

Range expansion and comparative habitat use of insular, congeneric lagomorphs: invasive European hares *Lepus europaeus* and endemic Irish hares *Lepus timidus hibernicus*

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Abstract The European hare (*Lepus europaeus*) has declined throughout its native range but invaded numerous regions where it has negatively impacted native wildlife. In southern Sweden, it replaces the native mountain hare (*L. timidus*) through competition and hybridisation. We investigated temporal change in the invasive range of the European hare in Ireland, and compared its habitat use with the endemic Irish hare (*L. timidus hibernicus*). The range of the European hare was three times larger and its core range twice as large in 2012–2013 than in 2005. Its rate of radial range expansion was 0.73 km year⁻¹ with its introduction estimated to have occurred ca. 1970. Both species utilised improved and rough grasslands and exhibited markedly similar regression coefficients with almost every land cover variable examined. Irish hares were associated with low fibre and high sugar content grass (good quality grazing) whilst the invader had a greater tolerance for low quality forage. European hares were associated with habitat patch

edge density, suggesting it may be more suited to using hedgerows as diurnal resting sites than the Irish hare. Consequently, the invader had a wider niche breadth than the native but their niche overlap was virtually complete. Given the impact of the European hare on native species elsewhere, and its apparent pre-adaptation for improved grasslands interspersed with arable land (a habitat that covers 70 % of Ireland), its establishment and range expansion poses a significant threat to the ecological security of the endemic Irish hare, particularly given their ecological similarities.

Keywords Invasive alien species · Spatial ecology · Niche overlap · Species replacement

Introduction

Invasive species have significant negative impacts on native species and ecosystems worldwide (Parker et al. 1999; Sakai et al. 2001; Montgomery et al. 2012). Potential issues include interspecific competition for resources (Hamel et al. 2013) and hybridization with related native species (Huxel 1999). Once established, invasive species are often difficult to manage or eradicate (Sandlund et al. 2001; Zavaleta et al. 2001). This is particularly true of invasive mammals on islands (Simberloff and Rejmánek 2011), including the British Isles (Harris and Yalden 2004). As such, the establishment of non-native species is of

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considerable concern among conservationists and land managers (Usher et al. 1986; Harris and Yalden 2004).

The European hare (*Lepus europaeus*, Pallas 1837) is an open-grassland specialist, native to much of mainland Europe and the Asian steppe (Flux and Angermann 1990). Populations in its native range have declined due to agricultural intensification (Hutchings and Harris 1996; Smith et al. 2005). However, European hares have been introduced to, and subsequently become established in, a wide range of regions, including Great Britain, Sweden, Australia, New Zealand, North and South America, and a range of small islands including the Falkland Islands (Flux and Angermann 1990; Tapper and Yalden 2010). The species was introduced to Ireland in the mid-to-late nineteenth century, primarily for field sports, with up to 15 separate introductions recorded between 1848 and 1892 (Barrett-Hamilton 1898). Despite initial establishment, most introduced populations subsequently died out (Barrett-Hamilton 1898). However, the species was confirmed as established at two locations in Northern Ireland in 2005: the central lowlands of mid-Ulster and West Tyrone (Reid and Montgomery 2007). Despite a number of reported sightings (Carlton 1978; Smiddy 1994; Fairley 2001; Sheppard 2004), presence of European hares has not been confirmed in the Republic of Ireland in recent decades (Reid 2011).

The Irish hare (*Lepus timidus hibernicus*, Bell 1837) is an endemic sub-species of mountain hare (*L. timidus*, Linnaeus 1758). However, research supports the contention that the Irish hare warrants full species status (Hughes et al. 2006). It seems certain that it represents a distinct, genetically diversified lineage dating from the middle part of the Quaternary, with its closest relatives being continental mountain hares, rather than neighbouring Scottish mountain hares (*L. t. scoticus*). Sub-fossil and fossil evidence (Yalden 1999) from around the time of the Last Glacial Maximum (ca. 28 kybp) suggests that the Irish hare was isolated from other lagomorphs well before Ireland became an island ca. 15 kybp (Clark et al. 2012). Prior to the introduction of alien mammalian prey species e.g. rabbits (*Oryctolagus cuniculus*) and deer species, the Irish hare was a key prey item for mammalian predators e.g. wolves (*Canis lupus*) and lynx (*Lynx lynx*), as well as golden eagles (*Aquila chrysaetos*), for which hares were a major dietary component (Brown and Watson 1964; Sleeman 2008).

