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Competitive interactions affect introgression and population viability amidst maladaptive hybridization

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Abstract

The deliberate release of captive-bred individuals, the accidental escape of domesticated strains, or the invasion of closely related conspecifics into wild populations can all lead to introgressive hybridization, which poses a challenge for conservation and wildlife management. Rates of introgression and the magnitude of associated demographic impacts vary widely across ecological contexts. However, the reasons for this variation remain poorly understood. One rarely considered phenomenon in this context is soft selection, wherein relative trait values determine success in intraspecific competition for a limiting resource. Here we develop an eco-genetic model explicitly focussed on understanding the influence of such competitive interactions on the eco-evolutionary dynamics of wild populations experiencing an influx of foreign/domesticated individuals. The model is applicable to any taxon that experiences natural or human-mediated inputs of locally maladapted genotypes ('intrusion'), in addition to phenotype-dependent competition for a limiting resource (e.g. breeding sites, feeding territories). The effects of both acute and chronic intrusion depended strongly on the relative competitiveness of intruders versus locals. When intruders were competitively inferior, density-dependent regulation 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 amplified 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 phenotype-dependent competitive interactions and maladaptive hybridization, which may be critical to determining the impact captive breeding programmes and domesticated escapees can have on otherwise self-sustaining wild populations.

KEYWORDS
adaptation, competitive interactions, demo-genetic, density dependence, fisheries management, gene flow, invasion

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Thomas Eric Reed and Ronan James O'Sullivan contributed equally to this work.

1 | INTRODUCTION

Free-living populations of animals and plants are typically, though not always, reasonably well-adapted to their local environments (Hendry & Gonzalez, 2008). Local adaptation can be disrupted, however, by various anthropogenic stressors such as climate change, pollution, habitat change and species introductions (Chevin et al., 2010). Human-mediated hybridization and repeated backcrossing (introgression), for example, can pull populations away from local adaptive peaks (extrinsic outbreeding depression) or lead to a breakdown of adaptive epistatic interactions (intrinsic outbreeding depression—(Grabenstein & Taylor, 2018)). The scope for introgressive hybridization has increased in the Anthropocene, as taxa shift their distributions in response to climate change, intentional introductions/translocations occur and domesticated individuals escape into wild populations (Brennan et al., 2015; Wayne & Shaffer, 2016). A major challenge for conservation biology is, thus, to anticipate and respond appropriately to such changes (Kinnison & Hairston, 2007).

The release of captive-reared individuals has long been used as a conservation strategy to replenish beleaguered populations (Fraser, 2008; Seddon et al., 2007), as well as a wildlife management tool to increase the number of individuals available for harvest (Barbanera et al., 2010; Claussen & Philipp, 2022). However, supplemental stocking often fails to provide the desired 'demographic boost' to populations that are already naturally self-sustaining and, in some scenarios, can lead to genetic homogenization (Karlsson et al., 2016) and reduced fitness of hatchery individuals and their hybrids in wild environments (Araki et al., 2008; O'Sullivan et al., 2020). For example, stocking of British rivers with hatchery-produced Atlantic salmon (*Salmo salar*) did not, on average, improve rod catches and, in some cases, apparently negatively affected them (Young, 2013). Nevertheless, the practice remains widespread among salmonines (salmon, trout, and charr), in particular, Pacific salmonids (*Oncorhynchus* spp.), where industrial-scale hatchery programmes exist for the purposes of enhancing fisheries or augmenting endangered populations (Naish et al., 2007). The reduced fitness of captive-reared individuals in the wild is likely due to various genetic, epigenetic and demographic mechanisms (Fraser, 2008; Le Luyer et al., 2017; Rodriguez Barreto et al., 2019; Waples, 1991) that arise as a result of adaptation/acclimation to the captive environment (Araki et al., 2007; Christie et al., 2012; Fraser et al., 2019; Milot et al., 2013).

Another major pressure in salmonines, in particular Atlantic salmon, is the escape of farmed fish. Farmed salmon are genetically divergent from wild salmon in a range of traits (Bolstad et al., 2017, 2021), owing to intentional artificial selection for commercially important characteristics, relaxed/domestication selection in captivity, founder effects and genetic drift (Gjedrem et al., 1991; Gjøen & Bentsen, 1997). 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; Reed et al., 2015; Skaala et al., 2012), 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 hybridization, whether it be from captive releases, farm escapes or introductions of 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 (Lehnert et al., 2020; White et al., 2018). Competitive interactions are likely key here (Glover et al., 2013; Heino et al., 2015). With purely ecological density dependence, survival or reproductive rates go down as population density increases, but all individuals are assumed to be equally affected. In reality, some individuals might be better able to compete for limiting resources than others, such that fitness depends on an interaction between phenotype and population density, that is, density-dependent selection (Travis et al., 2023). Competition for limited resources such as food, territories, or mates can also generate frequency-dependent selection, which can interact with frequency-independent selection (typically driven by abiotic factors) in complex ways to influence both evolutionary and demographic outcomes (Bell et al., 2021; Christie & McNickle, 2023; Svensson & Connallon, 2019).

The term hard selection has been used to describe situations where the fitness of an individual depends only on its phenotype with respect to some environmentally determined optimum and thus is independent of population density and the relative frequency of other phenotypes (Bell et al., 2021; Wallace, 1975). This is contrasted against soft selection, wherein the fitness of an individual depends on its phenotype relative to other conspecifics with which it interacts, and thus on both population density and composition (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). In order to survive or reproduce, an individual must acquire one of these vacancies, with relative rather than absolute trait values determining which individuals 'fill' them. A given trait can be under pure hard selection, pure soft selection, or some combination of the two. To illustrate, consider that body size could be under hard selection if absolute body size determines the match between phenotype and external environment (e.g. thermoregulatory ability), and/or soft selection if relative body size determines success in some intraspecific competition (e.g. resource defence) and there are more competing individuals than vacancies. Hard and soft selection, and interactions between abiotic and biotic drivers of selection more broadly, are highly relevant to understanding the consequences of hybridization, yet are rarely considered explicitly.

Here we present an eco-genetic model to explore the eco-evolutionary consequences of acute and chronic influx of foreign/domesticated individuals (intrusion) into a wild population. Though loosely based on a salmonine lifecycle, the model is generally applicable to any taxon that experiences an episode of competitively mediated biotic (soft) selection followed by hard selection, as well as artificial or natural inputs of genetically divergent immigrants (e.g. forestry contexts). In our model, individuals compete each generation for a limited number of breeding 'slots', with spawning success determined by a single quantitative trait, Z_{SOFT}, that is subject to soft selection. Following reproduction, the offspring experience an episode of hard selection wherein survival depends on the match between a second quantitative trait, Z_{HARD} and an environmentally determined trait 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 locals versus intruders, that is, how divergent the two forms are for Z_{SOFT}. One possibility is that intruders are competitively inferior to locals. For example, experimental studies in salmonines have shown hatchery-bred females to be at a competitive disadvantage relative to wild-bred females in acquiring and defending breeding sites, and hatchery-bred males to be less successful in obtaining mates (Fleming & Gross, 1993; Neff et al., 2015). Alternatively, intruders could be competitively superior, if they are, for example, larger. In the case of commercially cultivated Atlantic salmon, farm escapes are often larger as adults than wild fish, yet they seem to have lower spawning success (Fleming et al., 1996, 2000; Weir et al., 2004). However, the offspring of farm-farm or farm-wild matings can competitively displace wild-wild offspring, owing to their faster growth rates and hence larger fry sizes (Fleming et al., 2000; McGinnity et al., 1997, 2003). Whilst previous modelling studies have considered genetic and demographic interactions between cultured and wild salmon (Baskett et al., 2013; Bradbury et al., 2020; Castellani et al., 2015, 2018; Hindar et al., 2006; Sylvester et al., 2019), ours is the first, to our knowledge, to explicitly distinguish between hard and soft selection and to explore their interactive effects in this context.

