

Modeling future range expansion and management strategies for an invasive squirrel species

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Abstract Successful management of an invasive species requires in depth knowledge of the invader, the invaded ecosystem, and their interactions. The complexity of the species-system interactions can be reduced and represented in ecological models for better comprehension. In this study, a spatially explicit population model was created using the RAMAS software package to simulate the past and future

invasion dynamics of the eastern grey squirrel (*Sciurus carolinensis*) in the fragmented habitat in case study areas in Ireland. This invasive squirrel species causes economic damage by bark stripping forest crops and is associated with the decline of its native congener (*S. vulgaris*). Three combinations of demographic and dispersal parameters, which best matched the distribution of the species shortly after introduction, were used to simulate invasion dynamics. Future population expansion was modeled under scenarios of no control and two different management strategies: fatal culls and immunocontraceptive vaccination programmes. In the absence of control, the grey squirrel range is predicted to expand to the south and southwest of Ireland endangering internationally important habitats, vulnerable forest crops, and the native red squirrel. The model revealed that region-wide intensive and coordinated culls would have the greatest impact on grey squirrel populations. Control strategies consisting solely of immunocontraceptive vaccines, often preferred by public interest groups, are predicted to be less effective. Complete eradication of the grey squirrel from Ireland is not economically feasible and strategic evidence-based management is required to limit further range expansion. Ecological models can be used to choose between informed management strategies based on predicted outcomes.

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Introduction

Effective management of populations and landscapes requires an understanding of past events, current circumstances, and likely scenarios for the future. The complexity of ecological systems often necessitates the use of mathematical models with which simplified case studies can be created and manipulated. Such ecological models allow researchers insight into ecological processes such as *inter alia* dispersal or invasion speed (Caswell et al. 2003), effects of management or harvesting regimes (Taylor et al. 1987), and metapopulation patch occupancy (Hanski 1994). The development of spatially explicit population models (SEPMs), which combine landscape structure with metapopulation dynamics, has allowed for the incorporation of complex landscape/species interactions in models that consider species abundance, spatial distribution, and population viability (Dunning et al. 1995). These models are not only useful for those concerned with future scenarios for endangered or exploited species (Southwell et al. 2008) but also for those addressing the problems caused by expanding or invasive species (Kolar and Lodge 2002). Biological invasions now threaten biodiversity and ecological processes as well as agricultural and transport systems at local and global scales (Mack et al. 2000). Ideally, biological invasions should be addressed early to minimize negative consequences (Myers et al. 2000). However, if species invasions proceed past the point of easy eradication then SEPMs can assist managers and researchers in making predictions about future abundance (Meekins and McCarthy 2002), range extent (Higgins et al. 1996), and the effectiveness of control regimes (Vuilleumier et al. 2011). Here, we formulate SEPMs to predict the effectiveness of hypothetical lethal and contraceptive control strategies on the future spread of an invasive economic and ecological pest species, the grey squirrel (*Sciurus carolinensis*).

Arguably, the multiple introductions and fast expansion of grey squirrels outside of their native range is one of the most thoroughly documented cases of biological invasion (Gurnell et al. 2006). Additionally, the ecology of the grey squirrel in native and introduced areas, and the European red squirrel (*S. vulgaris*), the native squirrel most often affected by the invader, are well known. Competition between red and grey squirrels was modeled spatially for the first time

using a bespoke SEPM (Rushton et al. 1997). This research was built upon by studies examining future grey squirrel spread in Britain and Europe (Lurz et al. 2001; Tattoni et al. 2006; Bertolino et al. 2008) and effects of grey squirrel control (Rushton et al. 2002). Bespoke models hold the advantage of being precisely tailored to the relevant system but suffer from limited wider appeal due to lack of transparency. Highly customized models are less adaptable to other ecological systems and necessitate a high level of mathematical and programming literacy (Lurz et al. 2008). Recent advances in general population modeling software overcome many of the hurdles inherent in individual models and allow validated and transparent models to be designed that are tailored to specific ecological systems. Models of this type have successfully investigated population viability (Wood et al. 2007), effects of poaching and habitat fragmentation (Matsinos and Papadopoulou 2004), and range expansion and control programmes (Guichón and Doncaster 2008) for diverse sciurid species worldwide.

The economic and ecological costs of the many grey squirrel invasions have been high in Europe. Maximum annual estimates of the cost of grey squirrel tree damage at commercial harvest are as high as £10 million in Britain and €4.5 million on the island of Ireland (Kelly et al. 2013). Grey squirrels are associated with the disappearance of red squirrels from many areas of Ireland, Britain, and Italy, via reduced levels of juvenile recruitment (Gurnell et al. 2004) and disease transmission (McInnes et al. 2013; Shuttleworth et al. 2014). Irregularity characterised the early monitoring of the range expansion of the grey squirrel following the introduction of six male and six female animals to Ireland in 1911. The first distribution surveys were undertaken in the 1960s, though the frequency of surveys has since improved (Carey et al. 2007; Lawton et al. 2015). Grey squirrels have reached the north and east coasts of the island of Ireland and the population continues to expand at a rate of 1.75–1.94 km year⁻¹ (O'Teangana et al. 2000; McGoldrick 2011) to the south and south-west (Goldstein et al. 2014).

The most effective invasive species control programmes require support and funding at local and national levels (Bertolino and Genovesi 2003; Bryce et al. 2011; Bertolino et al. 2014). There is currently no coordinated grey squirrel control effort in Ireland as landowners typically cull on a property-by-property

basis. Though these local culls are effective at reducing squirrel numbers and limiting bark stripping damage in the short term, grey squirrel numbers recover to pre-cull levels within 2–3 months (Lawton and Rochford 2007). The need to control overabundant wildlife in areas of high human habitation, where fatal control is inappropriate or undesired, has prompted research into wildlife fertility control, which acts to reduce birth rates rather than survival rates (Fagerstone et al. 2010). Recent research in tree squirrel fertility reduction has achieved preliminary results through chemical interruption of reproductive hormone synthesis (Yoder et al. 2011; Mayle et al. 2013) and through the induction of an immune response against gonadotropin-releasing hormone (Pai et al. 2011; Krause et al. 2014).

We used SEPMs to examine the population and invasion dynamics of the grey squirrel in Ireland, where the species has never before been spatially explicitly modeled. The models were designed using a validated model creation software package, RAMAS GIS 6.0, and were calibrated to the species system through retrospective modeling of the invasion patterns following the initial introduction of the species. As the grey squirrel population in Ireland remains largely unmanaged, forecast modeling efforts were focused to the south and south-west of the country where range expansion continues (Goldstein et al. 2014), endangering vulnerable local hardwood plantations and robust local red squirrel populations. We used the predictions of range expansion under different control strategies and intensities to compare the efficacy of these methods in limiting grey squirrel abundance and slowing the pace of range expansion. Management goals should drive the choice and implementation of control strategies and we make recommendations for the use of these strategies in species management plans.

Methods

The island of Ireland (84,421 km²) encompasses the Republic of Ireland and Northern Ireland. Land use is primarily agricultural and forest cover currently stands at approximately 10 % and is increasing (Forest Service 2007b; Ní Dhubháin et al. 2009), though it remains highly fragmented. The initial expansion of the grey squirrel was retrospectively modeled in a

study area of approximately 18,000 km² in the Irish midlands (Fig. 1), which encompassed the site of introduction and the first recorded distribution in 1968 (NPWS 1968). Future expansion and effects of control strategies were modeled over a similar area in the south of Ireland (Fig. 1), where the grey squirrel continues to expand its range, as a case study. Killarney National Park (102.89 km²; 51°59'N 9°33'W), which contains oak and yew woodlands of international importance as well as many rare plant and animal species, was chosen as an example of a sensitive area at risk of grey squirrel invasion. This location, a designated UNESCO biosphere reserve, provides a tangible and ecologically relevant basis for comparison of long-term outcomes of different control strategies on grey squirrel range expansion.

