Long-term strategic recovery plan for pine martens in Britain

Jenny MacPherson and **Patrick Wright**

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Executive summary

The recovery plan outlined here aims to balance conservation of the recovering pine marten population in Scotland with growing interest in the use of conservation translocations as a means to restore the species to parts of its former range elsewhere in Britain.

The aim of this document is to set out a strategic, long-term recovery plan for pine martens in Britain. It follows on from a previous strategy produced in 2011 (Jordan, 2011), which outlined the practical work and research needed to restore and secure the future of pine marten populations in England and Wales up until 2020. We present a summary of what has been achieved so far and set out a continuing recovery plan for pine martens across Britain that maintains this strategic approach, while emphasising the importance of conserving recovering populations in Scotland.

Re-afforestation since the 20th century has improved habitat availability for pine martens, and legal protection in the 1980s played a significant role in enabling the species to recover some of its former range in Scotland. However, this recovery has been slow and the species is still vulnerable. For this reason, a strategic plan is needed to ensure that this recovery continues. The first priority must be to protect the integrity of existing populations and to promote natural recolonisation and range expansion. Where this is not possible, species restoration should be prioritised where it will be most effective and likely to succeed.

Source populations for conservation translocations should have appropriate genetic provenance, morphology, physiology and behaviour and be sourced from areas with similar prey species, competitors, predators and habitats. Therefore, the established population of pine martens in the Highlands of northern Scotland is currently the most suitable source of animals for translocations to England and Wales. With limited resources and suitable donor populations for actions such as reintroductions, it is important to identify how to achieve the maximum conservation benefit for pine martens for the minimum resource ‘costs’. We used modelling methods based on data and knowledge of pine marten ecology and distribution to develop a framework for optimising spatial targeting of conservation measures. This framework was applied to a number of regions in Britain to assess their potential for pine marten recovery or restoration. The results were used to inform a series of recommendations for long-term pine marten conservation in Britain.

There is currently an increasing interest in pine marten reintroductions and other conservation translocations, but proposed projects are often locally planned and motivated without knowledge of other similar projects or consideration of how they fit within the wider context of pine marten conservation. A national, strategic approach is needed to help guide project proposals and inform the decisions of stakeholders, funders, regulators and NGOs. Developing methodological approaches to identify and prioritise areas for species restoration is crucial, especially when resources (including suitable donor populations) are limited. The recovering population of pine martens in Scotland is currently the most suitable source of animals for translocations elsewhere in mainland Britain. However, there are still relatively few areas where pine martens have been established for a sufficiently long time and are at high enough densities to be able to sustain the removal of a limited number of animals for translocations. It is important to protect the recovering pine marten population in Scotland, as well as to monitor and facilitate natural spread and recolonisation where possible. Therefore, reintroductions should only be to the most optimal regions in priority order, and in such a way that has the minimum risk to donor populations and maximises the probability of reintroduced populations establishing, spreading and ultimately linking up.

Habitat suitability and connectivity modelling showed that the majority of well-connected, highly suitable habitat for pine martens is in the north and west of Britain. Translocations of pine martens have already taken place into the largest contiguous region of highly suitable habitat in mid Wales. A reintroduction is also underway into the Forest of Dean and Wye valley on the England/Wales border. This should consolidate the range of pine martens in Wales and the bordering counties. However, having discrete populations as a result of translocations is not ideal. A phased series of translocations to seed new populations in reasonable proximity to each other, with the capacity to increase, expand and form an effective meta-population, will increase gene flow and resilience. A robust metapopulation will expand and disperse into new patches of suitable habitat, with the advantage that natural recolonisation is perceived as less contentious than human-mediated releases.

We advise that, in the ten-year (2021-2031) timescale of the recovery plan presented here, there could feasibly be a maximum of two, properly researched and fully resourced pine marten reintroduction projects. This takes account of the need to ensure that the status of the recommended donor population in Scotland is not adversely affected. We set out a structured decision-making process for prioritising suitable regions for further investigation. However, this initial stage is very much focussed on the biological considerations associated with identifying potentially suitable landscapes for pine martens. It must be stressed that any conservation translocation also needs to consider and address relevant socio-economic and regulatory considerations. All conservation translocation projects should be planned and carried out in accordance with International Union for Conservation of Nature (IUCN) Guidelines for Conservation Translocations, as well as the Scottish and English Codes for Conservation Translocations.

We identified two regions that should be prioritised for further consideration based on analyses of habitat suitability, as well as other factors likely to affect survival and reproduction, key parameters in the establishment and spread of reintroduced populations. The first of these is south-west England. The results of our analyses suggest that it is highly likely that a viable population would result from pine marten reintroductions to the landscape spanning the counties of Somerset and Devon. Suitable habitats across these counties are in sufficiently close proximity to the restored populations in Wales and Gloucestershire for there to be a reasonable expectation of gene flow between them, should a reintroduction go ahead in the south west. The counties of Devon and Somerset could potentially be suitable for a landscape-scale pine marten reintroduction if other conditions are satisfied. These would include appropriate risk assessments (for disease, as well as impact on other species and habitats), minimal conflict with other land users and sufficient resources secured for a reintroduction and subsequent long-term monitoring and engagement.

The second region that warrants further investigation is south Cumbria. Modelling suggests that south Cumbria is likely to be recolonised by pine martens dispersing from the Scottish borders and Northumberland. However, there is an area of high landscape resistance across Carlisle and the M6 motorway, as well as the open fells of the northern Pennines. It is recommended that periodic distribution/expansion zone surveys are carried out, following on from previous work by the ***Back from the Brink*** project (https://naturebftb.co.uk/the-projects/pine-marten/) to monitor natural range expansion into the north of England. Habitat suitability might be further increased by providing additional resources such as artificial den sites for breeding females where appropriate. The potential for improving dispersal corridors from the current pine marten range should also be explored. Nonetheless, if there is no evidence of natural recolonisation in south Cumbria within approximately five to ten years, then we suggest that the potential for accelerating recolonisation by reintroductions should be explored. This might be an effective way of increasing the rate of spread of pine martens in northern England.

In south and south-east England, the high density of roads, traffic and other infrastructure pose a significant threat to founder populations of pine martens in the early stages of a reintroduction. These regions should not be a priority for pine marten translocations. However, the potential for increasing habitat connectivity to the reintroduced pine marten population in Gloucestershire should be explored. Creating dispersal corridor routes, as well as possible road crossings/green bridges/underpasses would increase landscape permeability for pine martens and benefit other wildlife.

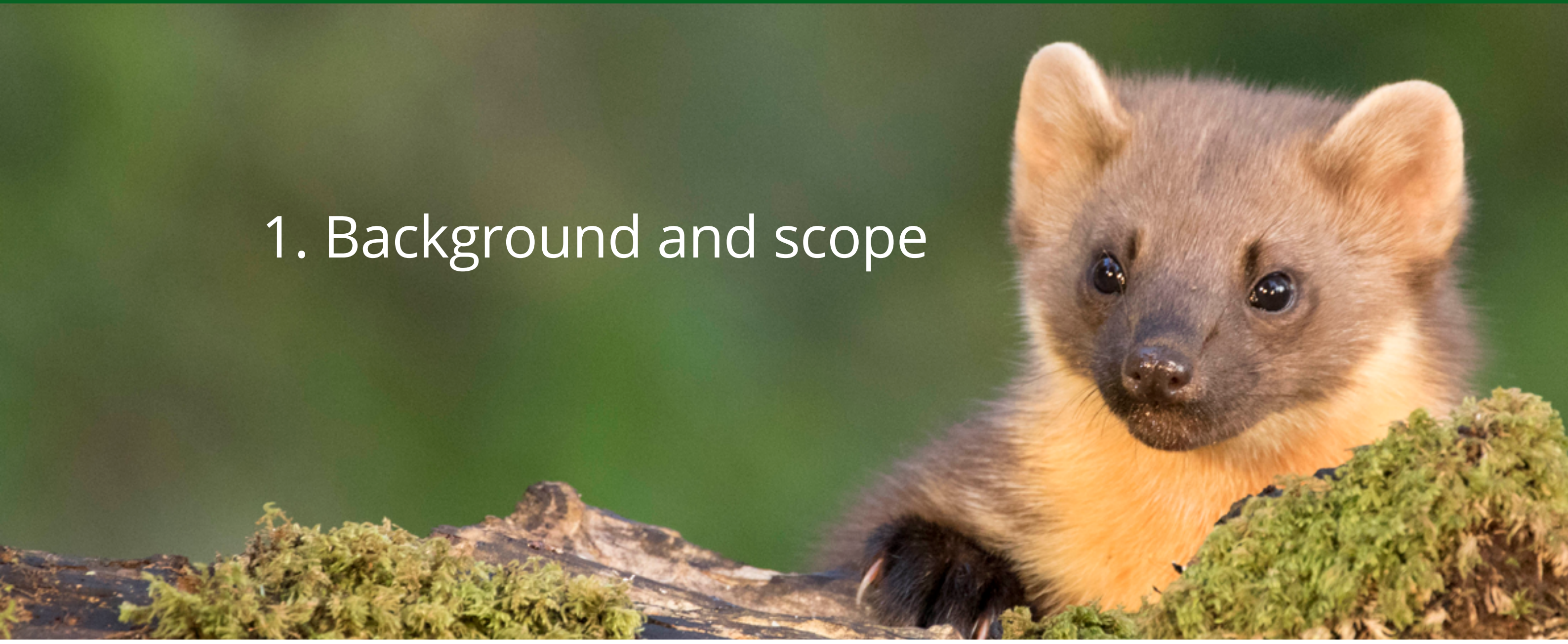
It is suggested that habitat enhancements are carried out in regions of Scotland where pine marten density or habitat connectivity is currently low, such as through the Central Belt and into southern Scotland. In northern Scotland, donor populations from which pine martens were removed between 2015 and 2019 have been monitored by VWT.

Population estimates derived from genetic analysis of non-invasively collected samples suggest that only a relatively small proportion of resident animals have been removed from the north Scotland donor populations. However, the sampling strategy could be improved to refine population estimates further and better inform the way in which donor populations are managed and conserved in the face of inevitable demand in future. Recognising the limitations of current population viability modelling, it is recommended that the current conservative harvesting strategy continues. Future translocations should be made up of a comparatively small number of animals taken from each of several different donor sites, with a minimum of five years between removals from any donor population. It is important that any donor population is monitored to assess the effects of removal, to ensure its conservation status is not adversely affected, and to inform the design of future ‘harvesting’ approaches.
It would be appropriate that this is undertaken by the relevant organisation(s) carrying out a reintroduction, and should be part of the project plan.

We recommend that work focusses on developing and implementing effective monitoring schemes for existing and expanding pine marten populations as well as further investigation of the highest priority regions for potential reintroductions. We suggest that these should be south-west England in the first instance, followed by a re-evaluation of south Cumbria, depending on the rate and patterns of natural recolonisation observed over the next five to ten years.

Monitoring range expansion, raising awareness of pine martens at the recolonisation front and across predicted expansion zones; carrying out targeted habitat improvements; provision of artificial den sites and increasing habitat connectivity where possible; and mediating with other land users to minimise the potential for future conflict are priority actions to benefit pine marten recovery in Britain. These will provide further information about the changing status and distribution of pine martens across Britain, as well as the need for more interventionist approaches such as reintroductions. This recovery plan emphasises the importance of compliance with published best practice approaches that have been produced to guide and inform conservation translocations (IUCN Guidelines for Conservation Translocations; Scottish Code for Conservation Translocations; Translocations, Reintroductions and other Conservation Translocations: Code and Guidance for England). This is the overarching framework that should be applied when designing any conservation translocation and will be used in assessing conservation translocation proposals for licensing.

Contents



1. Background and scope

The pine marten (*Martes martes*) is a medium-sized mustelid predominantly associated with forested habitat (Mitchell-Jones *et al*. 1999). Pine martens were once common and widespread throughout Britain (Maroo & Yalden 2000), but during the 19th and early 20th centuries the population suffered severe declines in numbers and distribution. This was a result of increases in predator control (Langley & Yalden 1977; Tapper 1992), coupled with the historical effects of loss and fragmentation of woodland habitat. By the beginning of the 20th century, pine martens were extinct in almost all of southern Britain, with the majority of the remnant population restricted to the north-west highlands in Scotland, and much smaller areas in the uplands of northern England and Wales (Langley & Yalden 1977). With increases in afforestation and legal protection, the pine marten population in Scotland has been recovering well and expanding its range since the 1980s, but this was not the case elsewhere in Britain.

By 2010, after 30 years of research and surveys by Vincent Wildlife Trust (VWT), there was no evidence of pine marten recovery in England and Wales. An external stakeholder group was set up, comprised of key representatives from SNCOs, NGOs, foresters and individual mammal research and conservation experts to focus on the objective of restoring pine martens to England and Wales. A strategy document was produced and agreed by the stakeholder group, which concluded that intervention was necessary to prevent complete extinction of the pine marten south of the Scottish border and to restore viable populations to the historical range of the species in southern Britain (Jordan 2011). The strategy outlined the practical work and research needed to restore and secure the future of pine marten populations in England and Wales across a timeline up until 2020. It is now appropriate, therefore, to summarise what has been achieved so far, and to set out a continuing recovery plan for pine martens in Britain that maintains this strategic approach.

The aim of this document is to outline a strategic, long-term (2021-2031) recovery plan for pine martens in Britain that will have the maximum conservation benefit at a national level, with the minimum impact on donor populations in Scotland. This emphasises the importance of conserving the recovering pine marten populations in Scotland, and monitoring and facilitating natural spread and recolonisation where possible. Reintroductions should be considered to the most optimal regions in England and Wales in priority order, and in such a way that maximises the probability of reintroduced populations establishing, spreading, and ultimately linking up. Regions that should be prioritised for further consideration have been identified based on analyses of habitat suitability, as well as other factors likely to affect survival and reproduction, key parameters in the establishment and spread of reintroduced populations.

Habitat loss and fragmentation, along with other factors, have led to population declines and local extinction for many species. In the UK alone, a recent assessment of more than 8,000 species using regional International Union for Conservation of Nature (IUCN) Red List criteria found that 15% are threatened with extinction from Britain, and 2% are already extinct (Hayhow *et al*. 2019). There is an imperative to find ways of reversing the loss of biodiversity which has led to a growing interest in rewilding and species translocations. Conservation translocation is the managed movement of organisms (including animals or plants) from one location to another to achieve a measurable conservation benefit for the population, species or ecosystem. The term covers reinforcement, where translocated individuals are adding to an existing, but often small, population; reintroduction, to restore a species to part of its natural range from which it has gone extinct; or conservation introduction, also called assisted colonisation, where the aim is to establish new populations of a species beyond what has previously been its natural range. Conservation translocations are a widely used management tool in situations where natural recovery or recolonisation is unlikely; however, they should only ever be used as a last resort. They are high cost (in terms of animal welfare and resources), and high-risk activities which need to have clear goals from the outset and be very carefully thought out.

The Conservation Translocation Specialist Group (CTSG) of the IUCN has published guidelines which have been developed over a number of years with input from experienced practitioners. These are designed to be applicable to all types of conservation translocations (IUCN, 1995; IUCN, 2013). They provide a series of checks and balances to ensure that any conservation translocation is justified because it will result in a quantifiable conservation benefit and will not cause adverse side effects of greater impact. The Scottish Code for Conservation Translocations, produced by the National Species Reintroduction Forum (NSRF), puts this into a national context and sets out more detail for projects arising in Scotland (NSRF, 2014), and the Department for Environment, Food and Rural Affairs (DEFRA) has produced a similar code and guidance for England (DEFRA, 2021). With limited resources available for conservation, objective prioritisation among potential reintroduction sites is important in order to maximise their effectiveness and conservation benefits at a national scale.

Following IUCN and NSRF guidelines, VWT carried out translocations of pine martens from Scotland to Wales in 2015-2017. Since then, there has been a growing number of pine marten reintroduction proposals from elsewhere. Recent studies in Ireland (Sheehy & Lawton 2014) and Scotland (Sheehy *et al*. 2018) suggested that pine martens may have a negative impact on grey squirrels, with a benefit to red squirrels where they are present and as a result, many organisations and partnerships in Britain are particularly interested in pine marten reintroduction projects for grey squirrel control. However, these are often locally designed initiatives, motivated by local conservation targets, without consideration of how they fit within the wider context of pine marten conservation and of other, similar projects. Reintroductions can offer a powerful conservation tool but when they are motivated and planned at a local scale this may hamper their ability to contribute to the long-term recovery of a species at the larger scale. This is particularly important for species such as the pine marten, which occupy large (c2-30km^2 per individual) home ranges and which, therefore, require suitable landscapes, rather than sites, in which to establish sufficient territories for a viable population.

Organisations with the responsibility to conserve species across large spatial scales have to prioritise in order to optimise use of resources. VWT, along with the statutory nature conservation agencies in Scotland (NatureScot), England (Natural England) and Wales (Natural Resources Wales), have been working with, and guiding, partner organisations for some time. However, the increasing number of proposals means that a more formal strategy is needed to help guide both project proposals and the decision of funders and statutory agencies to grant funding and licences where appropriate. Developing methodological approaches to identify and prioritise areas for species restoration is crucial, especially when resources (including suitable donor populations) are limited. Modelling methods and GIS spatial data can be utilised to devise an objective framework which can aid decision makers in prioritising the optimal areas for restoration initiatives, yet these approaches have rarely in the past been used specifically to prioritise sites for restoration or reintroduction of species (Noss, Nielsen & Vance-Borland 2009).

Long-term recovery goal
The long-term recovery goal is to improve the conservation status of the pine marten in Britain by:

- protecting the integrity of existing populations
- promoting natural recolonisation where possible to recover the species' former range
- prioritising species restoration where it will be most effective and likely to succeed

Objectives

1. Develop and demonstrate a transparent framework for decision makers to help optimise conservation actions for pine martens in a range of different circumstances including:
   a) promoting and facilitating natural recovery
   b) prioritising optimal areas in which to consider pine marten reintroductions
2. Protect existing populations in Scotland from negative impacts of over-harvesting

Past and present pine marten distribution in Britain
By the beginning of the 20th century, pine martens were extinct in almost all of southern Britain, with the exception of small, isolated pockets in the remote uplands of northern England and Wales (Langley & Yalden 1977). At this time, the pine marten's core range was restricted to the North West Highlands of Scotland. This stronghold held the largest remaining pine marten population in Britain, considerably larger than those pockets that persisted in England and Wales.

In the 1930s, the population in Scotland began to show signs of recovery with a reported increase in pine marten numbers in north-west Sutherland and a south-eastward range expansion. This is attributed to a reduction in lethal trapping pressure following the First World War (1914-18) (Lockie 1964). Pine martens subsequently recolonised the north side of Loch Ness by 1946 and were established south of the Caledonian Canal by the early 1960s (Lockie 1964).

By the early 1980s in Scotland, the pine marten population was continuing to expand its range and, although the main population was still north of the Great Glen, pine martens were recorded throughout the central and western Highlands (Velander 1983). The urbanised Central Belt was thought likely to be a barrier to natural recolonisation of southern Scotland so, in 1980-1981, 12 pine martens were reintroduced to Galloway Forest in the south-west, with six individuals released at two separate sites respectively (Shaw & Livingstone 1992). The released animals were not monitored, but it is thought that only one release was successful, due to a lack of subsequent sightings in the vicinity of the other release site (Shaw & Livingstone 1992).

