Forestry Commission

Research Note

Niches for species: a multi-species model to guide woodland management

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To protect biodiversity in the face of environmental change, there is a need to designate and manage areas of habitat for rare and threatened species. However, to identify the right areas usually requires detailed data on species distributions. Reliable data for rare and protected species are sparse as many species are cryptic and under-recorded. The challenge is greater when there are multiple species for which conservation decisions need to be taken within a habitat type. This Research Note describes how a model was developed to support woodland managers and policy makers in considering the conservation needs of protected species. The 'Niches for Species' model integrates species habitat requirements for multiple species and provides mapped outputs of their niches, and hence their potential occurrence in native woodlands. The Note presents the theoretical background to the creation of the model, and explains how it predicts the potential occurrence of species by linking species habitat requirements to spatial environmental data. The construction of the model from a classification of ecological niches using expert knowledge is described along with details of its validation testing and analysis of its strengths and weaknesses. The Niches for Species model may have many applications in forestry planning and management. Examples explored in this Note include its use in strategic targeting of conservation effort, comparing the likely benefits to biodiversity of different woodland expansion scenarios, visualising the configuration of species-rich and species-poor woodland, and highlighting the likely presence of a particular woodland species at a site.

Introduction

Woodlands are rich in biodiversity and there are many hundreds of species associated with woodlands, each of which has a level of legal protection. In the UK, the conservation of woodland biodiversity is promoted through various incentives and legal mechanisms as described in the UK Forestry Standard Guidelines on forests and biodiversity (Forestry Commission, 2017). For species, the highest level of protection is afforded to those listed in Annex II of the EU Habitats Directive (EU, 1992), and also by domestic legislation covering those species listed in the schedules for the relevant Acts (e.g. Schedule 8 of the Wildlife and Countryside Act covering Scotland (UK Government, 1981)). For rare or declining species identified on national lists, a general duty of care exists to further conserve them. Guidance is needed to help woodland managers, policymakers and planners make decisions on where to apply biodiversity management for the greatest conservation benefit. Knowing where rare and protected species are most likely to occur is fundamental to making such decisions.

Protected species can be found in a range of different woodland types of different stand structures, and have specific resource or microhabitat requirements (e.g. deadwood, wet rock faces and glades) for their habitats. Decision-makers are required to consider the needs of protected woodland species at a variety of scales. For example, forestry policymakers may need a national overview of the woodland resource and where protected species hotspots are located; forest planners may wish to visualise the configuration of the occurrence of protected species within a landscape; and forest managers may require fine-scale knowledge of potential species occurrence to direct operations within a particular woodland. Currently, a large number of species records are available via data portals such as the National Biodiversity Network and local environmental record centres. However, issues such as sampling bias and under-recording due to difficulties in detecting or identifying rare, inconspicuous or cryptic species mean that available records may not accurately reflect species distribution. Despite advances in data portal accessibility, extracting high-resolution records to compare with habitat data can be a lengthy and complicated process, and is unlikely to be fully utilised. To improve information provision, a niche-based model (Box 1), Niches for Species was co-developed to predict the potential occurrence of protected species in native woodlands, using Scotland as a case study.

Box 1 Niche-based models

Niche-based models provide predictions of where species are likely to occur. The model may define sites in which a set of conditions enable the species' long-term survival (the fundamental niche) or sites that the species actually occupies given other constraints such as dispersal limitations and competition (the realised niche) (Guisan, Thuiller and Zimmermann, 2017). There are two main approaches described in the literature concerning constructing niche-based models: species distribution models (SDMs) and expert-based habitat suitability models (HSMs).

SDMs have been widely used to characterise and map the fundamental niche of single (e.g. Bellamy, Scott and Altringham, 2013) or multiple taxa (Franco *et al*., 2009). Modelling uses statistical approaches to relate empirical species presence-absence, presence only, or abundance data with underlying environmental conditions, in order to determine species-environment relationships and predict species distributions (Elith and Leathwick, 2009). If species occurrence data are minimal or limited (e.g. confined to areas which do not represent the full range of variables where species actually occur), or location and not habitat is used for species dispersal, the resulting model may fail to fully describe suitable locations for the species.

Expert-based HSMs predict the occurrence of species based on their known habitat requirements and the availability of these habitats as described by spatial environmental datasets. This avoids the need to use species records, which may not comprehensively reflect habitat associations, and could be expensive to gather. HSMs have been extensively used by government conservation agencies in the USA and Canada for developing several expert-based species models, drawing on resources of species specialist knowledge (e.g. Leblond, Dussault and St-Laurent, 2014). The N4S model derives from the expert-based HSM approach.

The literature shows that expert-based HSMs are rarely validated (Iglecia, Collazo and McKerrow, 2012); but where reported, agreement has been found between the empirical data and the expert-based classifications of habitat choice (Reif, Jiguet and Šťastný, 2010; Leblond, Dussault and St-Laurent, 2014). However, in these examples, the validation tests used comprehensive species occurrence datasets from well-designed surveys (e.g. contemporary national caribou density assessments were used to test the caribou habitat suitability model).

Although the UK's species records resource is substantial, surveys are not always carried out systematically, and locations targeted for surveys or data-collection are typically selected on an ad hoc basis, usually close to roads and urban areas. It is uncommon for all areas to be surveyed regularly, and only very rarely is species absence data collected (National Biodiversity Network, 2017). Lack of species records or poor quality records have been reported as hindering useful model development (Phillips, Anderson and Schapire, 2006).

The Niches for Species model

The Niches for Species (N4S) model was created from a classification of ecological niches using expert knowledge on the habitats and resource requirements of 179 protected woodland species (69 lower plants – lichens, bryophytes and liverworts; 52 invertebrates; 21 fungi; 16 birds; 10 vascular plants; eight mammals; and three herptiles – amphibians and reptiles). Woodland type and structure data from the Native Woodland Survey Scotland (NWSS) (Patterson *et al*., 2014), and a combination of different types of spatial data were used to define microhabitats (i.e. detailed features of the habitats required by species). For a woodland polygon, (discrete, mapped area of woodland) the dominant woodland type, structure data and potential occurrence of microhabitats indicate which niches may be available, and the model determines those species for which the niches would be suitable. The model then uses predefined, current bioclimatic and/or species ranges to constrain the distribution of suitable niches to within the range area. This relationship between available data and species specific rules is demonstrated schematically in Figure 1. The resulting N4S model provides mapped outputs ranging from individual species occurrence and habitat use within a woodland polygon to a national map of species richness.

