Modelling the impacts of imports and non-native subspecies hybridisation in honeybees

Irene de Carlos[1,2*], Laura Strachan[2], Grace P. McCormack[1], Gregor Gorjanc[2], Jana Obsteter[3*]

[1] Galway Honey Bee Research Centre, Earth and Life Sciences, School of Natural Sciences, University of Galway, Galway, H91 TK33, Ireland .
[2] The Roslin Institute and Royal (Dick) School of Veterinary Studies, The University of Edinburgh, Easter Bush Campus, Edinburgh, EH25 9RG, Midlothian, UK .
[3] Agricultural Institute of Slovenia, Hacquetova ulica 17, 1000, Ljubljana, Slovenia .

*Corresponding author(s). E-mail(s): irenedecarlos@gmail.com; jana.obsteter@kis.si;
Contributing authors: L.K.Strachan-1@sms.ed.ac.uk; grace.mccormack@universityofgalway.ie; Gregor.Gorjanc@roslin.ed.ac.uk;

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Abstract

Human-mediated movement of organisms for agriculture and ecosystem services often results in hybridisation and introgression between native and non-native populations. While introgression may increase genetic diversity, it can erode unique adaptations and reduce fitness, threatening the survival of native lineages. Honey bees offer a good model with extensive records, queen trade and migratory beekeeping facilitating genetic exchange among subspecies.

To explore these dynamics, we used SIMplyBee to simulated hybridisation between native *Apis mellifera mellifera* and non-native (C lineage) honey bee populations. We adopted the parameters from the Irish honeybee population that still maintains relatively low levels of import, but is threatened by commercial imports. The model included colony honey yield and fitness as complex polygenic traits. We simulated varying import rates, genetic correlations between fitness in native and non-native environments, and spatial distributions of introgression over 20 years, measuring levels and rate of introgression and genetic means for both traits.

Increased imports accelerated introgression and induced a trade-off between higher honey yield and lower fitness, and decreasing genetic correlations between environments amplified fitness decline. Spatial simulations showed the spread of introgression across the entire simulated area. Halting imports reversed the trend, but purging of introgressed material was slow and varied among replicates. These findings highlight the trade-off between short-term production gains and long-term losses in fitness and adaptation. Our modelling framework provides a reference for exploring introgression in other systems, emphasising that sustainable management of introgression requires restricting imports and breeding locally adapted populations rather than relying on non-native imports.

Keywords: Introgression, *Apis mellifera*, Simulation, Queen importation, Fitness, Honey yield, GxE interaction, Ireland, SIMplyBee.

1 Introduction

Introgression is the transmission and integration of genetic material from one species, subspecies, or lineage into the genetic background of another with continued hybridisation and backcrossing (Ellis et al. 2018). Introgression can be associated with an increase in genetic diversity, which can boost the evolutionary potential of a species in changing environments (Jensen et al. 2005a). However, it can also lead to the loss of unique combinations of alleles that have emerged over long periods of adaptation and change adaptive traits in a population (Rhymer and Simberloff 1996; Benjamin et al. 2021). Persistent imports and introgression pose a risk of genomic extinction of lineages or subspecies, in turn leading to a homogenisation of the species (McKinney and Lockwood 1999; De la Rua et al. 2009).

In agricultural settings, the introduction of non-native (sub)species to a new environment can be voluntary or involuntary. Involuntary introductions are usually a consequence of anthropogenic activity, climate change, or transformation of natural landscapes. Such introductions can cause difficulties as seen for pest management. Hybridisation of pest species can lead to decreased susceptibility to pesticides and increased host range, as observed for one of the most important pest insect in the world, the bollworm (Corrêa et al. 2019).

Agriculture also intentionally introduces new organisms to increase the productive performance or for ecosystem services, such as pollination or biological control. Despite the deliberate introduction, introgression and hybridisation are usually an unwanted consequence. For example, rainbow trout is one of the most widely introduced fish species for hatchery cultivation or sport fishing. It's introduction resulted in hybridisation with local species that led to a decline of local populations and even to the extinction of native species (Metcalf et al. 2008). There are also examples of species introduced for biological pest control hybridising with local populations (e.g. (Havill et al. 2012)). This can have a negative impact through decrease fertility and

efficiency, and increased need for chemical control, or be beneficial and result in hybrid vigour (Corrêa et al. 2019).

Another example of intentional introduction is the translocation of honey bees and bumblebees for pollination services. Vast numbers of bee colonies are migrated for pollination. In the US alone, more than 2mio honey bee colonies are transferred to California every year for almond other crops pollination Glenny et al. (2017). In Europe, colonies are also transferred to harvest specific types of honey (Martínez-López et al. 2022). Migratory beekeeping thus converges multiple populations at one spot, enabling hybridisation. Migration of honey bees is exacerbated by a lively queen trade for improved food production. Beekeepers around the world import queens of two subspecies of C mitochondrial lineage, (*A. m. ligustica* from Italy and *A. m. carnica* from Central Europe), that are commercially popular for their high honey yield, gentle nature, low propolis usage, and high fertility (Hoppe et al. 2020; Minozzi et al. 2021; Péntek-Zakar et al. 2015).

Although there is economic benefit in honey bee trade, imports are contributing to a decline in locally adapted populations that are less commercially interesting. Introgression has already reduced the natural range of the European dark bee, *A. m. mellifera*, native in the north and west Europe , where distinct morphological and behavioural traits that assist survival, are at risk of being lost. (McCann and McCormack 2024; Valentine et al. 2024)

In Germany, the importation of *A. m. carnica* led to the near-total substitution of the local *A. m. mellifera* Jensen et al. (2005a). Comparable patterns are reported elsewhere: in Denmark, around 10% introgression was found in the protected Læsø population while the rest of the country, has become mainly C-lineage (Alice Pinto et al. 2014; Nielsdatter et al. 2021); in Poland in 2011 there was a 10–30% introgression reported (Oleksa et al. 2011); in the Urals 10 years ago this percentage was at 17.5% (Yanbaev 2024); in the UK, 20,000 non-native queens were imported in 2020, which

doubled the number from 2007 (Jensen et al. 2005a; Ellis et al. 2018; Henriques et al. 2018a; Momeni et al. 2021; McCann and McCormack 2024; Jones and Semmence 2021). Actual levels of introgression in these countries are likely to have increased since those estimates and research suggests that if imports continue, *A. m. mellifera* could disappear from these regions (Jensen et al. 2005a). Some countries have thus included *A. m. mellifera* in conservation programmes and have banned the import of non-native subspecies into some areas (Ruottinen et al. 2014).

In Ireland, a change in introgression levels from <3% to >18-25% between 2016 and 2023 has been reported, inline with an increase in imports (McCann and McCormack 2024). However these levels are still relatively low. Moreover, recent whole-genome analyses show that most Irish colonies are still largely pure *A. m. mellifera*, with only limited signs of C-lineage admixture (Buswell et al. 2025). Countries like Ireland are therefore still in a position to take preventive measures or conservation actions and would benefit from predicting outcomes of different measures via modelling.

Whether for conservation, preventing pest outbreaks, or introducing new beneficial species, modelling hybridisation is becoming increasingly important. For *A. mellifera*, introgression is being studied across the Nordic countries, Britain and in Ireland. Unfortunately, empirical studies directly quantifying the effects of introgression on fitness and honey production in native populations are still scarce. Simulations are a valuable tool for a time- and cost-effective evaluation of long-term effects of introgression, and hence a prediction of populations' evolution under such conditions. The results of such simulations could provide insights into ways of controlling imports and populations in practice. While simulations are widely used in animal and plant genetics research (Pook et al. 2020; Gaynor et al. 2021; Bančič et al. 2024), and are also gaining traction in honey bee research (Becher et al. 2014; Plate et al. 2019; Kistler et al. 2021; Bernstein et al. 2021; Obšteter et al. 2023; Strachan et al. 2024b), explicit applications to modelling introgression in honey bees are, to our knowledge, absent.

Honey bees offer a good model to study hybridisation in general due to the migratory nature of beekeeping, the relatively well-documented migration and production due to their economic importance, and their high population stratification.

The aim of this contribution was to build a stochastic simulation model for quantifying the magnitude and effects of introgression in native honey bee populations due to imports of non-native queens. We used the Irish native *A. m. mellifera* population as a case study to quantify the impact of the introgression on honey production and fitness.

2 Materials and Methods

The stochastic simulator SIMplyBee (an R package; Obšteter et al. 2023) was used to simulate a natural yearly cycle of honey bee colonies with import of queens from a non-native population. The R code for this simulation is open-source and available in the supplement and on-line (Data availability: 10). We chose Ireland as our model system because this issue is very current given recent increases in honey bee imports coinciding with increases in observed hybridization. Ireland was reported to have a significant population of *Apis mellifera mellifera* in 2018 (Hassett et al. 2018) so the question of the likely impact of imports there on introgression levels became urgent. Furthermore, Ireland provides publicly available, year-by-year data on queen imports, which facilitates parameterisation and validation of the analysis (Department of Agriculture, Food and the Marine 2024). We simulated two populations that resembled a native Irish population of *A. m. mellifera* and a non-native Central European population of C lineage. Two complex polygenic traits representing fitness and honey yield were simulated in these populations, but with a genetic correlation between the expression of these two traits in the two environments of the populations, giving rise to genotype-by-environment (GxE) interaction. We simulated 10 years of a burn-in phase followed by 10 years of scenarios varying the percentage of imported queens,

the magnitude of GxE interaction for the fitness trait, and the point of entry of the imports. We compared the scenarios based on the level of introgression and the genetic mean for fitness and honey yield.

