



Bidirectional hybridisation and introgression between introduced European brown hare, *Lepus europaeus* and the endemic Irish hare, *L. timidus hibernicus*

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Abstract

Introduced non-native species can threaten native species through interspecific hybridisation and genetic introgression. We assessed the prevalence of hybridisation and introgression between introduced European brown hare, *Lepus europaeus*, and the endemic Irish hare, *L. timidus hibernicus*. Roadkill hares ($n=56$) were sequenced for a 379bp section of the mitochondrial DNA D-loop and a 474bp segment of the nuclear transferrin (*Tf*) gene. A species-specific indel in the transferrin gene was present in *L.t. hibernicus* and absent in *L. europaeus*. Excluding three hares from which molecular data could not be recovered, 28 hares (53%) were native *L.t. hibernicus*, 7 (13%) were non-native *L. europaeus* and 18 (34%) were hybrids; of which 5 (28%) were first generation (F1) involving bidirectional crosses with mismatched nuclear and mtDNA (3 ♂ *europaeus* x ♀ *hibernicus* and 2 ♂ *hibernicus* x ♀ *europaeus*). Mixed nuclear transferrin sequences suggested 13 (72%) of hybrids were at least 2nd generation (F2) with 9 (69%) possessing *L.t. hibernicus* and 4 (31%) *L. europaeus* mtDNA (the latter indicative of hybrid backcrossing with the non-native). The prevalence of hybridisation at similar mountain-brown hare contact zones throughout Europe is notably lower (4–16%) and typically unidirectional (♂ *europaeus* x ♀ *timidus*). A high prevalence of bidirectional hybridisation and introgression (in association with projected climate change) may favour the introduced species over the native. Genetic surveillance and population monitoring are needed to further explore the potential conservation implications of European brown hare in Ireland.

Keywords D-loop · Hybridisation · Introgression · *Lepus* · mtDNA · Roadkill · Transferrin

Introduction

In some circumstances, introduced non-native species can negatively impact native species most often due to competition for space and resources but sometimes by hybridisation (Rhymer and Simberloff 1996) and introgression; the backcrossing of hybrids with either parental species (Harrison and Larson 2014). Hybridisation may contribute to the success of an invader with an initially low population density as

it reduces the Allee effect; the negative correlation between mean individual fitness and population size (Mesgarana et al. 2016). While hybrids are not always easy to identify from physical features, at the molecular level, hybridisation is clearly evidenced by introgression between species.

In conservation biology, hybridisation between introduced and native species is typically perceived as a threat to the native (Rosinger et al. 2021). Hybridisation and introgression can lead to genetic or demographic swamping by abundant hybrid individuals (Todesco et al. 2016). For example, non-native Sika deer, *Cervus nippon*, freely hybridise with native Red deer, *Cervus elaphus*, in Scotland and Ireland where hybrids can be more common than individuals with no hybrid ancestry (Abernethy 1994; Hayden and Harrington 2000; McDevitt et al. 2009; Smith et al. 2014). Similarly, the genetic integrity of the European wildcat, *Felis sylvestris*, is threatened due to introgression with hyperabundant domestic cats, *F.s. domesticus* (Nussberger

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et al. 2018). Native westslope cutthroat trout, *Oncorhynchus clarkii lewisi*, hybridise with introduced rainbow trout, *Oncorhynchus mykiss*, with first generation hybrids having a high reproductive success promoting introgression (Muhlfeld et al. 2009). In these cases and others, species range shifts due to climate change may increase interactions between introduced and native species driving further declines (Muhlfeld et al. 2014). Davis