The five stages of model development

1. Knowledge review

Available data describing the habitat requirements for 208 protected species considered to occur in Scotland using woodland as their primary habitat was reviewed (Scottish Action Co-ordination Group, 2008). The review consisted of scientific articles and other publications produced on species, as well as information from habitat association analyses conducted by species experts from statutory nature agencies and NGOs. Agency staff helped design the data tables which systematically collated and referenced information for each species, including its associations with woodland type, within-stand resource requirements from a broad to detailed scale, and other details relating to species requirements (including differences at early and mature life stages where appropriate).

2. N4S classification and matrix

A hierarchical classification of habitat based on species requirements was constructed and aligned with the NWSS classification (Patterson *et al*., 2014). The N4S classification consisted of three components, woodland type, woodland structure, and microhabitat. A unique woodland type–woodland structure–microhabitat combination was a niche. For those species where there was sufficient information on resource requirements (179 of the initial 208) a N4S matrix was created in which each one of the 179 protected species was associated with one or more niches based on species specificity or generality in resource needs (Table 1).

3. Spatially explicit habitat data

Attributes from different spatial data layers were combined using a carefully designed rule set to define woodland habitat

Figure 1 The integration of data (from spatial environmental datasets and species requirements knowledge), interpretation and processing performed by the Niches for Species model to map the potential occurrence of protected species in woodland across Scotland.

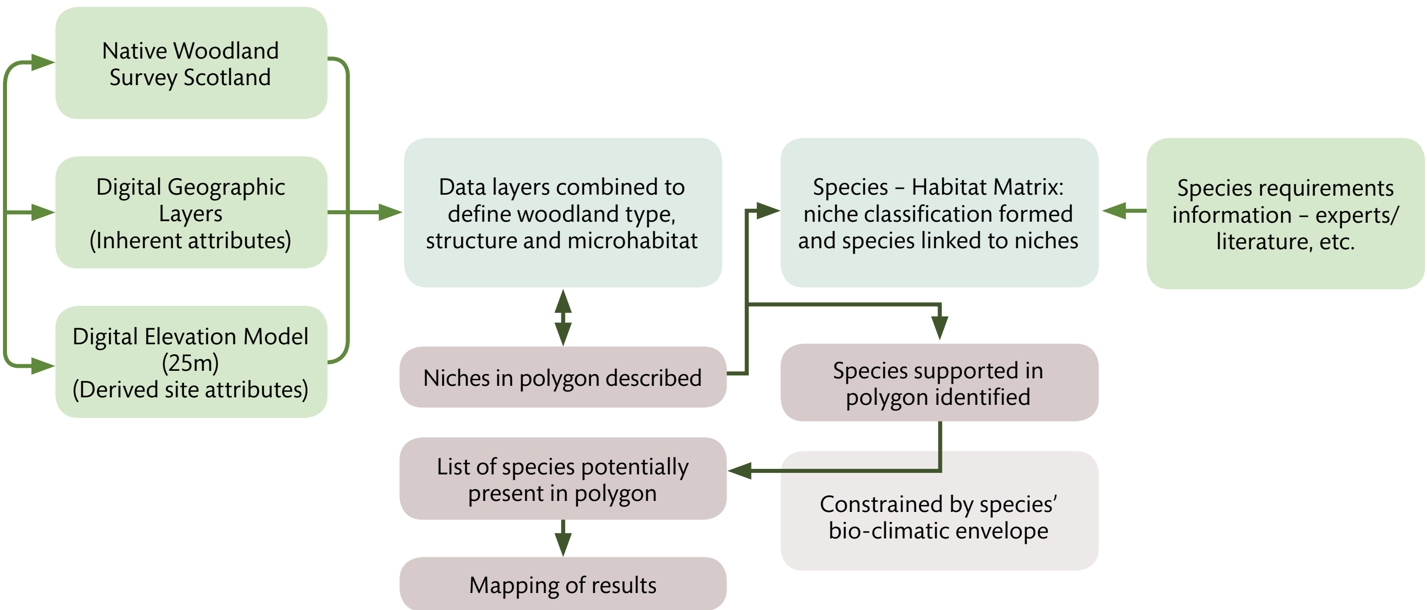


Table 1 Species included in the Niches for Species model and the approach used to constrain predicted distribution.

