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Modeling and assessing the current and future habitat of the Irish hare (*lepus timidus Hibernicus*) using GIS

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Author’s declaration

No portion of the work referred to in this thesis has been submitted in support of an application for another degree or qualification of this or any other university or other institute of learning.

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ABSTRACT OF THESIS submitted by:

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for the degree of Master of Science and entitled: *Modeling and assessing the current and future habitat of the Irish hare (lepus timidus Hibernicus) using GIS.*

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The Irish hare *lepus timidus Hibernicus* is endemic to the island of Ireland and has been subject to historic and current conservation concern due to a number of identified and perceived threats. Populations have experienced declines in recent years, and although often attributed to agricultural intensification, there are several other influencing factors. The invasive European hare *lepus Europaeus* has successfully naturalized in many countries across the Eurasian continent, including a small but established population in Northern Ireland. Changing climatic conditions are predicted to cause a contraction in the bioclimatic range of the endemic, and an expansion in favor of the invasive. Furthermore, existing bioclimatic models fail to account for the loss of available habitat due to anthropogenic disturbance, namely urban fabric and increasing human population densities.

The study aims to conduct a combined assessment of these threats, conducting a habitat suitability analysis using ArcGIS 10.2.2 to determine available territory, as well as predicting likely future distribution based on changing climatic conditions using the maximum entropy species distribution modeling approach (MaxEnt).

Although current conditions are favorable, suitable territory was determined to be circa 20% less than when calculated using solely bioclimatic variables as in previous studies. However, combined with predicted future climatic conditions, and accounting for a possible competitive exclusion due to European hare colonization, available habitat for the endemic is reduced to a fraction of its current size.

Keywords: Ecology; Irish hare; European brown hare; Ireland; Climate change; Habitat suitability; Species distribution; Invasive species; GIS.

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Abbreviations

AONB – Area of Outstanding Natural Beauty
ASSI - Area of Special Scientific Interest
BEM – Bioclimatic Envelope Model
CLC – Corine Land Cover
DPA – Designated Protected Area
ENM – Environmental Niche Model
EU – European Union
GIS – Geographic Information System
HSM – Habitat Suitability Model
IPCC – Intergovernmental Panel on Climate Change
NI – Northern Ireland
NISRA – Northern Ireland Statistics and Research Agency
NNR – National Nature Reserve
OSI – Ordnance Survey Ireland
OSNI – Ordnance Survey Northern Ireland
ROI – Republic of Ireland
SAC – Special Area of Conservation
SDM – Species Distribution Model
SPA – Special Protected Area
NHA – National Heritage Area

1 Introduction

1.1 Background & Research Justification

With an ever-increasing list of identified and potential threats to biodiversity, and in many cases statistical evidence highlighting the demise of many species globally, it is imperative that effective monitoring and management strategies are in place to mitigate and protect species.

The Irish mountain hare (*Lepus Timidus Hibernicus*, Bell 1837) is endemic to the island of Ireland and is Ireland's only endemic mammal (hereafter referred to interchangeably as 'the endemic' or 'Irish hare'). It has a unique phylogenic status, distinct morphology, and cultural value, granting it considerable intrinsic value (Reid *et al.* 2007a). The species faces a number of identified threats, which may be broadly categorized as:

I. **Agricultural intensification** – primarily increased pesticide application and increased farming mechanization. The species has undergone a dramatic population decline which peaked in 1980-90s and is largely attributed to agricultural intensification in traditional habitat spaces (Dingerkus and Montgomery 2002; Reid 2010).

II. **Climate change** – climate change projection models predict a dramatic contraction of the Irish hare's current bio-climatic range (Caravaggi *et al.* 2017).

III. **Invasive species** – The invasive European brown hare (*Lepus Europaeus,* Pallas 1837) (hereafter referred to interchangeably as 'the invasive' or 'brown hare') has established steady populations in some pockets of Northern Ireland (Reid and Montgomery 2007) where it competes for habitat space with the endemic. There are records of numerous historical introductions, primarily throughout the latter half of the 19th century, almost exclusively for coursing (hunting with dogs), and most of which subsequently died out (G. E. H. Barrett-Hamilton 1898). However, two established populations have been confirmed in mid-Ulster and West Tyrone (Reid and Montgomery 2007).

Recent literature (Thulin 2003; Reid and Montgomery 2007; Caravaggi *et al.* 2014; Caravaggi *et al.* 2017) highlights the emerging threat posed by the invasive, potentially compromising genetic integrity of the endemic, as well as out-competing the endemic in many of its traditionally preferred habitats, driving the endemic to the edges of its ecological niche.

Additionally, a variety of international obligations – the Convention on Biological Diversity (Anonymous 1992), the Bern Convention (Anonymous 1979), and the EU Habitats Directive (EEC 43/92) - compel the UK and Irish governments to respond to issues pertinent to invasive species, justifying further the need to address the threats facing Ireland's sole endemic mammal.

Given the potential for these threats to dramatically influence the capacity of the endemic to sustain or thrive in its natural - and presently, it's only – environment, an accurate assessment of its current and future habitat suitability on the island of Ireland is an important tool in ensuring its continued viability.

1.2 Aims

Macroclimatic factors are a key driver of distribution patterns at continental and global scales (Leach *et al.* 2017). Thus, Caravaggi *et al.* (2017) use macro-bioclimatic factors to predict shifts in home range for the two lagomorph species across Europe and Ireland (Bioclimatic Envelope/Environmental Niche Modelling). However, the literature (Pearson and Dawson 2003; Thuiller *et al.* 2003) indicates that at the community, landscape, and intermediate scale, biotic interactions, microclimatic factors and human impacts have a greater influence on range and distribution. Such factors are omitted from BEM/ENM, although utilized instead in Habitat Suitability Models (HSM), which focus on the immediate environmental conditions.

Both approaches have long been utilized in modelling for ecological research and management, but until recently, few attempts have been made to reconcile their respective selection criteria with each other with the aim of creating a more holistic and pragmatic ecological model for management.

The aim of the current study is to therefore model at the intermediate/species scale, the current and future ecological and environmental conditions for the endemic Irish hare in Ireland.

1.3 Research Questions

RQ1: What is the current environmental habitat suitability for the endemic Irish hare in Ireland?

- What impact are anticipated socio-economic factors, including urbanization, infrastructure and increasing population having on suitable habitat areal extent for the endemic?

RQ2: Based on future climate model projections, how could suitable habitat areal extent be affected by future climatic conditions in Ireland?

1.4 Objectives

1.4.1.1 Current Habitat Suitability Model

Conduct a geospatial analysis of current all island habitat suitability for the Irish hare, accounting for environmental suitability factors, including identifying anthropogenic and biotic influences which may influence suitability of conditions for the endemic, and integrate these into the suitability modelling process.

This integration of biotic interaction and human impacts aims to provide a finer scale model of the diminishing habitat suitability for the endemic. Biotic interaction will be represented by the presence of established brown hare populations, and human impacts will be examined through socio-economic factors including population density, urbanization, and transport infrastructure. Reconciling the bioclimatic restrictions represented in BEMs with environmental restrictions represented in HSMs is expected to yield different outcomes and therefore different management recommendations.

1.4.1.2 Future Habitat Suitability Projection

Develop additional habitat suitability models for a medium-term future scenario for the Irish hare, based on the original criteria as well as climate change projection model data and predictive outcomes of the competitive exclusion process triggered by invasive colonization.

The stated objectives are intended to produce a geospatial representation of changes in suitability for the endemic, drawing the most influential factors from different model approaches and reconciling them to provide an indication of the level of threat posed to the endemic.

2 Literature Review

Changes in climate are influencing the habitat suitability of the vast majority of species worldwide, and a host of evidence suggests geographic shifts in habitat suitability for the Irish Hare (Watts *et al.* 2013; Caravaggi *et al.* 2017; Marques *et al.* 2017). On the island of Ireland – currently the only home to this sub-species of the mountain hare - their habitat range is anticipated to contract north-westward due to predicted changes in local climate (Caravaggi *et al.* 2017). How rapidly this contraction may occur is subject to debate, and models based on different emissions scenarios produce somewhat varied results, but the overarching patterns remain the same.

Under various climate modelling scenarios (this project will utilize the UK Hadley model) both increasing temperature and increasing precipitation is projected for many more temperate Northern European regions in the coming decades. This will cause a shift in habitat suitability and while the Irish hare may be vulnerable, it will also potentially present new expansion opportunities for the invasive European brown hare (Leach *et al.* 2015), which has a small but established population spread across several geographical pockets in Northern Ireland. It is anticipated that the bioclimatic envelope for the brown hare in Ireland will expand approximately westward in tandem, encompassing the whole island by around 2070 (Caravaggi *et al.* 2017). The brown hare tends to both out-compete and hybridize with the Irish hare (Thulin 2003), also risking the genetic integrity of the endemic.

2.1 Threats to Biodiversity

2.1.1 Climate Change

Climate change has induced an increase in global temperatures over the course of the last century, and various global models predict it will continue to do so at an ever-accelerating pace. The Intergovernmental Panel on Climate Change (IPCC) fifth assessment report predicts global mean surface temperature will increase as much as 2-6°C to 4.8°C under RCP8.5 (see Figure 1) (IPCC 2014).

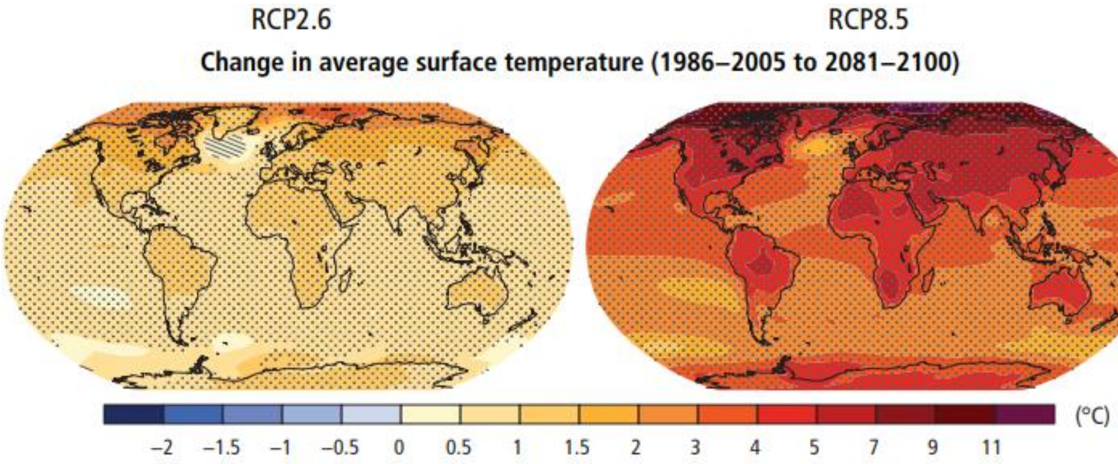


Figure 1: IPCC average surface temperature change predictions to 2100

This climatic shift is anticipated to have pronounced effects on global biodiversity, at all biological levels ranging from the individual organism to the biome (Bellard *et al.* 2012). (Parmesan 2006) discusses a detailed range of predicted impacts from reductions in allelic diversity at the genetic level, to reduced fecundity or changes in hibernation at the organism level, to reduced resilience, desertification and distribution shifts at the biome level. (Bellard *et al.* 2012) summarize the main climate change factors and their corresponding effects at different spatial and trophic levels in Figure 2.

Additionally, tropic interactions are expected to be drastically affected by climate induced population impacts (Gilman *et al.* 2010). This means that climate change impacts to one species population will have an additional effect on other, inter-linked species within their respective ecosystems, adding further complexity to the challenge of predicting outcomes.

Even at the biome level, the highest spatial categorization of biodiversity, climate change is expected to cause a spatial shift in distribution of 5-20%, according to the Millennium Ecosystem Assessment forecasts (Millennium Ecosystem Assessment 2005), with boreal forests expanding northward, and lakes at more central latitudes predicted to disappear completely.

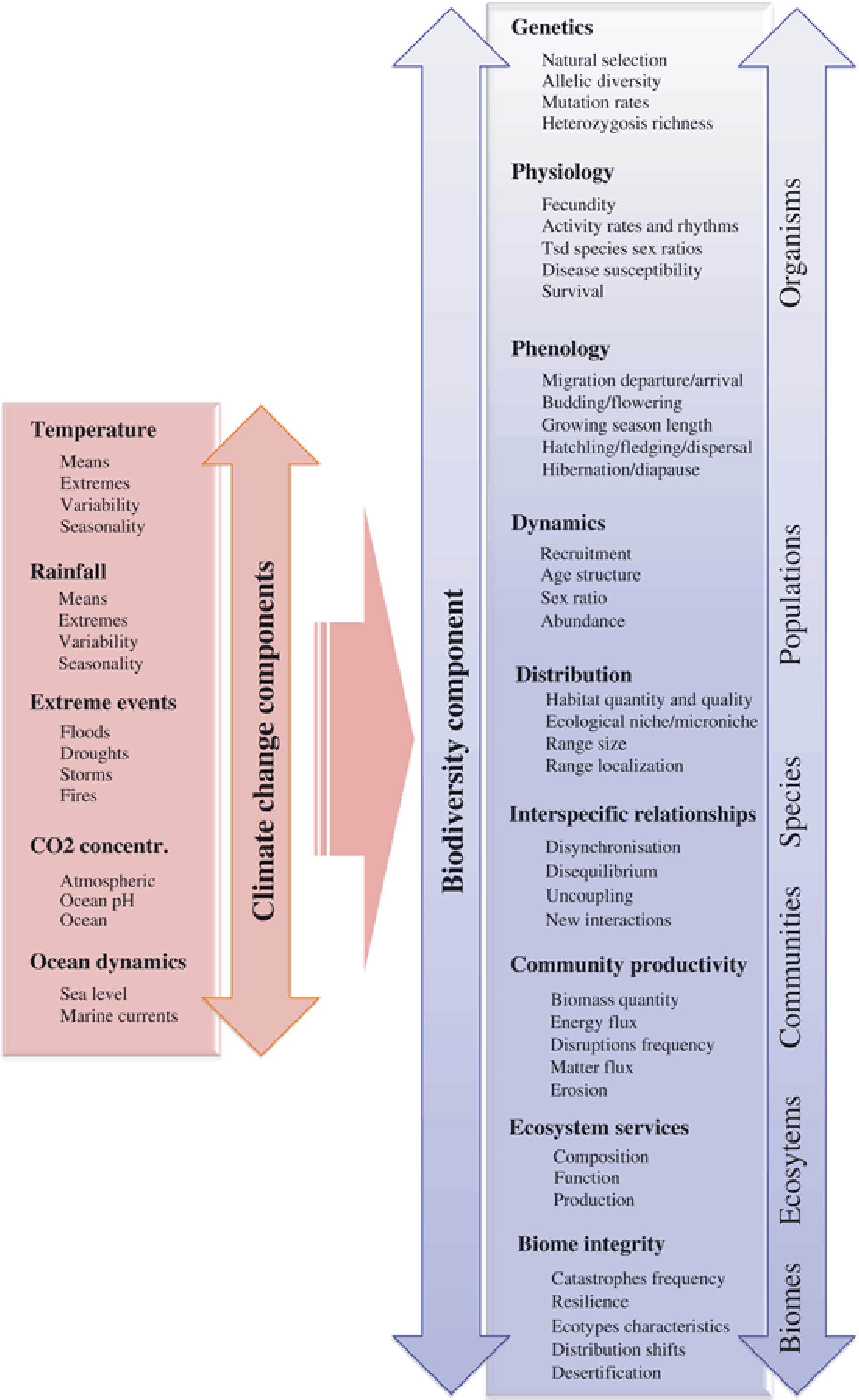


Figure 2: Summary of key climate change components and their corresponding impacts on biodiversity at different spatial and trophic levels

2.1.2 Invasive Species

Invasive species are a central issue in biodiversity management, particularly in the context of biodiversity preservation. The number of invasive species is increasing, as is the number of invasive species that successfully establish and colonize outside of their ‘natural’ home range (Blackburn *et al.* 2005), often to the detriment of native species.

Understanding the possible impacts an invasive species can have on a given ecosystem is complex and often unpredictable (Richter-Boix *et al.* 2013). Not all invasive-native species interactions are negative however, as numerous authors point out (Simberloff and Holle 1999; Grosholz 2005; Russell *et al.* 2014). Many of these examples in the literature demonstrate development of positive-mutualisms, and even ‘bio-control’ - managing high impact invasives using lower impact, ecologically similar invasive species, although these examples are certainly in the minority.

Quantifying and predicting the exact nature of the impact is challenging, but some overarching effects can be identified including ripple/knock-on effects through food-webs and across trophic levels as a result of interspecific competition for habitat space and food resources, as well as, in some cases, interspecific hybridization. For example, Castorani and Hovel (2015) demonstrate a case for cross-trophic level impact of invasives, as they examine the effect of invasive prey on native predators. As in this example, the literature focuses on inter-trophic interactions; however intra-trophic interactions are also prevalent.