By the 1990s, pine martens were no longer confined to the Highlands and had re-colonised further areas of central and eastern Scotland (Balharry *et al*. 1996). The most recent distribution surveys carried out in 2012 and 2013 show that there has been further range expansion, with the species having re-colonised much of Sutherland, Caithness, Aberdeenshire, Perthshire, southern Argyll, Stirlingshire, limited areas of western Angus and Fife and part of the industrialised Central Belt (Croose, Birks & Schofield 2013; Croose *et al*. 2014). In addition to range expansion of the core population, unofficial translocations and releases have resulted in the establishment of a pine marten population in the Scottish Borders (Croose *et al*. 2014) and the Isle of Mull (Solow *et al*. 2013). Pine martens are also now established on the Isle of Skye, having colonised from the mainland via the land bridge (Croose, Birks & Schofield 2013). In Scotland, pine martens now have an almost contiguous distribution north of the Central Belt, with a distinct but possibly contiguous population in south-west Scotland and the Scottish borders.

Throughout the 20th century, pine martens were occasionally recorded in the north of England, but until recently there had been no evidence of a viable population in this region. However, pine martens are now re-colonising parts of Northumberland and Cumbria from the Scottish borders where they are becoming more widespread. Between 2017 and 2020, over 50 records of pine martens in Northumberland and Cumbria have been collected in the course of the ***Back from the Brink*** project (https://naturebftb.co.uk/the-projects/pine-marten/). Since 2018, there have been regular records of pine martens in the Kielder Forest block, with occasional records further over the border in northern Cumbria. It is likely that this re-colonisation will continue but will be dependent on the availability of suitable habitat, low mortality, and minimal conflict with human interests.

Despite repeated surveys during the 1980s and 1990s, there was little evidence, beyond occasional sightings, to suggest that viable pine marten populations persisted elsewhere. There is sporadic evidence of animals in Shropshire and Hampshire, which may result from earlier, covert releases or escapes. In Wales, the population was thought to be functionally extinct and so, following a feasibility study, a total of 51 pine martens were translocated under licence from Scotland to Wales between 2015 and 2017. Translocated pine martens were released into woodlands around Devil's Bridge in north Ceredigion and the animals monitored using a range of methods including radio tracking, camera traps and scat surveys. Successful breeding has been recorded every year from spring 2016 through to 2020 and the population has expanded beyond the release region.

Eighteen pine martens were then translocated under licence from Scotland and released into the Forest of Dean, Gloucestershire, in autumn 2019. A small core population has settled in the Dean and Wye Valley, and successful breeding has been recorded. Further translocations are planned for autumn 2021.

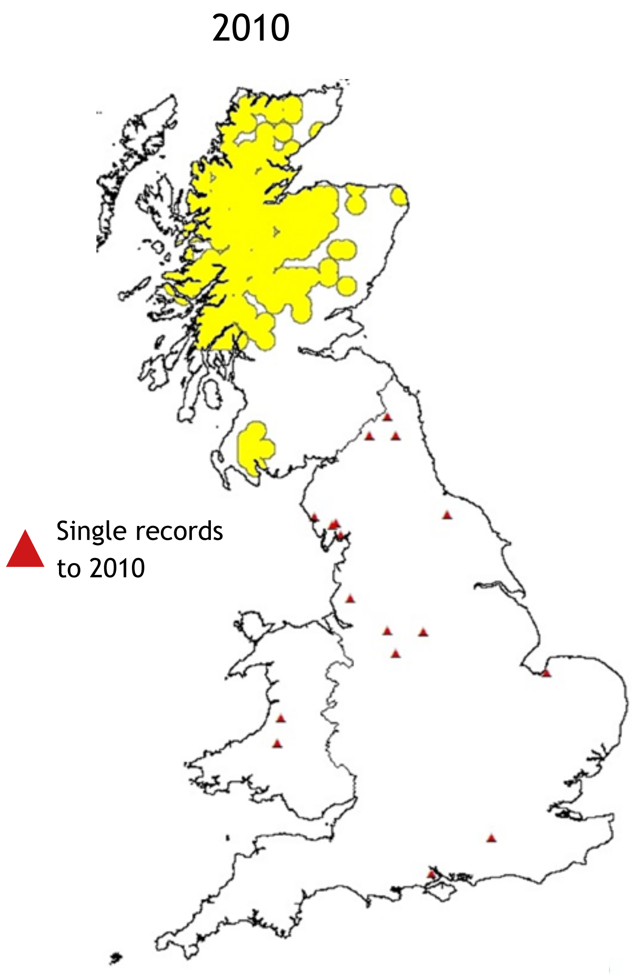


Figure 1. Pine marten distribution to 2010 (left) and to 2020 (right) (verified records, buffer applied to multiple records within 10km radius).

The most recent population estimate for the British pine marten population is 3,700 individuals (95%CI = 1,600–8,900).

(Mathews *et al*. 2018).

2. A Framework to optimise conservation actions for pine martens (objective 1)

We aim here to develop a simple and transparent framework based on widely used modelling methods that can be used to inform decisions around spatial targeting of pine marten conservation measures. Habitat Suitability Models or HSMs (also referred to as Ecological Niche Models, ENMs, or Species Distribution Models, SDMs) are increasingly being used to support conservation decision making. These models are used to derive spatially explicit predictions of environmental suitability for species. They have been developed for more than two decades now and have emerged as a set of tools with many potential conservation applications (Guisan & Thuiller 2005; Rodríguez *et al*. 2007; Franklin 2010). However, it has been argued that the decision framework within which HSMs are used is rarely explicit. Models are useful tools for use within a structured and transparent decision-making process and can be designed to suit a number of decision-making contexts. HSMs can be used to identify candidate locations for conservation actions that can then be evaluated in greater detail. Many other factors (such as stakeholder/social considerations, logistical constraints, costs or conflicting conservation priorities) will ultimately determine the feasibility of different actions, but the HSM provides information that can be used to evaluate a range of options when making decisions about where to translocate a threatened species.

HSMs can help inform the translocation decision process by identifying and prioritising regions of suitable habitat (under both current and future scenarios), that have the greatest potential as recipient sites. However, modelled probabilities of habitat suitability alone may not incorporate the population processes needed for species persistence (Guisan *et al*. 2013). Therefore, using process models such as population viability analyses (PVA) in combination with HSMs can provide more information on the likely effects of particular actions on long-term species persistence (Guisan *et al*. 2013). One published example of such an approach used to assess critical habitats for Ord’s kangaroo rat, *Dipodomys ordii*, in Alberta, Canada, showed that 39% of habitat predicted as suitable for this species was unlikely to contribute to population viability (Heinrichs *et al*. 2010). Heinrichs *et al*. (2010) highlighted the importance of using both HSM and spatially explicit PVA models with variables directly relevant to the species demography, when predictions of species persistence are the main concern.

There are a number of methodological choices to make when developing and applying an HSM. Their usefulness is often conditional on the availability of suitable data to train and build the models. Factors such as locational error or biased data can potentially affect HSMs and their predictions (Kadmon, Farber & Danin 2003; Cayuela *et al*. 2009).

Therefore, the usefulness of these models for decision makers is highly context sensitive. Choices between the various options for building and applying an HSM needs careful attention in a decision-making context, where modelling methods should be determined by the nature of the conservation problem being addressed and what decisions are being informed by the results. Habitat suitability model predictions can be subject to two types of errors: suitable habitat predicted as unsuitable (false negatives) and unsuitable habitat predicted as suitable (false positives) (Franklin 2010). Either can be critical, depending on the context, when using HSMs to support conservation decisions. If using an HSM to target survey effort for an under-recorded species, false negatives would be more of an issue than false positives, because underestimating the extent of a species potential distribution could lead to suitable areas not being surveyed. Conversely, false positives would be of greater significance if they resulted in management effort and resources being targeted in inappropriate areas. Deciding how to balance both types of error will differ from one decision making context to another, depending on the consequences of the errors in relation to the conservation objective. When using HSMs to inform decisions about translocations, it is important to err on the side of caution. If suitable habitat is underestimated (false negatives) then the worst outcome is that animals are not released into some potentially suitable areas. However, the consequences of false positives are much more significant as they could result in animals being translocated to unsuitable areas and failing to establish. Nonetheless, models should be validated and updated as and when more data become available.

Conservation translocation is defined as “the managed movement of animals or plants from one location to another to achieve a measurable conservation benefit for the population, species or ecosystem” (Seddon, Strauss & Innes 2012; IUCN 2013). This includes reinforcement, where animals are released to an area with an existing (but often small) population; reintroduction, which aims to restore a species to part of its natural range from which it has gone extinct; or conservation introduction, also called assisted colonisation, where the objective is to establish new populations of a species beyond what has previously been its natural range (Seddon 2010; IUCN 2013).

All translocations involve a specific set of decisions including if, where, when, and how to translocate and restore a species to part of its former range that it does not currently occupy. However, these decisions are often made more challenging as a result of multiple, and often competing, objectives. Therefore, it is recommended that a decision analytic approach is used. Decision analysis is defined as “a formalisation of common sense for decision problems which are too complex for informal use of common sense’ (Keeney 1982). Decisions are driven by objectives and measures of success that are clearly defined at the outset. Subsequent decisions can then be approached as an iterative sequence of steps. At each step, a set of potential alternative actions can be identified and assessed. For each potential alternative, it is then possible to evaluate any trade-offs and uncertainty and to make predictions of the likely outcomes in relation to the stated objectives. Finally, the optimal action(s) can be implemented, and the results monitored.

All projects should follow the guidelines for the justification, design and implementation of conservation translocations published by the International Union for Conservation of Nature (IUCN) (IUCN 1995; IUCN 2013) and incorporated into the Scottish and English Codes for Conservation Translocations (NSRF 2014; DEFRA 2021).

Conservation translocations are inherently complex, high risk activities and reviews of the outcomes have often reported low rates of success (Wolf *et al*. 1996; Fischer & Lindenmayer 2000; Seddon 2010; Sainsbury & Vaughan-Higgins 2012; Weise, Stratford & van Vuuren 2014; Berger-Tal, Blumstein & Swaisgood 2020). Nonetheless, in circumstances where natural recovery or recolonisation is unlikely, and other options are limited, then translocations may be needed, but they should only ever be considered as a last resort. Reintroductions are long-term projects that require the commitment of long-term financial and community support.

Methods summary

We developed a relatively simple framework to help guide spatial targeting, using modelling methods based on data and knowledge of pine marten ecology and distribution. This framework is illustrated in **figure 2**. We then applied the framework to a number of regions in Britain, where conditions might be suitable, to demonstrate its use and assess their potential for pine marten recovery or restoration. The results can be used to prioritise and inform future pine marten recovery projects.

We used MaxEnt (Phillips, Anderson & Schapire 2006) presence-only Habitat Suitability Modelling (HSM) to predict suitability of habitat for pine martens across the whole of Britain. Models were constructed using different combinations of training datasets to look at potential habitat suitability for pine martens under a range of conditions. In the context of the decision framework to which these models were applied, the consequences of overestimating habitat suitability would be far worse than those of underestimating it. Therefore, to minimise the risk of false positives, we used the most conservative model. We then used outputs from the Habitat suitability modelling in Circuitscape v4.0.5 (McRae *et al*. 2008) to map habitat connectivity for pine martens in Britain.

We carried out Population Viability Analyses (PVA) using HexSim (Schumaker & Brookes 2018), a spatially explicit individual-based population model, to link landscape structure from the habitat model with habitat quality and population dynamics. This approach provides a general method for identifying some of the biologically important elements of critical habitat that make a significant contribution to long-term regional population persistence. We used HexSim to run a series of simulations to look at likely patterns of pine marten persistence, dispersal and range expansion both at a national scale with and without translocations and, at a finer scale, to further investigate potential reintroduction regions.

Full accounts of all the modelling methods and data sets used are detailed and discussed in the appendix.

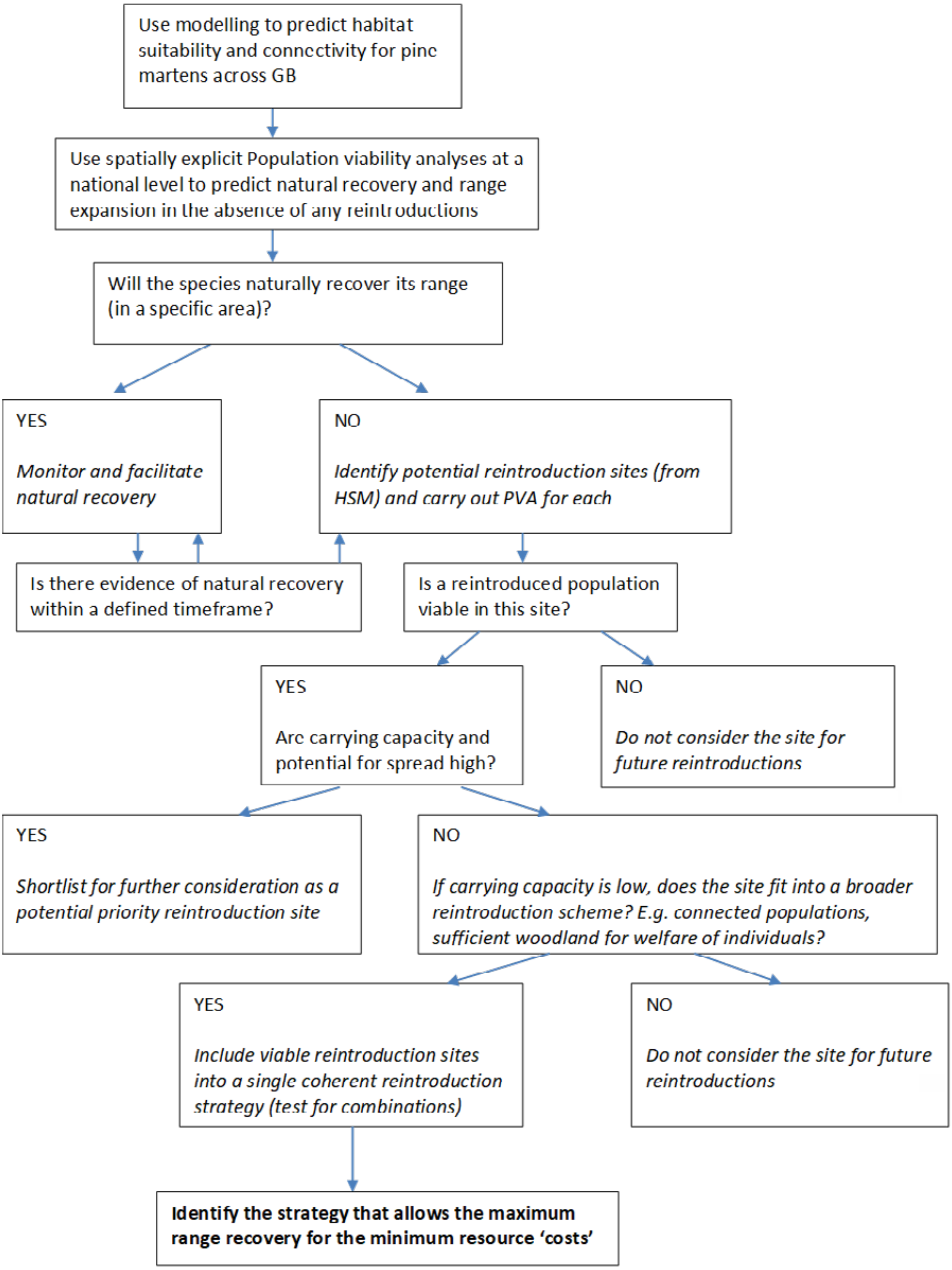


Figure 2. Summary of the framework developed and demonstrated here to optimise decisions around pine marten recovery and restoration.

3. Promoting and facilitating natural recovery (objective 1a)

The first question to ask when considering translocations is whether translocation is necessary, or the best option. Other conservation actions, such as habitat management to improve connectivity and facilitate natural recolonisation, could provide an alternative option with fewer risks and lower costs.

Habitat suitability modelling was carried out for Britain and the results used to generate HexSim spatially explicit population models (for methods see Appendix). The results of HexSim were used to look at where, in Britain, natural recolonisation is likely to occur in the next 25 years. For the 'natural recolonisation' model, we did not incorporate translocations to Wales and Gloucestershire. The results, shown in figure 3, predict that, within 25 years, it is highly likely that the population of pine martens in Scotland will have spread south and established in several of the northern counties of England, including Cumbria, Northumberland and Durham and will have begun to expand into Lancashire and North Yorkshire. However, without intervention, there would have been no natural expansion of pine marten populations south of the Humber in England.

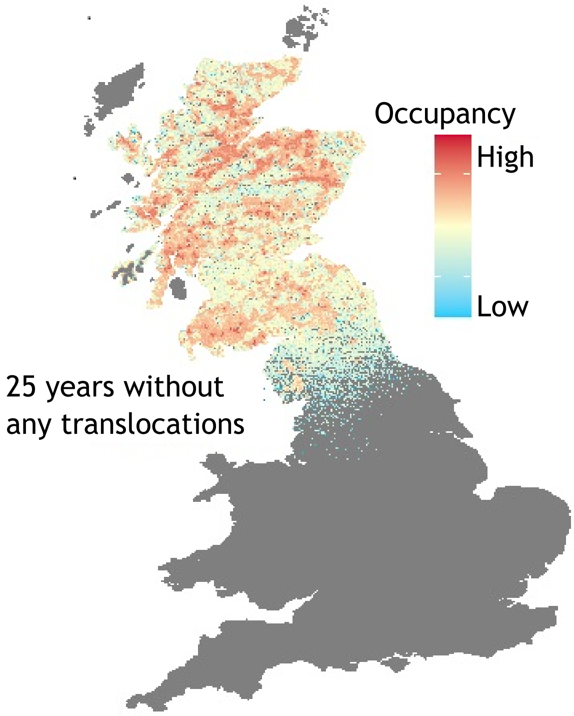


Figure 3. HexSim predictions of pine marten occupancy after 25 years without incorporating any translocations taking place outside Scotland.

We then ran simulations using the same parameters but with the inclusion of translocations that have already taken place into central Wales and the Forest of Dean, in Gloucestershire. The results of simulations 'with translocations' are shown in **figure 4**.

Figure 4. HexSim predictions of pine marten occupancy in southern Britain after 10 years including translocations to Wales only (left) or Wales and Gloucestershire (right).

The results of the real data model, incorporating translocations that have actually taken place to date, show that the re-established population in Wales would have taken time to expand beyond the Welsh Marches, but that the addition of the reintroduction in the Forest of Dean consolidates the range expansion into South Wales and should result in a robust Western metapopulation of pine martens within approximately ten years of the first releases into mid Wales. However, there is no natural recolonisation of suitable habitats in south-west England or in the east of the country within this timeframe. The likely impact of translocations so far on nationwide pine marten recovery in Britain is shown **figure 5**.

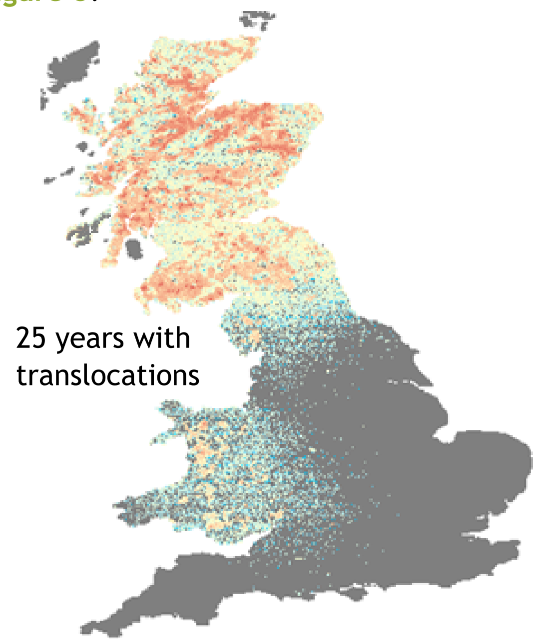


Figure 5. HexSim predictions of pine marten occupancy after 25 years incorporating translocations to date.