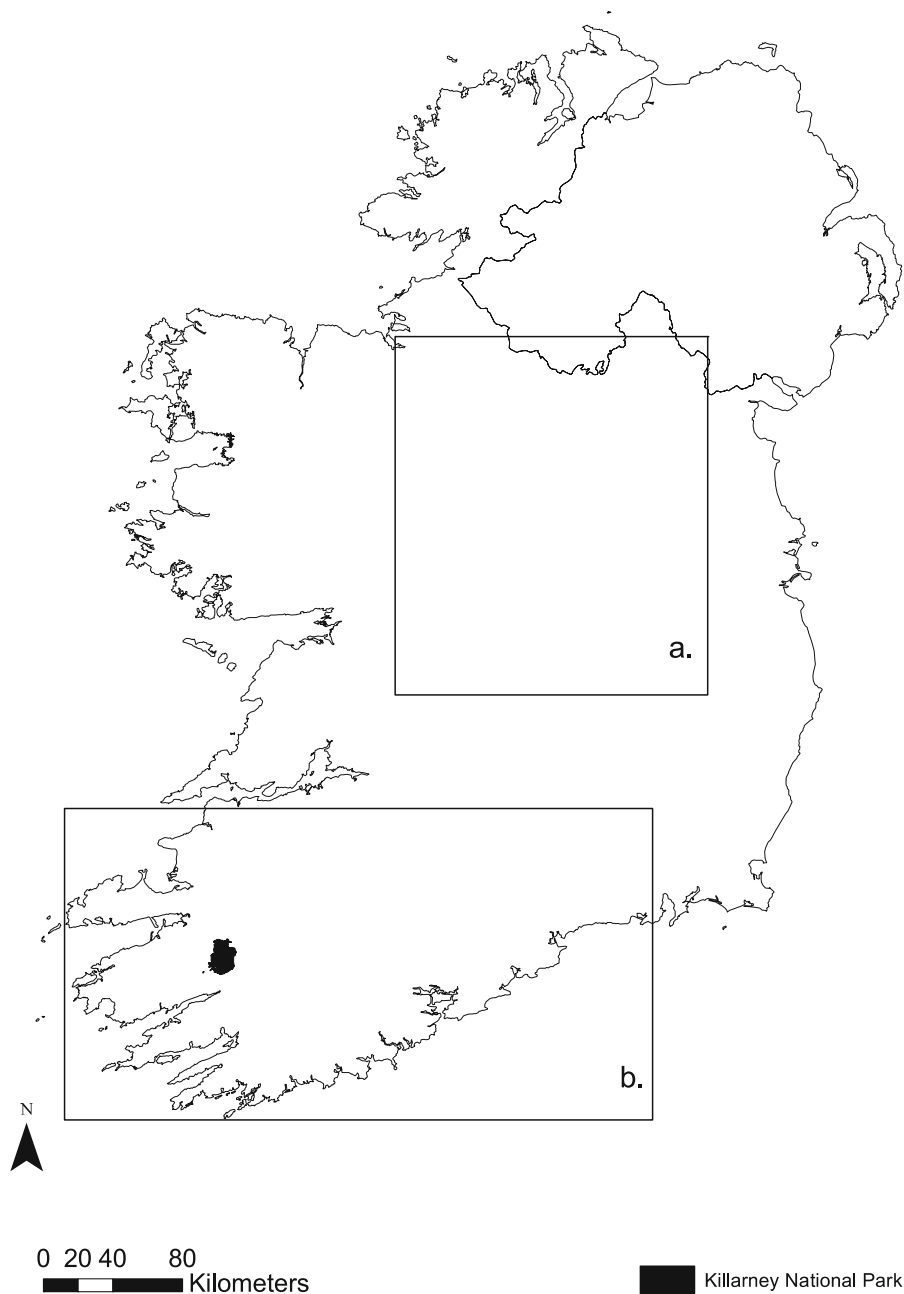
The model

A spatially-explicit, stage-structured stochastic model was developed to simulate the past and future grey squirrel invasion. Life-history parameters and carrying capacities required for the model were drawn from published data on the density and demography of introduced grey squirrel populations in Ireland, Britain, and continental Europe, and from populations within the native North American range, reviewed in Goldstein et al. (2015). The model was created using RAMAS GIS 6.0 software (Akçakaya and Root 2013), which is designed to link metapopulation models with spatial habitat data.

Several existing landscape datasets were consolidated and combined to create the habitat map. The 2006 Corine Land Cover inventory (minimum mapping unit: 25 ha) for Ireland (EEA 2007) was supplemented with the 2007 Forest Inventory (Forest Service 2007a) and Environmental Protection Agency Waterways data (EPA 2003). The land cover types defined in these datasets were dissolved into a limited number of habitats relevant to grey squirrels in ArcMap 10.0 (ESRI). Three types of habitat suitable for grey squirrels were defined; broadleaf woodland, mixed woodland, and urban area as well as non-suitable matrix habitat. The landscape raster had a cell size of 100 × 100 m.

Grey squirrels achieve highest population densities in broadleaf habitat in both their native and introduced ranges (Koprowski 1994; Goldstein et al. 2015). Broadleaf woodland was assigned the highest

Fig. 1 Map of Ireland showing **a** the extent of the study region in the introduction area and **b** the extent of the study area used to examine future expansion and control scenarios in the south and southwest of the country. Killarney National Park, which contains internationally valuable habitat and is vulnerable to *grey squirrel* invasion, is also highlighted



suitability value followed by mixed woodland and urban (including suburban) areas (Table 1) based on densities for each habitat derived from Irish live-trapping studies (O'Teangana 1999; Lawton and Rochford 2007; McGoldrick 2011; Sheehy and Lawton 2014; Goldstein et al. 2015). Grey squirrels are found at lower densities in Ireland than in their native North American range or in Britain (Goldstein et al.

2015) and therefore the carrying capacities for grey squirrels in different habitats in this model were held at the lower levels observed in Ireland in established and frontier populations. Conifer woodlands, a sink habitat for grey squirrels (Lurz et al. 1995; Kenward et al. 1998), mainly exist as large plantations in Ireland. Despite approximately 20 years of systematic squirrel research in Ireland (reviewed in Goldstein et al. 2015)

Table 1 Estimates of parameters used as model inputs for the spatially explicit population model designed to examine future grey squirrel (*Sciurus carolinensis*) expansion in Ireland

Parameter	Classification	Values (range)	
		Model trial A	Model trial B
Habitat quality (K)	Broadleaf	2 squirrel ha ⁻¹	
	Mixed	1.5 squirrel ha ⁻¹	
	Urban	1 squirrel ha ⁻¹	
	Matrix	0 squirrel ha ⁻¹	
Survival rates	Juvenile	0.4 (0.3–0.5)	0.5 (0.375–0.6125)
	Yearling	0.7 (0.525–0.875)	0.7 (0.525–0.875)
	Adult	0.7 (0.525–0.875)	0.7 (0.525–0.875)
Fecundity rates	Juvenile	0.03 (0.0225–0.0375)	0.0375 (0.0281–0.0459)
	Yearling	0.45 (0.3375–0.5625)	0.5625 (0.4219–0.6891)
	Adult	1.2 (0.9–1.5)	1.5 (1.125–1.838)
Finite rate of increase (λ)		1.0646 (0.7985–1.3308)	1.1859 (0.8894–1.4672)
Mean dispersal distance		1 km (0.5–2.0)	
Max dispersal distance		(2.5–9.0 km)	(5–9.0 km)
σ^2 relative dispersal	Juvenile	1:0.6	
	Yearling	0.5:0.3	
	Adult	0.25:0.15	
DDD constant ^a		0 (0.001)	
Competition type		Ceiling	

If a range of values was used these are shown in parentheses

^a Density dependent dispersal

only one population of grey squirrels has been studied in coniferous forestry, though the author noted that it was likely highly influenced by adjacent mature deciduous woodland (O’Teangana 1999). Recent systematic surveys have not detected grey squirrels in habitat that is 100 % coniferous (Carey et al. 2007; Goldstein et al. 2014; Lawton et al. 2015). Although grey squirrel populations have been observed with low densities and high turnover rates in coniferous woodlands in Britain (Lurz et al. 1995; Kenward et al. 1998; Lurz and Lloyd 2000), this is not a significant habitat for the species in Ireland due to current forest plantation design schemes and as such was considered as unsuitable matrix habitat in this model.

