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Niches for Species, a multi-species model to guide woodland management: an example based on Scotland's native woodlands

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Abstract

Designating and managing areas with the aim of protecting biodiversity requires information on species distributions and habitat associations, but a lack of reliable occurrence records for rare and threatened species precludes robust empirical modelling. Managers of Scotland's native woodlands are obliged to consider 208 protected species, which each have their own, narrow niche requirements. To support decision-making, we developed Niches for Species (N4S), a model that uses expert knowledge to predict the potential occurrence of 179 woodland protected species representing a range of taxa: mammals, birds, invertebrates, fungi, bryophytes, lichens and vascular plants. Few existing knowledge-based models have attempted to include so many species. We collated knowledge to define each species' suitable habitat according to a hierarchical habitat classification: woodland type, stand structure and microhabitat. Various spatial environmental datasets were used singly or in combination to classify and map Scotland's native woodlands accordingly, thus allowing predictive mapping of each species' potential niche. We illustrate how the outputs can inform individual species management, or can be summarised across species and regions to provide an indicator of woodland biodiversity potential for landscape scale decisions. We tested the model for ten species using available occurrence records. Although concordance between predicted and observed distributions was indicated for nine of these species, this relationship was statistically significant in only five cases. We discuss the difficulties in reliably testing predictions when the records available for rare species are typically low in number, patchy and biased, and suggest future model improvements. Finally, we demonstrate how using N4S to synthesise complex, multi-species information into an easily digestible format can help policy makers and practitioners consider large numbers of species and their conservation needs.

1. Introduction

Globally, biodiversity is under threat, many species are legally protected but resources for conservation are diminishing (Bottrill et al., 2008; MacDicken et al., 2015; Possingham et al., 2015). Maintaining habitat for species has been part of national and international conservation planning for decades and networks of protected areas exist globally (Orlikowska et al., 2016). However, whilst the IUCN has set a target of designating 10% of terrestrial habitats as protected areas (IUCN, 1993), it is recognised that this percentage of landcover, it's location, spatial configuration, and the actions prescribed within it may not be sufficient to support species, particularly in the face of rapid environmental change (Wiersma et al., 2018; Dinerstein et al., 2017; Rodrigues et al., 2004).

In the context of biodiversity protection in the temperate broadleaved and mixed forest biome, where habitat restoration is a priority, the choice of where to apply conservation effort for most benefit is critical (Dinerstein et al., 2017; Morales-Hidalgo et al., 2015). Such decisions are often directed by international conventions and directives on the environment, which are devolved to a regional level of administration for implementation (JNCC, 2018; EC, 2018). For example, in the UK, Scotland has listed 208 protected woodland species (mammals, birds, invertebrates, fungi, bryophytes, lichens, herptiles and vascular plants which are strongly associated with woodlands) (Scottish Action Coordination Group, 2008). Forestry policy and practice have been designed to deliver habitat enhancement and protection measures for these species (Forestry Commission, 2017), in line with wider conservation effort targeting species which are rare and/or at risk of extinction (Favaro et al., 2014; Winter et al., 2013). However, developing and adhering to these types of guidelines is contingent on knowledge of what habitat features a species requires and how these are distributed. This is complicated by the fact that many of these protected species are cryptic and poorly recorded (Minin and Moilanen, 2014). The challenge is further increased when there is a need to deliver conservation management for multiple protected and data-deficient species simultaneously. This challenge is faced by many land managers and owners.

To address gaps in species records and poor knowledge on habitat conservation needs, research has focussed on predicting where species are likely to occur using empirical models. These Species Distribution Models (SDMs) relate known species presence-absence or presence-only data with environmental variables to determine species-environment relationships and to predict habitat suitability over large extents (Elith and Leathwick, 2009; Guisan and Thuiler, 2005; Guisan and Zimmermann, 2000). They have been widely used to characterise and map habitat suitability for single species or taxonomic groups (e.g. Bellamy et al., 2013; Cooper-Bohannon et al., 2016; Johnson and Gillingham, 2008). However, SDMs may fail to accurately predict species habitat suitability when reliable occurrence data are sparse (Stockwell and Peterson, 2002; Wisz et al., 2008; although see Pearson et al., 2007), the full range of environmental variation across a species range is not represented (Austin 2002), the species is not in equilibrium with its environment (Dormann 2007; Soberon and Nakamura, 2009), or the impact of biotic interactions are not considered.

Whilst spatial data are available on broad woodland types across the UK (Forestry Commission, 2011) and other fine-scale attributes for some UK woodlands (e.g. dominant tree species, woodland structure, deadwood presence; Patterson et al., 2014), species records available via Local Environmental Record Centres or online data portals (e.g. NBN, 2017) typically suffer from sampling bias, low sample sizes and a lack of confirmed absences. This is particularly the case for rare, inconspicuous or cryptic species because of the difficulties in their detection or identification (Phillips et al., 2009; Newbold 2010). In addition, despite advances in data portal accessibility, the complexity and time investment involved in extracting high-resolution records for several hundred species, filtering them for reliability and accuracy, and interpreting the results alongside habitat data, means that this is unlikely to be undertaken by forestry decision makers. Using well recorded and better-known species as surrogates for wider biodiversity has been tested, but studies show surrogates perform less well when used to represent other taxa e.g. birds representing butterflies (Dorey et al., 2018; Margules and Pressey, 2000; Prendergast et al., 1993).

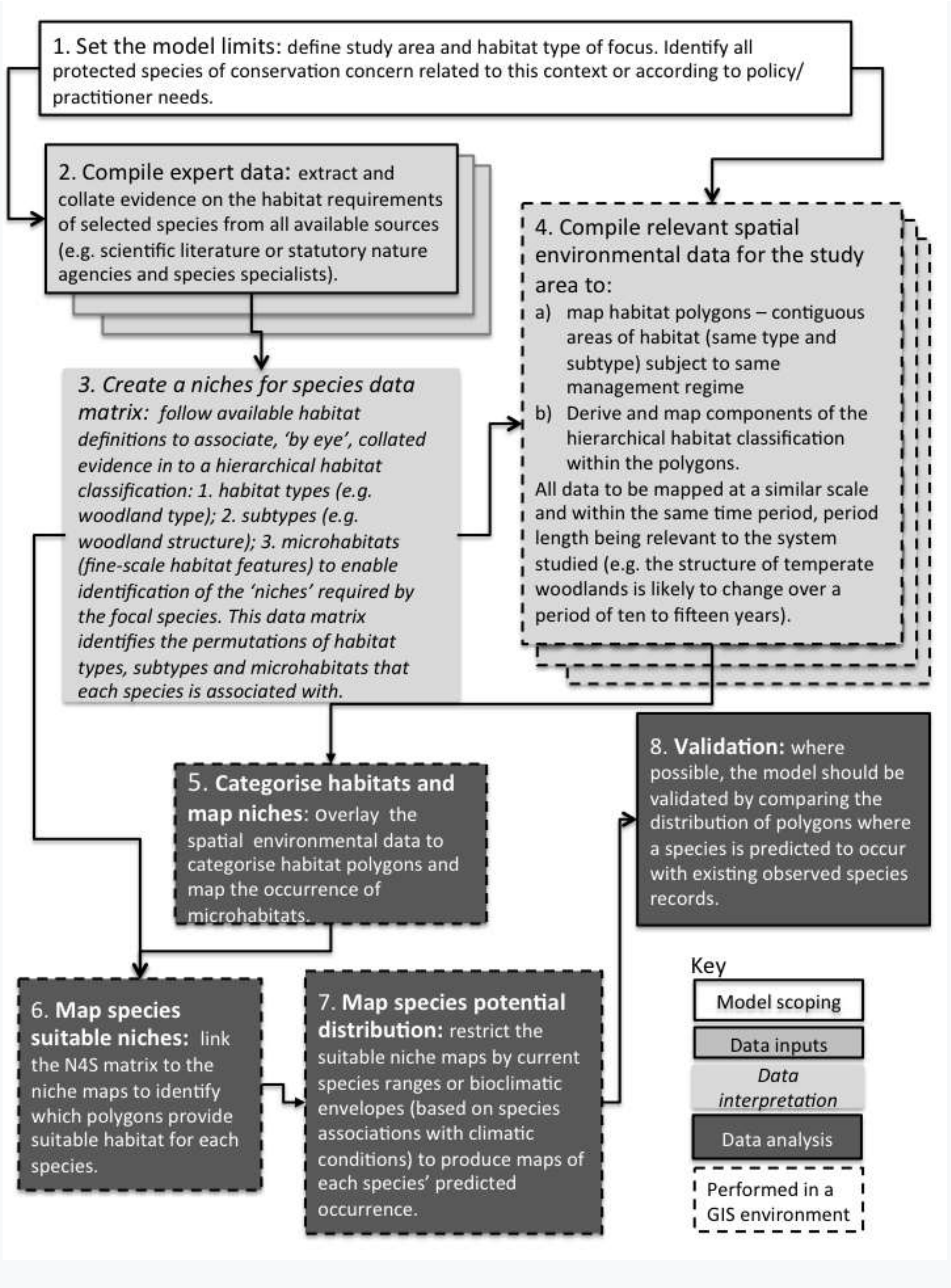
Expert-based habitat suitability models (EHSMs) provide a solution as useful alternatives to SDMs when inadequate occurrence records preclude accurate empirical modelling (Fourcade, 2016), or when funds for collecting new substantive datasets are limited (Doswald et al., 2007; Fourcade, 2016; Murray et al., 2009). EHSMs use both expert knowledge and evidence-based reviews from published scientific literature describing a species' habitat requirements and ecology, combined with spatial environmental datasets (e.g. land cover type, topography, aspect) describing the availability of these habitats, to predict the occurrence of species (e.g. Eycott et al., 2012; Ziegler et al., 2015). This approach has been extensively used by conservation agencies in the USA, where many EHSMs have been developed by drawing on the national resource of species specialist knowledge (Crance, 1987; Drew and Collazo, 2012; Drew and Perera, 2011). However, EHSMs are usually built for individual species (e.g. Leblond et al., 2014) and validation is nearly always neglected (Iglecia et al., 2012).

