**Abstract**

The deliberate release of captive-bred individuals, the accidental escape of domesticates, or the invasion of closely related conspecifics into wild populations can all lead to introgressive hybridisation, which poses a challenge for conservation and wildlife management. The rate of introgression and the magnitude of its demographic impacts vary widely across ecological contexts. Hoowever, the reasons for this variation remain poorly understood. One rarely considered phenomenon that likely plays a key role in mediating eco-evolutionary outcomes is soft selection, wherein relative rather than absolute trait values determine success in intraspecific competition for a limiting resource. Here we develop an eco-genetic model explicitly focussed on understanding the influence soft selection has on the eco-evolutionary dynamics of wild populations experiencing intrusion form foreign/domesticated individuals. The model is generally applicable to any taxon that experiences intrusion of locally maladapted genotypes, in addition to phenotype-dependent competition for a limiting resource (e.g., breeding sites, feeding territories). The effects of both one-off and continuous intrusion events depended strongly on the relative competitiveness of intruders versus locals. When intruders were competitively inferior, soft selection limited their reproductive success (ability to compete for limited spawning sites), which prevented strong introgression or population declines from occurring. In contrast, when intruders were competitively superior, this accelerated introgression and led to increased maladaptation of the admixed population. This had negative consequences for population size and population viability. The results were sensitive to the intrusion level, the magnitude of reproductive excess, trait heritability, and the extent to which intruders were maladapted relative to locals. Our findings draw attention to under-appreciated interactions between soft and hard selection, which may be critical to determining the impacts of captive breeding programmes and farm escapes on otherwise self-sustaining wild populations.

**Introduction**

Free-living populations of animals and plants are typically, though not always, reasonably well-adapted to their local environments (Hendry and Gonzalez 2008). This local adaptation can be disrupted, however, by various types of anthropogenic stressors, which induce maladaptation by affecting the abiotic or biotic selective landscape directly (e.g., climate change, species introductions), and/or by shifting trait distributions relative to the their optima on the adaptive landscape (Chevin, Lande, and Mace 2010). Human-mediated hybridisation, for example, can pull populations away from local trait optima (extrinsic outbreeding depression) or lead to a breakdown of adaptive linkage disequilibrium (intrinsic outbreeding depression - . The scope for such introgressive hybridisation has increased in the Anthropocene, as taxa shift their distributions in response to climate change, intentional introductions/translocations occur, or domesticated individuals escape., As a result,previously reproductively isolated populations come into contact (Wayne and Shaffer 2016; Brennan et al. 2015). A major challenge for conservation biology is, thus, to anticipate and respond appropriately to such changes.

The release of captive-reared individuals has been used as a conservation strategy to replenish depleted populations (Seddon, Armstrong, and Maloney 2007; Fraser 2008), or a management tool to augment natural production and increase the number of individuals available for commercial harvest or recreational angling/shooting (Claussen and Philipp 2022; Barbanera et al. 2010). However, such supplemental stocking often fails to provide the desired “demographic boost” to populations that are already naturally self-sustaining. For example, stocking of British rivers with hatchery-produced Atlantic salmon (*Salmo salar*) did not on the average improve, and in some cases apparently negatively affected, rod catches (Young 2013). Nevertheless, the practice remains widespread for many fishes, in particular Pacific salmonids (*Oncorhynchus* sp.) where industrial hatchery programmes exist for the purposes of enhancing fisheries or augmenting endangered populations (Naish et al. 2007). A range of genetic and demographic interactions between hatchery and wild populations can occur (Waples 1991; Fraser 2008), with potential demographic benefits of stocking being negated by genetic homogenisation and reduced fitness of hatchery fish and their hybrids in wild environments ( O’Sullivan et al. 2020) as a result of adaptation to the captive environment (Christie et al. 2012; Fraser et al. 2019; Milot et al. 2013). Whilst epigenetic mechanisms may play a role here (Rodriguez Barreto et al. 2019; Le Luyer et al. 2017; Venney et al. 2023), functional genetic changes are likely to underpin at least some of the phenotypic divergence between hatchery and wild fish, given the markedly different selective landscapes (Gross 1998) and the fact that many of the traits involved are heritable (Carlson and Seamons 2008).

Another major pressure in salmonids, in particular Atlantic salmon, is the escape of farmed fish into wild populations. Farmed salmon are genetically divergent from wild salmon, owing to intentional artificial selection for commercially important characteristics, relaxed/domestication selection in captivity, founder effects, and genetic drift (Gjøen and Bentsen 1997; Gjedrem, Gjøen, and Gjerde 1991). Escapes from marine fish farms or land-based hatchery units are frequent (Jensen et al. 2010; Naylor et al. 2005). Farmed fish and their hybrids can have substantially reduced fitness in the wild (McGinnity et al. 2003; Skaala et al. 2012; Reed et al. 2015), threatening the genetic integrity and viability of wild populations experiencing introgression (Glover et al. 2017) and altering their life histories (Bolstad et al. 2017; 2021).