2 | MATERIALS AND METHODS

2.1 | Model description

The model is based on a generalized anadromous salmonine life cycle but, for computational efficiency, with implicit freshwater and saltwater life-history stages. The life history is also greatly simplified, to focus directly on the processes of interest (eco-evolutionary interactions between soft and hard selection), without loss of generality. The sequence of model 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 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.

2.1.1 | Recruit stage

In all scenarios, the model is seeded with 500 local recruits ($N_R(locals) = 500$) in generation 1, just prior to competition for spawning slots. The initial trait values for Z_{SOFT} and Z_{HARD} are a function of the initial allele frequencies $p_{SOFT}(locals)$ and $p_{HARD}(locals)$. Thirty unlinked diploid loci affect each trait (i.e. 60 functional loci in total), and the 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 & Luikart, 2021), but this should not affect the qualitative outcomes of the model. The traits are assumed to be initially genetically uncorrelated, that is, no linkage.

Genotype matrices for each trait for local individuals are established in generation 1. These matrices are 500 rows (individuals) by 60 columns (alleles) in dimension. The first two columns store the alleles for the first locus, the second two columns store the alleles for the second locus, etc. Alleles were drawn in generation 1 from a binomial distribution setting the probability of success to $p_{SOFT}(locals)$ and $p_{HARD}(locals)$ for each trait.

In all simulations, the first 20 generations corresponded to a period during which no intrusion occurred. In the acute intrusion scenarios, a given number of intruders ($N_R(intruders)$) was introduced in generation 21 at the recruit stage, with no further intrusion occurring thereafter, whilst in the chronic intrusion scenarios, $N_R(nonlocals)$ were introduced in each generation starting from generation 21. The genotype matrices for the intruders for Z_{SOFT} and Z_{HARD} were set up in the same way as for the locals, with the initial allele frequencies corresponding to $p_{SOFT}(intruders)$ and $p_{HARD}(intruders)$ respectively. Immediately after intrusion occurred, the genotype matrices for each trait for locals and intruders were merged by row.

The genotypic value of each individual for each trait (Z_{SOFT} and Z_{HARD}) was then computed by summing the alleles across all 30 loci, assuming that '1' alleles increase the trait value by 1 unit (i.e. the additive allelic effect $\alpha = 1$ at all loci) and '0' alleles have no effect. Thus, genotypic values ranged from 0 to 60. The expected mean genotypic value is equal to $2np\alpha$, where n is the number of loci affecting the trait and p is the relevant allele frequency, and the expected genotypic variance is given by $2np(1-p)\alpha^2$. The genotypic means and variances for each trait thus differed between locals and intruders to the extent that p differed between them. Non-additive genetic effects were ignored for simplicity, so the genotypic variances corresponded to additive genetic variances (V_A).

The initial heritability, h^2, was assumed to be the same for both traits for both locals and intruders. The environmental variance for each trait, V_E, was assumed to be constant across generations and was computed as $V_E = V_P - V_A = \frac{V_A}{h^2} - V_A$, where V_P and V_A were the initial phenotypic and additive genetic variances respectively. Note that the actual heritability in any given generation can deviate from initial h^2, because V_A can change under the influence of selection, drift and introgression. For simplicity, no mutation was included in the model.

2.1.2 | Soft selection filter

Parental phenotypes are formed for Z_{SOFT} by drawing an environmental deviation for each individual from a normal distribution of mean 0 and variance equal to $V_E(soft)$. Note that in the acute intrusion scenarios, all fish were assumed to be locals from generation 22 onwards, that is, intrusion of foreign individuals occurred in generation 21 and then any hybrid offspring in future generations were, by definition, local. Environmental deviations were added to the genotypic values of individuals, to give individual phenotypic values for Z_{SOFT}.

The total number of available spawning slots was fixed at $K = 500$ in all simulations. In situations where $N_R(total) \leq K$, all recruits get a spawning slot and no soft selection occurs. In situations where $N_R(total) > K$ (i.e. when there is reproductive excess), only K individuals become spawners, with the surplus assumed to die. To determine which individuals get to spawn, individuals are ranked from top to bottom based on Z_{SOFT} and only the top $K / N_R(total)$ fraction of individuals are assigned a spawning slot, which imposes truncational soft selection. For example, if $K = 500$ and $N_R(total) = 600$, only five out of every six recruits get to spawn, with the top 83% ($100 \times \frac{500}{600}$) of individuals based on ranked Z_{SOFT} trait values 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 strength of directional soft selection. Here we assumed, for simplicity, that there is no stochasticity in soft selection, but we acknowledge that in nature competitively inferior individuals will sometimes get lucky, that is, the strength of soft selection can vary stochastically around some expectation.

2.1.3 | 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 $N_S k$, where N_S is the number of spawners and k the fecundity (number of offspring per parent). In reality, salmonine fishes can produce dozens to thousands of eggs, depending on female size, but for computational efficiency, we set $k = 2$. 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. In other words, all freshwater mortality is subsumed into k.

During reproduction, new empty genotype matrices for Z_{SOFT} and Z_{HARD}, each dimension N_O rows by 60 columns, are set up to store the offspring genotypes for each quantitative trait, where $N_O = N_S k$ is the total number of offspring produced. For each offspring, two parents are drawn at random from the pool of N_S 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 (assuming that loci are unlinked), followed by random fertilization. This process is repeated across all loci until the new offspring genotype matrices have been fully populated with 1 s and 0 s.

2.1.4 | Hard selection filter

In this next step, offspring phenotypes are first formed for Z_{HARD} by drawing an environmental deviation for each individual from a normal distribution of mean 0 and variance $V_E(hard)$. As all new offspring are by definition local, regardless of the provenance of their parents, the environmental variance was computed as $V_E = \frac{V_A}{h^2} - V_A$, where V_A 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 Z_{HARD}.

Hard selection 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. body size) and marine environment determines marine survival. The expected survival W_i of each individual is computed as a function of its phenotype for Z_{HARD} based on a Gaussian fitness function:

$$W_i = W_{max} e^{\frac{-(Z_{HARD} - \theta)}{2\omega^2}}.$$

Here, W_{max} is the maximum survival for individuals whose phenotype coincides with the optimum θ, and ω corresponds to the 'width' of the fitness function in units of phenotypic standard deviations ($sd(Z_{HARD})$). In all simulations, ω is fixed at a value of $3 \times sd(Z_{HARD})_t$, which corresponds to moderate to strong stabilizing selection (Estes & Arnold, 2007). The t subscript here indicates that $sd(Z_{HARD})$ 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 ω at a given value across all generations independently of $sd(Z_{HARD})_t$, but that would then mean that the effective strength of hard selection would vary as $sd(Z_{HARD})$ changes over time. A constant strength of selection (for a given deviation of $\overline{Z}_{HARD}$ from the optimum) was deemed a more parsimonious assumption.

Realized marine survival was then a random binary variable with an expected value W_i for each individual. This imposes hard directional selection on Z_{HARD} whenever the mean trait value deviates either side of the optimum θ. The survivors of hard selection then become the new locally bred recruits for the next generation, and the model cycles back to step 1.

In each generation, a series of output variables calculated at the recruit stage is stored in a results matrix. These include the phenotypic means and variances for Z_{SOFT} and Z_{HARD}, the additive genetic variance for each, the number of recruits N_R, and the number of spawners N_S. The realized recruits per spawner for each generation are then computed as $RPS = N_R / N_S$. For all scenarios, 1000 replicate simulations are run and the mean and 95% confidence interval of each output variable of interest are calculated across replicates.

The model was coded in R version 4.3.1 (R Core Team, 2023) using the RStudio programming environment (Posit Team, 2023). All model code is freely available here: https://github.com/Helsinki-Ronan/soft-selection.