Areas of habitat with a carrying capacity ≥ 1 squirrel ha⁻¹ were defined as patch habitat and the surrounding non-suitable habitat as matrix habitat to link the habitat and metapopulation functions of the model. Grey squirrels occupy non-exclusive home ranges varying in size from ≤ 1 to ≥ 5 ha dependent on resources and density (Kenward 1985) and also make routine extra-range movements across matrix habitat, especially in areas of fragmented woodland habitat (Gurnell 1987). The perceptual range of the grey squirrel, or the maximum distance at which it can perceive remote

habitat patches, is between 300 and 400 m (Zollner 2000; Goheen et al. 2003). Using these estimates of home range size, exploratory movement, and perceptual range, areas of suitable habitat within 400 m of each other were grouped as a single “patch”. The carrying capacity of each patch was equal to the total habitat suitability, which was calculated as the sum of the habitat values of the woodland and urban cells. Suitable habitat in Ireland is extremely fragmented at national and local scales. Smaller patches, with a carrying capacity (K_{min}) < 50 individuals, were treated as habitat fragments suitable for enhancing dispersal between larger populations. Including all smaller suitable habitat patches would have expanded the patch matrix drastically, exceeded programme limitations on number of populations, and limited programme functionality with regards to defining realistic dispersal pathways. Focusing analysis on the major patches allows for conservative estimation of the invasion dynamics of this system (Guichón and Doncaster 2008). We varied the minimum patch carrying capacity parameter ($K_{min} = 10, 25, 50, 75, 90$) to understand the sensitivity of yearly squirrel population increase rates to this model design requirement in the initial expansion area using the parameters of the “best fit” model (described below).

The elements of an age-structured Leslie matrix with three age classes for each sex were estimated using empirically collected and published demographic and density data (Goldstein et al. 2015). The age classes modeled were “juveniles” (0–1 year), “yearlings” (1–2 years), and “adults” (>2 years) following the example of Guichón and Doncaster (2008). This Leslie matrix was applied to each population once every time step (year). The following assumptions were required to fit this type of model to the grey squirrel system; (1) all litters are produced in one period each year, (2) each population is censused before the annual birth pulse (pre-breeding census) and (3) no deaths occur between the census and the completion of reproduction in a time step. Standard deviation matrices composed of elements equaling 5 % of the corresponding element in the Leslie matrix were also created for each set of demographic inputs.

Fecundity values for each age class were derived from maternity and juvenile survival rates, number of pups litter⁻¹ and number of litters year⁻¹, following the equation below from Akçakaya and Root (2013) using published grey squirrel reproduction data reviewed in Goldstein et al. (2015).

$$F_{age\ class} = \left(\frac{litters}{year}\right) * (litter\ size) * (juvenile\ survival) \\ * (sex\ ratio) * (proportion\ breeding\ \text{♀})$$

The average grey squirrel litter contains between two and four pups therefore every litter was assumed to consist of three pups, which also produced good fit in other models of grey squirrel expansion (Lurz et al. 2001). Grey squirrels rarely produce a litter in their first year of life (<12 months old), though such events have been recorded in Britain, mainland Europe, and North America (Shorten 1954; Smith and Barkalow 1967; Gurnell et al. 2001). For the purposes of calculating age class fecundity, it was estimated that 5 % of females would produce one litter in the year of their birth. Yearling females were estimated to breed 75 % of the time and to produce one litter year⁻¹, and 100 % of adult females were assumed to produce two litters year⁻¹ (Hayssen et al. 1993). These high rates of yearling and adult litter production were chosen after initial examination of the performance of a range of fecundity values using the simple matching coefficient as described below and are justified by high breeding

rates observed at invasion frontiers (Goldstein et al. 2015). The fecundity values were calculated as 0.03, 0.45, and 1.2 for females <12 months, yearlings, and adults respectively and were varied by ± 25 % of the value to account for uncertainty in estimation (Table 1). The sensitivity of the best-fitting model to variation in three components of the fecundity values: (1) number of litters year⁻¹ for adult squirrels (1, 1.5, 2), (2) number of pups litter⁻¹ (1, 2, 3) and (3) percent of adult females reproducing (25, 50, 100 %) was investigated over a period of 25 years with 1000 replications in the southern study region. Male squirrels were permitted to breed with a maximum of six females in the model, corresponding to the average overlap of male and female home ranges (Steele and Koprowski 2001).

Reported survival rates for juvenile squirrels vary widely from 18 to 70 % during average or good years (Goldstein et al. 2015) and therefore a rate of 40 %, close to the mean, was chosen as the input value. Greater consensus surrounds yearling and adult survival rates, which are recorded as 50–70 % (Goldstein et al. 2015). For this model the yearling and adult survival rates were set to 70 % following poor performance of trial models with lower survival rates. Fast population increase and low intraspecific competition rates at the invasion frontier (Gurnell et al. 2001) justify the choice of an adult and yearling survival rate at the upper end of the naturally observed range. The survival rates were varied by ± 25 % of the value to account for uncertainty in these estimates (Table 1). Density dependence of all vital rates was included in the model as “ceiling” competition in which the population grows exponentially up to the ceiling (carrying capacity) and then remains at that level until it experiences decline by random fluctuations or emigration (Akçakaya and Root 2013).

Dispersal of individuals between habitat patches in the model occurred once annually at a rate dependent on the inter-patch distance and the age and sex of the disperser. The dispersal process was simulated using a negative exponential equation with a defined maximum value. Mean and maximum dispersal distances were estimated at 1 and 5 km for the model respectively following published observations (Hungerford and Wilder 1941; Koprowski 1996). The dispersal values were varied by ± 50 % (Table 1) to account for uncertainty in estimates and in the creation of the

habitat suitability map. The inclusion of a higher mean dispersal distance of 2 km and maximum dispersal distance of 9 km accounted for high habitat connectivity. As settled adults rarely shift home range, dispersal in grey squirrels is biased towards younger animals and males (Gurnell et al. 2001). Although exact ratios of dispersers are difficult to obtain experimentally, Koprowski (1996) reported that 94 % of juvenile male and 63 % of juvenile female grey squirrels left the natal patch. Estimates of juvenile dispersal rate for the model were based on these figures and were decreased for each sex by 50 % for the yearling age class and again for the adult age class (Table 1). A positive density dependent dispersal effect, which causes a greater proportion of individuals to disperse as source population density increases, was evaluated in this simulation (Table 1) as this improved the fit of the *Callosciurus erythraeus* SEPM (Guichón and Doncaster 2008).

Demographic and environmental stochasticity were incorporated into the model at each time step. Numbers of offspring were sampled from a Poisson distribution and numbers of dispersers from a binomial distribution to model demographic stochasticity and avoid the unrealistic occurrence of fractional numbers of individuals (Akçakaya and Root 2013). Environmental stochasticity was accounted for in the model by randomly sampling the demographic rates from a lognormal distribution using means from the Leslie matrix and standard deviations taken from the standard deviation matrix (Akçakaya and Root 2013).

Validating the model

Validation trials of the model were performed in the introduction area surrounding the release site (Fig. 1) over the 57-year period between the initial release and the first systematic distribution survey (NPWS 1968). To find a model that adequately represented the invasion dynamics of the grey squirrel, three of the estimated input parameters [finite rate of increase (λ), mean dispersal distance, and maximum dispersal distance (Table 1)] were systematically varied. A modified 3×3 Latin square was used to test three levels (low, medium, and high) of each input parameter with a balanced design. Mean dispersal distances of 0.5 and 2 km and maximum dispersal distances of 2.5 and 9.0 km were always paired with the same demographic and dispersal parameters, which resulted

in 15 initial parameter input sets. Each parameter set was evaluated with and without density dependent dispersal on an approximately 18,000 km² extent of spatial landscape of identified patches in the introduction region. Multiple other combinations of input parameters were examined to ensure that a model with better fit did not exist outside of the original Latin squares (total initial runs of model trial A = 24). The model run for each parameter combination was run for 1000 replications and 57 time steps ensuring that the initial population at the release site matched the historical release. The proportion of area matching between the observed historical range and the ranges predicted by the models was ranked using the simple matching coefficient (SMC) (Rushton et al. 1997, 1999; Guichón and Doncaster 2008). This metric is calculated as $(a + b)/c$, where a is the specific area of suitable habitat that was both observed and predicted to be occupied, b is the specific area of suitable habitat observed and predicted to be unoccupied, and c is the total area of suitable habitat identified within the introduction region. SMC proportions closer to 1 indicate higher spatial similarity between observed and predicted ranges. All matches were improved by prohibiting dispersal across the Shannon River, which flows to the immediate west of the release site and is anecdotally responsible for the absence of grey squirrels in the west of Ireland (Carey et al. 2007), and this modification to the dispersal matrix was incorporated into the Latin Square analysis. Due to programme functionality limitations related to number of patches in the landscape, it was not possible to prohibit dispersal across the Shannon when analyzing the sensitivity of the model to minimum carrying capacity. Since the input value of λ for the model with the best SMC was high ($\lambda = 1.3308$), a further set of models with higher demographic rates was tested in a similar Latin square arrangement (model trial B in Table 1, total runs = 18) to ensure that a better match with a higher λ was not overlooked. The lowest maximum dispersal distance of 2.5 km was not used in model trial B as it led to poor SMC proportions in model trial A.