2.1 Simulation

We simulated the founder genomes with the Markovian Coalescent Simulation implemented in SIMplyBee, according to *A. mellifera* demographic model (Wallberg et al. 2014; Obšteter et al. 2023). We generated 500 *A. m. mellifera* and 500 *A. m. carnica* diploid genomes for the founders of each of the native populations. We generated 15 replicates of these base populations. Each genome contained 16 chromosomes with 1000 segregation sites per chromosome. From the founder genomes, we created the base populations of 500 *A. m. mellifera* colonies that represented the population in Ireland, and 500 *A. m. carnica* colonies that represented the population of in Central Europe providing the source of imports of C lineage queens. Each colony was simulated with one queen and 10 workers, which, to reduce computing time, represented the full size of a colony.

Within each native environment, we simulated two complex polygenic traits, fitness and honey yield. We simulated both traits as effected by 100 additive quantitative trait loci (QTLs) per chromosome (1600 QTLs per trait in total) and a trait mean of 0. For honey yield, we set genetic variance to 0.25, and residual variance to 0.75, which resulted in a heritability of 0.25, as estimated for natural honey bee populations (Maucourt et al. 2020). For fitness, we set the genetic variance to 0.1 and residual variance to 0.9, resulting in a heritability of 0.1, typical of fitness-related traits (Kruuk et al. 2000; Guichard et al. 2023). We modelled the GxE interaction by simulating fitness and honey yield in both environments as genetically correlated traits, resulting in four simulated traits: honey yield in Ireland, honey yield in Central Europe, fitness in Ireland, and fitness in Central Europe. Therefore, each simulated individual had a

genetic and phenotypic value for each of the four traits, regardless of their physical location. However, only the "local" values were used for selection, breeding, or import decisions. For honey yield, we fixed the genetic correlation between environments to 0.75, following Hatjina et al. (2014) that showed that honey bees produced more honey in their native environment than in a non-native one. For fitness, we varied the genetic correlation between the scenarios as described in the following.

2.2 Burn-in

During the burn-in phase, we kept the two populations closed and simulated 10 years of a beekeeping yearly cycle within each population. This cycle simulated three beekeeping seasons: spring, summer, and winter, with colony events occurring at different probabilities depending on the season (Table 1). These probabilities were estimated from the current literature (Mattila and Otis 2006; Seitz et al. 2015; Rangel et al. 2013; Brodschneider et al. 2018; Gray et al. 2023). We ran the 15 replicates of the base populations through the burn-in phase.

In the spring period (Figure 1 A), we first simulated the growth of existing colonies to their full size. Next, we split all colonies to simulate swarming prevention, which generated new colonies that were re-queened with age 0 virgin queens obtained from the original colonies. Then, we swarmed or superseded a percentage of colonies (Table 1). The remnant colonies of the swarms or supersedures were naturally re-queened with their own virgin queens. Next, we generated drones from colonies with queens of age 1 or older to create a drone congregation area (DCA) and mated all the new virgin colonies with an average of 15 random drones from the DCA. Finally, we ended the spring period with the collapse of a proportion of colonies, mimicking queen loss during a nuptial flight (Table 1).

In the summer period (Figure 1 B), we again swarmed a proportion of colonies (Table 1), though less than in the spring period, since swarms occur mostly in spring,

when the colonies outgrow their hive (Thomas 2016). We followed this by superseding or collapsing a percentage of colonies (Table 1). The resulting virgin colonies mated as in the spring period.

Finally, in the winter period (Figure 1 C), we collapsed a larger percentage of colonies due to overwintering challenges (Table 1). We collapsed colonies with the lowest phenotypic values for fitness in the corresponding environment to simulate *directional* selection, driving genetic differentiation between the two populations evolving in two different environments. As a result, the Irish population had a higher genetic mean for "fitness in Ireland" than the Central European population at the end of the burn-in phase. At the end of each yearly cycle, we removed some splits to maintain constant population sizes. In the Central European population, we removed the colonies with the lowest phenotypic value for honey yield to simulate directional selection on this trait. This selection reflected the long-term selective breeding for this trait and the presumed superior honey yields of the imported bees into Ireland.

Table 1 Probabilities of colony swarming, supersedure, and collapse in spring, summer, and winter simulated periods.

	Spring	Summer	Winter
Supersede	0.05	0.05	–
Swarm	0.05	0.01	–
Collapse	0.10	0.10	0.18

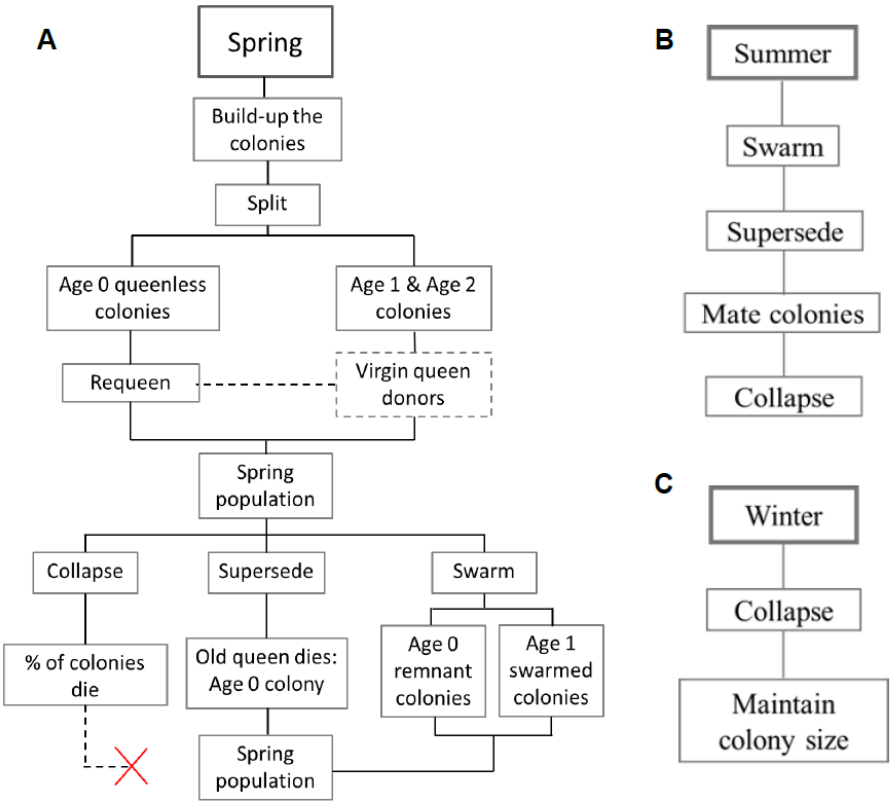

Fig. 1 Flow diagram of the simulated yearly cycle of honey bee colonies in A) the spring period, B) the summer period, and C) the winter period

2.3 Scenarios

After the burn-in, we continued running the 15 replicates for each of the three sets of scenarios for 10 additional years. In this phase, we transitioned from directional to stabilising selection on fitness, assuming that both populations had reached their optimal fitness levels after the burn-in. To implement this, we selectively collapsed colonies whose phenotypic value for fitness deviated most from the population's mean fitness during the winter period.

First, we simulated the import of queens from the C lineage into the Irish population by requeening a percentage of spring splits with imported virgin queens (Figure 2). We compared the scenarios with 0% (Control), 1.5%, 4%, and 10% of imports, which were determined based on the reported imports to Ireland (McCann and McCormack 2024).

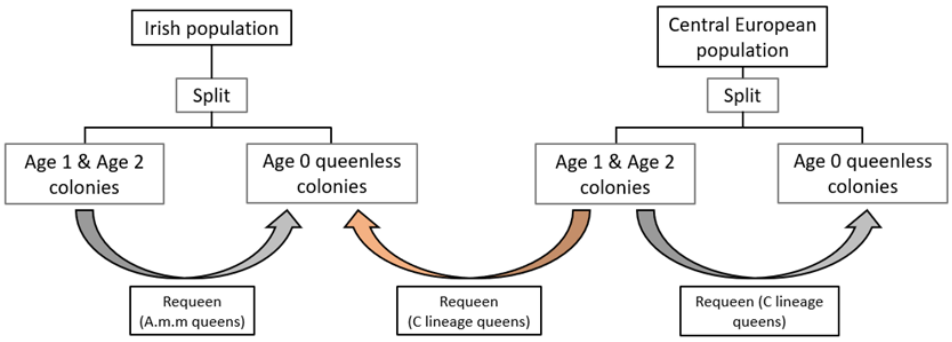

Fig. 2 Flow diagram of the import process: re-queening of age 0 queen-less colonies in the Irish population with C lineage queens from the Central European population after the burn-in phase

Second, to explore the effects of adaptation to the local environment and GxE interactions, we created a set of scenarios that varied the genetic correlation between fitness in Ireland and Central Europe. Büchler et al. (2014) found higher survival of honey bees with native genotypes over non-native genotypes, indicating the presence of GxE interactions and a past adaptation to the environment. However, given the lack of studies on the extent of the GxE interaction in honey bees, we evaluated a wide range of genetic correlations: -0.75, -0.25, 0.25, and 0.75 (base scenario).

