

Regime shift tipping point in hare population collapse associated with climatic and agricultural change during the very early 20th century

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Abstract

Animal populations at northern latitudes may have cyclical dynamics that are degraded by climate change leading to trophic cascade. Hare populations at more southerly latitudes are characterized by dramatic declines in abundance associated with agricultural intensification. We focus on the impact of historical climatic and agricultural change on a mid-latitude population of mountain hares, *Lepus timidus hibernicus*. Using game bag records from multiple sites throughout Ireland, the hare population index exhibited a distinct regime shift. Contrary to expectations, there was a dynamical structure typical of northern latitude hare populations from 1853 to 1908, during which numbers were stable but cyclic with a periodicity of 8 years. This regime was replaced by dynamics more typical of southern latitude hare populations from 1909 to 1970, in which cycles were lost and numbers declined dramatically. Destabilization of the autumn North Atlantic Oscillation (NAO) led to the collapse of similar cycles in the hare population, coincident with the onset of agricultural intensification (a shift from small-to-large farms) in the first half of the 20th century. Similar, but more recent regime shifts have been observed in Arctic ecosystems and attributed to anthropogenic climate change. The present study suggests such shifts may have occurred at lower latitudes more than a century ago during the very early 20th century. It seems likely that similar tipping points in the population collapse of other farmland species may have occurred similarly early but went undocumented. As northern systems are increasingly impacted by climate change and probable expansion of agriculture, the interaction of these processes is likely to disrupt the pulsed flow of resources from cyclic populations impacting ecosystem function.

KEYWORDS

agricultural intensification, climate change, game bag, landscape homogenization, North Atlantic Oscillation, population cycles, population dynamics, wavelet analysis

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1 | INTRODUCTION

Population cycles are fundamental to animals in northern latitudes (Lindström et al., 2001), where fluctuations in insects, grouse, voles and lemmings regulate much of the Arctic ecosystem (Ims & Fuglei, 2005; Linden, 1988). One of the greatest challenges in population biology remains determining the causes of cyclicity and their large-scale synchronicity (Krebs, 2020). Identifying the causes of collapse in cycles during regime shifts may elucidate how such cycles were generated in the first place (Brommer et al., 2010; Ims et al., 2008; Korpela et al., 2013). Collapse of cyclical population dynamics leads to a breakdown in the pulsed flow of resources and disturbs consumer–predator interactions resulting in a subsequent collapse of important ecosystem function (Ims et al., 2008). For example, reduced abundance of vole and lemming prey as a result of dampened amplitude has resulted in severe declines in many northern latitude predators (Ims & Fuglei, 2005). Thus, the effects of regime shifts cascade through multiple trophic levels and reverberate throughout ecosystems.

Most regime shifts are dramatic changes which lead to a breakdown in populations, communities and ecosystems (Folke et al., 2004; Harvey et al., 2020). Such shifts may be preceded by a slowing in system dynamics (Chisholm & Filotas, 2009), a skew in resources (Guttal & Jayaprakash, 2008) or an increase in system variance (Carpenter & Brock, 2006) but, more generally, occur without warning. Attempts to model state changes typically fail to forecast ecological thresholds (Hastings & Wysham, 2010). Tipping points occur when a change in system forcing triggers a non-linear response in dynamical structure (Andersen et al., 2009; Folke et al., 2004; Ims et al., 2008) and are generally attributed recently to the impacts of anthropogenic climate change (Harvey et al., 2020; Lenton, 2011).

Climate influences direct- and delayed density-dependent processes in cyclic populations through changes in temperature and precipitation (Root et al., 2003; Stenseth et al., 2002). First-order or direct density dependence characterizes population self-regulation or predator–prey functional responses while second-order or delayed density dependence reflects trophic interactions, for example, numerical responses of predators to prey, or disease and parasite dynamics (Ims et al., 2008; Townsend et al., 2011). Population cycles are frequently spatially correlated over large scales, the so-called Moran effect (Ranta et al., 1997). This occurs when local weather conditions are connected with planetary scale oscillators (Hurrell, 1995; Visbeck et al., 2001), frequently the El Niño Southern Oscillation and the North Atlantic Oscillation (NAO), which influence inter-annual variability in numerous ecological phenomena (Ottersen et al., 2001; Stenseth et al., 2002). It has been hypothesized that independent systems could lose their cycles with increasing irregularity in climate (Brommer et al., 2010). Inferring climate as a causal agent in the structuring or collapse of cyclical dynamics, however, is often difficult as ecological time series are usually short resulting in low statistical power (Cazelles et al., 2008; Murdoch et al., 2002).