Despite the widespread occurrence of anthropogenic hybridisation, whether it be from captive releases, farm escapes, or introductions of closely related conspecifics (e.g., Muhlfeld et al. 2009), considerable variation exists across ecological contexts in the extent of introgression and the magnitude of any associated demographic impacts(White et al. 2018; Lehnert et al. 2020). Density- and frequency- dependent processes are likely key here. In particular, the twin concepts of hard and soft selection (Wallace 1975; Bell et al. 2021) are highly relevant, yet are rarely considered explicitly. Hard selection refers to situations where the absolute fitness of an individual depends on its phenotype in absolute terms, e.g., the extent to which its trait value matches an environmentally determined optimum. Soft selection, in contrast, occurs when the absolute fitness of an individual depends on its phenotype relative to other conspecifics with which it interacts (Bell et al. 2021). For example, body size could be under hard selection if absolute body size determines the match between phenotype and environment (e.g., thermoregulatory ability), or soft selection if relative body size determines success in intraspecific competition. A given trait could be under pure hard selection, pure soft selection, or some combination of the two if both forms of selection affect fitness via multiple routes. Hard selection is independent of, whilst soft selection is dependent upon, the population density and phenotypic composition of that population (Bell et al. 2021). To understand soft selection, it is useful to conceive of the environment as containing a limited number of “ecological vacancies” (Reznick 2016). To survive or reproduce, an individual must acquire one of these vacancies, with relative rather than absolute trait values determining which individuals ‘fill’ them. So long as there are more individuals than ecological vacancies, all vacancies will be filled regardless of the phenotypic composition of the population, but soft selection will occur in a density and frequency dependent manner when individuals differ in their competitive abilities.

Here we present an eco-genetic model to explore the ecological and evolutionary consequences of one-off or continuous intrusion to a wild population by foreign/domesticated individuals, with a specific focus on the role of soft selection in mediating the outcomes. The model is generally applicable to any taxon that experiences sequential soft and hard selection as well as artificial or natural intrusion by genetically divergent immigrants. Individuals compete each generation for a limited number of “spawning slots” (ecological vacancies determining who gets to reproduce), with success determined by a single soft-selected quantitative trait, . Following reproduction, the offspring are subjected to an episode of hard selection wherein survival depends on the match between a second quantitative trait, , and an environmentally determined optimum (with locals assumed to be well-adapted and intruders maladapted). A key prediction we test is that the extent of introgression and its demographic consequences depend on the relative competitiveness of intruders versus locals, i.e., how divergent they are for . One possibility is that intruders are competitively inferior to locals, which could correspond to a captive-releases scenario, given that experimental studies in salmonids have shown hatchery-born females to be at a competitive disadvantage relative to wild-born females at acquiring and defending breeding sites, and hatchery-born males to be less successful in obtaining mates (Fleming and Gross 1993; Neff et al. 2015). Alternatively, intruders could be competitively superior to locals, which could correspond to a farm escapes scenario in which farmed individuals are for example larger, and hence more likely to acquire and defend a spawning slot or be chosen as a mate. Another, perhaps more likely, scenario is that farm-origin fry are competitively superior to local wild fry and displace them from feeding territories under high densities (McGinnity et al. 2003). Whilst our model assumes that soft selection occurs at the spawning stage, shifting soft selection to the fry stage (i.e., determines success in competition for limited fry territories, rather than limited spawning sites) would presumably have similar eco-evolutionary consequences, a point to which we return in the discussion. Whilst previous eco-genetic models have considered interactions between farmed and wild salmon (Hindar et al. 2006; Castellani et al. 2015; 2018; Sylvester et al. 2019) or between hatchery and wild salmon (Baskett and Waples 2013; Baskett, Burgess, and Waples 2013), ours is the first, to our knowledge, to explicitly distinguish between hard and soft selection and to explore their interactive effects on eco-evolutionary outcomes.

**Methods**

**Model description**

The model is inspired by a generalised anadromous salmonid life cycle but is not spatially explicit; freshwater and saltwater phases of the life history are rather implicit. The life history is also simplified greatly, to focus directly on the processes of interest (eco-evolutionary interactions between soft and hard selection), without loss of generality. The sequence of events is as follows: (1) the model is seeded with recruits at the pre-spawner phase; (2) phenotype-dependent competition (soft selection) for limited spawning slots occurs; (3) random mating among spawners and production of new offspring occurs; and (4) offspring survive from the juvenile to the recruit (pre-spawner) stage dependent on the match between phenotype and an environmental optimum (hard selection). Generations are discrete, and time is not explicit within generations.

*1. Recruit stage*

In all scenarios, the model is seeded with 500 local recruits () in generation 1, just prior to competition for spawning slots. The initial trait values for and are a function of the initial allele frequencies and . Thirty separate loci affect each trait (i.e., 60 functional loci in total), and the expected initial allele frequencies are assumed to be the same across all loci for each trait. In reality, a range of initial allele frequencies could occur (e.g., conforming to a beta distribution; Kardos and Luikart 2021), but this should not affect the qualitative outcomes of the model. The model includes an option to allow for some number of loci to overlap between both traits, i.e., loci with pleiotropic effects on and , but this functionality is not explored in the current paper. That is, the traits are assumed to be initially genetically uncorrelated, although some genetic association between them may emerge over time owing to a build-up of linkage disequilibrium. A third neutral trait is modelled via a single di-allelic locus, at which locals are assumed to be fixed for a “0” allele and intruders are fixed for a “1” allele. This facilitates the tracking of introgression of foreign/domesticated alleles into the mixed population over time.

