Climate and habitat configuration limit range expansion and patterns of dispersal in a non-native lizard

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Abstract

ABSTRACT Aim Invasive species are one of the main causes of biodiversity loss world-wide. As introduced populations increase in abundance and geographical range, so does the potential for negative impacts on native communities. As such, there is a need to better understand the processes driving range expansion as species become established in recipient landscapes. We investigated the potential for population growth and range expansion of introduced populations of a non-native lizard (*Podarcis muralis*), considering multi-scale factors influencing growth and spatial spread. Location England, UK Methods We collated records of *P. muralis* presence through field surveys and a citizen science campaign. We used presence-only models to predict climate suitability at a national scale (5km resolution), and fine-scale habitat suitability at the local scale (2m resolution). We then integrated local models into an individual-based modelling platform to simulate population dynamics and forecast range expansion for 10 populations in heterogeneous landscapes. Results National-scale models indicated climate suitability restricted to the southern parts of the UK, limited by a latitudinal cline in overwintering conditions. Patterns of population growth and range expansion were related to differences in local landscape configuration and heterogeneity. Growth curves suggest populations could be in the early stages of exponential growth. However, annual rates of range expansion are predicted to be low (5-16 m). Conclusions We conclude that extensive nationwide range expansion through secondary introduction is likely to be restricted by currently unsuitable climate beyond southern regions of the UK. However, exponential growth of local populations in habitats providing transport pathways is likely to increase opportunities for regional expansion. The broad habitat niche of *P. muralis*, coupled with configuration of habitat patches in the landscape, allows populations to increase locally with minimal dispersal.

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ABSTRACT

Aim

Invasive species are one of the main causes of biodiversity loss world-wide. As introduced populations increase in abundance and geographical range, so does the potential for negative impacts on native communities. As such, there is a need to better understand the processes driving range expansion as species become established in recipient landscapes.

We investigated the potential for population growth and range expansion of introduced populations of a non-native lizard (*Podarcis muralis*), considering multi-scale factors influencing growth and spatial spread.

Location

England, UK

Methods

We collated records of *P. muralis* presence through field surveys and a citizen science campaign. We used presence-only models to predict climate suitability at a national scale (5km resolution), and fine-scale habitat suitability at the local scale (2m resolution). We then integrated local models into an individual-based modelling platform to simulate population dynamics and forecast range expansion for 10 populations in heterogeneous landscapes.

Results

National-scale models indicated climate suitability restricted to the southern parts of the UK, limited by a latitudinal cline in overwintering conditions. Patterns of population growth and range expansion were related to differences in local landscape configuration and heterogeneity. Growth curves suggest populations could be in the early stages of exponential growth. However, annual rates of range expansion are predicted to be low (5-16 m).

Main Conclusions

We conclude that extensive nationwide range expansion through secondary introduction is likely to be restricted by currently unsuitable climate beyond southern regions of the UK. However, exponential growth of local populations in habitats providing transport pathways is likely to increase opportunities for regional expansion. The broad habitat niche of *P. muralis* , coupled with configuration of habitat patches in the landscape, allows populations to increase locally with minimal dispersal.

Keywords

climate matching, heterogeneous landscape, invasive species, lag phase,*P. muralis* , range expansion

Introduction

The global rise in the number of species introduced to regions beyond their native range via human-mediated translocation shows no sign of reaching saturation point (Seebens et al., 2017). While many species fail to establish or have little negative effect following introduction, a subset of these do spread and can have significant impact on economies, human health, native biodiversity and ecosystem services (Kolar & Lodge, 2001; Vila et al., 2010; Keller, Geist, Jeschke, & Kühn, 2011). The severity of potential negative impacts (e.g., extirpation and extinction of native species) are such that invasive non-native species (INNS) are justifiably regarded as one of the most significant threats to biodiversity worldwide (Genovesi, 2009; Simberloff et al., 2013).

For non-native species to become widespread and potentially damaging following introduction to new regions, introduced populations must negotiate the three stages of an introduction–establishment–invasion continuum (Blackburn et al., 2011). Evaluation of the likelihood of a species to be transported, establish, and to spread, as well as the potential for having ecological, economical, and health impacts, forms the basis of 'invasive' risk assessment for alien species (Bacher et al., 2018; Roy et al., 2019). Although it has been argued that the term 'invasive' doesn't always necessarily equate with a species' negative impact (Ricciardi & Cohen, 2007), the potential for damaging effects inherently increases as introduced species increase in population size and spread across novel landscapes, thus affecting broader areas and more ecological communities (Crooks, 2005). As such, there is great interest in understanding patterns and rates of expansion of introduced species, and the environmental factors which limit their distributions (Gallien, Munkemuller, Albert, Boulangeat, & Thuiller, 2010; Roy et al., 2019).

Following introduction and successful establishment beyond native ranges, species can further expand their range through local dispersal processes and/or by jump dispersal events that may be human-mediated (i.e., deliberate or accidental movement of individuals between habitats) or natural dispersal (i.e., long distance flight in birds) (Suarez, Holway, & Case, 2001; Ingenloff et al., 2017). Invading species typically exhibit several phases in the rate of spread. Firstly, there is an initial establishment phase where rate of spread is slow. Secondly, an expansion phase typified by increasing rates of spread, and finally, a saturation phase when available space is occupied and expansion rates reach a plateau (Arim, Abades, Neill, Lima, & Marquet, 2006).

A suite of factors influence patterns and rates of range expansion during these phases: propagule size, dispersal mode, matching of physiological and ecological traits of invading species with environmental conditions at the receptor site, vital rates (births and deaths) species interactions, evolutionary processes, spatial heterogeneity and temporal variability (reviewed in Hastings et al., 2005). Furthermore, our ability to assess and predict the temporal dynamics of invasions is often complicated by the phenomenon of lag phases, wherein an introduced species remains at low population levels in the early stages of establishment for a protracted period of time before the sudden onset of rapid range expansion (see Crooks (2005) for review of the causes of temporal lags at all stages in the invasion process). Introduced populations of the northern Racoon (*Procyon lotor*), for example, remained small for a number of years following introduction to Europe before a population explosion in the mid 1990's (Salgado, 2018). Similarly, landscape complexity can result in temporal and spatial patterns of invasion dynamics that deviate from classic theory of symmetrical, radial expansion from a central point (diffusion theory) (Skellam, 1951; Shigesada, Kawasaki, & Takeda, 1995; Kinezaki, Kawasaki, & Shigesada, 2010). The effects of landscape heterogeneity on patterns and rates of expansion have been demonstrated in the quick colonization of areas of suitable habitat in the early stages of the American mink (*Neovison vison*) invasion, compared to uptake in areas of low habitat suitability in Scotland (Fraser et al., 2015), and the fluctuating rates in range expansion of Cane toad (*Rhinella marina*) in response to changing environmental conditions in newly invaded areas of Australia (Urban, Phillips, Skelly, & Shine, 2008). Consideration of dispersal processes across heterogeneous landscapes is therefore central to predicting potential for range expansion during the invasion process (Travis, Harris, Park, & Bullock, 2011; Bocedi, Zurell, Reineking, & Travis, 2014; Grayson & Johnson, 2018). The development of platforms for spatially explicit individual-based modelling (Bocedi, Zurell, et al., 2014; Samson et al., 2017) have enabled the nested interactions between dispersal, landscape properties, and population dynamics to be considered in predicting species distributions, increasing the ecological realism of range expansion models (Andrew & Ustin, 2010; Ferrari, Preisser, & Fitzpatrick, 2014; Mang, Essl, Moser, Kleinbauer, & Dullinger, 2018; Hunter-Ayad & Hassall, 2020).

