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Ecological traps for large-scale invasive control: Predicting settling rules by recolonising American mink post-culling.

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Summary

1. Management programs worldwide seeking to reduce the density of invasive species must overcome compensatory processes, such as recolonisation by dispersers from non- or partially-controlled areas. However, the scale and drivers of dispersal in such context are poorly known.

2. We investigated the dispersal patterns of American mink reinvading 20,000 km^2 of their non-native range following a culling programme led by citizen conservationists. Using

multinomial models, we estimated the contributions of density dependence, proxies for patch quality and distance from the natal patch on mink settlement.

3. Seventy seven percent of mink dispersed and settled in non-natal patches. Dispersal distances were large with settlement probabilities only reduced by half at ~60 km, and 20% of mink dispersing > 80 km.

4. Females were more attracted to patches of high quality mostly found at low altitudes. Males favoured patches with intermediate current densities and consistently high quality.

Synthesis and applications. Predicting post-culling recolonisation by a non-native mobile carnivore over large spatial scale could was using information on relative densities obtained during management interventions largely implemented by citizen conservationists. This was made possible by a monitoring component designed to feed into the adaptive management process implemented in this project. High mink mobility dictates management should take place on very large spatial scales to minimise reinvasion from un-controlled areas. Both males and females were attracted to patches that were previously consistently occupied, providing a degree of predictability to patterns of recolonisation. Targeting control to patches attractive to immigrant mink requires knowledge of current mink density. Creating so-called ecological traps in the face of ongoing immigration from peripheral areas provides a promising tool to effectively control mobile invasive species.

Keywords: invasive species, dispersal, settlement, compensation, immigration, adaptive management, ecological traps

Introduction

Understanding the ecological processes governing invasive species population dynamics and mitigating their threat to native ecosystems is a focus of much research (e.g. Simberloff *et al.* 2013, Hastings *et al.* 2005). Efforts to reverse the spread of invasive mammals have become more rigorously designed and implemented, achieving eradications of e.g. rats, mice, cats and rabbits on islands of increasingly large size (Bester *et al.* 2002; Barun *et al.* 2011; Kessler

2011). Where eradication is not feasible, the management objective is suppressing numbers to near-zero density or to densities sufficiently low to allow the recovery of affected native species (Norbury *et al.* 2015); as with red foxes and feral cats in Australia, Moseby & Hill 2011; stoats in New Zealand, Veale, Clout & Gleeson 2011). However, management interventions focused on control must contend with compensatory recolonisation through dispersal from adjoining uncontrolled areas.

Reducing densities of invasive species by culling typically produces density dependent compensatory responses in surviving individuals, such as increased fecundity and survival (Boyce, Sinclair & White 1999; Pöysä 2004; Melero, Robinson & Lambin 2015). Reduced competition for resources may also stimulate dispersal from adjoining high-density areas towards culled low-density areas. If individuals are able to detect variations in resource availability, both residents that have escaped culling as well as immigrants may settle in productive low-density areas and partially or completely negate culling efforts through reinvasion (e.g. Matthysen 2005; Lieury *et al.* 2015). While such dispersal patterns would tend to accelerate the recovery of the culled population, they can be harnessed so as to create ecological traps in attractive but vacant areas where targeted ongoing culling would effectively prevent population recovery through immigration (Delibes, Ferreras & Gaona 2001; Robinson *et al.* 2008; Lieury *et al.* 2015; e.g. Gervasi *et al.* 2015; Oliver *et al.* 2016). Accordingly, understanding the drivers of dispersal, including settlement rules used by dispersers at low density, may be central for optimising the management of invasive species by spatially targeting control efforts (Glen, Pech & Byrom 2013).

Most studies of individual dispersal decisions have hitherto focused on emigration (Clobert *et al.* 2012; Altwegg *et al.* 2012; Furrer & Pasinelli 2015; but see Turgeon & Kramer 2012; Glen, Pech & Byrom 2013). The factors that determine settlement decisions are comparatively poorly known, even for the best-studied model organisms. Theoretical investigations predict that a disperser’s settling decision should depend on its ability to access information on the quality of potential patches (Ruxton & Rohani 1999; Vuilleumier & Perrin 2006). This in turn may be influenced by the perceptual range and mobility of dispersers and by the properties of the landscapes through which they move (Miller *et al.* 2011; Hovestadt, Mitesser & Poethke 2014). Most problematic predatory mammalian invasive non-native species are highly mobile (e.g. red fox, cats, stoats, mink and mongoose; Genovesi *et al.* 2012) and hence can acquire information about settlement opportunities over large areas. A fundamental question is therefore: how do individuals make decisions in relation to their settlement choices (Sutherland *et al.* 2013; Gilroy & Lockwood 2016).

Habitat quality and conspecific density are known to influence the attractiveness of potential settlement areas to dispersers (e.g. Turgeon & Kramer 2012; Glen, Pech & Byrom 2013). Therefore, the balance between quality and the positive and negative influences of density (due to e.g. conspecific attraction and competition for resources, respectively) might also shape individual decisions. Generally, relatively more individuals are expected to settle in poor quality sites at high-density than in low density populations (e.g. Gunnarsson *et al.* 2005). Indeed, in harvested cougar populations (*Puma concolor*), dispersers settled preferentially in high quality habitats where conspecific density was reduced by harvest (Robinson *et al.* 2008; Wolfe *et al.* 2013) and their settlement probability declined with distance from the location of birth (Morrison, Boyce & Nielsen 2015). Performing studies at sufficiently large scale relative to the large dispersal ability of predatory mammals is particularly challenging (Glen, Pech & Byrom 2013), such that, little is known about the dispersal and settling rules they (Glen, Pech & Byrom 2013; Oliver *et al.* 2016).

In order to provide the necessary understanding to optimally counter recolonisation through immigration, we sought to describe how dispersal distance, density dependence and patch quality affect settlement probability of the invasive American mink (*Neovison vison*). Mink is a globally widespread invasive species and the focus of much long-term control efforts (Bonesi & Palazón 2007; Genovesi *et al.* 2012). They are solitary, territorial carnivores inhabiting linear territories along watercourses. Mating occurs in February-March in Scotland, when rutting males, but not females, abandon their territories, travelling tens of kilometres in search of mating opportunities (Melero & Palazón 2011; Melero, Robinson & Lambin 2015). Dispersal is thought to occur once, when juveniles of approximately 5 months old leave the maternal territory seeking a vacant territory in which they typically settle by the end of the year (Gerell 1970; Dunstone 1993).