Genotype matrices for each trait for local individuals are established in generation 1. These matrices are of dimension 500 rows by columns, where rows correspond to individuals and columns to alleles, with the first two columns storing the alleles for the first locus, the second two columns storing the alleles for the second locus, etc. Each cell (allele) of the genotype matrix for was initiated in generation 1 by drawing a number between 0 and 1 from a random uniform distribution, and setting that allele to 1 if the number was less than and 0 if the number was greater than . The same procedure was repeated for the genotype matrix for , such that the expected initial allele frequency at each locus equalled . The genotype matrix for the neutral trait for local individuals was of dimension 500 rows (individuals) by 2 columns (alleles). Local individuals all had a genotype of {0,0} at this neutral diagnostic locus.

In all simulations, the first 20 generations corresponded to a “burn-in” period during which no intrusion occurred. In the one-off intrusion scenarios, a given number of intruders () was introduced in generation 21 at the recruit stage, with no further intrusion occurring thereafter, whilst in the continuous intrusion scenarios, were introduced in each generation starting from generation 21. The genotype matrix for non-local intruders for was of dimension rows by 60columns (30 diploid loci). The cells of this matrix (alleles) were populated by drawing a number between 0 and 1 from a random uniform distribution, and setting that allele to 1 if the number was less than and 0 if the number was greater than . The same process was repeated for the genotype matrix for , such that the expected initial allele frequency for intruders at each locus was . Intruders all had a genotype of {1,1} at the neutral diagnostic locus. Immediately after intrusion occurred, the genotype matrices for each trait for locals and intruders were merged by row, such that the new matrices were of dimensions rows by columns for and , and dimension rows by two columns for the neutral diagnostic locus, where .

The genotypic value of each individual for each trait ( and ) was then computed by summing the alleles across all 30 loci, assuming that “1” alleles at each locus increase the trait value by 1 unit (i.e., the additive allelic effect at all loci) and “0” alleles have no effect on the trait. Thus, genotypic values ranged from a minimum of 0, for individuals with a {0,0} genotype at all loci, to 60, for individuals with a {1,1} genotype at all loci. The expected mean genotypic value is then equal to , where is the number of loci affecting the trait (here always assumed to be 30), is the relevant allele frequency, and is the additive allelic effect. The expected genotypic variance is given by . For example, with , , and , the expected mean is 30 and the expected variance is 15. The genotypic means and variances for each trait thus differed between locals and intruders to the extent that differed between them. Non-additive genetic effects were ignored for simplicity, so the genotypic variances corresponded to additive genetic variances ().

The initial heritability, ), assumed to be the same for and , determined the magnitude of the environmental variance ) for each trait. was assumed to be constant across generations and was computed as , where and were the initial phenotypic and additive genetic variances, respectively. These parameters were defined in generation 1 for local individuals, and in the generation of intrusion for intruders. Note that the actual heritability in any given generation can deviate from ), because although was assumed to be constant, can change under the influence of selection, drift, and introgression. Mutation was assumed to be absent, which is reasonable on the evolutionary timescales of 100 to 150 generations under consideration.

*2. Soft selection filter*

Parental phenotypes are then formed for , by drawing an environmental deviation for each individual from a normal distribution of mean 0 and variance equal to ), where locals and intruders had potentially different values for the latter parameter, depending on the scenario. Note that in the one-off intrusion scenarios, all fish were assumed to be locals from generation 22 onwards, i.e., intrusion of foreign/domesticated individuals occurred in generation 21 and then any hybrid offspring in future generations were, by definition, locally born. Environmental deviations were added to the genotypic values of individuals, to give individual phenotypic values for .

The total number of available spawning slots was fixed at in all simulations. In situations where , all recruits get a spawning slot, but in situations where (i.e., when there is “reproductive excess”), only individuals become spawners, with the surplus assumed to die. To determine which fish get to spawn, individuals are ranked from top to bottom based on and only the top fraction of individuals are assigned a spawning slot, which imposes truncational soft selection. For example, if and , only 5 out of every 6 recruits gets to spawn, with the top 83% () of individuals based on ranked getting a spawning slot, and the lower 17% failing to spawn. Thus, the higher the reproductive excess, i.e., the more recruits there are relative to spawning slots, the stronger the truncational soft selection. No soft selection occurs when there are fewer recruits than spawning slots.

*3. Mating and reproduction*

Individuals assigned spawning sites then undergo random mating. Separate sexes are not considered, so random hermaphroditic mating based on a classic Wright-Fisher model is assumed. Each individual has an equal chance of becoming a parent, and each individual can produce more than one offspring (or no offspring), which guarantees an approximately Poisson distribution of offspring number per parent (Waples 2022). The total number of new offspring equals , where is the number of spawners and the fecundity (number of offspring per parent). In reality, salmonid fishes can produce hundreds to thousands of eggs, depending on female size, but here for efficiency . This is effectively equivalent to assuming random mortality of zygotes up to the smolt stage, such that each parent produces an average of two smolts, i.e., all freshwater mortality is subsumed into .