Modeling the effects of control strategies on future range expansion

Future squirrel expansion and control regimes were modeled in the southern region of Ireland using the

demographic and dispersal parameters that defined the three models best matching the initial range expansion (Fig. 2). Each model was used to predict the invasion outcomes under uncontrolled population growth and each hypothetical control scenario over a period of 25 years with 1000 replications from 2012, when the

southern range frontier was determined (Goldstein et al. 2014). Patches within the 2012 range were set at carrying capacity with a stable age distribution derived from the Leslie matrix for the first time step of each control scenario. The total squirrel abundances and range extents resulting from two intensity levels of the

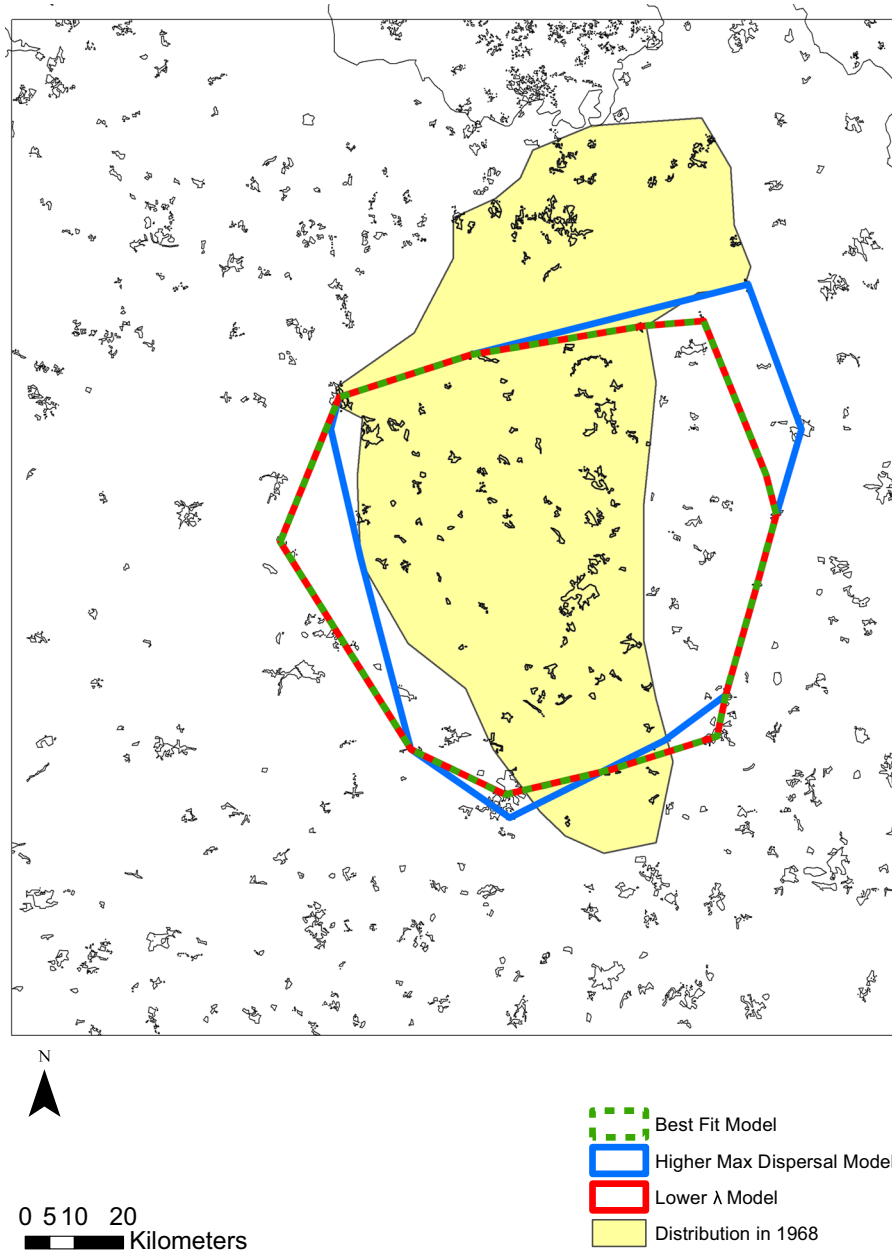


Fig. 2 Map showing habitat patches suitable for grey squirrels (*Sciurus carolinensis*) in the Irish midlands. The grey squirrel invaded area in 1968 is shaded yellow and the minimum convex polygons of three models for the extent of grey squirrel range in

the year 1968 which most closely matched the actual recorded distribution are shown. Parameter values for the “best fit”, “higher max dispersal” and “lower λ ” models are shown in Table 2

two distinct management actions, proportional culls and female immunocontraception, were compared for each model. Each management action was performed over two spatial extents: (1) all patches and (2) patches within a 20 km wide buffer zone of the 2012 invasion frontier to examine the suitability and relevance of frontier-based control programmes. Additionally, the effects of each management action were examined over a 200-year period to predict average year of arrival in Killarney National Park. The effects of the hypothetical culls (performed yearly for five consecutive years), carried out near the beginning of the simulation (2013–2018) at high and low intensity levels (70 and 30 % respectively of all adult and yearling squirrels removed during each year of the cull), were modeled at both spatial extents. Two hypothetical immunocontraceptive vaccination programme scenarios were modeled. In these two programmes high and low (70 and 30 % respectively) proportions of yearling and adult females were sterilized with a 100 % effective vaccine for 5 years from 2013. The effects of these fertility control regimes on grey squirrel invasion dynamics were modeled by adjusting the relative fecundities of yearling and adult females. Sterilization from this vaccine was assumed to be permanent but not to affect survival. The effects of the vaccine on relative fecundity were caused to taper off by 20 % each year for 5 years from the cessation of the vaccination programme, as the proportion of vaccinated females should naturally decrease over time.

Results

In the introduction region 465 patches of suitable habitat composing 506.64 km² (2.8 %) of the c. 18,000 km² with a carrying capacity >50 squirrels were identified (Figs. 1, 2). The area occupied by grey squirrels in 1968 ($t = 57$) included 103 of these patches and accounted for 114.07 km² (22.5 %) of suitable habitat in the region when dispersal across the River Shannon was prohibited through modification of the dispersal matrix. In the southern region, where control regimes and future expansion were modeled, 470 patches of suitable habitat occupied 595.6 km² (3.3 %) of the available land area (c. 18,000 km²). At the beginning of the control scenarios 126 patches were occupied at

carrying capacity by grey squirrels, which accounted for 155.9 km² of suitable habitat.

Model validation

The inclusion of positive density dependent dispersal in the models did not consistently improve the match between observed and predicted patch occupancy (Table 2). Good matching proportions ($SMC \geq 0.8$) occurred in models with population growth ($\lambda > 1$). Mean dispersal distances between 1 and 2 km and maximum dispersal distances of 7.5 and 9.0 km were also associated with good matches. Three models were chosen as the best representation of the natural system out of the 78 tested (Table 2), based on high matching proportions and a close match in area occupied. The chosen candidate models were termed “best fit”, “higher maximum dispersal distance (max DD)” and “lower λ ” based on their input parameters (Fig. 2). Two of the candidate models, “best fit” and “higher max DD”, slightly underestimated the area occupied though they produced two of the three highest SMC values. The third candidate model, “lower λ ”, was chosen for a comparable level of overestimation of area occupied. None of the models tested predicted the presence of squirrels in the northern part of the 1968 range (Fig. 2). At $t = 57$, the yearly increase in grey squirrel abundance (squirrels year⁻¹), as calculated by the derivative of the abundance curve evaluated at $t = 57$, was sensitive to variation in the minimum patch carrying capacity parameter ($K_{10} = 699$, $K_{25} = 812$, $K_{50} = 449$, $K_{75} = 198$, $K_{90} = 102$) in the initial expansion area when the dispersal matrix was unaltered. The “best fit”, “higher max DD” and “lower λ ” models had yearly increases of squirrel abundance of 314, 358, and 161 squirrels year⁻¹ at $t = 57$ respectively with the modified dispersal matrix. The models were more sensitive to variation in the number of pups litter⁻¹ and percent of adult females reproducing annually than in number of litters year⁻¹ for adult squirrels. Decreasing the number of litters year⁻¹, number of pups litter⁻¹ and percent of adult females reproducing resulted in a reduction in occupied patch area and metapopulation abundance (Table 3; Fig. 3).