We used multinomial models to analyse how recolonising mink selected settlement locations amongst available patches where their conspecifics had been removed by a large-scale citizen conservationist-based, project seeking to suppress mink populations in their invasive range in NE Scotland (Bryce *et al.* 2011). We predicted a negative influence of distance from the natal patch on settling probability (Oliver *et al.* 2016) and that dispersers would preferentially settle in patches of relatively high quality that host a moderate number of conspecifics, reflecting the dual influences of mate attraction and competition for resources.

Methods

STUDY AREA

The mink control program started in 2006 in the Cairngorms National Park (57º 0'N, 3º 30'W, Fig. 1a) NE Scotland and gradually expanded spatially in a non-systematic manner, reaching ~20,000km^2 by 2012 (Bryce *et al.* 2011). This area covers an heterogeneous landscape mixing highlands up to 1300 m altitude dominated by acidic grasslands and bogs with mean coverage 36.7% and 25.4% at 25 m-scale) and a coastal lowland plain partially dominated by rough and improved grass (mean 8% and 30%, ranges 0-100%) respectively (see Bryce *et al.* 2011) (Fig 1). The project area spanned 16 river catchments totalling 2,500 km of waterway, subdivided into 21 sections (patches hereafter) reflecting project management units where mink control and monitoring were instigated at the same time (see Bryce *et al.* 2011; Melero, Robinson & Lambin 2015). Patches had a mean waterway length of 153 km (SD 26; Fig. 1a). The asynchrony in the inception of comprehensive control in each river catchment led to a patchwork with different mink densities, each surrounded by variable numbers of other patches not yet subjected to control and variably fuelling recolonisation of adjacent patches. No mink were recorded or captured in one unit, so it was excluded from analyses.

DATA COLLECTION

Project activities were mostly undertaken by volunteers who detected, trapped and removed mink, and were coordinated by three to four project officers. Mink were detected using mink rafts (Reynolds, Short & Leigh 2004) deployed at regular intervals along waterways. A trap was placed on the raft following detection, and left in place for a few days or until a mink was caught and humanely dispatched. Sustained culling led to density reductions of 50% after the first year of fully-comprehensive control, achieving overall density reductions of 80% after 6 years (Melero, Robinson & Lambin 2015). The carcasses of 86% of 979 culled mink were collected from ca. 400 volunteers for later dissection of which 387 were females, 452 were males and 140 were of unknown sex (Fig. 1b). The carcasses of the remaining 14% mink were not retained. Mink sex was determined and a canine tooth and muscle tissue samples were removed for age determination and molecular analyses, respectively. Mink age was estimated through X-ray of canines (Helldin, 1997) and using tooth cementum analyses for non-juveniles performed by Matson's Laboratory LLC (Manhattan, USA).

CANDIDATE PREDICTORS OF SETTLEMENT DECISIONS

Dispersing mink are faced with a choice between multiple patches they could settle in. We modelled the probability that an individual chooses a specific patch amongst all possible candidates in relation to patch specific and individual-level covariates.

CHOICE-SPECIFIC VARIABLES

We were interested in understanding how the following environmental and population covariates at the patch-level affected patch choice: patch quality (constant), natal dispersal (individual specific) and conspecific density (time-varying).

Environmental covariates

Estimating spatio-temporal variation in prey resources for generalist predators over 20,000 km^2 was unachievable, so we used the data available in the control project to derive proxies of patch quality. First, we assumed that the most attractive patches would be those with consistently high occupancy. Thus we used as proxy of patch quality, *Q*, the maximum proportional length of a patch occupied by settled adult mink for the 6 year duration of the study (cumulative total km occupied/total patch length in km) following the procedure detailed in Melero, Robinson & Lambin (2015).

Calculations of *Q* did not exclude those mink focal to our inferences, which we acknowledge may impose a degree of non-independence between the explanatory and dependent variables. However, only 20% of the mink captures used to define *Q* were focal mink, such as their contribution in *Q* was per patch was low. To overcome potential caveats associated with using *Q*, we also used a set of habitat variables previously found to predict mink occurrence in Scotland (Fraser *et al*. 2015) at 1 km buffer (reflecting mink home ranges; Melero *et al.* 2008). These were mean altitude and proportion of improved grass, acid grass, rough grass, and bog, mapped at 25 m resolution, derived from Land Cover Map (LCM) 2007 data for the UK (Morton et al., 2011) using ArcGis 10.1 (ESRI, 2014) at 1 km^2 pixel. Because *Q* and candidate habitat descriptors were likely to be correlated, we fitted two distinct models to ensure interpretability. Model-1 included *Q* and all population and individual covariates described below but not the habitat covariates, whilst Model-2 included all covariates except *Q* (see below).

Approximate natal dispersal distances were taken as the distance between natal and culling patches. This distance was measured as the Euclidean distance between the arithmetic means of the capture locations of all mink culled in each patch (i.e. from the centroid of the natal to that of settlement patch) as mink appear unconstrained by waterways in their dispersal (Oliver *et al.* 2016). This reduced the error due to mink mobility within the patch (i.e., capture location does not necessarily relate to the location of activity), but reduced the resolution reported using exact locations (e.g. Oliver *et al.* 2016 Natal patch was inferred using a combination of information on pedigrees (Appendix S1, Supporting Information), and dates and locations of capture and birth following Telfer *et al.* (2003). The natal patch was deemed to be that of the capture location of an individual's mother. When the mother was unknown, it was taken as the capture location of an individual's full- or maternal half-siblings if siblings were captured prior to the seasonal initiation of natal dispersal (October). Fathers and paternal half-siblings were not used because males roam widely during the rut and their locations of capture poorly reflect the natal patch of their offspring (Dunstone, 1993). The settlement patch was taken to be the capture location of those individuals deemed to be holding a territory at the time of capture (i.e. settled mink). Thus, we excluded those mink likely to be transient (i.e. mink < seven months old, assuming all were born in June) and rut males (i.e. male mink caught during the mating season, February-March).