In the absence of ecological competitors, the Irish hare evolved to express marked ecological plasticity. Unlike other mountain hares which are restricted to upland habitats, Irish hares are found from the intertidal zone where they forage on seaweeds (Wolfe et al. 1996) to mountain summits (Walker and Fairley 1968), though they are most abundant in agricultural grasslands (Reid et al. 2007). Indeed, Ireland is the only temperate country in which mountain hares are observed over such a range of habitats. Due to their predominant grazing habit and dependence on grasses, they are ecologically more similar to the European hare than other mountain hares (Reid 2011). Agricultural intensification during the twentieth century is regarded as the main cause of a long-term decline in Irish hare abundance (Dingerkus and Montgomery 2002; Reid et al. 2010). Consequently, the Irish hare is a priority species for conservation action throughout Ireland (Anonymous 2000, 2005).

Most members of the genus *Lepus* occur in parapatry (Flux 1981). Whilst the separating mechanisms are not clear, competitive exclusion has been suggested as the most likely process (Flux 1981; Wolfe et al. 1996). Where species have evolved in close proximity, parapatric boundaries are usually relatively stable due to differential habitat requirements and spatial intolerance (Flux 1981). Where ecologically similar species come into first or secondary contact due to human-mediated introductions, sympatry is transient and usually short-lived (Flux 2008). For example, since the introduction of the European hare to Sweden in the mid- to late-1800 s, the native mountain hare declined over 210,000 km² of its range (Jansson and Pehrson 2007); an area 2.5 times the size of Ireland. Competition in combination with replacement mediated by hybridisation, have been posited as the main factors driving the decline and replacement of the native species (Thulin 2003).

On the island of Ireland, the European and Irish hare have comparable habitat niche breadths and near complete niche overlap (Reid and Montgomery 2007), indicating potential for interspecific competition. Both species occur in sympatry and have been observed engaging in pre-copula mating behaviour (Reid and Montgomery 2007). Hybridisation between introduced and native species is a common problem (Rhymer and Simberloff 1996); for example, introduced sika deer (*Cervus nippon*) freely hybridise with native red deer (*Cervus elaphus*) in Scotland and

Ireland, producing fertile offspring which are at no competitive disadvantage compared to either parental species (Abernethy 1994; Hayden and Harrington 2000). There is increasing evidence that the European hare poses a threat to the genetic integrity of the Irish hare with up to 30 % of road-casualty hares sampled within their invasive range being of hybrid origin (Hughes et al. 2009). This is much higher than hybrid prevalence estimates elsewhere in areas of naturally-expanding European hare range (Thulin and Tege-lström 2002; Thulin et al. 2006; Jansson et al. 2007; Zachos et al. 2010). The threat of hybridisation is particularly pronounced in the Irish hare due to its unique genetic status (Hughes et al. 2006). Consequently, both ecological and genetic mechanisms suspected as necessary for species replacement involving European and mountain hares in Sweden occur in Ireland leading Reid (2011) to suggest that co-occurrence in Ireland is likely to be transient whilst the European hare becomes sufficiently established to create a core zone of allopatry.

Here, we quantify temporal changes in the distribution and range of the European hare in Ireland by repeating a survey first conducted during 2005 (Reid and Montgomery 2007). We test the hypothesis that the European hare has expanded its range and that the ratio of invasive versus native hare records is likely to be more skewed towards the invasive species than in the past. We also describe comparative habitat use of the two species in order to establish the likelihood of interspecific competition for either space or resources. Such information is required to better understand the dynamics of invasive and native species interactions and inform invasive species management and/or eradication strategies.

Methods

Field surveys

Nocturnal spotlight counts were carried out in a 1,652 km² area of the mid-Ulster region of Northern Ireland during winter 2012–2013. Probability of detection was likely to be highest during winter, as hares are active immediately prior to, and including, their mating season which commences in January, vegetation is at its lowest height, and domestic livestock are typically housed indoors, reducing

disturbance. Roughly parallel transects along minor roads running southeast to northwest were exact repeats of a survey conducted during 2005 (Reid and Montgomery 2007). Additional transects running southwest to northeast were added to fill in gaps in the previous survey and provided a more even distribution of sampling effort. Surveys began 1 h after sunset and transects were driven at 15 km h⁻¹. A Toyota Hilux pick-up truck was fitted with a custom-built frame which elevated the observer's line of view above most hedgerows. Surrounding fields were swept with a 3 × 10⁶ candlepower spotlight with the observer systematically sweeping the light 180° on both sides of the road, working from the area closest to the vehicle towards the horizon. When a hare, or group of hares, was sighted, the vehicle was stopped and the phenotype of each examined using 8 × 50 binoculars and described as European-hare-like or Irish-hare-like. Positive identification of hares was not possible with 100 % accuracy due to the prevalence of hybrids in the area, as determined by genetic analyses (Hughes et al. 2009). Visual identification was based on pelage colour and texture, the length of the ears relative to the head, the presence of contrasting black tips to the ears, the shape of the head in profile, presence of white muzzle stripes, colour of the ventral surface of the tail (Fig. 1) and running gait. Following Reid and Montgomery (2007), each transect was surveyed during November 2012 (post-breeding), and again during February 2013 (pre-breeding). Note that both surveys (2005 and 2012–2013) were designed to establish the range of the European hare, including areas of sympatry and native Irish hare allopatry. Hence, they differed in the extent covered as the range of the European hare changed from 2005 to 2012–2013.