Here we present a multi-species EHSM approach, 'Niches for Species' (N4S), to enable forest policy makers and managers to consider multi-species management within Scottish forests. We use the term 'niche' to describe a set of habitat features that a species is strongly associated with, from which we can estimate species distributions whilst ignoring constraints such as competition. This is analogous to the 'potential niche', although we are only considering a narrow set of niche variables (Jackson and Overpeck, 2000). Our aim was to provide a simple-to-interpret spatial modelling framework for predicting the distribution of suitable habitat for multiple protected species. The main objectives were to develop an approach which could: incorporate all protected species associated with woodland for an entire (administrative) area; provide habitat requirement information for all those species; predict the potential distributions of those species consistently across a range of scales, whilst restricting predictions to climatically suitable areas where possible. Our modelling approach was wider and more ambitious in scope (a greater number of species and a wider range of taxa) than other attempts to inform conservation planning with multi-species models (e.g. Franco et al., 2009; Lentini et al., 2015; Minin and Moilanen, 2014) and as such is a novel application of EHSMs. Although developed for protected woodland species, the framework could be adapted for use with other habitats or suite of species. In addition, we aimed to test the model predictions against species occurrence records, despite our concerns that the low sample size, low resolution and high sampling bias associated with such records could limit agreement with EHSM predictions.

2. Material and methods

2.1 The Niches for Species framework

There are eight stages to the modelling framework (Figure 1). Stage 3 is unique to the N4S methodology; the development of a hierarchical habitat classification provided a structured system for categorizing species' niches. The incorporation of microhabitat information is rarely implemented in these types of landscape-scale, spatial approaches, despite their strong association with biodiversity (Michel & Winter, 2009). By nesting the levels, we take account of context dependency in species-microhabitat associations i.e. species microhabitats may only be important in certain types and structures of the habitat. Stage 8 (validation) is rarely performed in EHSM development. Details on how we have implemented these stages for woodland protected species in Scotland are given in Section 2.2., along with the list of attributes used and their sources (Tables 1 to 3). Output maps from Stage 7 can display single species predictions or aggregate information by polygon to show predicted species richness, for example.



1. **Set the model limits:** define study area and habitat type of focus. Identify all protected species of conservation concern related to this context or according to policy/ practitioner needs.

2. **Compile expert data:** extract and collate evidence on the habitat requirements of selected species from all available sources (e.g. scientific literature or statutory nature agencies and species specialists).

3. *Create a niches for species data matrix: follow available habitat definitions to associate, 'by eye', collated evidence in to a hierarchical habitat classification: 1. habitat types (e.g. woodland type); 2. subtypes (e.g. woodland structure); 3. microhabitats (fine-scale habitat features) to enable identification of the 'niches' required by the focal species. This data matrix identifies the permutations of habitat types, subtypes and microhabitats that each species is associated with.*

4. **Compile relevant spatial environmental data for the study area to:**
   - a) map habitat polygons – contiguous areas of habitat (same type and subtype) subject to same management regime
   - b) Derive and map components of the hierarchical habitat classification within the polygons.

   All data to be mapped at a similar scale and within the same time period, period length being relevant to the system studied (e.g. the structure of temperate woodlands is likely to change over a period of ten to fifteen years).

5. **Categorise habitats and map niches:** overlay the spatial environmental data to categorise habitat polygons and map the occurrence of microhabitats.

6. **Map species suitable niches:** link the N4S matrix to the niche maps to identify which polygons provide suitable habitat for each species.

7. **Map species potential distribution:** restrict the suitable niche maps by current species ranges or bioclimatic envelopes (based on species associations with climatic conditions) to produce maps of each species' predicted occurrence.

8. **Validation:** where possible, the model should be validated by comparing the distribution of polygons where a species is predicted to occur with existing observed species records.

Figure 1: A schematic flow chart illustrating the steps involved in Niches for Species (N4S) expert-based habitat suitability modelling framework to map the distribution of niches and species potential occurrence.

2.2 Our woodland application

We applied the N4S model to map the potential distribution of woodland protected species in Scottish native woodlands.

2.2.1 Expert knowledge on species-habitat requirements

We reviewed the available data documenting the habitat requirements for 208 protected species, considered to occur in Scotland and use woodland as their primary habitat (Scottish Action Coordination Group, 2008). These represented a wide range of taxonomic groups: lichens, bryophytes and liverworts; invertebrates; fungi; birds; vascular plants; mammals; reptiles and amphibians. Evidence sources were classified in to four categories:

Evidence type 1- information from habitat association analyses supplied directly to the authors by species experts in the statutory nature agencies (Scottish Natural Heritage, Natural England, Natural Resources Wales), and nature non-government organisations (NGOs) (Butterfly Conservation, Plantlife Scotland, British Trust for Ornithology). These sources were used particularly where peer reviewed information was lacking on habitat associations under British conditions.

Evidence type 2 – books and peer reviewed scientific articles detailing protected species requirements; these were sourced by searching online journals and journal directories. Example search strings and references used are shown in Table S1 in Appendix A (online supplementary material).

Evidence type 3 - information obtained from publications produced by nature agencies and nature NGOs and from websites likely to be subject to peer-review e.g. for Lepidoptera we used Butterfly Conservation (Butterfly Conservation, 2017)

Evidence type 4 – web sites where the review process was unconfirmed, and which might include anecdotal evidence.

For most taxa, roughly half of the sources of evidence were peer-reviewed websites and grey literature (evidence type 3), and the remainder were drawn evenly from the other three sources of evidence (Table 1). Differences in the use of evidence source by taxon is indicated when the percentage of data fields supported is considered (Table 1). Here there is a reliance on specialist and less available knowledge (type 1 and type 1) for the more cryptic species (e.g. lichens, fungi), compared to more widely accessible reports and information notes provided by nature conservation NGO’s and nature agencies (type 3), for the better-known taxa (e.g. birds, vascular plants). Overall, only a low proportion of data fields were supported by type 4 sources of evidence, where data accuracy is uncertain, as it may not have been confirmed or checked by species experts (Table 1).

We collated the information systematically for each species, recording associations with woodland type or tree species, and microhabitat requirements. Microhabitats represent features of the habitat that may be present at a particular location for a minimum of 5 to 10 years and offer particular microclimates and conditions which may be used by some species only at certain times of the year. Details on species requirements throughout the lifecycle, including differences at early and mature life stages, where appropriate (e.g. for invertebrate species) were also collected. All information included was referenced. A sample of the resulting database is given in Table S2, Appendix A (online supplementary material).

Table 1: Number of sources of evidence by evidence type (and the percentage of data field entries supported) used in identifying habitat requirements, by taxon.

Taxon (number species)	Collated expert knowledge covering individual species (type 1)	Peer-reviewed papers and books (type 2)	Websites (known quality review process) and nature agency reports (type 3)	Websites (unknown review process) and anecdotal evidence (type 4)
Lower plants (Lichens , Liverworts and Bryophytes)(69)	3 (82%)	6 (2%)	5 (16%)	0
Invertebrates (52)	8 (2%)	7 (53%)	36 (28%)	13 (17%)
Fungi (21)	1 (6%)	1 (58%)	9 (36%)	0
Birds (16)	1 (33%)	4 (11%)	7 (56%)	0
Vascular plants (10)	1 (20%)	2(21%)	6 (45%)	5 (14%)
Mammals (8)	2 (43%)	3 (9%)	8 (48%)	0
Herptiles (Amphibians and Reptiles) (3)	2 (70%)	0	2 (30%)	0

For 179 of the 208 protected woodland species (69 lower plants (lichens, bryophytes and liverworts); 52 invertebrates; 21 fungi; ten vascular plants; 16 birds; three herptiles (amphibians and reptiles) and eight mammals), there was sufficient information on habitat requirements for their inclusion in the N4S model. These species were allocated to woodland niches.

2.2.2 Habitat classification - Niches for Species (N4S) matrix

We constructed a hierarchical woodland classification which captured the habitat requirements for all species based on the collated expert information. Where possible, the classification used established descriptors of woodland habitat already familiar to forestry decision-makers e.g. woodland type and structure class (Figure 2):

i. Habitat type: At the highest level of the habitat classification is woodland type. Seven native woodland types are recognised and described (Maddock 2008) (Figure 2).

ii. Habitat subtype: At the second level of the classification hierarchy is structure type. Any woodland type may have stands (representing a portion of the woodland with the same structure, size and age, and considered a single management unit) according to six structure types – these include five stand development stages and a sixth *permanently open* type (Table 2).

Table 2: Summary of structure types used in the classification of niches providing habitat for 179 protected woodland species in Scotland in the Niches for Species model. The structure types are based on the Native Woodland Survey Scotland (NWSS) survey criteria (NWSS, 2013; Patterson et al., 2014)

Structure type	**Description**
Permanently Open	Open habitats: grassland, water or areas where there are constraints to planting trees e.g. rocks, geology, roads.
Temporary open	Area that has been thinned, clear felled, coppiced in last 4 years.
Regeneration and Scrub	Woodland without an overstorey - tree seedlings (< 1m tall), saplings (trees > 1m tall and with girth of up to 7cm diameter at breast height (1.5m)) and shrubs.
Pole stage	Trees and shrubs fill the area and compete, ground flora is shaded out and no other plants colonise. Some canopy trees and understorey shrubs die due to competition. Trees and shrubs not yet bearing seed/fruit (immature). Trees have a diameter at breast height of > 7cm and < 20-30cm and are usually above 5m height.
Mature	Trees producing seed/berries. Crown/canopy usually spreading and at its maximum development. Canopy die-back (up to 10%) from competition for light and/or wind/snow damage.
Veteran ancient	Characterised by the presence of individual trees which have a large girth and show least three signs of old growth and decay. e.g. major trunk cavities/progressive hollowing, fungal fruiting bodies (e.g. from heart rotting species), high aesthetic interest (e.g. pollard or old coppice stool).

Sources of expert knowledge often documented which of the woodland types, and which of the stand structure types, a species was associated with. However, where the expert review did not provide this information, we used the canopy or understorey tree species, or the ground flora the species was associated with to guide its allocation to the woodland type following the National Vegetation Classification (Rodwell, 1991). Where stand structure was not specified in the expert knowledge review for a species, we used information on species' detailed resource and microclimate preferences to inform the structure class within which a species was associated, such as: the use of old growth tree features; the requirement for openness or shade; a reliance on tree seeds; a preference for foliage density at different heights in the canopy.

iii. Microhabitat: From the Stage 2 review describing species resource needs we identified ten microhabitats (Figure 2) within each woodland type and structure class that covered various fine-scale requirements of every protected species. These microhabitat types nested within each structure type (Figure 2).