Third, to explore the effect of the spatial distribution of imports, we created spatially-aware scenarios. In the scenarios described above, the colonies have no notion of the location and can hence mate randomly (panmictic simulation). This was done to simplify the simulations, as we were mostly interested in the qualitative differences

between scenarios. However, colony locations and the locations of imports are likely to impact the introgression. SIMplyBee enables spatially-aware simulations, where each colony is assigned a location and the mating is restricted to a user-defined radius. To evaluate the effect of the point of import on the spread of introgression over time and place, we created a scenario by simulating an area with a single point of import at the center of the simulated area. We chose to place the point of import at the center of the simulated area to measure the effects of introgression symmetrically in all directions. We simulated an area of $150km^2$ with 500 colonies randomly placed. This mimicked the colony density in county Dublin (Department of Agriculture, Food and the Marine 2019), which receives the majority of imports in Ireland (about 3,000 reported honey bee colonies within $900km^2$ in 2020).

The 500 colonies were randomly placed into groups of between 5 and 15 colonies, representing the Irish apiaries. We restricted the mating to $15km$ radius and the new location of the swarms to $1.5km$ radius (Jensen et al. 2005; Schultz et al. 2008). Colonies created as splits were given the same location as the colony they originated from. Virgin colonies were re-queened with virgin queens sampled from a nearby area. For this, we divided the area into 16 smaller areas and sampled one colony as the virgin queen donor for each area.

Lastly, we simulated the effect of halting the import to evaluate if a population can recover after long periods of continuous imports. For this, we extended the spatially-aware scenario with a single point of entry for an additional 10 years (30 simulated years in total), where we halted imports to evaluate if the population can recover after long periods of continuous imports.

2.4 Analysis

To assess the level of introgression, we tracked recombination of genomes throughout the simulation and, with it, identity by descent inheritance of alleles from both base

populations. This enabled quantifying the proportion of alleles that originated from the native *A. m. mellifera* or the non-native C lineage population. We measured the level of introgression for each queen as 1 minus the proportion of alleles that originate from the founder *A. m. mellifera* alleles. Then we averaged the level over all queens by the year of birth.

We computed the rate of introgression as the slope of a linear model fitting the mean level of introgression over years for each replicate: $lm(\text{Introgression} \sim \text{Year} - 1)$. We omitted the intercept, because the level of introgression was 0 at the end of burn-in. We computed the average slope across the replicates of the scenarios, as well as the 95% quantiles.

We computed the genetic trend for "honey yield in Ireland" and "fitness in Ireland" traits by calculating the mean genetic value of queens by their year of birth in the Irish and the Central European populations for each replicate. These values were centered to have a mean of 0 in the last year of burn-in, year 10. Then we computed the average across the replicates of the scenarios as well as the 95% quantiles.

To assess the contribution of imported queens to genetic gain, we next partitioned the overall genetic trends for honey yield and fitness traits in the Irish population to the contribution of native *A. m. mellifera* and non-native C lineage population with AlphaPart R package (Obšteter et al. 2021).

In the spatially-aware scenario, we assessed the spread of introgression by plotting the proportion of introgression against the Euclidean distance of the colonies from the point of import. The Euclidean distance d between a colony located at (x_i, y_i) and the point of entry at $(75, 75)$ (centre of the $150km^2$ area) was calculated as $\sqrt{(x_i - 75)^2 + (y_i - 75)^2}$.

Moreover, we analysed the cline of introgression, to study gradual change across geographical distance. We fitted clines for each year of importation using the Hybrid

Zone Analysis R package (Derryberry et al. 2014). For each year of import, we collected the estimated c value, representing the centre of the cline. We averaged the c values across replicates to obtain the mean c value per year, as well as the 95% quantiles.

We performed ANOVA to assess the significance of differences in the collected quantities. We performed the post-hoc Tukey HSD tests to evaluate the differences between levels of a specific factor. All of these analyses were performed using the base R packages (R Core Team 2024).

3 Results

The results show (1) the effects of varying percentage of imports and the genetic correlation between fitness in two environments on the level and rate of introgression and mean honey yield in the Irish population, (2) the dispersion of introgression with a single point of entry, and (3) effect of halting imports. Increasing imports resulted in a proportional increase in introgression and honey yield; however, it also resulted in a notable decrease in fitness. Changing the genetic correlation between fitness in two environments did not significantly affect introgression or honey yield, but negative correlations led to a stronger decrease in fitness. Introgression from a single point of entry spread fast through the simulated area over the years. Halting imports led to a decay in introgression levels, but the rate of this decay was low.

3.1 Percentage of imports

The results showed that the level and rate of introgression increased from year 10 to year 20 in all scenarios that imported non-native queens (Figure 3). The increase became significantly more evident with higher import percentages (Supplementary information: Additional file 1 and Additional file 2). We observed the highest rate of introgression in the scenario with 10% imports (0.013). Here, the level of introgression

reached 0.39 by year 20, meaning that 39% of the population's genome was non-native. Decreasing the percentage of imports decreased the level of introgression, with the population being 18.3% and 7.4% introgressed in year 20 respectively with 4% and 1.5% imports (Table 2). The control scenario had no import and hence retained the level and rate of introgression at 0.

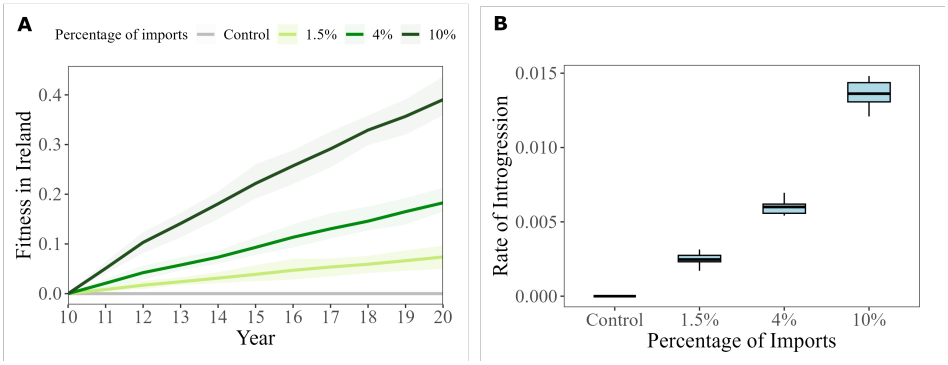

Fig. 3 Changes in the level and rate of introgression across replicates in scenarios with the varying percentage of imports of the C lineage into the Irish population: Control (0%), 1.5%, 4%, and 10%. A) The trend in mean level of introgression with the corresponding shaded regions indicating the 95% quantiles. B) Boxplot of the rates of introgression.

In accordance with the introgression, the mean genetic value for honey yield in the Irish population increased with increasing percentage of imports, while the mean genetic value for fitness decreased. In the control scenario, traits fluctuated around zero as honey yield in Ireland was not under directional selection, fitness was under stabilising selection at the optima, and there were no imports (Figure 4). We observed the highest increase in mean genetic value for honey yield in the scenario with 10% import, reaching +0.304 genetic standard deviations by year 20. This value was about 7 times higher than in the 1.5% import scenario and about 3 times higher than in the 4% scenario (Table 2, Supplementary information: Additional file 1). However, the 10% import scenario showed a significant and steep decrease in mean genetic value for

Table 2 Introgression metrics and genetic values in year 20 under different import and correlation scenarios.

	Scenario	Rate of introgression	Introgression at year 20	Honey yield at year 20	Fitness at year 20
Percentage of imports	Control (0%)	0.000	0.000	-0.008	-0.011
	1.5%	0.002	0.074	+0.041	-0.016
	4%	0.006	0.183	+0.119	-0.041
	10%	0.013	0.393	+0.304	-0.087
Changing genetic correlations	+0.75	0.0061	0.183	+0.119	-0.041
	+0.25	0.0058	0.175	+0.102	-0.066
	−0.25	0.0059	0.176	+0.134	-0.071
	−0.75	0.0057	0.171	+0.138	-0.078

Values of introgression rates, introgression levels, average honey yield genetic value, and average fitness genetic value in year 20 in the Irish population with varying percentage of imports: Control (0%), 1.5%, 4%, and 10%; and varying correlation between fitness traits in the two environments: +0.75, +0.25, -0.25, -0.75.

fitness, dropping to -0.087 genetic standard deviations by year 20, while the decrease in fitness in the 4% and 1.5% scenarios were less pronounced and not significantly different from the control group (Supplementary information: Additional file 2).