Contemporary realization of temporally changing cycles may be as much to do with better data (i.e. the relatively recent accumulation of long-term time series) and improved analytical techniques (i.e. advances in log-linear autoregression modelling, ARIMA and wavelet analysis) as much as recent global climate change.

Hare populations are renowned for their complex dynamics (Elton & Nicholson, 1942), and their widespread decline in abundance (e.g. Smith et al., 2005). Population cycles are characteristic of species at high latitudes, most notably the snowshoe hare (*Lepus americanus*; Erxleben 1777) and mountain hare (*Lepus timidus*; Linnaeus 1758), while population crashes have characterized recent temporal trends in more southerly species, most notably the European brown hare (*Lepus europaeus*; Pallas 1778). The 'tri-trophic' or 'predator-prey-winter food' hypothesis is invoked frequently to explain regular cycles in the abundance of high latitude species (Krebs et al., 2001), contingent on snow conditions affecting food availability and density-dependent predation, while agricultural intensification is regarded as the main cause of declines among farmland species throughout mainland Europe (Smith et al., 2005). Thus, climate change is regarded as being more important in range contraction in snowshoe hares than land use change (Sultaire et al., 2016). Nevertheless, it is important to consider the potential synergistic effects of climatic and other anthropogenic effects on distribution and abundance (Brodie, 2016).

Here, we examine a time series for the hare, *Lepus timidus hibernicus* population throughout Ireland which is situated at intermediate latitudes (ca. 51°–55°N) and has a temperate, maritime climate. Irish hares exploit rough grassland and intensive pasture that predominates lowland Ireland (Caravaggi et al., 2015). With virtually no snow cover food is never out of reach. Major predators of hares elsewhere including the wolf, *Canis lupus* are locally extirpated and while the golden eagle, *Aquila chrysaetos* has been re-introduced it is range restricted and locally rare (only the red fox, *Vulpes vulpes* and buzzard, *Buteo buteo* are widespread and common but both prey predominately on the more abundant European rabbit, *Oryctolagus cuniculus*). Thus, due to the absence of extreme winter weather and a lack of predators (i.e. failure to meet the conditions underpinning the predator-prey-winter food hypothesis), we posited that: (1) the hare population in Ireland should not exhibit cyclicity; and, (2) any decline observed in the hare population is likely to be associated with agricultural intensification in common with declines in hares elsewhere.

2 | METHODS

2.1 | Hare Index

Since the earliest work of Elton (1924) and Elton and Nicholson (1942), hunting records have been used as a proxy for hare abundance (e.g. Newey et al., 2007). Estate shooting records were acquired from the National Library of Ireland (Dublin), the Public Records Office of Northern Ireland (Belfast) and various private

estates throughout Ireland (Figure S1). The numbers of Irish hares shot annually between August and February were retrieved for 14 estates covering the period 1853–1970.

The software programme TRIM (Trends and Indices for Monitoring data; Pannekoek & van Strien, 2001) allows trends within time series to be established prior to, or after, specific events; these time points are referred to as 'change points'. Accounting for overdispersion, TRIM interpolates missing observations at each site from changes in all other sites using a Poisson log-linear model (McCullagh & Nelder, 1989). This technique is particularly useful as it accounts for spatial variation in the number of counts among sites, that is, hares shot among estates. Index values were standardized by corner point parameterization with the first year of the time series equal to 1 and all subsequent years relative to the first. Each year was tested as a candidate change point against a null model (i.e. no change point) and trends were fitted using a General Estimating Equation with model fit being quantified using change in the Akaike Information Criterion (ΔAIC). The model for change point selection which yielded the lowest AIC value was chosen as the best approximation of the beginning of the long-term decline in hare abundance. The game bag index is, hereafter, referred to as the 'hare index'.