Environmental parameters

As the survey methodology was based on continuously driven line transects we had geo-referenced locations for presence records only (i.e. where a hare was seen). Therefore, pseudo-absence points were generated randomly along the network of survey transects to match the number of presence records recorded for each species during November 2012. Pseudo-absences were generated: beyond 450 m from the nearest positive record i.e. beyond a putative mean home range of ~16 ha in area, or 225 m in radius (Reid et al. 2010); within 200 m perpendicular to the

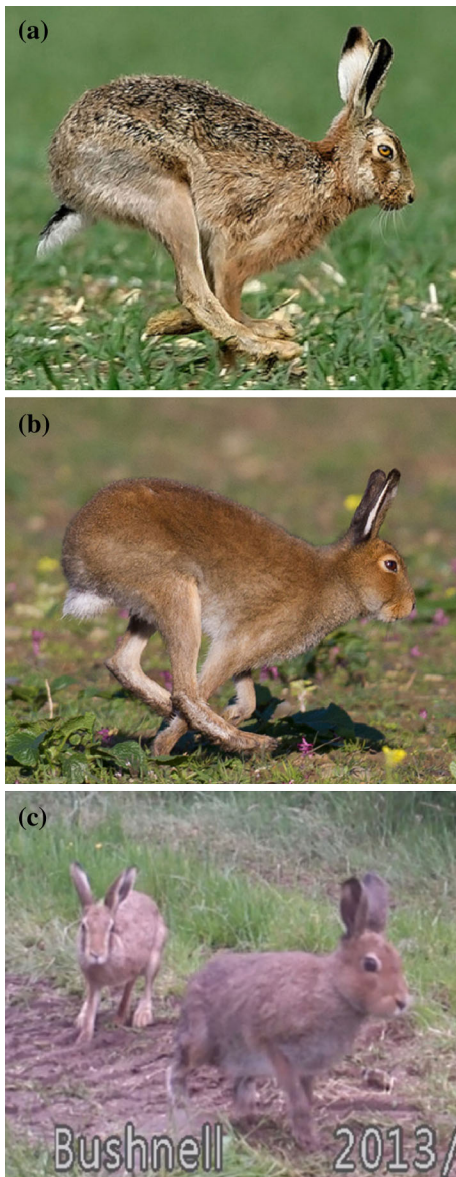


Fig. 1 **a** European hare (*Lepus europaeus*; image © Nigel Blake), **b** Irish hare (*Lepus timidus hibernicus*; image © Shay Connolly), and **c** both species together photographed by a Bushnell Trophy HD trail cam in mid-Ulster during June 2013

transect (with a normal distribution around a mean of 35 m to match the distribution of presence records with respect to the road); in grassland habitats only. All pseudo-absences associated with European hare data were generated *within* its invasive range to account for non-equilibrium (e.g. see Horak et al. 2013), i.e. pseudo-absences generated beyond the range of the invasive species would not have indicated

non-selection but merely that the species had not yet had time to colonise.

Land cover was extracted from the UK Land Cover Map 2007 (Morton et al. 2011) including improved grassland, rough grassland, arable, woodland (broad-leaved woodland plus coniferous plantations). Mean habitat patch size (ha) and mean habitat patch edge density (m/ha) were calculated using the CNFER Patch Analyst 5 (Rempel et al. 2012) plugin for ArcGIS 10.0 (ESRI 2011). Each land cover variable was extracted within six distances buffered around each record including: 225 m, 500 m, 1 km, 2.5 km and 5 km. An index of hilliness (or surface roughness) was extracted from a Digital Elevation Model of Northern Ireland. The latter was calculated within a buffer of 225 m only as the standard deviation of altitude (Newton-Cross et al. 2007), to explicitly account for varying detectability within fields due to the undulation of terrain. Soil drainage [a principal component (eigenvalue = 1.881) of soil clay content ($r = 0.971$) and sand content ($r = -0.971$) explaining 94 % of the variation in soil structural coarseness], was created from the Northern Ireland Soil Survey (Cruickshank 1997).