The partition of genetic trends for both traits further confirmed the positive contribution of imported queens to honey yield, with the imports accounting for 99% of the increase. This partition also confirmed the negative contribution of imported queens to fitness, with the imports accounting for 99% of the decrease (Supplementary information: Additional file 3 and Additional file 4).

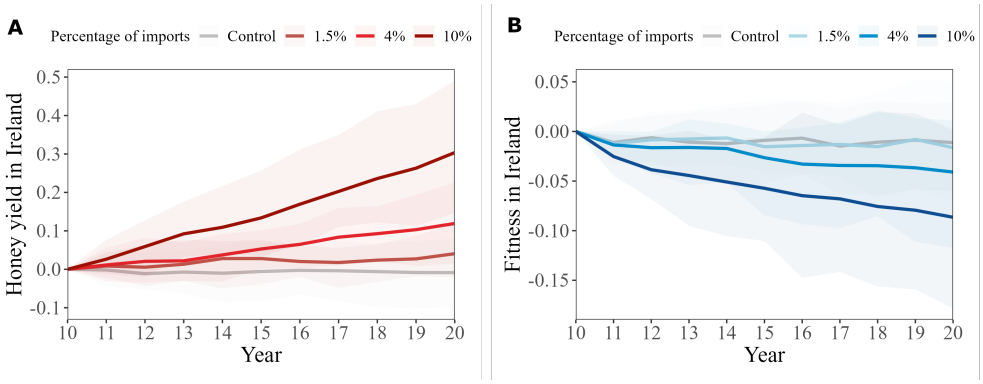

Fig. 4 Changes in the mean genetic value for (A) honey yield (red lines) and (B) fitness trait (blue lines) in the Irish population from year 10 to year 20 in scenarios with a varying percentages of imports: Control (0%), 1.5%, 4%, and 10%. The solid lines represent the mean genetic value across replicates with corresponding shaded regions indicating the 95% quantiles.

3.2 Genetic correlation between fitness in the two environments

The results revealed that the genetic correlation between fitness in Ireland and Central Europe had limited effects on the level and rate of introgression (Figure 5). Although the differences in introgression matched our expectations, there was a substantial variation between simulation replicates and the differences between scenarios were not statistically significant (Supplementary information: Additional file 1 and Additional file 2). The high genetic correlation of 0.75 gave the highest rate of 0.0061/year and the level of 0.183 in year 20. The low genetic correlation of -0.75 gave the lowest rate of 0.0057/year and the level of 0.171 in year 20.

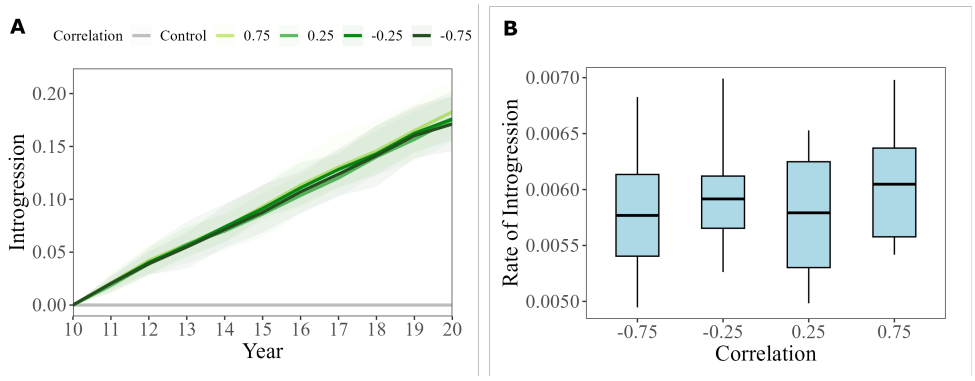

Fig. 5 Changes in the level and rate of introgression from year 10 to year 20 across replicates in scenarios with a varying genetic correlations between fitness traits in Ireland and Central Europe: +0.75, +0.25, -0.25, -0.75. The percentage of imports was set to 4% in all scenarios. A control population that received no imports is also represented. A) Trend in the introgression level with corresponding shaded regions indicating the 95% quantiles. B) Boxplot of the rate of introgression.

The mean genetic value for honey yield in the Irish population by year 20 did not follow a pattern regarding genetic correlation for fitness. With the -0.75 correlation scenario exhibiting the highest mean (0.138 genetic standard deviations) and the 0.25 scenario exhibiting the lowest (0.102 genetic standard deviations) (Figure 6, Table 2). However, none of the differences between the scenarios were significant given the high variation between replicates (Supplementary information: Additional file 1 and Additional file 2).

The partitioning of genetic trends for honey yield further confirmed that although the import increased the honey yield in all scenarios, there was no clear pattern in the size of contribution related to the genetic correlation for fitness in the two environments (Supplementary information: Additional file 5).

The mean genetic value for the fitness trait in the Irish population by year 20 decreased with decreasing the genetic correlation between fitness trait in Ireland and Central Europe (Figure 6, Supplementary information: Additional file 1). The scenario

with the +0.75 exhibited the smallest decrease in the value of fitness by year 20 (-0.041 genetic standard deviations), while the scenario with the -0.75 correlation exhibited the most significant decrease in the value of fitness by year 20 (-0.078 genetic standard deviations) (Table 2, Supplementary information: Additional file 2).

The partition of genetic trends for fitness further revealed the negative contribution of the imported honey bees to the genetic trend for fitness in the Irish population. While the domestic contribution to fitness fluctuated around zero due to stabilising selection, the contribution of the imports was increasingly negative as we decreased the fitness genetic correlation, with the maximum decrease observed with the -0.75 genetic correlation. Fitness declines were mostly driven by the imports, which accounted for 99% of the observed decline (Supplementary information: Additional file 6)

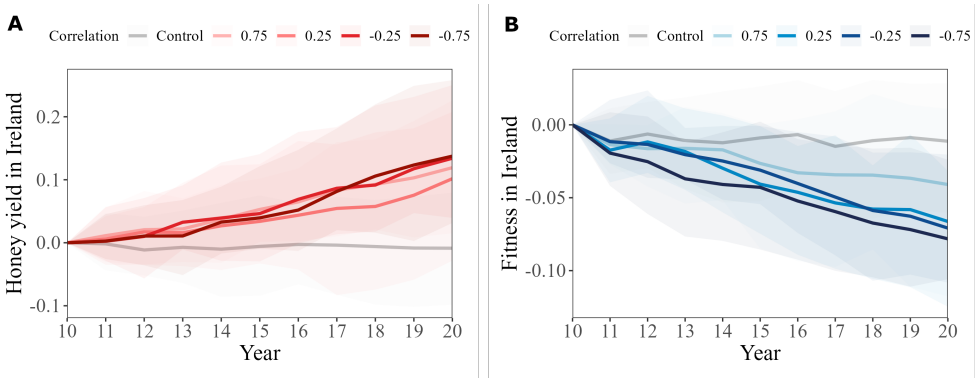

Fig. 6 Changes in the mean genetic value for (A) honey yield (red lines) and (B) fitness trait (blue lines) in the Irish population from year 10 to year 20 in scenarios across varying correlations between fitness traits: +0.75, +0.25, -0.25, -0.75. The solid lines represent the mean genetic value across replicates with corresponding shaded regions indicating the 95% quantiles. A control population that received no imports is also represented.

3.3 Point of entry

In the scenario with a single point of entry, colonies closer to the entry point exhibited higher levels of introgression compared to those further away. For instance, colonies located in a radius of 25km or closer to the point of entry showed levels of introgression that ranged between 75% to 100%, while colonies 100km away from the entry point showed no introgression over the simulated period (Figure 7a). The extensive spread of C lineage alleles was evidenced by the presence of some level of introgression even in colonies located 80km away from the point of entry at year 20. Moreover, the cline analysis revealed a significant increase in the c value over the years ($p < 0.001$) (Supplementary information: Additional file 8). Hence, the centre of the cline was moving away from the point of entry, also indicating that introgression was spreading progressively further from the point of entry as years passed (Figure 7b, Supplementary information: Additional file 7).

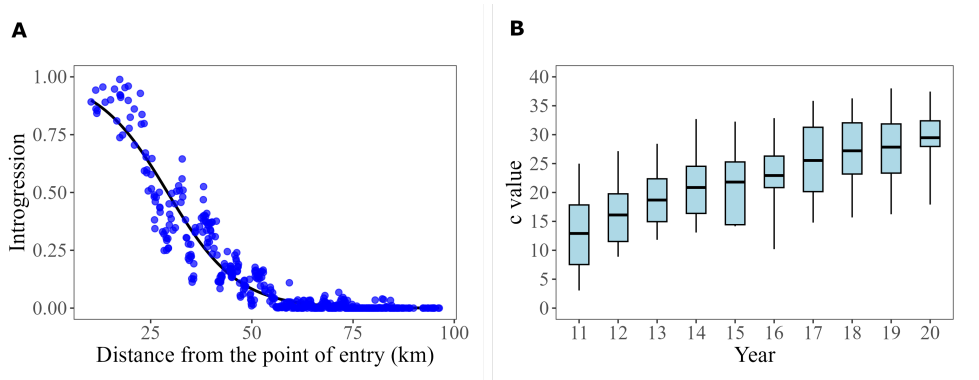

Fig. 7 A) Scatter plot of the introgression levels in honey bee queens in relation to the distance from the central point of entry after 10 years of importation. Each blue dot represents a honey bee queen. The black line indicates the fitted cline to the scatter plot. B) Box plot of the annual changes in the c value (centre of the cline), across 10 years of import over replicates.