Population density covariates

Due to the large scale of our study, it was unfeasible to estimate time-varying mink density. Instead, we used relative density values taken as the ratio of the number of captured territorial individuals in a calendar year relative to the maximum number of mink potentially settling in that patch (using Q as denominator). We did so in the knowledge that not all mink present in a given year and location were trapped but under the assumption that the number of mink caught was proportional to the number of mink present, and therefore that the estimate would capture biologically relevant variation in density. Relative density was calculated pooling males, females and mink of unknown sex as the later account for 14 % of 979 mink caught. Both relative density (RD) and its quadratic term (RD^2) were included as candidate explanatory covariates in the analyses to allow for positive and negative influences of density.

INDIVIDUAL-SPECIFIC COVARIATES

The influence of patch-specific covariates on settlement decisions is likely to differ between classes of individuals. Accordingly, we included sex as an individual-level covariate within all patch-specific covariates in our analyses. Dispersal distances inferred from pedigree assignments are not error-free in partially sampled populations (Leonarduzzi *et al.* 2012; Melero, Oliver & Lambin 2017). Hence, when considering dispersal distance, we first included the inferred relationship type (mother-offspring, full- or (maternal) half-siblings) used to infer natal patch as an individual-level covariate. We expected that the most error-laden assignments would see the greatest shrinkage of the effect of distance, with errors increasing from mother-offspring, to full- and half-sibling (Melero, Oliver & Lambin 2017). Relationships with the highest reliability (mother-offspring; Melero, Oliver & Lambin 2017) were then used to test the sex-distance interaction.

Finally, following Vardakis *et al.* (2015), we included a ‘home advantage’ variable in the models. This allows the probability of staying in the natal patch to be independent of the distance-to-travel effect.

All continuous variables were standardised by subtracting the mean and dividing by the standard deviation to assess the relative contribution of each variable to settlement probability.

MODELLING DISPERSAL DECISIONS

Dispersal movement data have recently been analysed using multinomial discrete choice models (multinomial regression models), where the probability of settling in a particular patch is a function of patch- and individual-level covariates (Vardakis *et al.* 2015). We used multinomial probit models to describe individuals’ choice from a finite set of mutually exclusive alternatives.

The models assume that an individual *i* selects its preferred settlement patch from the entire set of available patches $p = 1, \dots, P$. Relative preference by individual *i* is modelled through a $(P - 1) \times 1$ latent variable vector Λ_i. The chosen patch is assumed to be the one with the highest value of the latent variable:

$$Y_i(\Lambda_i) = \begin{cases} 0\ if\ \max(\Lambda_i) < 0 \\ p\ if\ \max(\Lambda_i) = \Lambda_{ip} > 0 \end{cases}, \text{for } i = 1, \dots, N \text{ and } p = 1, \dots, P\text{-}1$$

Where Y_i is the index of the chosen patch and $Y_i = 0$ is an arbitrarily chosen reference patch. The latent variable vectors Λ_i are defined as a function of k covariates:

$$\Lambda_i = X_i \beta + \varepsilon_i$$

X_i is a $(P - 1) \times k$ matrix of choice-specific and individual-specific covariates (listed in the previous section), and β is a $k \times 1$ vector of regression coefficients. ε_i is $(P - 1) \times 1$ multivariate normal vector of errors $\varepsilon_i \sim N(0, \Sigma)$ where Σ is a $(P - 1) \times (P - 1)$ positive-definite matrix which allows for some redundancy between alternative choices (Ray 1973).

We made the simplifying assumption that our study area included all possible alternatives, given the 20,000 km^2 size of our study area, even though not all patches were covered at the start of the project, such that some individuals may have died of natural cause undetected after settling. The models were fitted in a Bayesian setting using a Markov Chain Monte Carlo (MCMC) procedure, using package MNP in R 3.0.2 software (R Core Team 2016). We used the default non-informative priors (Gaussian with “infinite” variance) and drew 1,050,000 MCMC Gibbs samples, discarding the first 50,000 and retained one iteration in 100 for storage-saving purposes (for implementation see Appendix S2). We ran five independent MCMC chains, starting from overdispersed values and diagnosed their convergence with the Gelman-Rubin statistic (Table S1; Gelman & Rubin 1992).