In evolutionary biology, hybridisation can confer adaptive benefits improving the evolutionary success of hybrids. For example, obtaining maternally inherited mitochondrial DNA from another species whose metabolism is adapted to a different climatic zone can enhance local adaptation under a changing climate (Chunco 2014). Consequently, hybridisation occurs widely in some taxa, for example, hares, *Lepus* spp. (Ferreira et al. 2021), eroding genetic differences between diverging lineages driving reticulate evolution (Liu et al. 2011) and creating considerable taxonomic uncertainty (Thulin et al. 2006a, b; Melo-Ferreira et al. 2005, 2009, 2011; Alves et al. 2003, 2008a, b). For example, adaptive introgression underlies polymorphic seasonal camouflage in snowshoe hares, *Lepus americanus*, with brown winter coat colour (advantageous during the lower snowfall conditions) likely originated from an introgressed black-tailed jackrabbit, *Lepus californicus*, allele (Jones et al. 2018). The global rise in climate-change induced species range shifts and non-native species introductions, the intractability of their removal in most situations and equivocation over their impacts, have driven recent calls to stop demonising introduced species (Davis et al. 2021). Accepting the ecological change wrought by introduced species, and adopting a dispassionate evolutionary viewpoint, may lower the burden of interventionist conservation action but further biodiversity loss is to be expected in the immediate future (Simberloff 2011). As an example, the European brown hare, *Lepus europaeus*, was introduced to southern Sweden, where it hybridised and introgressed with the native mountain hare, the heath hare, *L. timidus sylvaticus*, replacing it and causing its virtual extinction in less than 200 years (Thulin 2003c).

The European brown hare has also been introduced to Ireland into the range of another endemic subspecies of mountain hare, the Irish hare, *L. timidus hibernicus*. It, along with the stoat, *Mustela erminea hibernica* (Martínková et al. 2007), grouse, *Lagopus lagopus hibernicus* (McMahon et al. 2012; Meyer-Lucht et al. 2016), dipper, *Cinclus cinclus hibernicus* (Hourlay et al. 2008), coal tit, *Periparus ater hibernicus*, and jay, *Garrulus glandarius hibernicus*, likely colonised Ireland naturally after the last glacial maximum and represent a community of genetically distinct endemic subspecies reflecting the island's unique continental biogeography. The Irish hare exists on the westernmost fringe of the mountain hare's distribution

and differs phenotypically, behaviourally and ecologically from other mountain hares (Barrett Hamilton 1898; Dingerkus and Montgomery 2002, Angerbjörn and Flux 1995; Reid 2011). The Irish hare is genetically distinct from its closest geographic neighbours possessing a comparatively high number of unique mitochondrial haplotypes (Hughes et al. 2006; Hamill et al. 2006). The genetic composition of its population is consistent with the long-term accumulation of genetic differences due to local adaptation to snowless conditions (Giska et al. 2022) resulting from its persistence in ice free refuges during successive glacial advances in, or around, Ireland (Montgomery et al. 2014). Thus, hybridisation and introgression with introduced the European brown hare has at least the potential to threaten the Irish hare's genetic integrity as an island endemic.

L. europaeus is one of a long line of mammalian introductions to Ireland by humans since the Holocene (Montgomery et al. 2014). Multiple deliberate introductions occurred throughout Ireland between 1848 and the 1890s (Reid 2011; Fig. 1a). Barrett-Hamilton (1898) reported that several populations established successfully and proliferated, but most disappeared by the end of the 19th century. While there have been isolated reports of European brown hares (Fairley 2001; Sheppard 2004), the only confirmed extant population is 1,000–2,000 individuals in Mid-Ulster spanning south-east County Derry and east County Tyrone (Reid and Montgomery 2007; Caravaggi et al. 2015, 2016). Irish hares have adapted to warmer conditions than elsewhere in the mountain hare range, exploiting habitats from mountains to the coast (Lysaght and Marnell 2016) in the absence of a lowland competitor. Comparison of habitat niches suggest that *L. t. hibernicus* and *L. europaeus* have comparable niche breadths that may completely overlap (Caravaggi et al. 2017a). Both species show a preference for improved grassland over other habitats (Reid and Montgomery 2007). A long-term decline in *L. t. hibernicus* abundance was associated with climatic and agricultural change (Reid et al. 2021). Climate change models predict greater extremes of precipitation and warmer summers in Ireland in the late 21st century (Nolan and Flanagan 2020) making it more suitable for arable agriculture which may favour *L. europaeus* (Caravaggi et al. 2017a).