Species group	Species	Approaches to constraint[1]		
		Bioclimatic envelope source[2]		MCP[3]
		A	B	
Bird	*Anthus trivialis*			X
Bird	*Caprimulgus europaeus europaeus*			X
Bird	*Carduelis cabaret*			X
Bird	*Coccothraustes coccothraustes*			X
Bird	*Cuculus canorus canorus*			X
Bird	*Loxia scotica*			X
Bird	*Muscicapa striata striata*			X
Bird	*Phylloscopus sibilatrix*			X
Bird	*Poecile montanus kleinschimdti*			X
Bird	*Poecile palustris*			X
Bird	*Prunella modularis occidentalis*			X
Bird	*Pyrrhula pyrrhula pileata*			X
Bird	*Tetrao tetrix britannicus*			X
Bird	*Tetrao urogallus*			X
Bird	*Turdus philomelos clarkei*			X
Bird	*Turdus philomelos subsp. hebridensis*			
Herptile	*Anguis fragilis*			X
Herptile	*Triturus cristatus*			X
Herptile	*Vipera berus*			X
Invertebrate	*Acronicta psi*		X	
Invertebrate	*Acronicta rumicis*		X	
Invertebrate	*Agrochola helvola*		X	
Invertebrate	*Agrochola litura*		X	
Invertebrate	*Agrochola lychnidis*		X	
Invertebrate	*Allophyes oxyacanthae*		X	
Invertebrate	*Amphipyra tragopoginis*		X	
Invertebrate	*Apamea remissa*		X	
Invertebrate	*Atethmia centrago*		X	
Invertebrate	*Blera fallax*			
Invertebrate	*Boloria euphrosyne*			X
Invertebrate	*Boloria selene*		X	
Invertebrate	*Brachylomia viminalis*		X	
Invertebrate	*Caradrina morpheus*		X	
Invertebrate	*Carterocephalus palaemon*			X
Invertebrate	*Chiasmia clathrata*		X	
Invertebrate	*Chrysura hirsuta*			
Invertebrate	*Cossus cossus*		X	
Invertebrate	*Cupido minimus*			X
Invertebrate	*Diarsia rubi*		X	
Invertebrate	*Diloba caeruleocephala*			
Invertebrate	*Ennomos erosaria*		X	
Invertebrate	*Ennomos quercinaria*		X	
Invertebrate	*Epione vespertaria*			
Invertebrate	*Erynnis tages*			X
Invertebrate	*Eugnorisma glareosa*		X	
Invertebrate	*Euxoa nigricans*		X	
Invertebrate	*Formica exsecta*			X
Invertebrate	*Formicoxenus nitidulus*			X
Invertebrate	*Graphiphora augur*		X	
Invertebrate	*Hammerschmidtia ferruginea*			X
Invertebrate	*Hoplodrina blanda*		X	
Invertebrate	*Lipsothrix ecucullata*			X
Invertebrate	*Lipsothrix errans*			X
Invertebrate	*Lochaea ragnari*			
Invertebrate	*Lycia hirtaria*		X	
Invertebrate	*Melanchra pisi*		X	
Invertebrate	*Monocephalus castaneipes*		X	
Invertebrate	*Mythimna comma*		X	
Invertebrate	*Notioscopus sarcinatus*		X	
Invertebrate	*Orthosia gracilis*		X	
Invertebrate	*Osmia uncinata*			X
Invertebrate	*Philodromus margariatus*			X
Invertebrate	*Rheumaptera hastata*			X
Invertebrate	*Saaristoa firma*		X	
Invertebrate	*Scotopteryx chenopodiata*		X	
Invertebrate	*Spilosoma luteum*		X	
Invertebrate	*Trichopteryx polycommata*		X	
Invertebrate	*Xanthia icteritia*		X	
Invertebrate	*Xanthorhoe ferrugata*			X
Invertebrate	*Xestia castenea*			X
Invertebrate	*Xylena exsoleta*		X	
Lower plant	*Acrobolbus wilsonii*			X
Lower plant	*Anaptychia ciliaris subsp. ciliaris*	X		
Lower plant	*Anomodon longifolius*			X
Lower plant	*Arthonia atlantica*			
Lower plant	*Arthonia cohabitans*			
Lower plant	*Arthonia invadens*			
Lower plant	*Arthonia patellulata*			X
Lower plant	*Arthothelium dictyosporum*			X
Lower plant	*Arthothelium macounii*			X
Lower plant	*Bacidia circumspecta*			X
Lower plant	*Bacidia incompta*	X		
Lower plant	*Bacidia subincompta*			X
Lower plant	*Biatoridium monasteriense*			
Lower plant	*Bryoria furcellata*			X
Lower plant	*Buellia violaceofusca*			X
Lower plant	*Buxbaumia viridis*			X
Lower plant	*Caloplaca ahtii*			X
Lower plant	*Caloplaca flavorubescens*			X
Lower plant	*Caloplaca lucifuga*			

Lower plant	*Caloplaca luteoalba*			X
Lower plant	*Catapyrenium psoromoides*			
Lower plant	*Catillaria alba*			
Lower plant	*Chaenotheca gracilenta*			
Lower plant	*Chaenotheca laevigata*			
Lower plant	*Cladonia botrytes*			X
Lower plant	*Collema fasciculare*	X		
Lower plant	*Collema fragrans*			
Lower plant	*Diplotomma pharcidium*			
Lower plant	*Dumortiera hirsuta*		X	
Lower plant	*Fuscopannaria sampaiana*	X		
Lower plant	*Gomphillus calycioides*	X		
Lower plant	*Graphis alboscripta*			X
Lower plant	*Gyalecta ulmi*			X
Lower plant	*Habrodon perpusillus*			
Lower plant	*Homomallium incurvatum*			
Lower plant	*Jungermannia leiantha*			
Lower plant	*Lecania chlorotiza*	X		
Lower plant	*Lecanographa amylacea*	X		
Lower plant	*Lecanora cinereofusca*			X
Lower plant	*Lecanora quercicola*			
Lower plant	*Lecidea erythrophaea*			X
Lower plant	*Lejeunea mandonii*			
Lower plant	*Leptogium saturninum*			X
Lower plant	*Megalospora tuberculosa*	X		
Lower plant	*Melanelia subargentifera*			
Lower plant	*Orthodontium gracile*			
Lower plant	*Orthotrichum gymnostomum*			
Lower plant	*Orthotrichum obtusifolium*			X
Lower plant	*Orthotrichum pumilum*			
Lower plant	*Pallavicinia lyellii*		X	
Lower plant	*Parmeliella testacea*	X		
Lower plant	*Peltigera malacea*			X
Lower plant	*Pertusaria velata*			
Lower plant	*Polychidium dendriscum*			X
Lower plant	*Porina hibernica*	X		
Lower plant	*Pseudocyphellaria intricata*	X		
Lower plant	*Pseudocyphellaria norvegica*	X		
Lower plant	*Pyrenula dermatodes*			
Lower plant	*Radula carringtonii*			X
Lower plant	*Ramonia chrysophaea*	X		
Lower plant	*Ramonia dictyospora*			
Lower plant	*Rinodina isidioides*			X
Lower plant	*Schismatomma graphidioides*			X
Lower plant	*Sclerophora pallida*			X
Lower plant	*Usnea florida*	X		
Lower plant	*Wadeana dendrographa*	X		
Lower plant	*Wadeana minuta*			X
Mammal	*Erinaceus europaeus*			X
Mammal	*Felis silvestris*			X
Mammal	*Lutra lutra*			X
Mammal	*Martes martes*			X
Mammal	*Nyctalus noctula*			X
Mammal	*Pipistrellus pygmaeus*			X
Mammal	*Plecotus auritus*			X
Mammal	*Sciurus vulgaris*			X
Vascular plant	*Cephalanthera longifolia*			X
Vascular plant	*Crepis mollis*			X
Vascular plant	*Juniperus communis*		X	
Vascular plant	*Linnaea borealis*			X
Vascular plant	*Melampyrum sylvaticum*			X
Vascular plant	*Moneses uniflora*			X
Vascular plant	*Monotropa hypopitys*			
Vascular plant	*Polygonatum verticillatum*			X
Vascular plant	*Sorbus arranensis*			X
Vascular plant	*Sorbus pseudofennica*			
Fungi	*Bankera fuligineoalba*			X
Fungi	*Hydnellum aurantiacum*			X
Fungi	*Hydnellum caeruleum*			X
Fungi	*Hydnellum concrescens*			X
Fungi	*Hydnellum ferrugineum*			X
Fungi	*Hydnellum peckii*			X
Fungi	*Hydnellum scrobiculatum*			X
Fungi	*Hydnellum spongiosipes*			
Fungi	*Hypocreopsis rhododendri*			X
Fungi	*Phellodon confluens*			X
Fungi	*Phellodon melaleucus*			X
Fungi	*Phellodon niger*			X
Fungi	*Phellodon tomentosus*			X
Fungi	*Phylloporus pelletieri*			
Fungi	*Piptoporus quercinus*			
Fungi	*Sarcodon glaucopus*			X
Fungi	*Sarcodon scabrosus*			X
Fungi	*Sarcodon squamosus*			
Fungi	*Stropharia hornemannii*			
Fungi	*Tricholoma colossus*			
Fungi	*Tricholoma robustum*			