In this study, we determine the potential for range expansion of the non-native common wall lizard (*Podarcis muralis*) in the UK.*Podarcis muralis* has a long history of introductions beyond its native range which covers most of Western and Southern Europe (Gassert et al., 2013). Many of these introductions have extended its range throughout continental Europe (Schulte, Gassert, Geniez, Veith, & Hochkirch, 2012; Wirga & Majtyka, 2015; Šandera, 2017), but the species also has several populations established in the New World, both in the United States (R. M. Brown, Gist, & Taylor, 1995) and Canada (Allan, Prelypchan, & Gregory, 2006).

Introduced to Vancouver Island, British Columbia, in 1970, the species persisted in isolated populations until 2006, but has since spread with alarming speed due to jump dispersal (human mediated) and natural radial dispersal of 40-70 meters a year in urban areas (Engelstoft, Robinson, Fraser, & Hanke, 2020){Engelstoft, 2020 #2101}.

To date there is no empirical evidence of negative ecological impacts of*P. muralis* introductions in the UK, and there is mixed social perception and opinion towards the species' presence (Williams, Dunn, Quinn, & Hassall, 2019). However, suspected declines in native lizards through interference and/or exploitation contest have been reported following introductions of *P. muralis* , to both Germany (Münch, 2001; Kühnis & Schmocker, 2008; Schulte, 2009) and the UK (Mole, 2010).

There have been multiple introduction events of *P. muralis* to the UK both as deliberate releases of captive animals and as cargo stowaways, with some extant populations having been established on the UK mainland as early as the 1970s (Michaelides, While, Bell, & Uller, 2013). More recent introductions (1980s onwards) have mostly arisen from movement of individuals from already established populations (secondary introduction) or captive-bred animals, rather than directly sourced from the native range (Michaelides, While, Zajac, & Uller, 2015). The UK populations represent the species at the northern extent of its range, with sites having markedly different climatic conditions compared with the native range. For example, air temperatures during the main activity season in populations in England are 5–10°C lower than their source regions in Tuscany and western France (While et al., 2015).

We investigated the potential for range expansion of *P. muralis*in the UK with models highlighting different (but complementary) parameters likely to influence spread at two spatial scales. Firstly, since long distance jump dispersal via translocation is important in facilitating spread of this species, we aimed to predict the national extent of the area potentially available for further colonisation by running a species distribution model (SDM) based on climatic suitability at these northern extremes. As has been speculated elsewhere, the ability to survive cold winters is likely limiting to the spread of introduced *Podarcis* populations (Burke, Hussain, Storey, & Storey, 2002). We therefore hypothesised that latitudinal clines in climate would restrict the area available for northward expansion of*P. muralis* via long distance human-assisted translocation in the UK. Second, to make predictions of population growth and dispersal patterns, as well as identify environmental features important to range expansion at a local level, we took a hybrid model approach combining SDMs, informed by variables characterising 10 local landscapes (i.e., microclimate, proximity to geographic features, and habitat type), with a high resolution (15 x15 m) spatiotemporal individual based model (IBM) simulating local population and dispersal dynamics. We expected that landscape characteristics (i.e., configuration and connectivity of suitable habitat patches), would result in asymmetrical patterns of predicted dispersal within populations, which in turn, would result in spatial and temporal variance in patterns of population growth and range expansion between populations. These analyses allow us to investigate the proximate and ultimate barriers to spread, as well as simulating the potential for invasion lag in each population.

Methods

The locations of known established *P. muralis* populations were obtained from the Surrey Amphibian and Reptile Group website (Langham, 2019). We determined the current geographic extent of as many of these populations as logistically possible using a combination of visual surveys, canvassing of the local public at sites of interest, and press releases in local and regional media encouraging members of the public to report their wall lizard sightings (see Appendix 1). Of the 30 extant populations recorded on the UK mainland, we visited 21 between three field seasons (April-September) of 2016, 2017, and 2018 (Fig 1). We did not visit the remaining nine locations because the lizard population were either known to be very small, access was restricted, and/or site locations were otherwise logistically challenging (i.e. distance from other populations). Specific attention was given to assessing the extent of *P. muralis* presence along railway habitat at West Worthing, Sussex (50.818° N, 0.390° W) during a five-week period in June-July 2018. The railway acting as a linear transect, along which we could assess the utility of railway habitat as a corridor for dispersal (Fig S1

Appendix 1). We also collected wall lizard location data from populations at two additional sites, Eastbourne (50.768° N, 0.291° E) and Kingswear (50.349° N, 3.568° W). The former was confirmed to be an established colony through a site visit, and the latter was reported to RW by a member of the public responding to a citizen science campaign in regional media. Sightings were confirmed for a further eight new locations as a result of the citizen science campaign (Fig 1) (see Appendix 1 for detailed methods).

Modelling climate suitability across the UK

A total of 1331 lizard sightings (presence) data (76 from online portal, 52 from postcard returns, 1203 from visual surveys) were used to develop relative habitat suitability maps at the UK national extent using MaxEnt v3.3.3k software (Phillips, Anderson, & Schapire, 2006). *Podarcis muralis* has demonstrated rapid adaptive responses following introduction to cool climates, with ability to evolve broader thermal tolerance at dispersal fronts (Litmer & Murray, 2019), and prolonged embryo retention and faster embryonic growth at low temperatures - compared to ancestral states (While et al., 2015). For this reason, we only used *P. muralis* presence records from the introduced UK range in our MaxEnt model, as they best reflect the current climatic tolerance of the species, and, secondary introductions from established populations are the primary concern for the species extending its range in the UK. We focused on seasonal averages of six climatic variables (predictors) at 5km resolution (Met Office, 2018) that have most relevance to wall lizard biology and therefore likely to influence distribution (Wirga & Majtyka, 2015) (Table 1). These six variables were refined from an initial input of 13 climate variables through an iterative process of removal/retention to limit covariate correlation (Spearman's rank correlation; correlated if r_s [?] 0.6) and maximise model performance (Glover-Kapfer, 2015). We kept parameter settings in MaxEnt the same for modelling at the national and local levels (see Appendix 1 for detailed method). The following Maxent parameters were used: Features used = Linear; Output format = logistic; Random Test % = 20; Regularization Multiplier = 2; Max number of background points = 10000; Replicates = 5; Replicated run type = Crossvalidate.