Having defined each unique woodland type-structure-microhabitat combination as a niche, each species was associated with one or several of these to reflect the range of woodland niches it is associated with according to the review evidence; these associations formed a N4S matrix.

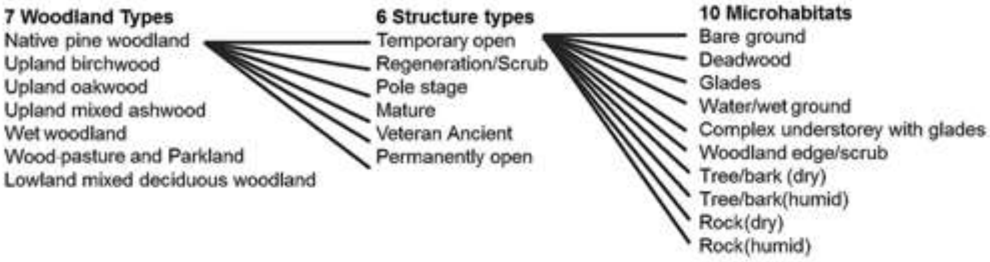


Figure 2: Hierarchical representation of the breakdown of a species resource requirement niche to illustrate the Niches for Species system of habitat classification into niche components.

2.2.3 Mapping woodland polygons and niche distributions

To map woodland polygons, we used the Native Woodland Survey of Scotland (NWSS) (Patterson et al., 2014). This spatial dataset provided information on native woodlands across Scotland according to their type (Biodiversity Action Plan Priority Woodland types: Maddock, 2008), structure and other features. The data were gathered from all of Scotland's native woodlands during 2006-2013 by trained surveyors according to a standard protocol (NWSS, 2013). Attributes are provided at the scale of the woodland polygon, which is defined as a discrete area ≥0.5ha and having a minimum width of 20 m, and in which structural elements occupying a minimum of 5% of the woodland area have been mapped. Therefore, a polygon can be considered analogous to a stand, and there are approximately 95,800 NWSS polygons mapped across Scotland, ranging in size from 0.5 ha to 800 ha with a mean size of c.4 ha (Figure 3).

The NWSS data provided information that allowed us to classify most woodland polygons into the two higher-level niche component categories, woodland type and woodland structure (Table 3). To identify 'wood-pasture and parkland' woodland type, which is not a NWSS woodland category, we overlaid Scotland's

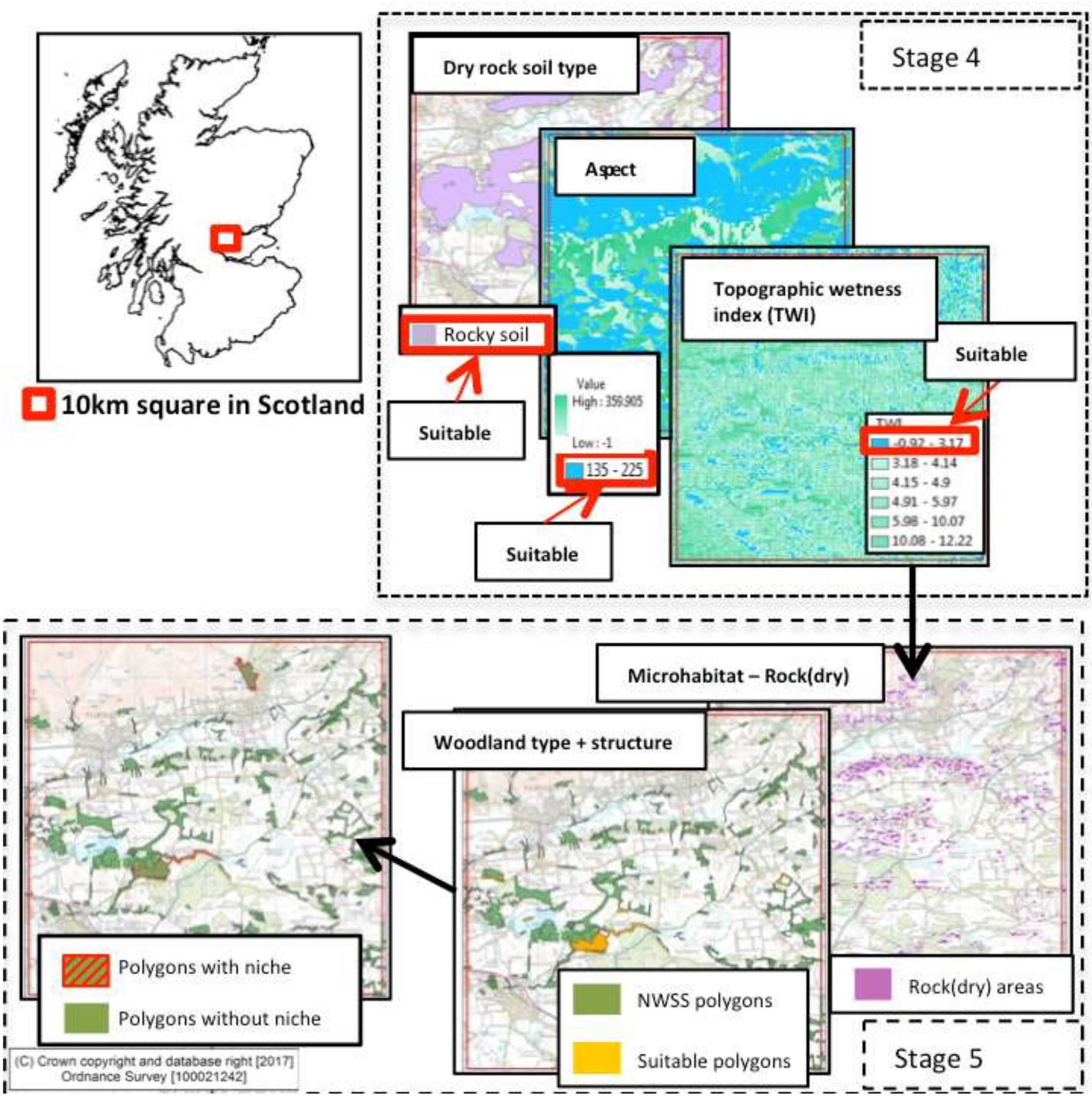


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Figure 3: Graphical representation of the Niches for Species model development for Stage 4- deriving niche components (this example for microhabitat type rock (dry)) from environmental spatial data, and Stage 5- categorising habitats and mapping niches by combining microhabitat presence with NWSS polygon information (in this example 'suitable' NWSS polygons are of habitat type upland oak woodland and subtype (structure) is mature).

Country Parks dataset (Scottish Natural Heritage) and updated the woodland type of any polygons with a centroid overlapping a park. The 'permanent open' or 'temporary open' woodland structures were identified as NWSS open habitat or clear fell polygons. These open polygons lacked woodland type information, so they were assigned the same woodland type as the adjacent woodland polygon with the shared longest border, calculated using a Geographic Information Software (GIS) (Esri, 2013). We made this assumption in the absence of historical NWSS data that might provide evidence of earlier woodland type.

To map the distribution of the 10 microhabitats, we reviewed the relevance of NWSS data attributes alongside various other spatial environmental datasets (singly or in combination) available for Scotland (Table 3). Data layers were extracted from non-NWSS data by selecting polygons (vector data) or cells (raster layers) using a GIS, that met specified attributes. For example, areas that were likely to have wet sites were identified as those falling within 25 m of linear water features or wetland habitat features identified from vector landcover maps, or as flat cells ($\leq 0.5^{\circ}$ slope) with high topographic wetness index values (Sørensen et al., 2006) using a 25 m digital elevation model (Table 3). Sources of all data layers used and whether vector or raster are provided in Table 3.

2.2.4 Mapping niche occurrence in polygons using spatial environmental data

Once the NWSS woodland polygons had been classified by type and structure, microhabitat presence-absence was predicted by overlaying the NWSS polygons with the various microhabitat input data layers in a GIS. A rule-set was established for mapping the presence of microhabitats that depended on particular combinations of microhabitat input layers. The simplest microhabitat to map was *deadwood*, as NWSS surveyors estimated deadwood volume on a single site visit per woodland polygon during the seven year-long field survey (Table 3) (NWSS, 2013). The remaining nine microhabitats were more complex to map, requiring more than a single data source (for details of data sources used to map the microhabitats see Table 3). For example, identifying the microhabitat *rock (dry)* used several spatial layers (Figure 3) combined using a logical rule-set to integrate information on land cover, soil and topographic position (e.g. slope and aspect) of the polygon. The rule-sets were automated in ArcGIS Model Builder (v10.2) (Esri, 2013). The ‘zonal statistics’ tool was used to identify polygons overlapping input raster cells, and ‘select by location’ used to identify polygons intersected by input vector layers. Any amount of overlap between a NWSS polygon and a microhabitat input layer resulted in recording the microhabitat ‘presence/absence’ in the polygon (although microhabitat ‘absence’ unused), and the area or amount of microhabitat cover within a polygon was not considered.

Table 3: Rule-set for combining spatial environmental data (type- vector=V, raster=R and sources of data shown in brackets) to describe potential niches present in the native woodlands of Scotland.