Here, we examine the genomic impact of *L. europaeus* on *L. t. hibernicus* in Ireland. *L. europaeus* may incorporate *L. t. hibernicus* mtDNA and nuclear DNA into its genome similar to *L. europaeus* with respect to native *L. timidus* in Sweden, the Alps and Russia (Zachos et al. 2010; Thulin et al. 2003a–c 2006a,b) which may lead to elevated fitness of the introduced species. Persistent introgression and possible fixation of introgressed mtDNA and nuclear DNA establishing a hybrid lineage, could render the native species vulnerable to replacement. The fate of earlier introductions and the

current status of European brown hares in Ireland, however, does not suggest that hybrids, if they exist, are undermining abundance of the native species. Alternatively, and perhaps more likely, introgressed nuclear and mtDNA genomes may be less fit and occur at reduced frequencies and disappear over subsequent generations as extant *L. europaeus* die out. We determine whether hybrids between *L. europaeus* and *L.t. hibernicus* exist in Ireland, estimate the prevalence of hybridisation, its directionality and the frequency of first and second generation hybrids and introgression, to assess the potential threat to the endemic Irish hare.

Methods

Tissue sampling

L.t. hibernicus is protected under the Wildlife and Natural Environment Act (Northern Ireland) 2011 (and its predecessors). Derogation under licence permits the taking of animals for scientific purposes, but systematic lethal sampling was deemed undesirable and incompatible with our conservation-orientated ethic. Thus, 56 roadkill hares were collected opportunistically from the vicinity of the non-native *L. europaeus* population established in Mid-Ulster (Counties Derry and Tyrone) accumulated between 2003 and 2008. Whilst sightings of *L. europaeus* have been made near Baronscourt Estate, west County Tyrone (Reid and Montgomery 2007), the population in Mid-Ulster is the only known extant population (Reid 2011; Caravaggi et al. 2016). No attempt was made to attribute a species phenotype to each carcass, which was determined genetically (see below), as many roadkill carcasses were badly damaged. An 8mm biopsy (Robbins Scientific Ltd.) was removed from the ear of each animal and preserved in 98% ethanol (Taggart et al. 1992).

Genetics

Taxonomic reliance solely on mtDNA may lead to erroneous conclusions, whilst a gene/marker in the nuclear genome that can accurately differentiate species based on unequivocal diagnostic sites, may be elusive (Alves et al. 2008b; Ben Slimon et al. 2008). Thus, to ensure reliable species identification, we used sequencing analysis of a 379 basepair (bp) segment of the mitochondrial DNA (mtDNA) D-loop, and a partial 474bp region, between exons 6 and 7 of the transferrin (*tf*) nuclear gene. Previous investigations (Hughes et al. 2006) revealed ≥ 32 fixed genetic differences (sequence mutations) between *L.t. hibernicus* and *L. europaeus* in the D-loop region. After careful examination of sequences of transferrin gene, we found a diagnostic

site that could reliably discriminate *L.t. hibernicus* and *L. europaeus*, based on the presence/absence (indel) of a single species-specific nucleotide in the partial transferrin gene region. All *L.t. hibernicus* had a T at position 158bp while all *L. europaeus* had a deletion at this position. This diagnostic site was reported as valuable in assessing phylogenetic relationships of *L. europaeus* and other hare species by Alves et al. (2003, 2008a,b). We examined the relationship between transferrin haplotypes from *L. europaeus* samples from Ireland (this study), *L. europaeus* and *L. timidus* from Europe including those available from Genbank, and *L.t. hibernicus* from across Ireland beyond the non-native range of *L. europaeus* (from Hughes et al. 2006), to determine the reliability of the species diagnostic characters in transferrin.

The mtDNA D-loop and nuclear *tf* gene were amplified using polymerase chain reaction (PCR) primers using conditions described in Wallner et al. (2001). Amplified PCR products were purified using Microspin columns (©Roche) and were bidirectionally sequenced (Macrogen Inc.). Resulting sequences for both mtDNA and nuclear regions were checked and assembled using the software packages Chromas v2.1 (Technelysium Pty Ltd.) and BioEdit v7.0.5.3 Multiple Sequence Editor (Hall 1999).

Discordant introgressions in nuclear and mitochondrial genomes are indicative of the direction of hybridisation i.e. assigning male and female parentage to species. The phylogenetic analysis based on separate mtDNA fragments were generally concordant. For nuclear DNA data, each individual bidirectional sequence and each polymorphic position in the dataset was carefully scanned to ensure that all double peaks were correctly identified and consistently scored across samples. We used offset chromatogram peaks to directly infer the phase of some or all heterozygous positions in those individuals that were heterozygous for an indel.