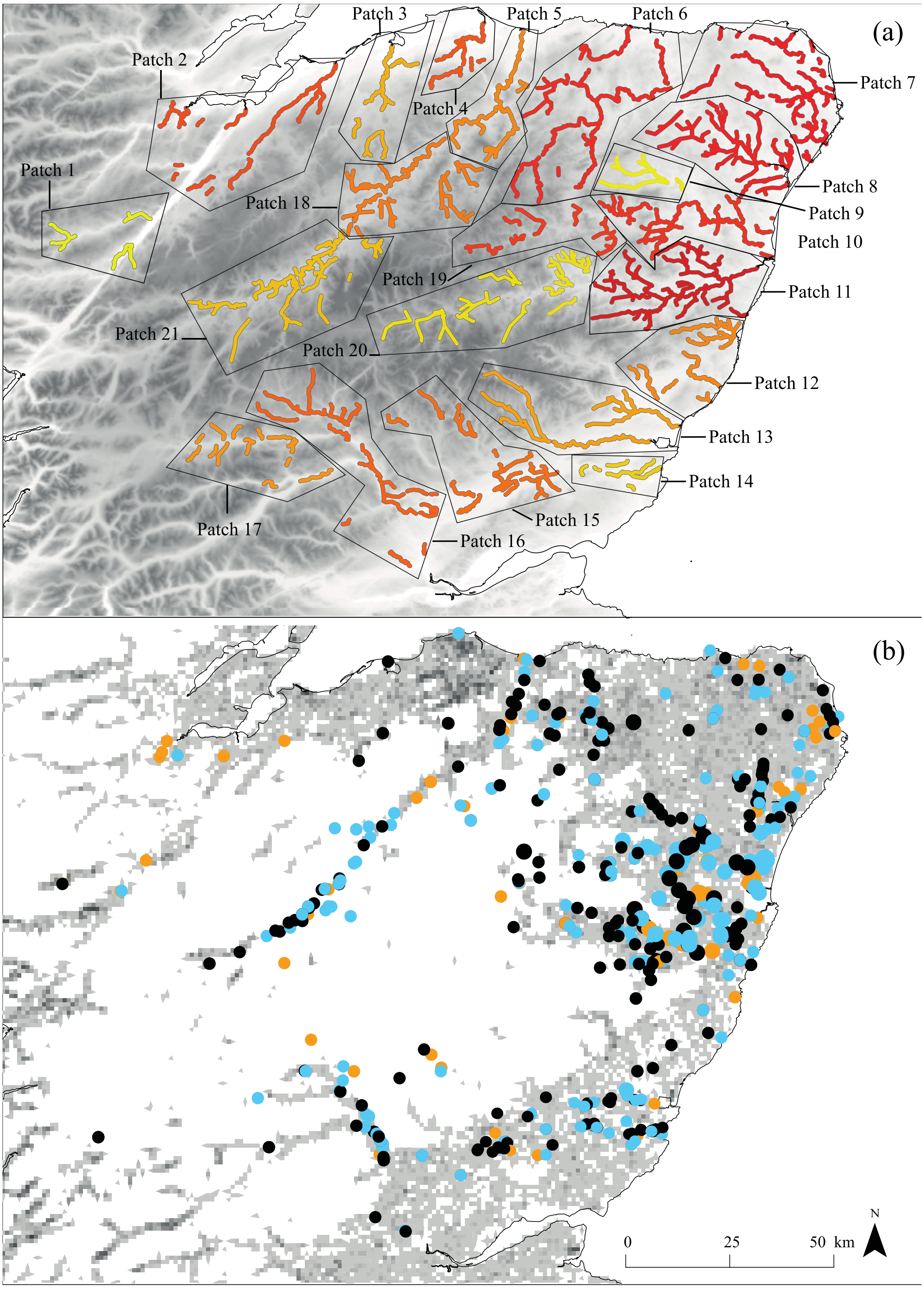

Figure 1. (a) The 21 patches coloured in yellow-to-red scale as per their gradient in quality *Q* (1-41% past use). The white-to-grey scale background relates to the gradient of altitude (spanning 0-1300 m). (b) Settled female (blue circles, N= 387), settled male (black circles; N

= 452) and mink of unknown sex (orange circles, N = 140). The grey scale background relates to the gradient of rough grass (1-100%, white relates to zero rough grass).

Results

All mink contributed to estimating the population density covariates, but only 479 out of 839 mink with known sex were successfully assigned to a relative (mother or pre-dispersal sibling) from which we could infer the natal location. Of these, 76.7% and 77% of adult females and males, respectively, were caught as outside their natal patch (Fig. S1).

Mink settlement decisions were influenced by both environmental and population covariates. Conspecific density (RD and RD^2) was a positive driver in both models, although the strength of its effect was lower in Model-2 (Table 1). Male probability of settlement increased with increasing conspecific density up to approximately 50% RD, but started to decline when RD exceeded ~60% RD, with no evidence of any effect at highest relative densities (Fig. 2). The influence of density on female settlement was comparatively weak (Fig. 2).