Iacarella *et al. (2015)* were the first to identify spatio-temporal variation in the competitive effects of an invasive species. As the author notes, as an invader spreads from the established source population area of intra-specific competition, it moves towards an invasion front, where interspecific competition then dominates. The authors provide evidence for potentially increased competitiveness of invasives based on their spatio-temporal positioning within the colonization process. That is, whether they are situated closer to the source, competing with their own, or at the frontier, competing with other species. This variation further adds to the complexity of quantifying the impacts to an ecosystem.

Furthermore, often many species live in sympatry, with a complex network of biotic interactions (mutualism, competition, predation, parasitism) constantly occurring between them, potentially influencing their respective niches (Pearson and Dawson 2003) as well as their actual distribution. This study will examine the nature of the intra-trophic/inter-specific interactions occurring between the endemic and the invasive hares in Ireland and further afield and incorporate an element of this biotic interaction into a GIS model.

2.1.3 Urbanization

The impacts of urbanization and an ever-increasing human population on biodiversity are undoubtedly profound in scope and extent. There is an obvious, observable negative correlation between urban density and species richness and abundance. Inner cities are not generally accommodating to nature; useable habitat space or food resources are few and far between for all but the smallest and most resilient species finding themselves within an urban environment, and urban sprawl is continually diminishing remaining potentially suitable habitat extent.

Elmqvist *et al.*(2013) discuss five major trends of the urbanization process, summarized as follows:

- Urban area physical extent is expanding faster relative to urban population growth.
- Urban heat island effects modify local climate and influence biodiversity processes.
- Urban expansion draws heavily on primary resources including water, timber and energy. The same expansion will continue at the expense of primarily agricultural land in previously peripheral areas, thereby further reducing habitat availability.
- The pace of urban expansion varies spatially. Areas of high biodiversity, low elevation and coastal areas are at greater risk.
- Most future urban expansion is anticipated to occur in developing areas with limited economic and institutional capacity to plan and implement appropriate biodiversity mitigation and conservation measures.

From a biodiversity perspective, urban infrastructure, namely transport and utilities lines, create a dense web of noisy, dangerous, and disruptive fragmentation lines across the landscape. Much of the literature points to the damaging effects at species level, including negative impact of roads on populations (Bissonette and Rosa 2009; Rytwinski and Fahrig 2015), and the fragmentation effect of transport infrastructure and barriers (Loro *et al.* 2015). These observable and quantifiable impacts result in less areal extent of potentially suitable habitats, with increased disruption and fragmentation to those that remain.

2.2 Biodiversity and Conservation Management with GIS

2.2.1 Bioclimatic Envelope Modeling

Assessing climate change induced impacts on biodiversity is executed primarily through the use of bio-climatic envelope (BEM), or ecological niche modelling (Dawson *et al.* 2011). Hutchinson (1957) defines the ecological niche of species as the range of environmental and biotic conditions within which it may persist without immigration. Hirzel and Lay (2008) succinctly summarize the key concepts of the ecological niche as follows:

- In the absence of immigration, a species must maintain a positive population growth rate facilitated by the local combination of environmental variables (predictors/covariates).
- The variables define the dimensions of the environmental space.
- The ecological niche is therefore the volume within the variable defined environmental space that facilitates positive population growth (Hutchinson 1957).
- Growth rates decrease across a spatial gradient ranging from the niche optimum to the niche envelope, at which growth is zero. Beyond this envelope, growth is negative.

BEM/ENM models anticipate changes to environmental conditions, relating them to physiological responses (Pacifici *et al.* 2015) and therefore the bioclimatic suitability of an area for a given species. Araújo and Rahbek (2006) contend that BEM is driven by the need for realistic and applicable outputs for biodiversity management.

2.2.1.1 BEM Limitations

BEMs operate at a coarse scale, and as such do not account for many biotic and micro-climatic factors that also play a substantial role in the suitability and potential dispersal of a given species.

Urban *et al.* (2016) highlight the relative absence of biological mechanisms from BEM, including those pertinent to dispersal, demography, physiology, species interactions, population interactions and adaptive potential.

2.2.2 Habitat Suitability Modeling

In more recent ecological theory, habitat suitability modelling (HSM) has risen to prominence in parallel to the ‘traditional’ BEM, as a tool for predicting the likelihood of species occurrence based on environmental variables (Hirzel and Lay 2008). HSM’s are developed through the compilation and integration of different influencing factors ranging from bioclimatic through to socio-economic and anthropogenic and are generally developed using Geographic Information Systems (GIS) and large datasets. Hirzel and Lay (2008) propose that the HSM may be viewed as the operational application of an ecological niche.

Their use and applicability varies with confidence levels in the model itself. Accuracy and veracity of input data, as well as finely tuned suitability selection criteria based on peer reviewed literature and expert consultation is vital to ensuring predictive and/or presumptive modelling approaches are pragmatically applicable to ecological management strategies. Hirzel and Lay (2008) argue that ‘Identifying the key environmental variables that determine the niche is one of the most crucial HSM operations.’

HSMs facilitate a number of additional 'off-shoot' spatial analyses that can provide further insight beyond potential suitability alone. Often HSMs can be taken a step further, to identify other influential factors pertinent to biodiversity conservation, such as connectivity of habitats (Marulli and Mallarach 2005; Fath *et al.* 2007; Gurrutxaga *et al.* 2010; Lookingbill *et al.* 2010; Teixeira *et al.* 2014; Loro *et al.* 2015), or conversely, their degree of fragmentation (Fulgione *et al.* 2009; Velázquez *et al.* 2017). Ayram *et al.* (2016) evaluate the recent integration of landscape connectivity in the identification and planning of conservation areas, reviewing 162 publications between 2010 - 2013, and note a substantial increase in number of studies pertinent to connectivity and conservation between 2008 – 2013. The authors also however note an absence of implementation of landscape connectivity recommendations provided within the study conclusions.

Loro *et al.* (2015) suggest that ecological connectivity modelling should occur as a baseline study measure during planning for transport infrastructure. They argue that this 'barrier effect' can be mitigated using HSM coupled with cost-distance analyses to determine not only the suitable areas to conserve for a given species, but also how that species might travel between areas, and therefore which areas to avoid fragmenting with transport urban infrastructure.

2.2.2.1 HSM Limitations

The strength of a distribution-niche link varies depending on species ecology, local environmental conditions, and historical events (Pulliam 2002) and is therefore ambiguous and difficult to ascertain. HSMs assume that species ecological requirements correlate with observed distributions, which is not always the case. Species may be observed outside of their anticipated suitable zones and conversely may be absent from zones deemed highly suitable.

Some HSMs amalgamate several, related environmental variables into summary representations of certain conditions, for example, representing ‘climatic conditions’ by combining mean temperature with precipitation and variability. As noted by Hirzel and Lay (2008) these synthesized factors can reduce model complexity but can also prove more difficult in the context of ecological interpretation. Furthermore, condensing or simplifying variables can result in a loss of detail and therefore reduced accuracy at finer scales.

2.2.3 Predictive Species Distribution Models Using BEM

Species distribution models (SDM) are widely utilized in the literature (Levinsky *et al.* 2007; Morin and Thuiller 2009; Vieilledent *et al.* 2013; Teixeira *et al.* 2014; Caravaggi *et al.* 2017; Leach *et al.* 2017), often to predict the potential impacts of climate change on a particular species or set of species. An SDM can be used to forecast future conditions by calculating probability of occurrence of a species based on current distribution (usually using presence records) and climate model data.

Much of the literature indicates predicted reductions in range for a number of species over the course of the next century, with some of the more severe predictions ending in extinction, such as the Vieilledent *et al.* (2013) analysis of the Malagasy Baobab.

Levinsky *et al.* (2007) use BEM/SDM to predict that as much as 10% of all European mammals are at risk of extinction within the next century, and up to 25% becoming critically endangered. They also note that even ‘less threatened' species will experience reductions to suitable habit space and therefore a reduction sustainable population numbers, potentially leading to further delayed extinction debts as competition for space and resources inevitably increases. Conversely, their model also predicts that over a third of European mammals will experience a bioclimatic range expansion. However, there are a number of additional factors for consideration that can influence actual future distributions, and that are not accounted for in an SDM process. Soberon and Peterson (2005) determine three constraints by which species geographical distributions are restricted:

- Local environmental conditions allow population growth.
- Inter-specific interactions (predations, competition, mutualism) allow species to persist.
- Accessibility based on dispersal ability of the species (can they disperse to a given location quickly enough; is altitude, slope, or land cover a logistical issue).

Habitat suitability models (HSM) are derived from this BEM/ENM, as an HSM aims to reconstruct the niche based on the environmental conditions observed in its present habitat, but then often takes this further by making spatial predictions), while accounting for additional influencing factors such as biotic interaction and accessibility.

2.2.3.1 MaxEnt Software

Maximum entropy (MaxEnt) models are commonly used in ecology spheres as the methodology for creating these future SDMs. MaxEnt uses the maximum entropy principle to estimate environmental niche and/or their probability of occurrence under stipulated environmental variables using presence-only data and the environmental conditions associated with those presence records (Phillips *et al.* 2006).

2.3 European Lagomorphs

2.3.1 Species Variation, Range & Distributions

In the order *lagomorpha*, Europe is home to five extant species of the genus *lepus*, although European geographic distribution tends to be dominated by the mountain hare (*Lepus timidus,* Linnaeus 1758) and the European brown hare (*Lepus Europaeus*, Pallas 1837) (Caravaggi *et al.* 2017).

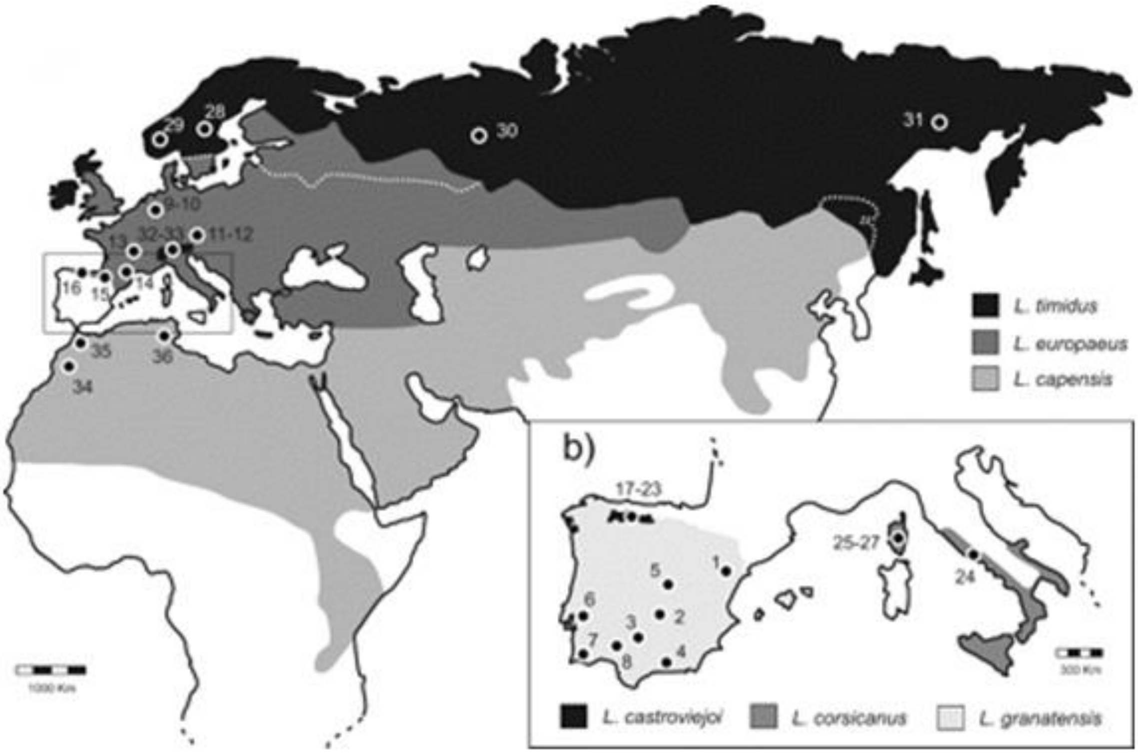


Figure 3: Distribution of extant hare species in Eurasia and Africa (Melo-Ferreira et al. 2012)

The mountain hare habitat is diverse and far reaching (see Figure 3), with distribution ranging from Scandinavia to the north, Ireland in the west, the Alps to the south, and as far east as Siberia, Kamchatka and Japan (Caravaggi et al. 2017).

There are also five extant mountain hare sub-species in Europe; each species being differentiated by ecological, physiological and behavioral characteristics (Angerbjörn and

Flux 1995; Caravaggi *et al.* 2017). However genetic differentiation is low, which Hamill *et al.* (2006) suggests is indicative of a post-glacial panmictic European population which then underwent a prolonged period of fragmentation, and in the case of the Irish hare, isolation caused by a rising Irish sea.

The Fennoscandian mountain hare sub-species refers to both the northern hare (*L.t. timidus*, Linnaeus 1758), and the heath hare (*L.t. sylvaticus*, Nilsson 1831). The northern hare widely considered the 'analogue' form of the species (most similar to ancestral form), and possessing the broadest geographic distribution, inhabits tundra and boreal forest ecosystems across the Arctic and Fennoscandia (Angerbjörn and Flux 1995; Caravaggi *et al.* 2017). The heath hare occurs only in southern Sweden and the Swedish island of Gotland (Winiger 2014; Caravaggi *et al.* 2017). It is evident from the literature that the taxonomic status of the heath hare has historically been subject for debate, with some arguing that it is not sufficiently genetically divergent from *L.t.timidus* to be considered a genuine sub-species, while others recognize its distinctiveness based on differences in winter pelage (Suchentrunk *et al.* 1999; Thulin 2003; Winiger 2014).

Unlike their Fennoscandian counterparts, the Scottish hare (*L.t. scoticus*, Hizheimer 1906), Alpine hare (*L.t. varronis*, Miller 1901), and Irish hare are characterized to an extent by their isolation (Caravaggi *et al.* 2017). The Scottish hare is distributed solely throughout the Scottish Highlands, in mountainous environments up to 1300m (Newey *et al.* 2011). The Alpine hare, also true to its namesake, is situated solely on forested slopes throughout the Alps (Bisi *et al.* 2013), at altitudes of up to 3500m (Thulin 2003).

2.4 The Irish Hare

The Irish hare is a sub-species of the mountain hare, and the only lagomorph - or indeed mammal - that is endemic to Ireland (Reid 2010). Hughes *et al.* (2006) estimate that the Irish hare diverged from its counterpart European sub-species approximately 360,000 years ago and has remained isolated for 30,000-60,000 years.

Although their specific habitat preferences are not well documented, they are known to occupy a diverse range of Irish habitat, ranging from coastal marsh to mountainous terrain (Reid 2006). At present, it can be found at all altitudes across the island but demonstrates a clear preference for lowland areas (Reid *et al.* 2007a) in the absence of any extenuating circumstances, such as competitive exclusion by an invasive species. It is evident from the literature (Angerbjörn and Flux 1995; Thulin 2003; Caravaggi *et al.* 2017) that the Irish hare and its associated mountain hare sub-species are opportunistic, and display marked ecological plasticity through their ability to survive in a hugely diverse breadth of habitat, often in poor environmental conditions or with limited food sources.

2.4.1 Numbers & Distribution

Reid *et al.* (2007a) highlight a host of surveys that indicate short-term population fluctuations to be the norm. Combined with an ongoing decline in overall numbers, accurate estimates can prove troublesome; this difficulty is reflected in the varied estimates of numbers and density across the literature.

2.4.1.1 Northern Ireland

(Dingerkus and Montgomery 2002) pooled data from several sources including historical game records, the Northern Ireland Rabbit Survey (1986-94), and the Northern Ireland Badger

Survey (hares were recorded when observed) (1990-93). They conduct estimates based on observed mean densities for different land class groups, placing minimum population numbers at circa 8250, and a maximum estimate at 21,000.

Tosh *et al.* (2005) estimated winter hare density for Northern Ireland at 3.1 hares/km2.

Reid and Montgomery (2007) estimated overall hare density in Northern Ireland at 7.99 hares/km2. They also stress that there is a host of evidence suggesting that hare numbers are still declining. Dingerkus (1997) observed that anecdotal evidence from farmers also suggest a continuing decline over the past 20 years. Furthermore, the various surveys used by Dingerkus and Montgomery (2002) provide further testament to this observed decline in hare numbers.