Niche Component	GIS rule
Woodland type[1]	
Upland mixed ashwood	Dominant NWSS woodland type for polygon (NWSS)
Upland birchwood	
Upland oakwood	
Lowland mixed deciduous	
Native pine	
Wet woodland	
Wood-pasture and parkland	Any NWSS polygon with centroids overlapping the Scotland's Country Parks dataset (NWSS; Scotland's Country Parks)
Structure type	
Permanently open	NWSS polygons recorded as 'open land' habitat type, which were ≥1 ha and shared an edge with a wooded NWSS polygon[2] (NWSS)
Temporary open	NWSS polygons recorded as 'clear fell' dominant habitat type which were ≥1 ha and shared an edge with a wooded NWSS polygon[2] (NWSS)
Regeneration or Scrub	'Native woodland' or 'Nearly-native woodland' NWSS polygons with dominant structure recorded as 'Visible regeneration', 'Established regeneration' or 'Shrub' or 'Scrub'(NWSS)
Pole	'Native woodland' or 'Nearly-native woodland' NWSS polygons with dominant structure recorded as 'Pole Immature' or 'Pole immature' (NWSS)
Mature	'Native woodland' or 'Nearly-native woodland' NWSS polygons with dominant structure recorded as 'Mature' (NWSS)
Veteran ancient	'Native woodland' or 'Nearly-native woodland' NWSS polygons with dominant structure recorded as 'Veteran' (NWSS)
Microhabitat	
Deadwood	NWSS polygons where deadwood was recorded by surveyor (NWSS)
Water/wet ground	NWSS polygons where (a) NVC[3] types associated with wet woodland habitats were recorded or, (b) they were intersected by: (i) inland water or wetland habitat polygons (OSMM or LCM inland water features) or, (ii) DEM cells with low slope (<=0.5°) and within the top seven deciles of topographic wetness index values (NWSS; OSMM; LCM; DEM)
Woodland edge/scrub	NWSS polygons where (a) scrub was recorded by the surveyor (NWSS) or, (b) that have 'hard edges' i.e. aren't completely surrounded by other woodland polygons (NWSS; NFI)
Tree/bark (dry)	NWSS polygons with hard woodland edges (see woodland edge / scrub description) that overlap DEM cells with a southerly aspect (135 - 225°) and are within the bottom decile of topographic wetness index values (NWSS; DEM)
Tree/bark (humid)	NWSS polygons that (a) overlap DEM cells with a northerly aspect (>315° or ≤45°) or, (b) overlap DEM cells with low slope (<=0.5°) and are (c) within the top seven deciles of topographic wetness index values (TWI) or, (d) within 25 m of inland water or wetland habitats (OSOR or LCM inland water

Niche Component	GIS rule
	features)(NWSS; DEM; TWI; OSOR; LCM)
Complex understorey with glades	NWSS polygons with 10 - 70% canopy cover and (a) regeneration (established or visible; ≥10% cover) and shrub structures (≥10% cover) or, (b) ≥6 canopy structure types recorded by the surveyor (NWSS)
Glade	NWSS polygons with 10 – 70% canopy cover (NWSS)
Rock (dry)	NWSS polygons intersected by soil polygons with 'rocky' properties and DEM cells with a southerly aspect (135 - 225°) and within the bottom decile of topographic wetness index values (NWSS; Scottish soils; DEM; TWI)
Rock (humid)	NWSS polygons intersected by rocky soil polygons and (a) overlap DEM cells with a northerly aspect (>315° or ≤45°) or, (b) overlap DEM cells with low slope (<=0.5°) and are (c) within the top seven deciles of topographic wetness index values or, (d) within 25 m of inland water or wetland habitats (NWSS; Scottish soils; DEM; TWI; OSOR; LCM).
Bare ground	NWSS polygons? intersected by a footpath or forest track feature (footpaths)

Data sources: NWSS = Native Woodland Survey Scotland (V) (Patterson et al., 2014); Scotland's Country Parks = Scottish Natural Heritage (V); OSMM = Ordnance Survey Master Map (V)(Ordnance Survey, 2016); LCM = Centre for Ecology and Hydrology Land Cover Map 2007 vector map (V)(Morton et al., 2011); DEM= 25 m resolution digital elevation model (R)(EU-DEM, 2016); NFI = Forestry Commission's National Forest Inventory map (V)(Forestry Commission, 2011); TWI = topographic wetness index (R)(Sørensen et al., 2006; EU-DEM, 2016); OSOR = Ordnance Survey Open Rivers (V); Scottish soils = a 'mash-up' of two different scale maps at 1:10,000 and 1:250,000 (V)(Lilly et al., 2010); Footpaths = Forestry Commission Scotland forest paths, tracks, rides, and boundaries (V)(FC Scotland, 2016).

[1] see Maddock (2008) for definitions

[2] Assigned the woodland type of the wooded polygon (those classified as Native woodland' or 'Nearly-native woodland') with which they shared the longest border length with.

[3] National Vegetation Classification (NVC) see Rodwell (1991).

2.2.5 Mapping species habitat suitability

Using Model Builder and Python scripts in ArcGIS, we implemented a rule-set to link the NWSS niche map with the N4S matrix. A NWSS polygon was predicted to be suitable when the combination of woodland type-woodland structure and microhabitat presence matched a species' habitat requirements. Binary fields were added to the spatial database to indicate a polygon's predicted suitability (0 or 1) for each species.

2.2.6 Mapping species potential distribution

As many of the protected species have restricted ranges across Scotland, we limited predicted species occurrence by classifying any NWSS polygons outside of modelled current bioclimatic envelopes as unsuitable. Bioclimatic envelopes were available for

51 species (23 species of invertebrate, 17 lower plants, 1 vascular plant (Ellis et al., 2014; Pearce-Higgins et al., 2015)) (Table S3, Appendix A – online supplementary material). In the absence of these data we mapped population ranges from 10 km resolution NBN Gateway species records (NBN, 2017) for all survey years using the Minimum Convex Polygons (MCPs) (Rurik and Macdonald, 2003) in ArcGIS. MCPs were generated for 90 species representing all taxa. For 38 species there was insufficient data (fewer than three 10 km squares adjacent to one another) (Table S3 Appendix A – online supplementary material).

2.3 Validation of model

2.3.1 Validation species occurrence data

We selected ten species to use in a validation exercise. The validation compared the potential distribution predicted by N4S with existing species occurrence records. The validation species were selected to represent a range of woodland types, taxonomic groups, and traits (wide to narrow niche breadth; vagile to sessile; easy to observe to cryptic). We used only data recorded at a 100 m resolution or finer (≥6 figure grid references) to ensure we could accurately attribute records to polygons (Dymytrova et al., 2016). Records were used from a sixteen-year period (2000 to 2016), in line with the NWSS data (surveyed 2006 – 2013). To gain insights into how well the N4S model predicted areas without the potential to support protected species, we incorporated pseudo-absence records into the analysis as adequate absence records were not available. Pseudo-absence records were created following the “surveyed absence” or “target group” strategy which uses location records of species from the same taxonomic group, where it is assumed that the focal species was not recorded as it was absent (Gomez-Rodriguez et al., 2012; Hanberry et al., 2012; Phillips et al., 2009). The choice of only 10 validation species was largely influenced by the availability of species records for which we could obtain some pseudoabsence data.

Ultimately, choice of validation species was constrained by data availability. For two bird species - *Muscicapa striata, Turdus philomelos* - data at the required resolution were available only from surveys of one woodland type (native pine woodland) limiting testing of model predictions to between woodland type and structure with and without microhabitat. N4S model predictions were fully tested for the remaining eight validation species: three lower plants- *Collema fasiculare, Pseudocyphellaria norvegica, Gomphillus calyciodes*; one vascular plant- *Linnaea borealis*; and four invertebrates- *Cupido minimus, Carterocephalus palaemon, Boloria euphrosyne, Osmia uncinata.*

2.3.2 Validation data analysis

Duplicate species records (same date and location) were removed. The proportion of field records falling within polygons predicted to be suitable or unsuitable for each of the validation species were calculated for presence and pseudo-absence records. We applied a cumulative binomial probability test (R Core Team 2012) to estimate whether the number of presence records lying within suitable polygons of the N4S model was greater than could have been predicted by chance alone, according to the area of suitable woodland habitat available within the species' range.

We also tested the degree of agreement between the N4S model predictions and the information from the presence/pseudo-absence datasets by constructing confusion matrices using SAS version 9.3 (SAS, 2011) (Table S1, Appendix B - online supplementary material) and generating Cohen's Kappa statistic (k), where k=1 indicates perfect agreement, k=0 agreement by chance alone and k<0 disagreement (Cunningham, 2009). A system of subdivision of k has been suggested, for which we tested the six categories: "No agreement" (k<0); "Slight agreement" (k≥0 and <0.2); "Fair agreement"(k≥0.2 and <0.4); "Moderate agreement"(k≥0.4 and< 0.6); "Substantial agreement" (k≥0.6 and <0.8); "Almost perfect agreement" (k≥0.8 and <1.0) (Landis and Koch, 1977). The deviation of k values from zero was tested statistically (H_0: k = 0; one-sided probability reported as testing agreement i.e. k>0). All tests were performed for each species and at three levels of the habitat classification hierarchy i.e. where occurrence of the target species was predicted from the presence of 1) suitable woodland type only, 2) woodland type + structure type or 3) woodland type + structure type + microhabitat type.

2.4 Choice of Niches for Species model outputs

The N4S model output (map of protected woodland species potential occurrence based on the availability of niches) can be viewed at a variety of scales. We selected three scales considered appropriate for different policy or practice queries: 1) a national-scale overview of species richness which may be applicable to supporting strategic forest policy decisions, 2) a landscape-scale assessment of species richness which may support tactical decision making in forest planning, and 3) an individual species map with associated habitat data which we envisaged might be used in practice for operational decisions guiding management interventions.

3. Results

3.1 Spatial environmental data used to map niche occurrence in polygons

Most of the niche components were derived directly from the NWSS data (Table 3). For the remainder, information was derived from other available spatial datasets and their reliability was limited by their relevance, accuracy and precision (Table 3; Table S4, Appendix A - online supplementary material). For example, there were no fine resolution spatial data available to describe the microhabitat *bare ground.* Therefore, we assumed this microhabitat would be found along footpaths and tracks, and used spatial data on these features to map the likely occurrence of this microhabitat.

3.2 Validation

The strength of the agreement (i.e. higher Kappa value) varied among species (Table 4). There was some agreement (Kappa>0) between model predictions and the occurrence for nine of the ten validation species (No agreement found for *T. philomelos*), but this was 'Slight' for seven of the remaining nine species' (Landis and Koch 1977). Higher Kappa values (Kappa = 0.296 - 'Fair agreement' to Kappa = 0.807- 'Perfect agreement') occurred for the species *O. uncinata* and for *L. borealis*. Results from the probability tests (Kappa and binomial) were largely consistent. For five of the ten validation species associations between distribution records and predicted availability of suitable polygons was better than would be expected if species occurrence had been allocated at random to the woodland polygons. For two species the results approached statistical significance, for one level of the habitat classification hierarchy (e.g. woodland type + structure) tested. Judged on the frequency of agreement (between actual and predicted occurrence of species when the

N4S model was run at the three levels of niche hierarchy complexity) the N4S model appeared to perform equally well at the intermediate (woodland type + structure) and most detailed (woodland type + structure + microhabitat) hierarchy levels (Table 4). However, the agreements with the highest levels of significance ($p<0.05$) for the binomial test and Kappa value occurred when the model included microhabitat (Table 4). This suggests that where agreements are found these are stronger when niche identification included microhabitat features.

