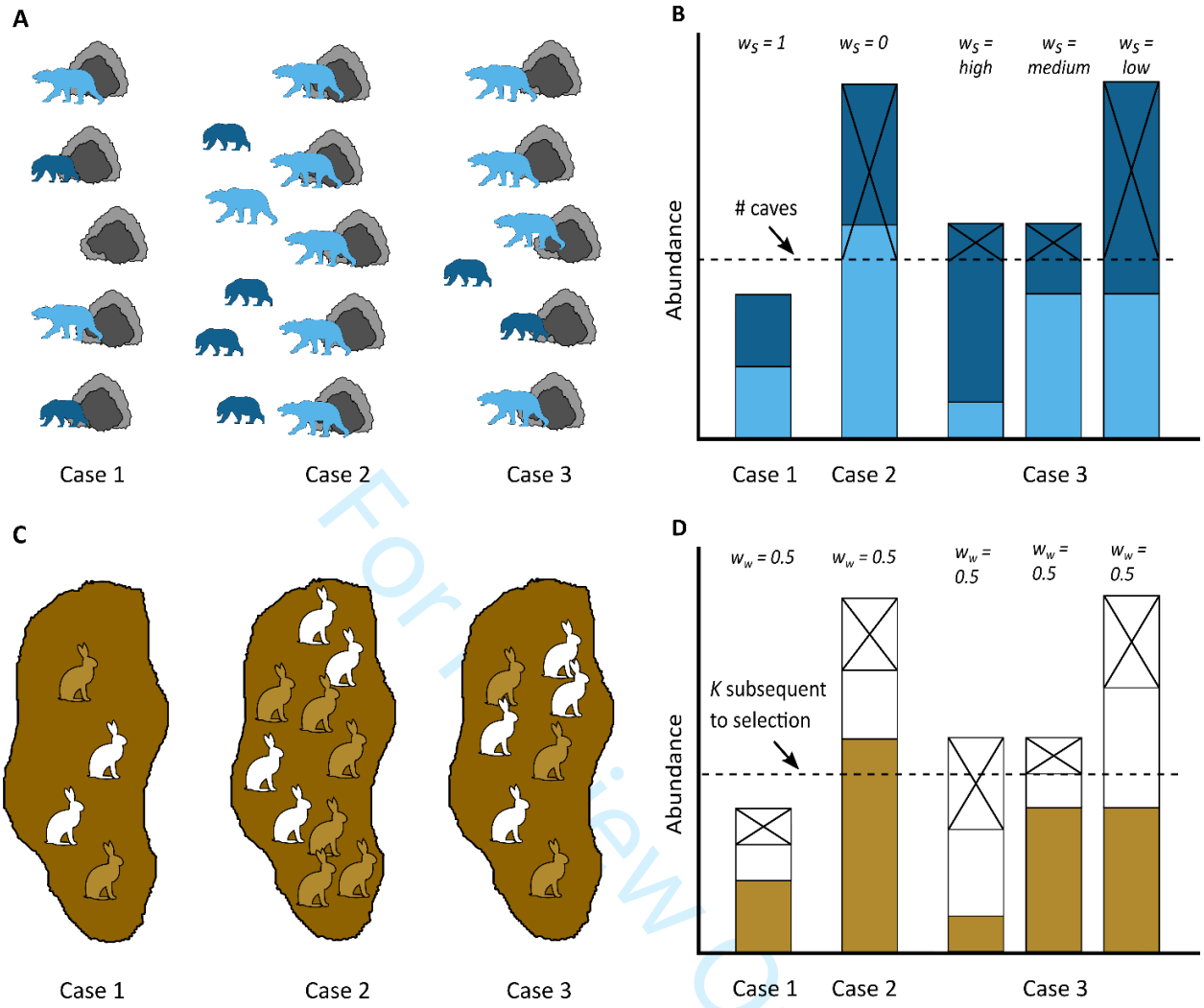


Figure 1. Depictions of soft selection occurring in bears competing for caves (A & B) and of hard selection for hares vulnerable to predation (C & D). In the soft selection example (A & B), aggressive bears (dark blue) always outcompete submissive bears (light blue) for a limited number of caves in which to hibernate. In case 1, all bears survive because there are fewer bears than caves and, hence, no selection. In case 2, aggressive bears obtain all caves, and submissive bears are eliminated from the population. In case 3, there are more bears than caves, but not enough aggressive bears to secure every cave, and the strength of selection is dependent on the phenotypic composition and density of the population. In the hard selection example (C & D), white (mismatched) hares have a 50% chance of surviving predation, while brown (matched) hares are resistant to predation. The relative fitness of white hares remains 0.5 irrespectively of the phenotypic composition and reproductive excess of the population (D). Selective mortalities are indicated by x's. w_s and w_w are the relative fitness of submissive bears and white hares, respectively. The dashed line is the number of caves in B, and a carrying capacity that is due to density regulation that occurs subsequent to selection in D. Cases 1-3 align with the soft selection equations

