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University College Cork, Ireland Coláiste na hOllscoile Corcaigh

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5 6	2	selection
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## 40 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.

# Ecology Letters

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2 3 4	57	Hard selection is both density- and frequency-independent. For that reason, it is the
5 6	58	mathematical geneticist's dream; for the same reason, it is the ecologist's nightmare".
/ 8 9	59	- Bruce Wallace, 1975
10 11	60	"Don't compare me to the Almighty, compare me to the alternative."
12 13	61	- Political proverb
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17 18	63	1. Introduction
19 20	64	The realization that evolution can occur on the same time scale as ecology has fueled renewed
21 22 23	65	interest in clarifying the links between natural selection and population dynamics (Carroll <i>et al.</i>
24 25	66	2007; Hendry 2017). This endeavor is especially critical as rapid anthropogenic change threatens
26 27	67	populations globally (Stockwell et al. 2003; Kinnison & Hairston 2007; Trisos et al. 2020).
28 29 30	68	Natural selection is often thought to incur a demographic cost (sensu Haldane 1957) through
31 32	69	either increased mortality or reduced fertility, which places an upper limit on the sustainable
33 34	70	rates of adaptive evolution that a population can endure without going extinct (Bürger & Lynch
35 36 37	71	1995; Gomulkiewicz & Holt 1995; Orr & Unckless 2008). Indeed, this may often be the case for
38 39	72	traits undergoing hard selection, where an individual's fitness (here referring to absolute fitness
40 41 42	73	unless otherwise stated; Box 1) is dependent on the match between its <i>absolute</i> trait value and
42 43 44	74	the environment and is independent of the phenotypic composition of the population (Wallace
45 46	75	1975; Box 1). For instance, individuals with lower thermal tolerances are more likely to perish as
47 48 40	76	temperatures rise, independent of the thermal tolerances of others in the population. Rising
49 50 51	77	temperatures can cause substantial population declines when many individuals are poorly
52 53	78	matched to the thermal environment, and population persistence then depends on whether
54 55 56	79	adaptive evolution can sufficiently reduce thermal mismatch (Killeen et al. 2017). The
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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.

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102 Consideration of hard and soft selection can alter predicted responses to anthropogenic 103 change (e.g., Day & Kokko 2015). Importantly, these concepts highlight that natural selection 104 and adaptive evolution can proceed with less influence on population growth than may often be 105 expected. However, interactions between hard and soft selection can both increase or decrease 106 extinction risk (Svensson & Connallon 2019), suggesting that their combined influence on 107 population dynamics can be complex.

108 Despite important differences in how hard and soft selection influence, and are 109 influenced by, population dynamics, these concepts have received infrequent attention in the 110 evolutionary and ecological literature. Although many researchers assume selection is hard, soft 111 selection might be the more common form of natural selection (Wallace 1991; Reznick 2016). 112 Here, we review the theoretical and empirical literature on hard and soft selection. Although 113 recent work has examined the evolutionary implications of hard and soft selection in meta-114 populations (e.g., Gallet *et al.* 2018), we focus on the local population scale and examine how 115 hard and soft selection influence population dynamics. Further, we place these concepts in the 116 wider context of eco-evolutionary dynamics and illustrate their relevance to a range of applied 117 questions involving population responses to anthropogenic stressors.

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## 119 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

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  $1-q^2$ , 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 aggressivebears to fill every cave (Case 3).

144 Case 1: s = 0 for K > N

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

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

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

160 Importantly, the type of frequency dependence Wallace referred to simply arises from the 161 fact that phenotypes are judged against the phenotypes of others in the population and is more 162 general than negative frequency-dependent selection (e.g., Gigord et al. 2001). The behavioral 163 phenotypes of Wallace's bears are under directional selection because the aggressive bears are 164 always at a competitive advantage, and negative frequency dependence never enters this 165 example. The manner in which Wallace used frequency dependence appears to be a source of 166 confusion surrounding hard and soft selection (Gromko 1976) and partly responsible for a 167 proliferation of uses of these terms that, although providing critical insights for evolution, 168 deviate from Wallace's initial concept to varying degrees (Box 2). Additionally, soft selection is

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.