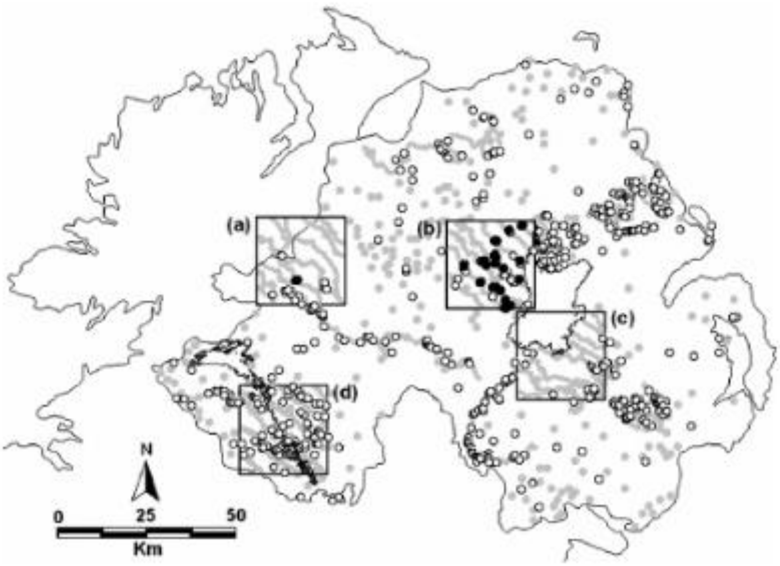


Figure 4: Irish and brown hare sightings during all surveys 1995-2005. Grey areas indicate survey effort; brown hares (black dots); Irish hares (white dots); 625km^2 squares indicate survey area for Reid and Montgomery (2007). (Taken from Reid and Montgomery 2007).

2.4.1.2 Republic of Ireland

The Hare Survey of Ireland (Reid *et al.* 2007a) surveyed 691 1km2 squares across Ireland during 2006-2007. Subsequent estimates place Republic of Ireland hare density at 3.33 hares/km^2 for 2006, with a marked increase the following year at 7.66 hares/km^2 in 2007, putting it to almost identical levels as its northern counterpart. The authors calculate total population estimates by multiplying estimated density by total area, producing a figure of 233,000 hares in 2006 and 535,000 in 2007.

2.4.2 Conservation Status

The literature (Dingerkus and Montgomery 2002; Reid and Montgomery 2007a; Reid *et al.* 2010) highlights the significant conservation concern directed towards the Irish hare following a sustained population decline during the latter half of the twentieth century, attributed primarily to agricultural intensification on the island. Reid (2010) lists the various legislative protections currently attributed to the Irish hare:

- Listed on Appendix III of the Bern Convention
- And Annex V(a) of the EU Habitats Directive (EEC 43/92 1992)
- The IUCN Irish Red Data Book also lists as an internationally important subspecies.
- Republic of Ireland: protection under the Wildlife Act 1976 and the Wildlife (Amendment) Act 2000.
- Northern Ireland: protection under the Wildlife Order (NI) 1985 and annual amendments to the Game Preservation (Special Protection for Irish Hares) Order (Northern Ireland) 2003.
- Species specific Northern Ireland and All-Ireland Species Action Plan in place.

Contrary to the regional conservation concern demonstrated towards the Irish hare, the IUCN red list assigns a ‘least concern’ assessment level for the broader mountain hare species (Smith and Johnson 2008), citing justification from Mitchell-Jones *et al.* (1999) stating its widespread distribution and relatively stable populations. The IUCN paper continues, citing from Thulin (2003) how isolated populations are experiencing declines, yet that such declines do not merit an escalation of conservation priority. While this paper does not claim to dispute these statements, it is prudent to highlight that the IUCN assessment is for the species in its entirety, which when averaged out would significantly dilute the proportionate representation of the Irish hare sub-species. Furthermore, some academic literature asserts that the Irish hare in fact merits a taxonomic upgrade to full species status (Barrett-Hamilton 1898; Thulin 2003; Hughes, *et al.* 2006; Reid 2006). Should a future IUCN assessment focus solely on the circumstances of the Irish hare, there is much evidence to suggest that the outcome would be significantly different.

2.4.3 Threats & Causes of Decline

There are numerous identified threats facing the Irish hare:

2.4.3.1 Agricultural Intensification

A somewhat overarching term which can constitute a number of more specific factors, this issue is widely cited in literature (Edwards *et al.* 2000; Reid 2006; Reid *et al.* 2007b; Flohre *et al.* 2011) as a primary cause of decline across many wildlife populations globally.

Agricultural practices constituting ’intensification’ include increased pesticide and fertilizer application; increased livestock densities; additional tillage; and the homogenization and simplification of agricultural landscapes (Flohre *et al.* 2011). Many of these factors are known to be detrimental to the hare: pesticide application reduces food availability and increases possibility of toxin exposure (van Klingeren *et al.* 1966), overgrazing livestock may further limit food resources (Karmiris and Nastis 2007), and increasingly mechanized tillage may increase mortality rates (Dingerkus and Montgomery 2002).

Benton *et al.* (2003) also observe the diminishing factor to biodiversity caused by agricultural simplification through loss of hedgerows, field amalgamation as well as the temporal and spatial synchronicity of farm management processes. These processes ultimately reduce habitat diversity and suitability, causing a decline in habitat extent for the hare.

Attaining accurate, georeferenced data for many of these factors would not fall within the scope of the current study however unsuccessful attempts were made to account for livestock density as an albeit incomplete representation of the impact of agricultural intensification. They did not aim to be a holistic representation of this diminishing factor, merely one spatially representable component. This attempt, explained in the methodology, further reinforces the inherent difficulties with quantifying this threat, as is cited in the literature (Pelorosso *et al.* 2008).

2.4.3.2 Climate Change

Caravaggi *et al.* (2017) developed an environmental niche model for the Irish hare and predicted a major shift in the bioclimatic suitability of the Irish environment for each of the two present hare species. The study predicts current range of the Irish hare to cover the whole island; however, by 2050 they anticipate the bioclimatic envelope to dramatically contract westward, declining to just 35,461 km^2 of a possible total of 83,497 km^2. By 2070 their model anticipated a further decline to 21,107 km^2, a 75% contraction in suitable bioclimatic envelope for the species.

The authors also calculate current and future bioclimatic envelope for the invasive, predicting current extent to be restricted to mostly to Northern Ireland, at around 12,417 km^2. By 2050 they project a substantial expansion to 53,874 km^2, in a south and westward direction. By 2070 they expect it will cover 66,312 km^2, a 79% expansion in suitable bioclimatic envelope.

2.4.3.3 Invasive Species Competition & Hybridization

The presence of an established European hare population in Northern Ireland presents a threat to the endemic through both interspecific competition and hybridization (Thulin 2003; Reid and Montgomery 2007; Reid 2010; Caravaggi *et al.* 2014). The extent of this threat is challenging to predict due to a host of other factors impacting the already naturally fluctuating mountain hare populations. Isolating and quantifying the impact of the presence of the invasive on the endemic's fecundity has not been attempted in the Irish context.

However, Caravaggi *et al.* (2014) note that in Ireland, the European and Irish hares currently exist in sympatry, due to a near total niche overlap (Reid and Montgomery 2007a). This is contrary to the lagomorphic norm, as most members of the genus *Lepus* in fact occur in parapatry (Caravaggi *et al.* 2014). The reason for this sympatric existence can be explained through the human introduction of the invasive (Flux 2008) rather than a co-evolutionary existence of the two species on the island. (Flux 2008) also observes that this type of sympatry is generally transient, meaning that in time, competitive exclusion will likely cause total retreat of the endemic as it yields territory to the more competitive invasive.

2.4.3.4 Urbanization

Increasing urbanization is a global biodiversity issue, cities and infrastructure are growing to accommodate an ever-increasing human population, encroaching into rural areas and reducing potentially suitable habitat for the majority of biodiversity that cannot adapt and survive in an urban environment. Furthermore, roads and other transport lines may act as barriers (Bissonette and Rosa 2009; Rytwinski and Fahrig 2015; Loro *et al.* 2015), fragmenting habitats and leading to isolated pockets of population which may reduce genetic diversity and overall fecundity. Road traffic also increases hare mortality rates (Roedenbeck and Voser 2008), further impacting population size and distribution.

2.4.4 Species Status Debate

It is widely accepted across the literature (Barrett-Hamilton *et al.* 1910; Reid 2006; Caravaggi *et al.* 2017) that the Irish hare is morphologically, ecologically and behaviorally distinct from its mountain hare sub-species counterparts. According to Reid (2010), the Irish hare is in fact more ecologically similar to the European hare than it is to other mountain hare sub-species due to similar grazing habits and a co-reliance on grasses.

Caravaggi *et al.* (2017) highlights key characteristics by which the Irish hare is distinguishable from its relatives. The author first notes observations by Hughes *et al.* (2006) of the relatively high number of unique genetic forms present in the Irish hare compared to other sub-species. Hughes *et al.* (2006) contend that its genetic composition supports the hypothesized paleoendemic origins of the species in Ireland, having survived the last ice age in a glacial refuge.

Additionally, almost all mountain hare sub-species exhibit camouflage whitening of fur during periods of snow cover (Hewson 1958). However, this trait has almost entirely eluded the Irish hare, which displays only marginal whitening of the ears and feet (Flux and Angermann 1990). Caravaggi *et al.* (2017) continue, arguing that literature (Wu *et al.* 2005; Cook and MacDonald 2010) contends that differences between the Irish hare and other mountain hare sub-species are as pronounced as those observed between the Arctic (*L. arcticus,* Ross 1819) and the Alaskan hares (*L. othus*, Merriam 1900), both of which are defined as separate species (Reid 2010), but whose phylogenetic relationship with the mountain hare have been a subject of contentious discussion.

Finally, the significant ecological plasticity displayed by the Irish hare is also worth noting in the context of the species status debate. Wolfe *et al.* (1996) observe the breadth of habitat in which Irish hare presence occurs, which ranges from intertidal zones to mountain summits. Caravaggi *et al.* (2014) note that this degree of variation in habitat range is unique to the Irish mountain hare, providing further endorsement to the stance that the species is deserving of full species status.

These distinguishing characteristics lead Hughes *et al.* (2006) to argue that the Irish mountain hare is deserving of a taxonomic ‘upgrading’, again highlighting the evolutionary and phylogenetic divergences as well as invoking the Arctic/Alaskan hare example as an additional point of reference. Caravaggi *et al.* (2017) also argues that reassessment of the species status of the Irish hare is justified and the evidence for at least upgrading to an 'Evolutionarily Significant Unit' is persuasive.

2.5 European Brown Hare

The European brown hare *L. Europaeus* (Pallas 1778) is thought to have evolved on the Asian steppes and gradually migrated, colonizing European agricultural habitats throughout the postglacial period (Linzey 2013). It is considered native to mainland Europe, with the except of the Iberian Peninsula, Scandinavia and parts of the Mediterranean (Reid 2010). The brown hare is however a formidable invasive species, having undergone extended range expansion throughout Europe, which Tapper and Barnes (1986) attribute to post-Holocene forest clearing and the spread of pastural agriculture. The literature also suggests that this spread was assisted through many human introductions, primarily for the purpose of coursing, with Linzey (2013) citing specific examples in various Mediterranean islands and Britain either pre or inter-Roman times. Britain later instigated further introductions in many historical colonies including Canada, Australia, New Zealand, and the Falkland Islands, in all of which the European hare has successfully naturalized (Reid 2010; Reid and Montgomery 2007; Caravaggi *et al.* 2014). Extant population distribution is displayed in Figure 3: Distribution of extant hare species in Eurasia and Africa (Melo-Ferreira et al. 2012).

According to Smith *et al.* (2005), the European hare has a preference for agricultural crop and pastures, primarily for the food and shelter provided by the generally heterogeneous landscape type. Research by Caravaggi *et al.* (2014) indicated a significant association with habitat patch edge density and therefore a preference for hedgerows and edge habitats as resting sites. The European hare does not utilize woodland or urban areas (Pelorosso *et al.* 2008).

2.5.1 Numbers and Distribution

European hare populations occupy most of continental Europe and central Asia (see Figure 3). Numbers are in decline across Europe, with decreasing populations largely attributed to intensification and spread of agriculture, and possibly exacerbated by hunting (Hutchings and Harris 1996; Linzey 2013). Roedenbeck and Voser (2008) highlight additionally the impact of roads and barriers on European hare populations, noting the cumulatively negative effect caused by increasing road densities in Switzerland, where the species is listed as ‘threatened’ on the Swiss red list (Schai-Braun *et al.* 2012).

2.5.2 Introduction to Ireland

The brown hare was extensively introduced throughout Ireland during the 19th and 20th centuries (Thulin 2003) however the Co. Tyrone and Co. Derry populations recorded by (Reid and Montgomery 2007) are thought to be the current extent of verifiable established populations on the island at present.

The Hare Survey of Ireland (Reid *et al.* 2007a), the most comprehensive and up to date all Ireland survey of lagomorphs, made no confirmed presence reports of the brown hare. However, the authors recognize the difficulty posed by identifying two species with such nuanced differences, often at dawn or dusk and at distance. They also reference to a number of anecdotal reports that indicate a population of brown hares exists between Julians town, Co. Meath (53°40’21’’N, 06°17’07’’W) and Balbriggan, Co. Dublin (53°36’28’’N, 06°11’03’’W), possibly extending up to southern Co. Louth. Additionally, Sheppard (2004) alludes to an additional population that may reside in east Donegal, not far from known introduction sites. The authors note in both (Reid and Montgomery 2007) and (Reid *et al.* 2007a) that although not detected, their presence is plausible, although distribution would likely be limited. Tosh *et al.* (2005) estimated the known Co. Tyrone (Strabane)/Co. Derry (mid Ulster) population at around 700 – 2000 individuals, while the Strabane population remains unknown.

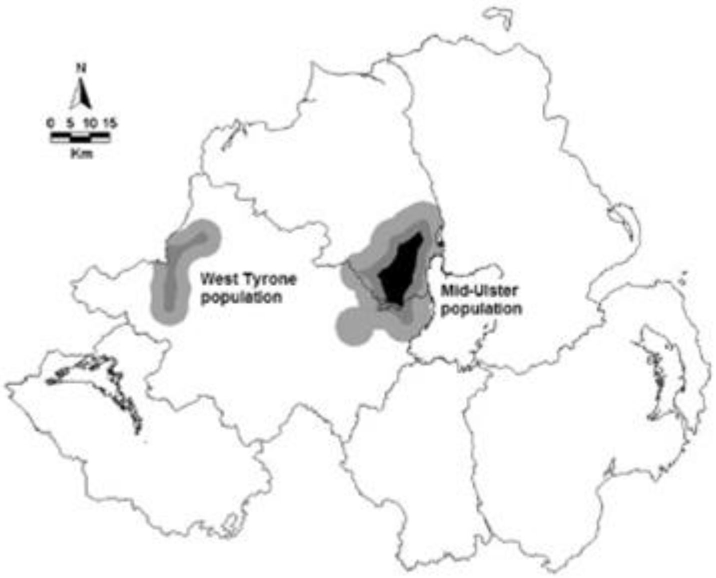


Figure 5: Known extant invasive brown hare populations, recorded during the Hare Survey of Ireland (Reid and Montgomery 2007). Black shading indicates core range; dark grey is areas of sympatry; light grey is dominated by the endemic. (Taken from Reid 2010).

Reid (2010) highlights the historic and current ambiguity around brown hare occurrence records in Ireland, noting that presence records dating as early as 1979 do exist for the northern counties as well as numerous others in the south west, however dubious georeferencing resulted in inaccurate data. The author points to additional anecdotal records, and again notes the difficulties with misidentification between the invasive and the endemic.

2.5.3 Success as an Invasive

The successful naturalization of the European hare in many non-native countries is testament to its success as an invasive colonizing species, despite substantial assistance through countless human introductions. Generally, lagomorphs in the genus *Lepus* co-exist in partial parapatry and this is mostly the case with contact zones between the European and the Mountain hare (Acevedo *et al.* 2007). Elevation and habitat preferences appear to play a role, with many contact zones seemingly stable, such as those that occur in the Alps or the Scottish Highlands (Leach *et al.* 2015). The author attributes this stability to a combination of differences in habitat and dietary preferences. They also predict that these elevationally defined contact areas will experience an upward shift in altitudinal separation in line with climate change induced warming.

Contrary to the hare frontiers of the Alps or the Scottish Highlands however, the brown hare and mountain hare exist in sympatry in Ireland, Sweden, Finland, and Russia (Flux 2008). The literature suggests that frontier stability is not uniform and does not extend to those areas in which there has been a recent introduction. For example, Jansson and Pehrson (2007) point to the widespread displacement of native mountain hares by the brown hare across much of southern Sweden. Levanen *et al.* (2015) confirm the same situation across southern Finland, and more recently in Northern Ireland (Reid and Montgomery 2007; Reid *et al.* 2010; Caravaggi *et al.* 2014; Caravaggi *et al.* 2017).