Results

All but one of 42 *L. europaeus* examined had a deletion in the nuclear transferrin gene. The sole exception was from Alava, Northern Spain. Thus, the presence of a T residue at 157bp as opposed to a deletion, is likely diagnostic of *L. timidus* and *L. europaeus*, respectively. Either mitochondrial or nuclear sequences could not be identified reliably in three hares (Supplementary Information, Table S1) which were excluded from subsequent analyses leaving $n = 53$. Twenty-eight hares (53%) were identified as endemic *L.t. hibernicus* and 7 (13%) were non-native *L. europaeus* with each possessing its own species-specific mtDNA and nuclear markers (Fig. 1b; Table S1). There were also 18 putative hybrids (34% of identified samples) which possessed a

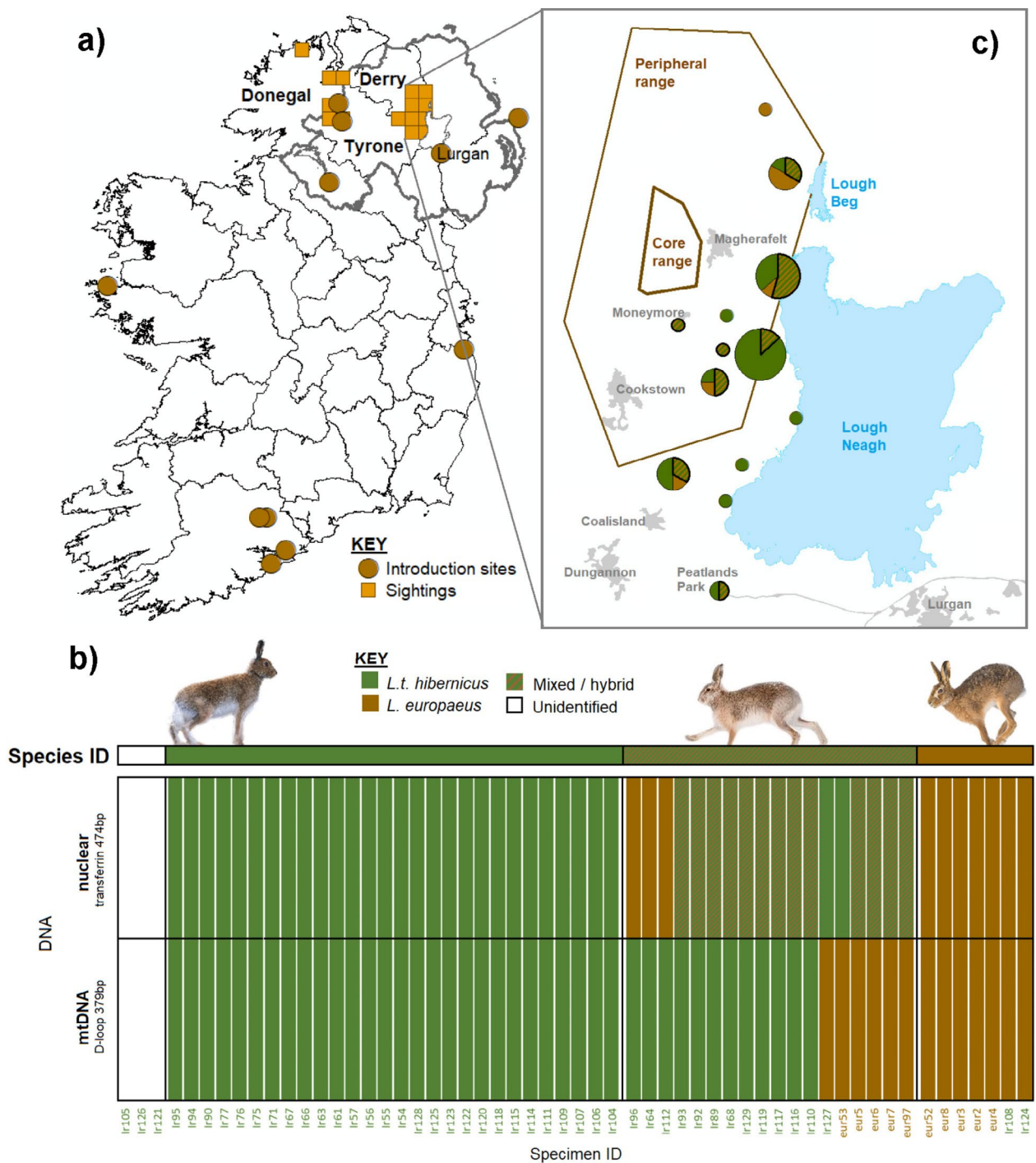


Fig. 1 (a) Known *L. europaeus* introduction sites (brown circles) in Ireland (showing county boundaries for orientation) as reported by Barrett-Hamilton (1898) though all died out except those at Baronscourt Estate, west Tyrone. Subsequently, sightings (tan 10km squares) were reported in north Donegal (Fairley 2001; Sheppard 2004) and Mid-Ulster spanning south-east Derry and east Tyrone (Caravaggi et al. 2016). (b) Infographic showing 53 specimens from Mid-Ulster identified using species-specific mitochondrial (bottom lane) and nuclear (top lane) DNA as *L.t. hibernicus* (green) or *L. europaeus*

(brown) or mixed sequences (hatched green/brown) and species ID (top). (c) Distribution of genetically identified samples relative to the non-native range of *L. europaeus* as surveyed during 2012-13 (Caravaggi et al. 2016) showing named urban areas (grey) for orientation. Pie charts show the percentage of specimens at each location which were native (green), non-native (brown) or hybrids (hatched green/brown) with bold boundary with charts scaled to represent sample sizes ($1 < n < 15$). Hare thumbnails show *L.t. hibernicus* (left ©Mike Brown), *L. europaeus* (right ©Mark Hamblin) and a *europaeus* x *timidus* hybrid during winter (middle ©Mark Hamblin)