1 2		
2 3 4	192	2020). Hard and soft selection can also be generalized to much more diverse ecological
5 6 7	193	scenarios.
7 8 9 10	194	
11 12 13 14	195	3. The ecological causes of soft and hard selection
15 16	196	Although Wallace was focused on intraspecific competition for abiotic resources, soft selection
17 18 10	197	can involve a range of interspecific biotic interactions (Chao et al. 2000; Start 2020). Returning
20 21	198	to the example of coat coloration in snowshoe hares (Section 2; Fig.1), we previously assumed
22 23	199	that predators simply cannot find well-matched hares (e.g., brown hares on brown backgrounds)
24 25 26	200	and hence this was an example of hard selection. Another possibility is that predators
20 27 28	201	preferentially target mismatched hares when they are frequent because the search times involved
29 30	202	are minimal, but switch to taking better-matched hares when mismatched hares become less
31 32	203	frequent because they have no option but to search for longer. This corresponds to soft selection
33 34 35	204	because the fitness of a mismatched hare now depends on how well matched other hares in the
36 37 38	205	population are.
39 40	206	Using a second heuristic example from Chao et al. (2000), if lions prey on the slowest
41 42 43	207	and most peripheral zebras in a herd, the phenotypic composition of the zebra herd determines
44 45	208	which, but not necessarily how many, zebras are captured. This example of zebras avoiding
46 47	209	predation mirrors bears competing for caves: the initial zebra population size minus the number
48 49 50	210	of predation events determines the number of ecological vacancies (i.e., survivors of a fixed
50 51 52	211	predation rate), and the relative speed and jockeying behavior of zebras determine which
53 54	212	individuals obtain those ecological vacancies. Generally, soft selection arising from interspecific
55 56	213	interactions can be broken into two categories: 1) intraspecific competition for a limited biotic
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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

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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).

240 Soft selection is often equated with intraspecific competition (e.g., Charlesworth 2013), 241 but intraspecific competition can also lead to hard selection. For example, under intraspecific 242 competition for resources due to high density, traits influencing resource use efficiency (e.g., 243 metabolic rates and digestive efficiency) are likely under hard selection because whether an 244 individual can survive on a given food ration is independent of the resource use efficiency of 245 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 246 247 resources than its neighbors to survive under conditions of high intraspecific competition. In 248 other words, both hard and soft selection can involve intraspecific competition and be density-249 dependent.

250 Additionally, soft selection is not density-dependent per se, but instead dependents on the 251 ratio of density to ecological vacancies (i.e., reproductive excess). If the number of bears stays 252 the same but a landslide buries half of the caves, the strength of soft selection will increase 253 because the ratio of bears to caves increased (i.e., reproductive excess was greater). Likewise, if 254 the number of zebras remains the same but the number of predation events increases, the strength 255 of soft selection will be greater because the ratio of initial zebras to survivors of predation 256 increased. More generally, the strength of soft selection depends on the per capita amount of 257 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 258 259 is involved. This suggests that soft selection will be more temporally dynamic than Wallace's

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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 Page 13 of 47

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283 1997; i.e., selection becomes harder). Similarly, when the mean level of inbreeding in a 284 population is low, individuals that are relatively more inbred than others might suffer from 285 reduced competitive ability or lower relative ability to escape from predators, for example, but 286 when the mean level of inbreeding is high, survival might plummet regardless of the competitive 287 or predatory environment (Frankham 1995; e.g., Robinson et al. 2019). 288 4. The demographic costs of hard versus soft selection 289 290 Hard and soft selection provide a useful lens to understand how natural selection influences 291 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, 292 293 we examine the demographic influences of evolutionary responses to selection. It is important to 294 distinguish between *immediate* reductions in mean stage-specific vital rates owing to phenotypic 295 selection versus *net* effects on mean fitness and, thus, population growth. Hard selection is 296 always associated with a reduction in survival or reproductive success during the life-stage at 297 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.