2.6 Competitive Exclusion

Much of the literature (Thulin 2003; Reid 2010; Caravaggi *et al.* 2014) contends that the invasion dynamics of the brown hare, as well as biotic interaction with the native mountain hare, are poorly understood and call for additional research. Thulin (2003) points to research by Angerbjörn and Flux (1995) and Mitchell-Jones *et al.* (1999), observing that comparisons of mountain hare and brown hare distribution in Europe reveal that in those areas where the latter occurs, the former appears to be restricted to high altitudes and forested regions. Indeed, the European hare has a feeding preference for agricultural grasses, and as the dominant competitor, consequently causes the displacement of the mountain hare from lowland farmlands (Thulin 2003). Angerbjörn and Flux (1995) previously noted a characteristic observation of hares that they were broadly divisible by habitat type.

Caravaggi *et al.* (2014) notes that although the separating mechanisms are not clear, competitive exclusion is suggested as the likely process that facilitates this parapatric relationship observed at most brown hare/mountain hare frontiers. Most hare species exist in mutually exclusive allopatry (Flux 1981) and in the absence of another hare species, each has a tendency to inhabit the potential range of its geographical neighbors, however usually retreating to their own optimum niche range upon contact (Reid 2010). It is from this attribute that inter-specific competition is inferred (Thulin 2003).

The relative stability attributed to the parapatric frontiers between hare species is partially a consequence of co-evolution in proximity to one another (Flux 1981). In the case of human induced introductions, the observed sympatry is temporally transient (Flux 2008), as the force of competitive exclusion causes separation and a drift toward the status quo of parapatric and allopatric relations.

2.6.1 Sweden Case Study

There are two extant hare species residing in the Fennoscandian region; the native mountain (heath & northern) hare and the recently established, invasive brown hare (Winiger 2014). Upon establishment, the brown hare expanded rapidly northwards, quickly outcompeting the endemic heath hare (Thulin 2003) to the point of virtual eradication, with the northern hare not faring much better (Caravaggi *et al.* 2017, via per.comm Thulin). ENMs for the Northern hare produced by Caravaggi *et al.* (2017) displayed a strong association with temperature and precipitation seasonality as well as coniferous forest land cover; conditions known to be unamenable to the brown hare, and the likely reason for the Northern hare's continued survival in the region.

Thulin (2003) speculates that brown hares facilitate this northward expansion through hybridization and introgression of mountain hare DNA. This would not be a trait unique to the brown hare; as the author notes, it is a commonly observed evolutionary adaptation force among plants. Jansson and Pehrson (2007) suggest that, in the case of Northern Sweden, where there is permanent seasonal snow cover, latitude is the primary limiting factor in further brown hare expansion. Consequently, they assign some blame to climate change for the growing threat to mountain hare populations in Sweden and elsewhere, as global warming causes snow lines to retreat ever further northward, facilitating further brown hare encroachment.

3 Methodology

3.1 Study Area

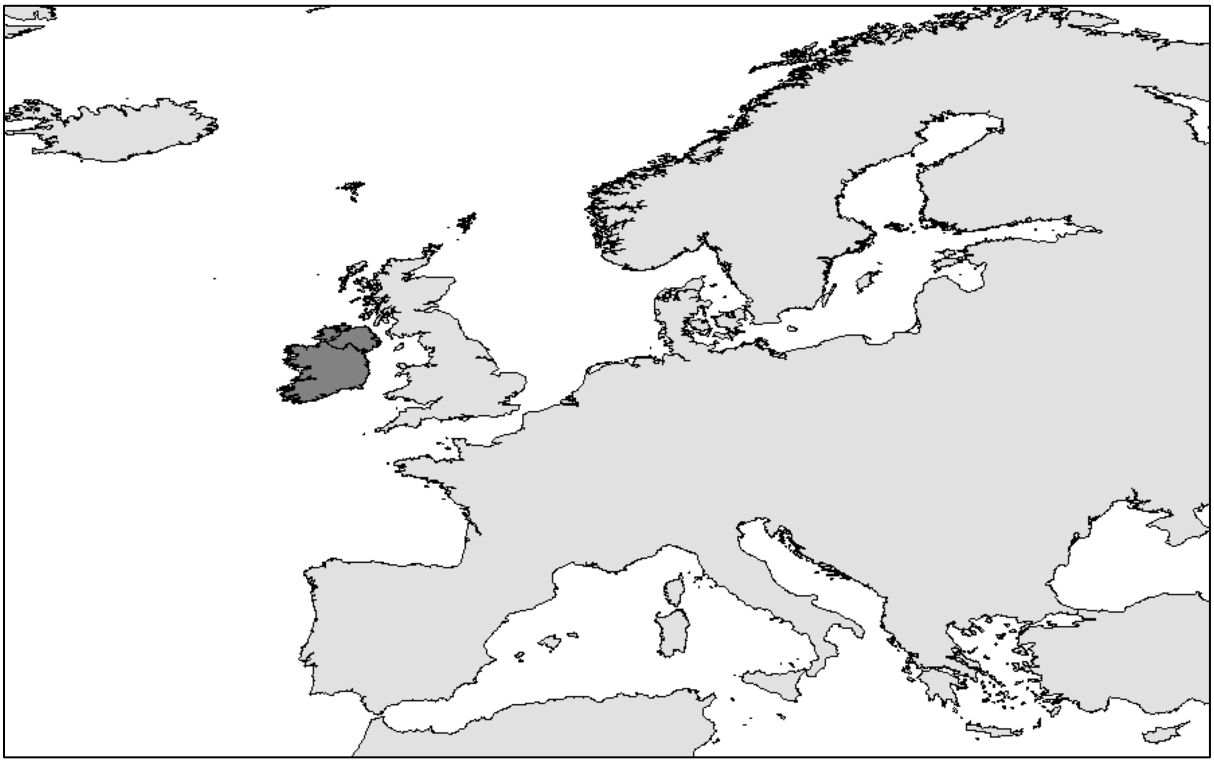


Figure 6: Study area within Europe

The chosen study area is the island of Ireland (52.1424° N, 7.6931° W) in its entirety (both Northern and Southern jurisdictions), encompassing approximately 84,000km^2 land surface area. The terrain is overwhelmingly dominated by pastureland, particularly in the center and east of the island. The main exceptions are the western coast which is lined by peat bogs and moorlands, and the south

eastern quarter which consists mostly of arable land. Mixed forests are scattered throughout, with somewhat higher concentrations in the south west of the island.

Figure 7: Study area within the British Isles

Ireland has few mountains, all of relatively modest elevation, with island-wide ranges from -3m bsl in coastal County Wexford to the highest peak of 1031m asl at Carruantoohil, County Kerry. This is particularly relevant to the study as, in the absence of competition, the endemic is inclined to occupy lowland areas, contrary to their other mountain hare subspecies counterparts, for example those situated in Scotland or the Alps. It is however anticipated that the endemic demonstrates sufficient ecological plasticity that it could adapt to higher altitudes should it be necessary.

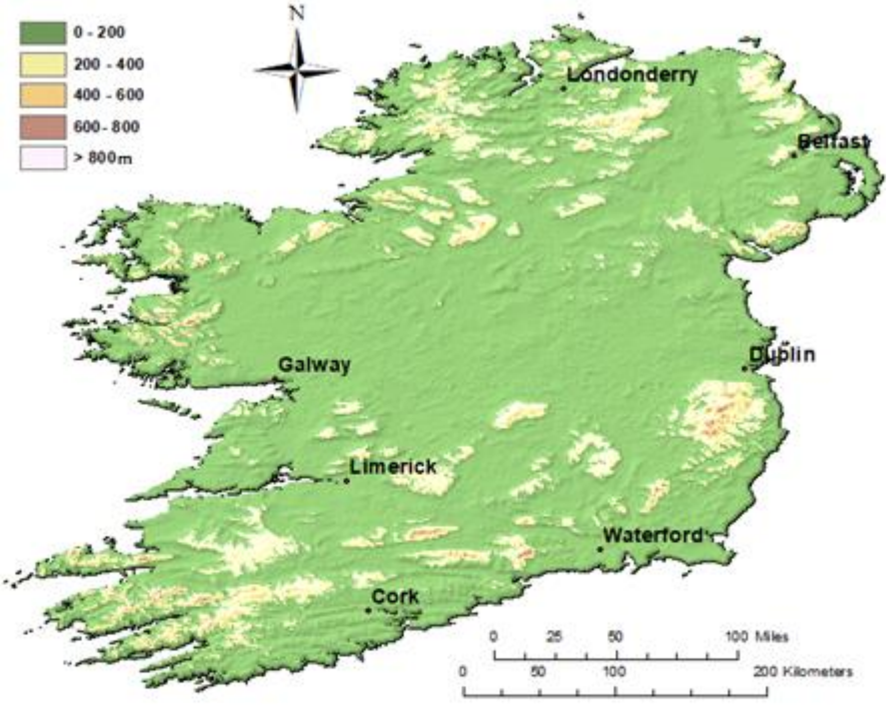


Figure 8: Map of Ireland showing population centers and topography

The Irish climate is defined by its adjacency to the North Atlantic Ocean, which brings temperate conditions and high levels of precipitation year-round. Current climate projection models predict some moderate changes in the coming decades however, and this will likely impact the suitability of habitats across the island for the endemic hare, and indeed for many other species as well.

There is relatively light transport infrastructure and urban fabric on the island by Western European standards, with the major cities being restricted to the Eastern coastline. This inevitably enhances overall habitat suitability for hares and other biodiversity. However, increasing urbanization is a global phenomenon and Ireland is no exception.

3.2 Research Design

The study draws upon numerous secondary data sources pertinent to Irish geography and biodiversity, particularly within the context of the Irish hare. The secondary data sources take two forms; firstly, the study utilizes current and past scientific literature in the area and draws upon this literature to determine the habitat and environmental preferences for the subject species. The next phase was collection of spatial data from a broad range of sources, which were deemed to be representative of the habitat variables to be examined. A series of variables/factors were selected that were deemed influential in determining the suitability of a given area for the endemic. Spatial data for these variables was collected and, based on peer reviewed literature, arbitrary values were assigned to the variables based on their perceived suitability for the endemic.

Determination of factors to analyze in a GIS environment was based on examination of previous habitat suitability models in the literature for a number of different species. This involved conducting a review of the biological requirements and environmental preferences of the species in question.

The data was subsequently processed, manipulated and ultimately combined on a spatial platform to provide meaningful output in relation to each other, using spatial analysis tools embedded in ArcGIS 10.2.2. software.

In order to provide a geospatially represented prediction of the anticipated home range shift for the endemic, and to estimate the potential loss to suitable habitat extent through climate change, MaxEnt (maximum entropy) software was utilized to create a 'probability of occurrence' model, which can then be overlaid with the original HSM to give a combined output representing how habitat suitability might look in 2050.

3.3 Data Collection & Processing

All the data utilized was determined to be of an appropriately high quality and from reliable sources, primarily government or government sponsored institutions. Occasionally, spatial data was in different coordinate systems, and had to be reconciled with each other. WGS 1984 was utilized as the default geographic coordinate system as the majority of data utilized was in this format. WGS is the World Geodetic System, a geocentric reference ellipsoid form of displaying geographic data.

For subsequent analysis, all layers that were not already in raster format were required to be converted. This was done using the '*polygon to raster*' tool in the '*conversion*' toolbox. The 'anthropogenic disturbance' layers were exceptions. As these layers were evaluated based on distance, the '*Euclidean distance*' tool within the '*spatial analyst*' toolbox was utilized. This tool displays straight-line distance to a source or sources in raster format.

3.3.1 Habitat Suitability Model

3.3.1.1 Land Mass & Provincial Borders

The Irish landmass, accompanying islands, and provincial borders were obtained from Global Administrative Areas (GADM). The shapefiles were downloaded by country, with both ROI and U.K required (to extract NI and merge with ROI landmass).

3.3.1.2 Water Bodies

Republic of Ireland – dataset maintained by the Department of Culture, Heritage and the Gaeltacht, and obtained via data.gov.ie, the Irish governments open source data portal.

Northern Ireland – dataset maintained by the Department of Agriculture, Environment and Rural Affairs, and obtained via OpenDataNI, the Northern Irish government open data source portal.

3.3.1.3 Designated Protected Areas

Republic of Ireland – Special Area of Conservation (SAC); Special Protected Area (SPA); and National Heritage Area (NHA) datasets maintained by the Department of Culture, Heritage and the Gaeltacht, and obtained via data.gov.ie.

Northern Ireland –Area of Special Scientific Interest (ASSI); National Nature Reserve (NNR); Special Area of Conservation (SAC); Special Protected Area (SPA); Area of Outstanding Natural Beauty (AONB); and RAMSAR (wetlands convention) datasets maintained by the Department of Agriculture, Environment, and Rural Affairs, Northern Ireland (DAERA-NI), and obtained via OpenDataNI.

Note that while the protected area categorizations vary slightly between the two political jurisdictions, they are all afforded similar levels of conservation status/protection and are therefore categorized as one broadly defined variable. The various vector shapefiles were combined using the '*merge*' tool to create a single vector shapefile containing all DPA polygons. The '*edit*' tool was then used to update the attribute table, and '*merge attributes*' used to combine all DPA polygons to streamline further data processing. This new merged DPA layer was then merged with a copy of the 'NI/IRE' landmass polygon. This final step was carried out so that when the layer was subsequently converted to raster for use in the final analysis, there is a binary value choice of either 1 'within DPA' or 0 'outside DPA' for the entire study area.

3.3.1.4 Digital Elevation Model (DEM)

A DEM displays terrestrial surface area in raster format, assigning values representative of height to each pixel. The ASTER Global Digital Elevation Model (G/DEM) was used to determine altitude and slope within the study model. ASTER GDEM is a product of a satellite-borne sensor 'ASTER', through a collaborative project between The Ministry of Economy, Trade and Industry of Japan (METI) and the National Aeronautics and Space Administration (NASA). The ASTER GDEM was obtained through Global Data Explorer (GDEx), a collaboration between the Land Processes (LP) Distributed Active Archive Center (DAAC) and George Mason University's Center for Spatial Information Science and Systems.

To attain DEM data for the entire island, the data had to be downloaded in 26 different grid tiles (.tif format), as file size exceeded the single download maximum allowance. '*Mosaic*' function was utilized to combine the different tiles into one DEM raster covering the entire study area. '*Extract by mask*' using the combined NI/ROI polygon as the mask, was used on the final DEM raster to trim it to the study area.

The DEM utilized had a 30m resolution and covered the entire study area, however due to pixel size, there were some omissions where the coast did not align with the edges of the pixels (resolution was too coarse). This is an unavoidable omission but should be considered during any subsequent analysis or assessment. It is of particular significance to the Irish hare, as it is known on occasion to occupy coastal regions, areas thought to be at best in the periphery of their environmental niche and indeed completely outside the niche of most other hare sub-species.

3.3.1.5 Land Cover

The EU 2012 Corine land cover dataset (CLC) was utilized (satellite IRS P6 LISS III) to determine predominant land cover types for the study area. Data was in raster format at 100m resolution and obtained from Copernicus Land Monitoring Service. Corine is a pan-European project which aims to produce uniform, interoperable environmental data and data standards for the EU bloc.

The dataset covers the entirety of the EU, so again '*extract by mask*' tool was utilized, using the combined NI/ROI polygon as the mask, to isolate land cover for the study area only (see appendice 1).

3.3.1.6 Transport Infrastructure

Northern Ireland – The Ordnance Survey Northern Ireland (OSNI) open data '50k transport lines' dataset was utilized and obtained via OpenDataNI. This layer contains all motorways, A B, C class and minor roads in Northern Ireland.

Republic of Ireland – The 'Roads - OSI National 250k Map of Ireland' dataset was utilized and obtained from data.gov.ie.

The island of Ireland has many minor, single lane countryside roads that can go for many hours without any traffic. These roads were not considered to be of significant disturbance, particularly as many hare sightings have been recorded in the immediate vicinity of such roads (Reid *et al.* 2007a). Rural roadside surveys are the predominant methodology and the method utilized during the Hare Survey of Ireland 2006-2007. These minor roads were therefore omitted from the model.

The OSI and OSNI transport layers were merged, after which a new layer was created by extracting the motorways, dual carriageways, A, B, C class roads, and railways only. This new layer was then converted to raster using '*Euclidean distance*' and masked to the study area.

3.3.1.7 Population Density

‘Small area’ geographical divisions were the smallest subdivision of geographical area with available population data. These were therefore utilized to maximize accuracy of population density representation.

Northern Ireland - ‘Small area’ vector shapefile is maintained by Northern Ireland Statistics and Research Agency (NISRA) and was obtained through OpenDataNI.