Data density of the time series was quantified as the number of estates contributing data to each year while effort was quantified as the number of days shooting per estate per year and the number of guns (shooters present) per estate per year.

2.2 | Climatic and agricultural data

Climatic data were downloaded from the National Centre for Atmospheric Research (<https://climatedataguide.ucar.edu/climate-data/hurrell-north-atlantic-oscillation-nao-index-station-based>). The NAO represents the ratio of sea level air pressure between Gibraltar and Reykjavik capturing weather conditions in northwest Europe with positive values associated with mild stormy weather and negative values cool clear settled conditions. Seasonal mean values were calculated for spring February–May (spNAO), summer May–August (sNAO), autumn August–November (aNAO), winter November–February (wNAO) and annually January–February (anNAO) for each year of the time series.

Declines in hare numbers throughout Europe during the 20th century have been attributed to agricultural intensification (Smith et al., 2005) while the effects of landscape homogenization on hare habitat availability and space use are most pronounced at scales approximating a hare's home range size (Reid et al., 2010). Using data downloaded from the Central Statistics Office (www.cso.ie), we captured change in the number of farms <40 ha in size (the closest size category of data available approximating an Irish hare's home range; Reid et al., 2010) to describe declines in extensively managed family small holdings and the shift to intensively managed large farm businesses during the 20th century (a proxy for change in landscape management at the spatial resolution mostly likely to impact hares).

2.3 | Statistical analyses

Differences in data density (estates year⁻¹) and shooting effort (days estate year⁻¹ or guns estates year⁻¹) were tested before and after the selected time series change point using t-tests. NAO metrics that might have explained variation in the hare index were selected using Pearson correlations and only those that were significant at $p < 0.05$ were retained for further analysis.

The cyclicity of ecological and environmental time series is often poorly structured with signal periods varying in intensity and duration. Wavelet analysis is useful as it can detect reoccurring periodic patterns at various frequencies within a noisy time series. Wavelet analysis, using a Morlet transformation tested against background red noise, was used to examine changes in the periodicity of both the hare and selected NAO indices. The hare index was detrended prior to analysis using a regression fitted before and after the time series change point. Wavelet coherency analysis, calculated against background red noise using a Monte Carlo simulation to describe the correspondence with a null model, was used to quantify covariance in the hare and NAO indices independent of the power of their periodicities. The direction of temporal synchrony was deduced by the degrees to which each Morlet wavelet was angled in a plane with respect to one another. For further details of methods, see Cazelles et al. (2008), Grinsted et al. (2004) and Torrence and Compo (1998).

Hare population growth was taken as $\lambda = \log_e (N_t/N_{t-1})$ where λ was the annual growth, N_t was the hare index at t and N_{t-1} was the hare index at $t-1$. Variance in λ was examined using General Linear Models (GLMs), assuming a normal distribution, an identity link function and an autoregressive AR1 error structure (to account for temporal autocorrelation) with one model fitted before and one after the time series change point. Independent covariates included direct density dependence, that is, N_{t-1} , delayed density dependence, that is, N_{t-2} , autumn or aNAO _{$t-1$} at a lag of 1 year and agricultural intensification captured using the number of farms <40 ha, that is, Farms_{<40ha}. Prior to analysis, all variables were standardized to have a $\bar{x} = 0$ and a $\sigma = 1$ to allow for the direct comparison of regression coefficients. Model fit was described using r^2 .

Correlations and GLMs were run in IBM SPSS Statistics 26 (IBM), wavelet analyses were conducted using Matlab (MathWorks) and graphs were produced using Sigmaplot v14 (Systat Software Inc).

3 | RESULTS

A total of 310 bag records (reported totals per estate per year) comprising 37,742 hares were collated throughout Ireland from 1853 to 1970 (Table S1). A time series for the hare index was reconstructed with standard errors (Figure 1a) and candidate change points evaluated (Figure S2) with 1908 being selected as the year that most closely approximated a change in temporal trend (describing the data better than a null model with no change point).