Modelling local habitat suitability

A total of 1083 presence records (all direct observations during visual surveys), across 10 study locations representing the range of habitats used by *P. muralis* (urban, suburban, rural), were used in producing relative habitat suitability maps and predictive models of local range expansion. These study sites encompassed heterogeneous land cover that helped in identifying variables affecting local habitat suitability and features acting as important corridors for range expansion. Data for six environmental variables at 2m resolution were used for the MaxEnt input and are summarised in Table 1. All variables were calculated and prepared in ArcGIS$^{(r)}$ (Esri 2017). We used the Phase One Habitat Survey Toolkit (Centre for Ecology Environment and Conservation, 2018) to create fine scale habitat type (categorical) data layers.

Modelling local range expansion (IBM)

Habitat suitability maps from our local scale MaxEnt models were prepared as habitat quality landscape layers by linear transformation of the MaxEnt logistic values (estimates between 0 and 1 of probability of presence) above the maximum test sensitivity plus specificity logistic threshold. This is the threshold at which the MaxEnt models maximize their discrimination of presences from background data (Jimenez-Valverde & Lobo, 2007; Glover-Kapfer, 2015). The resulting habitat quality landscape (scaled 0-100, and where cell values scale with cell carrying capacity in RangeShifter), provided the patch input for RangeShifter v1.1 (Bocedi, Palmer, et al., 2014), in addition to a cost layer to movement created by reclassifying (inverting) the habitat quality landscape layer. All inputs were resampled using bilinear interpolation to 15m x 15m cell size to reduce demands on computational memory whilst retaining biological relevance to wall lizard movement capabilities. A single cell in each landscape was identified as the initial species distribution (i.e., point of introduction for each population respectively) based on knowledge of the precise location of introduction when known, or by using the centre point of the current extent of sighting records for the population.

Parameterisation

Parameters of wall lizard demographics and behavioural attributes were based on empirical data in the published literature. Where published empirical data were not available, reasonable judgements and/or simplifying assumptions were made. The final parameter values used were biologically realistic and justifiably reflect the functional biology of*P. muralis* (Table S2 in Appendix 1). Parameterisation was further refined through an iterative process, where simulations were repeated across all study sites with fine parameter adjustments within biologically meaningful limits until a single set of parameters was found that modelled as closely as possible the currently observed spatial extent of each study population (Fraser et al., 2015).

Initialisation

Simulations were initialised using known founder size where documented (Michaelides et al., 2015; Langham, 2019). Where founder size was unknown, we used a minimal founder size that resulted in reasonable simulation outputs as per the iterative process mentioned above. We assumed adult age class for all founders. Local extinction probability was set at a constant of 0.003 across populations. Simulations (50 replicates) of population range expansion for the 10 study populations were then run for the period of time since introduction (which varies among sites) up to the year 2040.

Analysis

We investigated how landscape characteristics might influence population size, rate of population growth and range expansion, by first obtaining standard population growth metrics: carrying capacity (K), and intrinsic rate of increase (r), from linear growth curves applied to mean yearly population size data taken across all simulation iterations in R Studio (R Core Team, 2017) using the package Growthcurver (Sprouffske, 2018). We then created binary habitat suitability layers from our MaxEnt outputs for a radius of 200m around introduction points which served as inputs for the programme FRAGSTATS v4 (McGarigal, Cushman, & Ene, 2002). We ran linear regression models with two FRAGSTAT metrics describing heterogeneity of suitable habitat patches within the landscape (Normalised Landscape Shape Index – a measure of patch aggregation; and Connectance – a measure of functional joinings of patches) and average habitat quality as explanatory variables, and the growth rate parameters (k, r) and annual dispersal distance as response variables. We set the threshold distance within which patches are deemed ”connected” to an arbitrary 100m.

Results

National scale climatic suitability

The MaxEnt model fit at the national scale had an average test AUC score of 0.98 (SD $<$0.01). The most important variable to the model was ‘number of frost days’ which made the highest relative percent contribution to the model (38.1%) followed by ‘annual total hours of sun’ (26.2%), whereas ‘autumn max temperature’ had the lowest contribution (2.9%). The model indicates suitable climatic conditions for *P. muralis* in maritime climates all along the south coast of the UK – from Norfolk in the southeast, to the south coast of Wales. Favourable conditions inland diminish towards a latitude of ~52degN, but are particularly evident in the Greater London Metropolitan area (Fig 2). *P. muralis* probability of presence responded positively to increasing total hours of sunlight and mean maximum spring, summer, autumn and winter temperature, although probability of presence diminished past a peak of 3degC with the latter. Probability of presence declined with increasing number of frost days (Fig 3).

Local habitat scale suitability

The model fit to the local study areas had an average AUC of 0.88 (SD = 0.01) over the 10 areas and 50 replicated runs. The most important variable to the model was ‘habitat type’, which made the highest relative contribution to the model (66%). Ten habitat classes out of 44 stood out as being influential to increased probability of *P. muralis* presence; bare ground, residential garden, dense scrub, scattered scrub, rail track, road, introduced shrub, dry dwarf shrub, hard cliff, and quarry (Fig 4). Spring radiance had the second highest percent contribution to the model (15%), where the amount of spring solar insolation had a positive influence on probability of presence (Fig 4). Probability of occurrence was also greater closer to buildings, railtrack, and roads. The response to NDVI is one of increasing probability of presence with an increase in vegetation from bare ground, followed by a rapid negative response past NDVI = 0.25. Maps indicating configuration of suitable habitat within local landscapes are presented in Figure 5 and Appendix 2.

Individual-based models results

Patterns of range expansion from time since introduction to 2040, as determined by population dynamics and local landscape character, are presented in Figure 5 and Appendix 2. Growth curves for the 10 study populations are also presented in supplementary information (Appendix 3). Growth rates ranged from 0.07 (Shoreham) to 0.15 (Eastbourne). Following simple stepwise linear regression analysis (Table 2), growth rate (r) was positively related to the NLSI ($F_{(1,\ 9)} = 8.39$, $p = 0.02$,$R^2 = 51.13$), and negatively related to time since introduction ($F_{\ (1,\ 9)} = 5.80$, $p = 0.04$, $R^2 = 42.22$) (Fig 6 a, b). Branksome and Canford – two populations on the Bournemouth coast – had the highest carrying capacity (10443 and 10315 individuals, respectively). Eastbourne had the lowest carrying capacity (1447). A positive relationship between habitat quality and carrying capacity ($F_{(1,9)} = 6.22$, $p = 0.03$,$R^2 = 43.74$) was the only relationship observed between this growth parameter and the explanatory variables (Table 2). Annual dispersal distance was best explained by combined increases in NLSI and habitat quality ($F_{\ (2,9)} = 29.65$,$p <0.001$, $R^2 = 89.44$) (Fig 6 C), although habitat quality was not a significant predictor of annual dispersal distance on its own ($F_{\ (1,\ 9)} = 1.21$,$p = 0.34$, $R^2 = 13.14$). Greatest annual dispersal was predicted for the Eastbourne population (16 m), whilst the Shoreham, Wembdon, and Newton Ferrers populations had similar low dispersal of ~4 m per year. Connectance between suitable habitat patches had no relationship with any of the dependent variables.