Future range expansion and control strategies

The most valid models, when applied to the still progressing southern range frontier of the grey squirrel

Table 2 Model design and results for parameter input combinations leading to a simple matching coefficient (SMC) >0.8 between predicted and observed landscape area invaded by the grey squirrel 57 years after its initial introduction

	Model					Density dependent dispersal	
	λ	MeanDD	MaxDD	SMC	Area (km ²)	SMC	Area (km ²)
1	1.3308	1.0	7.5	0.864	111.45 (-2.62)	0.861	81.47 (-32.6)
2	1.1859	1.0	7.5	0.864	73.67 (-40.4)	0.854	60.14 (-53.93)
3	1.3308	1.0	9.0	0.862	112.85 (-1.22)	0.851	83.53 (-30.54)
4	1.0646	2.0	7.5	0.856	60.92 (-53.15)	0.849	56.89 (-57.18)
5	1.0646	1.5	9.0	0.854	59.58 (-54.49)	0.847	54.64 (-59.43)
6	1.0646	1.5	7.5	0.852	56.91 (-57.16)	0.833	48.88 (-65.19)
7	1.0646	2.0	9.0	0.849	64.45 (-49.62)	0.846	55.75 (-58.32)
8	1.1859	1.5	7.5	0.847	117.22 (3.15)	0.850	84.11 (-29.96)
9	1.1859	1.0	9.0	0.845	83.23 (-30.84)	0.831	72.49 (-41.58)
10	1.1859	2.0	7.5	0.835	127.17 (13.10)	0.830	97.44 (-16.63)
11	1.0646	1.0	9.0	0.828	47.10 (-66.97)	0.779	27.74 (-86.33)
12	1.0646	1.0	7.5	0.822	45.33 (-68.74)	0.780	28.24 (-85.83)
13	1.4672	1.0	7.5	0.819	134.2 (20.13)	0.838	123.85 (9.78)

The varied model inputs were the finite rate of increase (λ), mean dispersal distance (MeanDD), and maximum dispersal distance (MaxDD). The simple matching coefficient (SMC) ranks the absolute match between predicted and observed occupied patch area. The area predicted to be occupied by grey squirrels (with the difference from observed area in parentheses) 57 years after release. Models are shown without and then with the inclusion of the density dependent dispersal constant. The candidate models chosen for future range prediction are shown in bold and are Model 1: “best fit”; Model 3: “higher maximum dispersal distance (max DD)”; Model 8: “lower λ ”

Table 3 Predicted area of occupied suitable habitat, differences in grey squirrel (*Sciurus carolinensis*) abundance and time to reach Killarney National Park (KNP) when three demographic parameters, number of litters adult⁻¹ year⁻¹, number of young litter⁻¹, and % adults reproducing year⁻¹ were varied for the “best fit”, “higher maximum dispersal distance” (MaxDD), and “lower λ ” models

Variation to model	Area after 25 years			Abundance after 25 years			Year to reach KNP		
	Best fit	Max DD	Lower λ	Best fit	Max DD	Lower λ	Best fit	Max DD	Lower λ
None	334.7	336.4	331.3	27,962 ± 682	27,961 ± 681	19,947 ± 436	2072	2072	2093
1.5 litters adult ⁻¹ year ⁻¹	318.3	332.1	324.2	24,430 ± 427	24,479 ± 441	16,328 ± 281	2085	2085	2130
1 litter adult ⁻¹ year ⁻¹	305.6	327.3	318.4	20,301 ± 367	20,325 ± 352	11,316 ± 242	2104	2104	2263
2 young litter ⁻¹	306.2	342.6	318.8	22,333 ± 365	24,785 ± 464	13,486 ± 259	2094	2082	2179
1 young litter ⁻¹	296.6	321.1	261.6	14,953 ± 212	15,072 ± 195	2302 ± 139	2169	2168	Extinct in 2131
50 % adults reproduce	326.0	327.0	317.6	20,351 ± 345	20,325 ± 348	11,313 ± 240	2104	2104	2264
25 % adults reproduce	318.2	320.8	278.2	14,374 ± 199	14,266 ± 192	2586 ± 154	2179	2179	Extinct in 2156

Sensitivity analysis shows that the models were generally more sensitive to the number of young litter⁻¹ and % adults reproducing than number of litters adult⁻¹ year⁻¹

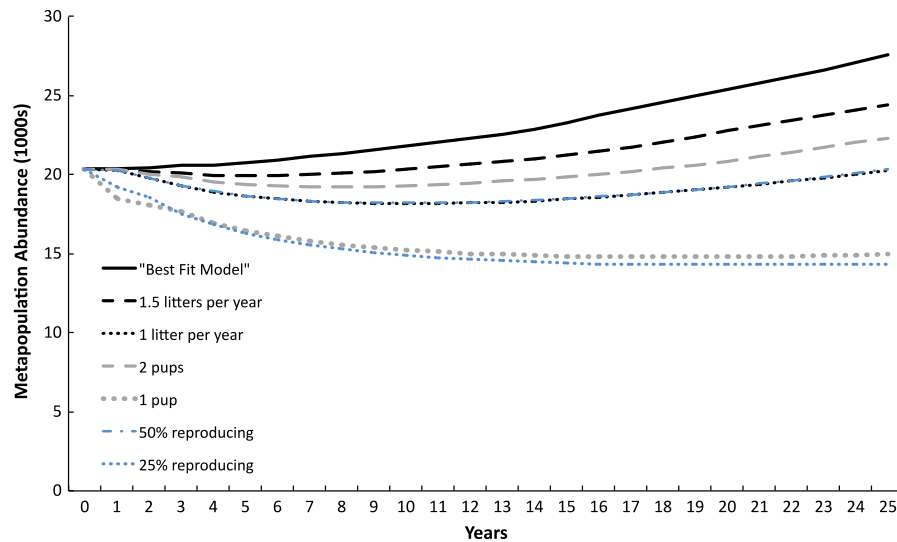


Fig. 3 Variation in mean metapopulation abundances for the “best fit” model under sensitivity analysis of three demographic parameters related to fecundity, number of litters adult⁻¹ year⁻¹, number of pups litter⁻¹, and % adults reproducing year⁻¹. Results for sensitivity analysis of “higher max DD” and “lower

λ ” are shown in Supplementary Material. The model of the expanding grey squirrel (*Sciurus carolinensis*) population in the southern region of Ireland was more sensitive to variation in number of pups litter⁻¹ and % of adults reproducing than to number of litters adult⁻¹ year⁻¹

in Ireland, predicted continuing range expansion towards the south and west (Fig. 4a–c) from the current 2012 range. After 25 years, uncontrolled populations were predicted to reach abundances of between 19,947 (± 436) and 27,962 (± 682) grey squirrels occupying 175.4–180.5 km² of suitable habitat patches beyond the 2012 invaded area (Table 4). The minimum convex polygon encompassing the grey squirrel range in the study area was predicted to extend 3773–4389 km² beyond the 2012 invaded range (Fig. 4a–c). Under these scenarios grey squirrels will reach Killarney National Park between 2072 and 2093.

High- and low-effort control strategies were modeled both in a focused buffer area and in all patches to gain insight into maximising benefit and minimising cost of population management strategies. A marked decrease in squirrel population abundance was predicted when 70 % of all yearling and adult squirrels were culled either in the buffer area or in all patches for 5 years, with effects lasting over 20 years from the cessation of the cull programme (mean of three models Fig. 5a, see Supplemental Material for individual model results). High intensity culls (70 % of all adults and yearlings culled) at both regional scales were predicted to cause larger decreases in overall

abundance and range expansion than lower intensity culls (Fig. 4d–f). Culling at high intensity in all populations delayed the invasion of Killarney National Park by 15–25 years while high intensity culls in buffer areas caused delays of only 8–13 years. The predicted decreases in abundance after a five-year immunocontraception programme for yearling and adult female squirrels did not last as long as those resulting from culls (mean of three models Fig. 5b, see Supplemental Material for individual model results). The decrease in predicted range expansion from “no control” scenarios was less pronounced for vaccination strategies than for culling strategies (Fig. 4g–i). A greater difference between the two strategies was observed in the overall abundance of the population with high intensity region-wide vaccination scenarios predicted to lower overall abundance after 25 years by 8–11 % percent compared to 26–43 % for high intensity culls at the same regional scale. Immunocontraception control delayed the invasion of Killarney National Park between 5 and 16 years. Both culling and immunocontraceptive strategies had the strongest effects on the “lower λ ” model and similar lesser effects on the “best fit” and “higher max DD” models.