shown in the main text. Note that in the hard selection example, K has no influence on selection, and is included so the ratio of N/K is consistent with the soft selection scenarios. Also note that soft selection does not influence the final population size, while hard selection reduces the final population size when selective mortalities exceed the reproductive excess (N-K).

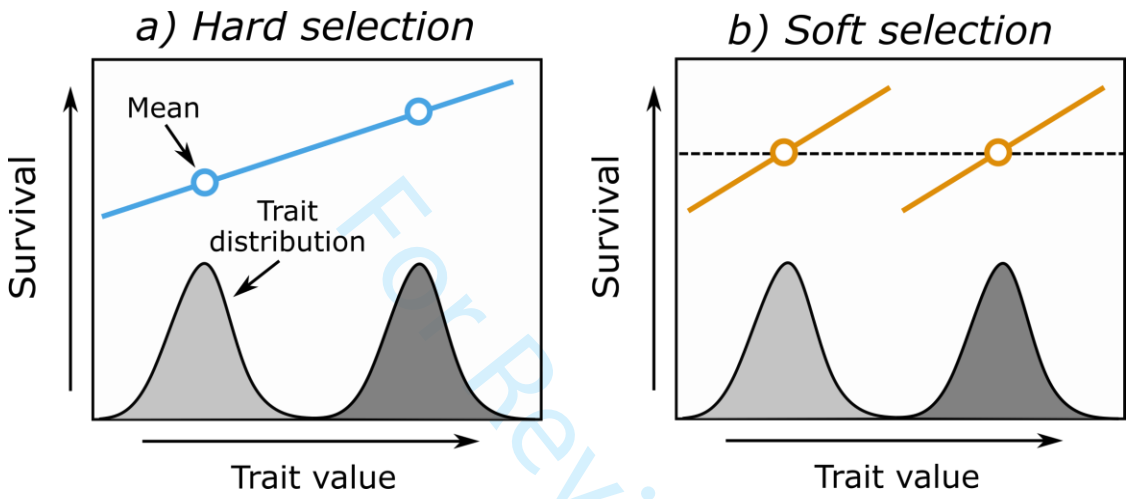


Figure 2. The relationship between individual trait values (e.g., thermal tolerance, breeding time, body size, running speed, etc.) and survival probability for hard versus soft selection assuming positive directional selection. The light and dark trait distributions represent two different populations that are otherwise experiencing the same environmental conditions. Under hard selection (A), the relationship between trait values and survival probability does not depend on the phenotypic composition of the population (i.e., trait distribution). The population with the higher mean trait value (dark grey) has higher mean survival (hollow points). Under soft selection (B), an individual's trait value relative to the population mean determines their survival probability, and the mean trait value of the population does not influence mean survival (hollow points; dashed line). Note that with compensatory hard selection, a lack of relationship can also result between mean fitness and mean trait value, but in this case mean fitness is some composite of survival/fertility across multiple life stages.