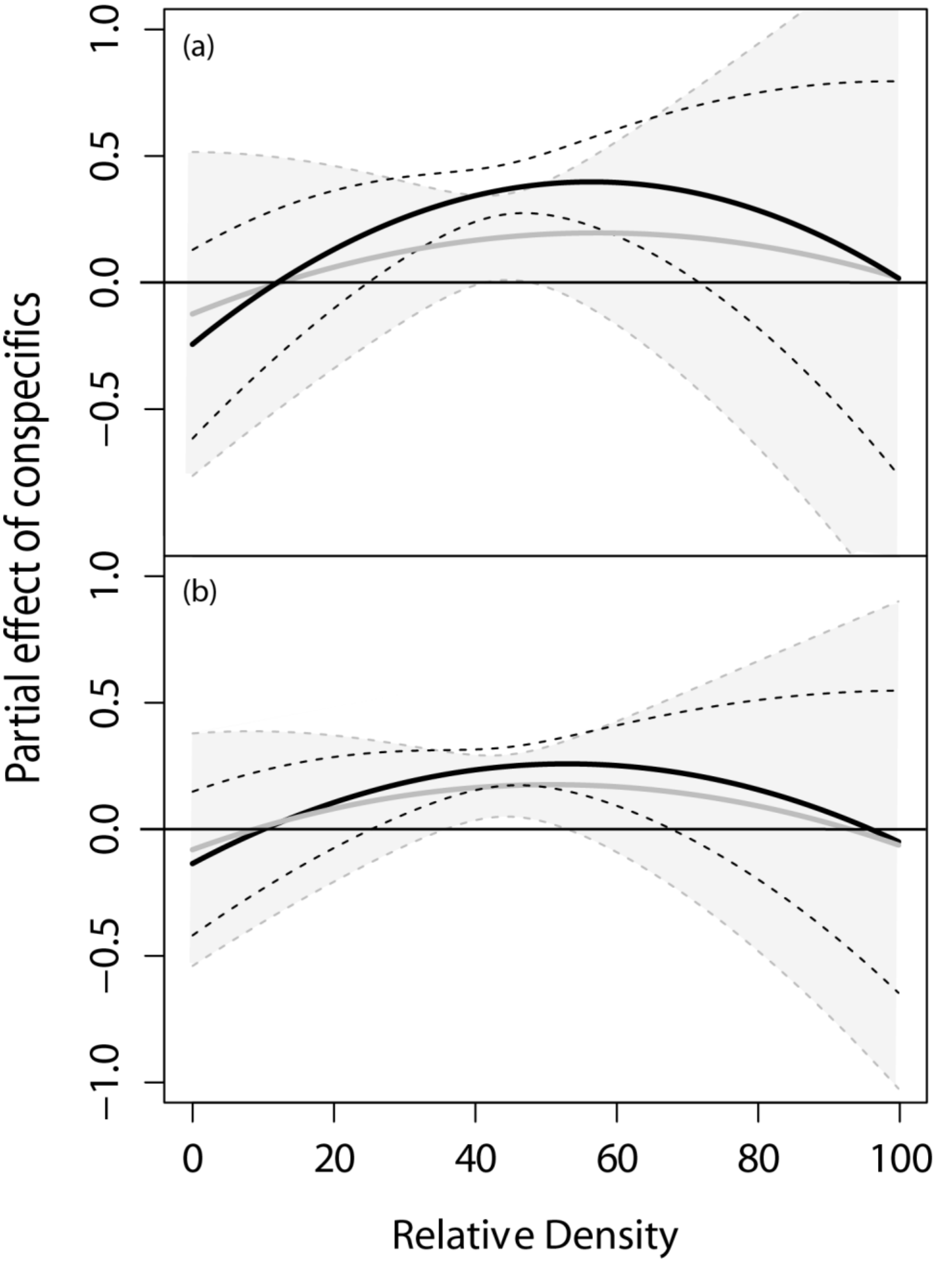

Figure 2. Estimated marginal effect of relative density (i.e., proxy of the saturation by conspecifics) on mink settlement probability (i.e. the additive effect on the link scale of relative density on the probability of choosing a patch) and 95% credible intervals (dashed lines) for (a) Model-1 (using occupancy as an indicator of patch quality) and (b) Model-2 (using habitat covariates as an indicators of patch quality), and for males (black lines) and females (grey lines and shadows). Solid horizontal lines represented no effect (y = 0).

Table 1. Posterior coefficient estimates for standardised patch-specific covariates (posterior mean, standard deviation and 95% credible intervals bounds). Covariates with the "female" subscript (e.g. "$\mathrm{RD}_{\mathrm{Female}}$") denote the difference between the effect of this covariate on females compared to its effect on the reference level, in this case, males. "$\mathrm{D}_{\mathrm{full\ sibling}}$" and "$\mathrm{D}_{\mathrm{half\ sibling}}$" are the difference between the effect of distance D for the reference level (D inferred from mother-offspring relationship) and the effect of D with D inferred from full and half sibling relationships respectively. *Q* relates to patch quality and RD to relative density. Bold indicates significant covariates.

	(a) Model-1				(b) Model2			
	Estimate	SD	2.5%	97.5%	Estimate	SD	2.5%	97.5%
RD	**0.86**	**0.17**	**0.54**	**1.20**	**0.60**	**0.13**	**0.35**	**0.87**
$\mathrm{RD}_{\mathrm{Female}}$	**-0.47**	**0.23**	**-0.94**	**-0.02**	-0.19	0.17	-0.51	0.13
RD^2	**-0.81**	**0.17**	**-1.15**	**-0.48**	**-0.61**	**0.14**	**-0.90**	**-0.35**
$\mathrm{RD}^2_{\mathrm{Female}}$	0.46	0.24	-0.01	0.93	0.17	0.17	-0.15	0.51
Q	**0.45**	**0.03**	**0.40**	**0.51**				
$\mathrm{Q}_{\mathrm{Female}}$	0.03	0.03	-0.03	0.08				
D	**-0.39**	**0.05**	**-0.51**	**-0.29**	**-0.31**	**0.05**	**-0.42**	**-0.22**
$\mathrm{D}_{\mathrm{full\text{-}siblings}}$	0.14	0.08	-0.02	0.29	**0.14**	**0.07**	**0.01**	**0.27**
$\mathrm{D}_{\mathrm{half\text{-}siblings}}$	**0.17**	**0.06**	**0.06**	**0.28**	**0.15**	**0.05**	**0.06**	**0.25**
Home Adv	**-0.18**	**0.07**	**-0.32**	**-0.04**	0.07	0.06	-0.05	0.19
Altitude					**-0.26**	**0.16**	**-0.61**	**-0.01**
$\mathrm{Altitude}_{\mathrm{Female}}$					**-0.10**	**0.05**	**-0.20**	**-0.02**
Rough					**-0.37**	**0.20**	**-0.80**	**-0.10**
$\mathrm{Rough}_{\mathrm{Female}}$					0.09	0.07	-0.03	0.22
Bog					0.05	0.07	-0.05	0.21
$\mathrm{Bog}_{\mathrm{Female}}$					0.02	0.03	-0.04	0.08

In both models, patch quality positively influenced mink settlement probability. Settlement by both sexes strongly increased similarly with *Q* (Model-1, Fig. 3a). Mink settlement decisions followed a distinct spatial pattern since patches with highest *Q* (3rd quartile *Q* = 19%, range 1-41; Fig. S2) were located in the coastal plain and along valleys floors. All patches had some coverage of rough grass (range 1-25%) but mink were attracted to those with lower than average cover and lower altitudes (both at 1 km-radius-scale), with lower altitude patches being more preferred by females relative to males (Table 1b, Fig. 3b-c). Other covariates either did not provide further explanation of habitat quality (Table 1 - Model 2) or were correlated with covariates already present in the model (Fig. S3).