Natural range expansion and recolonisation of former range is common for many species when conditions are suitable (Caniglia *et al*. 2014; Gadenne *et al*. 2014).
While habitat loss and persecution historically caused many predators, including pine martens, to be confined to areas with minimal human activity, attitudes towards predators are now changing. Following decreases in persecution, predators are often able to recolonise areas from which they were previously extirpated (Chapron *et al*. 2014). Pine martens are mobile and capable of relatively long-distance dispersal (of up to 103km reported by McNicol *et al*. 2020) and recolonisation, as has been seen in Scotland in recent years (Croose, Birks & Schofield 2013; Croose *et al*. 2014). However, it cannot be assumed that this will always be the case. It has been proposed that in some circumstances, for populations undergoing natural range expansion, individuals can be constrained by density-dependent effects.

In a low-density population, new recruits to the population are able to select optimal territories of high quality. As density increases and the best territories become occupied, more and more individuals may have to settle in poorer territories where their reproductive success is likely to be lower. As the overall population increases, therefore, its mean breeding success may be reduced. But when individuals are released into a new area, lack of competition means that individuals can select the most optimal territories, allowing them to achieve a mean productivity higher than in the original population (Morandini *et al*. 2017). In a natural colonisation with empty high-quality habitat outside the old population boundaries, high rates of productivity can also be achieved. However, if the only accessible habitat at the colonisation front is of low quality, then productivity will inevitably be affected. Natural colonisation is limited by the habitat quality that can conceivably be reached in the course of normal dispersal movements. In contrast, translocations are not restricted to areas surrounding existing populations, and the availability of good habitat for the species is one of the main criteria in release site selection (Armstrong & Seddon 2008). For this reason, new territories limited to areas surrounding existing populations can show lower productivity than territories in release areas selected by habitat quality values and without already established populations (Morandini *et al*. 2017). In addition to landscape and environmental factors, anthropogenic effects may limit natural range expansion if, for some reason, there is exceptionally high mortality at the expansion front, such as on a road or in an area of intensive predator control where there is a high risk of accidental mortality (Wabakken *et al*. 2001; Liberg *et al*. 2012; Nowak & Mysłajek 2016).

For the reasons discussed here, it is essential to monitor natural range expansion where it is predicted to occur and, if it has not, then question why and, if appropriate, take the necessary measures to assist the population to cross any natural or man-made barriers.

4. Prioritising optimal areas in which to consider pine marten reintroductions (objective 1b)

It has been shown repeatedly that quality and suitability of habitat are among the most important factors in determining the success of species reintroductions (Griffith *et al*. 1989; Wolf *et al*. 1996). Therefore, it is imperative that significant efforts are put into evaluating areas before considering them for potential reintroductions. It cannot be assumed that all the historical ranges of a species will still provide sufficient suitable habitat for a reintroduced population to establish, reproduce and persist. In fact, it may often be inappropriate to reintroduce within the former range (Seddon 2010).

The more time that has elapsed between local extinction and a planned reintroduction, the greater the likelihood that the habitat will no longer be suitable. This means there is a need to evaluate habitat suitability regardless of historical occupancy. Detailed knowledge of a species' ecology can provide information on the likely current suitability of a proposed release site, but modelling enables that knowledge to be put into a landscape context, projected into a range of current and future scenarios and compared against a number of objectively assessed alternative sites (Osborne & Seddon 2012). In this way, the effectiveness of species reintroduction programmes can be maximised (Razgour, Hanmer & Jones 2011).

Connectivity among habitats and populations is also crucially important in maintaining gene flow, metapopulation dynamics, demographic rescue, range expansion and, consequently, population persistence. In order to make effective conservation planning decisions to conserve species in increasingly fragmented landscapes, an understanding is needed of how connectivity is affected by landscape features. Many ways of predicting connectivity using landscape data have been developed recently, including connectivity models from electrical circuit theory. These can be used to model connectivity in ecology and conservation. We used Circuitscape (McRae & Shah 2009) methods here to determine likely corridors and other important elements of the landscape connecting suitable habitat for pine martens. For full details of methods, see the appendix.

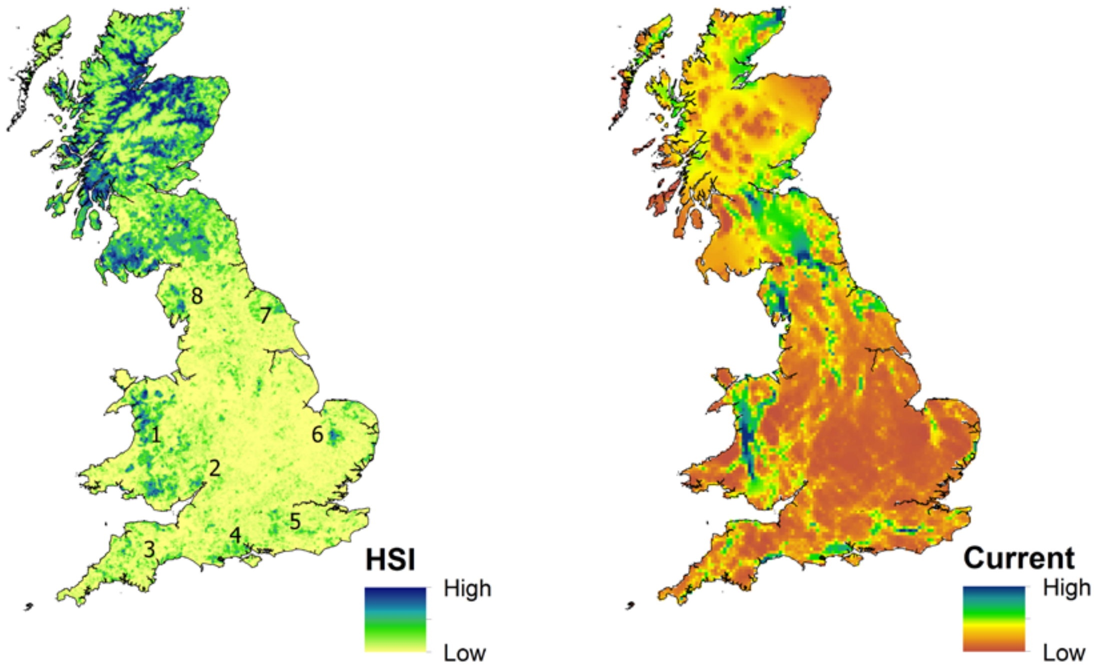


Figure 6. Predicted habitat suitability (left) and connectivity (right) for pine martens in Britain. Regions numbered anti-clockwise are: 1. Mid Wales, 2. Forest of Dean, Gloucestershire, 3. South-west England, 4. Hampshire, 5. South-east England, 6. East Anglia, 7. North Yorkshire, 8. South Cumbria.

Results of habitat suitability and connectivity modelling suggest that the majority of contiguous (or well connected) highly suitable habitat for pine martens is in the north and west of Britain. The areas numbered 3-8 are considered in more detail below. Translocations of pine martens have already taken place into the largest contiguous region of highly suitable habitat running from north to south Wales along the Cambrian mountain range (*number 1 in figure 6*). A reintroduction is also underway into the Forest of Dean (*number 2 in figure 6*) to the north of the Bristol channel. There are other areas in south-west England (*3*), south-east England (*5*) and East Anglia (*6*) that warranted further investigation as to their potential for re-establishing viable pine marten populations. It is thought that there is now a small population of pine martens in the south, around the New Forest in Hampshire (*4*). This should be monitored for evidence of breeding and future expansion, but is in an area that would likely be colonised by dispersers from an expanding western core once this exceeds carrying capacity. We used the modelling methods described previously (and in the appendix) to look at the impacts and likely establishment of future reintroductions to the regions predicted as having suitable habitat numbered 3-8 in **figure 6**.

South-west England

Whilst there are no large blocks of forest in the south-west that are of comparable size to those in Scotland and Wales, the counties of Somerset, Devon and Cornwall have reasonable percentages of woodland (7%, 9.9% and 7.5% respectively; Forest Research 2002) and a low density of roads (Department of Transport 2018). Predicted suitable habitat is dispersed throughout the landscape in the form of well-wooded valleys, many of which are connected via river catchment networks, although a high volume of traffic resulted in the low habitat suitability scores seen in some of south Devon. Circuitscape was used to examine landscape resistance and connectivity between areas of suitable habitat for pine martens in the three counties. The results suggest there is high current (connectivity) across the landscape in north Somerset, north-east and south Devon, with some further west from south-west Devon into the border with Cornwall (**figure 7**). Spatially explicit population viability analyses were carried out for south-west England with simulations run to investigate the population viability and potential spread of pine martens over a 50-year period. Models were used to compare the results of reintroducing individuals into north Somerset, into south Devon and into release sites in both counties. The results suggest that it is likely that a viable population would result from any of the three scenarios, but that a landscape scale reintroduction project across both counties would result in a (meta)population with the most resilience.

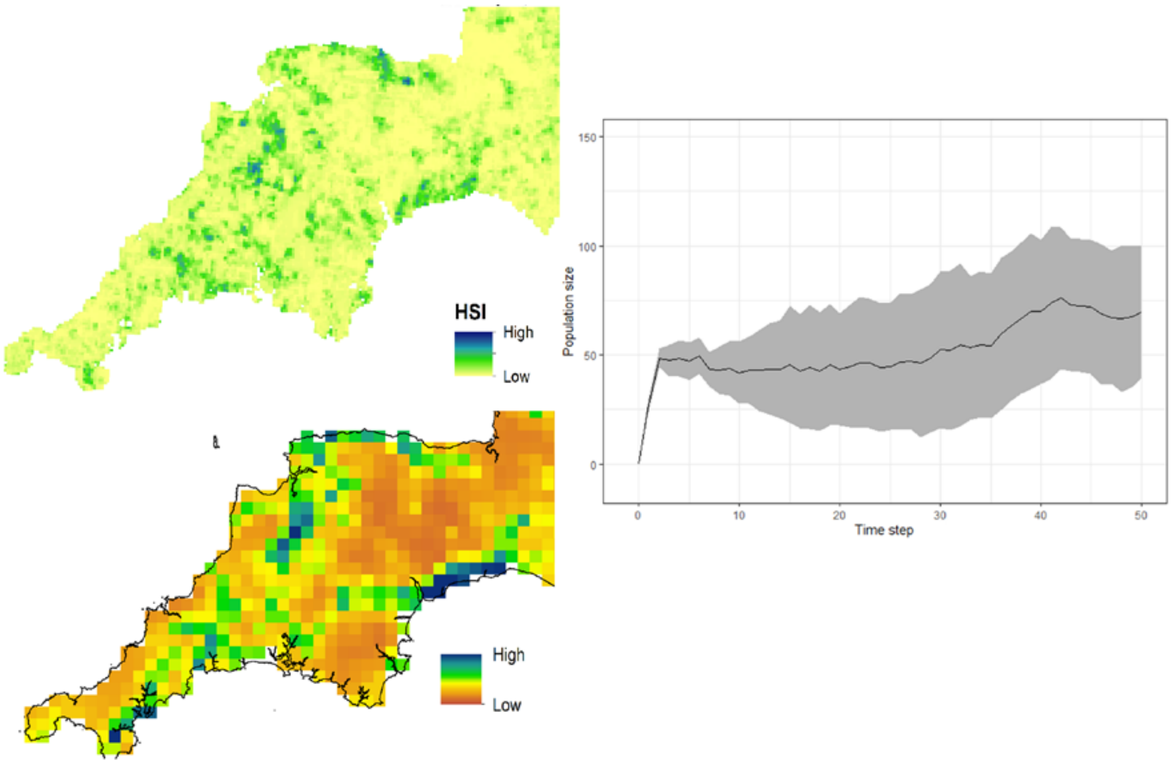


Figure 7. Predicted habitat suitability (top left) and current/connectivity (bottom left) for south-west England. Right: results of HexSim spatially explicit population viability analyses.

The results suggest that the counties of Devon and Somerset could be suitable for a future reintroduction project, subject to more detailed investigation of other factors. These include prey availability, any potential impacts on other species and habitats, as well as the likelihood of positive or negative perceptions or conflict with other land users.

East Anglia

There is a reasonably large area of suitable habitat centred on Thetford Forest in East Anglia. Results of spatially explicit PVA suggest that a reintroduced population here would be viable. However, the total amount of woodland in the region is small and the circuitscape model outputs show that there is very limited connectivity to any other suitable areas. Current (connectivity between suitable habitat) across the region is very low, therefore landscape resistance is high and pine martens would find it a challenge to disperse away from the release area once the carrying capacity of the woodland was exceeded. This could result in what was effectively an ‘island’ population with the consequent issues of genetic management. Thetford Forest was suggested as far back as the mid-1980s as a potential reintroduction site for pine martens (Yalden 1986). However, it covers a relatively small area and the county of Norfolk, in which the majority of Thetford lies, has a high density of gamekeepers (Bright & Harris 1994), and therefore there is likely to be potential for conflict with game shooting interests and predator control.

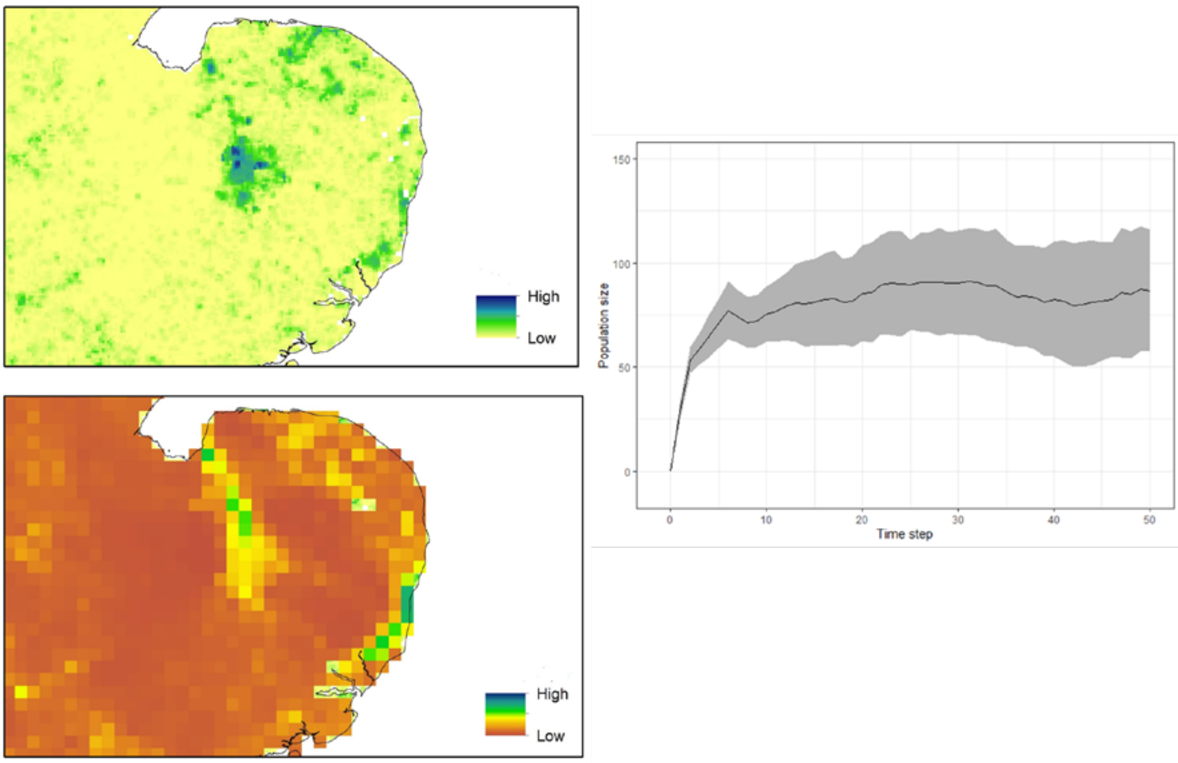


Figure 8. Predicted habitat suitability (top left) and current/connectivity (bottom left) for pine martens in East Anglia and results of population viability analyses (right) for reintroductions of pine martens into the region (20 iterations, mean and sd).

South-east England

This area encompasses both the North and South Downs to the west of London as well as the Weald region to the south and east of the capital. The south-east of England has a relatively high percentage of woodland cover and very extensive areas of broadleaf woodland. However, this region is very densely populated, covering just one tenth of the land area, but with over one third of the UK population living there. It also has significantly higher traffic flows than any other Department of Transport region in Britain (https://roadtraffic.dft.gov.uk/regions).

Pine martens are vulnerable to road traffic accidents (Velander 1983; Haigh 2012; Ruette *et al*. 2015), and animals exploring over large distances following release (Davis 1983; McNicol *et al*. 2020) might be especially so. Therefore, reproduction in this region may fail to keep pace with mortality. Pine marten populations are acutely vulnerable to increased mortality from direct persecution or traffic accidents. Sensitivity analyses of pine marten population viability models showed that persistence was highly sensitive to changes in adult mortality (Stringer *et al*. 2018) and that pine marten populations were unlikely to survive additional mortality of more than 30% per year (Bright & Harris 1994).

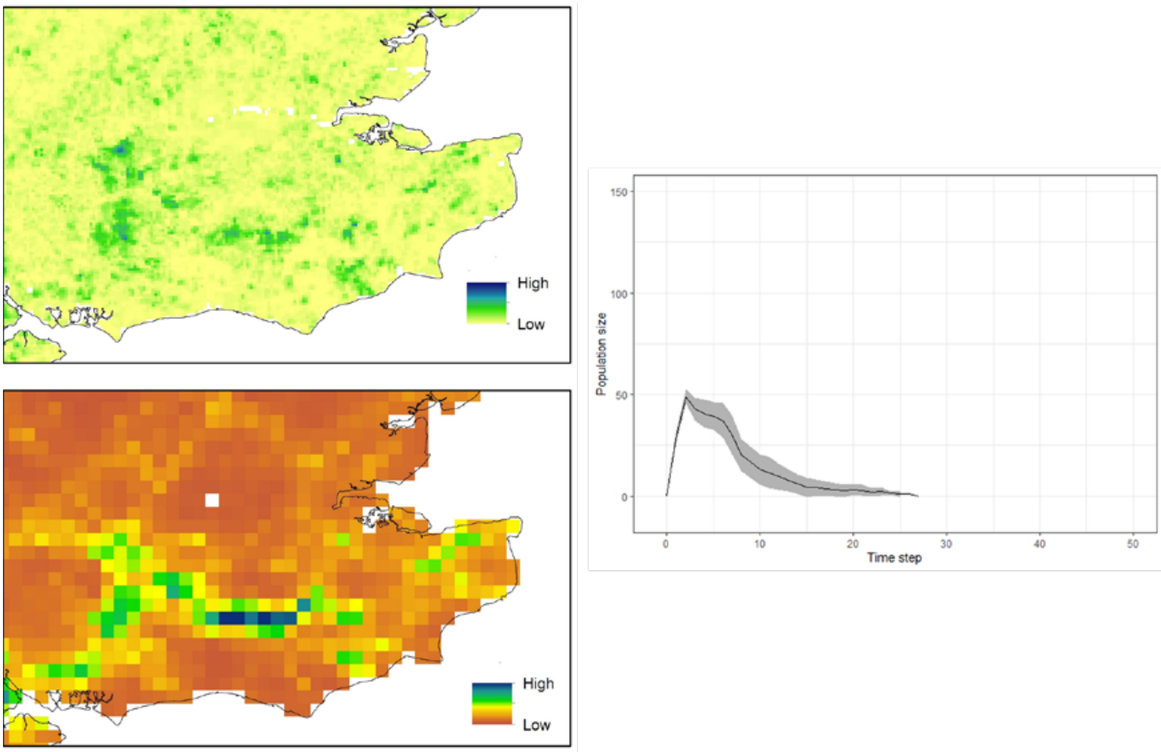


Figure 9. Habitat suitability (top left) and connectivity/current (bottom left) for pine martens in south-east England and results of spatially explicit PVA if 50 pine martens were reintroduced here.

