Projecting impacts of anthropogenic climatic change on the bird communities of southern Swedish spruce monocultures: will the species poor get poorer?

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The potential impact of climatic change on bird species' distributions in Europe was recently modeled for several scenarios of projected late 21st century climate. The results indicate mean range shifts of hundreds of kilometres north for many of European bird species. Here we consider the implications from such distributional shifts for the bird communities of Norway spruce (*Picea abies*) monocultures in southern Sweden, a forest type likely to remain prevalent due to forestry, despite climate change. Our assessment led us to three key findings. First, the monocultures offer suitable habitat to only two bird species projected to extend their breeding distribution northwards into southern Sweden this century. Second, species richness was projected to decline overall, which would accentuate the depauperate nature of these stands. Third, all conifer-associated arboreal granivores and three of four conifer-associated arboreal insectivores were projected not to occur, reducing both the functional richness and functional redundancy. We discuss caveats related to our approach, including the potential for bioclimatic projections – used in this study – to be hampered by the artificial retention of dominant vegetation. We also discuss the implications of our results for avian biodiversity in what is today the most prevalent forest type in southern Sweden and in many other regions of Europe.

1. Introduction

The potential impact of climatic change on breeding bird species' distributions in Europe by the end of this century was recently modeled (Huntley *et al.* 2007, 2008), with the results indicating mean range shifts of hundreds of kilometres north for many species. The climatic envelope models used in these studies are explicitly based on the assumption that, when species' distributions are considered at a sufficiently extensive spatial scale (continental in this case) and coarse enough grain (50 km × 50 km grid cells in this case), climate is the ultimate determinant of observed patterns of species' occurrence (Huntley *et al.* 2008, Araujo *et al.* 2009, Gregory *et al.* 2009). This expectation has been supported by comparisons of projected changes in the regional climatic suitability for bird species with observed population trends (Green *et al.* 2008, Gregory *et al.* 2009, Jiguet *et al.* 2010a), as well as by a modeling study using a range of grain sizes (Luoto *et al.* 2007). However, when attempting to apply the outcomes of such models to specific ecosystems at smaller spatial extents and finer grain, the complicating influence of vegetation structure and composition (Lee & Rotenberry 2005, Matthews *et al.* 2011), land-use practices (Peterson *et al.* 2002, Felton *et al.* 2010b), and species' habitat requirements (Fearer *et al.* 2007), need also to be taken into account.

Approximately one third of Sweden's bird species are associated with forests (Gerell *et al.* 1996). Nevertheless, only ca. 5% of Swedish forest areas are protected, with the rest having largely been transformed by production forestry in terms of tree species composition, age structure, spatial structure and disturbance regimes (Gustafsson & Perhans 2010). In the south of the country, production forestry has often led to the conversion of broadleaf and mixed broadleaf-conifer forests to even-aged monocultures of the Norway spruce (*Picea abies*, hereafter spruce) (Lindbladh & Foster 2010, Lindbladh *et al.* 2011). This has resulted in spruce monocultures becoming the most common forest type in southern Sweden, accounting for 50% of standing volume (SFA 2009). This dramatic increase in the abundance and distribution of spruce in the region (Lindbladh *et al.* 2000, Lindbladh & Foster 2010), has been to the detriment of deciduous and old-growth forests and

their associated bird communities (Felton *et al.* 2010b, 2011). As forest land in southern Sweden is dominated by spruce monocultures, projecting how climatic change will likely affect the bird communities found in these environments is relevant to understanding the future of southern Swedish forest-associated bird diversity in general.

Here, we use bird habitat associations, in combination with the climatic change modeling results from Huntley *et al.* (2007, 2008), to consider the potential bird-community composition of spruce monocultures in southern Sweden at the end of this century. Several features of our approach should increase the reliability of the projections. First, we focus on a specific managed habitat type that, due to production benefits, market incentives, long-term planning, and rotation periods of 60–70 years (Carbonnier & Hägglund 1969, Bergquist *et al.* 2009, Felton *et al.* 2010a), is likely to persist in southern Sweden over the course of this century, thus reducing confounding influences of climate-associated changes to vegetation structure and floristics. Second, the results of response-surface models are more reliable when applied to regions of low topographical relief, and in regions for which regular and widespread systematic monitoring of species take place (Huntley *et al.* 2007). Southern Sweden possesses both of these characteristics. Third, as spruce monocultures also occur in more temperate biogeographic zones of Western Europe, we can use bird surveys from these regions to identify species that use spruce monocultures as habitat, but do not as yet breed regularly in Sweden. We discuss our results with respect to the potential costs to forest bird communities from retaining boreal-associated tree species cover in what are increasingly temperate climatic conditions, and raise caveats relevant to our approach and the interpretation of bioclimatic projections.