At all points (presences and pseudo-absences) 300 g of ground-level vegetation was sampled and analysed for acid detergent fibre i.e. digestibility (Font et al. 2005) and water soluble carbohydrates i.e. readily available energy (Cosgrove et al. 2007). Both were expressed as percentage of dry mass, hereafter referred to simply as grass fibre and sugar content. Measurements were taken using Near-infrared Spectroscopy (NIRS) by the Agri-Food and Biosciences Institute (AFBI), Hillsborough, Northern Ireland.

To account for spatial autocorrelation i.e. aggregation of presence records, Moran's Z scores (Moran 1950) were calculated using the Spatial Analyst function in the ArcGIS toolbox for each spatial scale.

Statistical analyses

The range of the European hare was compared between 2005 (Reid and Montgomery 2007) and 2012–2013 using 100 and 50 % minimum convex polygons (MCPs) and mapped using ArcGIS. Radial range expansion was taken as the difference in the radius of two circles; one equal to the area of the range in 2005 and the other equal to the range in 2012–2013

divided by the time elapsed between surveys (i.e. 7 years). The period since the start of range expansion was calculated by dividing the maximum distance between the centroid of all records (taken as an approximation of the putative point of introduction) and the most distant record.

The degree of spatial autocorrelation in presence records for each species was evaluated by plotting their mean Moran's Z scores $\pm 95\%$ confidence intervals (CIs) against buffer radii where significance was taken as those values not overlapping a zone around 0 from -1.96 to $+1.96$ (Haining 1990). Comparative habitat use by each species was examined using generalized linear models (GLMs) assuming a binomial error structure and a logit link function where the presence and pseudo-absence of each species was fitted as the dependent variable. The effect of the spatial scale at which land cover variables were extracted was initially explored by plotting the regression coefficients (β -values) $\pm 95\%$ CIs against buffer radii. In the case of the Irish hare, variables of interest at each spatial scale were fitted along with Moran's Z scores at 5 km (as spatial autocorrelation was strongest and significant at this scale). However, for the European hare, Moran's Z scores were excluded (as spatial autocorrelation was not significant at any scale) and only the variable of interest at each spatial scale was included.

Subsequently, a single multiscale GLM was built for each species. Ordinarily, the optimum spatial scale for each variable (which may vary between species) would have been selected using the Akaike Information Criterion (AIC) if the purpose had been to predict the distribution of each species. However, the purpose here was to create a model of comparative habitat use, providing a means to interpret putative interspecific interactions. Consequently, rather than selecting different spatial scales for each variable for each species, a single spatial scale was chosen for each variable, a priori, based on an intuitive interpretation of univariate plots of regression coefficients from the initial exploratory models described above. All predictor variables were tested for multicollinearity to ensure that all Tolerance values were >0.2 . All variance inflation factor (VIF) values were <10.0 and all bivariate correlations had an $r < 0.5$ (Quinn and Keogh 2002). For those variables removed, the Pearson correlation coefficients are given in the results section and the variate with the greatest relationship

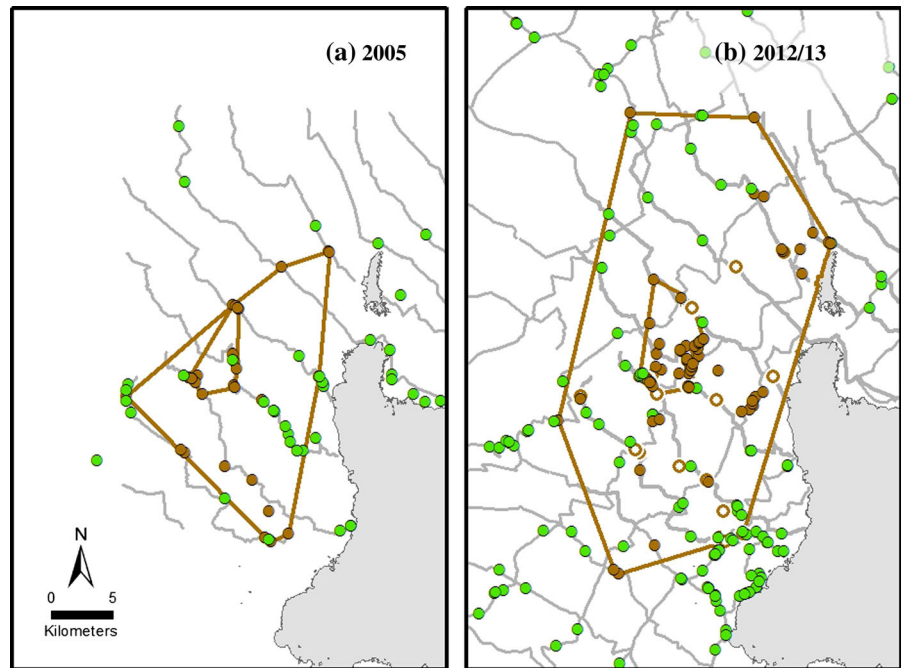
with the dependent variable (hare presence/pseudo-absence) was retained for inclusion in subsequent analysis. To allow for the direct comparison of regression coefficients, variables were standardized to have a $\bar{x} = 0$ and $\sigma = 1$ prior to analysis. All possible model permutations were created and ranked using AIC values. The Akaike weight (ω_i) of each model was calculated within the top set of N models defined as those with a value of $\Delta\text{AIC} \leq 2$ units (Burnham and Anderson 2002). The Akaike weight of each model is the relative likelihood of that model being the best within a set of N models. To calculate the importance of each variable relative to all other variables, the $\sum\omega_i$ of all models within the top set of models that contained the variable of interest was calculated and the variables ranked by $\sum\omega_i$ (McAlpine et al. 2006); the larger the value of $\sum\omega_i$ (which varies between 0 and 1), the more important the variable. Multimodel inference and model averaging was used to determine the effect size (β coefficient) of each variable across the top set of models (Burnham and Anderson 2002). Variables that had equal $\sum\omega_i$ values were ranked in order of the magnitude of their model averaged regression coefficients. The performance of the single best approximating model was assessed using the area under the curve (AUC) of the receiver operating characteristic (ROC) curve. Models were run using Genstat 16 (VSN International Ltd.).