3.4 Halt of imports

To evaluate the ability of the population to recover from imports, we extended the spatially-aware scenario (point of entry) by halting imports in year 20 and we continued the simulation for another 10 years.

By year 20, there was a clear increase in the level of introgression, as shown in the results above for the spatially-aware scenario, reaching a value of 0.14 and a rate of introgression of 0.006/year. In the following 10 years without import, we observed a slow decay for the rate of introgression (-0.001/year) compared to the increase observed in the importation period. This led to a gradual decline in levels of introgression, decreasing to 0.13 by the end of the simulation (Figure 8). There was however a substantial variation between replicates on how these levels changed over time.

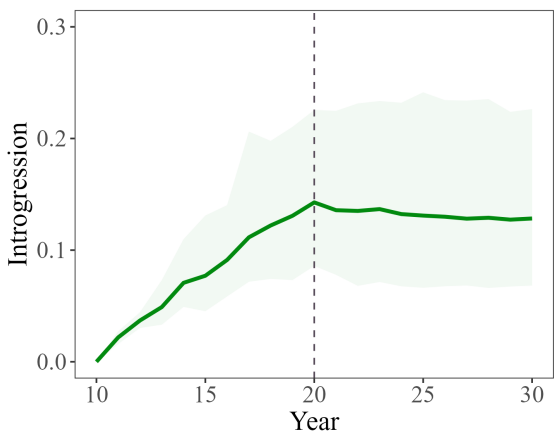

Fig. 8 Trend in the mean level of introgression from year 10 to year 30 across replicates with corresponding shaded regions indicating the 95% quantiles. The dashed line marks the halt of import.

4 Discussion

Hybridisation is an increasing phenomena in agricultural areas that significantly impacts populations management. Whether the goal is to preserve native species or harness hybrid vigor, modelling the outcomes of hybridization is essential to maintaining stable agricultural ecotypes. However, realistic modelling requires the knowledge of many parameters that are often unknown, such as the percentage of imports and fitness of hybrids. Interestingly, the former information would usually be recorded in managed agricultural populations, while the latter would more often be explored in wild populations, but both are seldom known together. In this study, we demonstrate a model of hybridisation between native and imported non-native populations on the example of Irish honey bee populations. Ireland represents a population largely composed of the native *A. m. mellifera*, offering a valuable opportunity to study the process before introgression becomes widespread, as in other European countries, and to take effective measures. We demonstrate the variables that need to be considered when modelling hybridisation and how varying these parameters affects the outcome.

Honey bees are highly migratory mainly due to anthropogenic activities, hence hybridisation is abundant and poses an issue for conservation and managing. There is thus an increasing need to model hybridisation to conserve populations, but also to ensure their productivity. Honey bees have established breeding programmes that genetically improve populations for production and workability traits, and hybridisation can dilute these efforts.

However, honey bees occupy a wide range with varying parameters and many unknowns. In this study, we explored the impact of varying the percentage of import and genetic correlation for the fitness trait between environments, as well as the spatial distribution of native and non-native populations. The model also considers the genetic divergence between the populations by simulating corresponding demographies. We parameterised the model on Irish data, however, we consider it representative of other

European countries that faced the same problem, as population dynamics and import pressures in Ireland are evolving similarly to other countries where this effect is now more notable Alice Pinto et al. (2014); Oleksa et al. (2011); Jensen et al. (2005); Yanbaev (2024).

Our simulation can also guide simulations of other species by offering a study design with a crucial set of parameters to consider when simulating or observing populations, as well as the order of impact for these parameters. Such modelling approaches may become increasingly important as other insect species are being used in commercial breeding programs for food and feed, where escaped individuals could potentially hybridise with native populations, a concern that has been raised in the context of emerging insect production industries (Kaya et al. 2021).

4.1 Percentage of imports

Our simulated import rates of 1.5%, 4%, and 10% captured the European spectrum: at the upper end, the UK imported 21,405 queens in 2020 (on the order of 10% of imports) (Department for Environment, Food and Rural Affairs 2021) while other European countries are reporting high introgression levels (Oleksa et al. 2011; Yanbaev 2024); mid-range values align with Ireland's 4% in 2012, with higher figures during the COVID period (McCann and McCormack 2024); and at the lower end, several Nordic conservation areas restrict non-native introductions (e.g. Læsø in Denmark; protected zones in Norway), implying low import rates (Groeneveld et al. 2020). Queen imports have increased introgression in Irish colonies, reaching 18-25% (Valentine et al. 2024; Smith et al. 2023). Our simulation with 4% of imports generated 18.3% of introgression after 10 years and the rate of 0.006/year, in line with these observations.

Raising imports from 4% to 10% in the simulation increased the level of introgression leading to introgression levels similar to the ones observed on the protected island of Læsø in Denmark, Poland, the Urals and the UK (Alice Pinto et al. 2014;

Oleksa et al. 2011; Yanbaev 2024; Ellis et al. 2018). This rise also increased the mean genetic value for honey yield, and decreased the mean genetic value for fitness. These results are expected since in the simulation the non-native population was under positive directional selection for honey yield, while the native was not. Also, the non-native population was selected for fitness in their own environment. Under such conditions, the expected contribution of imports to honey yield and fitness depends on genetic correlations for these traits between the two environments, as discussed in the following.

4.2 Genetic correlation between traits in the two environments

Results of the simulation depend critically on the assumed genetic correlation between traits in the two environments. For honey yield, we assumed the genetic correlation of 0.75 following Hatjina et al. (2014) that found large differences in honey yield among environmental clusters, with local genotypes generally yielding more than non-local ones. For fitness, we varied the genetic correlation to study its impact on introgression. Changing the correlation from +0.75 to -0.25 or -0.75 significantly decreased the native populations' mean fitness genetic value. This is expected since a negative genetic correlation between two environments implies that the animals performing best in one environment perform less well in the other environment (e.g. Bančič et al. 2023). Therefore, with negative correlations, as honey bees in the native Central European population were increasingly becoming adapted to their environment during the burn-in phase, they were indirectly becoming less adapted for the non-native environment.

Although GxE has not been extensively studied in honey bees, there are reports that honey bees show higher survival in their native environment compared to non-native environments (Ndiaye 2017; Meixner et al. 2015). Reports also show that importing non-adapted honey bees could decrease fitness and increase colony losses (Büchler et al. 2014; Henriques et al. 2018b).

Comparable GxE and fitness consequences of introgression are well documented in other taxa. In salmonids, introgression from domesticated or non-local stocks is associated with reduced fitness and altered life-history across wild populations, and modelling studies tracking fitness under different introgression pressures found that sustained introgression leads to clear declines in wild salmonids fitness (Castellani et al. 2018). These results support our use of different genetic correlations to project the effect of the environment. (Muhlfeld et al. 2009; Karlsson et al. 2016; Castellani et al. 2018)

While decreasing the genetic correlation for fitness decreased the mean genetic value for fitness due to imports, we did not observe the expected corresponding reduction in introgression. An explanation is that the simulated natural selection pressure was not strong enough to purge all non-native alleles. We assumed the native population to be at its fitness optimum and under stabilising selection, but also that fitness is a highly complex polygenic trait affected by 1600 QTLs and has the heritability of 0.1 (hence most of phenotypic variation in fitness is due to environmental effects). Taken together, these assumptions meant that introgressed non-native alleles were effectively largely hidden to selection and could "silently" increase in their frequency over time without major impacts on fitness. Consequently, varying the genetic correlation for fitness did not significantly impact the mean genetic value for honey yield. We hypothesise that implementing directional selection for fitness in the native population would result in a more efficient purging of the non-native alleles, with corresponding impact on both honey yield and fitness.

4.3 Point of entry

Next, we added a spatial component and modelled a single point of entry to explore the spread of introgression. After 10 years, introgression was observed in colonies located up to 80km away from the initial point of entry. This distance was influenced by the

parameters set in our model, particularly the queen mating radius, which was set to 15km based on Jensen et al. (2005). In Ireland, the majority of honey bee imports arrive at ports or major cities, such as Dublin, Belfast, and Cork (Valentine et al. 2024). Although most of these cities are coastal, we placed the import point in the center of the study area to (1) quantify the spread of introgression without being limited by coastline boundaries, (2) allow for a more generalizable scenario regarding the point of entry, and (3) ensure that sufficient data points were available around the point of entry for accurate analysis. We also assumed that there are no major geographical barriers, such as mountain ranges, within this study area. This mostly matches with the geography of Ireland and other European countries (Denmark, UK, Poland, etc). However, geographical barriers would significantly affect the spread of invasive species and could be accounted for when simulating areas with complex topography.