2. Materials and methods

2.1. Bird communities assessed

We used the Swedish standard for defining spruce monocultures, as managed stands of trees in which Norway spruce (*Picea abies*) comprise the majority of the stand's basal area, with no other species

Fig. 1. The location of the study area in Götaland, southern Sweden, and the spatial arrangement of the study sites.
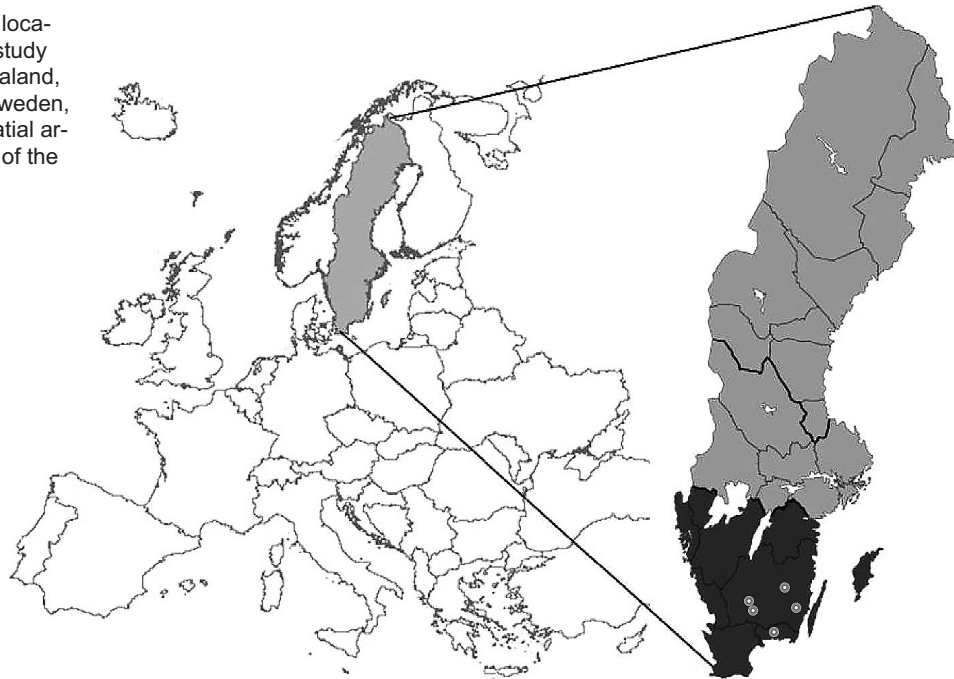
contributing ≥30% of total basal area (NFI 2007). Using electronic databases and Boolean search terms, we searched the scientific literature for studies that assessed bird-community composition for spruce monocultures in Southern Sweden and north-western Europe. To ensure all potentially relevant studies were considered, we used inclusive search terms: ("Picea abies" or "Norway spruce") and "bird*". The databases used were: Web of Science (http://www.isiwebofknowledge.com/), Google Scholar (http://scholar.google.se/) and Google (http://www.google.se/). Information on bird dietary guilds, foraging ecology, mass and migratory status were obtained from Birds of the Western Palearctic (BWPi 2007) and Lindell (2002).

Three published studies (Nilsson, 1979a, 1979b, Felton *et al.* 2011) surveying a total of nine mature stands were used to provide the bird-community composition and relative abundance for bird species currently associated with spruce monocultures in this region. These studies took place in the south eastern counties of Blekinge, Kalmar, and Kronoberg (Fig. 1), with stands located at least 2 km apart to ensure independence of the surveyed bird communities. The results from these studies enabled us to identify which species

occur in spruce monocultures, and their abundance. Although two of the studies are more than 30 years old, all of the species encountered are consistent with recent surveys (Lindström *et al.* 2012a) and the distribution maps for breeding European bird species in the present climate (Huntley *et al.* 2007, 2008).

We reviewed relevant literature on the habitat associations of all forest birds in Sweden and Western Europe (Lindell 2002, BWPi 2007). This review provided us with a list of European bird species considered to be associated with spruce monocultures, often due to their provision of suitable breeding sites or adequate food resources (Lindell 2002, BWPi 2007). Of the species associated with spruce monocultures, we refer to those projected to find suitable climatic conditions in southern Sweden by the end of this century as "establishing species", though we emphasise that establishment itself is not a given, and address this uncertainty as part of our analysis.

2.2. Background to climatic change projections

Huntley *et al.* (2007, 2008) simulated the potential distributions of bird species breeding in Europe at

the end of this century (2070–2099) for six IPCC climate-change scenarios. Their models were based on presence/absence records of breeding birds within 50 km × 50 km grid cells used by the European Bird Census Council (Hagemeijer & Blair 1997), and mean monthly climatic data at 0.5°C × 0.5°C resolution for 1961–1990 (New *et al.* 1999). Huntley *et al.* (2007, 2008) fitted response-surface models, using locally-weighted regression, to the distribution of each bird species, using three bioclimatic variables shown to give the best-fitting models of breeding distribution across all species. The three variables used were: mean temperature of the coldest month; annual temperature sum above 5°C; and an estimate of the ratio of actual to potential evapotranspiration. Model performance was assessed using area under the curve of a receiver-operating characteristic plot (Metz 1978). The probability of occurrence for a species for a given grid cell was simulated by the model, and was converted to presence/absence record using the threshold probability that maximises Cohen's *K* (Cohen 1960). See Huntley *et al.* (2007, 2008) for a detailed description of these methods.