The time series was characterized by two distinct regimes. In Regime 1, there was no overall temporal trend; however, distinct

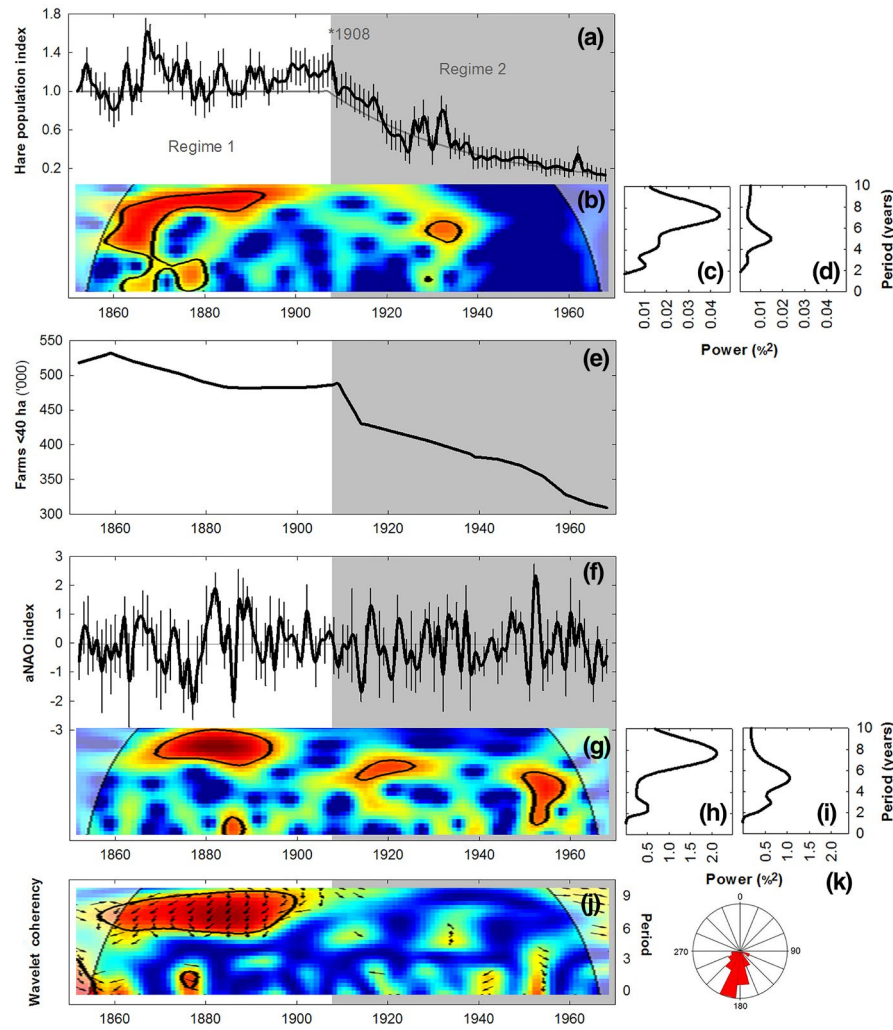


FIGURE 1 (a) Hare index (solid line) $\pm$ standard error (whiskers) showing the temporal trend (grey line) fitted before and after the 1908 change point. Regime 1 (stable phase) and Regime 2 (declining phase) are marked by white and grey shading throughout. (b) Continuous wavelet power spectrum for the cyclical dynamics of the detrended hare index. Dark blue indicates an absence of any signal and dark red indicates a strong signal. The regions enclosed by a bold black line indicate power that differed significantly from red noise ($p \leq 0.05$). Inferences cannot be made beyond the 'cone of influence' which is shown as a lighter area at the beginning and end of the time series. For simplicity and to avoid showing artificial harmonics, periods greater than 10 years are not shown. (c) Global power spectrum for the hare population wavelet during Regime 1 and (d) Regime 2. (e) Agricultural intensification as described by the change in the number of farms <40 ha throughout Ireland. (f) Autumn North Atlantic Oscillation (aNAO) Index (solid line) $\pm$ standard error (whiskers) showing the temporal trend (grey line). (g) Continuous wavelet power spectrum for the dynamics of the aNAO. (h) Global power spectrum for the aNAO wavelet during Regime 1 and (i) Regime 2. (j) Wavelet coherence transform showing cross correlation between the dynamics of both the hare and aNAO indices scaled for power. The direction of the arrows indicates whether the two wavelets are in phase (pointing right), anti phase (pointing left) or whether the hare index (pointing up) or aNAO index (pointing down) was leading. The direction in which the arrows point is indicative of the angle between the wavelets (pointing straight up or down equals 90°). (k) Circular histogram of the direction of arrows demonstrating a mean angle of 195° , that is, pointing down and to the left suggesting that the aNAO index was the leading wave