Note: no X indicates there were no constraints applied.
1 Where data were available, modelled current bioclimatic envelopes or Minimum Convex Polygons (MCPs) around species record locations were used to restrict the patches predicted to be suitable by the Niches for Species model. We applied the Ellis *et al*. (2014) envelopes in preference to the Pearce-Higgins *et al*. (2015) envelopes and either of these in preference to the MCPs. Where data were unavailable no restriction was applied for that species' range.
2 Bioclimatic Envelopes: when applying the bioclimatic envelopes developed by Ellis *et al*. (2014) (source A) we used the 'maximum training sensitivity plus specificity' threshold, a fixed threshold. As this detail was not available for the Pearce-Higgins *et al*. (2015) data (source B), we chose a fixed threshold of 0.7 to determine predicted suitable bioclimatic zones from the continuous logistic probability data.
3 Minimum Convex Polygons: species records were extracted at the 10 km square resolution from the UK national archive of biodiversity monitoring data (the National Biodiversity Network Gateway https://nbnatlas.org/). Minimum Convex Polygons (MCPs) were drawn around squares where three or more squares were adjacent to one another (isolated single or paired presence squares were excluded). All records were used with no date restriction applied.

and microhabitat describing niche types (Figure 2). For each polygon, the dominant woodland and structure type were identified, primarily using NWSS data. A predicted indicator (1: present, 0: absent) of the 10 possible microhabitats was added to the NWSS polygon component. The presence of microhabitat types were determined from multiple sources; for example, deadwood was accessed directly from measurements made by NWSS surveyors, but seven spatial datasets were combined following a logical rule set to assess wet rock.

4. N4S model construction

Using Geographic Information Software (GIS), ArcGIS (version 10.2) Model Builder and Python (version 2.7.5), each woodland polygon was assessed for its suitability to support each of the 179 protected species. A polygon was classed as suitable if the correct woodland type-woodland structure was present and it contained the suitable microhabitat, according to the N4S matrix. As many of the species have restricted ranges across Scotland, modelled bioclimatic envelopes were used (if available) to restrict the number of polygons predicted to be suitable (Ellis *et al*., 2014; Pearce-Higgins *et al*., 2015) (Table 1), or Minimum Convex Polygons (MCPs) were drawn around 10 km-species record datapoints (National Biodiversity Network, 2017). The N4S model output is a map of woodland polygons which have the potential to support different numbers of protected species.

5. Validation of the N4S model

The distribution predicted by the N4S model was compared with an actual distribution from species survey presence records. Species distribution data for 10 validation species displaying a variety of traits was used (wide-to-restricted distribution and niche preferences; vagile to sessile; easy-to-observe to cryptic); a pool of 752 species was utilised to provide pseudo-absence records. Pseudo-absence records were created following the 'surveyed absence' ('target group') strategy which uses location records of species from the same taxonomic group (i.e. those which would most likely have been recorded within the same survey as the validation species had they been reported) (Phillips *et al*., 2009; Hanberry, He and Palik, 2012). A measure of agreement was secured by performing a Cohen's kappa calculation on confusion matrices comparing actual and modelled record occurrences (Cunningham, 2009). Statistical tests were performed using binomial and one-sided kappa probability tests (Table 2).

Overall there was agreement between N4S model predictions and the occurrence of nine of the ten test species (no agreement was found with *Turdus philomelos*). The strength of agreement varied between the species and for half of the validation species, associations between record distribution and predicated availability of suitable patches was better than random (where the kappa value is positive and $p < 0.05$, or where the binomial test $p < 0.05$). For two other species this association was reaching significance (*Gomphillus calcyciodes, Carterocephalus palaemon*).

Figure 2 Schematic of the spatial forest type, habitat, and topographic data used to predict the presence of woodland type, woodland structure and microhabitat, which together describe available niches.