Discussion

The invasive grey squirrel, which has spread across much of the island of Ireland, continues to expand its range to the south, endangering internationally rare woodland ecosystems, hardwood plantations, and the native red squirrel. Continued expansion along the southern invasion frontier is predicted in the absence of intensive and prolonged control measures. In essence, these predictions generated by the SEPMS formulated here set the stage for proactive rather than reactive grey squirrel management. Long-term conservation or landscape management of areas within the predicted area of invasion must assess whether grey squirrel presence is incompatible with goals and formulate management strategies and budgets accordingly.

Model assumptions and demographic compensation

It is important to consider potential inaccuracies introduced by parameter estimation or simplification when formulating conclusions and recommendations based on model outputs. An honest accounting of the assumptions made during the design process can guide empirical work to ameliorate the resulting simplifying effects. Prediction error for the current grey squirrel model was addressed by estimating demographic and dispersal parameters from empirical data from intensively studied populations in both the native and introduced ranges of this species. Systematic variation of these parameters ensured that the combinations of parameters that led to distributions that best matched the earliest recorded range were retained and used for predictions of future population expansion. The effects of variation in three reproductive parameters that are components of λ were clarified using sensitivity analysis. The strong similarity in predicted range invasion between the “best fit” and “higher max DD” models (Fig. 4) is an indication that variation in maximum dispersal distance is less important than variation in λ . This greater importance of demographic variables (mortality and litter size, both components of λ in this study) over dispersal distances has also been noted in other applications of SEPMS to squirrel populations. Varying dispersal distance was shown to have less effect on the advance of the grey squirrel

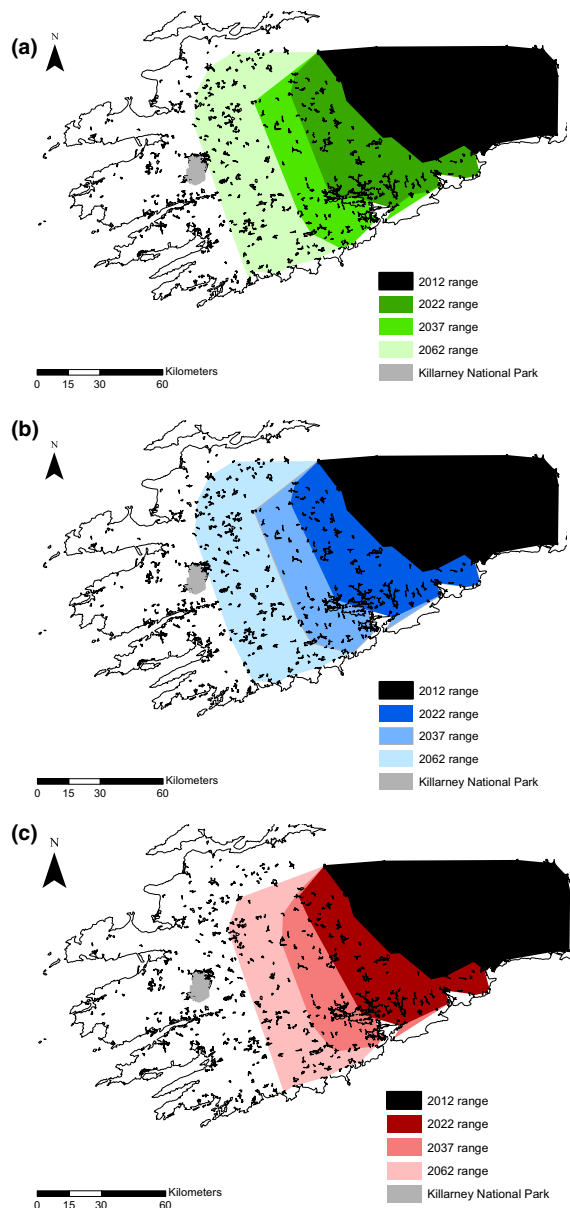


Fig. 4 Minimum convex polygons of 2012 grey squirrel (*Sciurus carolinensis*) range and predicted occupancy if no control measures are carried out 10, 25, and 50 years later in the southern region of Ireland (see Fig. 1 for study region extent) using **a** the “best fit” model **b** the “higher maximum dispersal distance” model and **c** the “lower λ ” model. The minimum convex polygons of predicted range expansion under four culling scenarios after 25 years are shown for **d** the “best fit” model **e** the “higher maximum dispersal distance” model and **f** the “lower λ ” model. Similarly, the predicted range expansion under immunocontraception vaccination scenarios after 25 years are shown for **g** the “best fit” model **h** the “higher maximum dispersal distance” model and **i** the “lower λ ” model

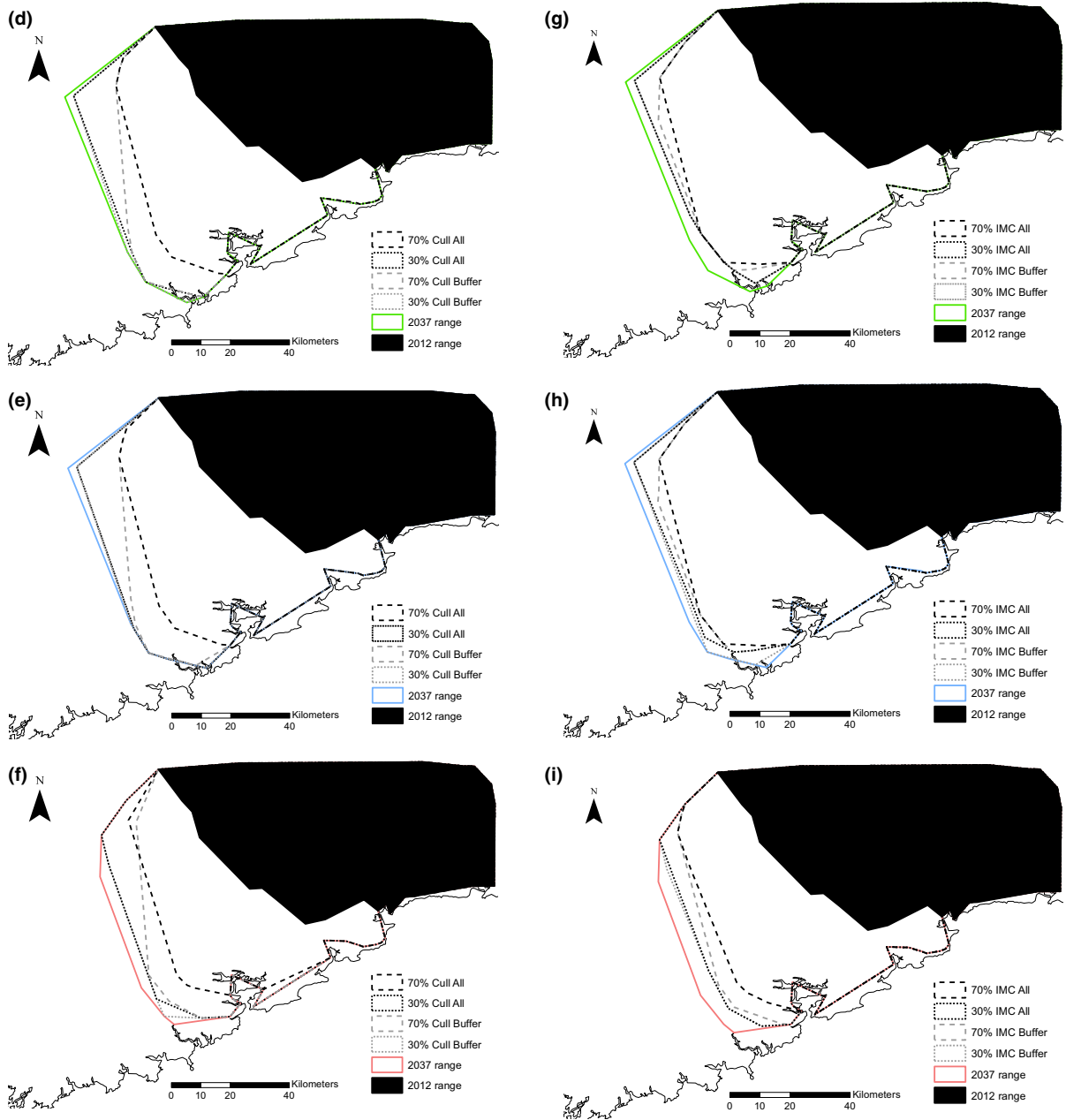


Fig. 4 continued

invasion in northern England (Rushton et al. 1997) and on the match between observed and predicted occupancy of red squirrels on the Isle of Wight (Rushton et al. 1999) and *C. erythraeus* in Argentina (Guichón and Doncaster 2008) than varying mortality or survival rates and litter sizes or fecundity.