inter-annual fluctuations were apparent. In Regime 2, the hare index declined by 87% (Figure 1a). Data density did not differ between regimes with 2.75 ± 1.54 estates year⁻¹ (SD) contributing data to Regime 1 and 2.52 ± 1.43 estates year⁻¹ contributing data to Regime 2 ($t_{d.f.=115} = 0.820$, $p = 0.414$). A total of 11 estates provided some measure of shooting effort. The number of days shooting per year did not differ between regimes with 29 ± 46 days estate year⁻¹ during Regime 1 and 29 ± 41 days estate year⁻¹ during Regime 2

($t_{d.f.=217} = 0.013$, $p = 0.989$). However, guns (shooters present) almost doubled increasing significantly from 26.3 ± 17.5 guns estates year⁻¹ during Regime 1 to 45.2 ± 31.1 guns estates year⁻¹ during Regime 2 ($t_{d.f.=74} = 3.206$, $p < 0.002$).

Wavelet analysis of the detrended hare index suggested that multiannual periodicity was a feature of Regime 1 which exhibited a significant 8-year cycle from 1860 until the mid-1890s (Figure 1b,c). This negated Hypothesis 1 with hares in Ireland exhibiting historical

cyclicality. While the effect of cyclicality ceased to be significant at $p < 0.05$, its influence evidently remained until the end of Regime 1. In contrast, there was no sustained period of cyclicality during Regime 2 (Figure 1b,d). Temporal trends in the hare index and $\text{Farms}_{<40\text{ha}}$ were similar and the change point in both roughly coincident (Figure 1e) consistent with Hypothesis 2 where landscape homogenization was posited to drive hare population collapse.

Autumn was selected as the seasonal NAO index that captured the greatest variation in the hare index during t ($r = 0.277$, $p = 0.038$) and $t-1$ ($r = 0.304$, $p = 0.023$) during Regime 1. No other NAO indices were significantly associated with the hare index in either Regime ($p > 0.05$). There was a high degree of inter-annual fluctuation in the aNAO index (Figure 1f). Wavelet analysis suggested multiannual periodicity with a significant 8-year cycle from 1870 to 1900 during Regime 1 (Figure 1g,h), coincident with a similar cycle in the hare index. Thereafter, sustained periodicity collapsed (Figure 1g,i). A wavelet coherence analysis suggested that the hare and aNAO indices were in phase synchrony being correlated for a period of ca. 30 years during Regime 1 (Figure 1j). The angle of the wave planes (Figure 1k) suggested that the aNAO index was the leading wave. There was no coherence between the hare and aNAO time series during Regime 2.

Hare population growth (λ) was negatively influenced by N_{t-1} during both Regime 1 and 2 suggesting a strong role for direct density dependence (Figure 2; Table S2). Delayed density dependence (N_{t-2}) had no significant influence during either regime. The aNAO positively influenced λ during Regime 1 but had no discernible influence during Regime 2 (Figures 2 and 3). In contrast, $\text{Farms}_{<40\text{ha}}$ had no significant influence on λ during Regime 1 but became a highly positive influence during Regime 2 (Figure 2; Table S2) as the numbers of small farm holdings declined throughout the 20th century (Figure 1e). Thus, the additive effects of early climate destabilization (collapse of cyclicality of the aNAO) and agricultural intensification (landscape homogenization i.e. fewer small farms) were associated