Republic of Ireland – ‘Small area’ vector shapefile is maintained by OSI and was obtained from data.gov.ie.

Population data was obtained separately, in the form of .csv spreadsheets, and was sourced from the NISRA (NI) and the CSO (ROI). Population density was calculated within the .csv file via MS Excel, using the following expression:

Pop. Dens = Total population / Area (m^2)

This dataset table was then joined to the vector shapefile for ‘small area’ divisions using the ‘*join table*’ function in ArcGIS and subsequently converted to raster.

3.3.1.8 Established Brown Hare Populations

Contact was made with Dr Neil Reid at Queens University Belfast, to request data for known brown hare sightings and populations. Dr Reid advised that this data was held by the Centre for Environmental Data and Recording (CEDaR). CEDaR was subsequently contacted, and the data request approved and released. Presence locations were based on the Northern Ireland Irish Hare Survey 2004 (Tosh *et al.* 2005), see Figure 9.

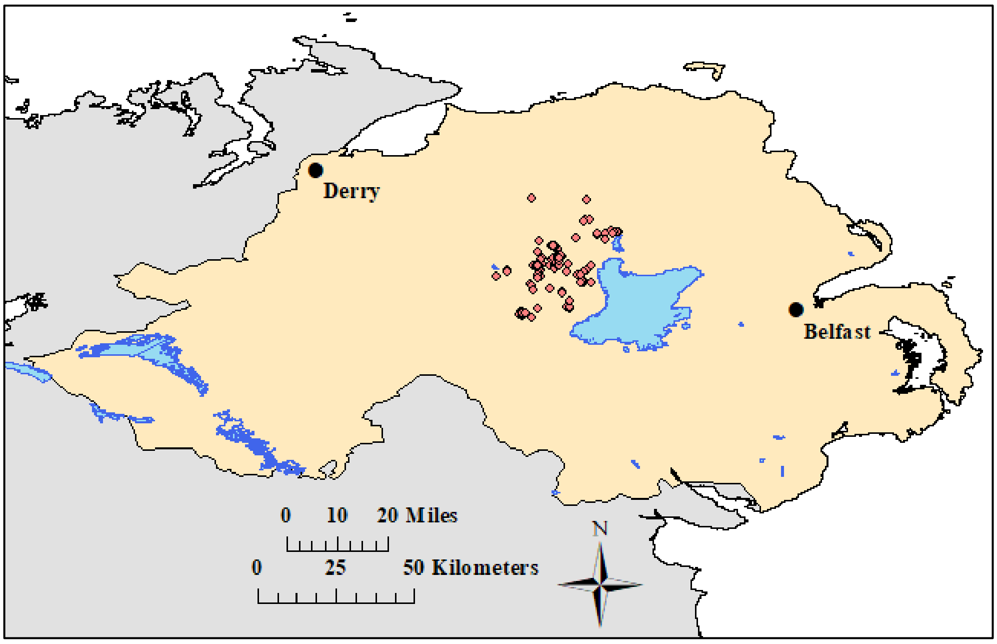


Figure 9: European hare survey 'presence' data locations map.

3.3.2 Predictive Species Distribution Model

3.3.2.1 Species Presence Data

Species presence data (sightings) for the Irish hare was obtained from the results of the Hare Survey of Ireland 2006-2007 and obtained via the Irish National Parks and Wildlife Service (NPRS) database in .shp format. To process this data in MaxEnt software, the following steps were taken:

1. presence data was required to be in .csv format, with XY coordinates for each presence record. As the .shp file was in TM65 (Irish National Grid) coordinate system, it was projected to WGS 1984 using the 'transformations' function in ArcGIS.
2. Each presence record was represented as a polygon; to obtain XY coordinates, these were converted into 'points' using the '*Feature vertices to points*' function, which converts the polygons into a single point using the starting corner of the shape.

3. XY coordinates were then calculated using the '*Add XY coordinates*' function. The attribute table, including the newly calculated XY values, was then converted to .csv format using the '*Table to excel*' function.

3.3.2.2 Current & Future Climate Data

The study incorporated climate model projection data (HadGEM2-ES) for the year 2050 into the completed habitat suitability model as a secondary analysis, demonstrating further expected reductions in suitable areal extent for the endemic.

Current and future climate projection data was obtained via WorldClim, an opensource climate global climate database designed for use in ecological modeling and GIS. Current climate data is required to for 'training' the model, which establishes a correlation between presence locations and their associated climatic conditions, and then projects these against the alternative (in this case, Hadley projections for 2050) climate data.

Data is gridded with a spatial resolution of circa 1km^2. WorldClim bioclimatic variables were utilized; these variables are derived from monthly temperature and rainfall values in order to generate more biologically meaningful variables. *Mean temperature (BIO1), temperature seasonality (BIO4)* and *precipitation seasonality (BIO15)* were the most significant contributing bioclimatic variables to suitability based on European ENMs, as identified in Caravaggi *et al. (*2017) and were therefore chosen to represent meteorological influence on future suitability.

4 Model Development & Analysis

For this study, a multi-criterial evaluation approach was utilized, and a habitat suitability model developed for the endemic. The '*weighted overlay*' function within the '*Spatial Analyst*' toolbox was chosen to evaluate the habitat. This tool overlays a number of rasters using a user defined common measurement scale and assigns a value to each based on user-defined % importance/weighting. The chosen methodology was designed to calculate actual available territory for the endemic, encompassing environmental and socio-economic variables, such as anthropogenic disturbance.

Determining an appropriate methodology is a compromise between model accuracy and cost, meaning that including all biotic and abiotic factors influencing the suitability of habitat for a given species would be impossible (Store and Kangas 2001). Often, appropriate spatial data for certain identified species traits or preferences is not feasible. For example, Karmiris and Nastis (2007) and Lush *et al. (*2014) highlight the negative influence of intense livestock grazing, which acts as both a physical deterrence to the brown hare as well as a drain on available food and shelter resources. This deterrence factor would likely extend to other hare sub-species as well. Pelorosso *et al.* (2008) note a conclusion also reached during this study; this information is rarely available in a format suitable for integration to habitat modelling.

This study explored the possibility of incorporating livestock density as a suitability condition for the endemic hare. Spreadsheet data was sourced from the Agricultural Census in Northern Ireland 2017 (DAERA 2017) which indicated total livestock numbers for specific geographical areas. A vector shapefile for the NI 2014 district electoral areas (DEA) was obtained from OSNI. Livestock density census data was integrated into the OSNI DEA vector shapefile to facilitate a representation of livestock density based on approximate geographical distribution.

The smallest available areal subset divisions were by ‘district electoral areas’, of which the smallest covered in the region of 9-14km^2 in the Greater Belfast area, and getting many magnitudes larger in the rural areas [see Figure 10]. At this size, densities are highly unlikely to be uniform throughout the region and would therefore be a very loose representation of on the ground realities at best. Similar data for ROI was also attained, although the smallest available geographical subset was larger still than those available for NI, and therefore deemed totally unsuitable for model integration.

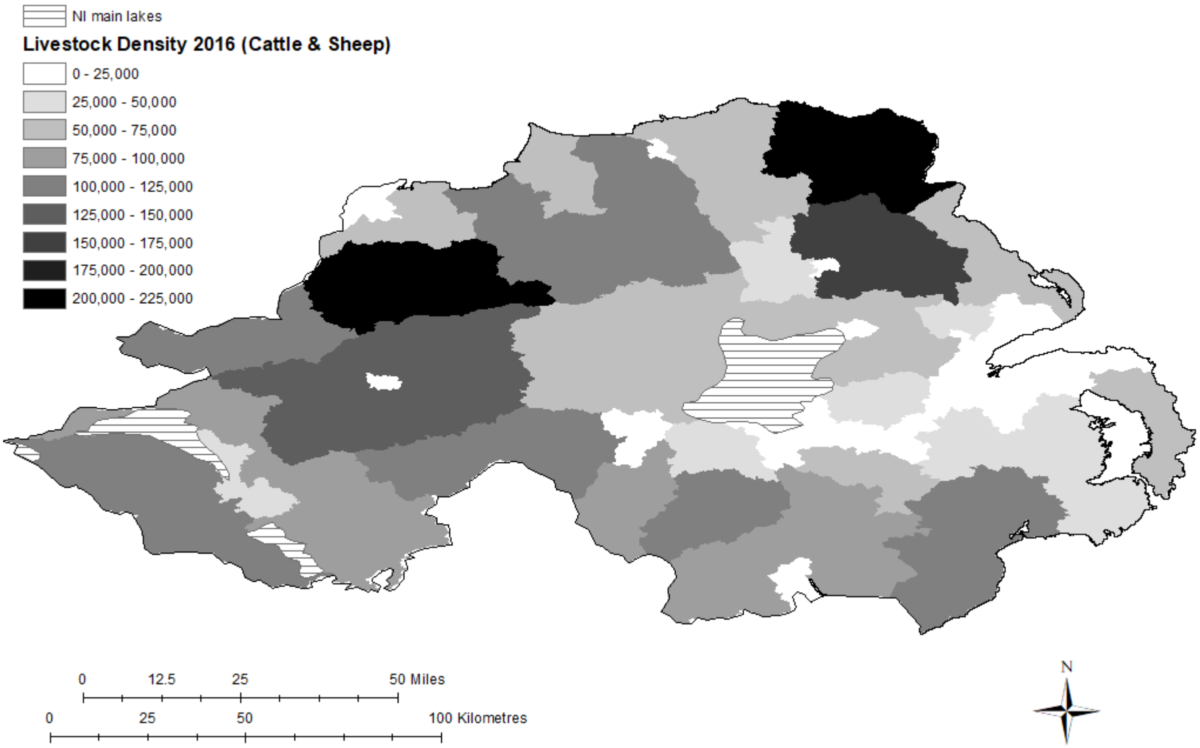


Figure 10: Livestock densities by District Electoral Area in NI.

4.1 Suitability Modeling Criteria (habitat preferences)

Modeling criteria were selected based on previous literature in the field, cross examining habitat suitability models both for various hare species, and for different species altogether. While the logic supporting the selection criteria is embedded in the literature, the exact values for most are arbitrarily assigned. For example, it is known that transport infrastructure is a deterrent to hares and most other species, due to noise disturbance, and the physical danger posed. However, exact distance data on the extent of this influence does not exist so 100m intervals were assigned. <200m is deemed totally unsuitable, <300m somewhat unsuitable, <400m somewhat suitable, and so on. See Table 2: Habitat suitability variables and their assigned values. for assigned suitability values.

4.1.1.1 Altitude

A difficult factor to accurately assess, as although the mountain hare is known to occupy primarily higher altitudes, the Irish mountain hare is an anomaly in this regard. This species most commonly occurs in temperate lowlands and is most abundant in agricultural pastures (Reid 2006; Reid and Montgomery 2007). The absence of competition and major predators in Ireland, coupled with a greater abundance of food and shelter resources in lowland areas would likely explain such an anomaly. For the purpose of the initial model, higher value (indicating greater preference) was assigned to lowlands, although high altitudes were also deemed acceptable, to a lesser extent.

4.1.1.2 Slope

Data on slope preference specifically for the endemic sub-species could not be found. Given the relatively low value weighting given to this component of suitability, and logical deduction that other sub-species of a similar size and physiology would have similar preferences, it was assumed that slope preference was the same as that of brown hares. Slope is therefore considered optimal in the range 0 to 30% (Pelorosso *et al.* 2008). Beyond 40% was deemed totally unsuitable/restricted.

4.1.1.3 Designated Protected Areas

It is demonstrated in literature and in general observation that areas assigned special protection designations enhance habitat suitability for all types of biodiversity, as anthropogenic disturbance is dramatically reduced in these zones. Often additional protection measures are in place, depending on the type of designation. For the purpose of the model, a high value was attributed to pixels falling within a DPA.

4.1.1.4 Anthropogenic Disturbance 1 (transport infrastructure)

A 200m buffer zone to major transport infrastructure (A-B-C roads, motorway/dual carriageways, railway lines) was established, and this area was deemed totally unsuitable/restricted. This approach is consistent with similar studies, such as Pelorosso *et al.* (2008). Scores became increasingly suitable with greater distance (100m intervals).

4.1.1.5 Anthropogenic Disturbance 2 (urban areas)

A raster representation of urbanized land area was derived from the EU CLC dataset. The following LC categories were extracted to create a new ‘urbanized area’ layer:

- 111 –Continuous urban fabric
- 112 – Discontinuous urban fabric
- 121 – Industrial or commercial units

- 122 – Road and rail networks and associated land
- 123 – Port areas
- 133 – Construction sites

A buffer zone of totally restricted/unsuitable area for < 500m distance to urban areas was established. Pixels were assigned an increasingly suitable score with greater distance (100m intervals).

4.1.1.6 Anthropogenic Disturbance 3 (population density)

Impact associated with population density cannot be fully representative of on the ground realities; rather this factor was included as a loose additional measurement of anthropogenic disturbance. For example, an area could have a high density if there are numerous high rise residential blocks, but this same area could be surrounded by lush pasture. While an unlikely scenario, this variable was assigned a low weighting (influence) percentage in the weighted overlay analysis and helped to filter out areas such as inner-city parks which may have been otherwise deemed suitable habitat. Observation and literature edifies that the mountain hare does not frequent urban green areas.

4.1.1.7 Land Cover

Land cover types were categorized using the standard CLC subdivisions, and arbitrary value assignments given for each land cover type based primarily on literature, although some logical assumptions were made as well (for example estuaries, lagoons, sea/ocean are deemed totally unsuitable). See Table 3 for scoring.

4.1.1.8 Brown Hare Source Areas (biotic interaction)

It is well established in the literature that the invasive will outcompete the endemic for habitat space and deter the endemic through competitive exclusion (Thulin 2003). Additionally, hare surveys such as Reid *et al.* (2007a) conducted in these established invasive source areas confirm that deterrent factor further.

The model therefore identifies the primary populations and establishes a buffer zone based on the home range extent of the invasive. Home range was established by collecting mean home range sizes (ha) from several previous studies and calculating a mean value. Schai-Braun and Hackländer (2014) compiled a list of studies and their respective mean home range sizes, from which the relevant data has been transcribed into Table 1 below.

Author(s)	**Year**	**Mean home range size (ha)**
Schai-Braun and Hackländer	2014	12
Ruhe and Hohmann	2004	21
Smith *et al.*	2004	29
Brockhuizen and Maaskamp	1982	29
Tapper and Barnes	1986	38
Reitz and Leonard	1994	113
Stott	2003	133
Marboutin and Aebischer	1996	138

Table 1: European hare range size data for agricultural areas (data taken from Schai-Braun and Hackländer 2014).

Mean value was calculated as 64.125 ha. The buffer zone was therefore set at 452m (radius of 64.125 ha circle). Again, suitability scoring increased with distance, with up to double this radius (904m), considered somewhat suitable, representing the area of known sympatry on the periphery of the invasive source areas, where the two species currently co-exist.

4.1.2 Reclassification Process

For the purpose of conducting a suitability analysis, in this case a '*weighted overlay'* analysis, each input variable must be assigned values based on a common value scale across all inputs.

In this case, a scale of 1 – 5 was selected, with 5 being the highest preference option. For example, a value of 5/5 was assigned to maximum distance from roads, > 800m, meaning that the hare displays a preference for those areas situated the greatest distance away from any roads.

4.1.2.1 Assigned Suitability Scores

Altitude (m)	**Assigned Suitability Score**	**% Influence**	**Additional Supporting Literature**
0 – 200	5	6	‘*..and, most notably the Irish hare, are adapted to a lowland ecology in the absence of contact with the European hare*.’ (Caravaggi *et al.* 2017).
200 – 400	5		
400 – 600	4		
600 – 800	3		
800+	2		
Slope (deg)			
0 – 10	5	4	‘*Slope is considered optimal in the range 0 to 30%.*’ (Pelorosso *et al.* 2008)
10 – 20	4		
20 – 30	3		
30 - 40	1		
40+	0 / RESTRICTED		
Designated Protected Area			
Yes	3	8	‘*Globally, species richness is 10.6% higher and abundance 14.5% higher in samples taken inside protected areas…*’ (Gray et al. 2016); (Xavier da Silva *et al.* 2018)
No	1		
Anthropogenic Disturbance 1 (roads dist, m)			
0 – 200	0 / RESTRICTED	18	‘*To simulate the negative effect of traffic and human activity on the hare, a 50 metres buffer was drafted around the road and rail networks and urbanised areas.*’ (Pelorosso *et al.* 2008); ‘*…three main effects potentially arising from roads on hare populations. (1)* Disturbance effects *caused by noise, dust and light and heavy metals may lead to avoidance of the areas adjacent to roads... (2)* Barrier effects…*This may be because animals avoid crossing heavily used roads or because animals do not reach the other roadside as they are killed by collisions with vehicles... (3)* Road mortality*…In the Czech Republic…brown hare is one of the species being most often killed by traffic’* (Roedenbeck and Voser 2008); (Loro *et al.* 2015).
200 – 300	2		
300 – 400	3		
400 – 500	4		
500+	5		

Anthropogenic Disturbance 2 (urban area dist, m)			
0 – 500	0 / RESTRICTED	15	‘*urbanised areas are not suitable for the Brown hare*’ (Pelorosso *et al.* 2008).
500 – 600	2		
600 – 700	3		
700 - 800	4		
800+	5		
Anthropogenic Disturbance 3 Urban Density (pop p/km)			
0 – 75	5	12	See ‘anthropogenic disturbance 2’.
75 – 150	4		
150 – 225	3		
225 – 300	2		
300+	/ RESTRICTED		
Brown Hare Source Areas			
0 - 452	0 / RESTRICTED	12	‘*Most members of the genus lepus occur in parapatry… Where ecologically similar species come into first or secondary contact due to human-mediated introductions, sympatry is transient and usually short-lived.*’; ‘*There is increasing evidence that the European hare poses a threat to the genetic integrity of the Irish hare’* (Caravaggi *et al.* 2014).
452 – 904	2		
904+	3		

Table 2: Habitat suitability variables and their assigned values.