combination of mtDNA from one species and nuclear DNA or mixed nuclear sequences from the another. Of these hybrids, 5 (28%) were first generation (F1) involving bidirectional crosses with mismatched nuclear and mtDNA i.e. 3 ♂ *europaeus* x ♀ *hibernicus* and 2 ♂ *hibernicus* x ♀ *europaeus* (Fig. 1b; Table S1). Mixed nuclear transferrin sequences suggested 13 hares (72% of hybrids and 25% of all hares) were at least 2nd generation (F2) of which 9 (50% of hybrids) had *hibernicus* and 4 (22% of hybrids) had *europaeus* mtDNA (the former indicative of hybrid backcrossing with the native and the latter indicative of backcrossing with the non-native i.e. bidirectional introgression). The generational timing of such backcrossing was undetermined.

Hybrids spanned an area 40km north to south along the eastern range edge margin of *L. europaeus* down the western shore of Lough Neagh (Fig. 1c). Both *L. europaeus* and hybrids were found up to 13km south of the former's known southerly range edge margin suggesting it may be more widespread than recorded by Caravaggi et al. (2016) with genomic impacts well beyond its known range.

Screening of an additional 24 *L.t. hibernicus* sampled throughout Ireland beyond the immediate vicinity of the range of *L. europaeus* (>15km) failed to provide any evidence of hybridisation or introgression suggesting known failed historical introductions elsewhere left no lasting genomic impact. The 12 hybrids from Mid-Ulster possessing *L.t. hibernicus* mtDNA D-loop haplotypes shared these with the additional 24 *L.t. hibernicus* sampled throughout Ireland.

Discussion

Molecular markers and species ID

Sequencing mtDNA (D-loop) and a portion of the nuclear gene transferrin (*tf*) revealed a deletion in the *L. europaeus* transferrin sequence that differentiated them from *L.t. hibernicus*. This deletion in the *L. europaeus* transferrin sequence not present in *L. timidus*, has been reported previously (Melo-Ferreira et al. 2009). With the exception of one out of 42 individuals, all *L. europaeus* had a deletion at this site, supporting this as a diagnostic marker for this species. The exception was a specimen from Alava, Northern Spain, a region with previous evidence of ancient and recent mitochondrial and nuclear introgression (Melo-Ferreira et al. 2009). Thus, it is likely that this *L. europaeus* acquired the T polymorphism from *L. timidus*.