Some population simulation tools now also enable spatially-aware simulation that enable a joint study of populations' genetics and ecology (Chevy et al. 2024), and allow for modelling any geographical barrier (Petr et al. 2023). Such modelling has already proven useful for managed pollinators around greenhouse or release hotspots and for large mammals with focal introductions, such as red–sika deer in mixed estates (Seabra et al. 2019; Goodman et al. 1999).

4.4 Halt of imports

Many countries have recognised the hybridisation of honey bees as a threat. The USA banned importation of adult honey bees in 1922 (U.S. House of Representatives, Committee on Agriculture 1962) while, in Europe, Slovenia banned the import of any honey bee species other than *A. m. carnica* in 2002, and new legislation to ban imports is being considered in Ireland. The question remains what effect does a ban have after the non-native (sub)species has been continuously introduced. We thus tested a scenario in which we halted importation after a series of repeated introductions.

Ten years after halting imports following a 10-year import period we observed only a slight reduction in introgression (rate of -0.001/year). Additionally, there was a large amount of variation in observed levels of introgression between replicates, ranging between 7% and 22%.

We hypothesise this is due to the simulated selection pressure being too weak. Under stabilising selection on a low-heritable polygenic fitness trait, introgressed alleles decline only slowly once established, as seen in other species (Hedrick 2009; Karlsson et al. 2016). For example, seven generations after releases ceased, two wild sea trout populations still retained large amounts of introgressed material (Bekkevold et al. 2025). Similarly, nine years after changes to rainbow-trout stocking in southeastern British Columbia, westslope cutthroat trout at open sites still carried substantial rainbow-trout ancestry (Bennett 2009), and non-native alleles have also been shown to persist after hybridization ceased in Anolis lizards (DeVos et al. 2023) However, the reason for the persistence of introgression could also be hybrid vigour, which we did not simulate. Furthermore, species can also become invasive even without enhancing local adaptation (Mesgaran et al., 2016).

These results highlight the difficulty of reversing introgression once it has occurred, especially in species with high dispersal like honey bees (Tallmon et al. 2004), and a need for an early implementation of preventing measures. For Ireland, where introgression remains relatively low, these results highlight the outcomes of taking preventative action, such as limiting or banning non-native imports, to avoid following the trajectory already observed in other European countries. In managed populations, the promotion of non-native alleles is also exacerbated by artificial maintenance by farmers/beekeepers due to positive effects on production despite potential negative effects on fitness.

4.5 Limitations

Although previous studies provide some qualitative results on the impact of non-native honey bees on native populations (Büchler et al. 2014; Meixner et al. 2015; Ndiaye 2017; Henriques et al. 2018b), no studies have quantified the impact and crucial parameters.

With respect to quantitative genetics, first, there is limited knowledge about the interaction between genotype and environment that significantly affects the consequence of importing. This knowledge is not limited only for honey bees, but also for other insect species. For instance, even for well studied populations such as among *Drosophila* species, the environmental factors shaping hybrid performance and the long-term stability of introgressed alleles are still largely unknown (Miller and Matute 2017).

Second, in honey bees, there is a lack of knowledge regarding artificial and natural selection coefficients, as well as a lack of quantified extent and distribution of dominance effects. The latter could confer hybrid vigour, which would facilitate introgression by increasing the fitness or production of hybrids.

Third, there is little knowledge about the selection mode (directional, stabilising, frequency-dependent, etc.) for different phenotypes, genotype to phenotype map, and environmental or management effects.

In the absence of this knowledge, our simulation was guided by qualitative reports on production and fitness differences between subspecies (Bernstein et al. 2020; Strachan et al. 2024a; Ndiaye 2017; Meixner et al. 2015), but due to the lack of quantitative measures, some of the quantitative genetics parameters needed to be varied in the simulation to include a range of possible outcomes. Varying over all genetic parameters would result in unfeasible number of scenarios, hence we assumed a complex polygenic architecture with only additive effects for honey yield and fitness, published level of heritabilities for honey yield and fitness, and a fixed genetic correlation

for honey yield, while we varied the genetic correlation for fitness and the extent of GxE. Regarding the selection mode for fitness, we assumed directional selection in both populations to generate genetic differentiation, while in the evaluation phase we assumed that both populations are at the optimal value for fitness and under stabilising selection around this value. For honey yield, we assumed directional selection in the non-native population, which is realistic since honey yield is improved through artificial selection that apply truncation selection.

The choice of complex polygenic architecture and low heritability for fitness is in line with published literature (Niklasson et al. 2022; Koeniger et al. 1999). The advent of genome-wide genotype data will hopefully enable studies that will provide more clarity about the form and strength of selection.

We made additional assumptions regarding mating. We assumed random mating in a non-spatial or spatial context, and did not account for mating preference or reproductive barriers between subspecies. However, there is evidence of behavioural differences between honey bees that would result in assortative mating, such as different vertical position of drones at mating (Koeniger et al. 1989), that would decrease the rate of introgression. Future work could include more complex models of bee flight and mating behavior.

We observed high variability across replicates. This is not a limitation, but shows that there is a huge amount of randomness in introgression outcomes driven by the randomness of genetic inheritance, coupled with selection on phenotypes that are a noisy representation of genetic value of individuals. Future work could focus on increasing the number of replicates to better quantify the outcomes and the variability itself. The number of replicates in this study was limited by required computational resources, but the SIMplyBee simulator (Obšteter et al. 2023) is being optimised to work with a larger number of colonies.

For the same reason, we simulated only 500 colonies, representing a fraction of the Irish population. This small population size might have exacerbated introgression and weakened the selection pressure on the imported individuals due to a sizeable drift effect. However, if import is limited to a few entry points with limited migration outside of these areas, our simulation represents the likely situation.

4.6 A way forward?

Assuming significant differences in production between native and non-native populations with medium-to-high genetic correlation, we observed that introgression will happen readily and rapidly spread from the point of entry, increasing genetic value for honey yield and decreasing genetic value for fitness. This process has already progressed substantially in the UK and Nordic countries, while Ireland remains at an earlier stage, with comparatively low levels of introgression but similar import pressures (McCann and McCormack 2024; Valentine et al. 2024; Oleksa et al. 2011; Alice Pinto et al. 2014; Yanbaev 2024; Buswell et al. 2025). So the pertinent question is: "What is the way forward"? While the short-term increase in production increases the commercial interest and benefit of import, it generates a long-term decrease in the native population's fitness. Beekeepers might overcome this with management, but beekeeping practices should be developed alongside native populations and their requirements. An increase in commercially relevant traits may negatively impact free-living honeybees. In the long term, introgression will depend on a complex interplay of the benefits in production and costs of adjusting the management, of beekeepers that want imports and those that do not, selective breeding actions, and strength and direction of natural selection. Climate change will likely be a significant factor in this process.

As shown in the results, even a small percentage of imports leads to introgression of non-native alleles. The effect of these non-native alleles in a new environment is largely

unknown and will depend on the origin of import. These effects could be negative and result in outbreeding depression, or positive as a new source of variation for selection to operate on. This stresses the need for further research on the extent of GxE and the differences in selection coefficients between honey bee populations and subspecies. Ireland thus serves as an important model for implementing conservation-by-use and selective breeding strategies before extensive hybridisation takes place.

The best course of action to prevent loosing the identity of the native populations and their adaptations due to imports is "conservation by use". Commercial beekeepers import non-native honey bee to improve short-term productivity and profitability. However, studies have reported that dark honey bee, native to Northern and Western Europe, has the capacity to forage, survive, and mate in lower temperatures (Jensen et al. 2005). These adaptations have evolved over many years and could be impacted or even lost due to introgression. By establishing selective breeding programmes aimed at enhancing production and workability traits of native populations (or even now introgressed/admixed populations) under local environmental conditions, beekeepers could improve commercial viability while preserving the past genetic adaptations and the identity of the populations. In fact, countries known for exporting their honey bee subspecies globally have established selective breeding programmes. For example, Italy has been selectively breeding for higher productivity and docility for decades (Bar-Cohen et al. 1978). Other European countries, such as Germany, Poland, and Switzerland, have also been successful at breeding for increased brood viability or hygienic behavior (Uzunov et al. 2014). Adopting these selective breeding concepts can lead to developing viable native honey bee populations while preserving the invaluable local adaptations.

5 Conclusion

Our work offers useful guidelines for modelling introgression in honeybees as well as other species with similar dispersal patterns. Here, we provide an open-source stochastic simulation and evaluation model with focus on complex traits, which can be revised and extended as needed and when new knowledge becomes available.