The representation of habitat in a SEPM is equally important to the quality of model outputs as are the

demographic and dispersal parameters of the focal species. Using land cover data from 2006 with a minimum mapping unit of 25 ha to model the initial grey squirrel invasion may have decreased the capacity of the metapopulation model to match the true demographic and dispersal dynamics of the time. A lack of connectivity between the introduction site and patches in the northern portion of the 1968 distribution

Table 4 Predicted area of occupied suitable habitat, differences in grey squirrel (*Sciurus carolinensis*) abundance and time to reach Killarney National Park (KNP) for each candidate model “best fit”, “higher maximum dispersal

distance (max DD)”, and “lower λ ” due to management strategies and spatial extents of management application 25 years after the latest distribution survey in 2012

Strategy	Control effort	Spatial extent	Area after 25 years			Abundance after 25 years			Year to reach KNP		
			Best fit	Max DD	Lower λ	Best fit	Max DD	Lower λ	Best fit	Max DD	Lower λ
No control			334.7	336.4	331.3	27,962 ± 682	27,961 ± 681	19,947 ± 436	2072	2072	2093
Cull	High	All	321.2	320.4	306.3	20710 ± 545	20696 ± 540	11247 ± 620	2087	2087	2118
	High	Buffer	322.2	321.9	305.4	23,795 ± 675	23,741 ± 646	16,319 ± 313	2080	2080	2106
	Low	All	345.6	346.7	333	26,317 ± 577	26,316 ± 593	18,528 ± 402	2073	2073	2097
	Low	Buffer	336.2	334.7	314.4	27,034 ± 664	27,046 ± 645	18,868 ± 410	2074	2074	2097
IMC	High	All	332	335.8	321.7	25,700 ± 449	25,673 ± 432	17,813 ± 359	2079	2079	2109
	High	Buffer	339	336	324	26,394 ± 475	26,365 ± 509	18,313 ± 353	2079	2079	2108
	Low	All	346.6	344.1	326.7	26,895 ± 550	26,888 ± 542	19,151 ± 393	2077	2077	2103
	Low	Buffer	345.7	345.7	328	27,190 ± 550	27,224 ± 574	19,307 ± 391	2077	2077	2103

The management strategies are: culls, and immunocontraceptive vaccination (IMC)

prevented this model from predicting expansion of squirrels into that area (Fig. 2), which suggests that small patches, not considered in the final model to avoid undue complexity, are important to invasion dynamics and species movement. This result is in agreement with findings on grey squirrel distribution in Italy where small habitat patches, often <5 ha, have been shown to be important in grey squirrel metapopulation dynamics (Wauters et al. 1997; Martinoli et al. 2010; Bertolino et al. 2014). Sensitivity analysis of minimum patch carrying capacity showed that grey squirrel populations increased most quickly when $K_{\min} = 25$ despite more potential patches being identified at $K_{\min} = 10$. This result suggests an interaction between patch size, patch density and dispersal distance that is important to invasion dynamics and supports ideas that populations may disperse through less preferred habitats more rapidly (Gonzales and Gergel 2007).

The finite rates of increase of the three models that best fit the initial expansion were composed of survival and fecundity values much higher than those observed in frontier grey squirrel populations in Ireland (Goldstein et al. 2015). These disparities indicate that assumptions made during model design are compensated for by the higher demographic rates retained in the final models. The simplification of habitat types, consideration of only major grey

squirrel populations ($K \geq 50$) as demonstrated in a sensitivity analysis, as well as the 100 m² raster cell size, likely led to higher demographic rates being retained to recapitulate observed spread over a more conservative simulated landscape. The models were designed to most closely match historical occupancy data in the initial expansion area rather than historical abundance data, which does not exist. Furthermore, as in other applications of the SEPM modeling framework to squirrels (Rushton et al. 1997, 1999; Guichón and Doncaster 2008), some of the assumptions related to the yearly time step are difficult to reconcile with grey squirrel ecology, namely the assumption of no mortality between the pre-breeding census and completion of reproduction, a period that may last longer than 5 months. It is important to recognise that demographic compensation can occur in population modeling and is a result of simplifying assumptions or estimation during model design. However, we stress that when a good match between model predictions and records of species occupancy is observed then the demographic and habitat assumptions and compensations are in balance (Guichón and Doncaster 2008; Wilson et al. 2010) and future predictions based on such a model for the specific system can be assumed to be validated and useful for management recommendations.

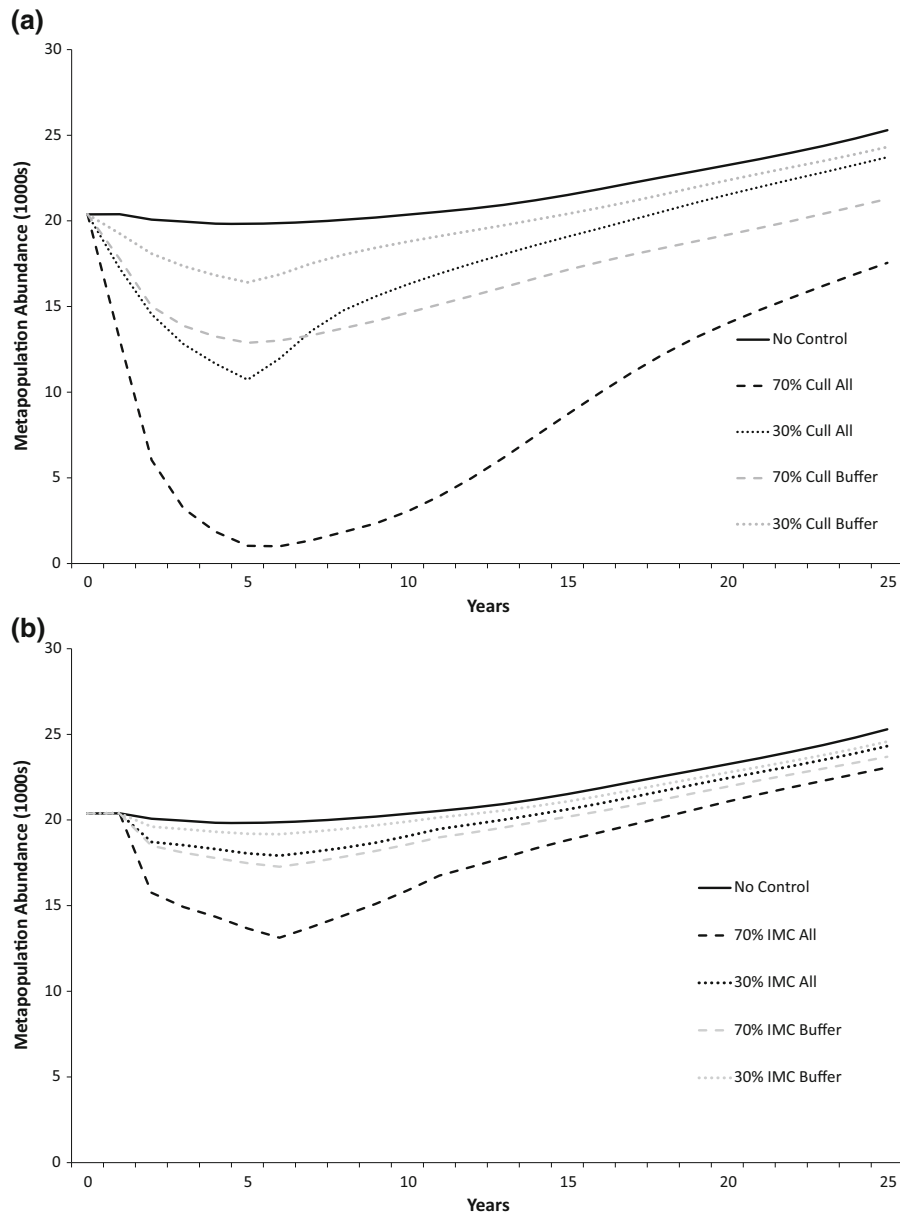


Fig. 5 Mean of the metapopulation abundances for the three candidate models for simulated **a** cull control scenarios and **b** immunosuppression (IMC) control scenarios of the expanding grey squirrel (*Sciurus carolinensis*) population in the southern region of Ireland. The *solid line* indicates abundance when no control measures were applied to the metapopulation.