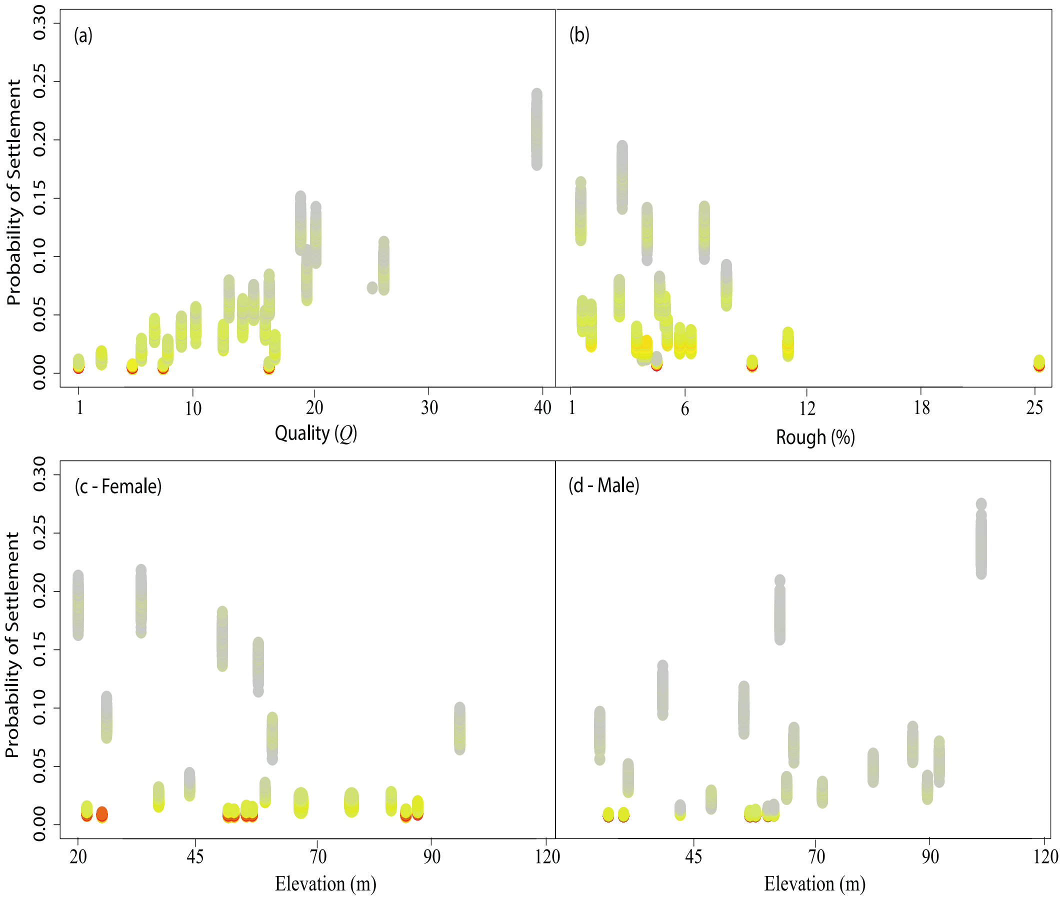

Figure 3. Partial predicted settlement probability for each mink and for each patch (i.e. each of the 479 mink is confronted with a choice of 21 potential patches, giving a total of 9009 probabilities), represented in relation to the patch variables (a) *Q*, (b) percentage of rough

grass, (c) altitude for females and (d) altitude for males. A gradient of colour has been linked to the density of predicted values (low to high: grey-to-yellow-orange-red). Predictions are based on holding all other covariates at their mean value.

Mink settlement probability declined with the distance from the natal patch in both models and for all three types of kin relationships used to infer natal location (mother-offspring, full- and half-siblings). The estimated negative slope of the relationship with distance was reduced by ≈ 33%, but not nullified, with assignment uncertainty levels, from mother-offspring to full- and half-siblings (Table 1, Fig. 4a). Consistently, estimated distances between centroids of natal and capture patches (Fig. S4) were longer when using half-siblings (mean 26.31, 3rd quartile 58 km, N = 324) and full-siblings (mean 25.44, 3rd quartile 55 km, N = 44) than when using mothers (mean 19.22 km, 3rd quartile 40 km, N = 112).

Considering only mother-offspring relationships, distance between patches had a similarly negative effect for both sexes (Fig. 4b, Fig. S5), reducing settlement probabilities to half (from approximately 0.20 to < 0.10) when patches were > 60 km distant from the natal patch in both models and with 20% of males dispersing > 80 km (Fig. 5). The significant effect of home advantage in Model-1 indicated that the probability of settling in the natal patch was less than predicted solely using the distance effect at distance zero; Model-2 did not capture this effect (Table 1).

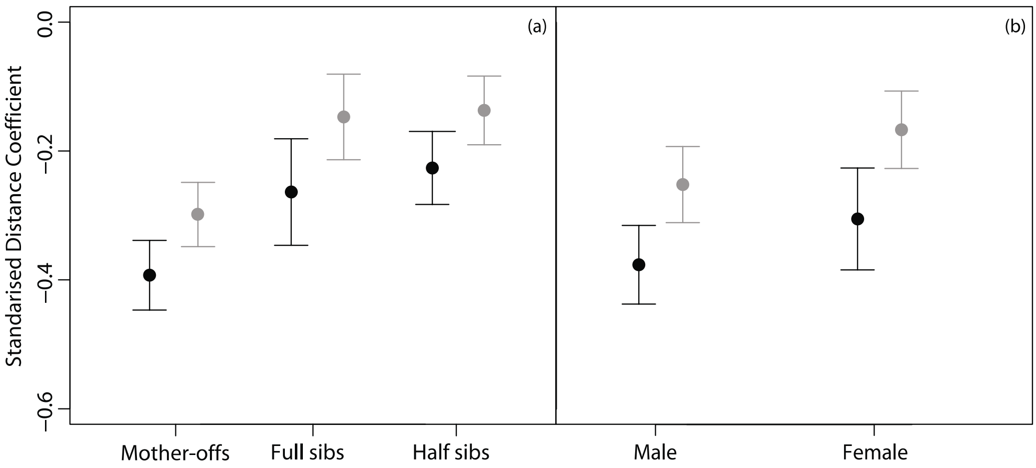

Figure 4. Estimated effect of the standardised distance from the natal patch on mink settlement probability in relation in relation to (a) the relationship type and (b) sex using only mother-offspring relationship for Model-1 (in black) and Model-2 (in grey).