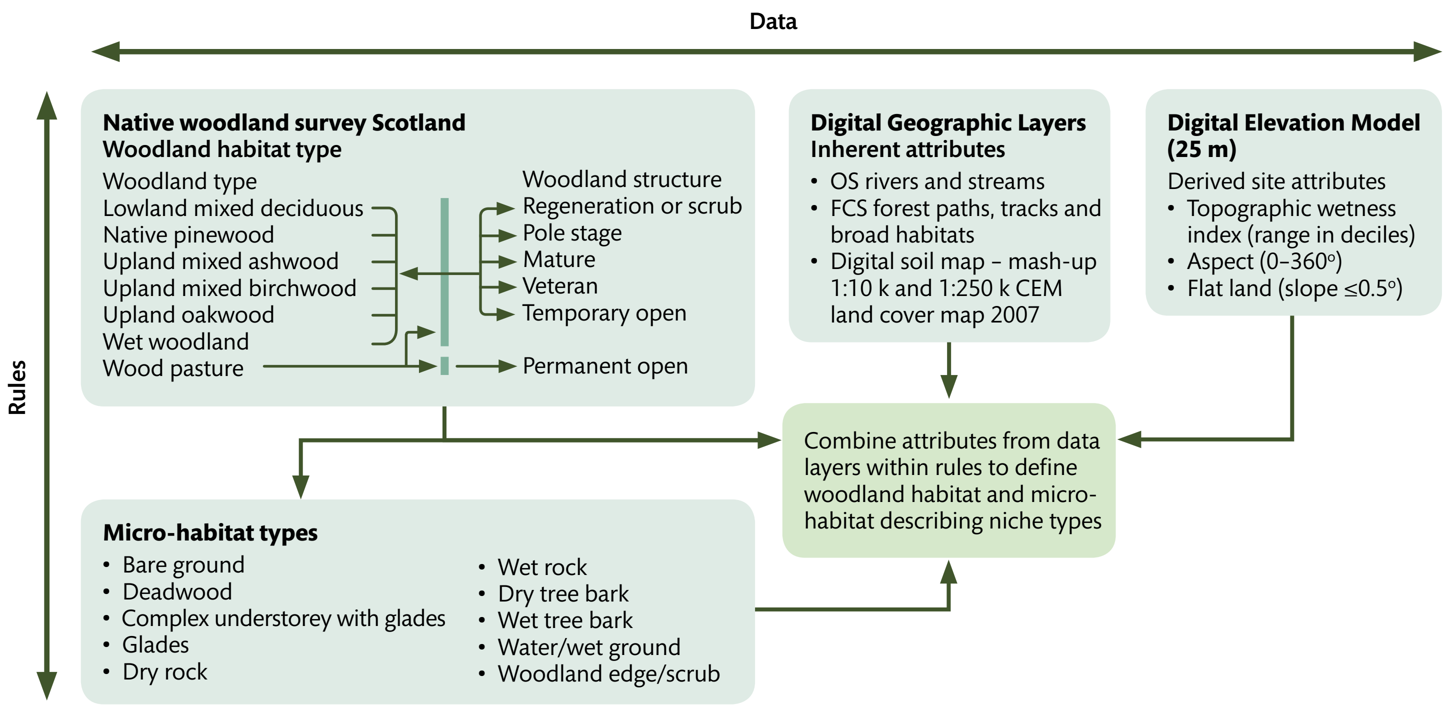


Table 2 Summary of statistical correspondence between the habitat availability for 10 validation species predicted using the Niches for Species model and records of species occurrence and pseudo-absence.

Validation species	Taxon	Kappa value[1] (p)[2]	Binomial[3]	Model complexity[4]
Collema fasciculare	Lichen	Slight agreement (ns)	ns	1
Pseudocyphellaria norvegica	Lichen	Slight agreement (ns)	ns	3
Gomphillus calyciodes	Lichen	Slight agreement (p = 0.053)	ns	2
Linnaea borealis	Twinflower	Slight agreement (****)	**	2
Cupido minimus	Small blue butterfly	Slight agreement (****)	***	3
Carterocephalus palaemon	Chequered skipper butterfly	Slight agreement (ns)	p = 0.056	2
Boloria euphrosyne	Pearl-bordered fritillary butterfly	Slight agreement (****)	**	1
Osmia ucinata	Mason bee	Fair agreement (****)	***	3
Muscicapa striata	Spotted fly catcher (bird)	Slight agreement (*)	ns	2
Turdus philomelos	Song thrush (bird)	No agreement (na)	ns	2

1 Kappa (k) subdivisions: 'No agreement' ($k < 0$); 'Slight agreement' ($k \geq 0$ and < 0.2); 'Fair agreement' ($k \geq 0.2$ and < 0.4); 'Moderate agreement' ($k \geq 0.4$ and < 0.6); 'Substantial agreement' ($k \geq 0.6$ and < 0.8); 'Almost perfect agreement' ($k \geq 0.8$ and < 1.0) (Landis and Koch, 1977).
2 One-sided probability reported when testing for where k is positive; H_0: k = 0.
3 'Binomial' probability test where H_0: the number of validation species records found within suitable woodland polygons is no better than random within the sampled woodland polygons; sampled woodland polygons either contain a pseudo-absence record or a validation species record or both. Probability test level of significance (for both Kappa and binomial tests): *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$, **** $p < 0.0001$, ns = non-significant, p value reported where nearing significance.
4 Tests were completed at three levels of model complexity (1 = woodland type only; 2 = woodland type + stand structure; 3 = woodland type + stand structure + microhabitat).

How the Niches for Species model can be applied to forestry

This section discusses the model's potential application to decisions made at three scales – national, landscape and woodland.