Discussion

The predicted suitable climate for *P. muralis* in the UK is contiguous along the southeast coast, the entire south coast through to the south coast of Wales, extending northwards to a latitude of ~52degN - a latitudinal range likely to reflect climatic conditions most akin to those found in the species' native origins. This northern limit to suitable conditions is in keeping with climate matching being an important limiting factor in determining establishment success and range expansion of introduced species, particularly significant for reptiles (Bomford, Kraus, Barry, & Lawrence, 2009; Pysek et al., 2010; Mahoney et al., 2015). Our climate suitability model output is similar to a previous SDM for *P. muralis* , which also highlighted favourable conditions in the UK up to ~53degN, (Wirga & Majtyka, 2015), despite a differing suite of climatic variables and species presence data informing models.

Our model shows that number of frost days and amount of annual sunshine were the most informative variables in predicting probability of occurrence. The hibernation period is short in *P. muralis* and individuals are often active in mid-winter during sunny mild spells, even in the northern extremes of their range, making them vulnerable to sudden or prolonged freezing (Claussen, Townsley, & Bausch, 1990). Measurements of critical thermal minimum temperature in an introduced population of *P. sicula* have been shown to be above temperatures likely experienced by some non-native populations in winter, suggesting individuals may need to find urban thermal retreats to survive winter conditions, or hibernate at a depth below soil freezing to survive (Burke et al., 2002; Liwanag, Haro, Callejas, Labib, & Pauly, 2018). Interestingly, our model accurately predicted the Greater London Urban Area as having relatively high habitat suitability, likely arising from matching to thermal characteristics associated with the "urban heat island" (UHI) effect (Trajer, Mlinarik, Juhasz, & Bede-Fazekas, 2014; Villalobos-Jimenez & Hassall, 2017). There are historic records of small, *P. muralis* populations persisting in this area (Langton, Atkins, & Herbert, 2011; Langham, 2019), and since we did not include these records in the input for the model (due to no recent confirmed sightings and no accurate location data), the predicted suitability in this area gives credence to the validity of the model and the theory of UHI in built environments facilitating overwintering for the species. Dependence on human structures to survive winter temperatures in northern extremes has been suspected for introduced populations of Mediterranean gecko (*Hemidactylus tursicus*) (Locey & Stone, 2006). Microclimatic conditions close to human habitations may have also facilitated establishment of Argentine ant (*Linepithema humilein*) in areas with otherwise unsuitable climate (Roura-Pascual et al., 2011). Such environments may, however, also act to shield populations from selective pressures that might lead to adaptive physiological responses that could facilitate more rapid diffusion and expansion across wider areas (Hulbert, Hall, Mitchell, & Warner, 2020).

Our fine scale modelling of probability of occurrence provides a detailed insight into local landscape structure and spatial pattern of available suitable habitat. The contribution of habitat classification and spring solar insolation to the model, and particularly the unimodal response observed toward vegetation cover (NDVI), is indicative of the species' affinities to disturbed habitats that provide resource for refugia (thermal and safety), egg deposition sites, and basking sites necessary for heliothermic temperature regulation (Bertram, 2004; Gherghel, Strugariu, Sahlean, & Zamfirescu, 2009). It is possible that although we took great effort to assign habitat type in as much detail as practical, generalisations made during the construction of the habitat classification layer could possibly lead to overestimation of the extent of suitable habitat (e.g., not all habitat classed as residential garden would in reality be suitable to *P. muralis*). However, the combined effect of the NDVI variable would go some way to enhance fine-scale delineation between suitable and unsuitable habitat type.

The relative importance of railway line and introduced shrub habitat in the model can be explained by the number of presence records associated with those habitats in relation to the relative scarcity of those habitats in the landscape. Habitat associated with railway lines is well documented as providing important habitat for *P. muralis* , facilitating both natural dispersal and accidental human movement of animals (Covaciu - Markov, Bogdan, & Ferenti, 2006; Kuhnis & Schmocker, 2008; Strugariu, Gherghel, & Zamfirescu, 2008; Gherghel et al., 2009). Dispersal of the introduced *P. muralis* population in Ohio, Cincinnati, has been reported to be more rapid along the continuous hospitable terrain of rail embankments compared to the relatively slow spread through highly fragmented residential and commercial areas (Hedeen & Hedeen, 1999). Although our simulations of the West Worthing (trackside) population (see Appendix 1) did have relatively higher dispersal distance than most other populations, the pattern of spread did not indicate extensive natural dispersal along the railway, despite the core population being centred on, and around, disused sidings and associated habitat. Instead, the simulated dispersal pattern is one of predominantly radial diffusion out into adjacent residential and commercial areas, where, although highly fragmented, the habitat was of suitable quality to facilitate this pattern of spread. Linear corridors may therefore only become important to natural dispersal when adjacent habitat is of low quality, or is less preferred, as is the case of invasive cane toads (*Rhinella marina*) selecting to use open roads for dispersal through less favourable vegetated habitat (G. P. Brown, Phillips, Webb, & Shine, 2006). The presence of other contiguous, linear habitat features in our landscape models also increased rates of annual range expansion (e.g., vegetated cliff faces at Branksome and Canford; sea front garden along the promenade at Eastbourne), but this is likely a result of there being restrictions to radial dispersal as suitable habitat is bordered by inferior inland habitat and the shore line. Our findings are congruent with the theory that corridors may be most effective when they actively influence, direct, and channel dispersal rather than simply provide additional suitable habitat (Andrew & Ustin, 2010).

Growth curves derived from our predictive models suggest all the populations studied may be in the early stages of exponential growth, and have demonstrated (or are demonstrating) a lag before the onset of appreciable population growth that is often associated with such a growth trajectory (Sakai et al., 2001). The negative correlation we found between intrinsic growth rate and time since introduction, is to be expected as a function of logistic growth, where the longer-established populations approach local carrying capacity and density dependence constrains growth (Sibly & Hone, 2002).