2.2 | Baseline scenario—no intrusion

To illustrate the basic functionality and behaviour of the model, baseline simulations were first explored in which no intrusion of foreign fish occurred and the evolutionary and population dynamics were tracked across 100 generations. Initial h^2 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 0.75 (i.e. $p_{SOFT} = p_{HARD} = 0.75$). The initial mean values of both traits were rescaled to reference values of 0, corresponding to mean-centring in generation 1 and the (closed wild) population was assumed to be well-adapted with respect to the hard-selected trait, that is, $\overline{Z}_{HARD} = \theta$. For simplicity, the optimum θ was kept constant over time.

To illustrate how the strength of soft selection depends on the magnitude of reproductive excess, the ratio of number of recruits N_R to number of spawning slots K was varied between ~1 and ~1.4. This was achieved by adjusting the W_{MAX} parameter. Three values of W_{MAX} were explored: 0.53, 0.63 and 0.73, corresponding to an expected RPS of approximately 1.0, 1.2 and 1.4 respectively. When $RPS \approx 1$ ($W_{MAX} = 0.53$), every recruit gained a spawning slot, so there was no reproductive excess. Note that, to generate a stable population the W_{MAX} parameter had to be set to slightly above 0.5 because of demographic stochasticity in the model. No evolution of Z_{SOFT} was then expected. When $RPS \approx 1.2$ ($W_{MAX} = 0.63$; moderate reproductive excess), there were more fish than spawning slots, hence phenotype-dependent competition will occur and Z_{SOFT} should evolve upwards. When $RPS \approx 1.4$ ($W_{MAX} = 0.73$; high reproductive excess), the competition intensified further and the rate of evolution of Z_{SOFT} should be correspondingly faster.

2.3 | Acute intrusion scenarios

2.3.1 | Acute intrusion simulations set 1

Here, we assumed that the wild population was initially well-adapted ($\overline{Z}_{HARD}(locals) = \theta$) and remained closed to intrusion for the first 20 generations, with $W_{MAX} = 0.58$ and $h^2(initial) = 0.25$. Thus, there was some reproductive excess, with ~550 recruits competing for 500 spawning slots each generation and $RPS \approx 1.1$. At generation 21, an acute intrusion event occurred wherein 500 foreign/domesticated fish intruded just prior to spawning. The total number of fish competing for spawning slots thus became ~1050, and soft selection intensified accordingly. From generation 21 onwards, all fish were 'locals' in the sense of being locally bred, but many would be of mixed ancestry. The intruders were assumed to be maladapted to the local environmental conditions, such that $\overline{Z}_{HARD}(intruders) < \overline{Z}_{HARD}(locals)$. This was achieved by setting $p_{HARD}(intruders) = 0.25$ and $p_{HARD}(locals) = 0.75$, such that $\overline{Z}_{HARD}(intruders)$ was 30 units less than $\overline{Z}_{HARD}(locals)$, corresponding to a difference of approximately 4.5 phenotypic standard deviations.

Three scenarios were explored: (1) intruders are competitively inferior to locals ($\overline{Z}_{SOFT}(intruders) < \overline{Z}_{SOFT}(locals)$); (2) intruders are competitively equal to locals ($\overline{Z}_{SOFT}(intruders) = \overline{Z}_{SOFT}(locals)$) and (3) intruders are competitively superior to locals ($\overline{Z}_{SOFT}(intruders) > \overline{Z}_{SOFT}(locals)$). This was achieved by varying p_{SOFT} for intruders relative to locals: in scenario 1, $p_{SOFT}(intruders) = 0.4$ and $p_{SOFT}(locals) = 0.6$; in scenario 2, $p_{SOFT}(intruders) = p_{SOFT}(locals) = 0.5$; and in scenario 3, $p_{SOFT}(intruders) = 0.6$ and $p_{SOFT}(locals) = 0.4$. With this parameterization, $\overline{Z}_{SOFT}(intruders)$ was 12 units lower than $\overline{Z}_{SOFT}(locals)$ at the time of intrusion in scenario 1, and 12 units higher in scenario 3. This corresponded to an absolute difference in trait means of ~1.6 phenotypic standard deviations.

2.3.2 | Acute intrusion simulations set 2

The above simulations were 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 were explored: low (250 intruders introduced at generation 21); moderate (500 intruders) and high (750 intruders), corresponding to $0.5 \times K$, $1.0 \times K$ and $1.5 \times K$ respectively. Three levels of reproductive excess were also explored: low ($W_{MAX} = 0.53$); moderate ($W_{MAX} = 0.58$) and high ($W_{MAX} = 0.63$), corresponding to expected RPS absent any intrusion of ~1.0, ~1.1 and ~1.2 respectively. As before, three levels of relative competitiveness of intruders versus locals were explored (intruders competitively inferior, equal or superior to locals) using the same parameterization as the *Acute intrusion simulations set 1*. This gave a total of 27 scenarios, that is, 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 were then run in which the difference between $\overline{Z}_{HARD}(intruders)$ and $\overline{Z}_{HARD}(locals)$ was assumed to be: (1) small ($p_{HARD}(intruders) = 0.35$; $p_{HARD}(locals) = 0.65$); (2) moderate ($p_{HARD}(intruders) = 0.25$; $p_{HARD}(locals) = 0.75$) and (3) large ($p_{HARD}(intruders) = 0.15$; $p_{HARD}(locals) = 0.85$). In all three cases, a moderate level of acute intrusion (500 intruders introduced at generation 21) and a moderate level of reproductive excess ($W_{MAX} = 0.58$) was assumed.

2.4 | Chronic intrusion scenarios

2.4.1 | Chronic intrusion simulations set 1

In the chronic intrusion scenarios, a constant number of foreign/domesticated fish were assumed to intrude each generation (from generation 21 onwards) just prior to spawning. In the first set of simulations, the per-generation intrusion rate was fixed at 5% of K, where $K = 500$. Thus 25 foreign/domesticated fish intruded each generation. As with the acute intrusion simulations, intruders were assumed to be maladapted with respect to Z_{HARD}, by setting $p_{HARD}(intruders) = 0.25$ and $p_{HARD}(locals) = 0.75$. As before, the same three levels of relative competitiveness were explored. The initial h^2 of both traits was set to 0.25 in all cases. The simulations were run for 150 generations, with intrusion starting at generation 21.

2.4.2 | Chronic intrusion simulations set 2

In the second set of chronic intrusion simulations, all parameters were the same as in set 1, except the per-generation intrusion rate was increased to 20% of K.

2.4.3 | Chronic intrusion simulations set 3

In the final set of simulations, a broader range of parameter values was explored. Specifically, the sensitivity of the chronic intrusion results to trait heritability and the level of reproductive excess was tested. In these simulations, the per-generation intrusion rate was set to 10% of K. Two levels of trait heritability (same value applies to both Z_{SOFT} and Z_{HARD}) were explored: $h^2(initial) = 0.25$ and $h^2(initial) = 0.50$. Three levels of reproductive excess were also explored: low ($W_{MAX} = 0.53$); moderate ($W_{MAX} = 0.58$) and high ($W_{MAX} = 0.63$), corresponding to an expected *RPS* absent any intrusion of circa 1.0, 1.1 and 1.2 respectively. Again, the same three levels of relative competitiveness of intruders versus locals were explored. This gave a total of 18 scenarios, that is, combinations of trait heritability, reproductive excess level and relative competitiveness.

3 | RESULTS

3.1 | Baseline scenario

The baseline simulations showed that, as expected, the rate of evolution of Z_{SOFT} depended on the extent of reproductive excess (Figure 1). With low reproductive excess, little to no directional evolution of Z_{SOFT} occurred (Figure 1a, orange curve) because all, or nearly all, recruits gained a spawning slot each generation, with *RPS* 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 *RPS* is by chance greater than one ($N_R > K$), but not when it is by chance less than one ($N_R < K$). This meant that a small amount of evolution of Z_{SOFT} accrued across multiple generations in the low reproductive excess case, which explains why the orange curve in Figure 1a shifted slightly upwards over time. With moderate reproductive excess (green curve in Figure 1a), the rate of evolution of Z_{SOFT} was faster, and with high reproductive excess (pink curve in Figure 1a) it was faster again. In all three scenarios, no evolution of Z_{HARD} occurred (Figure 1b) because the population was well adapted ($\overline{Z}_{HARD}$ coincided with θ).