Table 4 Summary of correspondence between the habitat availability for ten validation species predicted using Niches for Species (N4S) model and records of species occurrence and pseudo-absence at three levels of niche hierarchy (1 = woodland type only; 2= woodland type + stand structure; 3= woodland type + stand structure + microhabitat). Kappa (k) subdivisions: "No agreement" (k<0); "Slight agreement" (k≥0 and <0.2); "Fair agreement"(k≥0.2 and <0.4); "Moderate agreement"(k≥0.4 and< 0.6); "Substantial agreement" (k≥0.6 and <0.8); "Almost perfect agreement" (k≥0.8 and <1.0) (Landis and Koch, 1977). One-sided probability reported as testing for where k is positive; H_0: k = 0. “Binomial” refers to a binomial probability test; H_0: the number of validation species records found within suitable woodland polygons is no better than random within the sampled woodland polygons. Sampled polygons being those containing a pseudo-absence record a validation species record or both. Probability test level of significance (for both Kappa and binomial tests): *p<0.05, **p<0.01, ***p<0.001, na = not applicable for one-sided test, p value reported where non-significant.

	Niche hierarchy					
	1		**2**		**3**	
Validation species	**Kappa value (p =)**	**Binomial**	**Kappa value (p =)**	**Binomial**	**Kappa value (p =)**	**Binomial**
Collema fasiculare	Slight agreement 0.105 (p=0.067)	p=0.098	Slight agreement 0.095 (p=0.103)	p=0.147	Slight agreement 0.022 (p=0.386)	p=0.483
Pseudocyphellaria norvegica	No agreement -0.107 (na)	p>0.999	Slight agreement 0.005 (p=0.455)	p=0.444	Slight agreement 0.014 (p=0.358)	p=0.253
Gomphillus calyciodes	Slight agreement 0.008 (p=0.419)	p=0.518	Slight agreement 0.126(p=0.053)	p=0.078	Slight agreement 0.108(p=0.081)	p=0.118
Linnaea borealis	Almost perfect agreement 0.807 (***)	**	Slight agreement 0.128 (***)	**	Slight agreement 0.065 (***)	***
Cupido minimus	No agreement -0.0013 (na)	p=0.863	Slight agreement 0.042 (***)	**	Slight agreement 0.045 (***)	***
Carterocephalus palaemon	No agreement -0.018 (na)	p>0.999	Slight agreement 0.022 (p=0.075)	p =0.056	Slight agreement 0.004 (p=0.381)	p=0.262
Boloria euphrosyne	Slight agreement 0.013 (***)	**	No agreement -0.025 (na)	P=0.999	No agreement -0.016 (na)	P=0.999
Osmia ucinata	Slight agreement 0.006 (p=0.139)	p=0.231	Fair agreement 0.296 (***)	***	Fair agreement 0.223(***)	***
Muscicapa striata	NA	NA	Slight agreement 0.041 (*)	p=0.076	No agreement -0.016 (na)	p=0. 641
Turdus philomelos	NA	NA	No agreement -0.024 (na)	P=0.999	Insufficient values	p=0.999

3.3 Example N4S model outputs

3.3.1 National species richness map

The national scale map (Figure 4) highlights the extent of native woodlands covered by the NWSS dataset (included in the N4S model), and shows the potential occurrence of protected woodland species within these woodlands. Woodlands with high species richness (>20 to 30 protected woodland species per woodland polygon) are reasonably well spread throughout Scotland although the native woodlands of the River Dee valley and the River Spey valley in north-eastern Scotland stand out as being areas of particularly high species richness.

3.3.2 Landscape scale species richness output

The 10 km x 10 km area of upland Scotland selected to illustrate the N4S model landscape scale output (Figure 5) depicts a highly wooded landscape area, where nearly half of the area (4,377 ha) comprises native woodlands. A few polygons have the niche potential for a high number of protected woodland species (up to 31) and most have the potential to support ten or more species. However, several polygons have low species richness (0 to 10 protected species per polygon).

3.3.3 Individual species-niche output

More detailed information can be extracted from the N4S model (Figure 6). For example, the lower plant *Dumortiera hirsuta* was one of the species predicted to occur in the sample landscape we have used to illustrate the finest scale output from the N4S model. The model output gives the locations of the polygons *D. hirsuta* is predicted to occur within (Figure 6). These comprise woodland types *upland oakwood* and *upland mixed* *ashwood*, all with a *mature* stand structural stage. *Dumortiera hirsuta* is most likely to be associated with the *water/wet ground* and *rock*(*humid*) and *bare ground* microhabitats where available within these polygons.

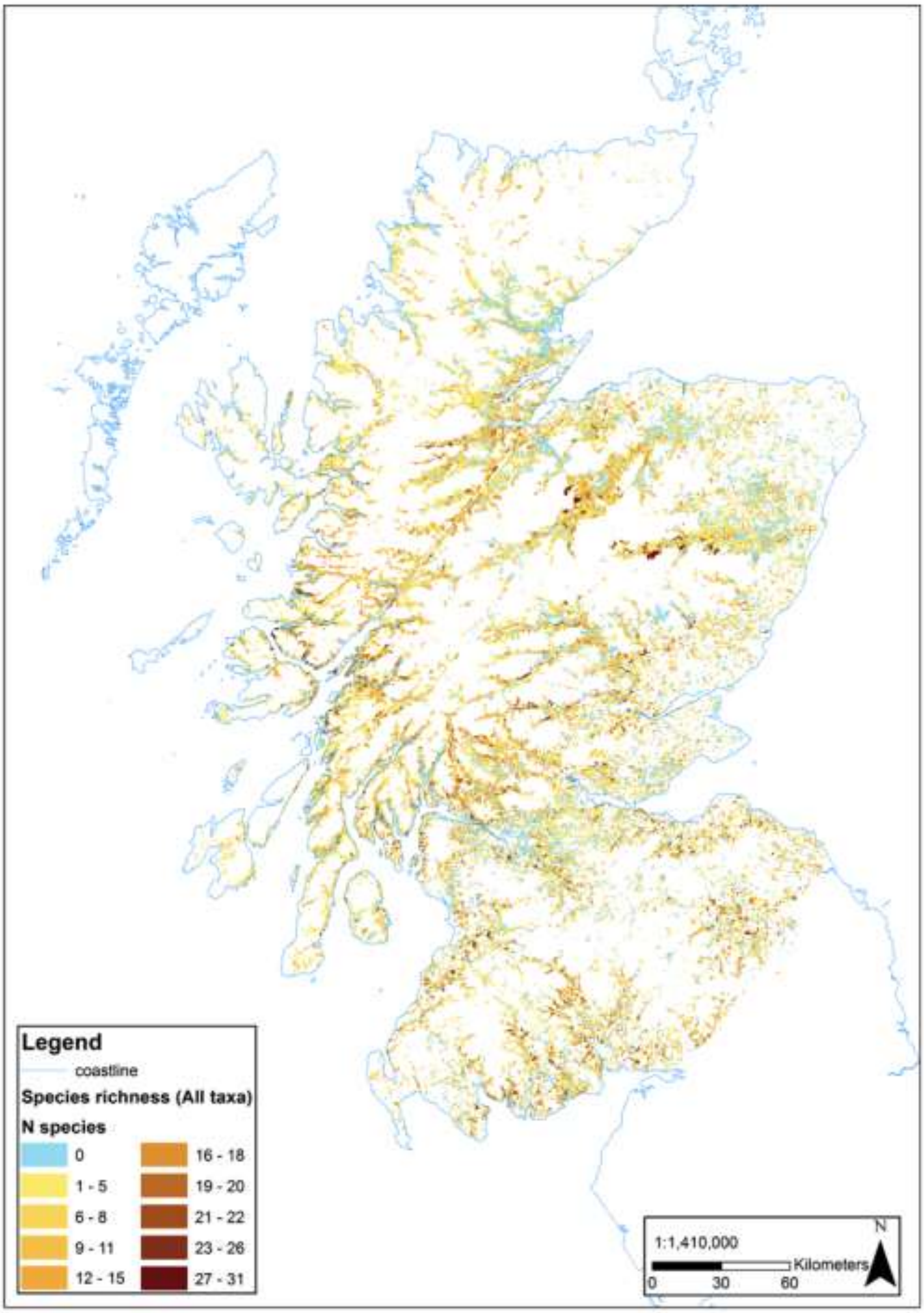


Figure 4: Species richness of native woodlands in Scotland based on the predicted potential distribution of all 179 protected woodland species.

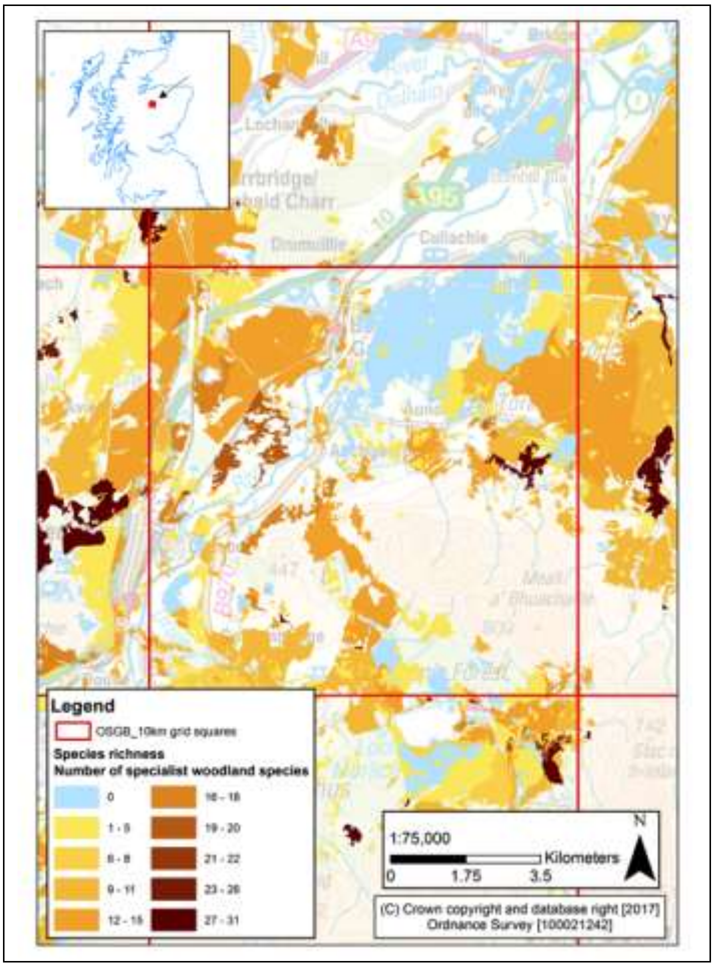
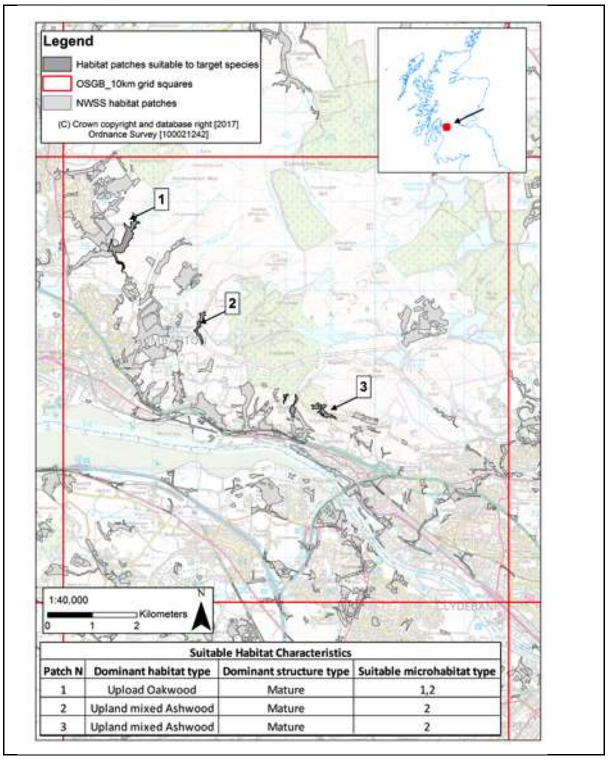