Our models concur, however, that natural dispersal of *P. muralis*from points of introductions in the UK is likely to be slow (Foster, 2015), with annual population range expansion of between 5 -16 meters. Spread distances were particularly small for populations in areas of relatively contiguous suitable habitat which allows for radial dispersal into suitable neighbouring habitat with limited search effort (i.e., rural villages with interconnected gardens, quarries) (Bonte et al., 2012; Baguette, Blanchet, Legrand, Stevens, & Turlure, 2013). In such instances it would appear that populations with limited opportunities/need for long distance dispersal are increasing their numbers locally, but will be limited for establishing a population over a large area (Lustig et al., 2017). Increasing disaggregation of suitable habitat had a joint positive influence on dispersal rate and growth rate in our models. We found this to be most apparent for the urban population of West Worthing, highlighting how the species' ability to exploit areas of human disturbance may facilitate overall invasion success (Marvier, Kareiva, & Neubert, 2004). Increasing abundance of discrete local patches of suitable habitat may provide opportunity for individuals to disperse more widely in the landscape, thus releasing density dependent constraints on population growth that would be in effect when suitable habitat is more aggregated and compact. This pattern is in line with the theories of a percolation threshold, where invasive spread may occur most rapidly and extensively above a threshold level of disturbance (i.e., amount of habitat fragmentation) (With, 2002). In addition, we found functional connectedness of suitable habitat patches had no relation to any of the growth parameters or rate of spread, indicating that localised habitat fragments are acting as stepping stones to dispersal (Alharbi & Petrovskii, 2019). Similar effects of landscape heterogeneity on range expansion of invasive species have been observed in introduced populations of whistling frog (*Eleutherodactylus johnstonei*) (Ernst, Massemin, & Kowarik, 2011), Eurasian collared dove (*Streptopelia decaocto*) (Ingenloff et al., 2017), and invasive weeds (Bergelson, Newman, & Floresroux, 1993).

Conclusions

Extensive nationwide range expansion through secondary introduction is likely to be restricted by currently unsuitable climate beyond southern regions of the UK. However, exponential growth of local populations in habitats providing transport pathways (i.e., movement of aggregates, timber, plants, general public) is likely to increase opportunities for regional expansion. A similar scenario has been described in the spread dynamics of invasive Pallas's squirrel (*Callosciurus erythraeus*), where a constant increase in the appearance of new populations occurred after a two decade lag, and could be explained by increased vector activity (intentional translocations) as the population size at the initial introduction foci increased – causing a potentially exponential increase of translocation events when translocated populations start acting as a source themselves (Guichon, Benitez, Gozzi, Hertzriken, & Borgnia, 2015).

Despite the fundamental physiological importance of sun exposure to diurnal reptiles, to the best of our knowledge, our models are the first to incorporate estimates of solar insolation into models of probability of occurrence at this fine scale (but see Bennie, Huntley, Wiltshire, Hill, and Baxter (2008) for a detailed discussion on use of solar influx as a variable in modelling fine scale topographic microclimate). Our models demonstrate the inclusion of the variable at this scale, and indeed our entire approach to developing a fine scale SDM, could be very useful in other applications relating to ectotherm ecology (e.g., in developing habitat suitability indices, directing habitat management, guiding survey effort for rare/cryptic species). Furthermore, whilst the use of SDMs and IBMs have become a widely used to further understanding of mechanisms driving invasion dynamics (Kadoya & Washitani, 2010; Fraser et al., 2015; Suzuki-Ohno et al., 2017), the benefits of incorporating spatially explicit individual based models into management plans for the control of invasive species has only recently been recognised (Day, Landguth, Bearlin, Holden, & Whiteley, 2018). In this regard, our models provide a best estimate for future expansion of *P. muralis* at both the UK national and local scale, providing essential information (i.e., dispersal patterns, key habitat, current and projected population sizes) on which management decisions could be made. As our models show UK populations may be approaching an end to an inherent lag phase, there is argument to suggest that a timely precautionary intervention may be justified to halt some populations before an abrupt end to the lag phase occurs.

Data accessibility: the following data is in the process of being deposited with EIDC

-MaxEnt (local and national scale) input files including presence and background samples with climate/environment data

- Inputs for Rangeshifter models and subsequent population outputs

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Table 1 Details of variables and their data source used in MaxEnt models *of P. muralis* probability of occurrence.

Model	Environmental variable	Description
National	*Spring max temp*	Average of monthly mean max temp °C (Mar, Apr, May) 1981-2010
	Summer max temp	Average of monthly mean max temp °C (Jun, Jul, Aug) 1981-2010
	Autumn max temp	Average of monthly mean max temp °C (Sep, Oct, Nov) 1981-2010
	Winter max temp	Average of monthly mean max temp °C (Dec, Jan, Feb) 1981-2010
	Frost days	Mean number of frost days in the year (minimum grass temperature below 0°C) 1981-
	Annual sunshine	Annual total hours of sunshine duration
Local	*NDVI*	Normalised difference vegetation index
	Distance to buildings	Euclidian distance to buildings
	Distance to roads	Euclidian distance to all roads
	Distance to rail	Euclidian distance to railway tracks
	Spring insolation	Mean incoming solar insolation for months Mar, Apr, May 1981-2017
	Phase 1 habitat	Habitat classification

Table 2 Summary of separate stepwise regression analysis showing significant variables predicting growth rate (r), carrying capacity (k), and annual dispersal distance of introduced *P. muralis* populations in the UK (N = 10)

		Predictors	β	SE	P	R^2
Population growth rate (r)	Population growth rate (r)	NLSI	0.30	0.10	<0.01	0.522
		Time since introduction	<-0.01	<0.01	0.04	
Carrying capacity (k)	Carrying capacity (k)	Habitat quality	218.8	87.8	0.03	0.437
Annual dispersal distance	Annual dispersal distance	Habitat quality	0.29	0.05	<0.01	0.894
		NLSI	68.18	9.59	<0.01	

Fig. 1 Locations of UK breeding populations of *P. muralis* from which presence data informed models of climatic suitability and locations of confirmed sightings arising from a citizen science campaign 2017-2019