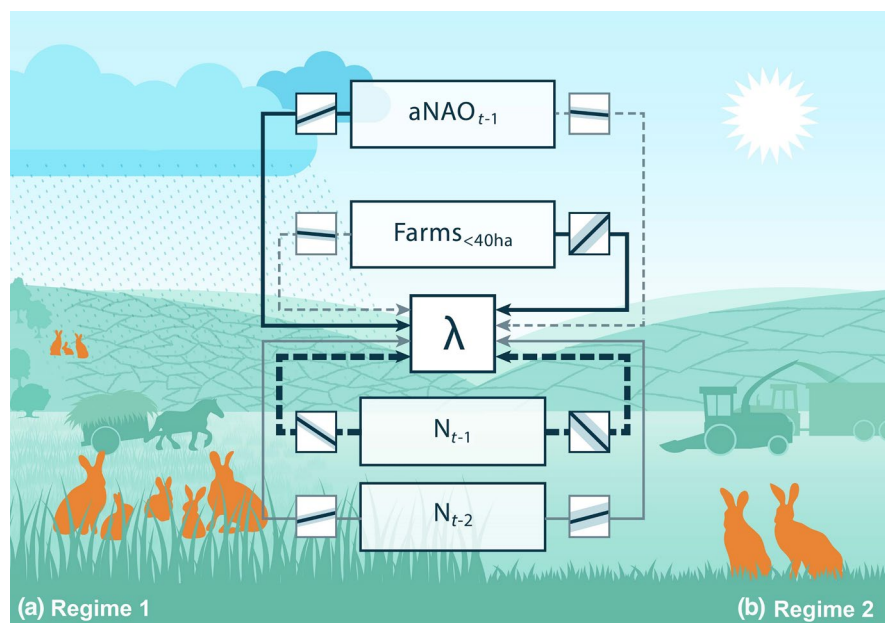
with the collapse of cyclicality in the hare population and the initiation of a long-term decline in abundance during the very early 20th century (Figure S3).

4 | DISCUSSION

Many studies have shown some correlation between climatic forcing and some aspects of a species' life history or population dynamics (Stenseth et al., 2002). Others relate extinction, for example, in large mammals, with extreme climate events and anthropogenic factors (Wan et al., 2019). Here, annual hare population growth was influenced by autumn weather, described by the NAO at a lag of 1 year, and agricultural intensification and landscape homogenization, described by a decline in farm small holdings. The hare population and autumn NAO indices shared a similar periodicity during the same period and were in phase synchrony, with annual hare population growth associated positively with the climatic index. Moreover, a destabilization and breakdown in the dynamical structure of the climate was mirrored by a synchronous collapse in the hare population cycle. This suggests that: (a) changes in climate can lead to a sudden and abrupt deterioration in the complex dynamical structures of cyclic populations (tipping points) making them more vulnerable to anthropogenic pressures such as agricultural intensification; or (b) the negative impact of agricultural intensification driving the long-term decline in abundance was sufficiently strong to mask any effects of climatic forcing. The initiation of both global warming (i.e. the change point in global temperatures) and the beginning of agricultural intensification in Europe (driven by World Wars I and II) was largely coincident during the early 20th century making it difficult to disentangle confounding effects; not least because agricultural change may be related to climatic change (Elmhagen et al., 2015).

Unlike more recent collapses in cyclicality in the populations of high latitude species in the northern hemisphere (Ims et al., 2008),

FIGURE 2 Autoregressive (AR1) General Linear Models of annual hare population growth rate (λ) during (a) Regime 1 (left) and (b) Regime 2 (right) with significant ($p < 0.05$) effects shown in black, non-significant ($p > 0.05$) effects in grey, positive relationships as solid lines and negative relationships as dashed lines. Line thickness reflects the strength of each relationship. Slope is shown as a plot insert where all y-axes represent λ and each x-axis represents the focal variable (with all axes standardized). Slope uncertainty is shown as grey shading. Illustration by Elfy Chiang (www.elfylandstudios.com)