Levins' niche breadth (Levins 1968) and Pianka's niche overlap (Pianka 1973) were calculated across habitat types for each species and compared using a Wilcoxon signed-rank test.

Results

A total of 267 hares were recorded in mid-Ulster during 2012–2013. The recorded range (100 % MCP) of the European hare was three times larger during 2012–2013 at 535 km² than during 2005 at 188 km², whilst the core range (50 % MCP) was twice as large during the current survey at 33 km² than during 2005 at 16 km² (Fig. 2). Leaving aside the caveat of increased survey effort, if we assume that the range expanded, this equated to a radial range expansion rate of 0.73 km year⁻¹ between surveys. The maximum distance between the centroid of all sightings i.e. the putative point of introduction (54°44'1"N, 6°38'55"W) and the most distant sighting was

Fig. 2 European hare range (outer 100 % MCP) and core range (inner 50 % MCP) during **a** 2005 and **b** 2012–2013 showing transects (grey lines), European hares (closed brown dots), Irish hares (closed green dots) and past records (open circles). Directly comparable transects during 2012–2013 are shown in bold. The maximum distance between the centroid of all sightings i.e. the putative point of introduction (54°44'1"N, 6°38'55"W) and the most distant sighting was 21.4 km



21.4 km. Thus we infer that range expansion started approximately 30 years before present (i.e. around 1983). Assuming a 10–15 years lag phase for most invasive mammals prior to active range expansion (e.g. see Jeschke and Strayer 2005; Clout and Russell 2007), the date of introduction for the European hare into mid-Ulster was estimated at around 1970.

Within the invasive species range, 91 (62 %) of animals expressed a European-like phenotype and 56 (38 %) expressed an Irish-like phenotype. This is comparable to the survey in 2005 in which 45 (65 %) expressed a European-like phenotype and 24 (35 %) expressed an Irish-like phenotype within the invasive range. In 2012–2013, five individuals were described as having intermediate phenotypes based on morphological traits, which differed between individuals, but included ear length, the degree of blackening of ear-tips, pelage colouration, and body size and shape. Putative hybrids were counted as European-like for the purposes of analysis. During 2012–2013, the putative species were observed interacting on two occasions.

All hares were observed in either improved or rough grassland. Both species exhibited positive Moran's Z scores at all spatial scales but this was significant only for the Irish hare at buffer radii of 2.5 and 5 km, being strongest at the largest scale (Fig. 3a). Accounting for spatial autocorrelation in Irish hare