During reproduction, new empty genotype matrices for and , each of dimension rows by 60 columns, are set up to store the offspring genotypes for each quantitative trait, where is the total number of offspring produced. Similarly, an empty genotype matrix for the neutral trait of dimension rows by two columns was set up. For each offspring, two parents are drawn at random from the pool of spawners by sampling with replacement. For each locus for each trait, the first offspring allele is drawn at random from the two alleles carried by parent 1 at that locus, and the second offspring allele is drawn at random from the two alleles carried by parent 2. This thus simulates random segregation and random assortment of alleles into gametes, on the assumption that loci are unlinked (on separate chromosomes, or far enough apart on the same chromosome that no recombination occurs), followed by random fertilisation. This process is repeated across all loci until the new offspring genotype matrices have been populated with 1s and 0s.

*4. Hard selection filter*

In this next step, offspring phenotypes are first formed for by drawing an environmental deviation for each individual from a normal distribution of mean 0 and variance ). Because all new offspring are by definition locally-born, regardless of the provenance of their parents, the environmental variance was computed as , where refers to the initial additive genetic variance of locals in generation 1. Environmental deviations are then added to the genotypic values, to give individual phenotypic values for .

Hard selection on is implicitly assumed to occur during the marine phase of the life cycle (although space and life stages are not explicit in the model), notionally corresponding to a scenario where the match between some phenotype (e.g., basal metabolic rate, gape size, growth rate) and marine environment determines marine survival. The expected survival of each individual is computed as a function of its phenotype for based on a Gaussian fitness function:

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Here, is the maximum survival for individuals whose phenotype coincides with the optimum , and corresponds to the “width” of the fitness function in units of phenotypic standard deviations ). In all simulations, is fixed at a value of , which corresponds to moderate to strong stabilising selection (Estes and Arnold 2007). The subscript here indicates that can vary across generations within model runs, in line with changes in the genetic variance in response to drift, selection and introgression. The alternative was to fix at a given value across all generations independently of , but that would then mean that the effective strength of hard selection would vary as changes over time. A constant strength of selection (for a given deviation of from the optimum) was deemed a more parsimonious assumption, but the basic results should be qualitatively robust to this.

Realised marine survival is then determined by drawing a number between 0 and 1 from a random uniform distribution, with the individual surviving if exceeded this number and dying otherwise. This imposes hard directional selection on whenever the mean trait value deviates either side of the optimum . The survivors of hard selection then become the new locally born recruits for the next generation, and the model cycles back up to step 1 above.

Each generation, a series of output variables calculated at the recruit stage is stored in a results matrix. These include the phenotypic mean and variance for each of and , the additive genetic variance for each, the frequency of the foreign/domesticated “1” allele at the neutral locus, the number of recruits , and the number of spawners . The realised recruits per spawner each generation is then computed as . For all scenarios, 1000 replicate simulations are run and the mean and 95% confidence interval of each output variable of interest is calculated across replicates.

The model was coded in R version 4.3.0 (R citation) using the RStudio programming environment (RStudio citation). All model code is available via a GitHub repository (insert GitHub url here eventually).

**Baseline scenarios – no intrusion**

To illustrate the basic functionality and behaviour of the model, a series of baseline scenarios was first explored in which no intrusion of foreign/domesticated fish occurred and the evolutionary and population dynamics were tracked across 100 generations. ) for both traits was 0.25, such that each had the potential to respond to selection, and the initial allele frequency at each locus for each trait was 0.5 (i.e., ). The initial mean values of both traits were rescaled to reference values of 0, corresponding to mean-centring in generation 1. In the first set of baseline simulations, the closed wild population was assumed to be well-adapted with respect to the hard-selected trait, i.e., . In the second set of baseline simulations, initial maladaptation was assumed (), such that the hard-selected trait experienced positive directional selection. The optimum did not vary over time in each case, for simplicity.

*Baseline simulations set 1:*

To illustrate how the strength of soft selection depends on the magnitude of “reproductive excess”, the ratio of number of recruits to number of spawning slots is varied between ~1 and ~1.4, achieved by adjusting the parameter. Three values of are explored: 0.53, 0.63 and 0.73, corresponding to an expected of approximately 1.0, 1.2 and 1.4, respectively. When (), every recruit gains a spawning slot, so there is little to no reproductive excess. No evolution of is then expected. When (; moderate reproductive excess), there are more fish than spawning slots, hence phenotype-dependent competition will occur and should evolve upwards. When (; high reproductive excess), the competition intensifies further, and the rate of evolution of should be correspondingly faster.

*Baseline simulations set 2:*

In the second set of baseline simulations, the closed wild population is assumed to be initially poorly adapted to the external environment, by setting and keeping initial at its reference value of 0. Such a situation could occur if the population experienced a sudden step change in the selective environment, or if it were introduced to a new environment to which it is not pre-adapted (Gomulkiewicz and Holt 1995; Kardos and Luikart 2021). is fixed at 0.63, such that expected would be greater than 1 in the absence of maladaptation () but less than 1 in the presence of maladaptation (). Thus, the population will initially decline in this scenario but gradually recover towards as evolves towards the new optimum, provided extinction does not occur in the interim, i.e., evolutionary rescue. During the period when , no soft selection should occur as everyone gets a spawning slot, but as recovers to , soft selection will kick back in.