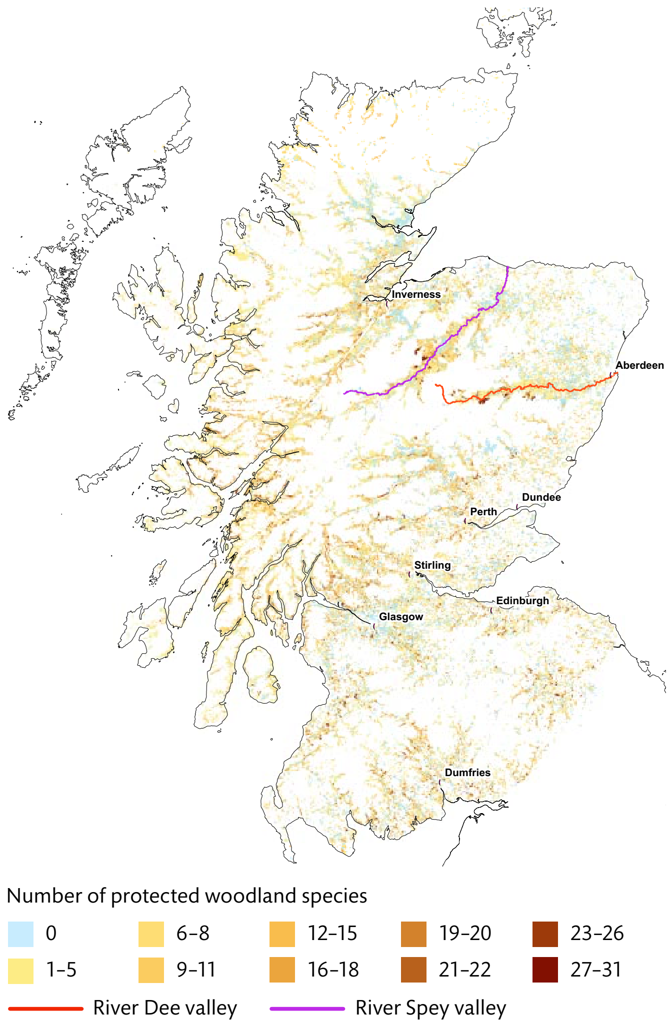
National – forest policymakers

The N4S model provides a method which consistently assesses and indicates the species richness across seven native woodland types, and provides a basis for the strategic targeting of conservation efforts at a national scale. This is demonstrated in the following two sections by a basic N4S model providing an overview of species richness, and also by a case study in upland Scotland illustrating how the N4S model uses scenarios to inform the targeting of regional woodland expansion.

An overview of the protected woodland species resource

For forestry policymakers, the N4S model provides analysis of the whole native woodland resource in Scotland (both within and outside protected areas), and indicates where there are species hotspots or habitats where particular sets of species may occur. The map of Scotland (Figure 3) highlights the extent of native woodlands covered in NWSS included in the N4S model (305 000 ha), and also shows the potential occurrence of protected woodland species within these areas.

Figure 3 Species richness (all taxa) of native woodlands in Scotland based on the predicted potential distribution of all 179 protected woodland species.



Overall, 284 000 ha of habitat considered suitable for protected species is identified within the model. Woodlands with high species richness (20–30 different protected woodland species per woodland polygon) are reasonably well dispersed throughout Scotland (Figure 3); the native woodlands of the River Dee and River Spey valleys in Northeast Scotland stand out as areas of particularly high species richness.

Exploring scenarios to inform the targeting of woodland expansion

The benefits of creating different types of woodland in a region can be assessed through simple scenarios. In this case study, expanding the native woodland cover in an upland landscape in Scotland is considered. Potential areas of native woodland were placed on sites suitable for native woodland expansion by choosing to either: (1) expand the native pinewood area (the conifer option); or (2) create a diversity of broadleaved woodlands (the broadleaf option). For the latter option, upland birch was substituted for the native pinewood expansion, and additional expansion areas were selected for upland oakwood or wet woodland, as informed by the current distribution of woodland in the landscape. For this scenario the key issue is deciding which protected woodland species could potentially be present within these new woodlands at each of the five stages of woodland development (temporary open habitat prior to woodland planting, regeneration/scrub stage, pole stage, mature and veteran/ancient). The assessment is based on species richness (the potential number of different species present) by woodland polygon. Only species likely to be in the area are included; all suitable microhabitats are considered to be present.

The scenario (Figure 4) shows that for either expansion option, species richness peaks in the mature stage (a maximum of 23–25 different protected species per polygon), and is higher in the regeneration/scrub (7–12 species) and veteran/ancient stages (10–12 species) compared to the temporary open (2–3 species) and pole stages (1–6 species). A comparison of the two options shows that the conifer option (Figure 4a) supports less species richness per polygon at the regeneration/scrub stage than the broadleaf option (Figure 4b), but when the woodlands reach the pole and mature stages, the conifer option supports a greater species richness per polygon. There is little difference between the two options at the temporary open and veteran/ancient stages. The N4S model outputs can also provide information on which protected species could potentially occur in each new native woodland polygon (but without providing an estimate of the potential abundance of individual species). Other scenarios can be explored by using the model to reflect different objectives.

Landscape – forest planners

For forest planners, the N4S model can be used to make predictions about protected species occurrence at both a regional and forest scale. At the forest scale, visualising the configuration of species rich polygons in a landscape can help planners decide how to minimise potential impacts on the most species-rich areas. This is demonstrated in the following section by an output from the N4S model on a 10 x 10 km area of upland landscape in Scotland.

Protected species richness in an upland landscape

The 10 x 10 km area in upland Scotland (Figure 5) is a highly wooded landscape and nearly half of the area (4377 ha) is comprised of native woodlands. A few polygons have the potential to contain a high number of protected woodland species (up to 31) and most have the potential to support 10 or more species. However, several polygons have a low species richness (0–10 protected species per polygon).

For forest planners, this information might indicate that there is considerable sensitivity in the polygons to disturbance or intervention within this landscape, and this could inform decisions about where to locate recreational activities or silvicultural interventions, for example, assuming that different options are possible. Alternatively, polygons indicated as having low species richness could become the focus for habitat improvement measures, if maximising biodiversity is an objective.