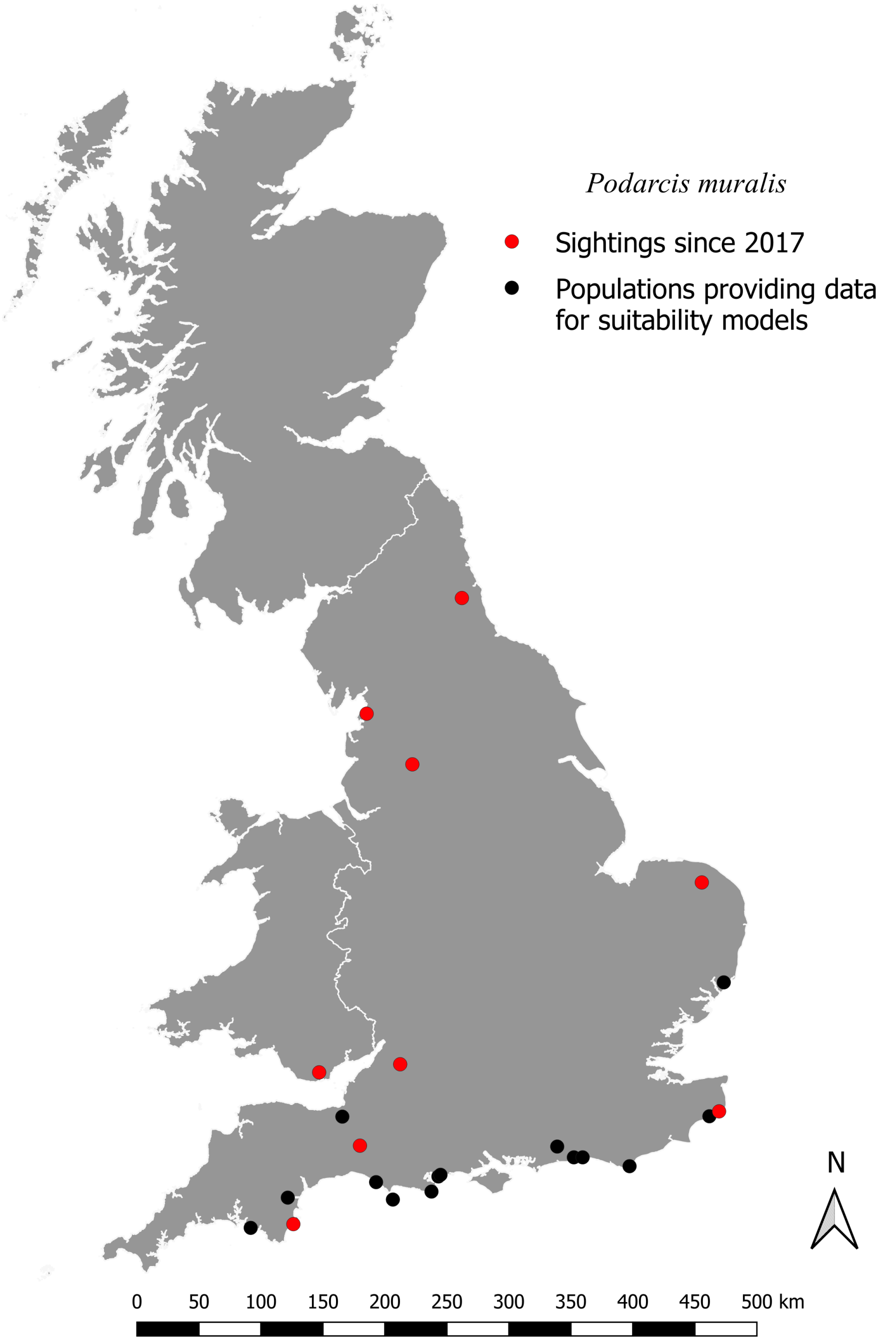
Fig. 2 Regions of climatic suitability for *P. muralis*in the UK as predicted by MaxEnt models considering seasonal averages of six climatic variables. Locations of major populations from which presence data informed model output: WE, Wembdon; NF, Newton Ferrers; KW, Kingswear; NA, Newton Abbot; PO, Portland; PQ, Purbeck quarries; DS, Durleston Head; BC, Bournemouth coast; BU, Bury; WW, West Worthing; SH, Shoreham; EA; Eastbourne; FO, Folkestone; FE, Felixstowe

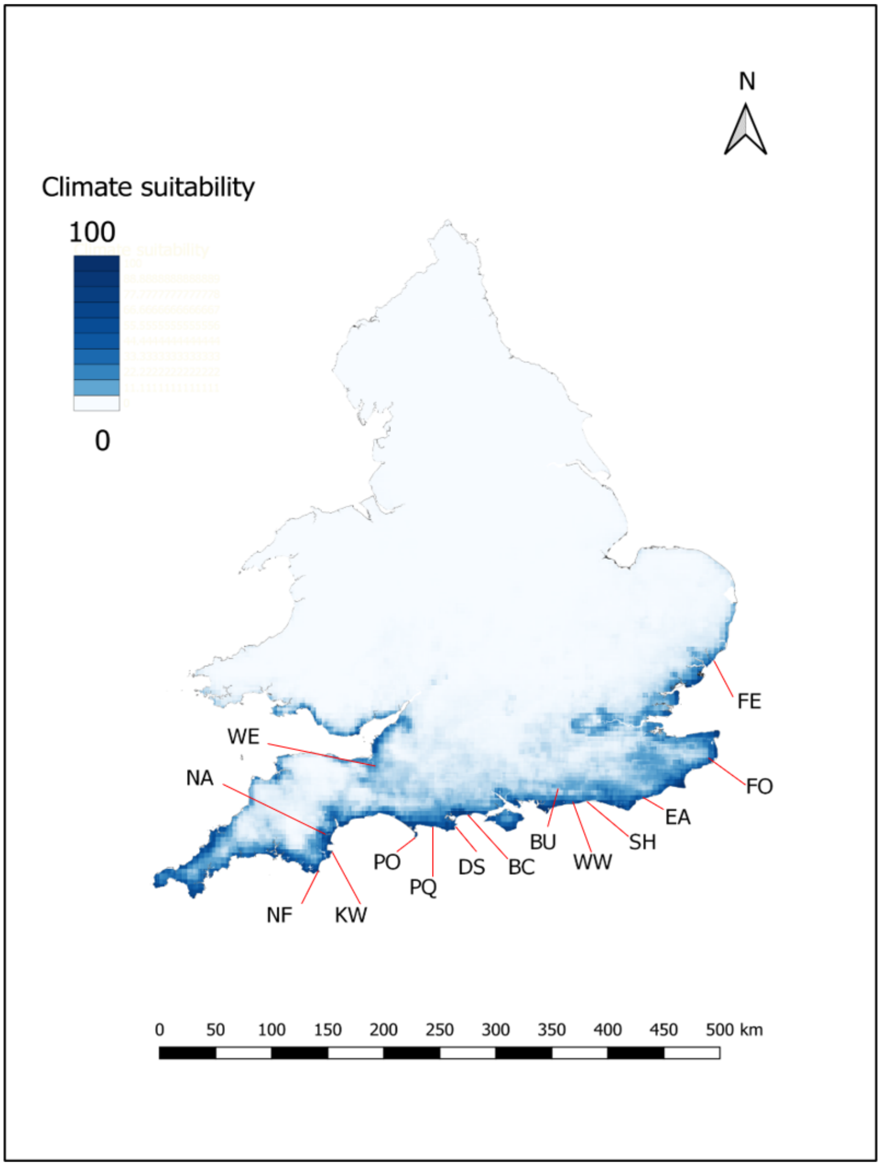
Fig. 3 Response of *P. muralis* (probability of presence) to six climate variables as modelled in MaxEnt at the UK national scale: a) Maximum Spring temperature, b) Maximum Summer temperature, c) Maximum Autumn temperature, d) Maximum Winter temperature, e) Number of frost days, f) Annual duration (hours) of bright sun shine