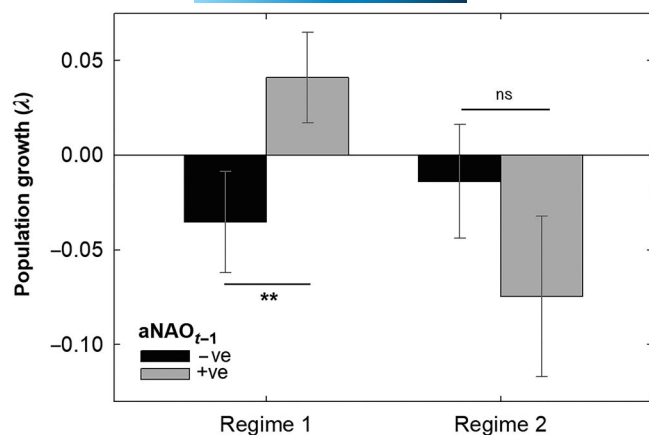


FIGURE 3 Mean hare population growth rate (λ) $\pm$ SE in positive and negative polarity of the autumn NAO_{t-1} during Regime 1 (stable phase) and Regime 2 (declining phase)

the collapse of mid-latitude hare cycles in Ireland occurred more than a century earlier during the very early 20th century. Data density, that is, the number of estates contributing game bags and the number of days spent shooting did not differ between Regimes 1 and 2. However, the number of guns present almost doubled during Regime 2. Notwithstanding possible overharvesting (unlikely as hares are usually robust to high harvesting rates; Marboutin et al., 2003), the temporal trend observed may reflect real population change (a decline in availability) rather than being an artefact of changes in data quantity, quality or shooting effort. Factors contributing to the regime shift in the hare population of Ireland are likely to have impacted other species throughout Europe. For example, the populations of many farmland species such as ground-nesting birds (which have a similar ecology to hares), including the corncrake (*Crex crex*), grey partridge (*Perdix perdix*) and skylark (*Alauda arvensis*), all collapsed during the 20th century (Green & Stowe, 1993; Lynas et al., 2007). Detecting abrupt population changes is problematic and such phenomena could have occurred widely but gone undocumented.

Regular cyclicity in population abundance can emerge spontaneously without exogenous forcing from intrinsic regulation by delayed density-dependent processes (e.g. Brigatti et al., 2007) encoded genetically (Montgomery, 2021). As N_{t-2} did not influence the hare index, we conclude that cyclicity detected during Regime 1 was exogenous driven by climatic oscillation. The precise mechanisms by which climate interacted with the hare population remain unknown. There were no significant interactions between the NAO index and direct- or delayed density-dependent parameters. Only first-order parameters were significant in models of population growth suggesting that whatever mechanisms were in operation they were likely to be self-regulation, a predator functional response or their interaction (Ims et al., 2008).

The time series of game bags from the 14 estates used here were discontinuous with some stretches of time during which little or no data were recorded and thus not all estates contributed data equally to each year of the time series. For this reason, we aggregated the data by interpolating missing observations at each site from changes

in all other sites. Population cyclicity is generally spatially synchronized changing as a travelling wave across the landscape (e.g. Sherratt & Smith, 2008). Thus, aggregating data across multiple sites could obscure, weaken or, conceivably, generate or strengthen any detected cycles due to constructive or destructive interference. The maximum distance between any two sites in the current study was 350 km, far smaller than the continental scales over which spatial synchronicity of population dynamics has been detected before. The 8-year periodicity of hare cycles in Ireland was similar to the periodicity reported for other mountain hare populations throughout Europe (Newey et al., 2007) while wave synchrony with climate and the coincident collapse of their dynamics provides compelling support that the patterns observed reflect real change rather than statistical artefact(s). Notwithstanding issues to do with missing data, reanalysis of the unaggregated dataset following, for example, the methods of Cornulier et al. (2013) would provide a further test of whether the effects detected here hold at the individual site level.