The Netherlands is often cited as an example where pine marten populations persist alongside human and road densities that are equivalent to those in the south of England. There was increased urbanisation and the construction of a dense road network in the Netherlands from the 1960s to 1980s. The pine marten population was thought to have declined to around 400 individuals in the 1990s, but population sizes started to increase again after 2000 (De Groot *et al*. 2016). Nonetheless, the distribution of pine martens in the Netherlands still centres around a few core habitats, and genetic analysis suggests that they can be subdivided into a northern and a central subpopulation, which may reflect limited dispersal between core habitats in the two areas. Pine marten abundance in the Netherlands has been increasing and dispersal into the surrounding habitats has been observed, however roads do cause large numbers of traffic casualties each year and act as barriers for dispersal (De Groot *et al*. 2016). The first individuals to be released into a new area may be more likely to leave the vicinity of release sites, due to the inherent absence of resident conspecifics (McNicol *et al*. 2020). Sites in close proximity to dense or heavily used road networks, or other potential causes of conflict or mortality pose a higher threat in the early stages of reintroduction.

Therefore, based on our analyses, the south-east of England is not a region that should be prioritised for pine marten reintroductions, as mortality is likely to be high which would impact the establishment of a relatively small founder population. However, there is suitable habitat and, provided there was a source of recolonisers in the surrounding landscape, the high rates of additional mortality could be compensated for. Improving connectivity to other regions where reintroductions have a higher likelihood of establishment could promote dispersal and natural recolonisation to suitable habitats in the south east in future.

South Cumbria

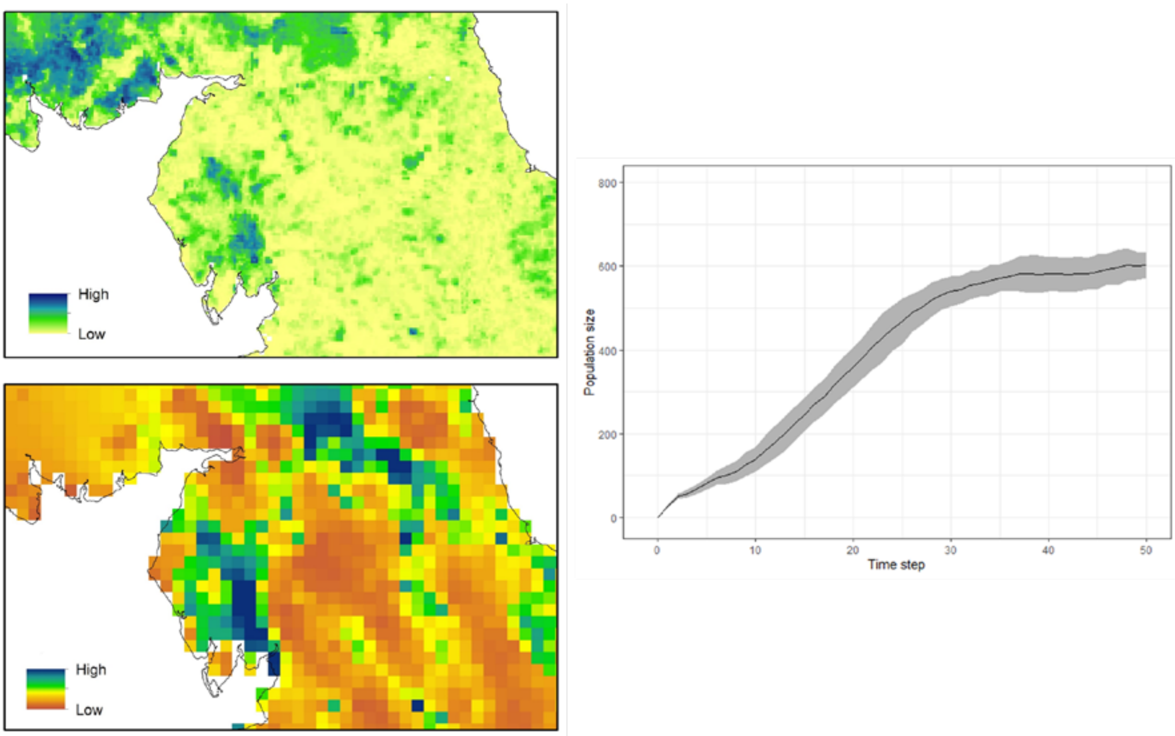


Figure 10. Habitat suitability (top left) and connectivity/current (bottom left) for pine martens in the north of England and results of spatially explicit PVA if 50 pine martens were reintroduced into south Cumbria.

Modelling suggests that there is a large amount of suitable habitat for pine martens in the Lake District, particularly around Grizedale. The PVA model for Britain predicts that this region will be naturally recolonised by pine martens within 25 years. This should be monitored and natural recovery facilitated where possible. Circuitscape results indicate that, although there is relatively good current (connectivity) between the western edge of Kielder Forest on the Scottish border and the suitable habitat further west, there is an area of higher landscape resistance across Carlisle and the M6 motorway, as well as the open fells of the northern Pennines. Future work could look at improving connectivity to reduce this. HexSim simulations with pine martens reintroduced to south Cumbria show that a population would be viable and highly likely to establish (**figure 10**).

North Yorkshire

North Yorkshire is an area with occasional records of pine martens in recent years. The HSM and circuitscape models suggest that there is an area of high habitat suitability and connectivity on the eastern side of the North York Moors. However, this is relatively isolated from other areas to the north and the HexSim model for Britain (**figure 5**) shows that this region is unlikely to be colonised naturally from an expanding Scottish population. The main barriers are likely to be the conurbations of Middlesborough, Darlington, Newcastle and Sunderland with their associated road networks. When HexSim was used to simulate pine marten reintroductions to this region, the population slowly declined over time. Although it persisted for the modelled timeframe of 50 years, it was at lower levels than the number of animals released and would be vulnerable to stochastic events. (**figure 11**). Nonetheless, if there was a small but constant influx of individuals dispersing from further north, this might make a population of pine martens here more resilient.

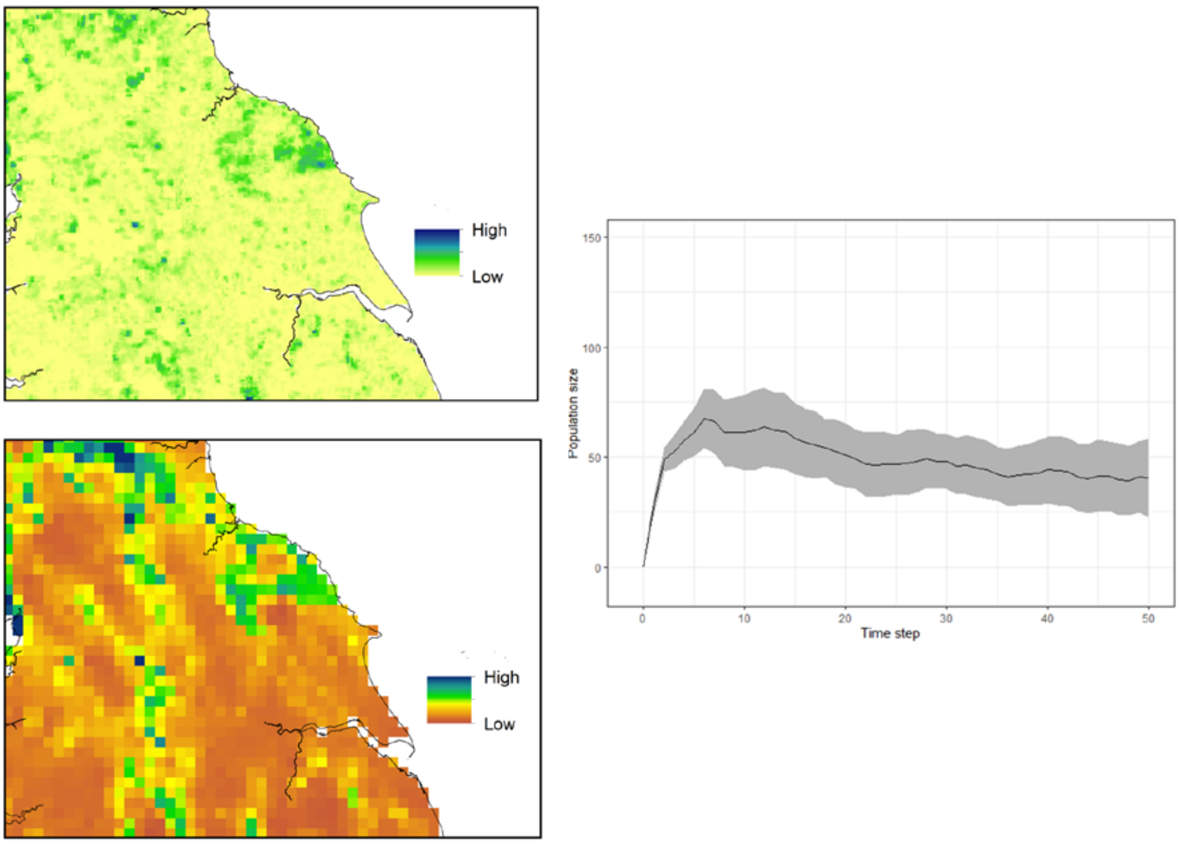


Figure 11. Habitat suitability (top left) and connectivity (bottom left) for north Yorkshire and (right) HexSim results for simulated reintroductions.

Hampshire/New Forest

There have been intermittent unequivocal records of pine martens present in this region, from the 1970s through to 2020, including animals of both sexes and some that were identified as juveniles from road casualty carcases. Their origin is unknown, but it suggests that there may be a very small number of pine martens living wild, at least for a time, and possibly breeding. Our HexSim simulations of the outcome of translocating a viable number of founder animals to this region declined rapidly but did persist for 50 years, albeit at very low levels. This may give some indication of why pine martens have failed to establish a significant population here and warrants further investigation. The New Forest has a reasonable amount of woodland and predicted highly suitable habitat for pine martens. However, there is a dense road network here and gamekeeper density is also relatively high so there are increased risks of accidental mortality. Field voles, the pine martens' main prey, may also be at lower density here than in other regions due to the heavy grazing pressure (Putman, 1986) from ponies and deer. Intensive outdoor recreational use may also make this region unsuitable for translocations of pine martens as a result of high levels of disturbance.

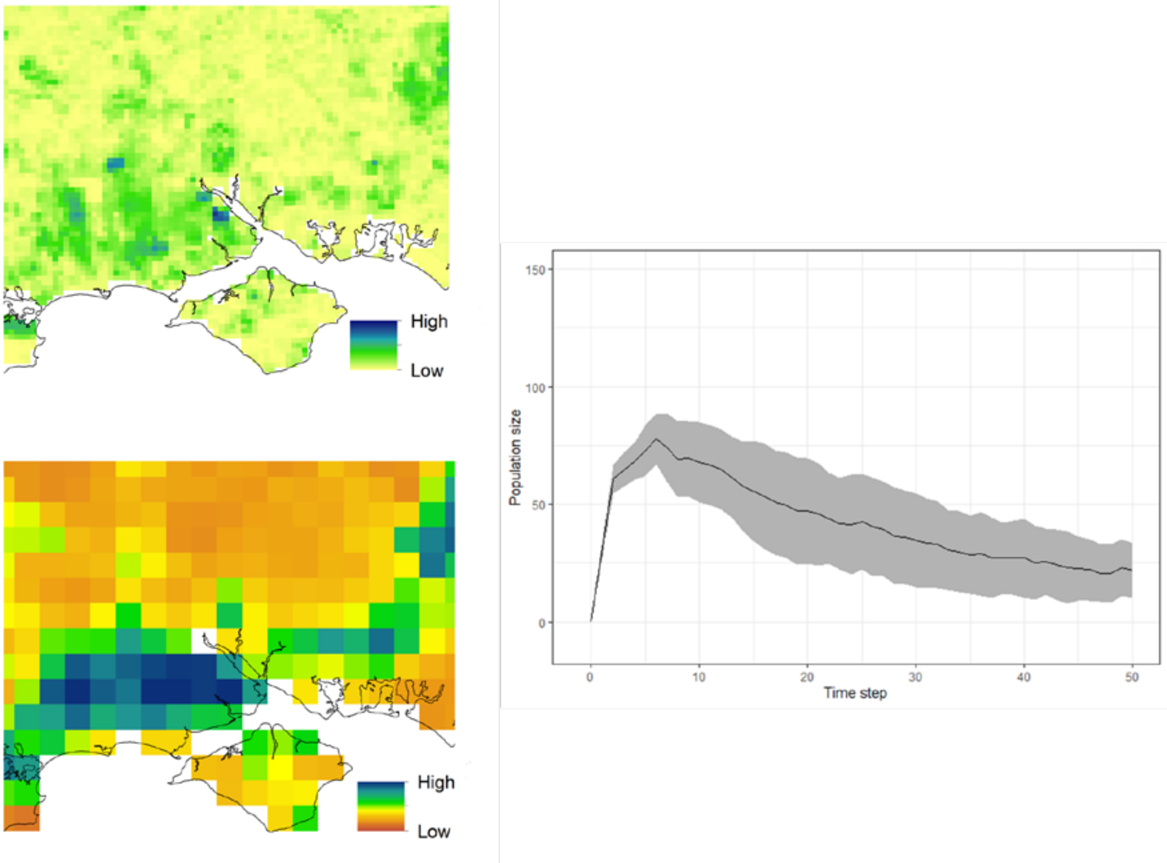


Figure 12. Habitat suitability (top left) and connectivity (bottom left) for Hampshire and (right) HexSim results of reintroductions.

The Circuitscape analysis shows that there is low resistance/high current throughout the New Forest area and again to the east, and across to the suitable habitat in the South Downs and beyond. However, because the Solent and Southampton would act as a barrier to pine martens, any animal dispersing eastwards would first have to go north, into relatively impermeable habitat, in order to cross. Improving habitat connectivity along this west-east corridor in the south would facilitate natural range expansion and recolonisation from the establishing reintroduced pine marten populations in Wales and Gloucestershire. The circuitscape map for Britain in **figure 6** suggests that there is a route of moderate current running southwards from the Forest of Dean to the New Forest and on into the South Downs. A landscape project with the aims of increasing this potential connectivity could have significant benefits for pine marten conservation in the south east of England. It is suggested that this should be explored within the next five to ten years, once there is more information on the movement and range expansion of the reintroduced pine marten population in Gloucestershire.

Discussion

Modelling can play a key role in informing species reintroduction decision making (Seddon, Armstrong & Maloney 2007). The IUCN guidelines recommend that modelling is used to explore different scenarios and to devise an optimal strategy. This should take account of intraspecific variation and dispersal as well as the fundamentally important objective of matching habitat suitability and availability to the target species (IUCN 2013). Habitat suitability modelling in conjunction with spatially explicit population viability models are useful tools with which to contribute vital information into the broader, more complex decisions made by policy makers and conservation practitioners of whether to proceed.

Reintroductions, especially those of carnivores, are often complex and costly, making efficiencies in planning highly beneficial. Time spent on modelling the likely outcomes of different scenarios is disproportionately valuable, compared with the financial, welfare and reputational costs of repeated reintroduction failures.

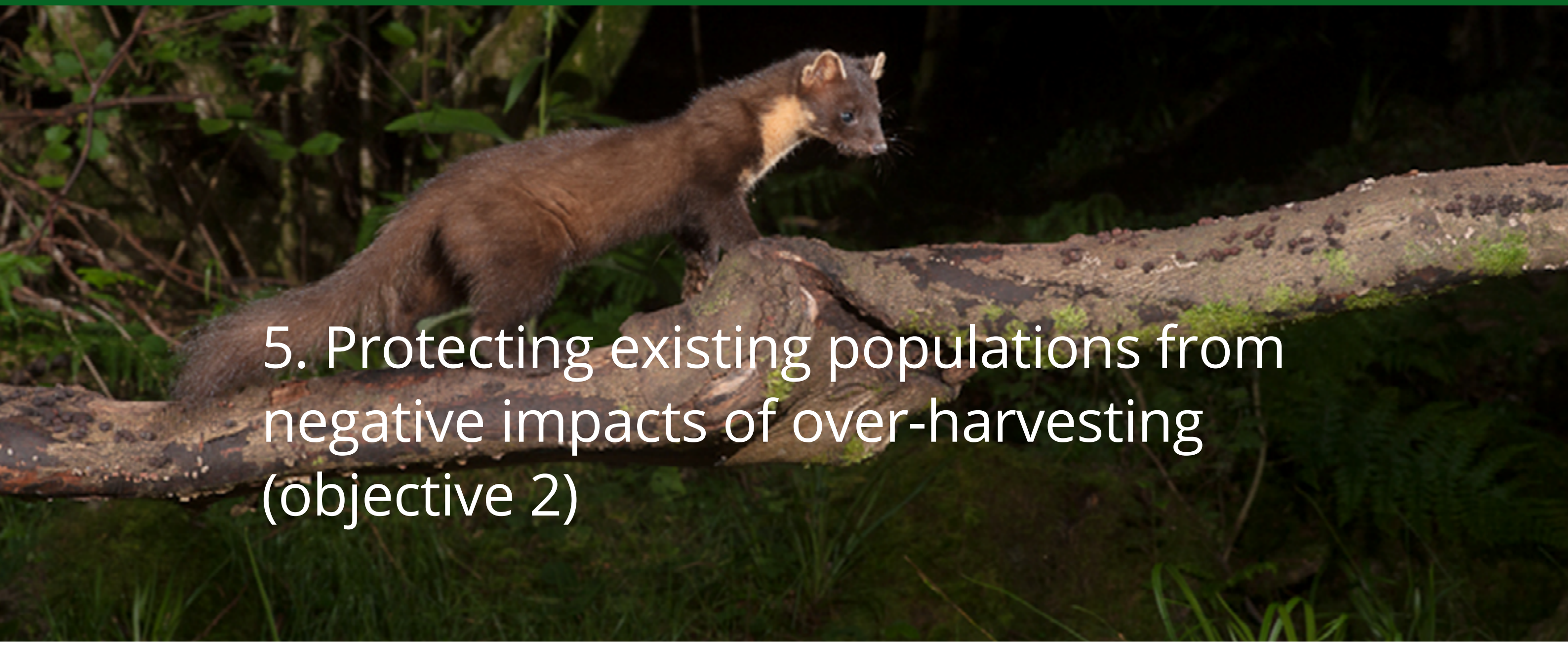
Table 1. Summary of positive and negative results for each of the regions.

	Natural recolonisation	Habitat	PVA	Connectivity
Cumbria	+	+	+	+
South-west	-	+	+	+
South-east	-	+	-	-
Hampshire	-	+	-	-
East Anglia	-	+	+	-
North Yorkshire	?	+	?	-

The prioritisation exercise carried out here suggests that south-west England merits further consideration as a potential pine marten reintroduction region. Some areas in south-west England may be suitable for reintroductions contingent on the results of appropriate disease risk analysis, as well as risk assessments for other species and habitats and minimal conflict with other land users. It would then depend on sufficient resources being secured for a reintroduction and subsequent long-term monitoring and engagement.