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

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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).

308 In an empirical example that mirrors Wallace's illustration of bears competing for caves, 309 the survival of aggressive and submissive strains of Drosophila melanogaster was compared 310 under different densities and phenotype frequencies (Kilgour et al. 2018). Aggressiveness was 311 found to be under negative frequency-dependent selection, with the strength of selection 312 increasing under high density, competitive conditions (i.e., as the ratio of *Drosophila* to 313 ecological vacancies increased). Survival of aggressive and submissive phenotypes only differed 314 in mixed-phenotype treatments, suggesting selection was soft. Further, mean survival of 315 experimental populations did not differ between uniform and mixed-phenotype treatments, or 316 across mixed treatments with different phenotypic frequencies, suggesting that soft selection 317 involved a zero-sum game.

318 However, soft selection can influence stage-specific vital rates when the phenotypic 319 composition of a population not only influences which individuals obtain ecological vacancies, 320 but also the *number* of ecological vacancies. For example, territorial defense can influence 321 territory size, and thus the number of territories (López-Sepulcre & Kokko 2005). Some 322 resources (e.g., food) need to be obtained throughout an organism's life span, and the number of 323 ecological vacancies can be considered the number of individuals the resource-base (e.g., food-324 base) can support. Strong asymmetries in acquisition ability can create big winners that horde a 325 disproportionate share of the resources (Weiner 1985; Weiner & Freckleton 2010; Yun & 326 Agrawal 2014), which can reduce the total number of ecological vacancies and, hence, soft 327 selection will reduce vital rates. However, when resources are extremely limited, such that equal

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	329	dying (Nicholson 1957; Miller 1967), competitive asymmetries may allow some individuals to
	330	hoard enough resources to survive, thus potentially increasing the mean survival. A similar
	331	process could also occur during interspecific avoidance. For example, asymmetries in
	332	palatability could create big losers that receive an unequal share of herbivore grazing, potentially
	333	increasing or decreasing mean survival. Overall, while hard selection will always result in a
16 17 18	334	decrease in survival or fecundity, soft selection may either increase, decrease, or have no effect
19 20	335	on stage-specific vital rates. These caveats to zero-sum games under soft selection do not change
21 22	336	the general expectation that soft selection is less likely to depress vital rates than hard selection.
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24 25 26 27 28 29 30 31 32 33 34 35 36 37 38 39	337	An experiment on emergence timing in Brassica rapa demonstrated that survival can be
	338	reduced by soft selection (Weis et al. 2015). Mortality was higher in mixed cultures of early and
	339	late-emerging plants compared to monocultures because the early-emerging plants gained a
	340	substantial competitive advantage for access to light which inhibited late-emerging plants from
	341	growing. However, despite differences in early life survival, the total reproductive output was
	342	similar in monocultures and bicultures (Weis 2015), suggesting that increased mortality due to
	343	soft selection was compensated for by increased reproductive output of the survivors, consistent
40 41 42	344	with the law of constant yield in the plant literature (Weiner & Freckleton 2010). This
43 44	345	experiment highlights that even when selection does reduce a vital rate, population growth can
45 46 47	346	remain unaffected.
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49 50	347	There are at least three reasons why an immediate reduction in a vital rate due to
51 52	348	selection may not translate into a decrease in population growth. First, selection simply may not
53 54	349	be strong enough to appreciably influence population growth. Second, the vital rate that selection
55 56 57	350	affects may have a limited influence on population growth (Mills 2013). For example, inbreeding
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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