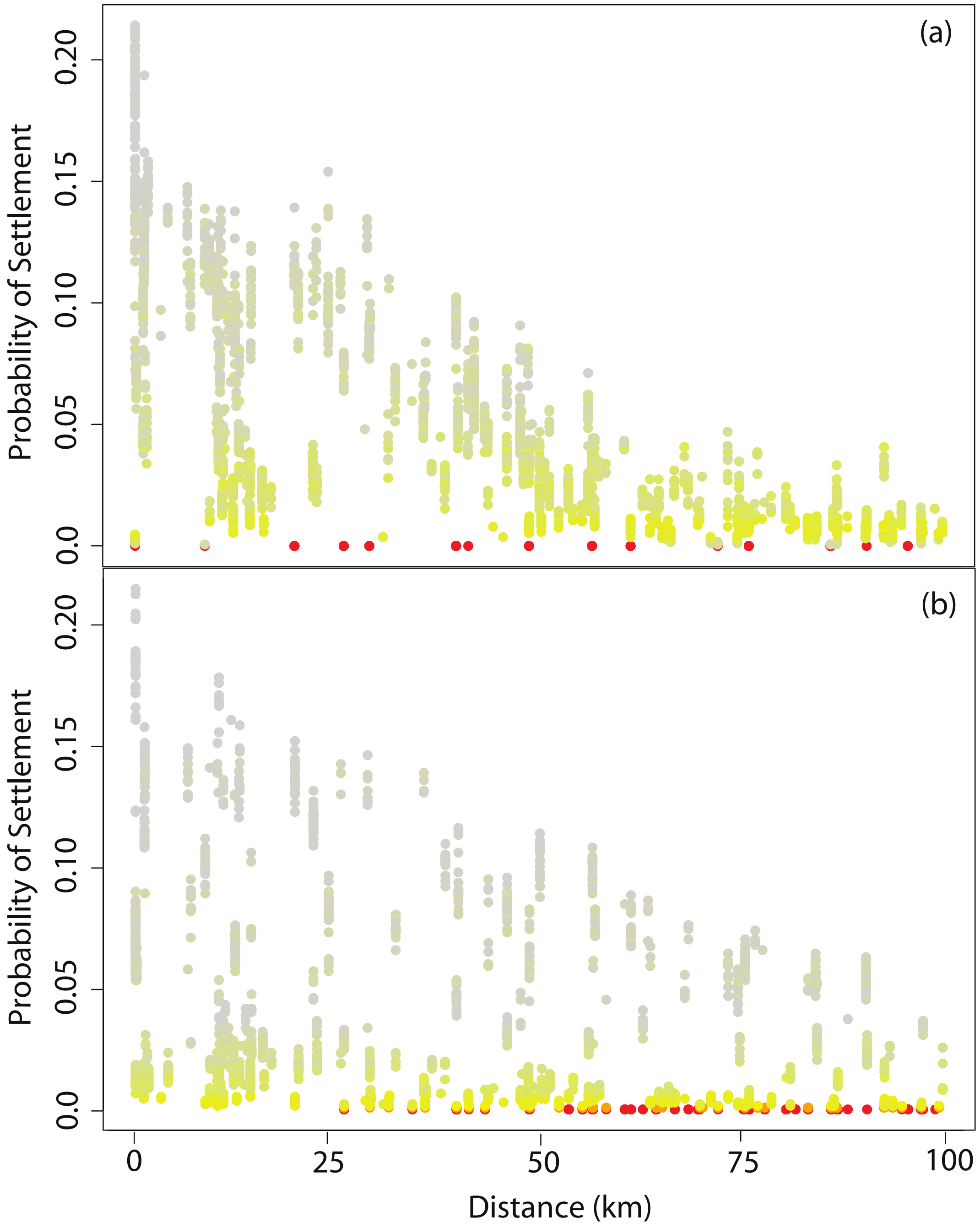

Figure 5. Partial predicted settlement probability for each mink and for each patch (i.e. each of the 112 mink using only mother-offspring relationship is confronted with a choice of 21 potential patches, giving a total of 2352 probabilities), represented in relation to the distance from the capture to the natal patch for (a) Model-1 and (b) Model-2. A gradient of colour has been linked to the increasing frequency of predicted values (grey-to-yellow-orange-red). Predictions are based on fixing all other covariates values at their mean. Predictions at distance zero include a "home advantage" effect.

Discussion

We used discrete choice models similar to Vardakis *et al.* (2015) for considering dispersal as a choice process whereby individuals' decisions are ruled by the characteristics of the chosen patch and of alternative choices. Using this relatively novel methodological approach, and utilising dispersal data from mink recolonising a large area repeatedly depleted of conspecifics by culling implemented by citizen conservationists, we provided evidence of both density dependence and habitat quality affecting mink settlement decisions. Mink selected high quality patches to settle in. Probability of settlement decreased with distance from natal areas in a similar way for female and male mink but the distances reached were long (mean 19 km, max 100 km), therefore not constituting a strong limitation. Our findings indicate that large-scale mink control could be optimized by turning preferential settlement areas in ecological traps.

Dispersal distances and mink settlement

The precision of natal dispersal distances estimates using inferred pedigrees depends largely on the type of kinship relationship between mother and descendants (Melero, Oliver & Lambin 2017). We pragmatically ensured that our inferences are robust by accounting for the influence of relationship type on the estimated effect of distance in the models. Not all dispersers were detected and some mink immigrated and emigrated from our study area. While these issues introduce a negative bias in estimations of dispersal distance in all studies (Koenig, Van Vuren & Hooge 1996), their impact was likely minimal owing to the exceptionally large size of the study area and the fact that it was bounded over roughly 75% of its periphery by the North Sea and the semi-permeable Cairngorms Mountains (Zalewski *et al.* 2009; Fraser *et al.* 2013). Re-invading mink of both sexes may have dispersed long distances. Both mean (19 km) and maximum (100 km) dispersal distances are well in excess of values predicted for carnivorous mammals of the size of mink (Sutherland *et al.* 2000) and may have contributed to mink's success as an invasive species. Long-range dispersal by mink and other mobile invasive species dictates that vast areas should be monitored and removal after an initial knock down phase to prevent re-establishment of a breeding population (e.g. Oliver et al 2016; Lieury *et al.* 2015). Given the range of natal dispersal in mink, the resource expenditure required would be unmanageable without some way of targeting monitoring based on habitat selection.

Environmental quality and mink settlement

We evaluated two sets of candidate proxies for patch quality, giving pragmatic consideration to the challenges of characterising 2,500 km of waterways. Both indices similarly had a positive influence on the settlement decisions of male and female mink. This provides scope for targeting monitoring to intercept and removing dispersers settling in areas turned into ecological traps through culling (Delibes, Gaona & Ferreras 2001; Delibes, Ferreras & Gaona 2001).