Hybridisation in Ireland

A mismatch between species-specific mitochondrial and nuclear DNA indicated animals had hybrid ancestry. At contact zones between *L. timidus* and *L. europaeus* throughout Europe, hybridisation is typically unidirectional between female *L. timidus* and male *L. europaeus* (Alves et al. 2003; Thulin et al. 2003a-c, Melo-Ferreira et al. 2005; Zachos et al. 2010) which are larger and more likely to engage in mate guarding behaviour than male *L. timidus* (Flux and Angerbjörn 1990). In Ireland, we detected bidirectional, first generation (F1) hybrids with three examples of the former direction and two examples of male *L.t. hibernicus* mating with female *L. europaeus*. Despite a small sample size, it seems that bidirectional crosses occurred at a similar frequency (17% and 11% of hybrids respectively). Irish hares (3.5–4.5kg) are the largest of the 16 subspecies of *L. timidus* (others being 2.5–3.5kg typically; Angerbjörn and Flux 1995) and may compete more effectively with *L. europaeus* males than their smaller relatives, thus evening up the odds for successful hybrid mating in either direction. *L. timidus* male x *L. europaeus* female crosses have been achieved by artificial insemination in captivity in Sweden (Gustavsson and Sundt 1965), but such hybrids (and their descendants) may suffer a competitive disadvantage in the wild (Thulin and Tegelström 2002).

Bidirectional introgression was also recorded in the present study with hybrids backcrossing predominately with the native (69% of individuals with mixed nuclear sequences had *L.t. hibernicus* mtDNA) with *L. europaeus* backcrossing more limited: 31% of individuals with mixed nuclear sequences had *L.t. hibernicus* mtDNA). This >2:1 ratio reflects the 3:1 non-native:native ratio in population density at the invading wavefront of *L. europaeus* (Caravaggi et al. 2016) suggesting the frequency of bidirectional introgression reflects the populations of parental and hybrid stock and availability of potential mates.

Notwithstanding any potential skew or bias due to our opportunistic sampling strategy (and associated small sample size), the prevalence of hybridisation and introgression in Ireland at 33% of sampled individuals was notably higher than (unidirectional hybridisation and introgression) reported from Sweden at 7–16% (Thulin and Tegelstrom 2002; Jansson et al. 2007), and Russia and Switzerland, both at 4%, where *L. europaeus* is expanding its range (Thulin et al. 2006c; Zachos et al. 2010). Bidirectional hybridisation and introgression has also been reported at much lower frequencies than in Ireland (present study), in Russia (Thulin et al. 2006a), Scandinavia (Thulin et al. 2006b; Melo-Ferreira et al. 2009) and the Alps (Suchentrunk et al. 2005, 2006; Melo-Ferreira et al. 2009, 2011; Zachos et al. 2010).

Irish hares screened throughout Ireland beyond the range of *L. europaeus* revealed no evidence of any *L. europaeus* genomic legacy beyond their current range. Hughes et al. (2006) examined >100 hares for mtDNA and screened >1,100 hares throughout Ireland for microsatellite markers exhibiting variation in allelic frequency between *L. timidus* and *L. europaeus* (OCMSAT5, SAT5 and IH270) but found no evidence consistent with the presence of *L. europaeus*. Thus, despite sightings (Dingerkus 1997; Shepard 2004), and notwithstanding unknown populations, most historical *L. europaeus* introductions to Ireland appear to have died out without trace except for those reported here, in Northern Ireland, within which hybridisation and introgression with the endemic Irish hare is extensive. This suggests that the future of *L. timidus hibernicus* may not be threatened genetically by the presence of introduced *L. europaeus* under prevailing conditions without substantial expansion of the non-native's population. Speculatively, introgression has the potential to convey adaptive potential, for example, *L. europaeus* hybrids could acquire mountain hare mitochondrial DNA enhancing metabolism such as a homeostatic ability to tolerate cool, damp conditions typical throughout Ireland while *L.t. hibernicus* hybrids could acquire the European brown hare's tolerance for higher temperatures potentially mitigating the impacts of climate change.