**One-off intrusion scenarios**

*One-off intrusion simulations set 1:*

Here, we assume that the wild population remains closed to intrusion for the first 20 generations, with =0.58 and =0.25. Thus, there is some reproductive excess absent any intrusion, with ~550 recruits competing for 500 spawning slots each generation and . At generation 21, a one-off intrusion event occurs wherein 500 foreign/domesticated fish intrude just prior to spawning. The total number of fish competing for spawning slots thus becomes ~1050, and soft selection intensifies accordingly. From generation 21 onwards, all fish are “locals” in the sense of being locally born, but many will be of mixed ancestry. The intruders are assumed to be maladapted to the local environmental conditions, such that . This was achieved by setting and , such that was 30 units less than , corresponding to a difference of approximately 4.5 phenotypic standard deviations.

Three scenarios are explored: (1) intruders are competitively inferior to locals (; (2) intruders are competitively equal to locals (; and (3) intruders are competitively superior to locals (. This was achieved by varying for intruders relative to locals: in scenario 1, and ; in scenario 2, ; and in scenario 3, and . With this parameterisation, was 12 units lower than at the time of intrusion in scenario 1 (intruders competitively inferior), and 12 units higher in scenario 3 (intruders competitively superior). This corresponded to an absolute difference in trait means of ~1.6 phenotypic standard deviations.

*One-off intrusion simulations set 2:*

The above simulations are then repeated under a broader range of parameter values, to explore the sensitivity of the results to the level of intrusion and the level of reproductive excess. Three levels of intrusion are explored: low (250 intruders introduced at generation 21); moderate (500 intruders); and high (750 intruders), corresponding to , , and , respectively. Three levels of reproductive excess are also explored: low (); moderate () and high (), corresponding to expected absent any intrusion of ~1.0, ~1.1 and ~1.2, respectively. As before, three levels of relative competitiveness of intruders versus locals are explored (intruders competitively inferior, equal, or superior to locals) using the same parameterisation as the *one-off intrusion simulations set 1*. This gives a total of 27 scenarios, i.e., combinations of intrusion level, reproductive excess level, and relative competitiveness.

To explore the effects of the level of maladaptation of intruders relative to locals, three additional scenarios are then run in which the difference between and is assumed to be (1) small (; ); (2) moderate (; ); and (3) large (; ). In all three cases, a moderate level of one-off intrusion (500 intruders introduced at generation 21) and a moderate level of reproductive excess () is assumed.

**Continuous intrusion scenarios**

*Continuous intrusion simulations set 1:*

In the continuous intrusion scenarios, a constant number of foreign/domesticated fish are assumed to intrude each generation (from generation 21 onwards) just prior to spawning. In the first set of simulations, the per-generation intrusion rate is fixed at 5% of , where =500. Thus 25 foreign/domesticated fish intrude each generation. As with the one-off intrusion simulations, intruders are assumed to be maladapted with respect to , by setting and . Thus, for the intruders is 30 units (~4.5 phenotypic standard deviations) lower than for the locals. As before, the same three levels of relative competitiveness are explored, i.e., intruders competitively inferior, equal, or superior to locals. The initial heritability of both traits is set to 0.25 in all cases. The simulations are run for 150 generations, with intrusion starting at generation 21.

*Continuous intrusion simulations set 2:*

In this second set of continuous intrusion simulations, all parameters are the same as in set 1, except the per-generation intrusion rate is increased to 20% of , i.e., 100 foreign/domesticated fish intrude each generation, again starting at generation 21.

*Continuous intrusion simulations set 3:*

In this final set of simulations, a broader range of parameter values is explored. Specifically, the sensitivity of the continuous intrusion results to trait heritability and the level of reproductive excess is tested. In these simulations, the per-generation intrusion rate is set to 10% of , i.e., 50 foreign/domesticated fish intruded each generation, starting at generation 21. Two levels of trait heritability (same value applies to both and ) are explored: = 0.25 and = 0.50. Three levels of reproductive excess are also explored: low (); moderate () and high (), corresponding to an expected absent any intrusion of circa 1.0, 1.1 and 1.2, respectively. As before, the same three levels of relative competitiveness of intruders versus locals are explored (intruders competitively inferior, equal, or superior to locals). This gives a total of 18 scenarios, i.e., combinations of trait heritability, reproductive excess level, and relative competitiveness.