Our results demonstrate that although importing non-native honey bees can increase production traits, is also increases introgression of the non-native alleles, which is associated with a decline in fitness and the loss of native adaptation to the environment. Moreover, the spread of non-native alleles can be fast and substantial with continued imports and introgression can not be reversed quickly, resulting in long-term segregation of the introgressed alleles. These findings highlight the importance of strategies to manage genetically distinct and locally adapted subspecies of honey bees. Imposing strict import regulations may be a necessary solution to preserve native populations as has been applied by some countries and regions. However, it is important to understand and address the reasons for importing non-native honey bees. A comprehensive approach would be (1) to restrict levels/locations of imports of non-native honey bees, (2) to enhance economically important traits of the native honey bees via selective breeding, (3) to raise awareness of the expected level of production of different genotypes in different environments, and (4) to communicate about the risk of short- versus long-term effects of introgressing non-native alleles. To support such an approach, it is important to expand population and quantitative genetics research of honey bee populations.

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7 Author information

7.1 Authors' contributions

IC: conceptualization, simulation coding, data curation, formal analysis, visualization, writing – original draft.

LS: conceptualization, simulation coding, methodology, writing – review and editing.

GM: conceptualization, funding acquisition, supervision, project administration, writing – review and editing.

GJ: conceptualization, funding acquisition, supervision, project administration, methodology, validation, writing – review and editing.

JO: conceptualization, supervision, simulation coding, methodology, validation, writing – review and editing.

7.2 Corresponding author

Correspondence to Jana Obsteter & Irene de Carlos.

8 Availability of data and material

The datasets generated and/or analysed during the current study are available in the idecarlos_honeybee_import repository, https://github.com/HighlanderLab/idecarlos_honeybee_import.

9 Ethics declarations

9.1 Competing interests

The authors declare that they have no competing interests.

9.2 Research Ethics statement

Research ethics committee's approval was not required for this study.

10 Supplementary information

Link to the GitHub repository with code for the simulations:
https://github.com/HighlanderLab/idecarlos_honeybee_import.

Additional file 1. ANOVA results for introgression and genetic values under different import and correlation scenarios.

	Rate of introgression	Introgression at year 20	Honey yield at year 20	Fitness at year 20
Percentage of imports	<2e-16	<2e-16	7.69e-15	3.99e-05
Fitness genetic correlations	0.4760	0.2210	0.2260	0.0093

ANOVA p-values for the rate of introgression, introgression at year 20, honey yield at year 20, and fitness at year 20 across different import percentages and genetic correlation scenarios.

720 **Additional file 2.** Tukey post-hoc comparisons.

	Scenario	Rate of introgression	Introgression at year 20	Honey yield at year 20	Fitness at year 20
Percentage of imports	Control – 1.5%	0.0000	0.0000	0.2780	0.9858
	Control – 4%	0.0000	0.0000	0.0001	0.2006
	Control – 10%	0.0000	0.0000	0.0000	0.0000
	4% – 1.5%	0.0000	0.0000	0.0267	0.3571
	4% – 10%	0.0000	0.0000	0.0000	0.0108
	10% – 1.5%	0.0000	0.0000	0.0000	0.0000
Genetic correlations	0.25 – –0.25	0.9230	0.9933	0.4100	0.8576
	0.75 – 0.25	0.9095	0.7120	0.8172	0.0180
	0.25 – –0.75	0.9994	0.8660	0.5053	0.7157
	0.75 – –0.75	0.4983	0.1640	0.8903	0.0086
	0.75 – –0.25	0.5715	0.5470	0.9032	0.1216

Post-hoc Tukey pairwise comparison p-values between the different percentage of imports scenarios and the different fitness genetic correlation scenarios for the rate of introgression, introgression at year 20, honey yield at year 20, and fitness at year 20.

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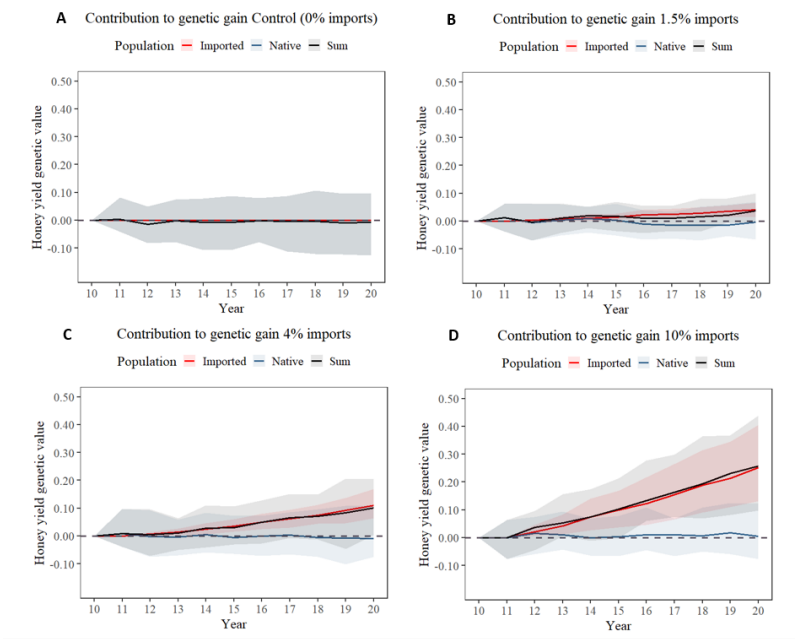
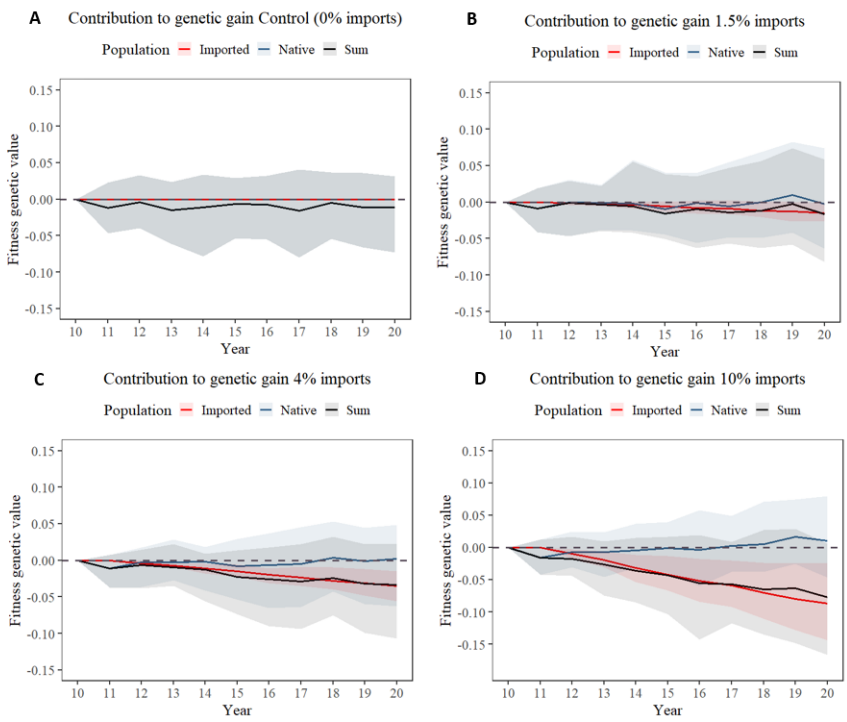
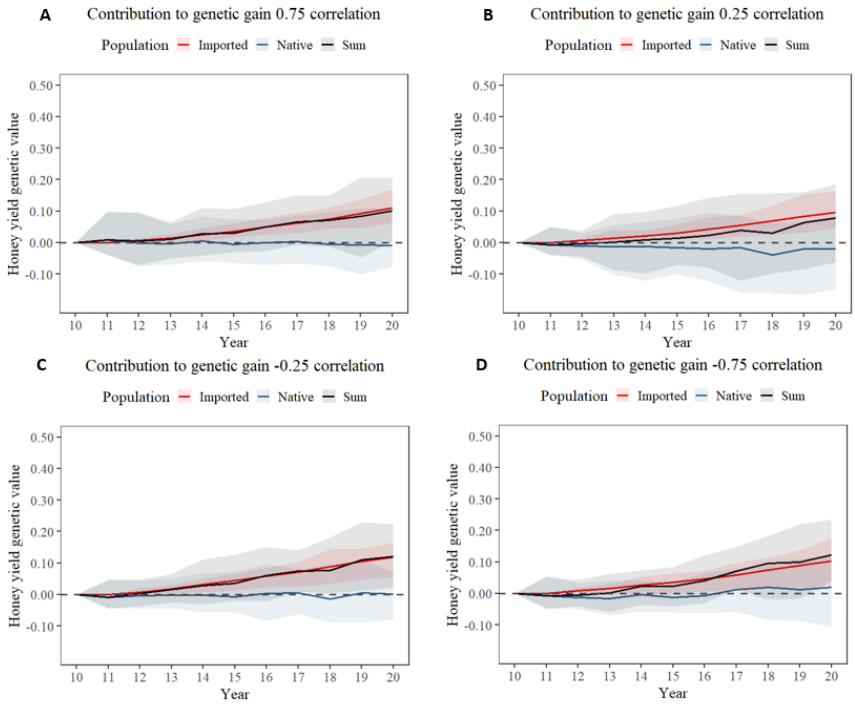