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374 population of pink salmon (Oncorhychus gorbuscha) that has undergone a rapid evolutionary 375 change in adult migration timing (Kovach et al. 2012, 2013b). The near elimination of late 376 migratory phenotypes aligned with the second-highest stream temperatures on record (Kovach et 377 al. 2012), suggesting hard selection due to thermal mismatch. However, shifts in migration 378 timing did not influence population growth (Kovach et al. 2013a), possibly because density-379 dependent reproductive success compensated for reduced adult survival (Fukushima et al. 1998). 380 Hard and soft selection can also interact to influence population growth (Svensson & 381 Connallon 2019), and soft selection can either increase or decrease the demographic cost of 382 subsequent or concurrent hard selection on the same, or a correlated, trait. Using body size as an 383 example, soft selection can favor larger individuals that have a competitive advantage for 384 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 385 386 reasons (Gardner et al. 2011; Sheridan & Bickford 2011; but see Siepielski et al. 2019). If hard 387 and soft selection act on body size in the same direction, soft selection helps to improve the 388 match between the mean body size and the optimal body size, reducing the strength of hard 389 selection and thus its influence on vital rates and population growth (Fig. 3a). Soft selection may 390 instead oppose subsequent hard selection on body size, which would lead to a greater decline in 391 survival or reproduction (Fig. 3b).

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## 393 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 hardand soft selection can also have unique influences on how the evolution of heritable traits affects

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396	population dynamics. Although hard selection can reduce population growth in the generation
397	that selection occurs, it is expected to increase mean fitness in subsequent generations (Fisher
398	1930). In cases where the environment changes abruptly or gradually across generations,
399	adaptive evolution via hard selection can sometimes avert extinctions (i.e., evolutionary rescue;
400	Hufbauer et al. 2015; Bell 2017). For example, yeast (Saccharomyces cerevisiae) exposed to
401	mostly lethal salinity initially experienced a rapid decline, but as salt-tolerant phenotypes
402	increased in frequency population declines were often reversed within several generations (Bell
403	& Gonzalez 2009). With continuous environmental change, evolutionary trait shifts are expected
404	to lag behind a moving environmental optimum (Lynch & Lande 1993; Bürger & Lynch 1995),
405	leading to sustained hard selection. The inability of adaptive evolution to keep pace with
406	environmental change can threaten long-term population viability (Quintero & Wiens 2013;
407	Radchuk <i>et al.</i> 2019).

408 However, adaptive evolution can sometimes have negligible effects on population growth 409 or abundance. Soft selection involving a zero-sum game allows for rapid trait evolution over 410 multiple generations with minimal influence on population dynamics (e.g., Fisher & McAdam 411 2019), and thus high rates of sustainable evolution (e.g., Maynard Smith 1968; Sved 1968). The 412 population size may also remain stable under evolution via hard selection when selective 413 reductions in vital rates are compensated for. This is a type of cryptic eco-evolutionary dynamics 414 (Kinnison et al. 2015) because although natural selection appears to not influence population 415 growth, evolution in response to hard selection is preventing or limiting maladaptation that might 416 otherwise result in a population decline (e.g., Reed et al. 2013b).

417 In addition to influencing population growth, evolution under hard and soft selection may418 influence the number of individuals the environment can support. For example, hard selection

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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 prev 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.

442 For example, oscillations in r-K selection promoted stable population cycles in side-blotched
443 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**

Climate Change

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466	Climate change is expected to become a leading driver of extinction in the near future (Urban
467	2015; Trios 2020), and a major concern is that adaptive responses to climate change will be
468	insufficient (Quintero & Wiens 2013; Radchuk et al. 2019). However, soft selection and
469	compensatory selection might buffer against population declines driven by poor phenotypic
470	matches with changing climatic conditions. For some climate-influenced traits, soft selection
471	may often work in the same direction as, and thus reduce the demographic influences of, hard
472	selection (Fig. 3a), which might be the case for thermal adaptation. Sexually-selected traits are
473	often condition-dependent (Kotiaho et al. 2001), and individuals better matched to the changing
474	thermal environment should have higher conditions and gain reproductive advantages, in turn
475	improving thermal adaptation (García-Roa et al. 2020). Experiments comparing populations that
476	evolved with weak versus strong sexual selection demonstrate that soft (sexual) selection can
477	increase persistence probability at high temperatures (Plesnar-Bielak et al. 2012; Parrett & Knell
478	2018). However, large temperature increases will drive populations toward extinction regardless
479	of buffering from soft selection (e.g., Parrett & Knell 2018).
480	Compensatory selection can also buffer against climate-driven extinction, which could
481	partly explain why evidence for population impacts of climate-induced phenological mismatch