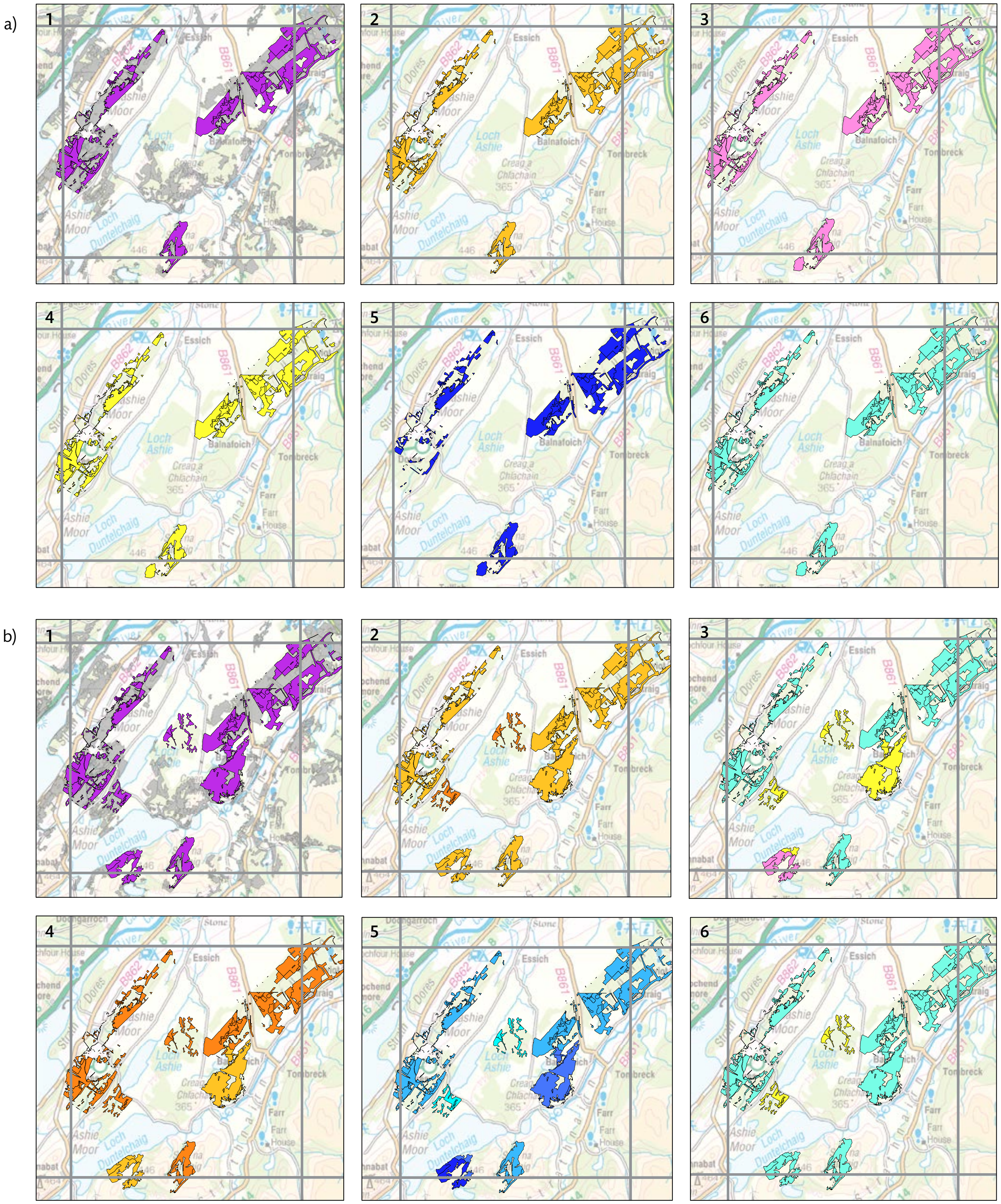
Woodland – forest managers

For forest managers, the model can be used to predict the occurrence of protected species at the woodland scale. At this fine scale, knowledge of the potential occurrence of a particular protected species within a woodland polygon may alert the forest manager to the need for an expert survey to confirm a species' presence. Alternatively, when managers do not have the resources available for conducting specialist surveys, they could utilise the ecological information provided by the N4S model when scheduling work, paying particular attention to locations and timing so as to minimise the risk of impacting a species that could be present within the stand (e.g. avoiding particular structures or microhabitats within the woodlands). This is demonstrated in the following section by an output from the N4S model for one woodland protected species.

Information on individual species

The occurrence of individual protected woodland species by native woodland polygons in a landscape can be predicted

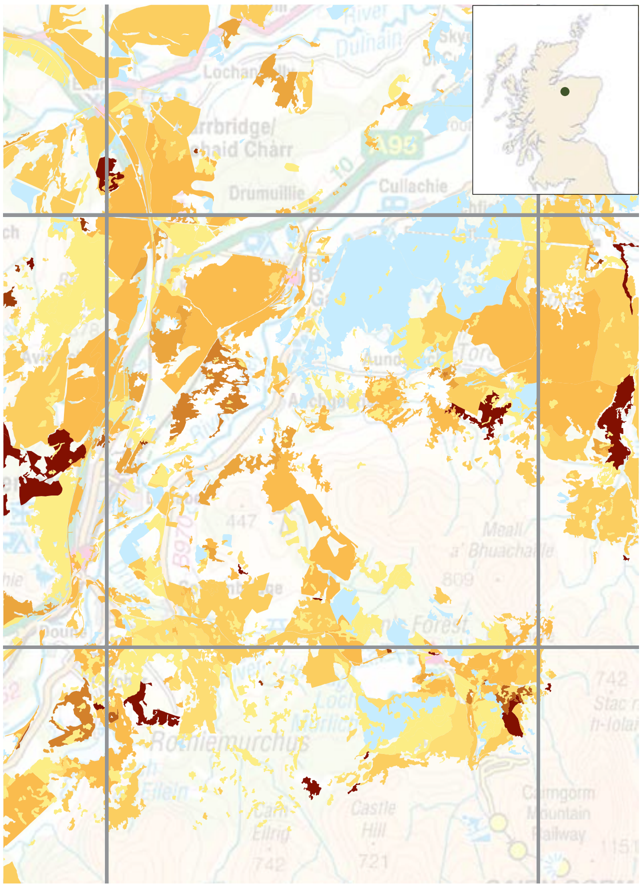
Figure 4 Species richness by native woodland polygon under two woodland expansion scenarios: (a) conifer and (b) broadleaf. For each scenario, box 1 shows the expanded woodland area. The following five boxes (2-6), show the level of species richness for each of the five stages of woodland development: (2) temporary open habitat prior to woodland planting, (3) regeneration/scrub, (4) pole, (5) mature, (6) veteran/ancient. It should be noted that the tree species selected for planting should be suited to site conditions (e.g. using Ecological Site Classification (Pyatt, Ray and Fletcher, 2001)).