Corine Code	Land Cover Type	Suitability Score	Additional Supporting Literature
111	**Continuous urban fabric**	**0**	
112	**Discontinuous urban fabric**		
121	**Industrial or commercial units**		
122	**Road and rail networks**		
123	**Port areas**		
131	**Mineral extraction sites**		
132	**Dump sites**		
133	**Construction sites**		
124	**Airports**	**1**	‘*...Irish hares are often seen feeding during the day, sometimes in large herds, notably at Aldergrove Airport, Belfast.*’ (Walker and Fairley 1968).
141	**Green urban areas**	**1**	
142	**Sport and leisure facilities**	**1**	
211	**Non-irrigated arable land**	**4**	Fig 4(b) (Caravaggi *et al.* 2014)
222	**Fruit trees and berry plantations**	**0**	‘*Woodlands…are not suitable for the Brown hare.*’ (Pelorosso *et al.* 2008).
231	**Pastures**	**4**	‘*The Irish hare was associated with temperate, highly productive pastures.*’ (Caravaggi *et al.* 2017)
242	**Complex cultivation patterns**	**3**	Fig 4(b) (Caravaggi *et al.* 2014)
243	**Land principally occupied by agriculture…**		
311	**Broad-leaved forest**	**0**	‘*Woodlands…are not suitable for the Brown hare.*’ (Pelorosso *et al.* 2008). Fig. 4(b) (Caravaggi *et al.* 2014).
312	**Coniferous forest**		
313	**Mixed forest**		
321	**Natural grasslands**	**4**	Fig 4(b) (Caravaggi *et al.* 2014); ‘*Both species occupied improved and rough grassland*’ (Dingerkus and Montgomery 2002); ‘*...feeds predominately on grasses*’ (Caravaggi *et al.* 2014; Caravaggi *et al.* 2017); ‘*The native species was positively associated with improved grasslands…*’ (Dingerkus and Montgomery 2002).
322	**Moors and heathland**	**3**	
324	**Transitional woodland-shrub**	**3**	
332	**Bare rocks**	**1**	
333	**Sparsely vegetated areas**	**2**	
411	**Inland marshes**	**3**	‘*Irish hares are found from the intertidal zone where they forage on seaweeds…’* (Caravaggi *et al.* 2014).
412	**Peat bogs**	**3**	‘*(uplands, bogs, moorlands and coastal habitats) …might remain the sole preserve of the Irish hare.’* (Caravaggi *et al.* 2014)
331	**Beaches, dunes, sands**	**1**	
	Salt marshes	**2**	
423	**Intertidal flats**	**2**	
511	**Water courses**	**0**	
512	**Water bodies**		
	Coastal lagoons		
522	**Estuaries**		
523	**Sea and ocean**		

Table 3: Assigned suitability scoring for Corine land cover categories.

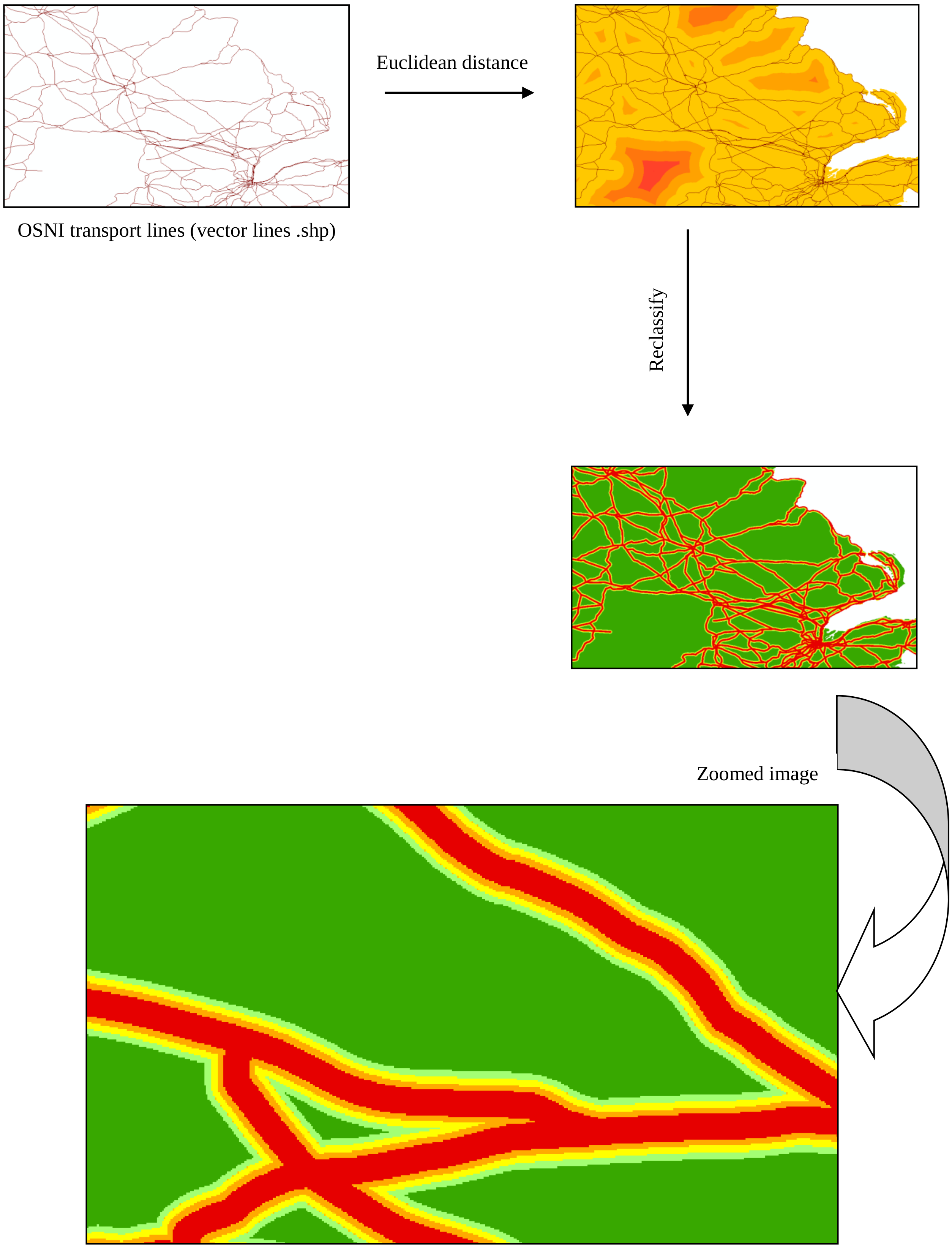
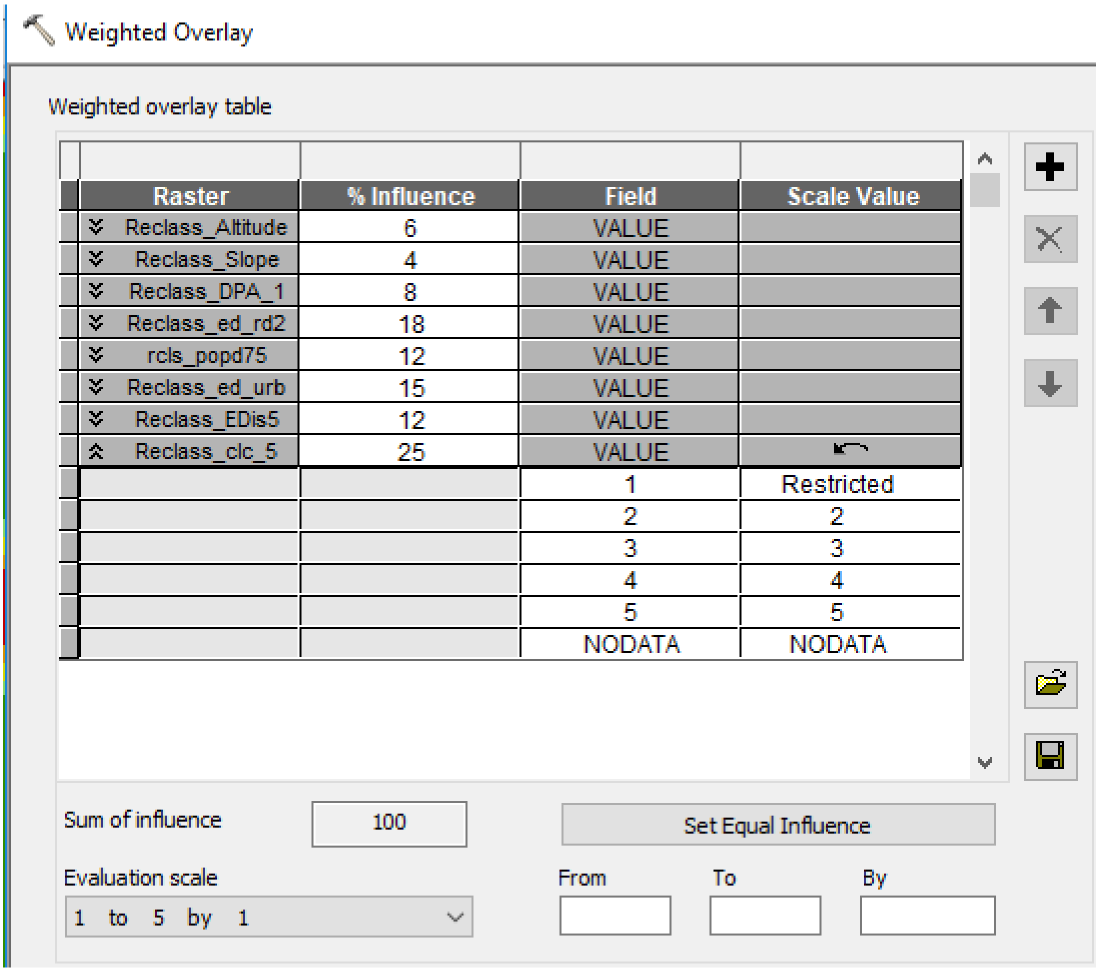


Figure 11: Reclassification process example: anthropogenic disturbance 1 (roads) layer

4.1.3 Weighted Overlay Analysis

For each variable in the weighted overlay analysis, a percentage '*influence*' must be assigned, indicating its degree of importance in the output. For example, land cover was assigned a greater value than slope as this has a substantially more significant impact on the spaces hares choose to occupy. The '*evaluation scale*' was set at '1 to 5 by 1', producing 5 output classifications or 'scores', where the highest would indicate most suitable, after which the geoprocessing was executed. The output is displayed in Figure 14.



Weighted overlay table

Raster	% Influence	Field	Scale Value
Reclass_Altitude	6	VALUE	
Reclass_Slope	4	VALUE	
Reclass_DPA_1	8	VALUE	
Reclass_ed_rd2	18	VALUE	
rcls_popd75	12	VALUE	
Reclass_ed_urb	15	VALUE	
Reclass_EDis5	12	VALUE	
Reclass_clc_5	25	VALUE	
		1	Restricted
		2	2
		3	3
		4	4
		5	5
		NODATA	NODATA

Sum of influence: 100

Evaluation scale: 1 to 5 by 1

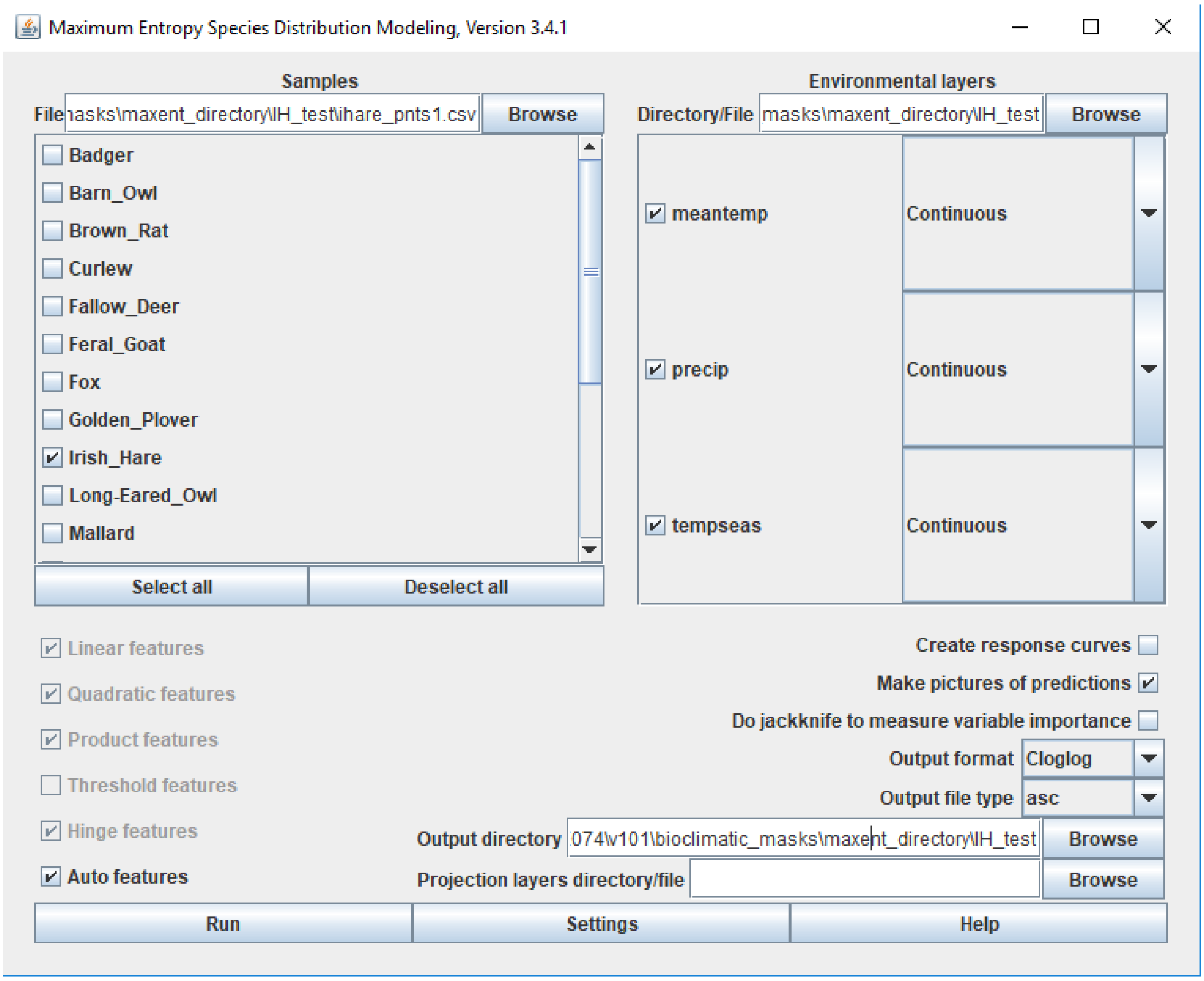
Figure 12: Screenshot of weighted overlay influence levels

4.2 MaxEnt Probability of Occurrence Model

MaxEnt software was utilized to create a ‘probability of occurrence’ model, using species presence data from the Hare Survey of Ireland 2006-2007, and the WorldClim 2050 climate projections (Figure 13). The survey data is a formal biological survey and the most comprehensive of its kind.

MaxEnt creates a species distribution model (SDM) by calculating the relationship between geospatially referenced species presence records and associated environmental conditions (Franklin and Miller 2010). In this instance, future climate data was analyzed against current presence records and their associated climatic conditions, providing an output indicating the likelihood of their occurrence based on the ‘new’ climatic conditions.