483 Visser & Gienapp 2019). For example, cavity-nesting birds are typically regulated by

484 competition for nest sites and food (Newton 1998), and climate-driven hard selection acting on

has remained elusive despite being predicted by the match-mismatch hypothesis (Cushing 1969;

485 phenology expressed before density regulation can have a limited impact on population growth,

486 provided that climate change is not too extreme (Reed *et al.* 2013a, b). These examples have a

487 common theme: soft selection and compensatory selection may buffer against climate-driven

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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511 2006), range shift dynamics (Best *et al.* 2007; Cotto *et al.* 2017), and altered interspecific
512 interactions (Cahill *et al.* 2013).

514 *Small populations and the extinction vortex* 

15 Small, isolated populations face increased extinction risk due to interactions between 16 demographic effects and inbreeding depression (i.e., extinction vortex; Soulé & Mills 1998). 17 Note that inbreeding depression is the reduction in fitness of inbred *individuals* (Charlesworth & 18 Willis 2009; Box 1) and does not require that mean fitness decreases. For example, inbreeding 19 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 20 21 drive population declines through hard selection (e.g., Whitlock & Agrawal 2009; López-22 Cortegano et al. 2016), thus weakening the extinction vortex (Lumley et al. 2015). Soft selection 23 could help explain why some small, inbred populations manage to persist (e.g., Benazzo et al. 24 2017; Grossen et al. 2020).

25 Consideration of soft selection could potentially improve the predicted influences of inbreeding depression in population viability analyses (PVAs). The magnitude of inbreeding 26 27 depression can have strong influences on predicted extinction probability (O'Grady et al. 2006), 28 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 29 30 depression is due to soft selection (e.g., Schmitt & Ehrhardt 1990; or hard selection is 31 compensatory), these PVA frameworks will likely overestimate the effect of inbreeding depression on extinction risk. Accounting for the influences of soft selection and compensatory 32 33 selection in PVAs would be highly informative but challenging. In any case, soft selection

> 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 3/2 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

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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.

564 Oftentimes, outbreeding depression should be due to both hard and soft selection. This is 565 likely the case for Pacific salmon, where captive-bred (i.e., hatchery-produced) individuals and 566 their hybrids tend to have markedly reduced fitness in the wild due to rapid adaptation to the 567 captive rearing environment (Araki et al. 2008; Christie et al. 2014). Reduction in fitness is 568 likely cumulative over many traits, but it generally appears to result from reduced marine 569 survival (Jonsson et al. 2003) and reproductive success during spawning (Thériault et al. 2011). 570 The latter is due, at least in part, to soft selection. Experimental studies have demonstrated that, 571 compared to wild-born fish, hatchery-born females are competitively inferior at acquiring and 572 defending breeding sites, and males have a substantially lower ability to obtain mates (Fleming 573 & Gross 1993; Neff et al. 2015). However, competitive disadvantages of hatchery-born fish were 574 generally weaker at low densities (Fleming & Gross 1993), and hatchery-born fish readily breed 575 in the absence of wild-fish (Fleming & Gross 1992). Therefore, low abundance of wild-born fish 576 can increase the reproductive success of hatchery-born fish, thereby producing offspring with 577 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 578 579 declines, the exact opposite of the desired outcome of captive breeding programs.