With moderate or high reproductive excess, the rate of evolution of Z_{SOFT} gradually plateaued, as selection limits were reached due to the erosion of genetic variation. With only 30 loci contributing to each trait, genetic variation will be lost even under pure drift (in the absence of mutation or gene flow), as loci drift away from their initial allele frequency p (with genetic variance being maximal at $p = 0.5$) and alleles eventually go to fixation. Thus, additive genetic variation in Z_{SOFT} went down slowly over time in the scenario with low reproductive excess (largely drift only) and more rapidly in the moderate and high reproductive excess scenarios (selection + drift; Figure 1c). Z_{HARD} experienced no directional selection, so the rate of loss of genetic variance (Figure 1d) in all three scenarios was similar to that for Z_{SOFT} in the low reproductive excess scenario.

3.2 | Acute intrusion scenarios

3.2.1 | Acute intrusion simulations set 1

Prior to intrusion, Z_{SOFT} evolved gradually upwards from generation 1 to 20 (Figure 2a), as there were approximately 1.1 recruits for every spawner (i.e. reproductive excess). Z_{HARD} remained static during this pre-intrusion phase (Figure 2b), as the optimum was constant. The subsequent effects of acute intrusion depended strongly on the relative competitiveness of intruders and locals. When intruders were competitively equal to locals (green curves in Figure 2), consistent soft selection occurred and so Z_{SOFT} evolved gradually upwards (Figure 2a, green curve). When intruders were competitively inferior to locals, Z_{SOFT} exhibited a sudden drop in generation 21 when intrusion occurred (Figure 2a, orange curve). However, Z_{SOFT} rapidly jumped back up within a few generations, because any mixed ancestry individuals with lower Z_{SOFT} would have experienced a strong selective disadvantage (reduced likelihood of attaining a spawning site). Z_{SOFT} continued to evolve gradually upwards thereafter, as ongoing competition and soft selection played out.

In contrast, when intruders were competitively superior, Z_{SOFT} rapidly jumped up in generation 21 as a direct result of the intrusion (Figure 2a, pink curve). For the next 25 generations or so, Z_{SOFT} remained relatively static, because little soft selection occurred. The latter reflected the fact that Z_{HARD} was pulled strongly off its optimum by introgression (Figure 2b, pink curve). The effect of this maladaptation is seen in the much lower dip below 1 that was exhibited by *RPS* compared to the other two scenarios (Figure 2c, pink curve). The greater maladaptation in this scenario was due to the highly

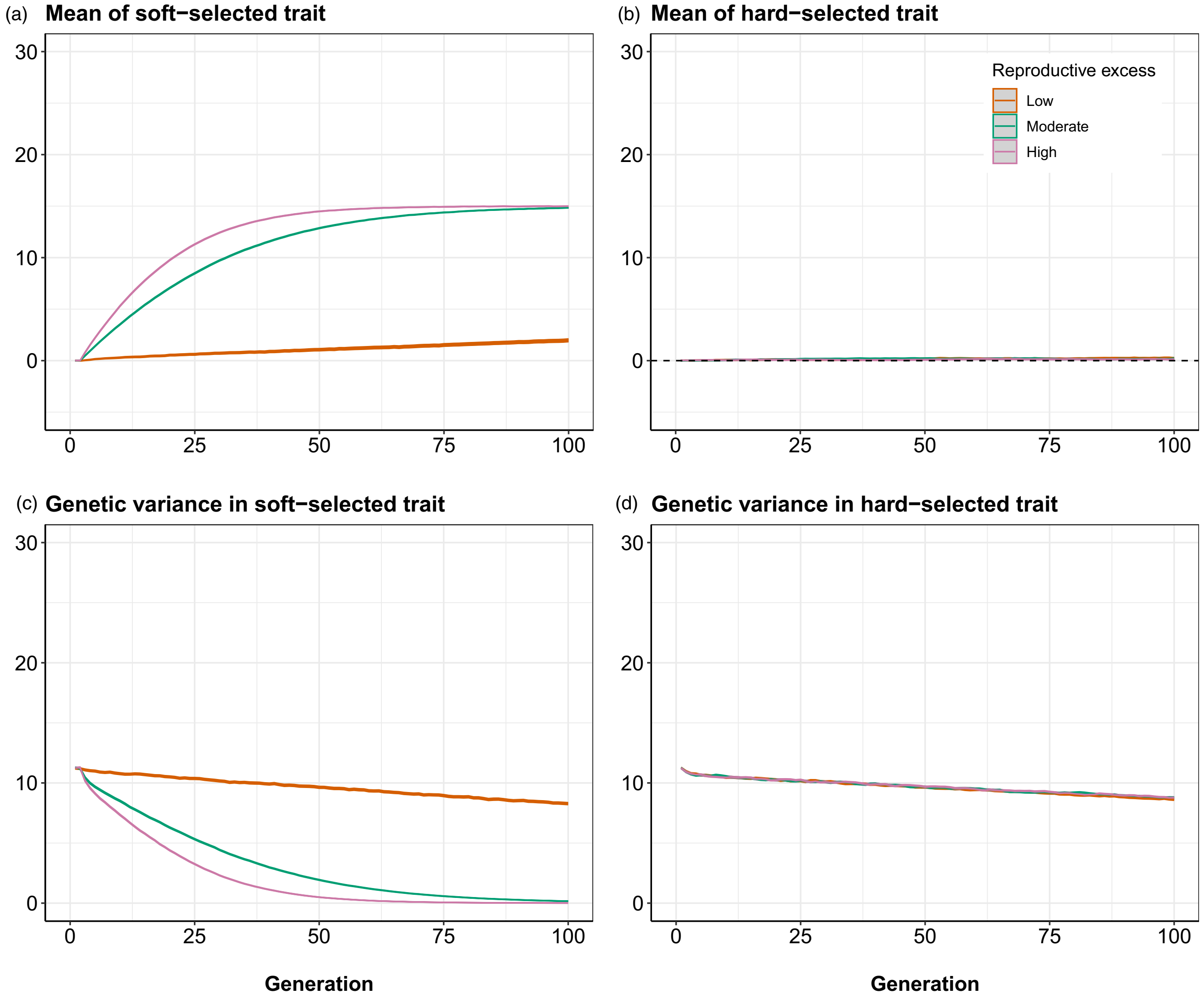

FIGURE 1 Results of baseline simulations. No intrusion of foreign/domesticated fish occurred, and the population was assumed to be initially well-adapted with respect to the hard-selected trait. Orange = low reproductive excess ($W_{MAX} = 0.53$); green = moderate reproductive excess ($W_{MAX} = 0.63$); pink = high reproductive excess ($W_{MAX} = 0.73$). Mean and 95% confidence intervals (grey ribbons) across 1000 replicate simulations are shown. (a) Changes in mean of soft-selected trait ($\overline{Z}_{SOFT}$) over time. (b) Changes in mean of hard-selected trait ($\overline{Z}_{HARD}$) over time (dashed line indicates optimum). (c) Changes in genetic variance of Z_{SOFT} over time. (d) Changes in genetic variance of Z_{HARD} over time.

competitive intruders (and their hybrid/backcrossed descendants in the generations immediately post-intrusion) having high spawning success, which led to higher introgression of foreign/domesticated alleles into the population. 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 (Figure 2d). Nevertheless, evolutionary rescue occurred in all three scenarios.