1. **Presence localities:** ‘Samples’ (presence data) was uploaded in .csv format, and the relevant species selected.
2. **Environmental variables:** ‘Environmental layers’, the variables by which MaxEnt calculates occurrence likelihood, were uploaded as .ascii raster grids. This is the training data; worldclim bioclimatic variables for present day.
3. **Projection layers directory/file:** This contains the alternative, future climate conditions against which the presence data will be projected.



Maximum Entropy Species Distribution Modeling, Version 3.4.1

Samples

File asks\maxent_directory\IH_test\ihare_pnts1.csv

☐ Badger
☐ Barn_Owl
☐ Brown_Rat
☐ Curlew
☐ Fallow_Deer
☐ Feral_Goat
☐ Fox
☐ Golden_Plover
☑ Irish_Hare
☐ Long-Eared_Owl
☐ Mallard

Environmental layers

Directory/File masks\maxent_directory\IH_test

☑ meantemp	Continuous
☑ precip	Continuous
☑ tempseas	Continuous

☑ Linear features
☑ Quadratic features
☑ Product features
☐ Threshold features
☑ Hinge features
☑ Auto features

Create response curves ☐
Make pictures of predictions ☑
Do jackknife to measure variable importance ☐
Output format Cloglog
Output file type asc
Output directory 074\v101\bioclimatic_masks\maxent_directory\IH_test
Projection layers directory/file

Figure 13: MaxEnt interface.

5 Results & Discussion

5.1 Habitat Suitability

Habitat suitability	Classification No.	% areal extent
totally unsuitable/restricted	1	22.5334
Marginal	2	0.0003
Somewhat suitable	3	0.245
Suitable	4	74.3993
Optimal	5	2.8213

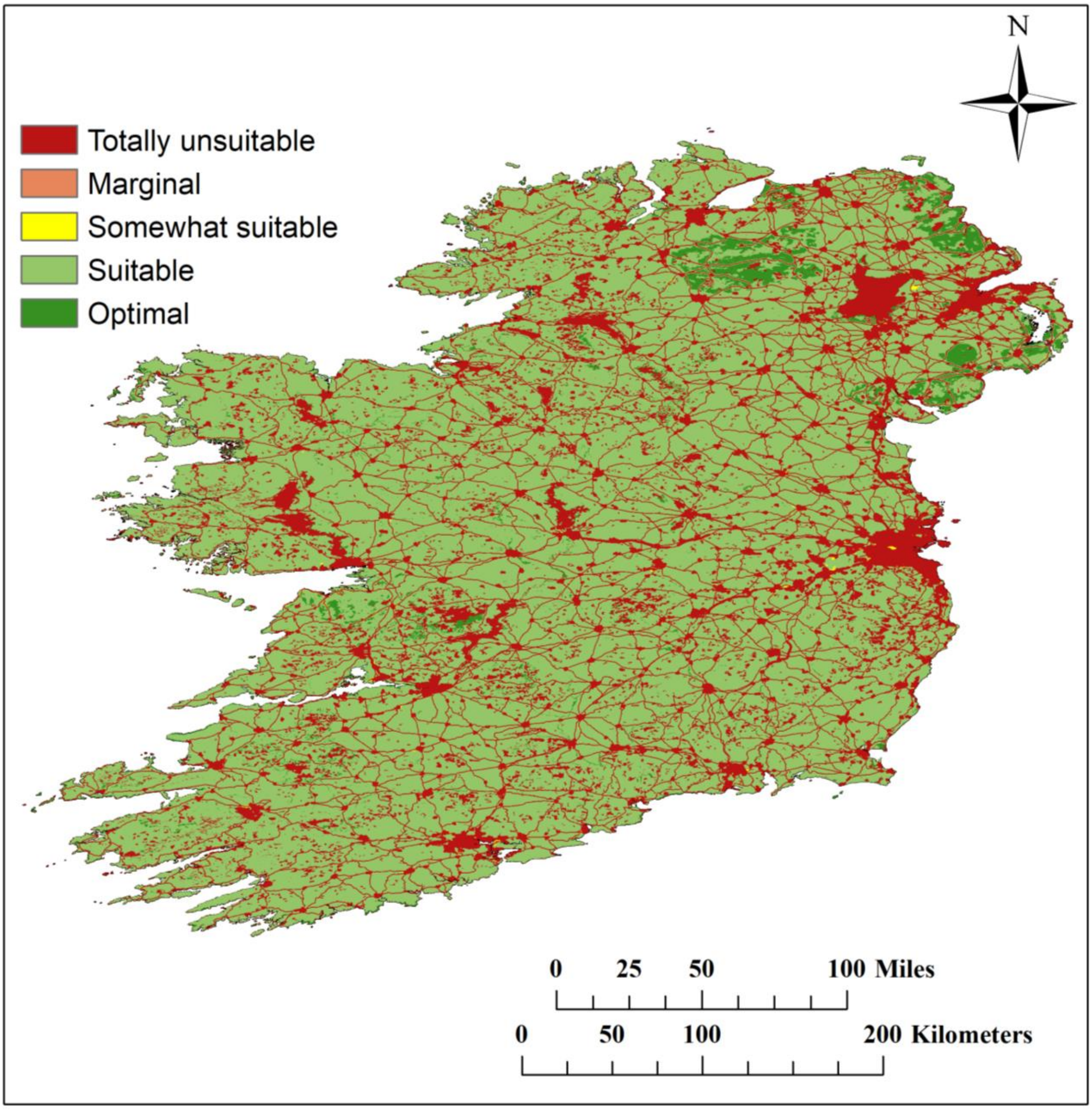


Figure 14: Weighted overlay analysis output - map indicating calculated suitability level for the endemic hare.

The model output indicates that across the island, there are indeed vast swathes of suitable territory for the endemic, with 77.22% of total area being deemed suitable (4) or highly suitable (5). Prior models relying purely on bioclimatic factors (Caravaggi *et al.* 2017) indicated that circa 100% of the total area was suitable, however once the additional anthropogenic and biotic factors were accounted for, the model identified 22.53% of area as totally unsuitable (1). This is primarily due to the lack of suitability associated with urban fabric, areas of high population density, and transport infrastructure (roads and rail). This is visible in the map, as major transport infrastructure and settlements are visibly demarcated within the restricted zones. Marginal (2) habitats were almost in complete omission, with 0.0003% of territory falling into this category, and somewhat suitable (3) habitats followed a similar trajectory, covering only 0.245% of the total available land mass.

Altitude and slope had minimal influence on the model output as the endemic, in the absence of the invasive or threat of predation, is adapted to lowland landscapes in Ireland. While there are many rolling hills in the study area, there are few truly mountainous areas and therefore few areas where altitude or slope have the potential to influence suitability.

Designated protected areas, despite being assigned a low weighting/influence percentage in the model, correlate strongly with optimal (5) zones.

Overall, the suitable (4) category overwhelmingly dominates at 74.3993% of total available land mass, correlating strongly with land cover. Land cover was assigned a high influence percentage in the model, and accordingly, the majority of pastures, grasslands and other agricultural land, which covers approximately 70% of the island (EEA 2018), fell into this category.

5.2 Predicted Range Shift

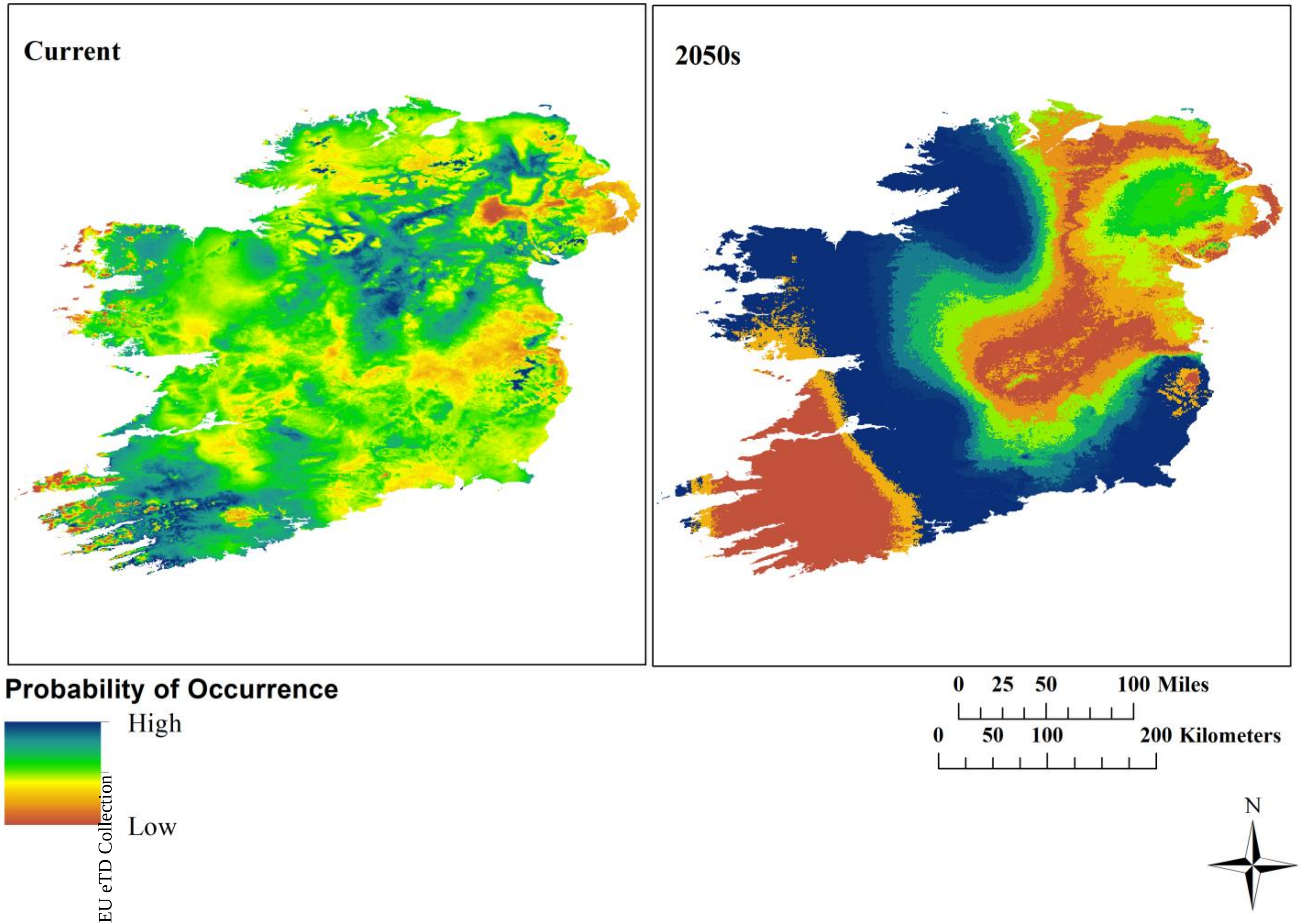
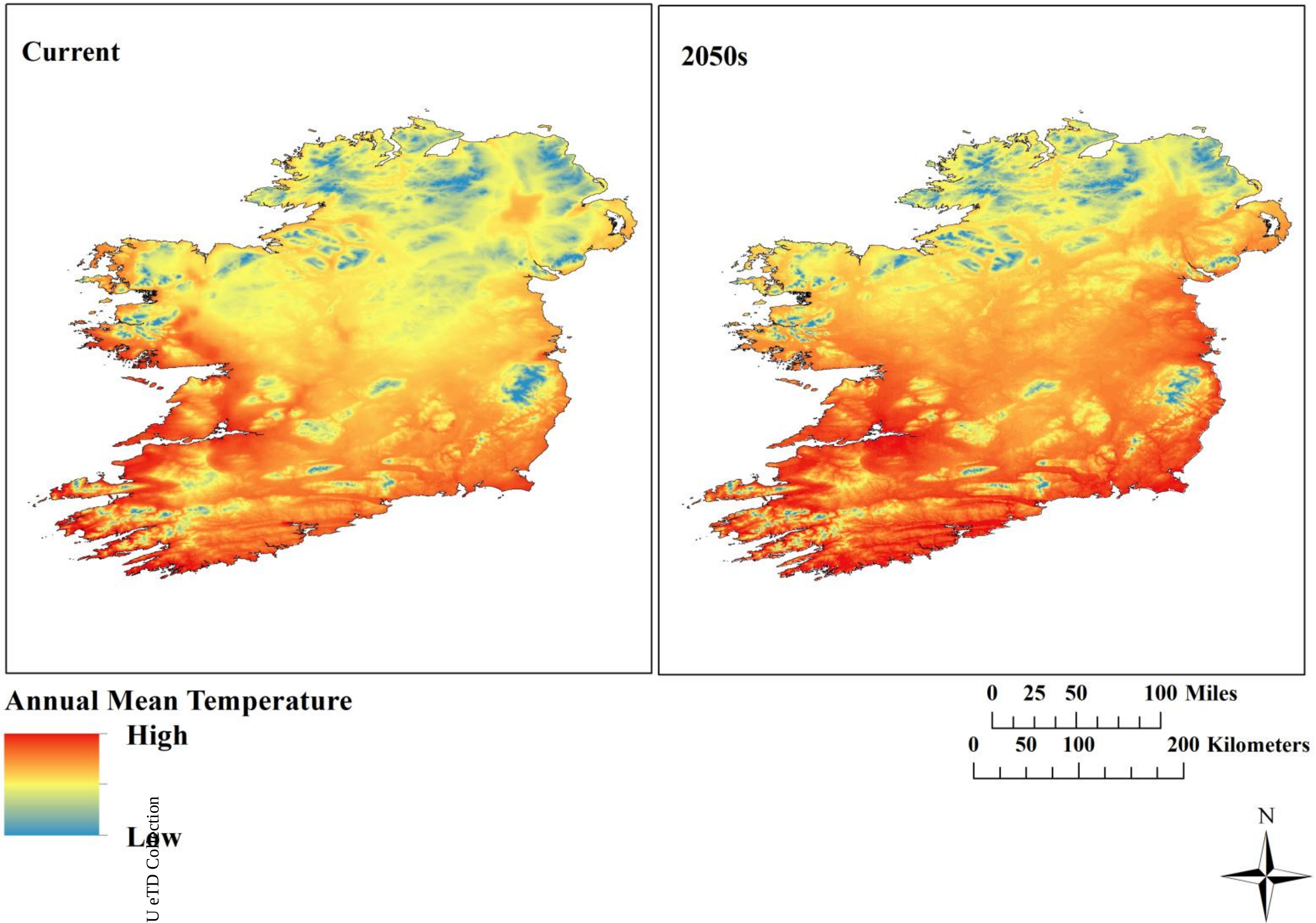
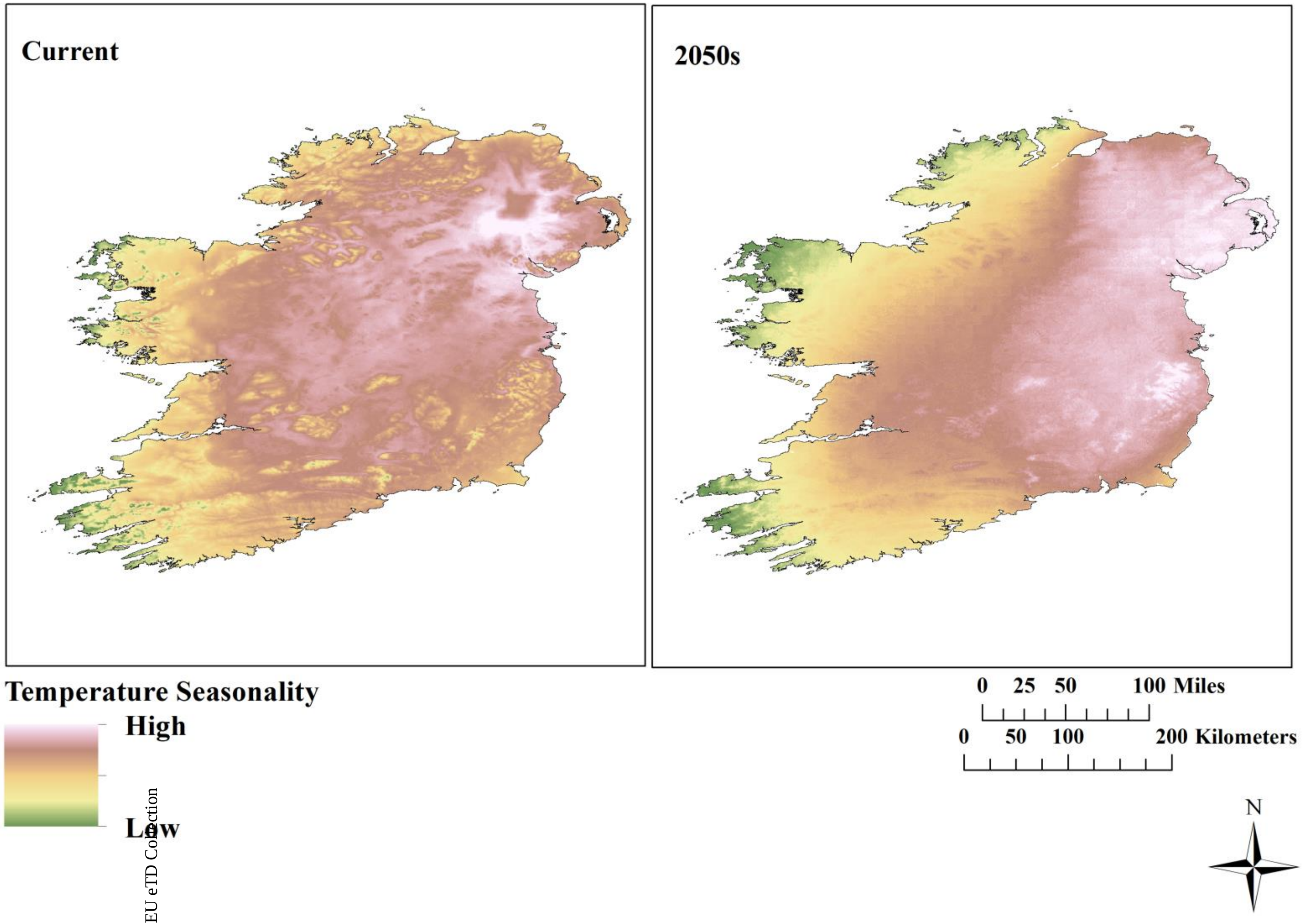