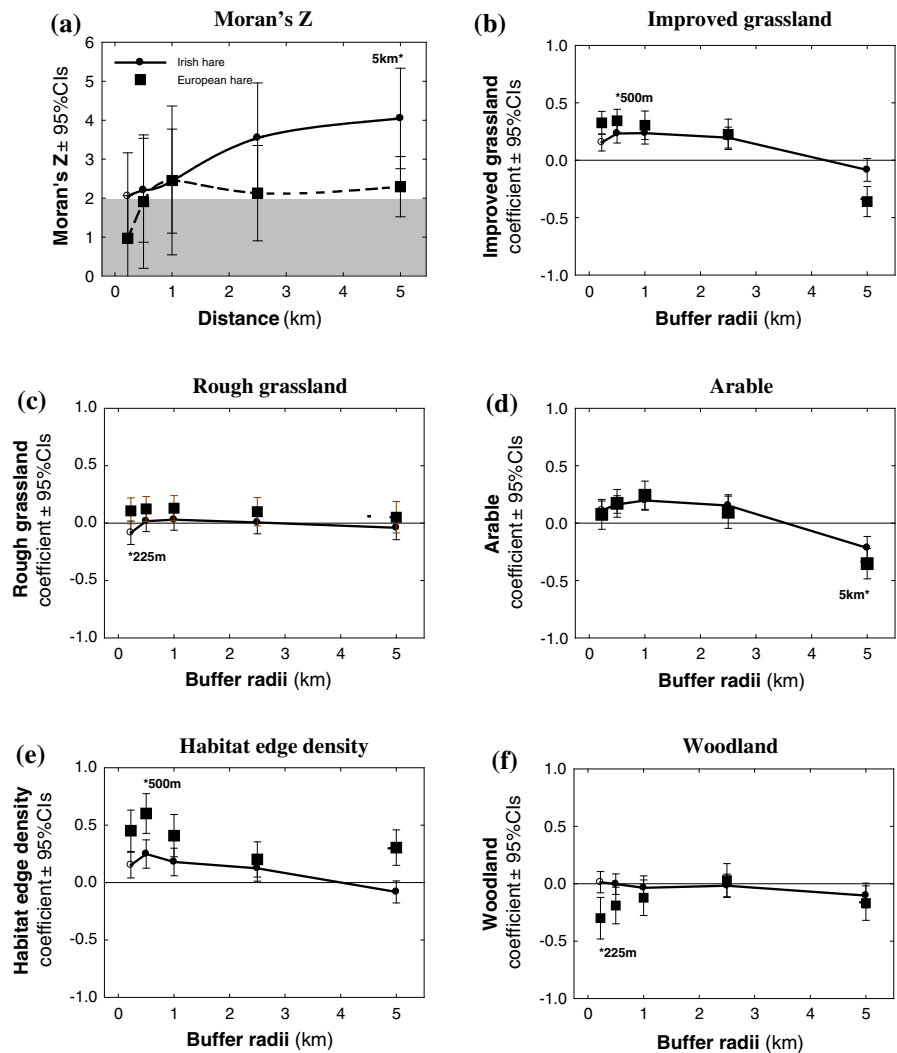
presence but *not* in European hare presence, both species exhibited notably similar responses to land cover variables at varying spatial scales from 225 m to 5 km (Fig. 3b–f). Comparative habitat use models suggested that detection of both species was negatively associated with local hilliness and both had similarly strong negative associations with arable coverage at the landscape (i.e. 5 km) scale (Fig. 4a, b).

The best approximating model for the European hare was most strongly influenced by a positive association with habitat edge density (hedgerows) at 500 m. The converse was true of habitat patch size (field size), which was negatively correlated with habitat edge density ($r_p = -0.578$, $p < 0.001$). European hare presence exhibited a positive association with the rough grassland cover at 225 m (Fig. 4a).

In addition to significant spatial autocorrelation at 5 km, the best approximating model for the Irish hare also demonstrated a significant negative association with grass fibre content (Fig. 4b, c). This suggested an association with grasses with high sugar content, as both measures were negatively correlated ($r_p = -0.765$, $p < 0.001$; Fig. 4c, inset). Irish hare presence was also significantly associated with improved grassland cover at 500 m.

There was a trend for the European hare to exhibit wider Levin's habitat niche values than the Irish hare

Fig. 3 The effect of spatial scale (buffer radii) on: **a** spatial autocorrelation (Moran's Z scores). Irish hare presence was significantly spatially autocorrelated at 2.5 km and 5 km but European hare presence was unaffected. The regression coefficients (β -value) \pm 95 % confidence intervals (95 % CIs) of **b** improved grassland, **c** rough grassland, **d** arable, **e** habitat edge density and **f** woodland. Models for Irish hare presence also included Moran's Z scores at 5 km whilst evaluating the effect of land cover variables whereas those for the European hare excluded spatial autocorrelation. Those scales selected for inclusion in comparative models of habitat use are denoted using *asterisks* (*)



(Wilcoxon signed-rank test $Z = 1.753$, $p = 0.080$) with larger values at most scales except the largest (5 km), and increasing similarities at larger spatial scales (Table 1). Despite the Irish hare's niche being, on average, 14 % narrower than that of the European hare, their niche overlap was virtually complete at all scales (Table 1).