3.2.2 | Acute intrusion simulations set 2

The basic patterns found in the first set of acute 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 acute intrusion on the number of spawners (Figure 3, compare bottom panels to top panels). The number of spawners was reduced to a lower level when the intrusion rate was higher, because Z_{HARD} was dragged more from the optimum (Figure S1). In contrast, the greater the reproductive excess, the weaker the negative impact of acute intrusion on population size (Figure 3, compare right panels to left panels), because N_R remained above K for longer (Figure S2). The level of reproductive excess did not affect the level of maladaptation (Figure S1), but rather the effects of a given level of maladaptation on the number of spawners. *RPS* was negatively affected by intrusion in all cases, but this translated into strong impacts on number of spawners only in those scenarios where *RPS* was reduced below

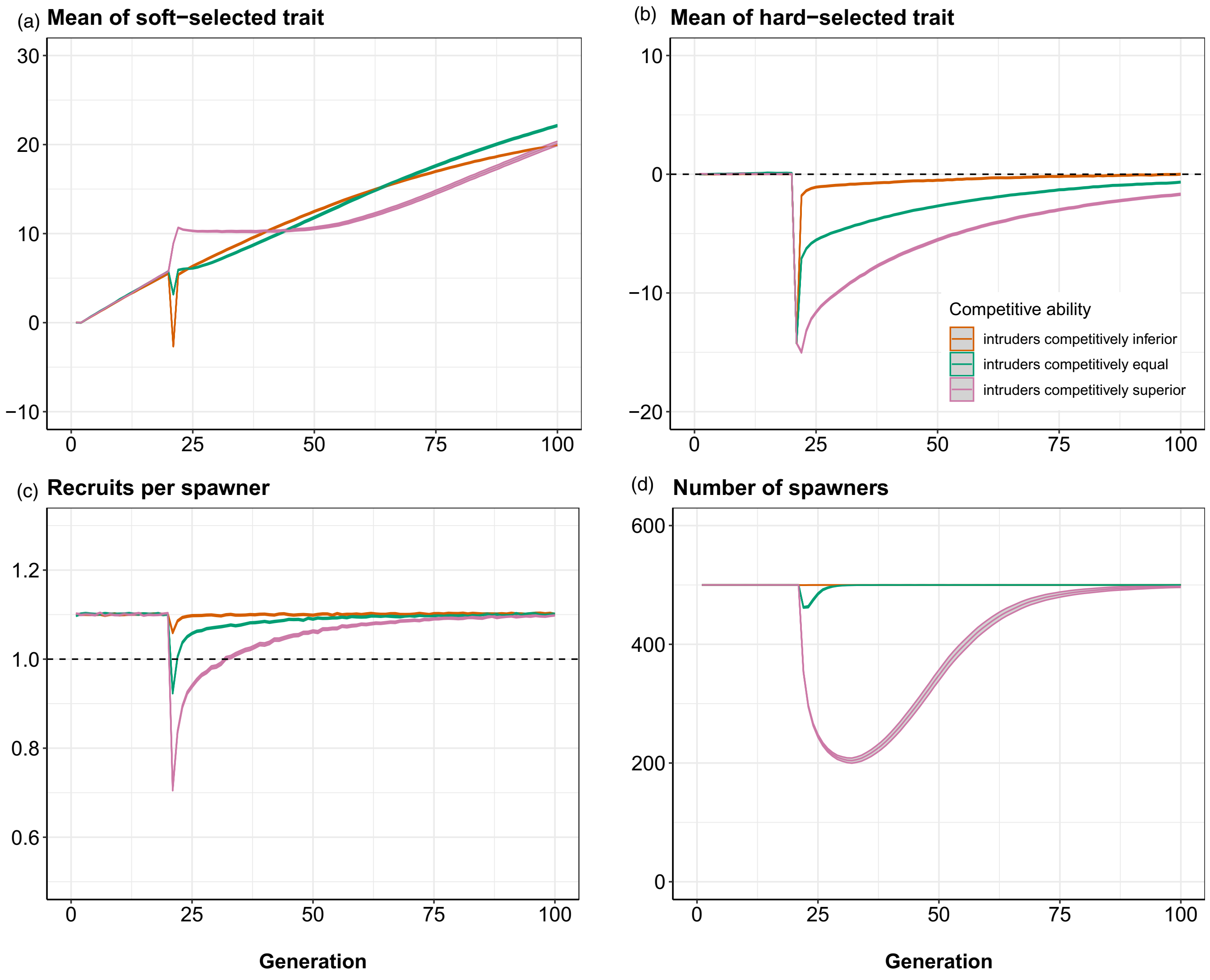

FIGURE 2 Results of acute intrusion simulations set 1. Prior to intrusion in generation 20, the wild population has a *RPS* of ~1.1 ($W_{MAX} = 0.58$), such that ~550 recruits compete for $K = 500$ spawning slots. At generation 20, 500 foreign/domesticated fish intrude just prior to spawning, giving ~1050 fish in total, greatly intensifying competition for the 500 spawning slots. Results of three scenarios (mean and 95% confidence intervals across 1000 replicates) are shown: orange = intruders competitively inferior to locals; green = intruders competitively equal to locals and pink = intruders competitively superior to locals. The intruders are maladapted with respect to Z_{HARD} in all three cases, so *RPS* goes down in generation 20 but then slowly recovers as $\overline{Z}_{HARD}$ of the mixed population evolves back up towards the fixed optimum ($\theta = 0$; dashed line in B). (a) Evolutionary trajectory of Z_{SOFT}. (b) Evolutionary trajectory of Z_{HARD}. (c) Trajectory of *RPS* over time (dashed line = replacement). (d) Trajectory of number of spawners N_S over time. Initial $h^2 = 0.25$.

1 (Figure S2). For a given level of intrusion and reproductive excess, intrusion had a greater negative impact on the number of spawners 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 (Figure S3).

The patterns were the same (results not shown) when $\overline{Z}_{HARD}(intruders)$ was greater, rather than less than, $\overline{Z}_{HARD}(locals)$, because the adaptive landscape was symmetrical about the optimum. The patterns were also more pronounced when a bigger absolute difference between $\overline{Z}_{HARD}(intruders)$ and $\overline{Z}_{HARD}(locals)$ was assumed (i.e. greater maladaptation of intruders), and less pronounced when a smaller absolute difference was assumed (i.e. weaker maladaptation of intruders; Figure S4).

3.3 | Chronic intrusion scenarios

3.3.1 | Chronic intrusion simulations set 1

Chronic intrusion exerted a consistent downwards pull on Z_{HARD}, because the intruders were maladapted to the local environmental conditions. This was counteracted, however, by evolution of Z_{HARD} back towards the fixed optimum ($\theta = 0$). When the intruders were competitively equal to the locals, Z_{HARD} gradually evolved downwards