The socio-economic context, specifically human attitudes, is fundamental to the success of carnivore reintroductions and its importance cannot be underestimated.
In south-east England and Hampshire/New Forest, the high density of roads, traffic and other infrastructure probably pose too high a threat to a founder population of pine martens that would, inevitably, be relatively small in the early stages of any reintroduction, in comparison to one at carrying capacity (Deredec & Courchamp 2007). Considerable effort should be put into expanding and improving existing habitat in terms of size, quality and connectivity, providing good natural and artificially enhanced dispersal corridors. The potential for increasing habitat connectivity and linkages with the pine marten population in Gloucestershire should be explored to create dispersal corridor routes, as well as possible road crossings/green bridges/underpasses to increase landscape permeability for pine martens and other wildlife

Modelling suggests that, within the next 25 years, south Cumbria is highly likely to be recolonised by pine martens dispersing from the Scottish borders and Northumberland. It is recommended that periodic distribution/expansion zone surveys are carried out to compare with model predictions and refine these with more data. Habitat suitability might be increased by providing additional resources such as artificial den sites for breeding females where appropriate. The potential for improving dispersal corridors from the current pine marten range should also be explored. However, the population of pine martens in southern Scotland may derive from a relatively small number of animals including 12 that were translocated to two sites in Galloway Forest in the early 1980s (Shaw & Livingstone 1992) as well as some rehabilitated pine martens that have subsequently been released in the Scottish Borders by the SSPCA (Croose *et al*. 2014). This relatively small number of founders and consequent likely low levels of genetic diversity may have led to the slow rate of range expansion from Galloway (c21.2km per decade) observed so far (Croose, Birks & Schofield 2013). Similarly on the island of Skye, which pine martens colonised after the road bridge to the mainland was built in 1995, the rate of population expansion by 2011 was estimated at only 26.6km per decade (Roy *et al*. 2014). Therefore, subject to further investigation, reintroductions of pine martens to the area around Grizedale in south Cumbria might be an efficient way of accelerating their spread in northern England and should not be ruled out.



5. Protecting existing populations from negative impacts of over-harvesting (objective 2)

To safeguard viable populations of pine martens throughout their range in Britain requires effective monitoring of population changes and tools to ensure that harvesting of donor populations for reintroductions is sustainable.

A key element of successful reintroduction programmes, and the removals associated with them, is the integration of genetic considerations of both donor and founder populations into the scientific design (Robert, Couvet & Sarrazin 2007). In addition to any impact on absolute numbers, harvesting donor populations can potentially cause a genetic bottleneck leading to inbreeding and loss of genetic diversity, and as a result may have hidden consequences. Therefore, the size and genetic diversity of potential donor populations are central points to consider when assessing impacts of removals on both genetic diversity and population persistence (Jamieson & Lacy 2012; IUCN 2013).

Population viability analyses suggest that between 30 to 40 pine martens need to be released in an area to maximise the viability of the founder population (Bright & Halliwell 1999; MacPherson 2014, *unpubl.data*). Where possible, if there are still suitable donor populations in the wild, it is recommended that wild caught animals are used for reintroductions (Griffiths & Pavajeau 2008). These generally show higher survival and better adaptation to new environments than captive bred animals, and this is especially true for carnivores (Jule, Leaver & Lea 2008). Ideally, donor populations should show characteristics based on genetic provenance, morphology, physiology and behaviour that are appropriate to the reintroduction sites. Animals sourced from areas with similar prey species, competitors, predators and habitats often show higher rates of post-release survival and reproduction (Aber *et al*. 2013). A published study comparing the haplotype composition of historical and current pine marten populations in England, Scotland and Wales found no differences between the main haplotype of contemporary (post-1950) populations across Britain (Jordan *et al*. 2012). Therefore, in comparison with other options (discussed on p36) the increasing and expanding population of pine martens in Scotland is currently the most suitable source of animals for translocations elsewhere in mainland Britain. However, any harvesting must be carefully managed to avoid negative impacts on recovering Scottish populations. It is important to conserve the recovering pine marten population in Scotland, as well as to monitor and facilitate natural spread and recolonisation where possible. Reintroductions should only be to the most optimal regions in priority order, and in such a way that has the minimum risk to donor populations and maximises the probability of reintroduced populations establishing, spreading and ultimately linking up.

Since 2015, VWT has carried out pine marten translocations from Scotland for population restoration in Wales (MacPherson 2018) and, more recently, England (Gloucestershire). A primary consideration in these translocations was to minimise the potential for negative impacts on recovering donor populations in Scotland. Regions likely to contain suitable pine marten donor populations for translocations to date have been identified on the basis of woodland cover, altitude and known length of occupancy by pine martens. Initially the maximum number of pine martens taken from each source site was proposed based on a combination of the following: indices of pine marten activity from scat surveys carried out in the preceding March (VWT unpubl. data); and conservative estimates of the number of adult pine martens present, derived from correlates of pine marten density (prey indices and forest cover) and woodland area (as per Bright and Halliwell 1999).

The donor populations identified by VWT were those within large forest blocks where the removal of between two and four individuals per forest in late summer (at the end of the breeding season) was unlikely to have an impact on viability of the source population as these individuals would quickly be replaced by dispersing juveniles. Timing of removals is key as there is a higher risk that removing animals in late winter would be additive to other winter mortality and have a greater impact on the donor population.

In addition to scat surveys and habitat assessments at each proposed donor site, informal consultations were carried out with local stakeholders and residents to ascertain if there were any concerns about a small number of animals being removed from the area, or any other projects, research or businesses (e.g. commercial hides or tourism enterprises) that might be impacted. As a result, VWT avoided trapping in areas which were in the proximity of businesses or local people who enjoy watching and interacting with their local pine martens.

Surveys and monitoring have been carried out each year from 2015 to 2020 at the donor sites. Based on precautionary principles, VWT has taken a highly conservative approach to trapping and removing pine martens from Scotland. Data on indices of pine marten activity at donor sites to date suggest that this has proved effective, and population estimates derived from genetic analysis of non-invasively collected samples suggest that only a relatively small proportion of resident animals have been removed (Powell, MacPherson & O'Reilly 2017). However, the sampling strategy could be improved to refine population estimates further and better inform the way in which donor populations are managed and conserved in the face of inevitable demand in future.

By only removing a maximum of four pine martens from any one forest, in autumn, it was expected that territories left vacant by these removed animals would soon be filled by dispersing juveniles or non-territory holding adults and this has been confirmed by subsequent monitoring of these populations since (MacPherson *et al*. 2020). As pine martens are territorial, it is suggested that leaving untrapped 'refugia', at least twice the size of a mean pine marten home range, may protect a population reservoir from which trapped areas will quickly recolonise (Strickland 1994). All trapping and removal so far has been carried out in woodland owned and managed by Forestry and Land Scotland (FLS). However, these are set within a wider, forested landscape and so it is highly likely that there are further sources of recolonisers in privately-owned woodland adjacent to each of the donor sites.

Intensive harvesting of a population with a low rate of increase, in a changeable environment can lead to its extinction or severe depletion (Lande, Engen & Saether 1995). Pine marten populations can be susceptible to overharvest (Helldin 2000), therefore the effects of removing individuals from source populations must be monitored. Preliminary work using scat surveys as an index of pine marten presence and genetic analysis of scats and hairs, indicate that the conservative harvesting approach undertaken to date has been successful in minimising the impact on the donor populations. However, the sampling strategy could be improved to better inform how donor populations are managed and conserved as demand for source animals increases. Advances in molecular methods mean that it is now possible to use non-invasive methods to acquire genetic data to inform conservation decisions. We were able to make some useful preliminary inferences about the impact of harvesting at donor sites in the short term (Powell, MacPherson & O'Reilly 2017). Nonetheless, there are limitations to using scat and hair samples collected on single sampling occasions each year. Further surveying will be required to achieve a higher confidence population estimate and determine whether or not the removal of the pine marten at these sites will have long-term effects on the integrity of the populations.

Juvenile to adult ratios in marten populations vary from year to year, depending on abundance of food resources which affects fecundity as well as recruitment (Flynn and Schumacher 2000). The impact of removing adults, particularly adult females, is likely to have a higher impact on donor populations than that of removing juveniles and sub-adults. However, this must be balanced against the benefits of translocating only adult animals of breeding age to increase the chances of successful reintroduction. There may also be changes in population productivity (i.e. female fecundity or recruitment rate) following removal of pine martens. This may be affected positively, as a result of reduced intra-specific competition, or negatively if removals disrupt territorial behaviour.

The PVA model on which the initial harvesting protocol was based, predicted that two years after 15% of adult animals were removed there was a more than 80% probability that populations would have returned to their initial size. However, even if 25% of the population was removed, there was a high (>90%) probability that five years after the removal the population would have returned to its initial size (Bright & Halliwell 1999). Therefore, it is suggested that currently, it would be prudent NOT to re-trap at sites from which animals have already been removed for translocations, until at least five years have elapsed since they were last trapped. However, one of the limitations of these harvesting models is that they require accurate population estimates in order to be implemented (and tested) effectively.

Age structure and survival can fluctuate considerably in marten populations in the short term. For example, following years when there is an abundance of prey, such as a peak in microtine vole population cycles, marten reproduction and survival increases (Powell *et al*. 1994). It is therefore recommended that a rigorous, cost-effective monitoring protocol be established to monitor medium to long-term impact on donor sites, building on the preliminary work done to date. A combined sampling approach comprising hair tubes and scats following the methods of Croose *et al*. (2019) has been shown to be effective at detecting a significant proportion of individuals. Hair tubes yielded the highest number of observations per individual ("recaptures") which, combined with scats, resulted in the population estimate with the smallest 95% confidence interval.

VWT is currently designing such a protocol which, subject to funding, could begin as early as 2021.

Donor sites used so far have been north of Speyside and all along the Great Glen. Some of the other more northerly forest blocks, such as those around Loch Shin, could also be considered in future. They have a long history of pine marten occupancy, but they would be logistically more challenging because of their remoteness. They would also necessitate a longer journey by road for those animals that were trapped and translocated to sites in southern Britain, so the potential welfare issues of this should be taken into account.

There are pine marten populations in areas further south that were considered as potential donor sites, such as those around the Trossachs. However, given its relatively southern location and proximity to the Central Belt, the Trossachs population could be an important source of dispersers to the largely un-colonised area to the south of the Central Belt, despite the risks of dispersing through a highly populated area with its associated roads and infrastructure. This is also an area where the recovering pine marten population is thought to be having a negative impact on the grey squirrel population and consequently benefiting native red squirrels (Sheehy *et al*. 2018). For these effects to occur requires a high-density pine marten population. Therefore, it is recommended that no pine martens are removed from populations in areas that overlap with current grey squirrel distribution in Scotland. This includes all of the sites south of the line shown in **figure 13**.

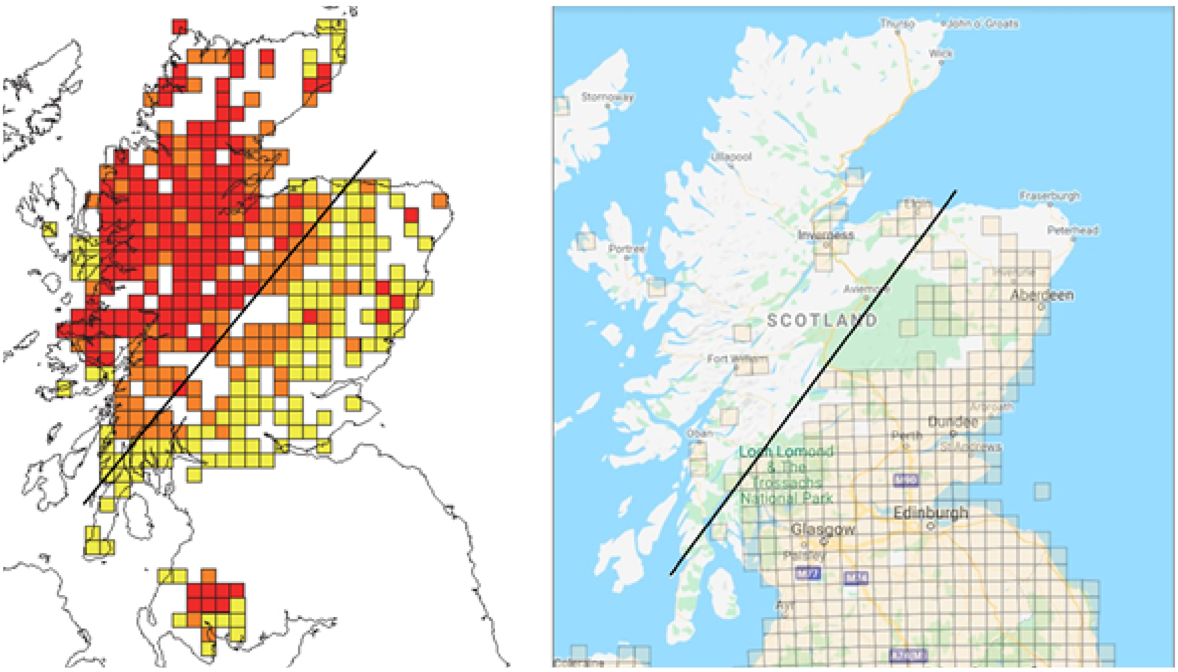


Figure 13. (Left) Distribution of the pine marten in Scotland, comprising records collected from 1980 to 2012. Positive hectads from the 1980-1982 distribution survey (Velander 1983) are shaded red; positive hectads from the 1994 distribution survey (Balharry *et al*. 1996) are shaded orange; and positive hectads from the 2012 Expansion Zone Survey (Croose, Birks & Schofield 2013) are shaded yellow (reproduced from Croose *et al*. (2014)). (Right) distribution of grey squirrel in Scotland (data from NBN gateway downloaded October 2020). Maps based upon Ordnance Survey material with the permission of the Controller of HMSO © Crown Copyright (2013) Licence no. 100017908.

We recommend that there should be a presumption *against* removing pine martens from central or southern Scotland where recolonisation has only occurred relatively recently. It is suggested that further habitat enhancements are carried out in regions where pine marten density is currently low (Central Belt and southern Scotland, northern England, east and west Wales). This could include the provision of artificial den boxes to increase the availability of natal den sites for breeding females, where natural sites in tree cavities may be a limiting resource. Further research is needed to quantify the benefit of this. Periodic surveys at the expansion fronts within southern Scotland and northern England as well as in the Welsh Marches and Gloucestershire are recommended to monitor the status and recovery of pine martens in Britain.

Other potential sources for reintroductions

Captive breeding and rehabilitated animals

Captive breeding for reintroduction is a well-established conservation measure (McGowan *et al*. 2017; IUCN SSC 2013), and release of captive bred animals is a conservation intervention that is also considered here.

Some mustelids, such as sable *Martes zibellina* and American mink *Neovison vison*, are bred in captivity on a commercial scale due to their economic value as furbearers (Lagerkvist 1997; Kashtanov *et al*. 2016). Pine martens, however, despite also being historically exploited for their fur, have never been captive bred in the same large numbers. The pine marten's low reproductive rates and relatively small litters (mean litter size three (Harris & Yalden 2008)) is why so few of them were raised in captivity for commercial breeding (Markley & Bassett 1942). In contrast, captive sables are capable of litter sizes of up to nine per female, making them much more economically viable (Kashtanov *et al*. 2016). Out of the breeding season, pine martens of opposite sexes, if paired in captivity, do not mate but usually interact aggressively. Breeding in all martens involves a long series of complex behavioural interactions eventually leading to mating (Heath *et al*. 2001). Even during the mating season, the results of many attempts at breeding pine martens in captivity have failed because the animals simply would not breed in cage conditions (Landowski 1962). American and Pacific martens (*M. americana* and *M. caurina*), close relatives of the pine marten, were historically used in the fur trade in the USA (where they were known as "Hudson Bay sable"). These two species were the subject of numerous studies in captive breeding at the U.S. Fur Animal Experiment Station over many years. Over a 21-year study period from 1920 to 1941 there was an 80 percent failure in litter production and, of 18 females that died, nine did so as a result of injuries sustained during the mating season (Markley & Bassett 1942).

Much more is known now about the reproductive biology of mustelids (Mead 1989; Murphy 1989; Amstislavsky & Ternovskaya 2000) but there are very few pine martens in captivity in Britain and they remain a species that is extremely difficult to breed in captive conditions. Wildwood in Kent is one of a small number of British wildlife parks that have had some success, by adapting their enclosures to incorporate a tunnel system that allows the pine martens to meet one another prior to pairing. The current focus is on maintaining a small population of pine martens in captivity in Britain for public engagement, education and research, and the capacity for captive breeding is low. The *ex situ* breeding population currently consists of fewer than 20 (mostly older) animals. A conservation breeding programme would therefore require considerable financial investment, continued stud book co-ordination and the addition of further, wild caught animals to increase numbers and genetic diversity of the breeding stock (J.Palmer Pers. comm.). This would take some time to develop. The number of animals released is a key factor in reintroduction success (Griffith *et al*. 1989). It is unlikely that there would be sufficient captive bred stock available in the foreseeable future for a viable founder population (30-40 pine martens) to consist solely of captive bred animals. Nonetheless, the release of captive bred pine martens to augment larger, viable numbers of translocated wild caught pine martens in future should not be ruled out, provided there is sufficient evidence to show that such animals are suitably equipped for life in the wild. This is important as many published studies of carnivore reintroductions have found that captive bred animals have lower post-release survival than wild-born translocated animals (see review by Jule, Leaver and Lea (2008)). However, this can be mitigated by providing captive born animals with an environment that allows them to develop the behaviours and survival skills necessary for life in the wild (Jonas *et al*. 2018). There has been some success, for example with survival of released captive-bred black footed ferrets *Mustela nigripes* (Grenier, McDonald & Buskirk 2007; Biggins, Livieri & Breck 2011), but with no comparison with wild-wild translocations. If the release of captive bred pine martens is considered, it is recommended that research is carried out to assess their suitability for release into the wild, and monitor post release survival alongside that of wild-caught animals released under comparable conditions.

At the time of writing, pine martens are legally protected by inclusion on Schedule 5 of The Wildlife and Countryside Act 1981, which in Scotland is amended by the Nature Conservation (Scotland) Act 2004 and the Wildlife and Natural Environment (Scotland) Act 2011. Under this legislation it is an offence to intentionally kill, injure or take a wild pine marten; or to possess or control, sell, offer for sale or possess, or transport for the purpose of sale, any live or dead wild pine marten. The release of captive bred animals without adequate effort to ensure their future well-being may be an offence under the Abandonment of Animals Act 1960 in England and Wales, and Section 29 of the Animal Health and Welfare (Scotland) Act 2006. However, there is currently no requirement for a licence to release captive bred pine martens in their native range. In Scotland, this is understood to encompass the mainland population north of the Central Belt only. Unlicensed releases further south in Scotland would be considered outwith the current native range and therefore illegal (see the NatureScot guidance on native range for further detail: https://www.nature.scot/professional-advice/protected-areas-and-species/protected-species/invasive-non-native-species/native-range). However, the situation is dynamic as the pine marten populations north and south of the Central Belt are expanding their range and are expected to eventually merge. Therefore, at present, north of the Central Belt in Scotland, and in England and Wales, there is no obligation for such releases to comply with national guidelines and codes of best practice, or to submit proposals to SNCOs for scrutiny and approval, but if doubt remains, captive martens should not be released into the wild and further advice from the appropriate SNCO sought. Unregulated releases may not be in the best interests of the species and/or the released animals and changes to the current legislation should be considered to close this loophole. It is recommended that in Scotland, pine marten south of the Central Belt only is added to the list of former native species in Table 1 of Annex 2 in the NatureScot native range guidance. In England and Wales, in addition to remaining fully protected under Schedule 5, it is suggested that pine marten is added to the list of species in Schedule 9 of the Wildlife and Countryside Act of animal species that may not be released or allowed to escape into the wild without a licence.