Lepus hybridisation and introgression

Hybridisation and introgression are ubiquitous throughout the genus *Lepus* and throughout their distribution and involve ancient as well as recent phenomena (Alves et al. 2003; Liu et al. 2011; Acevedo et al. 2012; Melo-Ferreira et al. 2014a, b; Marques et al. 2017a; Seixas et al. 2018; Ashrafzadeh et al. 2018; Momhammad et al. 2020). Phylogenetic or deep introgression is associated with species replacements during glacial advances and retreats (Melo-Ferreira et al. 2014c; Kinoshita et al. 2019). More recent introgression occurs where there are parapatric distributions, perhaps leading to a hybrid zone, or species expansions due to climate change or introductions (Zachos et al. 2010; Cheng et al. 2014; Schenker et al. 2020). Deep introgression can result in a gradient in introgression which is a record of species replacement and a similar phenomenon is apparent in expanding populations. In both scenarios, the level of introgression is highest close to the invasion wavefront (Marques et al. 2017a). Introgression in hares mainly involves mtDNA and is generally unidirectional (Melo-Ferreira et al. 2012, 2014a) but there are exceptions to both generalisations (Wu et al. 2011; Levanen et al. 2018a, b). Whilst phylogenetic studies produce bifurcating trees, the level of introgression in past and current relationships amongst hare

lineages is best represented by a network referred to as reticulate evolution e.g. Liu et al. (2011), Acevedo et al. (2015) and Tolesa et al. (2017).

Introgression in hares may be selected for and is adaptive: for example, camouflage in snowshoe hares *Lepus americanus* (Jones et al. 2018), coat colour variants (Giska et al. 2019, 2022); structural and physicochemical properties of proteins encoded by the OXHPOS complex in Arctic lineages of Northern American hares (Melo-Ferreira et al. 2014b); and genes associated with spermatogenesis, immunity and mitochondrial metabolism in northern populations of *L. granatensis* (Seixas et al. 2018). Thus, hares are excellent models for research on the interplay of biogeography and evolution where there are marked discontinuities in global change due to climate change and anthropogenic introductions (Acevedo et al. 2012; Marques 2017b; Reid et al. 2021).

Future of european brown hare in Ireland

The current restricted geographical distribution of *L. europaeus* in Ireland suggests that it has not spread far from its point of introduction in Mid-ulster and that its origin may be as recent as the 1970s (Caravaggi et al. 2016). *L.t. hibernicus* possesses a high level of genetic diversity being isolated in Ireland for a longer period of time and adapted to a wider range of lowland and upland conditions than *L. timidus* subspecies in Scandinavia and the Alps (Hughes et al. 2006; Giska et al. 2022). As such, *L. t. hibernicus* may be a stronger ecological competitor for *L. europaeus* than its continental relatives. Thus, the outcome for this population may follow the pattern of earlier introductions of *L. europaeus* throughout Ireland becoming extinct leaving little or no genetic trace. However, it is still possible that the high degree of hybridisation and introgression described here in conjunction with climate change or some other environmental factor(s) may result in a more persistent interaction and a long-lasting genomic legacy.

Model simulations suggest that if an invasion is recent and interbreeding events are infrequent, introgression of genes tends to be from the native to the invader irrespective of relative densities of the two, and symmetrical (bidirectional), but becomes asymmetric (unidirectional) with increasing interbreeding levels (Currat et al. 2008). This is consistent with empirical data with 32 cases (82%) of invasions and range expansion showing this pattern (Currat et al. 2008). In Sweden, most of the asymmetric transfer of *L. timidus* mtDNA into *L. europaeus* may have occurred during the initial rapid expansion of the invader with hybrid frequency declining 10–20 years following introduction, indicating that interspecies mating occurs when there is a lack of conspecific partners. Thus, initial impact on the

genetic make-up of the species is worse at the beginning of the invasion but should decline over time. Hybrid occurrence was higher in areas of current sympatry with 9 of 12 *L. europaeus* carrying *L. timidus* mtDNA at the wavefront of the invasion compared to 11 of 70 in former areas of sympatry (Jansson et al. 2007). This process did not apparently impact Swedish *L. timidus* genetically, but caused *L. timidus* to retreat northwards with the near extinction of the heath hare, *L.t. sylvaticus*, whose range was restricted to south Sweden (Thulin 2003c). Swedish *L. timidus* are limited by resources in the lowland grasslands in the south while the northward expansion of *L. europaeus* is constrained by the snowline (Jansson et al. 2007).