For Review Only

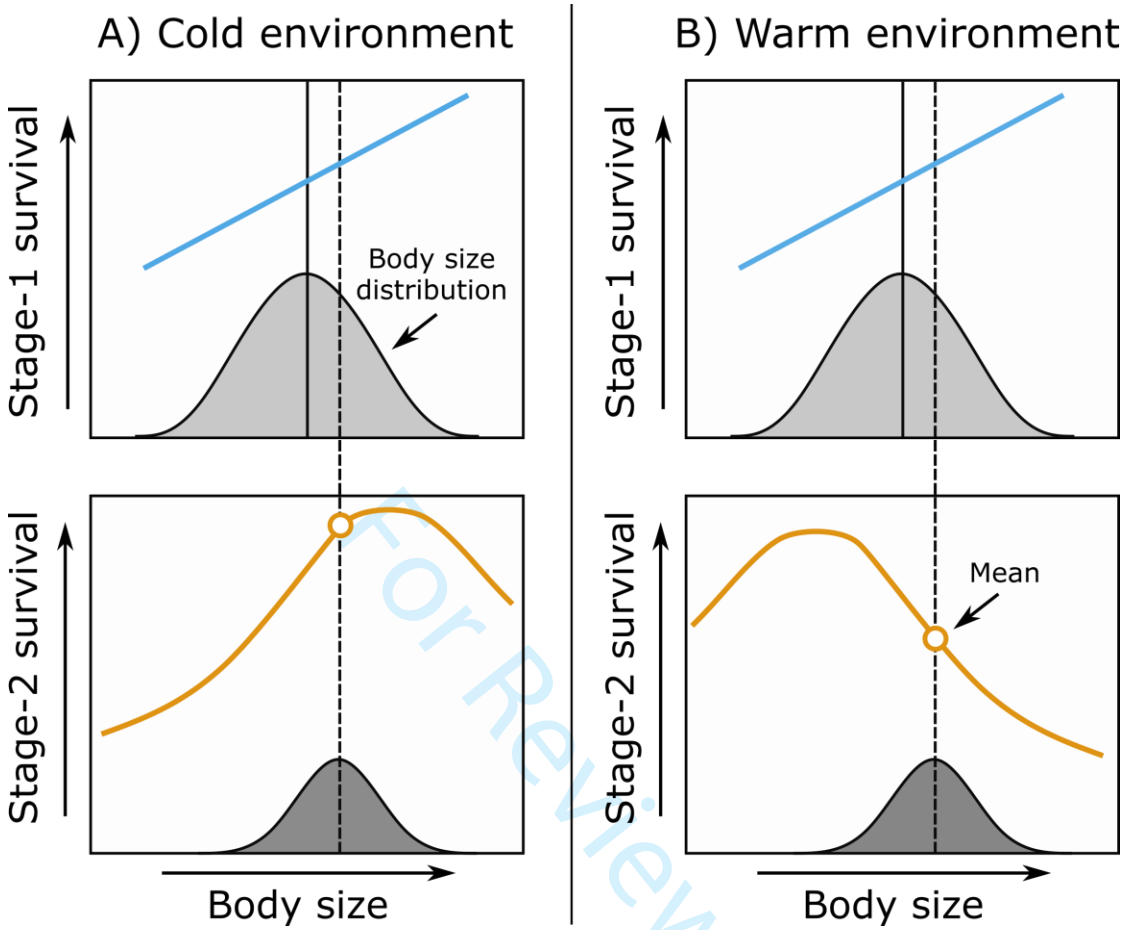


Figure 3. A hypothetical example of soft selection followed by hard selection at a later life-stage on body size in two populations inhabiting cold (A) versus warm (B) environments. At life stage-1, larger individuals outcompete smaller individuals for a limiting resource and thus have higher survival (orange lines; upper panels). The solid and dashed vertical lines represent the mean body size before and after soft selection, respectively. The survivors of stage-1 are larger on average at the start of stage-2 due to soft selection. The strength of hard selection during life stage-2 depends on how close the mean phenotype (post-soft selection) is to an environmental optimum (blue curves; lower panels). During stage-2, the optimal body size is larger in the colder environment and smaller in the warmer environment for thermoregulatory reasons. In the cold environment (A), soft selection during stage-1 decreases the strength of hard selection on stage-2, and mean stage-2 survival is high (hollow point). In contrast, in the warm environment (B), soft selection increases the strength of subsequent hard selection, and mean stage-2 survival is low (hollow point). The light grey and dark grey distributions represent the trait distributions prior to soft selection and hard selection, respectively.

Box 1: Glossary

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Soft selection – a type of natural selection in which absolute fitness of an individual depends on its trait value relative to other conspecifics with which it interacts (i.e., the phenotypic composition of the population).

Hard selection – a type of natural selection in which individual absolute fitness depends on their absolute trait value and is independent of the phenotypic composition of the population.

Population growth – the growth of a population over a given (e.g., annual) time step (N_{t+1}/N_t).

Absolute fitness – an unscaled measure of life-time individual fitness. Population growth is proportional to the mean absolute fitness of individuals in the population. In this paper, fitness refers to absolute fitness unless stated otherwise.

Relative fitness – a scaled measure of individual fitness, where individual fitness is expressed as a proportion of the mean fitness in the population (typical in quantitative genetics), or as a deviation from the maximum fitness (common in population genetics)

Inbreeding depression – reduced fitness of offspring with related parents compared to those with unrelated parents.

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Box 2: Competing definitions of soft selection