The same is true of rehabilitated animals: each year, wildlife centres, including the Royal Society for the Prevention of Cruelty to Animals (RSPCA) and the Scottish Society for Prevention of Cruelty to Animals (SSPCA) rescue and rehabilitate wildlife casualties and orphaned animals of many species (Molony *et al*. 2007; Grogan & Kelly 2013) including pine martens. Wildlife rehabilitation is defined as "the treatment and temporary care of injured, diseased and displaced indigenous animals, and the subsequent release of healthy animals to appropriate habitats in the wild" (Miller 2012). The release of an animal is often considered to be the measure of success; however, the animal's chance of surviving in the wild should be as good as that of its wild counterpart and it is not always possible to collect data to confirm whether this is the case. There have been post-release studies of some of the more commonly rehabilitated mammals including hedgehogs (Morris, Meakin & Sharafi 1993; Morris & Warwick 1994) and polecats (Kelly, Scrivens & Grogan 2010), which suggest that these species at least do have a reasonable chance of survival following release, although not whether they become part of the breeding population in the longer term. Of three orphaned pine marten kits taken into care and captive reared in County Mayo, Ireland in 2012, two (males) were subsequently radio tracked for a short time after their release. At the end of the two- month tracking period in December, both were still alive and in good condition (McGloughlin *et al*. 2018). One appeared to have established a home range while the other was dispersing south when the radio collar was removed. Since 2007, there have been a number of releases of rehabilitated orphaned or abandoned pine marten kits in the Scottish borders. When the most recent survey was carried out in 2014, there was evidence of pine martens in the area (Croose *et al*. 2014), suggesting that these animals were still present and may have established a breeding population. Future releases of rehabilitated pine martens could provide valuable information on their survival and behaviour in the wild and be incorporated into planned reintroductions with animals from other sources.

Source populations outside mainland Britain

The use of donor sites outside of mainland Britain has also been suggested for future pine marten reintroductions to England (Jordan *et al*. 2012; Bamber *et al*. 2020). Although pine marten populations across central and northern Europe are likely descended from a single glacial refugium (Ruiz-González *et al*. 2013), they are now significantly differentiated into a number of mitochondrial DNA control region haplotypes (Davison *et al*. 2001; Kyle, Davison & Strobeck 2003; Pertoldi *et al*. 2014), many of which are unique and limited to a single country (Pertoldi *et al*. 2014). Species can have very specific genetic adaptations to their local area, even if they have very similar haplotypes, which might be driven by climate or other factors. Local adaptations can be a major determinant of the adaptive capacity of populations in the face of changing environmental conditions (Savolainen, Lascoux & Merilä 2013). This has been studied most often in the context of climate change (Ikeda *et al*. 2017; Razgour *et al*. 2019), however when there are greater intraspecific than interspecific ecological niche dissimilarities, this must also be considered when selecting donor populations for translocations.

IUCN guidelines for conservation translocations recommend that founder selection should aim to provide adequate genetic diversity and that donor populations physically closer to, or from habitats that are similar to the recipient sites may be more genetically suited to destination conditions. Numerous studies on the genetic outcomes of conservation translocations recommend comparing donor populations to the recipient ones to ensure that there is no adaptive divergence and to minimise the potential for genetic ‘swamping’ (Hedrick & Fredrickson 2010; Hedrick & Garcia-Dorado 2016).

Inbreeding depression is a consideration when there are few source populations available for multiple translocations, and many studies have looked at the genetic benefit of translocations of wild (Grauer *et al*. 2017; Manlick *et al*. 2017) or captive (White *et al*. 2018; Wirtz *et al*. 2018) animals. These point out that the source population should be genetically suitable, which may mean similar or different (He, Johansson & Heath 2016; Malone *et al*. 2018) depending on the specific circumstances of the translocation. However, it is often the case that little or no data are presented on the genetic composition of the source before or after the translocation.

The pine marten population in Scotland has been through a relatively recent bottleneck, as a result of the severe decline in the 18th and 19th centuries, giving rise to concerns that this may have had an impact on its genetic diversity. However, as can be seen from **table 2**, the genetic diversity of the Scottish population is comparable to that elsewhere in Europe and higher than that recorded in Ireland. Therefore, provided donor sites in Scotland are well spaced out, there would seem to be sufficient variation in Scottish pine martens for it to be possible to mitigate against inbreeding depression in founder populations of Scottish origin.

Population	*n*	*A*	*HE*
Translocated[5]	38	3.42	0.55
All donor sites[5]	149	3.19	0.52
Ardennes[1]	102	3.42	0.61
Bresse[1]	126	3.49	0.6
Isere[1]	62	3.5	0.62
Ariege[1]	88	2.77	0.48
Scotland[2]	59	3.86	0.42
Ireland[2]	9	1.86	0.34
Ireland[3]	29	2.29	0.35
Ireland[4]	24	2.86	0.39
England[2]	7	3.57	0.66
Germany[2]	10	3.86	0.56
Sweden[2]	16	3.86	0.57
Finland[2]	26	4.57	0.57
Netherlands[2]	10	3.57	0.54
Latvia[2]	8	3.86	0.64
Italy[2]	15	4.57	0.61

Table 2. Summary of genetic variation in pine marten populations from published studies ([1]Mergey *et al*. (2012); [2]Kyle, Davison and Strobeck (2003); [3]Mullins *et al*. (2010); [4]Sheehy *et al*. (2014)), compared with that of pine martens translocated from Scotland to Wales in 2015-2016 (Translocated) and samples from all donor sites 2015-2016 (All) [5](Powell, MacPherson & O’Reilly 2017). N Sample size, A average number of alleles per locus, HE unbiased expected heterozygosity.

Sourcing animals from Ireland or from elsewhere in northern Europe has been discussed in recent years. Ireland has been considered as a potential source of donor populations of pine martens, as the haplotype found in Ireland suggests that the Irish pine marten population is derived from stock that may have been introduced there from southern Britain up to 1000 years ago (Yalden 2010; Jordan *et al*. 2012). However, Ireland has a smaller suite of mammals than Britain or continental Europe, consequently the pine marten there has fewer competitors and potential prey, so its ecology and dietary niche may be very different from that in the rest of its range. Conversely, in mainland Europe, there is a wider range of small mammals, but the pine marten's ecological niche may be more constrained than in Britain as it has to co-exist with the closely related stone marten, *Martes foina*, as well as many other carnivores. When animals are sourced from donor sites with similar prey species, competitors, predators and habitats to those in release sites, they have higher rates of post-release survival and reproduction (Aber *et al*. 2013), therefore the ecological suitability of animals from outside the British mainland needs to be assessed, along with the risks of genetic swamping and outbreeding depression.

A major consideration when translocating animals from anywhere, but even more so between different land masses, is the associated disease risk. Many parasites and pathogens are highly localised in their distribution as a result of the specific ecological requirements of them and their vectors, so even translocating wild-caught animals over short distances can result in them being exposed or contributing to new disease problems. However, animals from different islands or land masses may be more likely to have been exposed to diseases endemic to their area of origin (and may be symptomless carriers of the pathogens), but they may lack acquired immunity or resistance to the parasites and pathogens which they will encounter at the release site. Any translocated animal, whatever its origin and whether wild-caught or captive bred, can bring new pathogens into a release area where these can cause disease among co-existing, immunologically naïve wild or domestic animals (Kock, Woodford & Rossiter 2010). Therefore, before any wild animal is translocated from one place to another, the health risks to that animal, its conspecifics, other (wild and domesticated) species, humans and the wider environment must be assessed (Jakob-Hoff *et al*. 2014; OIE & IUCN 2014). Disease risk analysis (DRA) is a fundamental element of wildlife translocations, although it is still often overlooked (Lewis *et al*. 2020). A detailed DRA should be integral to any pine marten reintroduction proposals, irrespective of where animals are sourced from. There are also increased welfare considerations when capturing and moving animals from longer distances and from abroad. This is likely to elevate any stressor-associated disease risks (Dickens *et al*. 2010).

6. Summary of conclusions and recommendations

The recovery plan outlined here, aims to balance conservation of the recovering pine marten population in Scotland, with growing interest in the use of translocations as a means to restore the species to parts of its former range elsewhere in Britain. It is recommended that wild caught pine martens from Scotland are used for conservation translocations to other parts of Britain, rather than captive bred pine martens or those sourced from Ireland or elsewhere in Europe.

The distribution of pine martens in Scotland has been expanding south and eastwards from its former stronghold in the North West Highlands. There have now been populations established in Aberdeenshire, Perthshire, Argyll and the Trossachs since at least 2012 (Croose, Birks & Schofield 2013) and pine martens have also recolonised most of Stirlingshire and some parts of western Angus and Fife. However, there is still a relatively small pool of potential donor populations, that have been established for a sufficiently long time and are at high enough densities to be able to sustain the removal of a limited number of animals for translocations. These are largely in the former counties of Inverness-shire, Ross and Comarty, plus Lochaber and northern Argyll.

It has been shown that, although a population may be able to sustain a one-off harvest of a relatively high number of animals, the genetic profile of a donor population is likely to be affected if the proportion of animals removed is above a threshold (Pacioni, Wayne & Page 2019). If donor populations are to be used more than once, then the number of animals removed has to be relatively small to preserve the integrity and genetic diversity of the source population. Lower harvest limits are advisable if there is low confidence in the accuracy of population size estimates and if population growth rates are low or variable, as is the case with pine martens. Recognising the limitations of current population viability modelling and the natural annual variability in survival and recruitment in martens, it is recommended that the current conservative harvesting strategy continues. Future translocations should be of a comparatively small number of animals taken from several different donor sites. A minimum of five years should elapse before any donor population is trapped again. For some species it can be advantageous to release family groups but for pine martens it is optimal to release animals of breeding age that are unrelated and as genetically diverse as possible. They should be obtained from widely dispersed northern subpopulations of the total Scottish population to maximise genetic capture and minimise the likelihood of adversely affecting donor sites.

Pine marten populations in the Trossachs, Perthshire, Angus and Aberdeenshire have been established relatively recently and could be important sources of dispersers to the counties south of them. The proximity of southern Argyll and the Trossachs, as well as Perthshire and Stirlingshire, to the largely uncolonised counties south of the Central Belt means that pine marten populations here could be an important source of dispersers south. This is also an area where the recovering pine marten population starts to overlap with the current range of grey squirrels in Scotland and may be having a negative impact on grey squirrel populations, to the advantage of native red squirrels (Sheehy *et al*. 2018). There is some evidence that this effect is dependent on pine marten density exceeding a threshold so it is recommended that pine marten density should not be reduced by any removals from populations that overlap with current grey squirrel distribution in Scotland.

It is recommended that habitat enhancements are carried out in regions of Scotland where pine marten density or habitat connectivity is currently low, such as through the Central Belt and into southern Scotland. This might include the provision of artificial den boxes to increase the availability of natal den sites for breeding females, where natural sites in tree cavities may be a limiting resource. Further research could quantify the impact of this on breeding success.

With limited resources and suitable donor populations for actions such as reintroductions, it is important to identify how to achieve the maximum conservation benefit for pine martens for the minimum resource ‘costs’. Using modelling methods, based on data and knowledge of pine marten ecology and distribution, the framework, demonstrated here can inform spatial targeting of conservation measures and help to prioritise projects in future with the goal of improving the conservation status of the pine marten in Britain.

When we applied this framework to a number of regions in Britain to assess their potential for pine marten recovery or restoration, the results suggest that the south west of England should be prioritised for further investigation as a potential reintroduction region. Habitat suitability and connectivity modelling showed that the majority of well-connected, highly suitable habitat for pine martens is in the north and west of Britain. Translocations of pine martens have already taken place into the largest contiguous region of highly suitable habitat in mid-Wales. A reintroduction is also underway into the Forest of Dean and Wye valley on the England/Wales border. This should consolidate the range of pine martens in Wales and the bordering counties. However, having discrete populations as a result of translocations is not ideal. It is suggested that a translocation of around 50 individuals, capturing at least 95% of the source population’s standing genetic variation, needs to reach an effective population size of approximately 1000 individuals as quickly as possible (Weeks *et al*. 2011). This is considered an approximate minimum threshold to maintain sufficient adaptive potential in the face of environmental change (Willi, Van Buskirk & Hoffmann 2006) and, ideally, should be achieved within several generations of the translocation. This is also in line with the IUCN Red List Criterion D where minimum viable population size for isolated (i.e. island) populations is 1,000 individuals (IUCN 2012). This may take some time for pine marten populations to achieve in southern Britain, but should be the objective. A series of translocations to seed new populations in reasonable proximity to each other, with the capacity to increase, expand and form an effective meta-population, will increase gene flow and resilience. A robust metapopulation will expand and disperse into new patches of suitable habitat, with the advantage that natural recolonisation is perceived as less contentious than human mediated releases (Auster, Barr & Brazier 2020).

The results of our analyses suggest that it is highly likely that a viable population would result from pine marten reintroductions into the south-west of England. Therefore, the counties of Devon and Somerset could potentially be suitable for a future reintroduction project and it is recommended that this area is prioritised for more detailed investigation. Some of this work is already underway. When considering potential reintroduction, it is important to consider not only the characteristics of a specific area, but also the metapopulation potential of the landscape that surrounds the area of interest (Armstrong 2005). Suitable habitats in Somerset and Devon are in sufficiently close proximity to the restored populations in Wales and Gloucestershire for there to be a reasonable expectation of gene flow between them, should a reintroduction go ahead in the south west. HexSim models incorporating the south-west illustrate predicted occupancy across the region, as shown in **figure 14**.

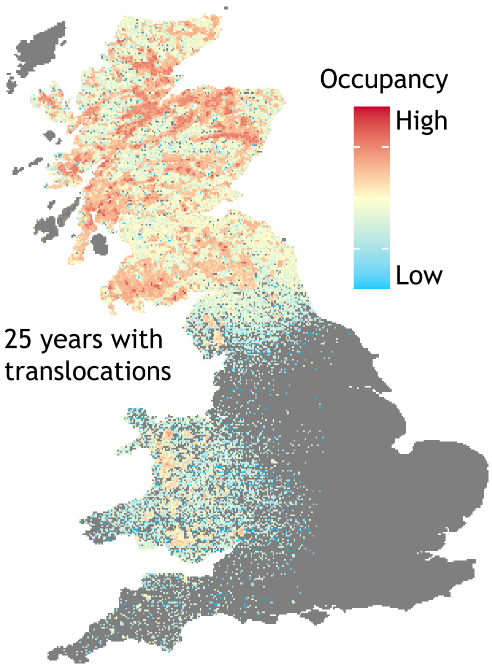


Figure 14. HexSim predictions of pine marten occupancy within 25 years of first translocations to Wales, incorporating subsequent reintroductions to Gloucestershire and south-west England.

There is a large amount of suitable habitat for pine martens in Cumbria, particularly in the south around Grizedale. Our HexSim models predict that this region will be naturally recolonised by pine martens within 25 years. However, the higher landscape resistance of the open fells of the northern Pennines and possible barrier of Carlisle and the M6 motorway could impede the movement of pine martens to this region. It is recommended that range expansion across northern England is monitored and further facilitated where possible. If there is no evidence of natural recolonisation in this region within a reasonable timeframe (five to ten years), then we suggest that 'assisted recolonisation' by reintroductions should be explored. This might be an effective way of accelerating the spread of pine martens in northern England.

In East Anglia, although there is an area of suitable habitat, it is surrounded by a (predominantly arable) landscape with very high resistance values. If pine martens were reintroduced here, they would find it a challenge to disperse away from the release area once the carrying capacity of the suitable woodland was exceeded. This could result in what was effectively an island population, which would require long-term monitoring and management to mitigate against the consequences of genetic isolation. For this reason, it would not be a priority area for pine marten restoration at present but should be revisited in the next iteration of the recovery plan (from 2030), in the context of the landscape then, as changes in land use in the next ten years may have a significant effect on future landscape permeability.

The HexSim models for Britain show that north Yorkshire is unlikely to be colonised naturally by significant numbers of pine martens from an expanding Scottish population. There is some suitable habitat but when modelling was used to simulate pine marten reintroductions to this region, the population slowly declined over time. Although it persisted for the modelled timeframe of 50 years, it was at lower levels than the number of animals released and would be vulnerable to stochastic events. However, our models did not include any additional animals that might enter the population intermittently. If there was a small but constant influx of individuals dispersing from further north or west, this might increase the resilience of a reintroduced population of pine martens here. This should be included in monitoring and facilitating further range expansion in northern England.

Despite an apparently high amount of suitable habitat, based on our analyses, the south east of England is not a region that should be prioritised for pine marten reintroductions. Mortality is likely to be high which would impact the establishment of a relatively small founder population. Given the existence of better quality potential reintroduction sites elsewhere, south-east England is outranked by other sites. Consequently, the valuable limited donor source should be directed at these, provided that other considerations are also favourable. Nonetheless, there is suitable habitat and, in the future when pine martens disperse into the landscape beyond established reintroductions, some sites in the south-east, albeit with high mortality, may be colonised. It is likely that these would function as sink populations, which may go extinct at times but are 'rescued' by dispersal from source populations. These are subpopulations that have enough individuals to sustain themselves and supplement other subpopulations through migration (Howe, Davis & Mosca 1991). Improving connectivity to other regions where reintroductions have a higher likelihood of establishment, could promote dispersal and natural recolonisation to suitable habitats in the south-east in future.

There have been intermittent records of pine martens in Hampshire and the New Forest, suggesting that there may be a very small number of pine martens living wild, and possibly breeding. Our HexSim simulations of the outcome of translocating a viable number of founder animals to this region declined rapidly but did persist for 50 years, albeit at very low levels. This may give some indication of why pine martens have failed to establish a significant population here. The New Forest has a reasonable amount of woodland and predicted highly suitable habitat for pine martens. However, there is a dense road network here and intensive outdoor recreational use may also make this region unsuitable for translocations of pine martens as a result of high levels of disturbance. This is not a region that would be a priority for reintroductions, but the Circuitscape map for Britain suggests that there is a route of moderate current running southwards from the Forest of Dean to the New Forest and on into the South Downs. Therefore, a landscape project with the aims of improving connectivity could have significant benefits for pine marten conservation in the south-east of England. It is suggested that the potential for this is explored further in the next five to ten years, once the pine marten population in Gloucestershire has had time to establish, increase and start to expand its range.

Animal welfare is a key consideration in any reintroduction (IUCN 1995; IUCN 2013) and should be considered for all individual animals and at all stages of the translocation process (Harrington *et al*. 2013). Methods that minimise the suffering of translocated individuals should always be used, in line with ethical considerations when using animals in research (Thulin & Röcklinsberg 2020). The welfare implications of transporting pine martens over the large distances from northern Scotland to the far south of Britain need to be considered in any proposed future reintroduction plans. Whilst this is a risk, it has to be balanced with other risks in terms of alternatives such as captive breeding or bringing in animals from elsewhere. Ways of minimising transport stress should be explored with a multi-disciplinary team including wildlife veterinarians.