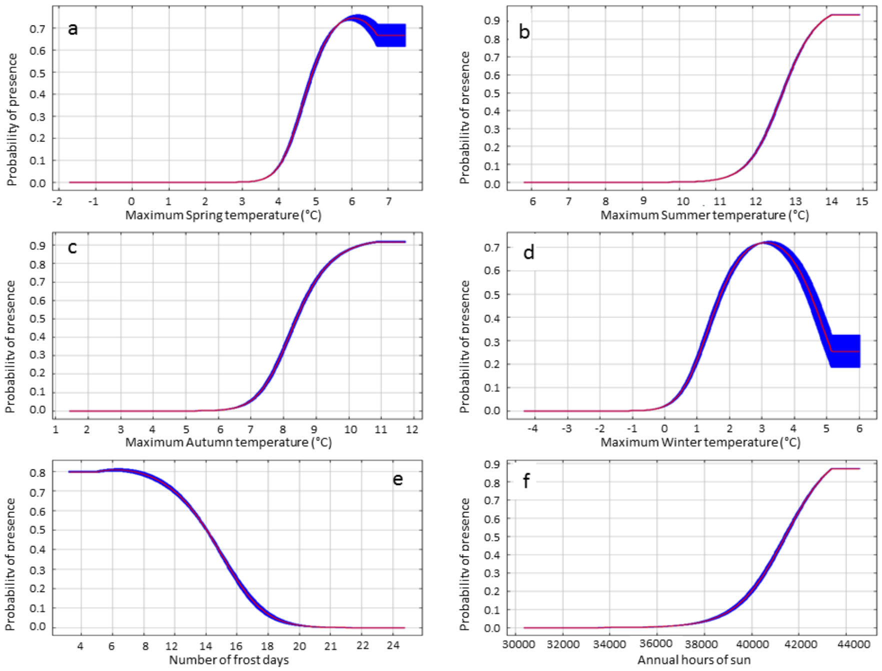
Fig. 4 Response of *P. muralis* (probability of presence) to six environmental variables as modelled in MaxEnt at the UK local scale: a) Distance to buildings, b) Distance to rail, c) Distance to roads, d) NDVI, e) Habitat type, f) Spring solar insolation

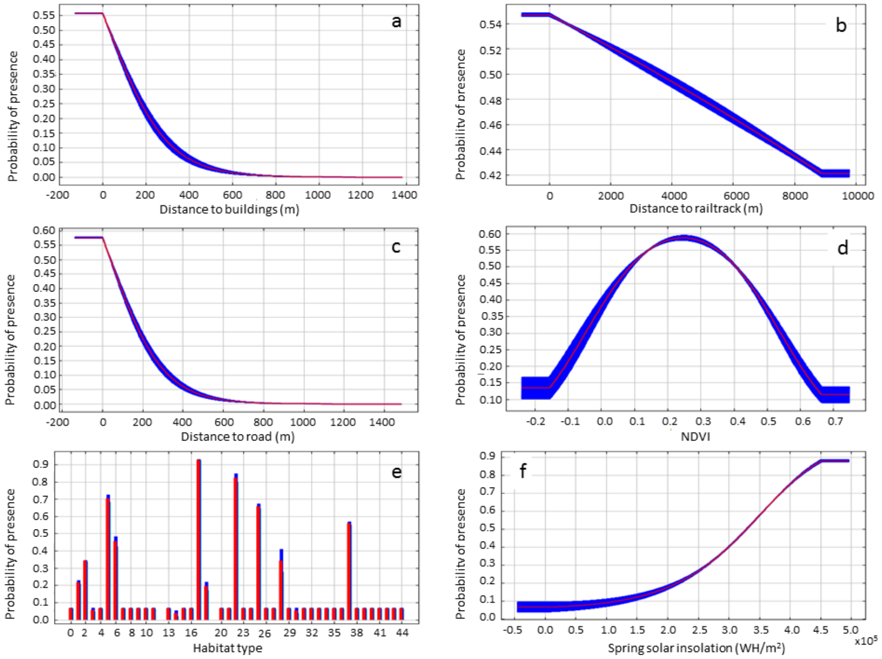
Fig. 5 MaxEnt outputs showing local extent and configuration of suitable habitat for *P. muralis* populations in the UK. Order demonstrates the range of variance in patch fragmentation, patch isolation, and linear features of suitable habitat across local landscapes: a) West Worthing, b) Bournemouth (including Boscombe and Canford populations), c) Portland, d) Wembdon, e) Newton Ferrers. Outputs from RangeShifter models are overlain, indicating patterns of population dispersal projected from year of introduction to 2040 and number of lizards per occupied 225m^2 cell

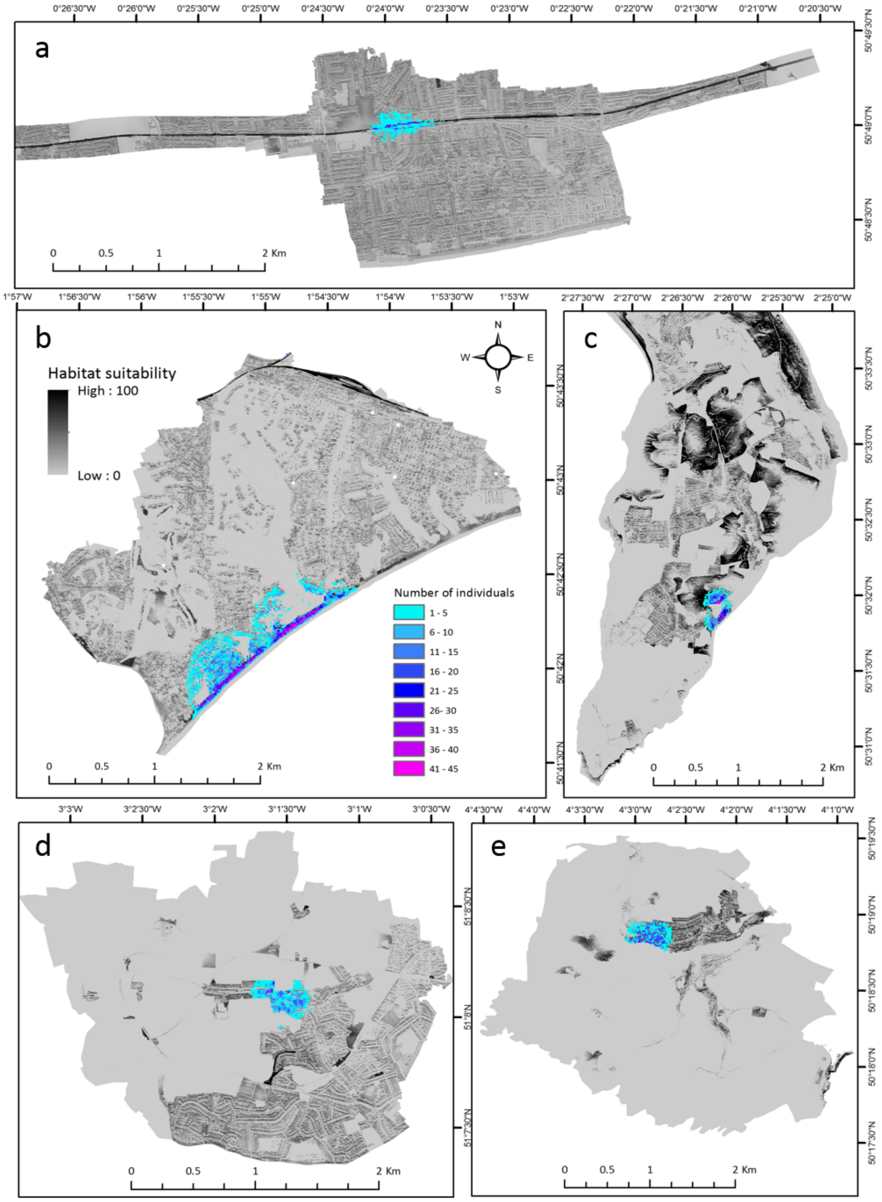
Fig. 6 Relationship between growth rate (r) and a) aggregation of suitable habitat (NLSI), time since introduction b), and c), relationship between NLSI and annual dispersal distance in non-native population of *P. muralis* in the UK