The application of control strategies was modeled in the metapopulation for 5 years. After this period control was halted and the metapopulation was allowed to recover for 20 years. See Supplemental Material for metapopulation abundances under cull and IMC control scenarios for each of the candidate models individually

Minimum convex polygons, the standard method for estimating ranges, are prone to overestimate range and to be insensitive to occupancy changes inside vertices (Burgman and Fox 2003). The polygons used

here (Fig. 4), though modified to respect coastlines, likely mask effects of habitat and connectivity on the invasion frontier. Events not considered in the simulations, such as human-mediated long-distance

movement events (Guichón et al. 2015), variation in resource availability (Lurz et al. 2001; Bertolino et al. 2008) or predator population dynamics (Sheehy and Lawton 2014) could significantly alter future grey squirrel invasion dynamics. The likelihood of occurrence of such events, along with other factors that contribute to change in population dynamics and distribution such as climate and land-use change, becomes higher as simulation time is extended in the model. Therefore long model runs, such as those in this study where time to invasion of Killarney National Park was considered, should be interpreted cautiously and seen as a guide rather than a certain forecast. Models should be frequently updated and grounded to real-time data. Remaining mindful of such sources of error, short- and long-term predictions of future grey squirrel range expansion are valuable to diverse interest groups including red squirrel conservation managers and silviculturalists whose projects and interests have varying timescales.

Control strategies

Successful eradication and long-term control of invasive species has rarely been achieved in Europe, where high costs and ethical resistance to fatal measures (Bertolino and Genovesi 2003; Bremner and Park 2007) have hampered efforts (but see Gosling and Baker (1989); Tonkin and Mackenzie (2011); and Adriaens et al. (2015)). Predictive models can guide managers toward effective strategies by allowing for the avoidance of expensive and potentially unproductive experiments in control methodology and for the speedy implementation of effective regimes. SEPMS have repeatedly identified large-scale culls as the most effective method of invasive squirrel control (Rushton et al. 2002; Bertolino et al. 2008; Guichón and Doncaster 2008) and intensive culls were again found to be the most effective abundance reduction method here. Results of the model indicate that 5-year intensive region-wide culls would be successful in sharply reducing squirrel numbers in the short and medium term. However, a faster rate of abundance and range extent increase was predicted to follow the cessation of low intensity culls, suggesting that unfavourable density-dependent consequences occur at low levels of fatal control. These results further support assertions that successful control measures should be nationally or internationally managed

(Mack et al. 2000; Bertolino and Genovesi 2003; Bertolino et al. 2014) and that sporadic, uncoordinated, or low-intensity culling may cause faster increases in population abundance or range. Co-funded programmes within the European Union (EU), under the environmentally focused LIFE funding instrument, are an opportunity to combine EU and national funding sources to improve control programme outcomes. To-date there have been 86 invasive species management LIFE co-funded programmes in Europe (EU 2015) including two that focus on controlling grey squirrels in Italy: “EC-SQUARE” (2010–2015) and “U-SAVEREDS” (2014–2018).

Though an immunocontraceptive vaccination programme succeeded in preventing reproduction in a fox squirrel (*S. niger*) population (Krause et al. 2014), the capacity of a large-scale vaccination programme to control invading squirrel populations is unknown and a vaccine is currently not commercially available for grey squirrels though testing is ongoing (Pai et al. 2011; Yoder et al. 2011; Mayle et al. 2013). Rushton et al. (2002) showed that a hypothetical immunocontraceptive vaccine was ineffective at controlling a grey squirrel invasion, unless applied at large scale. Here, results indicate that a 5-year intensive and region-wide vaccination programme would cause a short-term reduction in population abundance but that medium and long-term effects would be negligible. The nature of this control method, which requires more extensive training for control staff and material expense than culling programmes, makes it likely that programmes at a larger-than-local scale would be economically unfeasible. Compensatory mechanisms acting to boost survival of juveniles (Jacob et al. 2004) or fecundity of untreated females could also act to diminish achievable population size reductions if less than 100 % cover is achieved. However, utilisation of immunocontraceptive vaccination strategies could improve management outcomes if used to complement traditional culls in areas where fatal control is inappropriate or unwanted (e.g. suburban areas) (Lauber and Knuth 2004). The 5-year culls and vaccination programmes resulted in predictions of up to one to two decade delays in arrival year to Killarney National Park compared to uncontrolled scenarios. Long-lasting decreases in squirrel abundance or delay in range expansion require that control programmes do not cease after short- or medium-term goals are realised,

as management gains can be lost after the restoration of natural survival and fecundity rates.

Invasion frontier-based control programmes offer a less expensive alternative to region-wide strategies. However, when the application of hypothetical control strategies was confined to the buffer areas, the effects were not consistently comparable to region-wide action. Frontier-based culling efforts were much less effective than region-wide programmes in slowing expansion. This contrasts with results found in Argentina, where the difference in squirrel expansion after priority and region-wide culls was much smaller (Guichón and Doncaster 2008). Immunocontraception vaccination programmes carried out in the buffer populations, or at a lower intensity, were not effective at decreasing abundance and bring further support to large coordinated control campaigns over local or low-intensity efforts. When examined locally from a cost-effectiveness standpoint, the cost savings associated with a limited control region may outweigh decreased management effectiveness depending on the local situation and goals. A formal cost-benefit analysis and a public education campaign regarding control methodologies should be carried out to objectively evaluate control regimes.

The grey squirrel has featured prominently in species modeling literature in recent decades with many proof-of-concept studies (Rushton et al. 1997; Di Febbraro et al. 2013) choosing to focus on this species undoubtedly due to the thorough understanding of its habitat requirements and population dynamics, and the well-publicised impact on the red squirrel through competition and disease. Such models have ranged in scale from local models, which can identify likely dispersal or invasion corridors through least-cost pathways (Gonzales and Gergel 2007; Stevenson-Holt et al. 2014), to continental and global scale models of potential invasion areas identified through ecological niche and species distribution modeling (Di Febbraro et al. 2013). The SEPM approach applied here, based in linking individual-based population dynamics models with spatial data, is best suited to regional applications. A number of regional investigations using bespoke SEPMs grew out of the original work by Rushton et al. (1997) in northern England. These models have considered grey squirrel expansion under varying resource conditions (Lurz et al. 2001; Bertolino et al. 2008) and culling regimes (Tattoni et al. 2006) in Italy and examined the costs and

impacts of culls and immunocontraception on grey squirrels (Rushton et al. 2002) and the influence of squirrelpox virus on red and grey squirrel dynamics in the UK (Rushton et al. 2000). The major difference between these bespoke models and our models is the use of a validated and transparent model creation software package. This tool ensures that our models, via the systematic and step-by-step process outlined here, are repeatable, accessible, and customisable by researchers and landscape managers in any region. The input values for carrying capacity and dispersal distance were generally lower, and the values for fecundity generally higher, in our models than those used in the bespoke SEPMs. In this study the initial range of input values was based on a combination of locally collected and published demographic data, and final inputs were chosen systematically and without bias through range matching. The spatial landscapes used in the bespoke models were often more complicated (Lurz et al. 2001; Tattoni et al. 2006; Bertolino et al. 2008) than the simplified landscape we considered but as a consequence relied heavily on estimated carrying capacities in many habitat types rather than published measurements. Despite these differences, our practical conclusions on grey squirrel control largely agree with those derived from the bespoke SEPM studies, namely that region-wide intensive control is more effective than spatially limited or less intense strategies (Tattoni et al. 2006), and that culling is a more effective control method than immunocontraception (Rushton et al. 2002). This agreement supports the utility and relevance of customisable software packages in spatial species modeling projects aimed at practical conservation and species management programme design.

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Compliance with ethical standards

Conflict of interest The authors declare they have no conflicts of interest.

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