Figure 5: Sample output from the Niches for Species model showing predicted distribution of protected woodland species richness by native woodland polygon in a 10 km x 10 km (Ordnance Survey Great Britain) area of a typical upland landscape in Scotland.



Suitable Habitat Characteristics			
Patch N	Dominant habitat type	Dominant structure type	Suitable microhabitat type
1	Upload Oakwood	Mature	1,2
2	Upland mixed Ashwood	Mature	2
3	Upland mixed Ashwood	Mature	2

Figure 6: Sample output from the Niches for Species model showing predicted location of *Dumortiera hirsuta*, a protected woodland species in native woodland polygons in a 10 km x 10 km area (Ordnance Survey Great Britain). Niche information associated with *D. hirsuta* is included; a niche is defined by the combination of *woodland type*, *structure type* and *microhabitat* (1 = *water/wet ground*, 2 = *rock*(*humid*)). (NWSS- Native Woodland Survey Scotland).

4. Discussion

We provide a framework to link expert species knowledge with spatial environmental datasets to predict simultaneously, for multiple taxa, the availability of habitat for protected species. In applying our N4S model to protected woodland species in Scotland, we found that the type and accessibility of expert knowledge on habitat requirements varied between taxa, but that there was sufficient information to include 179 of the 208 species. Relevant spatial environmental data were also available to classify native woodlands into type and structure, and to map the distribution of most microhabitats with confidence. Species records did not consistently accord with the predictions of species occurrence by the model: good agreement was shown for five out of ten of the validation species, based on the niche hierarchy giving best results. By mapping protected species potential occurrence, the quality of habitat for supporting biodiversity can be visualized in a simple form by spatial outputs of protected species richness by woodland polygons; interpreted from the same input data either at the whole administrative region, landscape or forest level.

4.1 Adequacy of data and model strengths

The relatively simple species-habitat association evidence in the N4*S* model has been drawn from information provided by species experts, and, although of good quality, much of the information was not published and therefore needed to be sought directly from the experts. Based on the percentage of data field entries for different taxa supported by each of the four evidence types, it appears information for cryptic species is less accessible (mostly via expert knowledge- evidence type 1 and peer-reviewed journals- evidence type 2) than for the better-known species, as expected. The literature on biodiversity indicators suggests there is a sound basis to making links between habitat features and species occurrence (Regnery et al., 2013; Gao et al., 2015) and the inclusion of fine scale habitat features (e.g. structure type and microhabitats in the N4S model) can be important for certain species (Harvey and Platenberg, 2009; Dymytrova et al., 2016; Horak, 2017).

We have high confidence in the quality of the spatial data as 65% of the 23 different habitat categories and microhabitats used in the N4S model (7 woodland types, 6 structure types and 10 microhabitat types) were derived directly from existing attributes in the input datasets. A third of these attributes relied on information derived from various other spatial data. However, we had low confidence in predicting just one attribute - the *bare ground* microhabitat. Although beyond the scope of this study, we recommend validating the N4S model using a targeted survey of polygons in which an assessment of the predicted niche occurrence has been verified. This would increase our confidence in how well spatial data combine to describe features on the ground. We have relied on the detailed woodland survey NWSS data to locate many of the niches and such data may not be universally available. Nevertheless, the approach illustrated, of classifying habitat niches and describing these using spatial data would allow the use of alternative or replacement spatial datasets. We recommend sourcing and integrating alternative spatial data to ensure that habitat layers remain current. For example, we could integrate a forest structure layer interpreted from aerial photography or LiDAR data (where this is available) to update the woodland structure information within the polygons (McInerney et al., 2011).

The N4S model does not take account of interactions among species and assumes that if the correct habitat is available there will be no constraints on potential species use. This assumption, like SDMs in general, may lead to over prediction of species occurrence (Phillips et al., 2006). Although N4S does not account for the landscape surrounding a woodland patch, broader scale influences that affect species distribution are factored in to the N4S model by constraining predictions by bio-climatic or distribution envelopes. Inclusion of envelopes has been shown to improve model performance in SDMs based on species records (Lobo et al., 2011; Zarnetske et al., 2007), primarily because it enables some environmental data to be incorporated.

4.2 Model validation

Consistent with our expectations, validation showed limited correspondence between predicted potential species locations (woodland polygons) and recent species presence records (agreements were significant for half of the validation species). Including detailed information about species' resource requirement (microhabitat) in our expert-based habitat suitability model did appear to improve the model performance in the validation tests for the subset of species where agreement was found between predicted and recorded species occurrence. It is possible that this is due to weak relationships between some but not all taxa represented by the validation species and microhabitats (Goa et al., 2015; Regnery et al., 2013) and could also result from poor spatial definition of microhabitats from the data sets we have used. However, we anticipated that poor model performance could also result from the lack of availability of high-resolution species presence records available for validation. Although the resource of species records for Britain is large, surveys are not always carried out systematically (instead favoured locations are targeted for survey), it is uncommon for all areas to be surveyed regularly, and only rarely is species absence data collected (NBN, 2017). In studies when data meeting these survey criteria are deployed, good agreement has been found between the empirical data and the expert-based classifications of habitat choice (Leblond et al., 2014; Reif et al., 2010). The lack of availability of good quality species records has been argued (e.g. Phillips et al., 2006) as a reason to develop predictive models of distribution based on knowledge, as in N4S, rather than records.

4.3 Application

Niches for Species is now being applied in several ways with model uncertainty described according to the scale of application. For forest policy makers, the model provides an analysis of the whole of the native woodland resource in Scotland (both within and outside protected areas) and indicates where there are species 'hotspots' or habitats where particular sets of rare or threatened species are likely to occur. As N4S considers all the protected species of interest for the region, it performs as well, or better than the current alternative national analysis method conducted for the UK using coarser (2km resolution) data, and the better recorded species e.g. birds as surrogates (Franco et al., 2009). Furthermore, the N4S model has the advantage of providing information on the habitats associated with areas that may be prioritised due to potential protected species occurrences: Franco et al. (2009) recognised that the lack of such information was a shortcoming in their SDM. For forestry decision making, visualising the configuration of potential protected species occurrence at the landscape-scale can help planners consider how to minimise forest operations impacts on species rich areas (Forestry Commission 2017; UKWAS, 2008). When used in a scenario analysis, N4S can provide planners with estimates of how potential species lists and overall species richness may vary with choice of woodland type and location, as a result of decisions to meet woodland expansion targets (Sing et al., 2013). At this scale of application, uncertainties regarding the accuracy of the model should be checked by applying local experience to compare habitat types, and likely diversity of niches with the location of species rich areas indicated by the model. At a finer scale, knowledge of potential occurrence of a protected species within a woodland polygon may alert the need for an expert survey to confirm species presence. This is consistent with the recommended application of many SDMs (Buechling and Tobalske, 2011; Dymytrova et al., 2016; Lentini et al., 2015).

Forestry practitioners and policy makers are tasked with applying management in ways that will meet international and national obligations for conserving biodiversity in the most efficient manner (CBD, 2010; Forestry Commission, 2017). Obligations are articulated through law and policy devolved to a country/regional level. In all cases information is needed on where the most threatened species occur within the landscape, and how species presence may change in response to habitat management at a variety of scales (Barrows et al., 2005; Egoh et al., 2014;). Our challenge was to produce a model which encompassed all the protected species Scottish forestry decision makers are legally obliged to consider. Our approach incorporates the available wealth of ecological knowledge on species using high resolution spatial data, and avoids the need to rely solely on species records or surrogate species. The N4S model provides forest decision makers with information on the occurrence of niches for nearly all the protected species associated with woodlands in Scotland. For many species, actual locations may not be known due to their rarity and/or their cryptic nature; and additionally, there may be uncertainty about habitat features to which their location is related. The output map format with associated attribute table listing the woodland type, structure and predicted presence and absence of each microhabitat and protected species, helps to improve knowledge of species needs and location of potential niches.

Niches for Species can help forest practitioners guide conservation management, but we acknowledge some weaknesses, which may limit its application, and suggest improvements. The model may lack high levels of accuracy that would otherwise be valuable to forest policy makers and practitioners. However, high levels of accuracy are not always needed by decision makers, and more timely action may ultimately be more cost effective than delayed action (Cook et al., 2013). This is particularly so at a time of austerity and a decline in priority afforded to biodiversity policy. We recommend this expert-based EHSM approach as a method to integrate complex information relating to multiple and often data-deficient species in a format which allows land policy makers and managers to consider equally, large numbers of species and their conservation needs.

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References

Austin, M.P., 2002. Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. *Ecol. Model.* 157(2–3), 101–118.