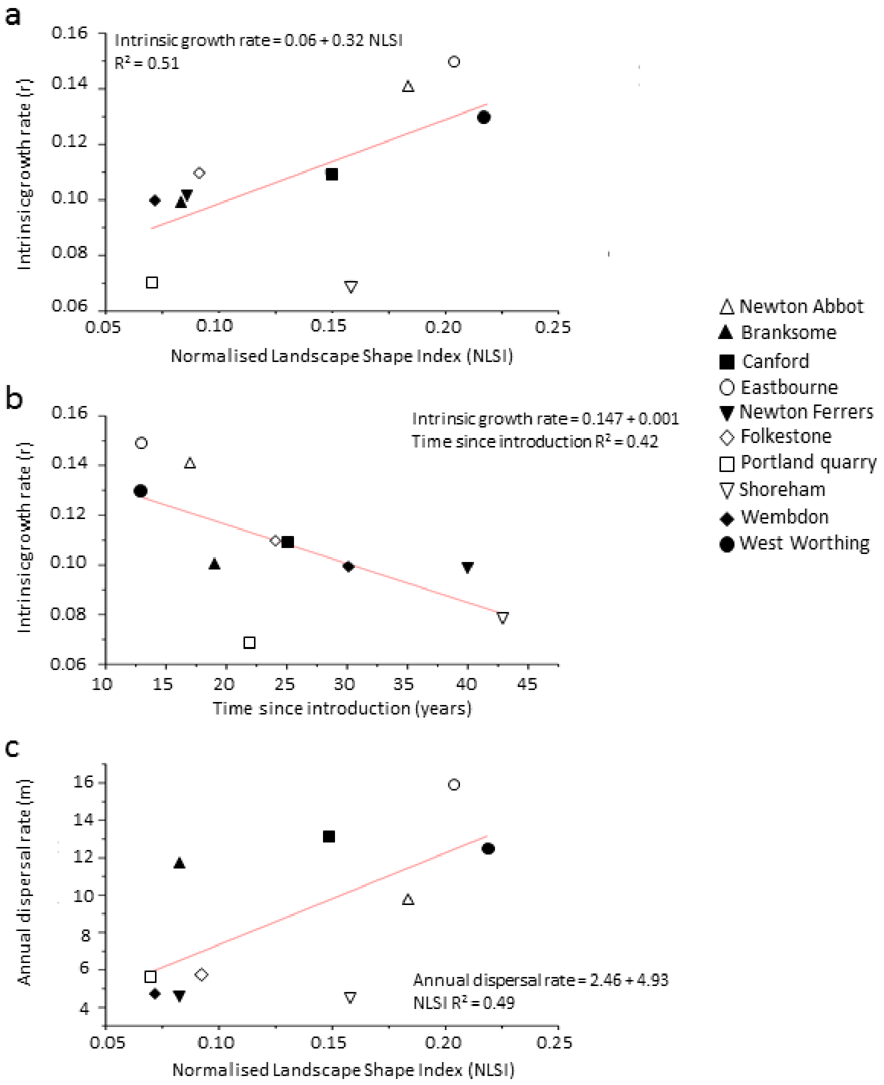

Podarcis muralis
● Sightings since 2017
● Populations providing data for suitability models
N
0
50
100
150
200
250
300
350
400
450
500 km


N
Climate suitability
100
0
WE
NA
FE
FO
EA
SH
WW
BU
BC
DS
PQ
PO
NF
KW
0
50
100
150
200
250
300
350
400
450
500 km


a
Probability of presence
Maximum Spring temperature (°C)
b
Maximum Summer temperature (°C)
c
Maximum Autumn temperature (°C)
d
Maximum Winter temperature (°C)
e
Number of frost days
f
Annual hours of sun


a
Probability of presence
Distance to buildings (m)
b
Distance to railtrack (m)
c
Distance to road (m)
d
NDVI
e
Habitat type
f
Spring solar insolation (WH/m²)
x10⁵


a
0°26'30"W
0°26'0"W
0°25'30"W
0°25'0"W
0°24'30"W
0°24'0"W
0°23'30"W
0°23'0"W
0°22'30"W
0°22'0"W
0°21'30"W
0°21'0"W
0°20'30"W
50°49'30"N
50°49'0"N
50°48'30"N
0 0.5 1 2 Km
b
1°57'W
1°56'30"W
1°56'W
1°55'30"W
1°55'W
1°54'30"W
1°54'W
1°53'30"W
1°53'W
50°43'30"N
50°43'N
50°42'30"N
50°42'N
50°41'30"N
N
W
E
S
Habitat suitability
High : 100
Low : 0
Number of individuals
1 - 5
6 - 10
11 - 15
16 - 20
21 - 25
26- 30
31 - 35
36 - 40
41 - 45
0 0.5 1 2 Km
c
2°27'30"W
2°27'0"W
2°26'30"W
2°26'0"W
2°25'30"W
2°25'0"W
50°33'30"N
50°33'0"N
50°32'30"N
50°32'0"N
50°31'30"N
50°31'0"N
0 0.5 1 2 Km
d
3°3'W
3°2'30"W
3°2'W
3°1'30"W
3°1'W
3°0'30"W
51°8'30"N
51°8'N
51°7'30"N
0 0.5 1 2 Km
e
4°4'30"W
4°4'0"W
4°3'30"W
4°3'0"W
4°2'30"W
4°2'0"W
4°1'30"W
4°1'0"W
50°19'30"N
50°19'0"N
50°18'30"N
50°18'0"N
50°17'30"N
0 0.5 1 2 Km


a
Intrinsic growth rate = 0.06 + 0.32 NLSI
R² = 0.51
Intrinsic growth rate (r)
0.16
0.14
0.12
0.10
0.08
0.06
0.05
0.10
0.15
0.20
0.25
Normalised Landscape Shape Index (NLSI)
b
Intrinsic growth rate = 0.147 + 0.001
Time since introduction R² = 0.42
Intrinsic growth rate (r)
0.16
0.14
0.12
0.10
0.08
0.06
10
15
20
25
30
35
40
45
Time since introduction (years)
c
Annual dispersal rate (m)
16
14
12
10
8
6
4
0.05
0.10
0.15
0.20
0.25
Annual dispersal rate = 2.46 + 4.93
NLSI R² = 0.49
Normalised Landscape Shape Index (NLSI)
△ Newton Abbot
▲ Branksome
■ Canford
○ Eastbourne
▼ Newton Ferrers
◇ Folkestone
□ Portland quarry
▽ Shoreham
◆ Wembdon
● West Worthing