**Results**

**Baseline scenarios**

*Baseline simulations set 1:*

The results of the first set of baseline simulationsshowed that, as expected, the rate of evolution of depended on the extent of reproductive excess (Fig.1). With low reproductive excess, little to no directional evolution of occurred (Fig.1A, red curves) because all, or nearly all, recruits gained a spawning slot each generation, with fluctuating around 1. Because soft selection only occurs when there are more recruits than spawning slots, this creates an asymmetric situation where a small amount of soft selection will occur whenever is by chance >1 (and hence , but not when it is by chance <1 (). This meant that a small amount of evolution of accrued across multiple generations in the low reproductive excess case, which explains why the red curves in Fig.1A crept upwards slightly over time. With moderate reproductive excess (green curves in Fig.1A), the rate of evolution of was faster, and with high reproductive excess (blue curves in Fig.1A) it was faster again. In all three scenarios, no evolution of occurred (Fig.1B) because the population was well adapted ( coincided with ) so no directional selection occurred.

With moderate or high reproductive excess, the rate of evolution of gradually plateaued, as selection limits were reached owing to the erosion of genetic variation. With only 30 loci contributing to each trait, allelic variation will be lost even under pure drift, as loci go to fixation. Thus, additive genetic variation went down slowly over time in the scenario with low reproductive excess (weak to no directional selection on , i.e., largely drift only) and more rapidly in the moderate and high reproductive excess scenarios (selection + drift) (Fig.1C). experienced no directional selection, so the rate of loss of genetic variance (Fig.1D) in all three scenarios was similar to that for in the low reproductive excess scenario. If some mutation had been included in the model, this would have countered the loss of additive genetic variation.

*Baseline simulations set 2:*

Here, the wild population was again closed to intrusion but now the optimum was 20 units higher than  in generation 1. As a result of this maladaptation, evolved upwards towards (Fig.2A). The rate of evolution of slowed down as the generations progressed for two reasons: (1) selection weakened as the new optimum was approached (because the Gaussian fitness landscape is flatter near the optimum), and (2) genetic variance was progressively lost owing to both directional selection and drift (Fig.S1).

Up until generation 25 or so, owing to the maladaptation (Fig.2B), so no soft selection occurred and correspondingly no directional evolution of was observed (Fig.2C). During this early period of maladaptation, the population size (number of spawners) declined but then recovered in a classic U-shape pattern under evolutionary rescue (Fig.2D) as positive population growth was restored. Twenty percent of replicate populations went extinct in the interim. From about generation 25 onwards, had recovered to above 1 (Fig.1C), so soft selection kicked in and gradually evolved upwards (Fig.2D).

**One-off intrusion scenarios**

*One-off intrusion simulations set 1:*

Prior to intrusion, evolved gradually upwards from generation 1 to 20 (Fig.3A), as there were approximately 1.1 recruits for every spawner (i.e., some reproductive excess). remained static during this pre-intrusion phase (Fig.3B), as the optimum was constant. The subsequent effects of one-off intrusion depended strongly on the relative competitiveness of intruders and locals. When intruders were competitively equal to locals (green curves in Fig.3), consistent soft selection occurred and so evolved gradually upwards (Fig.3A, green curve). When intruders were competitively inferior to locals, exhibited a sudden drop in generation 21 when intrusion occurred (Fig.3A, red curve). However, rapidly jumped back up in the ensuing few generations, because any mixed ancestry individuals with lower would have experienced a strong selective disadvantage (reduced likelihood of attaining a spawning site). continued to evolve gradually upwards thereafter, as ongoing competition and soft selection played out.

In contrast, when intruders were competitively superior, rapidly jumped up in generation 21 as a direct result of the intrusion (Fig.3A, blue curve). For the next 25 generations or so, remained relatively static, because little soft selection occurred. The latter reflected the fact that was pulled strongly off its optimum by the intrusion (Fig.3B, blue curve), such that exhibited a much lower dip below 1 compared to the other two scenarios (Fig.3C, blue curve). The greater maladaptation in this scenario in turn stemmed from the fact that the highly competitive intruders (and their hybrid offspring in the generations immediately post-intrusion) had high spawning success, driving higher introgression of foreign/domesticated alleles into the population (Fig.S2). The net result was that the number of spawners in this scenario dipped to a much lower nadir compared to the scenarios where intruders were competitively equal or inferior to locals (Fig.3D). Evolutionary rescue nonetheless occurred in all three scenarios.

*One-off intrusion simulations set 2:*

The basic patterns found in the first set of one-off intrusion simulations were emulated in the second set, with the effects scaling with the degree of intrusion and the degree of reproductive excess. The higher the intrusion rate, the greater the negative impact of one-off intrusion on population size (Fig.4, compare bottom panels to top panels). The number of spawners was reduced to a lower level when the intrusion rate was higher, because was dragged more from the optimum (Fig.S3). In contrast, the greater the reproductive excess, the weaker the negative impact of one-off intrusion on population size (Fig.4, compare right panels to left panels), because remained above for longer (Fig.S4). The level of reproductive excess did not affect the level of maladaptation (Fig.S3), but rather the effects of a given level of maladaptation on the number of spawners. was negatively affected by intrusion in all cases, but this translated into strong impacts on number of spawners only in those scenarios where was reduced below 1 (Fig.S4). For a given level of intrusion and reproductive excess, intrusion had a greater negative impact on population size when intruders were competitively superior. The probability of extinction (fraction of replicate populations that went extinct) was higher when the level of intrusion was higher, when the level of reproductive excess was lower, and when intruders were competitively superior to locals (Fig.S5).