The correlation of the hare and autumn NAO indices, rather than annual NAO values, suggests that the influence of climate may be restricted to relatively short, critical periods and, thus, are likely to be species-specific (Lima et al., 2006; Stenseth et al., 2002) with climatic forcing highly context dependent (Brommer et al., 2010). Climate change exerts its influence through changes in temperature and precipitation (Root et al., 2003; Stenseth et al., 2002) while affects may be spatially idiosyncratic. Positive polarity in the NAO index has been associated with increased rainfall and mild temperatures in Great Britain and Ireland (Butler et al., 1998). Korpimäki et al. (2004) suggested that increased survival rather than reproductive rate may drive population increases during the upward phase of cyclic mammal populations. Consequently, we posit that survival and maturation of late born leverets, rather than reproductive rate per se, may be aided by extended grass growth associated with warmer and wetter autumn weather. Likewise, adult hare body condition may be improved for similar reasons increasing over-winter survival during high NAO index years. Schmidt et al. (2004) found a similar effect on European brown hare populations in Denmark and suggested that the persistence of the ongoing positive NAO phase experienced during the late 20th century (Visbeck et al., 2001) should have resulted in population increases. However, such is the negative effect of agricultural intensification that the positive influence of climate has been unable to reverse ongoing declines in hare numbers (Schmidt et al., 2004).

Hares require discrete and varied resource requirements satisfied by a complex landscape structure composed of a matrix of high-quality grassland providing nocturnal foraging and tall rough vegetation providing diurnal cover and shelter (Reid et al., 2010). Moreover, hares in Ireland have notably small home ranges within the genus *Lepus* (Wolfe & Hayden, 1996). Thus, individuals require a habitat patchwork within an area less than 40 ha and unless landscapes are composed of such fine-scale heterogeneous structure they are unlikely to support high densities. Ireland shifted throughout the 20th century from being a heterogeneous landscape composed of numerous farm small holdings supporting

mixed agriculture, to a very homogenous, pastoral landscape composed of fewer, larger farm businesses (many >200 ha) focussed on grass production (Bell & Watson, 2014). Moreover, there was a move from extensive hay making during the early to mid 20th century, to intensive silage production during the mid to late 20th century (Mayne & O'Kiely, 2005). Silage harvesting is synchronous with peak parturition in hares between May and July (Flux, 1970), while mechanization endangers young hares and causes significant mortality (Kaluziński & Pielowski, 1976; Marboutin & Hansen, 1998; Milanov, 1996; Milanova & Dimov, 1990). Thus, improved grassland represents an ecological trap for hares (Reid et al., 2010). Agricultural intensification has been identified as the main cause of long-term population declines in hares throughout Great Britain and mainland Europe (Smith et al., 2005) and together with changes in climatic forcing was likely to be a significant driver of the observed long-term decline of hares in Ireland.

We demonstrate that the dynamical structure of cyclic populations and exogenous forces (principally climatic variability) is structurally interrelated. Anticipating change in ecological phenomena due to the impacts of future climate change is an increasingly important area of research (Stenseth et al., 2002; Walther et al., 2002). Global temperatures increased by 0.6°C during the 20th century and are predicted to increase by up to 6°C further over the current century (IPCC, 2014). Global circulation models (GCMs) suggest that projected climate change is likely to be most pronounced in Arctic regions (King et al., 2018) potentially opening up new areas for agriculture. If climatic forcing influences many cyclic populations, our results suggest that we should expect more tipping points or dampened amplitude such that cycles fade while increasing resource exploitation in northern regions is likely to drive further population declines.

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AUTHOR CONTRIBUTIONS

Neil Reid was the lead author and collated and analysed the data and drafted the manuscript. Jon E. Brommer conducted wavelet analysis. Nils C. Stenseth and Ferdia Marnell provided intellectual input in developing ideas. Robbie A. McDonald conceived of the study and won funding under competitive tender while W. Ian Montgomery contributed intellectual input throughout and editorial oversight. Both Robbie A. McDonald and W. Ian Montgomery should be considered joint senior authors.

DATA AVAILABILITY STATEMENT

Data are available from the primary author upon reasonable request.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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