Discussion

The range of the European hare in Ireland substantially expanded between 2005 and 2012–2013. However, the proportion of animals observed within the invasive range that expressed a European-like phenotype was

similar between both surveys (i.e. 62 and 65 % respectively). The invader had a marginally wider niche breadth than the native species, indicating a tolerance for a range of habitats, a characteristic common to many successful invasive species (Mayr 1965; Holdgate 1986; Shea and Chesson 2002; Lambon 2008). This supports previous studies which suggested that the European hare has a competitive edge over *L. timidus* in open, agricultural, anthropogenic landscapes (Hewson 1991; Thulin 2003; Jansson and Pehrson 2007). Nevertheless, niche overlap between the species was near complete, indicating the potential for strong interspecific competition for habitat space should resources be limiting (Reid and Montgomery 2007), particularly during winter when

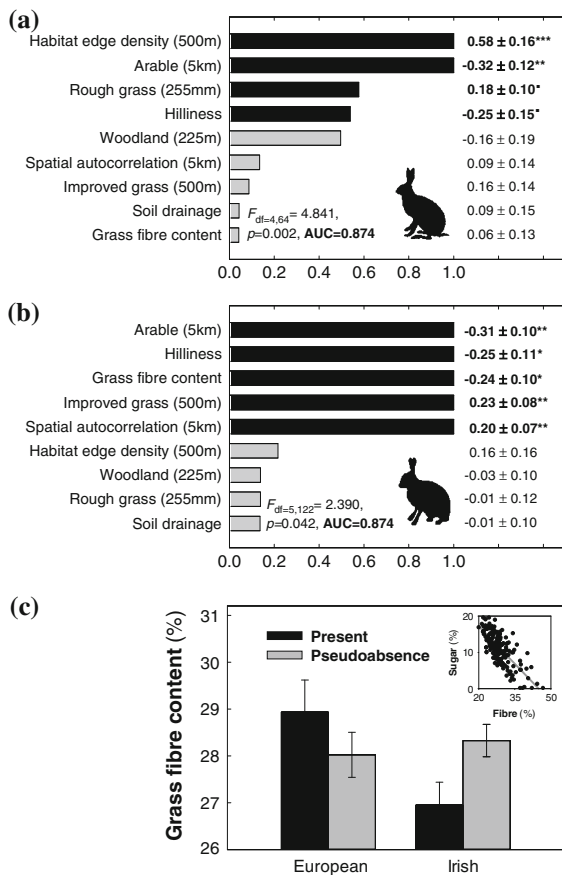


Fig. 4 Relative importance of explanatory variables in explaining the occurrence of: **a** European hare and **b** Irish hare in the landscape at multiple spatial scales (extracted from buffers ranging from 225 m to 5 km). Variables were ranked in order of the sum of their Akaike weights (Σw_i) within the top set of models i.e. models with $\Delta AIC \leq 2$. *Black bars* indicate those variables that were retained in the best single approximating model (i.e. that with the lowest AIC value) and *grey bars* indicate variables included in all other models within the top set. Standardised β values \pm SEs are given to the right of *each bar* and *p* values of each variable in the top model are denoted as * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$. **c** Grass fibre content (%) ± 1 standard error (SE) at locations where European and Irish hares were present with associated pseudo-absences. *Inset* shows the negative correlation between grass fibre and sugar content as a percentage of dry mass

the species are forced into close proximity by a paucity of forage. Consequently, competition may have limited the rapidity of the European hare's establishment and subsequent rate of spread in Ireland ($0.73 \text{ km year}^{-1}$) to below that observed in other regions within its invasive range where close ecological competitors are absent (most notably, native leporids), or offer insufficient competition. During its

colonisation of South America, expansion rates varied between 10 and 37 km year^{-1} (Grigera and Rappoport 1983; Bonino et al. 2010) and were substantially higher in Australia, at 60 km year^{-1} (Jarman and Johnson 1977).

Social associations, inferred from the degree of spatial autocorrelation exhibited by presence records, differed between the native and invasive species, with the native being positively autocorrelated at the largest scales. However, it may be that the invasive population, which currently occupies a relatively small range, has yet to reach equilibrium even within the colonised area. Expanding invasive populations often exhibit high dispersal rates (e.g. Phillips et al. 2007; Kraan 2008; Bonino et al. 2010). If indeed the European hare population in mid-Ulster represents a recent introduction exhibiting a competitively-constrained extended lag phase (i.e. 15 years or more), the rate of expansion presented here may be a conservative estimate. Core population disequilibrium and post-lag-phase expansion may account for the lack of significant clustering within European hare records.

Hilliness, as measured by the deviation of elevation, within the immediate vicinity of each survey point (225 m) had a negative effect on hare detectability. This suggests that either both species prefer flat ground allowing the early detection of approaching predators, or that hills and hollows adversely affected observer ability to detect animals which are more readily seen in open flat fields.