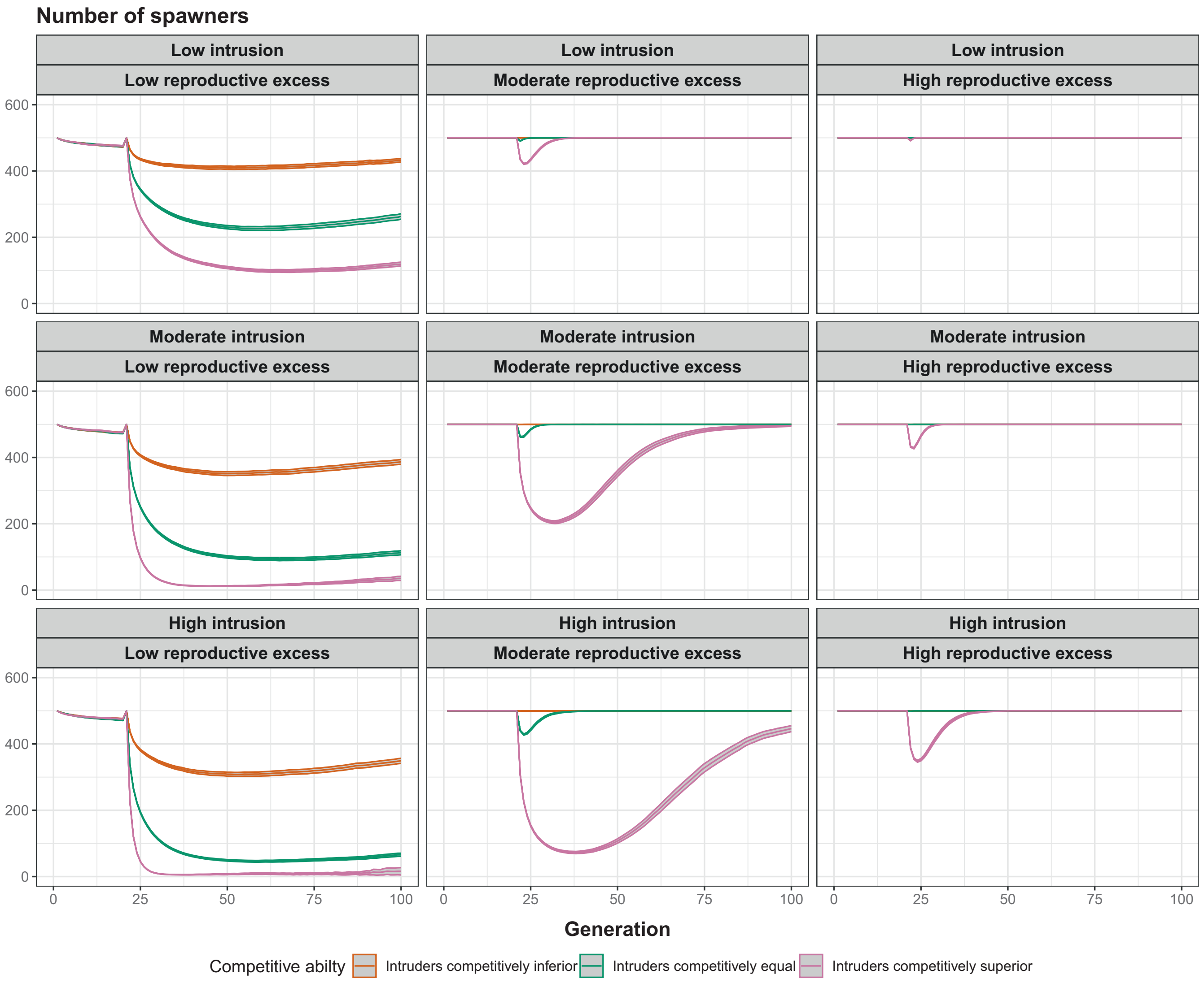

FIGURE 3 Results of acute intrusion simulations set 2. Mean and 95% confidence intervals across 1000 replicates are shown. Orange = intruders competitively inferior to locals; green = intruders competitively equal to locals and pink = intruders competitively superior to locals. $K = 500$ in all scenarios. Low intrusion = 250 intruders introduced in generation 21; moderate intrusion = 500 intruders introduced; high intrusion = 750 intruders introduced. Low reproductive excess: $W_{MAX} = 0.53$; moderate reproductive excess: $W_{MAX} = 0.58$; high reproductive excess: $W_{MAX} = 0.63$. Each panel shows the trajectory of number of spawners over time, with the average taken each generation over only those replicate populations that persisted ($N_S > 0$). Initial $h^2 = 0.25$.

towards a value of −30 (Figure 4a, green curve), because chronic intrusion resulted in the 'genetic extinction' of the wild population. As the degree of maladaptation went up, *RPS* went down accordingly, approaching a minimum of around 0.5 (Figure 4b, green curve). Z_{SOFT} went up initially, during the pre-intrusion period (generations 1 to 20), as positive soft selection was occurring. Once *RPS* dipped below 1 by around generation 25, however, soft selection no longer occurred and hence Z_{SOFT} was dragged downwards (Figure 4c, green curve) by the continual influx of foreign/domesticated fish each generation. Once Z_{SOFT} approached the reference value of 0, it remained there as soft selection was no longer occurring given that $RPS < 1$. The number of recruits declined to less than 50 by around generation 100, with the number of spawners levelling out at between 50 and 70 (Figure 4d).

When intruders were competitively superior, the results were similar to the 'intruders competitively equal' scenario, except that maladaptation increased faster (Figure 4a, pink curve) and hence *RPS* declined faster (Figure 4b, pink curve). Z_{SOFT} stabilized around +10 (Figure 4c, pink curve), reflecting the fact that gene swamping again occurred so that the original wild population was replaced genetically by foreign/domesticated alleles. Only around 20–25 recruits were produced each generation, and the number of spawners per generation bottomed out at between 30 and 40 (Figure 4d, pink curve).

The results were very different when intruders were competitively inferior to locals. Soft selection filtered out most intruders in each generation, such that little maladaptation occurred (Figure 4a, orange curve). As a result, *RPS* remained steady above 1 (Figure 4b,

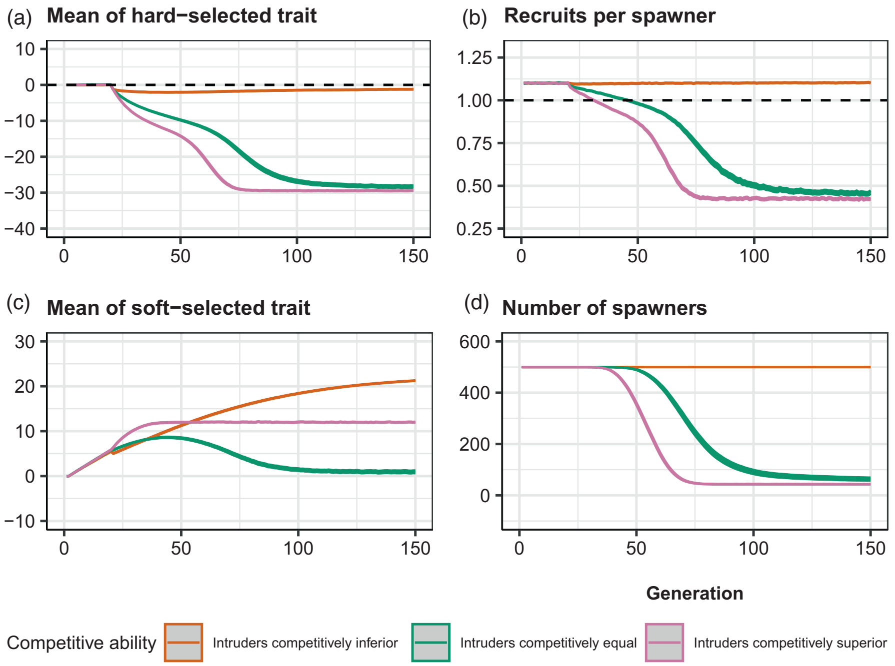

FIGURE 4 Results of chronic intrusion simulations set 1. Prior to intrusion in generation 21, the wild population has a *RPS* of ~1.1 (W_{MAX} = 0.58), such that ~550 recruits compete for $K = 500$ spawning slots. From generation 21 onwards, 25 foreign/domesticated fish intrude each generation just prior to spawning. Results of three scenarios (mean and 95% confidence intervals across 1000 replicates) are shown: orange = intruders competitively inferior to locals; green = intruders competitively equal to locals and pink = intruders competitively superior to locals. Each panel shows the trajectory of number of spawners over time, with the average taken each generation over only those replicate populations that persisted ($N_S > 0$). Initial $h^2 = 0.25$.