Christiansen (1975) applied Wallace's hard and soft selection to two competing models of spatial heterogeneity in selection across discrete habitats (Levene 1953; Dempster 1955). Although much of the current use of soft and hard selection is in reference to these models, Levene's model is not soft selection under Wallace's initial intent. In Levene's model, individuals first disperse into two or more habitats, and selection occurs within each habitat. Within-habitat selection depends only on the match between phenotype and the habitat. Next, local density regulation occurs within each habitat type, which results in a consistent contribution of each

habitat to the total population size (i.e., compensatory hard selection). Finally, individuals from all habitats re-pool and mate panmictically. Density and negative frequency-dependent selection emerge in Levene's models at the *global* level, which led to this model being called soft selection. However, relative trait values of individuals never entered this model, which is the critical component of Wallace's soft selection.

A variety of subsequent models (reviewed by Ravigné *et al.* 2004; also see De Lisle & Svensson 2017) and some empirical studies (Gomulkiewicz & Kirkpatrick 1992; Gallet *et al.* 2018) have invoked soft selection *sensu* Christiansen in the context of evolution in spatially heterogeneous environments or metapopulations (Whitlock 2002; Agrawal 2010; Ho & Agrawal 2012). Their common denominator is the idea that the 'softness' of selection is determined by the extent to which individual fitness depends on phenotype relative to a local average (soft selection) or a global average (hard selection). However, soft selection can also occur globally. For example, global soft selection would occur if individuals from different demes pool in a common habitat during a certain life stage and phenotype-dependent competition for ecological vacancies occurs among them. Likewise, hard selection does not require a 'global optimum' and habitat heterogeneity can create local optimum trait values against which organisms are judged (i.e., hard selection). The key for Wallace's soft selection is that, at some time or place, selection occurs based on relative trait values among individuals, and frequency and density dependence can emerge at the scale and time that selection occurs.

Research on hard and soft selection *sensu* Levene has provided important insights into evolution including the maintenance of genetic variation (e.g., Vale 2013; Gallet *et al.* 2018), and strict adherence to any particular definition is unnecessary. We suggest that authors specify

For Review Only

which version of soft selection they are using and acknowledge that the different models of soft selection (Wallace vs. Christiansen) are not synonymous.