Both species occupied improved and rough grassland, the former offering grazing whilst the latter also offers stands of rushes (*Juncus* sp.) indicating the importance of potential cover in which hares typically rest during the diurnal period. The native species was positively associated with improved grasslands within 500 m of each observation, indicating a preference for open areas. Indeed, the Irish hare usually prefers open field habitats (Dingerkus and Montgomery 2002) perhaps due to the long-standing association of its mountain (*L. timidus*) and Arctic (*L. arcticus*) hare ancestors with open upland landscapes or flat tundra habitats (MacPherson 1965; Flux and Angermann 1990). European hares were associated with high habitat patch edge density, and, hence, small habitat patches, suggesting that it may make greater use of hedgerows and edge habitats as diurnal resting sites (Hutchings and Harris 1996; Neumann et al. 2011) than the Irish hare.

Table 1 Levin's niche breadth for the European and Irish hare and Pianka's niche overlap at multiple spatial scales

Spatial scale	Levin's niche breadth			Pianka's niche overlap
	European hare	Irish hare	Δ	
225 m	2.10	1.57	0.53	0.98
500 m	2.04	1.61	0.43	0.99
1 km	2.06	1.74	0.30	0.99
2.5 km	2.03	1.78	0.25	0.99
5 km	1.92	2.01	0.09	1.00
\bar{x} (95 % CIs)	2.03 (1.97–2.09)	1.74 (1.59–1.89)	0.32 (0.18–0.47)	0.99 (0.98–1.00)

Grass fibre comprises lignin and cellulose (Stubbs et al. 2010), the least digestible part of forage, and thus is inversely correlated with digestibility and readily available energy (Font et al. 2005). Irish hares preferentially utilised forage which was easily digestible and, hence, had a high nutritional content. In contrast, the invasive species exhibited a greater tolerance for less digestible, lower energy forage. Avoidance of low-quality habitats by the native species, combined with potential exclusion from those same habitats due to the competitive edge of the invasive, may facilitate further invasive range expansion.

Both species were positively associated with arable land at 225 m, though this was not significant for the invader, while being strongly and negatively associated with arable farming on a scale of 5 km. European hares are commonly associated with arable agriculture throughout their native range (Frylestam 1980; Chapuis 1990; Smith et al. 2005), while Irish hares have always been assumed to avoid arable fields (Reid et al. 2007; Reid and Montgomery 2007). However, it is clear from the current analyses that the response of the native species to arable is virtually identical to that of the invasive. The strength of the association between the invader and arable agriculture might be diminished in Ireland relative to Great Britain or Europe, as the extent of arable land, and the composition of the wider agricultural matrix within which it is farmed, may be very different in Ireland. Elsewhere, arable farming is more intensive with fields being substantially larger (e.g. Marboutin and Aebischer 1996; Pépin and Angibault 2007), whereas in Ireland few farms are completely arable, with any arable fields being embedded within a predominant matrix of pastoral agriculture.

European hares in England occur at higher densities in arable (7.1 hares km²) than in pastoral landscapes

(3.3 hares km²; Hutchings and Harris 1996). Consequently, the Irish landscape may represent a suitable but suboptimal habitat matrix for the invasive species, further limiting its rate of spread. Nevertheless, pastoral farming (improved and rough grasslands), arable agricultural (crops and complex cultivation patterns) and natural grass (acid, calcareous and neutral grasslands) occupy approximately 70 % of Ireland (EEA 2010). Consequently, a substantial majority of the island is available for colonisation by the European hare, whilst the remaining area (uplands, bogs, moorlands and coastal habitats), assuming no other environmental change, might remain the sole preserve of the Irish hare. However, some invasive species undergo spatial sorting of dispersal traits (Hui et al. 2012; Berthouly-Salazar et al. 2013) which result in shifting habitat associations throughout the invasion process. Thus, future habitat associations of the European hare in Ireland may not necessarily reflect those reported here whilst any threat(s) to the native Irish may well shift as the colonisation process continues.

The ability of the European hare to become a highly effective alien invasive species has been demonstrated both in Sweden, where it has displaced the native mountain hare (Thulin 2003; Jansson and Pehrson 2007), and in northern Patagonia where mara (*Dolichotis patagonum*) populations have been depressed or displaced since its introduction in the late 1800 s (Puig et al. 2006). The present study indicates that the European hare poses a significant threat to the ecological security of the Irish hare. As signatories to the Convention on Biological Diversity (1992), the Bern Convention (1979) and the European Habitats Directive (EEC 43/92 1992), the authorities in both political jurisdictions of Ireland are obliged to address invasive species issues. Further studies are required to re-evaluate: (1) the invasive species' rate of spread to

document the colonisation process; (2) the extent of interspecific hybridisation between the native and invasive hare; and (3) the likely efficacy of population control measures to inform appropriate management.

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