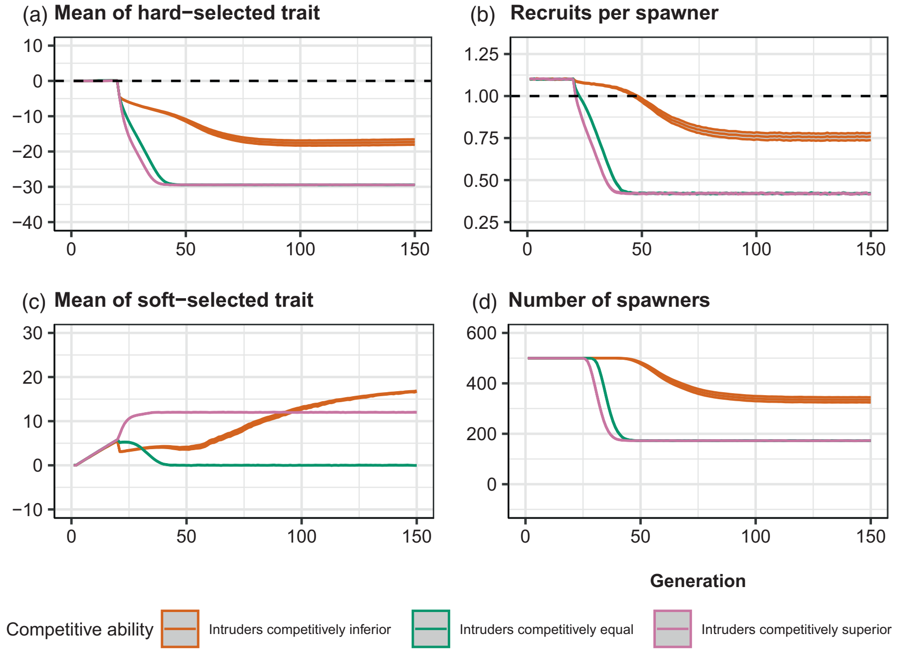

FIGURE 5 Results of chronic intrusion simulations set 2. Prior to intrusion in generation 20, the wild population has a *RPS* of ~1.1 (W_{MAX} = 0.58), such that ~550 recruits compete for $K = 500$ spawning slots. From generation 20 onwards, 100 foreign/domesticated fish intrude each generation just prior to spawning. Results of three scenarios (mean and 95% confidence intervals across 1000 replicates) are shown: orange = intruders competitively inferior to locals; green = intruders competitively equal to locals and pink = intruders competitively superior to locals. The intruders are maladapted with respect to Z_{HARD} in all three cases. (a) Evolutionary trajectory of Z_{HARD} (dashed line = optimum). (b) Trajectory of *RPS* over time (dashed line = replacement). (c) Evolutionary trajectory of Z_{SOFT}. (d) Trajectory of number of spawners N_S over time. Initial $h^2 = 0.25$.

orange curve). Z_{SOFT} continued to evolve upwards (Figure 4c, orange curve). Very little introgression of foreign/domesticated alleles occurred, and the number of recruits remained steady at around 550 and the number of spawners remained at $K = 500$ (Figure 4d, orange curve).

3.3.2 | Chronic intrusion simulations set 2

The results of the second set of chronic intrusion simulations (in which 100 foreign/domesticated fish intruded each generation) were similar to the first set (in which only 25 intruded), except Z_{HARD}

declined faster towards its equilibrium value (Figure 5a). In the 'intruders competitively equal' and 'intruders competitively superior' scenarios, complete genetic replacement of locals by the foreign/domesticated type occurred, and the number of spawners equilibrated at just under 200 (Figure 5d, green and pink curves). With the higher intrusion rate, some introgression occurred even in the 'intruders competitively inferior' scenario, indicative of a hybrid swarm. Some maladaptation occurred (Figure 5a, orange curve), albeit less than in the 'intruders competitively equal' and 'intruders competitively superior' scenarios (Figure 5a, green and pink curves respectively). *RPS* equilibrated at a value below 1 (Figure 5b, red curve). The number of spawners stabilized at around 350 (Figure 5d, orange curve), which was considerably higher than the 'intruders competitively equal' and 'intruders competitively superior' scenarios (Figure 5d, green and pink curves respectively).

3.3.3 | Chronic intrusion simulations set 3

The results of the chronic intrusion scenarios were sensitive to both trait heritability and degree of reproductive excess. In the low reproductive excess scenario (Figure S5), 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 fish. Trait heritability had little effect on these outcomes.

The dynamics changed when there was moderate reproductive excess (Figure S6). 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. In contrast, under the 'intruders competitively inferior' scenario, soft selection filtered out most intruders each generation so little maladaptation or introgression occurred. As a result, population size remained stable at *K*. 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, but different for the 'intruders competitively equal' scenarios (Figure S6). In the latter case, continued intrusion resulted in a small amount of maladaptation, but not enough to cause an appreciable decrease in *RPS*, so the number of spawners remained close to *K*.

The dynamics changed yet again when there was high reproductive excess (Figure S7). When trait heritability was 0.25, the results were similar to the moderate reproductive excess scenario, but only in the 'intruders competitively superior' scenario. Strong maladaptation occurred, and population size was reduced by about generation 50–100 or fewer spawners. In contrast, in the 'intruders competitively equal' and especially the 'intruders competitively inferior' scenarios, soft selection filtered out many intruders each generation. The number of spawners remained stable at *K* in both cases. When heritability was increased to 0.5, little to no introgression or maladaptation occurred in the 'intruders competitively inferior' and 'intruders competitively equal' scenarios, whilst a small amount of introgression and maladaptation occurred in the 'intruders competitively superior' scenario (Figure S7), with the number of spawners remaining stable at *K* in all three cases.

4 | DISCUSSION

Our modelling results showed that the eco-evolutionary consequences of maladaptive hybridization depend on the relative competitiveness of intruders versus locals. In both the acute and chronic intrusion scenarios, competitive superiority of intruders over locals acted as a 'Trojan Horse' for accelerated introgression of foreign alleles into the admixed population, reducing the average degree of adaptation and population productivity. Under certain parameterizations, this led to population decline (acute intrusion scenarios) or genetic replacement of local genotypes by non-local genotypes (chronic intrusion scenarios). However, these negative outcomes were much less pronounced, or absent altogether, when intruders were competitively inferior to locals. In that case, soft selection effectively cushioned the wild population against maladaptive hybridization by filtering out foreign genotypes each generation at the spawning stage and hence limiting the scope for introgression. Taken together, these findings emphasize how interactions between hard and soft selection play a crucial role in determining the evolutionary and demographic implications of hybridization between divergent gene pools.

Soft selection remains a relatively poorly appreciated aspect of eco-evolutionary dynamics, yet one that is highly relevant to a range of applied problems including artificial propagation, farm escapes, climate change, harvest and habitat alterations (Bell et al., 2021). The term soft selection has been mostly used in the context of models of evolution in spatially heterogeneous environments or metapopulations (e.g. Christiansen, 1975; Hadfield & Reed, 2022; Ho & Agrawal, 2012; Levene, 1953; Ravigné et al., 2004), in which density regulation is local and the contribution of each habitat/deme to total population size is fixed. Here, however, we did not consider spatial heterogeneity or metapopulation structure; our focus was on a single undivided population. We thus use the term soft selection as originally conceived by Wallace (1975), in that the expected fitness of an individual with a given trait value for Z_{SOFT} depended on both the number of other conspecifics and their phenotypic composition for this trait. The density-dependent nature of soft selection can be seen clearly in our baseline simulations, where greater reproductive excess (more recruits relative to spawning slots) was associated with faster evolution of Z_{SOFT} (Figure 1a). Z_{HARD}, in contrast, was unaffected by the magnitude of reproductive excess (Figure 1b), because hard selection is independent of both population density and composition (Bell et al., 2021). In our simulations, we assumed that Z_{SOFT} and Z_{HARD} were genetically independent traits, but future extensions could consider pleiotropy between them. This would generate more complex outcomes, as soft selection would then have indirect consequences for Z_{HARD}, whilst hard selection would have both direct and indirect consequences for Z_{SOFT}.