Barrows, C.W., Swartz, M.B., Hodges, W.L., Allen, M.F., Rotenberry, J.T., Li, B.-L., Scott, T.A., Chen, X., 2005. A framework for monitoring multiple-species conservation plans. *J. Wildl. Manage*. 69, 1333–1345.

Bellamy, C., Scott, C., Altringham, J., 2013. Multiscale, presence-only habitat suitability models: Fine-resolution maps for eight bat species. *J. Appl. Ecol.* 50, 892–90, doi: 10.1111/1365-2664.12117.

Bottrill, M.C., Joseph, L.N., Carwardine, J., Bode, M., Cook, C., Game, E.T., Grantham, H., Kark, S., Linke, S., McDonald-Madden, E., Pressey, R.L., Walker, S., Wilson, K.A., Possingham, H.P., 2008. Is conservation triage just smart decision making? *Trends Ecol. Evol.* 23, 649–654, doi: 10.1016/j.tree.2008.07.007.

Buechling, A., Tobalske, C., 2011. Predictive habitat modeling of rare plants species in Pacific Northwest forests. *West. J. Appl. For.* 26, 71–81.

Butterfly Conservation, 2017. Factsheets, downloads, resources and reports. Butterfly Conservation, Wareham, UK, https://butterfly-conservation.org/ (accessed November 2017)

CBD (Convention on Biological Diversity), 2010. Strategic Plan for Biodiversity 2011–2020 and 20 Aichi targets. CBD, Nagoya, Japan, https://www.cbd.int/sp/elements/ (accessed November 2017).

Cook, C.N., Mascia, M.B., Schwartz, M.W., Possingham, H.P., Fuller, R.A., 2013. Achieving conservation science that bridges the knowledge-action boundary. *Conserv. Biol.* 27, 669–678, doi: 10.1111/cobi.12050.

Cooper-Bohannon, R., Rebelo, H., Jones, G., Cotterill, F.W., Monadjem, A., Schoeman, M.C., Taylor, P., Park, K., 2016. Predicting bat distributions and diversity hotspots in Southern Africa. *Hystrix, Ital. J. Mammal*. doi: 10.4404/hystrix-27.1-11722.

Crance, J.H., 1987. Guidelines for using the Delphi technique to develop habitat suitability index curves. *US Fish Wildl. Serv. Washingt.* 21.

Cunningham, M., 2009. More than just the kappa coefficient: A program to fully characterize inter-rater reliability between two raters. *SAS Glob. Forum 2009 Stat. Data Anal.* 242, 1–7.

Dinerstein, E., Olson, D., Joshi, A., Vynne, C., Burgess, N.D., Wikramanayake, E., Hahn, N., Palminteri, S., Hedao, P., Noss, R., Hansen, M., Locke, H., Ellis, E.C., Jones, B., Barber, C.V., Hayes, R., Kormos, C., Martin, V., Crist, E., Sechrest, W., Price, L., Baillie, J.E.M., Weeden, D., Suckling, K., Davis, C., Sizer, N., Moore, R., Thau, D., Birch, T., Potapov, P., Turubanova, S., Tyukavina, A., De Souza, N., Pintea, L., Brito, J.C., Llewellyn, O.A., Miller, A.G., Patzelt, A., Ghazanfar, S.A., Timberlake, J., Klöser, H., Shennan-Farpón, Y., Kindt, R., Lillesø, J.P.B., Van Breugel, P., Graudal, L., Voge, M., Al-Shammari, K.F., Saleem, M., 2017. An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* 67, 534–545, doi:10.1093/biosci/bix014.

Dormann, C.F., 2007. Promising the future? Global change projections of species distributions. *Basic Appl. Ecol.*, *8*(5), 387-397.

Dorey, K., Walker, T.R., 2018. Limitations of threatened species lists in Canada : A federal and provincial perspective. *Biol. Conserv.* 217, 259–268, doi:10.1016/j.biocon.2017.11.018.

Doswald, N., Zimmermann, F., Breitenmoser, U., 2007. Testing expert groups for a habitat suitability model for the lynx *Lynx lynx* in the Swiss Alps. *Wildlife Biol.* 13, 430-446.

Drew, C. A., Collazo J. A., 2012. Expert knowledge as a foundation for the management of secretive species and their habitat. Chapter 5 in A. H. Perera, C. A. Drew, and C. J. Johnson, editors. Expert knowledge and its application in landscape ecology. Springer, New York, New York, USA, doi: 10.1007/978-1-4614-1034-8_5.

Drew, C. A., Perera A. H., 2011. Expert knowledge as a basis for landscape ecological predictive models. Chapter 12 in C. A. Drew, Y. F. Wiersma, F. Huettmann, editors. *Predictive species and habitat modeling in landscape ecology: concepts and applications* Springer, New York, New York, USA, doi: 10.1007/978-1-4419-7390-0_12.

Dymytrova, L., Stofer, S., Ginzler, C., Breiner, F.T., Scheidegger, C., 2016. Forest-structure data improve distribution models of threatened habitat specialists: Implications for conservation of epiphytic lichens in forest landscapes. *Biol. Conserv*. 196, 31–38, doi:10.1016/j.biocon.2016.01.030.

EC (European Commission), 2018. How EU environment law works. EC environment pages, EC, Brussels, Belgium, http://ec.europa.eu/environment/basics/benefits-law/eu-environment-law/index_en.htm (accessed May 2018).

Egoh, B.N., Paracchini, M.L., Zulian, G., Schägner, J.P., Bidoglio, G., 2014. Exploring restoration options for habitats, species and ecosystem services in the European Union. *J. Appl. Ecol.* 51, 899–908, doi:10.1111/1365-2664.12251.

Elith, J., Leathwick, J.R., 2009. Species distribution models: Ecological explanation and prediction across space and time. *Annu. Rev. Ecol. Evol. Syst*. 40, 415–436, doi:10.1146/annurev.ecolsys.l.

Ellis, C.J. Eaton, S., Theodoropoulos, M., Coppins, B.J., Seaward, M.R.D., Simkin, J., 2014. Response of epiphytic lichens to 21st century climate change and tree disease scenarios. *Biol. Conserv*., 180, 153–164, doi:10.1016/j.biocon.2014.09.046.

Esri, 2013. ArcGIS v.10.2, Esri, Redlands, CA, USA, www.esri.com. (accessed September 2015).

EU-DEM 2016 European Digital Elevation Model (EU-DEM) Version 1, 25m resolution, Copernicus Programme, European Environment Agency, copernicus@eea.europa.eu

Eycott, A.E., Stewart, G.B., Buyung-Ali, L.M., Bowler, D.E., Watts, K., Pullin, A.S., 2012. A meta-analysis on the impact of different matrix structures on species movement rates. *Landsc. Ecol.* 27, 1263–1278, doi:10.1007/s10980-012-9781-9.

Favaro B., Claar D.C., Fox C.H., Freshwater C, Holden J.J.,Roberts A., 2014. Trends in extinction risk for imperiled species in Canada. *PLoS ONE*, 9(11): e113118.

Franco, A.M.A., Anderson, B.J., Roy, D.B., Gillings, S., Fox, R., Moilanen, A., Thomas, C.D., 2009. Surrogacy and persistence in reserve selection: Landscape prioritization for multiple taxa in Britain. *J. Appl. Ecol.* 46, 82–91, doi:10.1111/j.1365-2664.2008.01598.x.

Forestry Commission, 2011. National Forest Inventory Report, 2011. NFI 2011 woodland map GB. Forestry Commission. Edinburgh.

Forestry Commission, 2017. The UK Forestry Standard (Fourth Edition). Edinburgh.

FC Scotland (Forestry Commission Scotland), 2016. Open Data, http://data-forestry.opendata.arcgis.com/datasets?t=Scotland (accessed November 2017).

Fourcade, Y., 2016. Comparing species distributions modelled from occurrence data and from expert-based range maps. Implication for predicting range shifts with climate change. *Ecol. Inform*. 36, 8-14.

Gao, T., Nielsen, A.B., Hedblom, M., 2015. Reviewing the strength of evidence of biodiversity indicators for forest ecosystems in Europe. *Ecol. Indic.* 57, 420–434, doi:10.1016/j.ecolind.2015.05.028.

Gómez-Rodríguez, C., Bustamante, J., Díaz-Paniagua, C., Guisan, A., 2012. Integrating detection probabilities in species distribution models of amphibians breeding in Mediterranean temporary ponds. *Divers. Distrib*. 18, 260–272.

Guisan, A., Thuiller, W., & Zimmermann, N. E., 2017. *Habitat Suitability and Distribution Models: with Applications in R*. Cambridge University Press, Cambridge.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. *Ecol. Lett.* 8, 993-1009.

Guisan, A., Zimmermann, N.E., 2000. Predictive habitat distribution models in ecology. *Ecol. Model.* 135, 147–186, doi:10.1016/S0304-3800(00)00354-9.

Hanberry, B.B., He, H.S., Palik, B.J., 2012. Pseudoabsence generation strategies for species distribution models. *PLoS ONE*, 7(8), 7–10.

Harvey, D.S., Platenberg, R.J., 2009. Predicting habitat use from opportunistic observations: A case study of the Virgin Islands tree boa (*Epicrates granti*). *Herptological Journal*, 19(3), 111–118.

Horák, J., 2017. Insect ecology and veteran trees. *J. Insect Conserv.* 21, 1–5, doi:10.1007/s10841-017-9953-7.

Iglecia, M.N., Collazo, J. A, McKerrow, A.J., 2012. Use of occupancy models to evaluate expert knowledge-based species- habitat relationships. *Avian Conserv. Ecol.* 7, 5, doi:10.5751/ACE-00551-070205.

IUCN, 1993. Parks for Life Report of the IVth World Congress on National Parks and protection Areas, IUCN. Gland, Switzerland. 260pp

Jackson, S. T., & Overpeck, J. T. (2000). Responses of plant populations and communities to environmental changes of the late Quaternary. *Paleobiology,* 26, 194-220.

JNCC (Joint Nature Conservation Council), 2018 Conventions and Legislation. JNCC, Peterborough, UK, http://jncc.defra.gov.uk/page-1359 (accessed May 2018).

Johnson, C.J., Gillingham, M.P., 2008. Sensitivity of species-distribution models to error, bias, and model design: An application to resource selection functions for woodland caribou. *Ecol. Model*. 213, 143-155.

Landis, J.R., Koch, G.G., 1977. The measurement of observer agreement for categorical data. *Biometrics* 33, 159–174, doi:10.2307/2529310.