The patterns were the same (results not shown) when was instead assumed to be greater, rather than less than, , because the adaptive landscape was symmetrical about the optimum. The patterns were also more pronounced when a bigger absolute difference between and was assumed (i.e., greater maladaptation of intruders), and less pronounced when a smaller absolute difference was assumed (i.e., weaker maladaptation of intruders; Fig.S6).

**Continuous intrusion scenarios**

*Continuous intrusion simulations set 1:*

The results of the continuous intrusion scenarios depended strongly on the relative competitiveness of intruders versus locals. In this first set of simulations, 25 foreign/domesticated fish intruded each generation from generation 21 onwards. This exerted a downwards pull on , as the intruders were maladapted to the local environmental conditions. This was in turn counteracted by an upwards pull on , as evolution tried to bring it back towards the fixed optimum (). When the intruders were competitively equal to the locals, gradually evolved downwards towards a value of -30 (Fig.5A, green curve), because continual intrusion resulted in the effective “genetic extinction” of the wild population. As the degree of maladaptation went up, went down accordingly, bottoming out at around 0.5 (Fig.5B, green curve). went up initially, during the pre-intrusion period (generations 1 to 20), as soft selection was occurring and favouring individuals with higher values. Once dipped below 1 by around generation 25, however, soft selection no longer occurred and hence was dragged downwards (Fig.5C, green curve) by the continual influx of foreign/domesticated fish each generation, whose average value for was assumed (in the “intruders competitively equal” case) to be equal to that of the locals in generation 1. Once bottomed out at the reference value of 0, it stayed there as soft selection was no longer occurring given that . The frequency of the foreign/domesticated allele at the neutral locus increased steadily in this scenario and reached 1.0 by around generation 100 (Fig.5D, green curve), indicating effective genetic replacement of the original wild population by the intruders. The number of recruits declined to <50 by circa generation 100 (Fig.5E), with the number of spawners bottoming out at around 50-70 (Fig.5F).

When intruders were competitively superior, the results were similar to the “intruders competitively equal” scenario, except that maladaptation increased faster (Fig.5A, blue curve) and hence declined faster (Fig.5B, blue curve). equilibrated at around +10 (Fig.5C, blue curve), reflecting the fact that “gene swamping” again occurred such that the original wild population was effectively replaced genetically by foreign/domesticated alleles (Fig.5D, blue curve). Only around 20-25 recruits were produced each generation (Fig.5E, blue curve), and the number of spawners per generation bottomed out at around 30-40 (Fig.5F, blue curve).

The results were very different, however, when intruders were competitively inferior to locals. Soft selection each generation filtered out most of the intruders, such that little maladaptation occurred (Fig.5A, red curve) and hence remained steady above 1 (Fig.5B, red curve). thus continued to evolve upwards (Fig.5C, red curve). Very little introgression of foreign/domesticated alleles occurred (Fig.5D, red curve), and the number of recruits remained steady at around 550 (Fig.5E, red curve) and the number of spawners remained at (Fig.5F, red curve).

*Continuous intrusion simulations set 2:*

The results of the second set of continuous intrusion simulations (in which 100 foreign/domesticated fish intruded each generation) were similar to the first set (in which only 25 intruded), except declined faster towards its equilibrium value (Fig.6A). In the “intruders competitively equal” and “intruders competitively superior” scenarios, complete genetic replacement of locals by the foreign/domesticated type again occurred (Fig.6D, green and blue curves), and the number of spawners equilibrated at just under 200 (Fig.6F, green and blue curves). With the higher intrusion rate, some introgression of foreign/domesticated alleles occurred even in the “intruders competitively inferior” scenario (Fig.6D, red curve), representing a “hybrid swarm” type situation. Some maladaptation occurred (Fig.6A, red curve), albeit less than in the “intruders competitively equal” and “intruders competitively superior” scenarios (Fig.6A, green and blue curves respectively), and equilibrated at a value below 1 (Fig.6B, red curve). The number of spawners equilibrated at around 350 (Fig.6F, red curve), which was considerably higher than the “intruders competitively equal” and “intruders competitively superior” scenarios (Fig.6F, green and blue curves respectively).

*Continuous intrusion simulations set 3:*

The results of the continuous intrusion scenarios were sensitive to both the trait heritability and the degree of reproductive excess. In the low reproductive excess scenario (Fig.S7), no soft selection occurred (as was always <1), so trait heritability had no effect on the dynamics of . The continual intrusion pulled down to a minimum of -30 (the expected mean for intruders) and genetic replacement (i.e., complete introgression of foreign/domesticated alleles) occurred. Population size was reduced to 100 or fewer spawners by generation 50 or so. Recruitment at this point was close to zero, so new spawners each generation effectively consisted of fresh waves of intruding immigrants. Trait heritability had little effect on these outcomes.