Box 3: Measuring hard and soft selection

Experiments that manipulate phenotypic composition are required to fully disentangle hard and soft selection and measure their relative strengths. For example, experiments can compare monocultures (uniform social environments) and mixed cultures (heterogeneous social environments) of the phenotype of interest under the same environmental conditions. A relationship between absolute fitness and phenotypes in monocultures provides evidence for hard selection, and a change in that relationship in mixed cultures provides evidence for soft selection (e.g., Weis *et al.* 2015). For traits that are more continuously distributed, manipulating the mean value (or variance) of the trait, while holding all else constant, should change the absolute fitness of individuals with a given trait value under soft selection (because relative trait values then change), but not hard selection (Lande 1976; Svensson & Connallon 2019). Additional experimental treatments can further disentangle the dynamics of hard and soft selection. For example, when examining soft selection due to intraspecific competition, researchers will typically also want to add density treatments (while resource amounts stay constant), as the strength of soft selection should increase with density in this case. Other treatments of interest including altering the abiotic environmental conditions, and the ratio of focal to interactor species for studies examining soft selection due to avoidance of negative interactions.

Deciphering between hard and soft selection in wild populations presents a greater challenge. Showing that a measure of absolute fitness depends both on an individual's phenotype

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and the phenotypic composition of the population (i.e., mean and/or variance for continuous traits) provides evidence that soft selection is occurring. This will require measuring a phenotype over multiple selective episodes, either over space, time, or both. However, studies must also account for temporal and spatial variation in agents driving selection before inferring to what extent hard and soft selection occurred.

Studies should also aim to examine the demographic costs and evolutionary responses to hard and soft selection. In both observational and experimental studies, the demographic costs of hard and soft selection can be estimated by examining associations between mean absolute fitness (or population growth) and the strength of selection. Additionally, evolutionary changes (i.e., temporal trends in breeding values) in the focal trait, and in theory also fitness itself, can be estimated when phenotypic information on traits and fitness are combined with direct or indirect (e.g., pedigree-derived) genetic information (Kruuk *et al.* 2008; Hadfield *et al.* 2010; Hendry *et al.* 2018; Fisher & McAdam 2019). Further, modeling approaches that combine selection, inheritance, and demography allow exploration of population responses to environmental change (e.g., Coulson *et al.* 2017), and will be critical for improving our understanding of the complexities of hard and soft selection.

Further mathematical development is needed to distinguish between hard and soft selection. Models for determining the relative strength of hard and soft selection have been derived for related, but distinctive, versions of the concept (Laffafian *et al.* 2010; Ho & Agrawal 2012; Weis *et al.* 2015). These models can provide results consistent with Wallace's conception of hard and soft selection under some conditions, and might also serve as useful starting points to derive additional equations.