In summary, it is recommended that work focusses on continuing to develop and implement effective methods to monitor donor sites north of the Great Glen where pine martens are removed. This will inform future management decisions. The pine marten populations in central and southern Scotland should be surveyed at suitable intervals to monitor their status and document range expansion. At the same time, the highest priority regions for potential reintroductions should be investigated further. The results of our modelling framework suggest that these should be south-west England, in the first instance, followed by a re-evaluation of south Cumbria depending on the rate and patterns of natural recolonisation observed over the coming five to ten years. Monitoring range expansion, raising awareness of pine martens at the recolonisation front and across predicted expansion zones; carrying out targeted habitat improvements; provision of artificial den sites and increasing habitat connectivity where possible; and mediating with other land users to minimise the potential for future conflict are priority actions to benefit pine marten recovery. These will provide more information for statutory agencies and decision makers about the changing status and distribution of pine martens across Britain, as well as the need for more interventionist approaches such as reintroductions.

Research priorities

Data on indices of pine marten activity at donor sites to date suggest that VWT's conservative harvesting protocol has proved effective, and population estimates derived from genetic analysis of non-invasively collected samples suggest that only a relatively small proportion of resident animals have been removed. However, the medium to long-term effects of removing individuals from source populations must be monitored. It is recommended that a rigorous, cost effective protocol be established, building on the preliminary work done to date, to improve the confidence around current harvesting models and monitor medium to long-term impact on donor sites.

It is unlikely that there will be sufficient captive bred stock available in the foreseeable future to sustain reintroductions solely of captive bred animals. However, captive bred pine martens could be used to augment larger, viable numbers of translocated wild caught pine martens in future if there is sufficient evidence to show that such animals are suitably equipped for life in the wild. Therefore, it is recommended that research is carried out that will enable their suitability for release into the wild to be evaluated, and to assess post release survival and behaviour to that of wild-caught animals released under the same or comparable conditions.

The goal in selecting source populations for translocations is to release a cohort of individuals that are genetically diverse and to minimise founder effects by translocating a sufficient number of pine martens. For some species it can be advantageous to release family groups (Fritts *et al*. 1997; Rantanen *et al*. 2010), but for pine martens it is optimal to release animals of breeding age that are unrelated and as genetically diverse as possible. The genetic diversity of the Scottish population is within the range of that reported elsewhere in Europe and higher than that recorded in Ireland. Therefore, provided donor sites in Scotland are well spaced out, and not over-harvested, there would seem to be sufficient variation in Scottish pine martens for it to be possible to mitigate against inbreeding depression in founder populations of Scottish origin.

There is an argument for mixing animals from different populations to increase genetic diversity and potential for adaptation, unless there is a strong indication that this could affect the overall fitness. For inbred populations there are some reports in the literature of dramatic recovery once admixing occurs (Weeks *et al*. 2017; Gille *et al*. 2019). However, there is currently no evidence that inbreeding is a concern with the wild population of pine martens in Scotland. There is also a very real risk that 'outbreeding' with animals from another source would result in a reduction of fitness (Laikre *et al*. 2010; Colella *et al*. 2019), so it is not recommended before research can demonstrate the likely effect and a genetic 'cost benefit' analysis is undertaken.

The primary motivation for the interest in pine marten reintroductions expressed by many individuals and organisations is the expectation that they will provide a biological control for grey squirrels. There are ethical and welfare considerations in any translocation, but particularly so if the primary purpose is for the animals to provide a service to humans. In all cases an ethical cost (harm)-benefit analysis for achieving the specific goals of the proposed action should be carried out before proceeding (Thulin & Röcklinsberg 2020). Studies in the UK and elsewhere show that the interactions between pine martens and squirrels are clearly complex and influenced by a number of different factors such as the abundance and types of alternative prey/food sources, habitat type and the densities of both pine martens and squirrels. Much more research is needed under a range of different conditions before regarding pine martens as a panacea for the problems caused by the grey squirrel in Britain. While there is evidence from Ireland and Scotland to suggest that, at relatively high densities, pine martens may have a negative effect on the occupancy of grey squirrels (Sheehy & Lawton 2014; Sheehy *et al*. 2018; Flaherty & Lawton 2019; Twining, Montgomery & Tosh 2020), it is not certain that grey squirrel numbers will be reduced to extinction where pine martens occur. Furthermore, even if this were the case, grey squirrels are still likely to persist in urban and other habitats that are avoided by, or unsuitable for, pine martens (Twining, Montgomery & Tosh 2020). As a result of persecution in the past, it is likely that pine martens have been unable to achieve their natural carrying capacity in many parts of Britain for centuries. Further research is needed to establish what densities pine marten populations could achieve in Britain and under what conditions, if any, they might have a similar effect on grey squirrels as observed in the Irish midlands.

1. Pine marten is included on the Scottish Biodiversity list under the criterion “insufficient data to assess their populations”
2. Under the Natural Environment and Rural Communities (NERC) Act 2006, pine marten is a Species of Principal Importance in England and Wales. Sections 41 (England) and Sections 42 (Wales) of the NERC Act 2006 require that species listed as being “of principal importance for the purpose of conserving biodiversity” therefore need to be taken into consideration by a public body when performing any of its functions with a view to conserving biodiversity.

Table 3. Summary of recommended actions.

Action	Suggested lead and partner organisations	Timeframe
Periodic distribution/expansion zone surveys in southern Scotland/northern England; Wales/Marches; Gloucestershire/SW	VWT, SNCOs	2024, 2029
Further investigation of south-west England as potential reintroduction region	Wildlife Trusts, National Trust, NPAs, Woodland Trust, VWT	2021-23
Re-evaluate need/potential of south Cumbria as a potential reintroduction/assisted recolonisation region	University of Cumbria, Wildlife Trusts, NPA, other NGOs, VWT	2025-2028
Improve and establish standardised monitoring protocols for donor sites, including data on pine marten densities	VWT, NatureScot, FLS	2021-2023
Establish standardised annual den box monitoring scheme at representative sample of sites, so data are comparable	VWT, Myotismart (JB, JM), FLS, FE, NRW, NE, SWT, GWT	2021-
Devise monitoring protocols for 2/3 species interactions (pine martens, red and grey squirrels) where pine martens have been reintroduced	University, Forest Research, GWT, VWT	2021-25
Look at ways to facilitate/improve dispersal in areas of high landscape resistance (Central Belt, southern Scotland, northern England, Welsh Marches)	VWT, local Wildlife Trusts, relevant Highways Agencies	2023-
Raise awareness of pine martens and develop conflict management strategies at expansion fronts	VWT, SNCOs	2021-2030
Research into behavioural suitability of captive bred/ rehabilitated pine martens for incorporation into future planned reintroductions	VWT, SSPCA, zoo partners	2021-24
Ensure pine marten remains fully protected on Schedule 5 and discuss potential implications of recommending pine marten be added to Schedule 9 of the WCA, making unlicensed releases of pine martens into the wild an offence	DEFRA, Natural England, Natural Resources Wales	
Risk/benefit analysis and investigation of future potential of source populations outside Britain	VWT, University, genetics and wildlife health specialists	2025-28
Risk/benefit analysis of source populations outside Britain	VWT, University, genetics and wildlife health specialists	2025-28

Review dates:

2025 Interim report on progress
2030 Review and report on progress, renew plan going forward

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Appendix

Modelling methods and results

Habitat suitability modelling
We used MaxEnt (Phillips, Anderson & Schapire 2006), a presence-only Habitat suitability modelling (HSM) approach, to predict suitability of habitat for pine marten. All analyses were carried out using R (v. 3.5.3; R Core Team 2013) in R Studio (v.1.2.5042; RStudio Team).

Presence records consisted of pine marten scats, confirmed by DNA testing, which had been collected during recent surveys between 2005-2007 in Ireland, and 2012-2013 in Scotland (for details see O'Mahony, O'Reilly and Turner 2012 and Croose, Birks and Schofield 2013). Both surveys were based on 1-3 transects of 1-1.5km in length within 10km national grid squares. Experienced surveyors walked transects located along forest tracks or paths in wooded habitat searching for pine marten scats. Each transect was walked only once between May and September. Additional confirmed pine marten records from the ***Back from the Brink*** project in northern England (https://naturebftb.co.uk/the-projects/pine-marten/ were also included in the analysis. We also obtained pine marten records in Northern Ireland and Scotland from the GBIF database (https://www.gbif.org/) where only records of a sufficient resolution dating from 2005 onwards were kept. For each model, we filtered records to retain a single record per grid square.

Given the differences in datasets available (presence and environmental data) for modelling pine marten habitat, we explored multiple models and measured the correlation between these outputs (Schoener's D) to assess the consistency in our predictions throughout the study area. Here, we expected models to differ not only because of differences in data input (presence records and explanatory variables), but also because of differences in the conservation status or biogeographical context of the species throughout the extent of each model.

Model 1 (Britain + IRL + NLD): Here, we used primarily Land Cover variables from the CORINE land cover 2018 dataset (Supplementary X; Büttner *et al*. 2004) and pine marten presence location records from Britain, Ireland, Northern Ireland and the Netherlands. This model contained information from two countries where the species is currently widespread and found in areas with high road densities and other types of habitats where the species is currently not found in Britain. Pine marten data from the Netherlands were validated records provided by the Dutch Nationale Database Flora en Fauna (NDFF).

Model 2 (Britain + IRL): This model was identical to Model 1, but did not use any data from the Netherlands. By keeping records from Britain and Ireland in this model, we expect to provide information from the widespread Irish population which shares similar climatic and latitudinal characteristics to southern Britain. This model should remove any bias from continental records resulting from the presence of stone martens, intra-guild competitors and differences in prey base availability.

Model 3 (Britain): This model contained fewer records than model 1 and model 2, as it included records from Britain only. However, we could provide more information on the impact of road density and traffic on pine marten presence in Britain by using landscape variables derived from Wright *et al*. (2020). This model should also provide more conservative predictions as the records will be representative of a recovering population and might not identify the species' fundamental niche. Records from Wales were excluded to avoid bias that may have arisen from pine martens being released into specific, pre-selected areas and habitat types.

All explanatory variables were measured at two candidate scales — 1km and 3km. The optimal scale was identified for each predictor by creating univariate models using default settings with threshold features disabled (Hijmans *et al*. 2017; Bellamy *et al*. 2020; Wright *et al*. 2020). The scale with the highest training gain measure was then selected (Merow, Smith & Silander Jr 2013).

For each model, we removed highly correlated variables using the 'vifstep' stepwise function of the 'usdm' package (Naimi *et al*. 2014) and a conservative VIF threshold of three (Zuur, Ieno & Elphick 2010). We used the package 'ENMeval' (Muscarella *et al*. 2014) to identify the optimal MaxEnt model settings. We tested combinations of feature types (L, linear; H, hinge; Q; quadratic; P, product) and disabled threshold features to reduce overfitting. We varied the regularisation multiplier in steps of 0.5, from 0.5 to 4. Then, we performed a final model using the optimal settings to produce model predictions. Predicted HSI values were then partitioned into a binary response using the Maximum Training Sensitivity and Specificity (MTSS) occupancy rule (Liu, White & Newell 2013). Finally, we calculated Schoener's index between all HSM outputs in order to assess the degree of similarity between our models in Britain and in the south-west of England (Dorset, Somerset, Devon, Cornwall).

Connectivity modelling

We used Circuitscape v4.0.5 (McRae & Nürnberger 2006), a software linking circuit and random walk theories, to visualise the amount of connectivity for pine martens in Britain (5km resolution). As opposed to least-cost-path analysis, Circuitscape calculates all possible pathways connecting points (or habitat patches) through the landscape based on a resistance surface and provides a current map identifying areas of high connectivity in the landscape.

Here, the resistance surfaces were based on the conservative pine marten HSM (model 3). To transform the habitat suitability values into a resistance surface, we used a negative exponential function where c = 32 (Trainor *et al*. 2013; Mateo-Sánchez *et al*. 2015; Keeley, Beier & Gagnon 2016):

$$R=100-99\,(1-\exp(-cH))/(1-\exp(-c))$$

H = habitat suitability value   c = 32

We used two types of focal nodes with Circuitscape. First, we used suitable habitat patches identified from each HSM as the focal nodes, then we created a buffer zone surrounding Britain and placed 50 points (focal nodes) on this buffer area. We ran Circuitscape using the pairwise modelling mode which calculates movement probability between all possible pairs of nodes for both types of focal nodes.

Table 4. List of explanatory variables used for each model. In model 3, we prioritised Land Cover 2007 (Morton *et al*. 2011) variables over CORINE LC 2018 (Aune-Lundberg & Strand 2010) if these were duplicated in the model.

Model	Explanatory variable	Source
Model 1 and 2	Arable (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Broadleaved (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Coniferous woodland (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Mixed woodland (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Woodlands (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Coastal habitat (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Heathland (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Natural grassland (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Pasture (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Scrub (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Urban (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Water (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Major road density	DIVA-GIS (2020)
Model 3	All road traffic	GB Road Traffic Counts (data.gov.uk, 2019)
	B-road density	OS Open Roads (2019)
	Major road density	OS Open Roads (2019)
	Major road traffic	GB Road Traffic Counts (data.gov.uk, 2019)
	Minor road density	OS Open Roads (2019)
	Minor road traffic	GB Road Traffic Counts (data.gov.uk, 2019)
	Coastal habitat (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Heathland (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Natural grassland (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Pasture (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Scrub (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Woodlands (% cover)	CORINE LC 2018 (Aune-Lundberg & Strand 2010)
	Arable (% cover)	Land Cover 2007 (Morton *et al*. 2011)
	Broadleaved (% cover)	Land Cover 2007 (Morton *et al*. 2011)
	Coniferous woodland (% cover)	Land Cover 2007 (Morton *et al*. 2011)
	Urban (% cover)	Land Cover 2007 (Morton *et al*. 2011)
	Improved grassland (% cover)	Land Cover 2007 (Morton *et al*. 2011)
	Rough grassland (% cover)	Land Cover 2007 (Morton *et al*. 2011)
	Freshwater (% cover)	Land Cover 2007 (Morton *et al*. 2011)

HexSim models

HexSim is a life history simulator used for building population viability models, but also looking at interactions, and responses to disturbance. These models are spatially explicit and individual-based. Individuals can be assigned dynamic life history traits.

In these simulations, we first investigated the spread of pine martens from the Scottish borders across Britain more than 25 years with and without reintroductions in central Wales and the Forest of Dean. Then, we examined separately the spread of pine martens in England and Wales from the two sites (central Wales and Forest of Dean) having already undergone translocations. Here, the translocations were designed to replicate previous translocations by introducing 20 pine martens (10 males and 10 females) in central Wales for the first three years; and a separate one which also included the following reintroductions in the Forest of Dean on year five and six.

In the first model, the initial population was set at 3,700 individuals according to the most recent estimates by Mathews *et al*. (2018). Then, at year 6 for the first year of translocations in central Wales took place, followed by the Forest of Dean.

A separate model was run which included the actual translocations that have taken place to Wales and the Forest of Dean, but also included translocations to an additional site in south-west England at year eight and nine years after the first releases in Wales, to look at how this would affect occupancy over time. Reintroductions were also performed at a regional scale for each site still being considered to assess the viability of isolated reintroduced populations over 50 years.

The models were designed to replicate the life-history of pine martens (home range, dispersal, survival, etc.) as far as possible. Population and life history parameters were derived from Powell *et al*. (2012), consistent with Stringer *et al*. (2018). As in the wild, the pine martens in the model were set to maintain territorial home ranges and would not tolerate overlap with territories of individuals from the same sex. The males had larger home range sizes than females and could overlap with more than one female. The model used separate movement events for subadults and adults, whereby adults were able to move and claim resources before subadults.

For the models, we assumed that values from HSMs would correlate with habitat quality and, therefore, population density. The hexagon size was set at 25ha for local reintroductions and 1km for national models and values derived from the HSM ranged between 0 and 100. Other settings are listed in **table 5**.

Sample sizes, optimal settings and results for each model are presented in **table 6**. The number of records used ranged from 2,920 in model 1 (**figure 15**; **table 6**) and 1,808 in model 3 (**table 6**). For each model, the optimal settings included LQHPT feature types and a regularisation multiplier between 1 and 2.5 (**table 6**).

The niche overlap index (Schoener's D index) between model 1 and 2 in Britain was high (0.93). Model 3, on the other hand, had the lowest niche overlap with overlap values of 0.73 with model 1 and 0.75 with model 2.

Table 5. Summary of settings and values used to set the home range of individual pine martens.

Setting	Value
Maximum lifespan	8 years
Maximum litter size	4
Maximum Range Area	120 hexagons (30km^2)
Minimum Range Resource	800 (equivalent to 2km^2 of very good habitat)
Female Resource Target	(Maximum territory size x [(MTSS+10th percentile)/2]) + 1,000
Male Resource Target	Female Resource Target x 2
High Resource threshold	MTSS value from the HSM model
Medium Resource threshold	10th percentile threshold value from the HSM model

Table 6. Model performance of the final MaxEnt models for model 1 (Britain + IRL + NLD), model 2 (Britain + IRL) and model 3 (Britain).

	n	Feature types	Regularisation multiplier	AICc	Mean AUC ± var	Non-independent AUC
Britain + IRL + NLD	2,920	LQHPT	1	68,754.99	0.82 ± 0.003	0.87
Britain + IRL	2,061	LQHPT	2.5	46,908.5	0.83 ± 0.012	0.87
Britain	1,808	LQHPT	2	37,336.56	0.91 ± 0.002	0.93

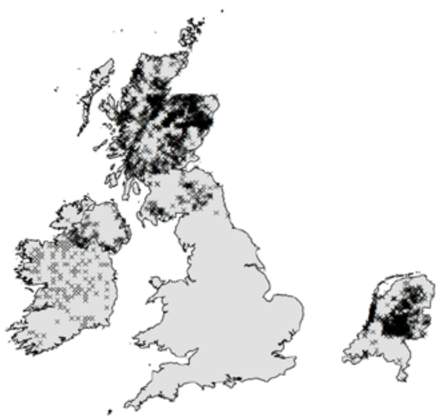

Figure 15. All 2,920 pine marten records used in Britain, Ireland and the Netherlands for model 1.

Table 7. Schoener's D index scores representing the niche overlap between all three models in Britain only (bottom) and south-West England (top).

	Model 1	Model 2	Model 3
Model 1	-		
Model 2	0.93	-	
Model 3	0.73	0.75	-

Suitable habitat was widespread throughout the Netherlands (shown bottom right in Figure 16a) and Ireland (shown in Figure 16a, b). In Britain, however, areas of suitable habitat were primarily identified in Scotland, northern England and Wales. Other areas were identified in south-west England but also in south-east England in model 1 (Figure 16). In all three models, most of England remained largely unsuitable (Figure 16).