The picture changed when there was moderate reproductive excess (Fig.S8). When trait heritability was 0.25, the results were similar to the low reproductive excess scenario, but only in the “intruders competitively equal” and “intruders competitively superior” scenarios (green and blue curves in Fig.S8, respectively): strong maladaptation occurred, and population size was reduced by generation 50 or so to 100 or fewer spawners. The genetic composition of the population (at both the neutral locus and the functional loci affecting and ) also shifted towards that of intruders, i.e., genetic replacement. In contrast, under the “intruders competitively inferior” scenario (red curves in Fig.S8), soft selection effectively filtered out most intruders each generation so little maladaptation or introgression of foreign/domesticated alleles occurred. As a result, population size remained stable at . When heritability was increased to 0.5, the outcomes were the same as the heritability=0.25 case for the “intruders competitively superior” and “intruders competitively inferior” scenarios (blue and red curves in Fig.S8). The outcomes were different, however, for the “intruders competitively equal” scenario (green curves in Fig.S8). In that case, continued intrusion resulted in a small amount of maladaptation, but not enough to make an appreciable dent in , so the number of spawners remained close to (albeit with more variability compared to the “intruders competitively inferior” scenario). A small amount of introgression occurred in the “intruders competitively equal” scenario at the neutral locus.

The picture changed again when there was high reproductive excess (Fig.S9). When trait heritability was 0.25, the results were similar to the moderate reproductive excess scenario, but only in the “intruders competitively superior” scenario (blue curves in Fig.S9): strong maladaptation occurred, and population size was reduced by about generation 50 to 100 or fewer spawners. In contrast, under the “intruders competitively equal” and “intruders competitively inferior” scenarios (red and green curves in Fig.S9), soft selection filtered out many intruders each generation (especially in the “intruders competitively inferior” case), so little maladaptation or introgression of foreign/domesticated alleles occurred in the “intruders competitively inferior” case and a small amount of introgression occurred in the “intruders competitively equal” case. The number of spawners remained stable at in both cases. When heritability was increased to 0.5, little to no maladaptation occurred in the “intruders competitively inferior” and “intruders competitively equal” scenarios (red and green curves in Fig.S9), while a small amount of maladaptation occurred in the “intruders competitively superior” scenario (blue curves in Fig.S9). Little to no introgression occurred in the former two scenarios, whilst a small amount of introgression occurred in the “intruders competitively superior” scenario. The number of spawners remained stable at in all three cases.

**Discussion** (a stream of consciousness for now!!)

Section 1: a recap of the key results, with some big statements on their general importance.

Section 2: brief discussion of the baseline scenario simulations, hammering home how the strength of soft selection scales with the magnitude of reproductive excess (the more recruits than spawning slots, the stronger the selection). Discuss interactions between hard and soft selection – e.g., when there is strong maladaptation (strong hard selection), recruits per spawner falls below 1, which shuts off any soft-selection. Our model assumed genetic independence between and , but if they were genetically correlated, this would lead to further interactions between them mediated by indirect selection. For example, if soft selection favours higher values and the traits are positively genetically correlated, this would drag off its optimum as a correlated response, thereby leading to maladaptation and an associated demographic penalty. If the latter is strong enough, this in turn would feed back to reduce or shut off soft selection. Our model contains the option for a certain fraction of loci to be shared between and , so these interactions can be explored in future work.

Section 3: a discussion of the one-off intrusion scenario results, framed in the context of captive releases and farm escapes in salmonids (as well as a more general framing). Hammer home the importance of the relative competitiveness of intruders versus locals. Discuss evidence for hatchery fish being less competitive than wild fish, and for farm escapes being more competitive than wild fish. In the latter case, the more realistic scenario is probably where farm genotypes are more competitive at the fry stage in terms of feeding territory acquisition (McGinnity papers, Norwegian studies, etc.). If we had shifted soft selection in our model to the fry stage, rather than the spawning stage, the same qualitative outcomes would likely have been observed (might even try running these simulations, as will be easy to tweak the model!!). Higher competitiveness of farmed genotypes at the fry stage would accelerate the introgression of domesticated genes, and thereby increase maladaptation with respect to and impose a stronger demographic penalty.

Section 4: discuss continuous intrusion results, which largely showed similar patterns to the one-off intrusion results, although with some interesting differences. E.g., genetic replacement can occur under continual intrusion, or hybrid swarms may emerge, even though the population size may equilibrate a lower size (compared to no intrusion). Ecological extinction has not occurred, but genetic extinction has effectively resulted. Discuss how likely it is in salmonids for intrusion to involve one-off events (e.g., a load of fish escape from sea-net pens in a big storm, a one-off stocking event of hatchery fish occurs), versus low-level continual intrusion (e.g. continual leakage from a farm; continual stocking each generation).

Section 5: compare our model and findings to previous eco-genetic models with salmonids, i.e., Hindar et al, Castellani et al, Sylvester et al, Baskett and Waples. Some of these models allowed for density-dependent competition, I think, but none mention soft selection (need to check this!!). In the case of Castellani, they assumed I think that a single set of loci affect a bunch of different fitness-related traits (so genetic non-independence across traits), including I think competitive ability of fry?? Did this result in similar outcomes to our model? Baskett and Waples also might have included density/frequency dependence, but again need to look into how they modelled things exactly and what they found.

Section 6: limitations and possible future extensions of our model.

Section 7: Management/conservation implications.

Section 8: Conclusions (one paragraph wrap-up).

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