Leblond, M., Dussault, C. St-Laurent, M., 2014. Development and validation of an expert-based habitat suitability model to support boreal caribou conservation. *Biol. Conserv*. 177, 100–108, doi:10.1016/j.biocon.2014.06.016.

Lentini, P.E., Wintle, B.A., 2015. Spatial conservation priorities are highly sensitive to choice of biodiversity surrogates and species distribution model type. *Ecography* 38, 1101–1111, doi:10.1111/ecog.01252.

Lilly, A., Bell, J.S., Hudson, G., Nolan, A.J., Towers, W., 2010. National Soil Inventory of Scotland: site location, sampling and profile description protocols (1978-1988), NSIS1. Technical Bulletin, Macaulay Institute, Aberdeen, UK.

Lobo, J.M., Tognelli, M.F., 2011. Exploring the effects of quantity and location of pseudo-absences and sampling biases on the performance of distribution models with limited point occurrence data. *J. Nat. Conserv.* 19, 1–7, doi:10.1016/j.jnc.2010.03.002.

MacDicken, K.G., Sola, P., Hall, J.E., Sabogal, C., Tadoum, M., Wasseige, C. De, 2015. Global progress toward sustainable forest management. *For. Ecol. Manage.* 352, 47–56.

McInerney, D., Suarez, J., Nieuwenhuis, M., 2011. Extending forest inventories and monitoring programmes using remote sensing : A review. *Irish For.* 68, 6–22.

Maddock, A., 2008. *UK Biodiversity Action Plan: Priority Habitat Descriptions*, Peterborough, UK. http://jncc.defra.gov.uk/PDF/UKBAP_PriorityHabitatDesc-Rev2011.pdf (accessed November 2017).

Margules, C.R., Pressey, R.L., 2000. Systematic conservation planning. *Nature* 405, 243–253, doi:10.1038/35012251.

Michel, A. K., and Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, USA. *For. Ecol. Manage*. 257, 1453-1464, doi:10.1016/j.foreco.2008.11.027

Minin, E., Di, Moilanen, A., 2014. Improving the surrogacy effectiveness of charismatic megafauna with well-surveyed taxonomic groups and habitat types. *J. Appl. Ecol*. 51, 281–288, doi:10.1111/1365-2664.12203.

Morales-Hidalgo, D., Oswalt, S.N., Somanathan, E., 2015. Status and trends in global primary forest, protected areas, and areas designated for conservation of biodiversity from the Global Forest Resources Assessment 2015. *For. Ecol. Manage*. 352, 68–77, doi:10.1016/j.foreco.2015.06.011.

Morton, D., Rowland, C. Wood, C., Meek, L., Marston, C., Smith, G., Wadsworth, R., Simpson, I.C., 2011. Final Report for LCM2007 - the new UK Land Cover Map, CS Technical Report No 11/07, Centre for Ecology and Hydrology, Natural Environment Research Council, Wallingford, UK.

Murray, J.V., Goldizen, A.W., O'Leary, R.A., McAlpine, C.A., Possingham, H.P., Choy, S.L., 2009. How useful is expert opinion for predicting the distribution of a species within and beyond the region of expertise? A case study using brush-tailed rock-wallabies *Petrogale penicillata*. *J. Appl. Ecol.* 46, 842–851, doi:10.1111/j.1365-2664.2009.01671.x.

NBN (The National Biodiversity Network), 2017. Web platform for UK biological records. https://nbn.org.uk (accessed November 2017).

Newbold, T., 2010. Applications and limitations of museum data for conservation and ecology, with particular attention to species distribution models. *Prog. Phys. Geog.*, *34*(1), 3-22.

NWSS 2013. Native Woodland Survey of Scotland Field Survey Protocol – attributes, definitions and pick-lists. Mauld Environmental & Forestry Commission Scotland, pdf, 12pp (https://scotland.forestry.gov.uk/images/corporate/pdf/NWSSProtocolAbridged.pdf) - accessed February 2019

Ordnance Survey, 2016. MasterMap Sites Layer user guide contents v1.2 – 06/2016 © Ordnance Survey Limited, UK.

Orlikowska, E.H., Roberge, J., Blicharska, M., Mikusiński, G., 2016. Gaps in ecological research on the world 's largest internationally coordinated network of protected areas : A review of Natura 2000. *Biol. Conserv*. 200, 216–227, doi:10.1016/j.biocon.2016.06.015.

Patterson, G., Nelson, D., Robertson, P., Tullis, J., 2014. Scotland's Native Woodlands Results from the Native Woodland Survey of Scotland. Forestry Commission Scotland. Edinburgh, UK.

Pearce-Higgins, J.W., Ausden, M.A., Beale, C.M., Oliver, T.H. and Crick, H.Q.P. (eds)., 2015. Research on the assessment of risks and opportunities for species in England as a result of climate change. Natural England Commissioned Reports, Number 175. Peterborough, UK.

Pearson, R. G., Raxworthy, C. J., Nakamura, M., Townsend Peterson, A., 2007. Predicting species distributions from small numbers of occurrence records: A test case using cryptic geckos in Madagascar. *J. Biogeogr. 34*(1), 102-117.

Phillips, S.J., Anderson, R.P., Schapire, R.E., 2006. Maximum entropy modeling of species geographic distributions. *Ecol. Model.*,190, 231–259, doi:10.1016/j.ecolmodel.2005.03.026.

Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models : Implications for background and pseudo-absence data. *Ecol. Appl.* 19, 181–197.

Possingham, H.P., Bode, M., Klein, C.J., 2015. Optimal conservation outcomes require both restoration and protection. *PLoS Biology* 13(1), 1–16.

Prendergast, J.R., Quinn, R.M., Lawton, J.H., Eversham, B.C., Gibbons, D.W., 1993. Rare species, the coincidence of diversity hotspots and conservation strategies. *Nature* 365, 335–337,doi:10.1038/365335a0.

R Core Team 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/

Regnery, B., Couvet, D., Kubarek, L., Julien, J.-F., Kerbiriou, C., 2013. Tree microhabitats as indicators of bird and bat communities in Mediterranean forests. *Ecol. Indic*. 34, 221–230.

Reif, J., Jiguet, F., Šťastný, K., 2010. Habitat specialization of birds in the Czech Republic: comparison of objective measures with expert opinion. *Bird Study* 57, 197–212, doi:10.1080/00063650903477046.

Rodrigues, A.S., Andelmann, S.J., Bakarr, M.I., Boitani, L., Brooks, T.M., Cowling, R.M., Fishpool, L.D., da Fonseca, G.A.B., Gaston, K.J., Hoffmann, M., Long, J.S., Marquet, P.A., Pilgrim, J.D., Pressey, R.L., Schipper, J., Sechrest, W., Stuart, S.N., Underhill, L.G., Waller, R.W., Watts, M.E.J., Yan, X., 2004. Effectiveness of the global protected area network in representing species diversity. *Nature* 428, 640–643, doi:10.1038/nature02422.

Rodwell, J.S. 1991. British plant communities, I: Woodlands and Scrub. Cambridge University Press, Cambridge, UK.

Rurik, L., Macdonald, D.W., 2003. Home range and habitat use of the kit fox (*Vulpes macrotis*) in a prairie dog (*Cynomys ludovicianus*) complex. *J. Zool*. 259, 1-5, doi:10.1017/S0952836902002959.

SAS 2011. SAS Institute Inc., 2011. *SAS/STAT® 9.3 User's Guide: The FREQ Procedure (Chapter).*Cary, NC: SAS Institute Inc.

Scottish Action Coordination Group, 2008. ACG 1-spreadsheet 2- mapping priority species to habitats and ecosystems- August 2008.xls. The Scottish Biodiversity Strategy. http://www.biodiversityscotland.gov.uk/doing/scottish-biodiversity-governance/habitats-and-species-group/ (accessed October 2010).

Sing, L., Towers, W., Ellis, J., 2013. Woodland expansion in Scotland: An assessment of the opportunities and constraints using GIS. *Scottish Forestry*, 67(4), 18–25.

Soberon, J., Nakamura, M., 2009. Niches and distributional areas : Concepts, methods, and assumptions. *PNAS* 106, 19644–19650.

Sørensen, R., Zinko, U., Seibert, J., 2006. On the calculation of the topographic wetness index: Evaluation of different methods based on field observations. *Hydrol. Earth Syst. Sc*. 10, 101–112.

Stockwell, D. R., Peterson, A. T., 2002. Effects of sample size on accuracy of species distribution models. *Ecol. Model. 148*(1), 1-13.

UKWAS (United Kingdom Woodland Assurance Standard), 2008. The UK Woodland Assurance Standard. Second edition (amended). UKWAS, Edinburgh. (online) Available at: http://www.ukwas.org.uk/assets/documents/UKWAS%20Second%20Edition%20%28Amended%20November%202008%29%20Web.pdf (accessed February 2017).

Wiersma, Y.F., Sleep, D.J.H., 2018. The effect of target setting on conservation in Canada's boreal: What is the right amount of area to protect? *Biodivers. Conserv.* 27(3), 733–748.

Winter, M., Devictor, V., Schweiger, O., 2013. Phylogenetic diversity and nature conservation: Where are we? *Trends Ecol. Evol*. 28, 199–204, doi:10.1016/j.tree.2012.10.015.

Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., Elith, J., Dudík, M., Ferrier, S., Huettmann, F., Leathwick, J.R., Lehmann, A., Lohmann, L., Loiselle, B.A., Manion, G., Moritz, C., Nakamura, M., Nakazawa, Y., Overton, J.M.C., Phillips, S.J., Richardson, K.S., Scachetti-Pereira, R., Schapire, R.E., Soberón, J., Williams, S.E., Zimmermann, N.E., 2008. Effects of sample size on the performance of species distribution models. *Divers. Distrib*. 14, 763–773, doi:10.1111/j.1472-4642.2008.00482.x.

Zarnetske, P.L., Edwards, J., T.C., Moisen, G.G., 2007. Habitat classification modeling with incomplete data: Pushing the habitat envelope. *Ecol. Appl*. 17, 1714–1726, doi:10.1890/06-1312.1.

Ziegler, C.R., Webb, J.A., Norton, S.B., Pullin, A.S., Melcher, A.H., 2015. Digital repository of associations between environmental variables: A new resource to facilitate knowledge synthesis. *Ecol. Indic*. 53, 61-69.