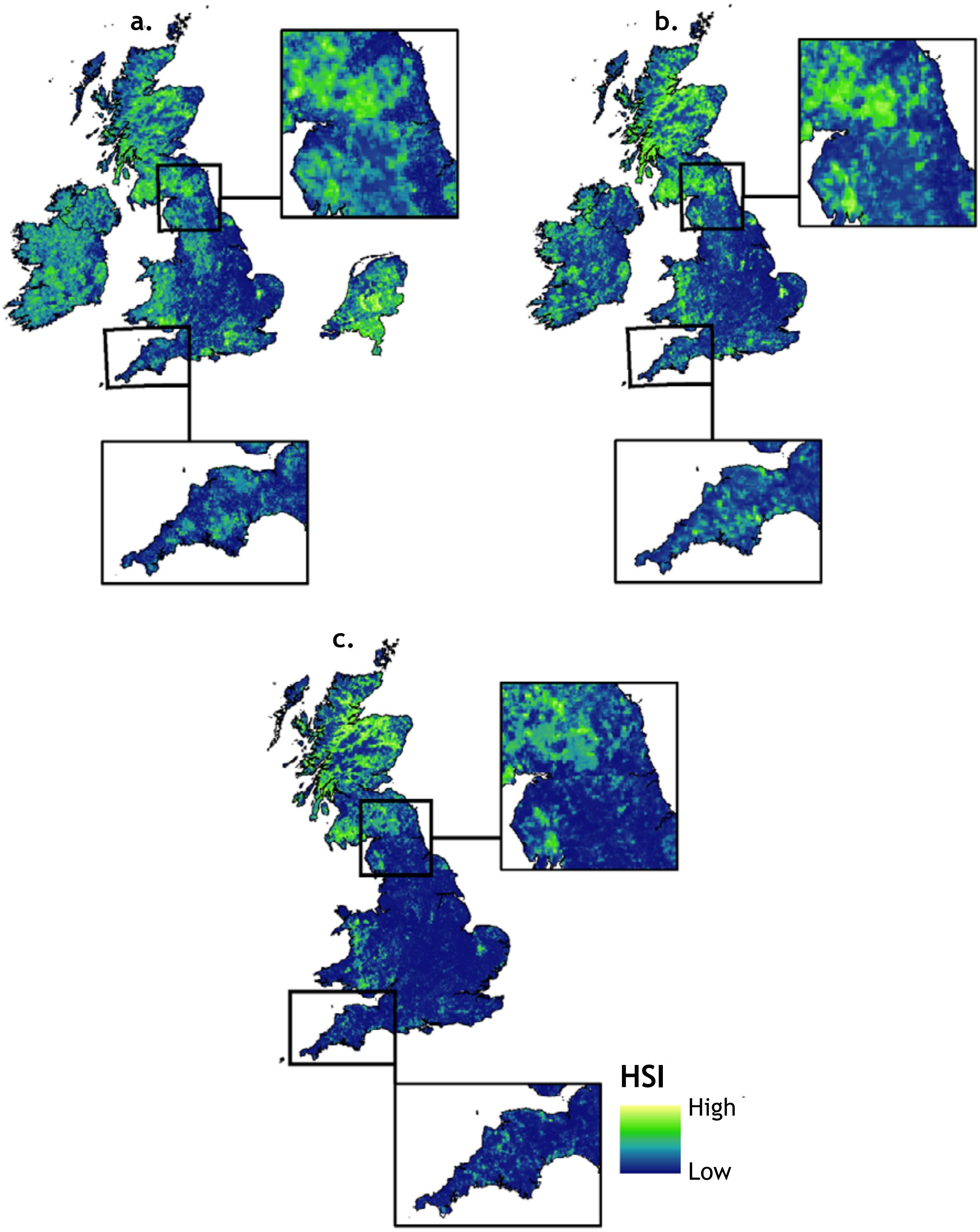

Figure 16. Logistic output model 1(a), model 2(b) and model 3(c).

For model 1 and 2, suitable habitat was characterised primarily by high woodland cover and reduced arable, pasture and urban cover at a 3 km scale (Figure 17a-h; Table 8). In model 3, pine marten presence was strongly associated with reduced road traffic (1km scale) and high coniferous woodland (3km scale) and woodland cover (3km scale) (Figure 17 i-l; Table 8).

Table 8. Predictor contribution values. Any missing variables from **Table 4** were removed due to multicollinearity.

Model	Environmental variable	Optimal scale (km)	Permutation importance (%)
Model 1 (Britain + IRL + NL)	Woodland cover	3	65.1
	Arable cover	3	14.8
	Pasture cover	3	7.8
	Urban cover	3	2.7
	Coastal habitat cover	3	0.2
	Road density	1	2.5
	Water cover	3	3.7
	Scrub cover	3	3.2
Model 2 (Britain + IRL)	Woodland cover	3	70.5
	Arable cover	3	10.4
	Pasture cover	3	5.7
	Urban cover	3	4.6
	Scrub cover	3	4.0
	Road density	3	3.6
	Water habitat	3	1.1
	Coastal habitat cover	3	0
Model 3 (Britain)	All road traffic	1	30.9
	Coniferous cover	3	23.7
	Woodland cover	3	20.3
	Pasture cover	3	8.4
	Arable cover	3	7.9
	Minor road traffic	3	3
	Broadleaved woodland	1	1.7
	B-road density	3	1.1
	Improved grassland	1	1
	Scrub cover	3	0.8
	Rough grassland	1	0.5
	Freshwater cover	3	0.4
	Urban cover	3	0.3
	Coastal habitat cover	1	0.0

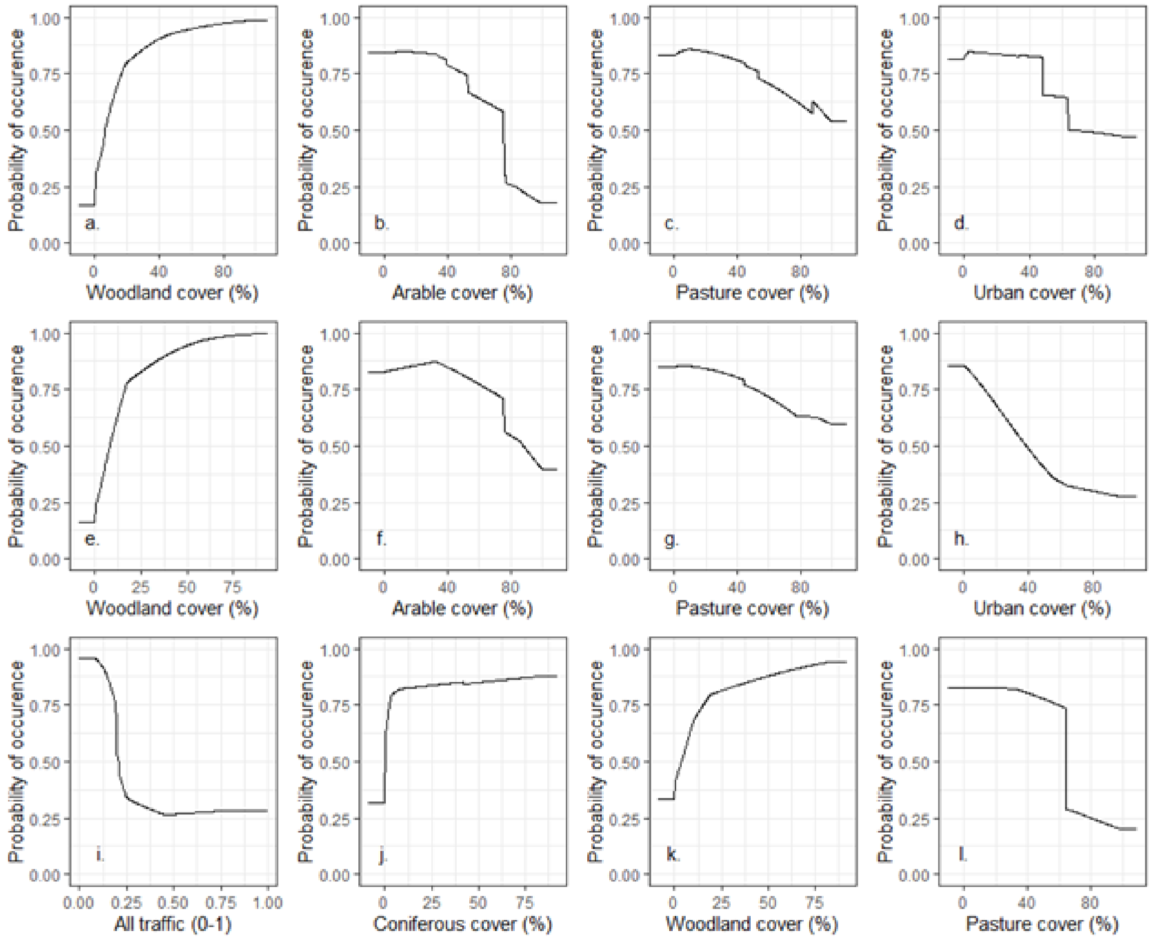

Figure 17. Response curves of the four variables showing the highest permutation importance for pine martens in model 1(a, b, c and d), model 2 (e, f, g and h) and model 3 (I, j, k and l). Response curves are plotted from the most important (a) to the least important (d) permutation importance.

The use of HSM/SDMs increasingly involves prediction to new environments such as new places or times (Elith & Leathwick 2009). This can be contentious as it makes strong assumptions (Elith *et al*. 2010) and usually requires prediction to environments not sampled by the training data. Our confidence in a model's output, should be directly linked with the degree to which the assumptions of the model are met. One important assumption is that the range of covariates sampled is similar to the range of covariates and values in the overall landscape. We included data from the Netherlands in our initial exploratory models of habitat suitability for pine martens in Britain, as there are some similarities between the two countries, particularly with respect to human population and road densities. However, geographical biases can influence predictions of species distribution and there are some marked differences between the Netherlands and Britain. Upland habitats (including mountain, moorland, blanket bogs, heaths and rough grassland) cover almost 40% of Britain's land surface (Bunce 1987), whereas much of the Netherlands is flat and low lying with nearly half of the land at or below sea level, only rising in the extreme south where it meets the foothills of the Ardennes.

A MaxEnt model using just data on pine marten presence from the Netherlands projected to Britain predicted absence from almost all of Scotland, other than the heavily urbanised central belt and an area along the Aberdeenshire coast down to Angus. In the same model, almost all of Wales was predicted as being unsuitable for pine martens with most of the suitable habitat being along the M4 corridor going west from London, as well as in Norfolk, the Suffolk coast and around Southampton (Sturton 2019). This does not correlate with actual data on pine marten distribution in the Britain, illustrating some of the issues when extrapolating across different geographical areas. For this reason, our models 1 and 2 were not used as the final model on which to base the analyses and recommendations presented in this report. Model 3 had the highest AUC and predicted habitat suitability with the closest similarity to current pine marten distribution in Scotland, giving the most confidence in its suitability for extrapolation to the rest of Britain.

Connectivity modelling

The resistance surfaces for all models had areas of high resistance throughout most of eastern England, while Scotland and Wales were mostly areas of low resistance. In model 1 and 2, we found low resistance values in southern England (**figure 18a, b**). In model 3, however, areas of high resistance extended throughout most of England (**figure 18c**).

Large contiguous patches of habitat were observed in Scotland and Wales. Habitat was more fragmented south of the Scottish border and connectivity was only preserved up to the Midlands. Some connectivity was observed in southern England (**figure 18d, e**), but this was considerably reduced in model 3 (**figure 18f**). In all model outputs, central and eastern England had low connectivity (**figure 18d, e, f**).

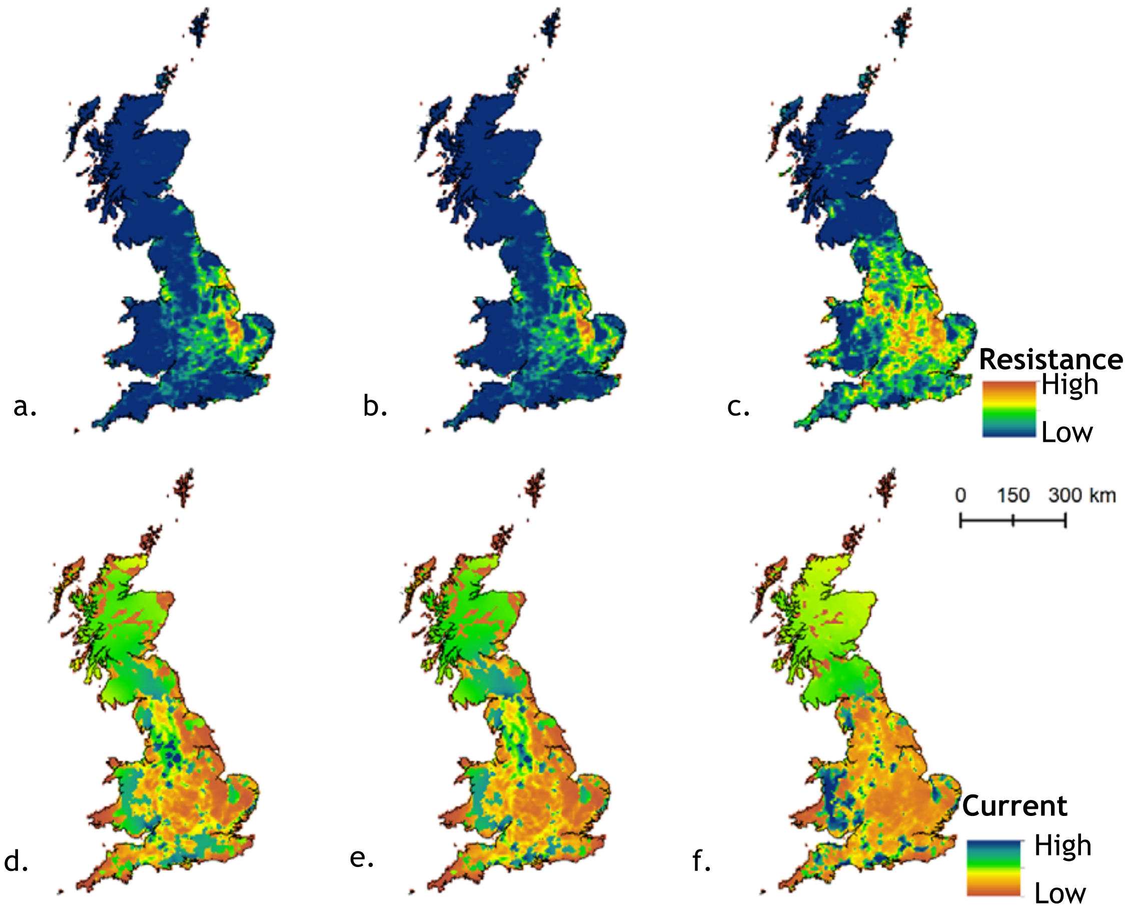

Figure 18. Resistance surfaces of Britain at a 5km resolution for model 1(a), model 2(b) and model 3(c); and the Circuitscape output in the form of a current map representing the amount of connectivity between habitat patches for model 1(d), model 2(e) and model 3(f).

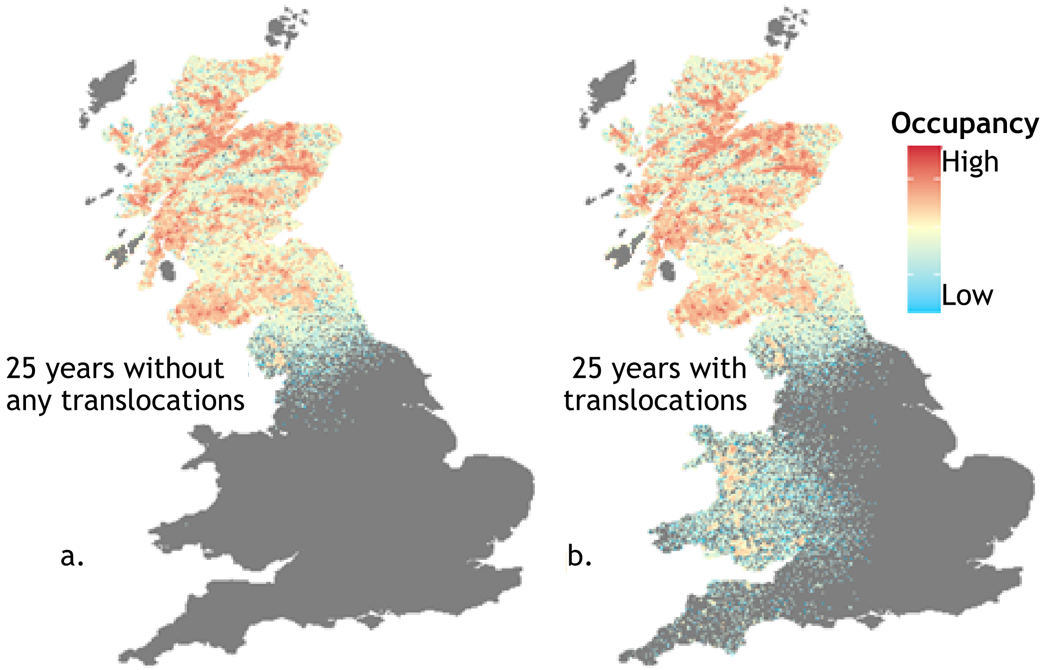

Figure 19. Results of HexSim models without translocations (a) and (b) including translocations to Wales and the Forest of Dean, followed by hypothetical translocations to south-west England.

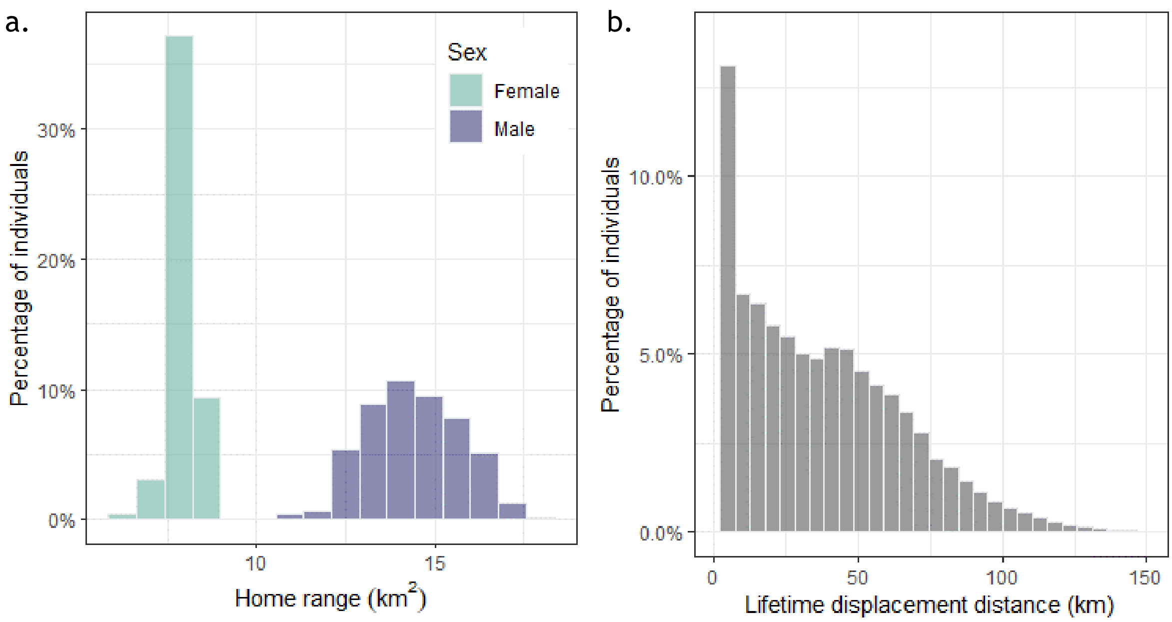

Figure 20. Frequency histograms of predicted home range size (left) and lifetime displacement/dispersal distances (right) for pine martens (From the SW HexSim model)

The frequency distributions of male and female pine marten home range sizes, as well as (lifetime) displacement distances following reintroductions that were generated by our final HexSim model is very similar to those from analyses of post-release radio tracking data from Wales (McNicol *et al*. 2020; MacPherson *unpubl data*) (**figure 20**). This supports our assumption that the parameter values used in the final model are appropriate.

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Contact us

3-4 Bronsil Courtyard, Eastnor, Ledbury, Herefordshire HR8 1EP
01531 636441 enquiries@vwt.org.uk
www.vwt.org.uk

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