The proxies of quality in Model-2 were remotely-sensed properties of the riparian habitat. Unlike Q, they have the benefits of being available from the outset of any control project or in any future expansion area. Consistent with female mammals being constrained by the energetic demands of lactation, they indicated that female mink settled preferentially in river sections located in the fertile lowland plain of the North-East portion of the project area where arable farming is the dominant land use. The level of discrimination these proxies provided was however limited, leaving 1,500 km of river with high quality scores, hence with high priority for ongoing monitoring.

The second proxy, the consistency of patch use as defined by mink occupancy (Q) was a good predictor of settlement consistent with inference from remote-sensed covariates. It was the main factor predicting female mink settlement, with greater influence than distance to the natal patch according to standardised regression coefficients. High quality patches were mostly at low altitudes ($Q_{lowlands}$ mean = 22.4, $SD_{lowlands}$ = 10.1; $Q_{highlands}$ mean = 8.8, $SD_{highlands}$ = 4.8; Fig. S2) but not all lowland patches had high Q values. Unlike remotely-sensed habitat proxies, *Q* is derived from the management process and relies on mink captures gradually accumulating.

Using *Q* as proxy of patch quality as perceived by mink themselves to predict settlement by immigrants and spatially prioritise management is a technique broadly applicable to other species, even where detectability of settlers is <100%. It can be particularly useful when measures of resources (e.g. food, shelter) are not attainable. Indeed past occupancy is widely used as a proxy of quality where gradients of quality are steep, as in metapopulation studies (Hanski & Gilpin 1991; Johnson 2007).

Density dependence and mink settlement

Our metric of density was a time-varying relative estimate based on the number of mink culled reported by volunteers. As the ratio of the number of occupied inferred territories per patch in a calendar year relative to the maximum potential number of mink settling in that patch, it is as a pragmatic measure of saturation relative to a notional carrying capacity. Averaged annual relative patch density ranged from 6-90.4%; median 20%, overall range 0-100%). There was evidence of non-linear effect of conspecific density (RD + RD^2 effects) with highest probability of settlement at intermediate densities; the effect being stronger for male than for female. This density dependence supports the hypothesis of a trade-off between the benefits of the presence of conspecifics, which may inform prospective immigrants about patch quality and on the presence of females, and the costs of competition.

Detecting the dual influences of quality patches and conspecific density on settlement probability was facilitated by the reduction in mink population density through culling. Indeed density dependence in saturated conditions in the early stages of the project likely contributed to some female mink settling in low quality patches in the upland reaches of the river catchments (Aars *et al.* 2001; Bryce *et al.* 2011). Our analyses imply that mink settled preferentially in the more productive lowland patches as relative densities decreased, and adds to the evidence of compensatory immigration that is known to occur in other controlled mammalian species (e.g. Loveridge *et al.* 2007; Lieury *et al.* 2015).

Management implications

Our results exemplify that, despite the unavoidable incomplete reporting and associated loss of information, engaging citizen-scientists in a conservation project makes it feasible to carry out management and collect data at an exceptionally large spatial scale while learning about key ecological processes.

Where the objective of invasive-species management is control rather than eradication, identifying and focussing control effort on attractive areas is an effective option for preventing reinvasion of an area following an initial knock down of the population. These attractive areas where individuals are more likely to settle, can be used as ecological traps by managers (Delibes, Ferreras & Gaona 2001) by enhancing trapping effort via e.g. higher volunteer deployment and renewal of rafts. These attractive areas are not of high conservation value; which will mandate interception of mink before arrival. The promise of increasing efficiency resulting from an adaptive management process should contribute to reducing the vulnerability of invasive non-native species management efforts to fluctuations in funding, which, in the UK, typically consist of discrete projects of 3-4 years duration in lieu of long term strategic funding.

Remotely-sensed habitat variables identified clear gradients of attractiveness to prospective immigrants but were not sufficiently descriptive to efficiently target long term monitoring aimed at thwarting recolonisation of very large areas. A better characterization of habitat variables defining attractiveness of river section within the productive lowlands would be beneficial and applicable in newly controlled areas where mink resettlement information is lacking. Variation in patch quality gathered from historical settlement decisions by previous individuals can help ranking the attractiveness of potential settling areas and more sharply focus monitoring and removal effort. The approach of relying on habitat selection to spatially focus invasive control is however not without risk, as it relies on statistically defined settling rules being faithfully used by all individuals. As such, it may not be suited to eradication attempts, where it is crucial to remove all individuals. In an ongoing control program, evidence of variation in patch quality will become increasingly valuable to refine knowledge of the location of potential attractive areas that can be used as ecological traps as capture of immigrants accumulate and the predictive power of models improve. Despite patches being large in our study due to historical management and sample size limitations, the effects of the covariates were clear. Their scale, while ideally refined over time as data accumulate, is nevertheless suitable for targeting control or volunteer staff deployment to those portions of the overall project area most attractive to the immigrants and suppress reinvasion.

A corollary is that while proxies of quality can be used to predict settlement, accurate prediction of patch relative attractiveness to prospective immigrants at a given time ideally requires knowledge of current density, or an appropriate proxy thereof. Supporting the approach of spatiotemporal predictions for management (e.g. Baker 2017).

Authors' Contributions

Y.M and XL conceived the study, all authors interpreted the results and wrote the manuscript. Y.M. performed the genetic analyses and estimated dispersal distance with M.K.O, and the statistical analysis with T.C. X.L. supervised the research and management project.

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Data Accessibility

Data of the culled American mink in NE Scotland (ID), their settlement choice and the related covariates formatted for the multinomial model will be archived in Dryad.

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Supporting Information

Additional supporting information may be found in the online version of this article.

Appendix S1. DNA extraction, genotyping and pedigree analyses

Appendix S2. R code and dataset for the Bayesian multinomial probit model (Model-1)

Table S1. Convergence statistics of the five MCMC chains for each model

Fig. S1. Matrix of the accumulative number of settled mink from natal to settlement patch.

Fig. S2. Quality (*Q*) per patch.

Fig. S3. Correlations between habitat variables.

Fig. S4. Patches coloured as per Q and their centroid of mink captures.

Fig. S5. Histogram of distances between patches.