2 3 4	580	
5 6	581	Harvest
7 8 9	582	Strategic harvest of reproductive excess is at the core of sustainable fisheries and wildlife
10 11	583	management (e.g., Boyce et al. 1999). While theoretically and empirically justified when viewed
12 13	584	solely in the light of population abundance, the harvest of population excesses can decrease the
14 15 16	585	efficacy of soft selection on traits mediating success in intraspecific competition and reduce the
17 18	586	buffering capacity afforded by compensatory selection (Young 2003). Furthermore, harvest often
19 20	587	acts as a selective force (Allendorf & Hard 2009), especially on traits that are subject to strong
21 22 23	588	sexual selection (e.g., body size, horn size). In a population harvested exactly at maximum
23 24 25	589	sustainable yield, and hence kept at population sizes below which there is strong intraspecific
26 27	590	competition for a limiting resource (e.g., breeding territories), the strength of soft selection will
28 29 20	591	likely be reduced and hence these traits might be more vulnerable to the effects of genetic drift.
30 31 32	592	At best, this might create situations where natural selection cannot act to shift populations toward
33 34	593	fitness peaks that are desired by humans (e.g. larger body sizes). At worst, harvest could act to
35 36 27	594	increase the phenotypic maladaptation that many populations of conservation concern already
37 38 39	595	face (Waples et al. 2008), which might prove increasingly worrisome as populations are subject
40 41	596	to novel or more acute selective pressures under global change. In either scenario, it is clear that
42 43	597	consideration of soft selection is fundamental in predicting the ecological and evolutionary
44 45 46	598	implications of harvest.
40 47 48	599	
49 50 51	600	7. Conclusion
52 53	601	Hard and soft selection are neglected topics of broad relevance for uniting ecology and evolution

602 (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

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.



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) haves are resistant to predation. The relative fitness of white haves 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.





677 Figure 3. A hypothetical example of soft selection followed by hard selection at a later life-stage on body 678 size in two populations inhabiting cold (A) versus warm (B) environments. At life stage-1, larger 679 individuals outcompete smaller individuals for a limiting resource and thus have higher survival (orange 680 lines; upper panels). The solid and dashed vertical lines represent the mean body size before and after soft 681 selection, respectively. The survivors of stage-1 are larger on average at the start of stage-2 due to soft 682 selection. The strength of hard selection during life stage-2 depends on how close the mean phenotype 683 (post-soft selection) is to an environmental optimum (blue curves; lower panels). During stage-2, the 684 optimal body size is larger in the colder environment and smaller in the warmer environment for 685 thermoregulatory reasons. In the cold environment (A), soft selection during stage-1 decreases the 686 strength of hard selection on stage-2, and mean stage-2 survival is high (hollow point). In contrast, in the 687 warm environment (B), soft selection increases the strength of subsequent hard selection, and mean stage-688 2 survival is low (hollow point). The light grey and dark grey distributions represent the trait distributions 689 prior to soft selection and hard selection, respectively.

## 691 Box 1: Glossary

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3 4	692	Soft selection – a type of natural selection in which absolute fitness of an individual depends on
5 6	693	its trait value relative to other conspecifics with which it interacts (i.e., the phenotypic
7 8 0	694	composition of the population).
9 10 11	695	Hard selection – a type of natural selection in which individual absolute fitness depends on their
12 13	696	absolute trait value and is independent of the phenotypic composition of the population.
14 15 16	697	Population growth – the growth of a population over a given (e.g., annual) time step $(N_{t+1}/N_t)$ .
10 17 18	698	Absolute fitness – an unscaled measure of life-time individual fitness. Population growth is
19 20	699	proportional to the mean absolute fitness of individuals in the population. In this paper, fitness
21 22 22	700	refers to absolute fitness unless stated otherwise.
23 24 25	701	Relative fitness – a scaled measure of individual fitness, where individual fitness is expressed as
26 27	702	a proportion of the mean fitness in the population (typical in quantitative genetics), or as a
28 29	703	deviation from the maximum fitness (common in population genetics)
30 31 32	704	Inbreeding depression – reduced fitness of offspring with related parents compared to those with
33 34	705	unrelated parents.
35 36 37	706	
38 39 40	707	Box 2: Competing definitions of soft selection
41 42 43	708	Christiansen (1975) applied Wallace's hard and soft selection to two competing models of spatial
44 45	709	heterogeneity in selection across discrete habitats (Levene 1953; Dempster 1955). Although
46 47 48	710	much of the current use of soft and hard selection is in reference to these models, Levene's
48 49 50	711	model is not soft selection under Wallace's initial intent. In Levene's model, individuals first
51 52	712	disperse into two or more habitats, and selection occurs within each habitat. Within-habitat
53 54	713	selection depends only on the match between phenotype and the habitat. Next, local density
55 56 57	714	regulation occurs within each habitat type, which results in a consistent contribution of each
58 59 60		32