The acute intrusion of maladapted invaders had similar consequences to a sudden shift in the optimum caused by environmental change in the absence of intrusion. That is, $\overline{Z}_{HARD}$ was dragged away from the optimum, such that directional selection on Z_{HARD}, and potential evolutionary rescue, then ensued. The key difference, however, was that intrusion altered the competitive dynamics whenever Z_{SOFT} of intruders and locals was different. When the intruders were competitively inferior, many of them simply failed to spawn, and hence the demographic penalty on the admixed population owing to maladaptation of Z_{HARD} was much lower, relative to a scenario where intruders and locals were competitively equal (Figure 2). In contrast, competitive superiority of intruders over locals exacerbated maladaptation and increased extinction risk. These effects scaled, in turn, with the degree to which intruders were locally maladapted (differed in mean Z_{HARD}) relative to locals (Figure S4). Similar results were found in our chronic intrusion scenarios, except that 'genetic extinction' rather than demographic extinction was more likely to occur when the intruders were competitively superior (Figures 4 and 5). The productivity (recruits per spawner) of the admixed population was still greatly depressed in the chronic intrusion scenarios, however, relative to cases where intruders were competitively inferior or equal.

Acute or chronic intrusions can occur under both hatchery release and farm escape contexts. For example, stocking of rivers or lakes with hatchery fish (and their potential subsequent straying into neighbouring catchments) might occur on a once-off or intermittent pulse basis, or more regularly on an annual basis. Similarly, escapes from fish farms might involve large episodic events (e.g. Sylvester et al., 2019), or continual low-level 'drip leakage' (Glover et al., 2017). Whether, and by how much, the intruders differ from locals in competitive ability will depend on the specific types of traits and life stages involved, and the extent to which soft/density-dependent selective pressures under artificial propagation differ from those in the wild.

In our model, we assumed that competition occurred over access to limited spawning sites, which has certainly been a major factor in the historical evolution of salmonine life histories (Young, 2004). Hatchery-bred salmonines tend to be competitively inferior to wild-bred fish at acquiring/defending breeding sites and mates, which may reflect a relaxation of natural and sexual selection in captivity (Fleming & Gross, 1993; Neff et al., 2015). Similarly, escapees from commercial aquaculture facilities (fish farms) seem to be at a competitive disadvantage (particularly males) during spawning under natural conditions, although their spawning success relative to wild fish varies across contexts depending on, for example, the life stage at which the fish escape (Fleming et al., 1996, 2000; Weir et al., 2004). The specific traits mediating these spawning interactions, and their genetic basis, remain largely unknown, but behavioural phenotypes might be more important than body size, given that farmed adults are often larger than wild adults and hence should be superior competitors on that basis alone. However, competition for limited fry territories might also be important in determining whether farm genes can or cannot introgress into wild populations. Selection in the farm typically favours rapid growth, so the offspring of farm escapes are typically larger as fry than offspring of wild fish, with hybrids intermediate (see Glover et al., 2017 and references therein). As a result, pure farm or hybrid offspring can competitively displace pure wild offspring to poorer quality habitats where survival is lower (Fleming et al., 2000; McGinnity et al., 1997, 2003). Whilst we did not model such a scenario, competitive superiority of intruder genotypes at the fry/parr stage (Sundt-Hansen et al., 2015) would presumably have similar qualitative effects in our model as competitive superiority at the spawning stage, because soft selection and hard selection would still interact in the same way.

Our modelling framework is similar in some ways, but fundamentally different in others, to previous modelling studies that have considered genetic and demographic interactions between cultured and wild fish (Baskett et al., 2013; Bradbury et al., 2020; Castellani et al., 2018; Hindar et al., 2006; Sylvester et al., 2019). Although not an explicitly eco-genetic model (sensu Dunlop et al., 2009), the model of Hindar et al. (2006) did explore the effects of varying spawning success of escaped farmed salmon relative to wild salmon. The results suggested that low relative spawning success of farm escapees substantially reduces the proportion of farmed genotypes in the admixed population in subsequent generations, similar to our finding that competitive inferiority of intruders leads to lower introgression. They also showed that spawning by mature male parr may act as a conduit for gene flow from farmed to wild salmon (Garant et al., 2003), an interesting complication that we did not consider in our model but which clearly also involves density- and frequency-dependent processes (Kane et al., 2022). The eco-genetic model of Baskett et al. (2013) showed that an intermediate degree of maladaptation of aquaculture escapees relative to wild fish has the most serious consequences because extremely maladapted escapees are purged before they get a chance to reproduce. For a given degree of maladaptation, the mean fitness taken across all individuals in the admixed population was higher, and the recovery rate faster, when density dependence in their model occurred after selection (what they called soft selection) rather than before (what they called hard selection). However, selection itself was not density/frequency dependent in their model (i.e. not soft selection as defined by Wallace, 1975). Baskett et al. (2013) did not model the potential competitive superiority of cultured fish over wild fish, which they argued (in their discussion) would likely '*increase the demographic effect of aquaculture escapees on wild populations and the importance of the relative timing of escape and density dependence*'. In our model, density dependence and (soft) selection occur simultaneously at the spawning stage, but adding a subsequent round of ecological (i.e. phenotype-independent) density dependence either before or after hard selection would likely lead to similar findings as Baskett et al. (2013).

The IBSEM model of Castellani et al. (2015) is much more mechanistic and specifically tailored to salmon biology than our model (see also Piou & Prévost, 2012; Reed et al., 2011), and is thus better suited to applications where the goal is to generate predictions specific to a given stock or region (e.g. Bradbury et al., 2020; Castellani et al., 2018; Sylvester et al., 2019). IBSEM incorporates density-dependent growth and survival at different life stages, but interactive effects of genotype and density on these vital rates are not included, to the best of our knowledge. Thus, selection is effectively assumed to be hard. Like Hindar et al. (2006), IBSEM assumes that domesticated escapees have lower spawning success (30% for females, 5% for males) relative to wild spawners, which effectively limits introgression of farm alleles, but competitive abilities (during spawning or any other life stage) are genotype independent. It would be interesting to see how the eco-evolutionary dynamics predicted by IBSEM would be affected by including soft selection dynamics. Likewise, future extensions of our model could consider additional complexities such as mutation, simultaneous gene flow from multiple farm strains (Besnier et al., 2011), dispersal of farm escapes (Bradbury et al., 2020), straying from nearby wild populations (Bradbury et al., 2020), mature male parr (Castellani et al., 2015; Hindar et al., 2006), correlational selection (Tufto, 2010) or uneven distribution of allelic effects across loci (Castellani et al., 2015; Kardos & Luikart, 2021). However, increasing model complexity can come at the cost of generality and interpretability, so the appropriate amount of biological detail will depend on the specific research questions being addressed. Finally, we note some similarities with the modelling results of Svensson and Connallon (2019) who showed that, under many scenarios, frequency-dependent truncation selection reduces the rate of environmental change that is evolutionarily tolerable, although immigration was not considered.

5 | CONCLUSIONS

We have demonstrated that considering interactions between soft and hard selection can be crucial in evaluating the potential eco-evolutionary consequences of influxes of genetically divergent intruders into wild populations. Our model broadens the scope of previous modelling studies (Baskett et al., 2013; Bradbury et al., 2020; Castellani et al., 2015, 2018; Hindar et al., 2006; Sylvester et al., 2019; Tufto, 2010) by allowing for genotype-dependent variation in competitive abilities, which may be a key determinant of introgression levels. Aquaculture escapes, in particular, are recognized as an ongoing threat to the productivity and persistence of wild salmonine populations (Forseth et al., 2017; Glover et al., 2017), and our results inform aquaculture risk assessments and salmon conservation more generally. They also emphasize the importance of obtaining better information across a range of ecological or invasion contexts on the relative competitiveness of domesticated/foreign individuals and their wild counterparts. Climate change will likely exacerbate the consequences of maladaptive hybridization, so better knowledge of the processes influencing a population's ability to resist intrusion should ultimately foster evolutionarily informed conservation decisions.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest with the work herein.

DATA AVAILABILITY STATEMENT

This study produced no empirical data, but the code for running the model and generating all outputs is available here: https://github.com/Helsinki-Ronan/soft-selection.

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SUPPORTING INFORMATION

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