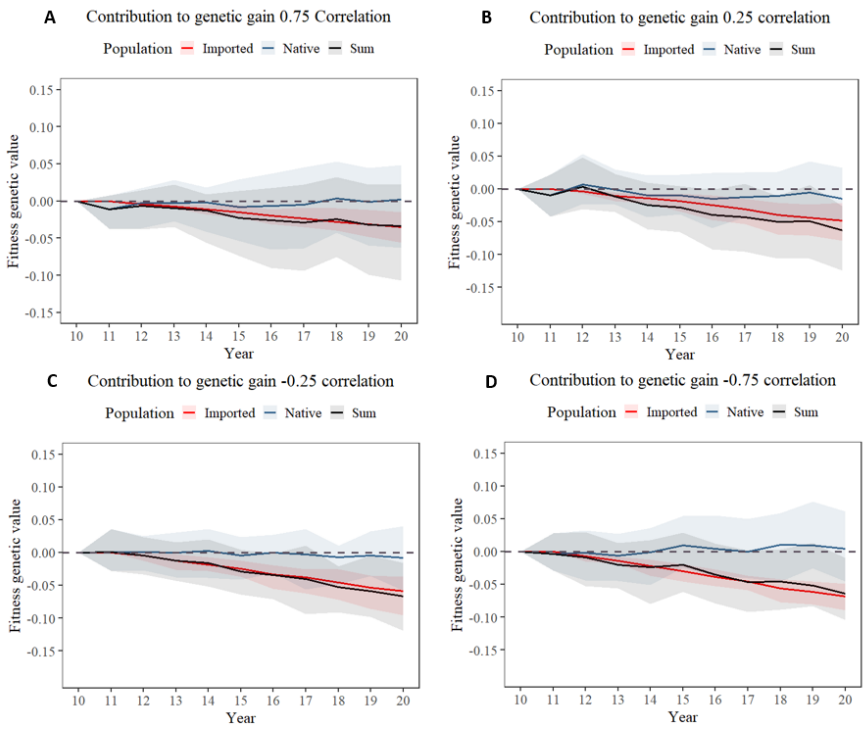
Additional file 3. Contribution to genetic gain of honey yield from year 10 to year 20, comparing the imported (red line) and native contributions (blue line) to the overall honey yield genetic value for the Irish population or Sum (black line). This is represented across varying percentages of imports of C-lineage bees to the Irish population: A) Control (0% imports), B) 1.5% imports, C) 4% imports, and D) 10% imports. Shaded regions indicated the 95% confidence intervals. The contribution of imported C-lineage honey bees increased the genetic value of honey yield for the Irish population. This increase became more evident as the percentage of imports was incremented.



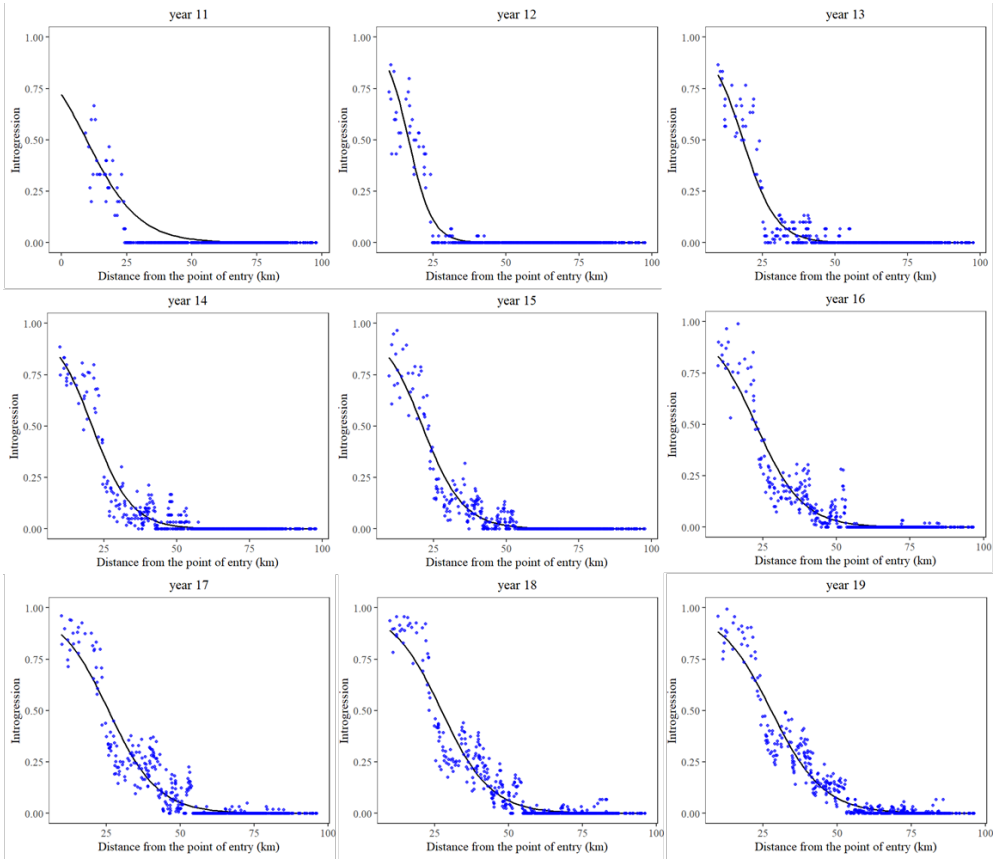
Additional file 4. Contribution to genetic gain of fitness from year 10 to year 20, comparing the imported (red line) and native contributions (blue line) to the overall fitness genetic value for the Irish population or Sum (black line). This is represented across varying percentages of imports of C-lineage bees to the Irish population: A) Control (0% imports), B) 1.5% imports, C) 4% imports, and D) 10% imports. Shaded regions indicated the 95% confidence intervals. The contribution of imported C-lineage honey bees decreased the genetic value of fitness for the Irish population. This decrease became more evident as the percentage of imports was incremented.



Additional file 5. Contribution to genetic gain of honey yield from year 10 to year 20, comparing the imported (red line) and native contributions (blue line) to the overall honey yield genetic value for the Irish population or Sum (black line). This is represented across varying genetic correlations between fitness traits: A) Genetic correlation of 0.75, B) Genetic correlation of 0.25, C) Genetic correlation of -0.25, and D) Genetic correlation of -0.75. Shaded regions indicated the 95% confidence intervals. The contribution of imported C-lineage honey bees increased the genetic value of honey yield for the Irish population. However there was no clear pattern among the different fitness genetic correlations.



Additional file 6. Contribution to genetic gain of fitness from year 10 to year 20, comparing the imported (red line) and native contributions (blue line) to the overall fitness genetic value for the Irish population or Sum (black line). This is represented across varying genetic correlations between fitness traits: A) Genetic correlation of 0.75, B) Genetic correlation of 0.25, C) Genetic correlation of -0.25, and D) Genetic correlation of -0.75. Shaded regions indicated the 95% confidence intervals. The contribution of the imported C-lineage honey bees is in generally negative. The contribution became increasingly negative as the fitness genetic correlation was decreased.



Additional file 7. Scatter plot of the introgression levels in honey bee colonies across the distance from the central point of entry on the first (year 11) to the 9th (year 19) year of importation. Each blue dot corresponds to a honey bee colony, with the y-axis indicating the level of introgression and the x-axis representing the distance from the point of entry, which is marked at 0 km. The black line indicates the fitted cline to the scatter plot.

Additional file 8. Tukey p-value matrix for cline centers pairwise comparisons.

	11	12	13	14	15	16	17	18	19	20
11	–	0.9368	0.2996	0.0305	0.0804	0.0015	0.0031	0.0001	0.9841	0.0000
12	0.9368	–	0.2996	0.0305	0.0804	0.0015	0.0031	0.0001	0.9841	0.0000
13	0.2996	0.2996	–	0.3208	0.6913	0.0342	0.0181	0.0004	0.0734	0.0001
14	0.0305	0.0305	0.3208	–	0.0194	0.0595	0.1534	0.9954	0.9465	0.0000
15	0.0804	0.0804	0.6913	0.0194	–	0.1843	0.1116	0.0103	0.0000	0.0033
16	0.0015	0.0015	0.0342	0.0595	0.1843	–	0.2411	0.9204	0.9939	0.0000
17	0.0031	0.0031	0.0181	0.1534	0.1116	0.2411	–	0.5094	0.0000	0.0000
18	0.0001	0.0001	0.0004	0.9954	0.0103	0.9204	0.5094	–	0.9999	0.9999
19	0.9841	0.9841	0.0734	0.9465	0.0000	0.9939	0.0000	0.9999	–	0.9999
20	0.0000	0.0000	0.0000	0.0000	0.0033	0.0000	0.0000	0.9999	0.9999	–

Table of pairwise Tukey comparison p-values between c values (center of cline) for all years of importation (year 11 to 20).

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