Figure 15: maximum entropy 'probability of occurrence' model of the Irish hare for present day and 2050 bioclimatic conditions


Current
2050s
Annual Mean Temperature
High
Low
0 25 50 100 Miles
0 50 100 200 Kilometers
N


Current
2050s
Temperature Seasonality
High
Low
0 25 50 100 Miles
0 50 100 200 Kilometers
N

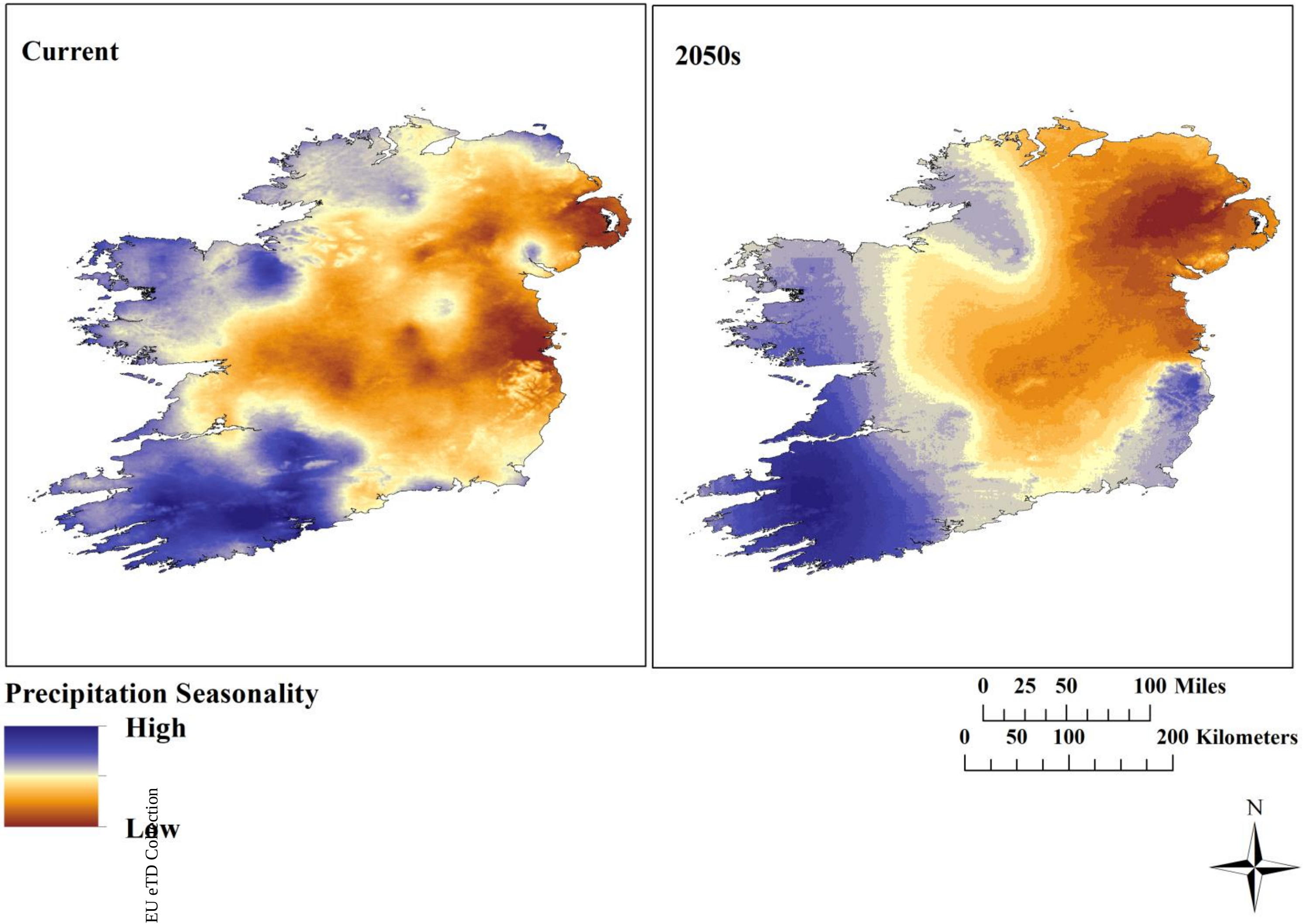


Figure 16: Current and 2050 bioclimatic data utilized in MaxEnt projection model for each variable (pp61-63)

5.2.1 Current

The ‘current’ output shows a large area of highly suitable territory in the center to north eastern region, covering significant portions of Northern Ireland, including the known locations of the established invasive populations. Any advance of the invasive population frontier will therefore quickly reduce the areal extent of a key endemic territory, increasing the probability of hybridization, further risking the genetic integrity of the endemic.

Territory indicating low probability of occurrence is scarce and is contained mostly to small patches on the eastern coastline, particularly in the region of the islands two capital cities. *Annual mean temperature* in the capital regions is already disproportionately higher than the surrounding areas, likely due to the urban heat island effect.
There are also some low probability zones on the far western tips of coastline, where both *annual mean temperature* and *precipitation seasonality* are highest.

5.2.2 2050

The model output indicates a significant geographic shift in bioclimatic suitability for the endemic in a generally westward direction, which accurately reflects current scientific assessment on the issue. Highly suitable territory correlates with high *precipitation seasonality* however there are exceptions, notably in the green mid-range patch in the north east, where *precipitation seasonality* is lowest.

5.2.3 Fundamental and Realized Niches

Hutchinson (1957) defines a specie's fundamental and realized niche as follows:

'*A specie's fundamental niche consists of the set of all conditions that allow for its long-term survival, whereas its realized niche is that subset of the fundamental niche that it actually occupies.*'

In other words, the realized niche is the geophysical space the species actually occupies when all preventative factors are considered. These may include geographic boundaries such as being situated on an island, but also account for biotic and anthropogenic interaction that may deter a species from occupying otherwise suitable territory.

The SDM model relies on species 'presence' data, and therefore represents the realized niche of a species rather than the more holistic fundamental niche. As an extension of this, any projections made therefore are also predictions of a future realized niche, and as biotic and anthropogenic influences may shift temporally, so too would the future realized niche. Phillips *et al.* (2006) elaborate further, highlighting the likely exacerbation of this issue when presence data is derived from smaller geographical areas. Smaller geographical areas will inevitably represent a smaller fraction of the total variation in species community composition and skew projection models. This issue could therefore be mitigated through maximizing the areal extent of any presence data utilized in the model.

This study relied on the 1695 presence records contained within the Hare Survey of Ireland 2006-2007, which surveyed a total of 691 1km^2 grids, an area which covered the entirety of the island, except for some minor omissions primarily caused by access or health and safety issues. The survey is therefore considered comprehensive and robust, maximizing the portion of the fundamental niche represented by the presence data (Peterson and Holt 2003). However, as Peterson and Holt (2003) also note, the fundamental niche is merely a theoretical construct, and so the divergence from the observable realized niche will always remain an unknown factor.

5.2.4 Survey biases

There are a number of unavoidable pitfalls associated with the implicit and explicit assumptions that are required to execute a maximum entropy, probability of occurrence SDM. In the context of sampling bias, distinguishing between areas receiving largest search effort, and actual species preference is impossible (Phillips *et al.* 2009). The MaxEnt model assumes that all locations in the study area are equally likely to be sampled when in reality, species presence data is generally inherently bias as some areas inevitably receive heavier sampling than others, due to local environmental conditions (Merow *et al.* 2013). For example, the Hare Survey of Ireland 2006-2007, from which this study derived its species presence data, utilizes the most south-westerly 1km^2 in each 10km Irish grid square. However, the 1km^2 required the presence of a minor road from which to conduct the survey. In the absence of a suitable road, the sampling location shifted to the next nearest suitable square. This methodology is inherently biased towards those areas in closest proximity to minor roads; these areas therefore receive the highest sample record numbers and are disproportionately represented in comparison to those areas situated further away from the road.

Additionally, use of MaxEnt modeling requires an assumption that detection probability is uniform across the geographic area studied (Yackulic *et al.* 2013). While any comprehensive, scientifically conducted ecological survey will take steps to minimize any bias, certain external influences are unavoidable, for example local traffic flow the area of the survey location may influence probability of detection, as the noise and visuals may deter some species.

5.2.5 Future Land Use and Land Use Change

A difficulty that arises with SDM projections is an inability to account for future land use and land use change. There are simply too many variables, both socio-economic and climatic, that may influence how land use in the future could look. Predictions can be made using remote sensing technology and historical records to identify historical temporal trends and therefore possible future trajectories. Perhaps therefore future studies may explore the possibility of combining land use projection models with bioclimatic SDMs.

5.3 Further Considerations

5.3.1 Invasive Brown Hare Colonization

The Irish hare is widespread in Northern Ireland; however, densities appear to be markedly lower than the rest of the island, and numbers are in decline (Dingerkus and Montgomery 2002). Relatively low densities of the endemic in the north only strengthen the potential for expansive colonization by the invasive brown hare.

Assuming the two species have shifted from a sympatric to allopatric co-existence as anticipated and observed on other mountain/brown hare frontiers (Scotland, Alps, Sweden), dramatic reductions in available territory for the endemic are anticipated. Indeed, most hare species exist in mutually exclusive allopatry (Flux 1981) and in the absence of another hare species, each has the capacity to inhabit the potential range of its geographical neighbors, usually however retreating to their own optimum niche range upon contact (Reid 2010). This means that the invasive is capable of occupying the full current range of the endemic where it is known to out-compete it. Should total colonization of lowland areas occur, the outcome for the endemic is much more severe. Available territory would likely be confined to small areas of high altitude in Ireland's few mountainous regions, as well as some peatland regions along the west coast were bioclimatic and land cover conditions are still favorable.

5.3.2 Potential Habitat Preference Shifts

Caravaggi *et al.* (2014) note a trend among colonizing invasive species that may create a divergence between models and future realities. They highlight that invasive species may undergo spatial sorting of dispersal traits resulting in a shift in habitat preference as a consequence of the invasion process. Therefore, the current observed preferences of the brown hare in Ireland could become different in future as they adapt and colonize their new environment. This has implications for the endemic too, as perceived threats in a given habitat type may be over or underestimated based on the shifting preferences of the invasive.

The endemic has a preference for open field habitats (Dingerkus and Montgomery 2002), in contrast to the invasive, which according to Caravaggi *et al.* (2014) has a preference for high habitat edge densities and smaller habitat patches. As Ireland is expected to continue to experience ever increasing agricultural intensification in the coming decades, field sizes are anticipated to increase, therefore increasing mean habitat patch size and reducing the number of edge habitats (hedgerows, farm walls). These preferences would imply a favorable outcome for the endemic, however the literature (Thulin 2003; Jansson and Pehrson 2007) indicates that the invasive has a competitive edge over the endemic in open, agricultural landscapes. Caravaggi *et al.* (2014) results also show that the invasive has a wider niche breadth which suggests a greater tolerance for a range of habitat types, perhaps therefore exhibiting even greater ecological plasticity than the endemic.

5.4 Implications for the Irish Hare

The expected reductions in available habitat for the Irish hare will undoubtedly further exacerbate the numerous threats it is already facing today. This means that without additional mitigating management strategies in the form of ecological management regimes, the endemic will continue to experience declines in population across it's only current habitat.

The disproportionately high seasonal and annual fluctuations observed in hare populations make the task of monitoring population size and breeding rates particularly difficult, which only serves to compound the issue further. Given that the IUCN, and subsequently the Irish/UK governments, currently deem the conservation status of the endemic to be of low to moderate concern, with only continued monitoring suggested in relation to mitigating measures, the fate of the Irish hare is uncertain.

Taking Sweden as a model, the mountain hare has been made all but extinct with the exception of the far northern territories where the Northern hare retreats to the permanent snow cover, driven by the invasive European hare colonization. There is little to suggest that the same fate does not lie in store for the Irish hare in Ireland. In Ireland, an island, there is no area of permanent snow cover, nor is there any significant elevational barriers in place to halt the advance of the invasive (Reid 2010), and future dispersal stops at the coastline, in the absence of human intervention. Current models (Caravaggi *et al.* 2017) suggest bioclimatic suitability for the invasive is limited to Northern Ireland at present, but climate change is tipping conditions further in the favor of the invasive, to the detriment of the endemic. Furthermore, current suitability for the endemic indicated by models in this study (see Figure 14 and Figure 15) overlaps with the established invasive population locations. This suggests that any advance of the invasive population frontier will inevitably encroach into optimal endemic territory from the outset.

6 Conclusion

In conclusion, the study outcome indicates that available territory for the endemic Irish hare is widespread at present, although significantly lower than that represented by bioclimatic conditions alone. Bioclimatic conditions indicate that the vast majority of the island is suitable or optimal at present. However, anthropogenic disturbance factors including urbanization and transport infrastructure, as well as loss of territory to invasive species, reduce the available habitat for the endemic. Projections of likely expansion of urban fabric may provide further indication as to how much territory is at risk. Research of the impact of habitat fragmentation due to road barriers on local hare populations could provide further indication as to the extent of the risk posed by this factor.

The SDM projection for 2050 climate conditions produce similar results to those indicated in prior literature; the bioclimatic envelope for the endemic is contracting in a generally westward direction. This contraction, coupled with the other anthropogenic and biotic environmental variables suggest a much greater ecological threat to the endemic than previously anticipated, and does not correlate with the present IUCN assessment of a ‘least concern’ conservation status.

HSMs and SDM projections tend to rely on assumptions and generalizations. This approach presents a host of issues that bring their utility into question in the context of ecological management, however it is unquestionable that these models have been critical tools in alerting us to the magnitude of climate change impacts (Sinclair 2010). When all signs are pointing in approximately in the same direction, it would be prudent to take notice and factor this into future ecological management regimes.

6.1 Recommendations/Further Study

6.1.1 Model Validation

The final step of the overlay analysis process is to validate the model to make sure what the model indicates is at a site reflects the on-the-ground reality. A more comprehensive study should validate the analysis by ‘ground truthing’ a sufficient sample of the model output, verifying that the input variables match the reality on the ground. Furthermore, there is scope for error in that any influencing suitability factor omitted from the model (of which there will always be many, as not all variables can be condensed into a geospatial dataset), such as livestock density would not be accounted for. The model output could indicate a full score, perfect habitat patch based on the stipulated model criteria, but only ground truthing could identify that this patch has hundreds of cattle and is heavily overgrazed at present.

6.1.2 Mapping the Colonization Process

A cost-distance analysis, essentially an inversion of the suitability map, could be conducted to determine likely dispersal patterns, based on overall brown hare amenability to adjacent geographic spaces. For example, agricultural areas within 0-600m elevation, situated away from urbanized areas will be highly likely dispersal regions.

Source regions are identified by recent previous studies in which ecological surveys were carried out, and sightings of the invasive have been spatially documented. Cost-distance analysis conducted between the known source locations would further inform the likely colonization process, identifying likely dispersal routes and identifying patterns. This information would undoubtedly prove a useful tool for wildlife managers and ecological planners tasked with stemming the spread of the invasive and/or identifying key conflict areas and therefore areas to apply enhanced protection for the endemic.

7 References

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8 Appendix

Corine Land Cover – map and categories