For Review Only

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For Review Only

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For Review Only

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Supplementary materials

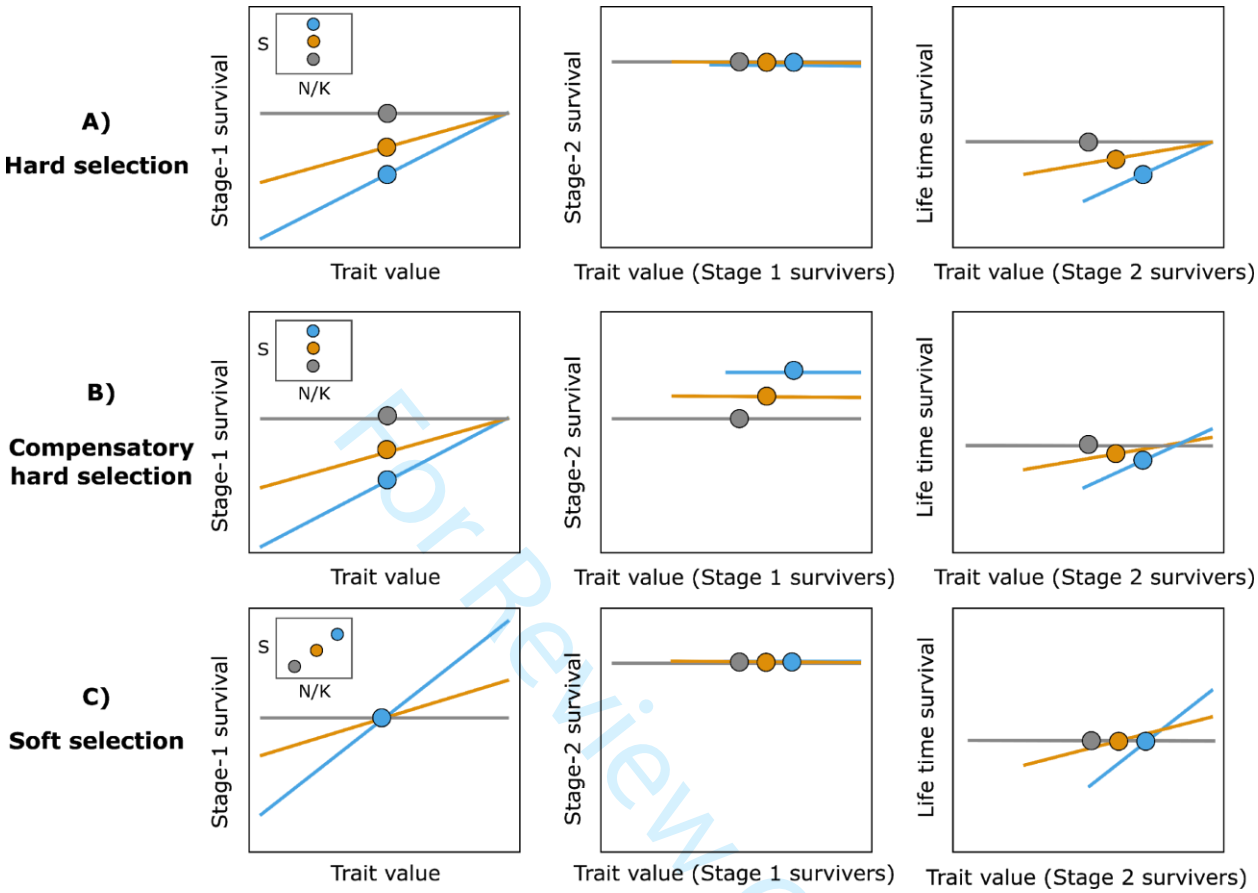


Figure S1. Schematic depiction of the net demographic costs of (A) HS, (B) partially compensatory HS and (C) SS. In each scenario, a single episode of selection occurs during life stage-1 (left-hand column) and three different years are depicted (grey, orange, blue) across which linear selection strength varies. The steeper the relationship between individual survival during life stage-1 and the trait value, the stronger the selection differential (S). The small inset graphs present the relationship between population density (N relative to K) and selection differentials. Selection differentials under hard selection are dependent upon the external environment (e.g., climate) and are independent of density. In contrast, the strength of SS is correlated with population density. Under HS (A), selection is followed by density- and trait-independent mortality in stage-2. Under compensatory HS (B), selection is followed by density

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dependence at stage-2, hence the stronger the reduction in mean survival in stage-1, the higher the mean survival in stage-2 owing to release from competition (note that compensation is partial as depicted). Under SS (C), survival at stage-2 could be density dependent or independent, but either way the expected mean is the same across years as SS at stage-1 has not impacted the number of survivors. The right-hand panels show the net outcomes in terms of life time survival (product of survival in stage-1 and stage-2). Circles represent population means.

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