Number of protected woodland species

0	2–3	7–9	13–16	20–22	New native woodland planting
1	4–6	10–12	17–19	23–25	Existing native woodland
					Ordnance Survey Great Britain 10 km grid squares

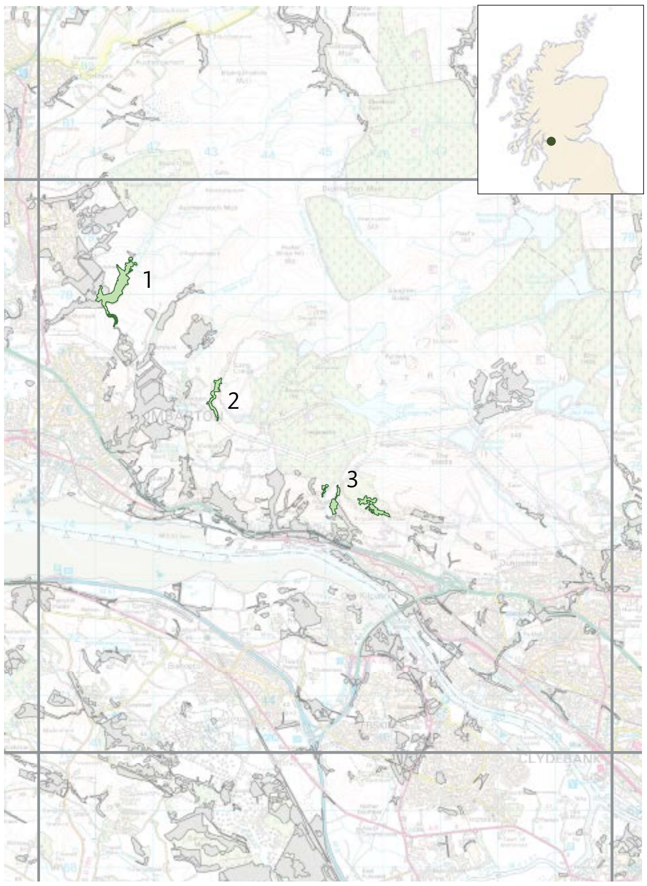
Figure 5 Potential distribution of protected woodland species richness by native woodland polygon in an upland landscape.



Number of protected woodland species

- 0
- 1–5
- 6–8
- 9–11
- 12–15
- 16–18
- 19–20
- 21–22
- 23–26
- 27–31
- Ordnance Survey Great Britain 10 km grid squares

Figure 6 Potential locations of the liverwort *Dumortiera hirsuta* and associated niche requirements.



- Habitat patches suitable to target species
- Native Woodland Survey Scotland habitat patches
- Ordnance Survey Great Britain 10 km grid squares

Suitable habitat characteristics			
Patch	Dominant habitat type	Dominant structure type	Suitable microhabitat type
1	Upland oakwood	Mature	water/wet ground, rock (humid)
2	Upland mixed ashwood	Mature	rock (humid)
3	Upland mixed ashwood	Mature	rock (humid)

using the N4S model. For example, the model output identifies the locations of the polygons where the lower plant, *Dumortiera hirsuta*, is predicted to occur (Figure 6). Polygons include upland oakwood and upland mixed ashwood woodland types, all with a mature stand structural stage. *D. hirsuta* is most likely to be associated with the water/wet ground, rock (humid) and bare ground microhabitats where available within these polygons. In the example, three polygons are identified where it may be advisable to avoid disturbing areas of the woodland containing their microhabitats. As an added precaution, a specialist survey could be focused on these polygons to confirm occurrence of the species prior to any woodland intervention or activity that might change or disturb the habitat.

Strengths and weaknesses

The N4S model has strengths and weaknesses. Like many models, it is only a quantitative expression reflecting the best working understanding of the relationships between species and habitats (Van Horne and Wiens, 1991). The N4S model has been constructed using an expert-based habitat suitability modelling (HSM) approach (Box 1). Poor species record availability is advanced as a reason to develop predictive models of distribution based on knowledge rather than records. Therefore, attempting to validate the N4S model with records which are considered inadequate for building a model may explain why the validation results are mixed.

Limitations to application

Because the performance of the N4S model in validation tests was mixed, its application may be limited, depending on the scale at which the model is applied.

National scale

For applications to decision-making at a national scale, the limitations relating to the accuracy of the N4S model may not hinder its use. With analysis on a broad scale, any uncertainties concerning the N4S model may be deemed less important in comparison to the usefulness of a method which can be consistently applied. The N4S model may perform equally as well or better than the current national analyses for Britain which uses relatively coarse (e.g. 2 km resolution) data and only the better known species (e.g. birds as surrogates for other taxa) (Franco *et al*., 2009), as N4S covers all protected species of interest for which expert knowledge on habitat requirements are available. Furthermore, the N4S model has the advantage of providing information on the habitats associated with areas that may be prioritised, which is an aspect regarded as a shortcoming in other approaches (Franco *et al*., 2009).

Landscape and woodland scale

Given the uncertainties regarding the accuracy of the N4S model, it is recommended that planners sense-check N4S model outputs by applying local knowledge when comparing habitat types, and the likely diversity of niches with the locations of species-rich areas as indicated by the N4S model. Decisions on the distribution of individual species within woodlands or groups of woodlands may require more stringent checks, for instance, commissioning an expert survey to confirm a species presence. Several researchers have proposed there could be benefits from ground-truth models (e.g. Lentini and Wintle, 2015), and have suggested methods for updating and improving model performance and utility by collecting field data on agreements and miss-matches with model predictions.

N4S model improvements

Three improvements could be made to the N4S model to increase its utility in forestry decision-making: (1) increasing confidence in the accuracy of model predictions by carrying out a targeted survey of polygons in which an assessment of both the predicted niche occurrence, and the predicted protected species occurrence, has been verified; (2) sourcing and integrating alternative spatial datasets would ensure the habitat layers remain as up-to-date as possible, for example, by incorporating a forest structure layer interpreted from aerial photography or LIDAR data (McInerney, Suarez and Nieuwenhuis, 2011); and (3) by building more species and habitat niches into the N4S model; ideally it should include non-native woodlands and be applicable to other parts of the UK, but this may be constrained by a lack of ecological knowledge supporting the species-habitat relationships which underpin the model.

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