In Ireland, bidirectional hybridisation and symmetrical transfer of genetic material may become more asymmetric, *L. europaeus* absorbing *L.t. hibernicus* mtDNA, as the invasion progresses, and transfer of nuclear *L.t. hibernicus* DNA to *L. europaeus* becoming less likely. If both species remain at low densities, *L. europaeus* may simply die out in common with previous introductions. Nevertheless, the *L. europaeus* population has expanded in Ireland since its first discovery perhaps indicating a growing propensity for persistence. Certainly, future change in climate (and likely associated changes in agriculture) in Ireland are likely to favour the invader and disadvantage the native (Caravaggi et al. 2017a).

Nineteenth century densities of *L.t. hibernicus* were probably much higher and widely adapted to the habitat in Ireland (Reid et al. 2021). However, *L.t. hibernicus* numbers declined dramatically during the early 20th century due to habitat fragmentation and landscape homogenisation due to agricultural intensification, and climatic change (Reid et al. 2021), to reach current low densities (McGowan et al. 2019). Early introductions of *L. europaeus* during the mid- to late-1800s, therefore, may have been met with greater resistance than the more recent introduction to Mid-Ulster where low densities of the native offer little resistance to invasion. Hybrid hares in Sweden and Russia occur where densities of each species are low, and, hence, frequency dependent, assortative mating can arise (Thulin et al. 2006a, b; Jansson et al. 2007). This can occur when one species dominates the other or when both species occur at low density allowing the two species to hybridise due to low availability of conspecific partners, known as Hubbs' principle (Chan and Levin 2005). *L.t. hibernicus* occurs at around 3 hares/km² in allopatry, *L. europaeus* in their core range are up to 5 hares/km², with densities of both species roughly equal in sympatry (Caravaggi et al. 2016). The balance of competition between both species likely pivots on subtle differences in habitat choice with the *L.t. hibernicus* preferring pastoral agriculture and *L. europaeus* preferring areas with a higher coverage of arable crop.

Monitoring, surveillance and sampling

In the Republic of Ireland, *L. timidus* is listed on Annex V of the EU Habitats and Species Directive 92/43/EEC with Articles 11 and 17 requiring regular monitoring and reporting on its conservation status while monitoring and surveillance, management and eradication of non-native species like *L. europaeus* is covered by the EU Regulation 1143/2014 on Invasive Alien Species. Northern Ireland is no longer an EU member after the United Kingdom left the EU in 2021 with the impact of legislative transition on conservation priorities unclear. Regardless, being one of Ireland's few truly endemic mammals (Montgomery et al. 2014), any potential threat to the status of *L.t. hibernicus* should be taken very seriously by Government agencies and Departments in both jurisdictions north and south of the border. A European brown hare invasive Species Action Plan (iSAP) is required galvanising stakeholders (Government, landowners, farmers and the public) to support monitoring and surveillance of hare distribution and abundance and systematic sampling of hares to evaluate genomic impacts. The attitudes of landowners and others are important in setting an agenda for conservation of Irish hare such that a program of outreach and engagement may be required to attain majority support for lethal control of invading *L. europaeus* (Caravaggi et al. 2017b). Notwithstanding calls for eradication, this interspecific interaction zone offers an excellent study system by which to test ideas and concepts involved in invasion biology, population dynamics and evolutionary biology.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s10592-022-01471-5>.

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Author contribution N.R. identified presence of European brown hares in Mid-Ulster, verified their history and absence elsewhere in Ireland, collected samples, drafted the manuscript including production of the figures and is the corresponding author. M.F.H collected samples, extracted DNA and conducted genetic analyses. R.A.H. developed molecular markers and supervised laboratory training and analyses. W.I.M. secured funding and contributed intellectually throughout. P.P. supervised genetic work and contributed intellectually throughout. N.R., W.I.M and P.P. edited the manuscript.

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Data Availability The datasets generated are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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