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1 2		
2 3 4	715	habitat to the total population size (i.e., compensatory hard selection). Finally, individuals from
5 6	716	all habitats re-pool and mate panmictically. Density and negative frequency-dependent selection
7 8 9	717	emerge in Levene's models at the global level, which led to this model being called soft
9 10 11	718	selection. However, relative trait values of individuals never entered this model, which is the
12 13 14	719	critical component of Wallace's soft selection.
15 16 17	720	A variety of subsequent models (reviewed by Ravigné et al. 2004; also see De Lisle &
17 18 19	721	Svensson 2017) and some empirical studies (Gomulkiewicz & Kirkpatrick 1992; Gallet et al.
20 21	722	2018) have invoked soft selection sensu Christiansen in the context of evolution in spatially
22 23 24	723	heterogeneous environments or metapopulations (Whitlock 2002; Agrawal 2010; Ho & Agrawal
24 25 26	724	2012). Their common denominator is the idea that the 'softness' of selection is determined by the
27 28	725	extent to which individual fitness depends on phenotype relative to a local average (soft
29 30	726	selection) or a global average (hard selection). However, soft selection can also occur globally.
32 33	727	For example, global soft selection would occur if individuals from different demes pool in a
34 35	728	common habitat during a certain life stage and phenotype-dependent competition for ecological
36 37	729	vacancies occurs among them. Likewise, hard selection does not require a 'global optimum' and
38 39 40	730	habitat heterogeneity can create local optimum trait values against which organisms are judged
41 42	731	(i.e., hard selection). The key for Wallace's soft selection is that, at some time or place, selection
43 44	732	occurs based on relative trait values among individuals, and frequency and density dependence
45 46 47 48	733	can emerge at the scale and time that selection occurs.
49 50	734	Research on hard and soft selection sensu Levene has provided important insights into
51 52	735	evolution including the maintenance of genetic variation (e.g., Vale 2013; Gallet et al. 2018),
53 54 55 56 57	736	and strict adherence to any particular definition is unnecessary. We suggest that authors specify

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

## 

## 740 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. 

757 Deciphering between hard and soft selection in wild populations presents a greater758 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.

764 Studies should also aim to examine the demographic costs and evolutionary responses to 765 hard and soft selection. In both observational and experimental studies, the demographic costs of 766 hard and soft selection can be estimated by examining associations between mean absolute 767 fitness (or population growth) and the strength of selection. Additionally, evolutionary changes 768 (i.e., temporal trends in breeding values) in the focal trait, and in theory also fitness itself, can be 769 estimated when phenotypic information on traits and fitness are combined with direct or indirect 770 (e.g., pedigree-derived) genetic information (Kruuk et al. 2008; Hadfield et al. 2010; Hendry et 771 al. 2018; Fisher & McAdam 2019). Further, modeling approaches that combine selection, 772 inheritance, and demography allow exploration of population responses to environmental change 773 (e.g., Coulson et al. 2017), and will be critical for improving our understanding of the 774 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.

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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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2 3	1160	dependence at stage-2, hence the stronger the reduction in mean survival in stage-1, the higher the mean
4 5 6	1161	survival in stage-2 owing to release from competition (note that compensation is partial as depicted).
0 7 8	1162	Under SS (C), survival at stage-2 could be density dependent or independent, but either way the expected
9 10 11 12	1163	mean is the same across years as SS at stage-1 has not impacted the number of survivors. The right-hand
	1164	panels show the net outcomes in terms of life time survival (product of survival in stage-1 and stage-2).
13 14	1165	Circles represent population means.
14         15         16         17         18         19         20         21         22         23         24         25         26         27         28         30         31         32         33         34         35         36         37         38         39         40	1166	
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