The reliability of the climate-envelope approach at projecting shifts in species distributions due to climatic change has been questioned (Araújo & Rahbek 2006, Pearson *et al.* 2006, Zimmer 2007). Gregory *et al.* (2009) addressed such concerns by (1) simulating observed species' distributions in one part of a species' range using a model based on data fitted from another part of the species' range; (2) comparing observed changes in species' distribution with projected changes to distribution (eliminates effect of spatial auto-correlation); and (3) comparing the capacity to project changes for species for which climatic envelope models were fitted to all or only part of their geographic range. Their results support

Huntley *et al.* (2007, 2008) and justify the use of climate-envelope approaches as a means of projecting shifts in bird species distributions due to climatic change.

We used a subset of results from Huntley *et al.* (2007, 2008) that were based on the HadCM3 general circulation model (Gordon et al., 2000) and the IPCC 2001 synthesis SRES B2 and A2 emission scenarios (Nakicenovic & Swart 2000, Cubasch et al. 2001). We restricted our assessment to the results provided for the HadCM3 model, be-

cause it is a "middle-of-the-road" model with respect to simulating global mean temperature and precipitation changes (Huntley *et al.* 2008). We used the A2 emission scenario because it assumes rapid human population growth and high emissions, with end-of-the-century CO_2 emissions equating to approximately five times the 1990 values. In contrast, we used the B2 emission scenario because it assumes relatively slower population growth, with more diverse technological advancements contributing to the end-of-the-century CO_2 emissions equating to slightly more than two times the 1990 values (see Cubasch *et al.* 2001, IPCC 2007).

2.3. Avian community composition

We used presence/absence results from Huntley *et al.* (2007, 2008) for grid cells proximate to the spruce stands considered to determine which of the baseline "present" bird species for each stand were projected to persist under A2 and B2 scenarios. We applied the same approach to identify the spruce-associated bird species projected to arrive in southern Sweden for these scenarios. We then considered two alternative outcomes: one in which no new species would establish in spruce monocultures by the end of this century ('Not establishing species'), and another in which spruce-associated bird species do establish ('Establishing species'). Projected species-richness results were based on the net results of these two outcomes (not establishing or establishing species) for the two climate-change scenarios (A2 or B2).

2.4. Statistical analysis

To assess whether statistically significant differences occur between present and projected species richness, we conducted paired *t* tests contrasting present species richness with projected species richness as response variables, after testing for normally distributed errors. We repeated this approach for A2 and B2 scenarios, and for the two establishment scenarios. To compensate for the inflated risk of false discovery arising from multiple comparisons, we applied the FDR correction procedure (Benjamini & Hochberg 1995). We also

used Cohen's *D* to calculate the effect size of the projected response (Cohen 1988). We ran all statistical tests using R (R Development Core Team 2010).

3. Results

3.1. Bird communities in spruce monocultures, and projected climatic suitability

We recorded a total of 36 bird species to use the managed spruce monocultures of southern Sweden (Nilsson 1979a, 1979b, Felton *et al.* 2011). The analysis by Huntley *et al.* (2007, 2008) then enabled us to consider which of these and additional species are likely to shift their distributions to the inclusion or exclusion of southern Sweden over the course of this century for different climate-change scenarios. Of those bird species projected to encounter suitable climate in southern Sweden later on this century, most will not find suitable breeding habitat or resources in spruce production stands (Lindell 2002, BWPi 2007). For example, although the Melodious Warbler (*Hippolais polyglotta*), Nightingale (*Luscinia megarhynchos*), and Bonelli's Warbler (*Phylloscopus bonelli*) are all projected to experience suitable climatic conditions in southern Sweden by the end of this century for either the B2 or A2 scenarios (Huntley *et al.* 2007, 2008), none of these have habitat associations that overlap with the conditions provided in dense coniferous production forests (BWPi 2007). Firecrest (*Regulus ignicapilla*) and Short-Toed Treecreeper (*Certhia brachydactyla*) are projected to experience suitable climates in southern Sweden under the A2 and B2 SRES scenarios (2007, 2008), have a defined breeding habitat association with production coniferous forests (BWPi, 2007), and are found in spruce monocultures in at least part of their present range, albeit at low density (Steverding & Leuschner 2002, Paquet *et al.* 2006, BWPi 2007, de Warnaffe & Deconchat, 2008). The former of these two is an extremely rare breeder in Sweden, and the latter appears a vagrant (Lindell 2002, Ottosson *et al.* 2012).
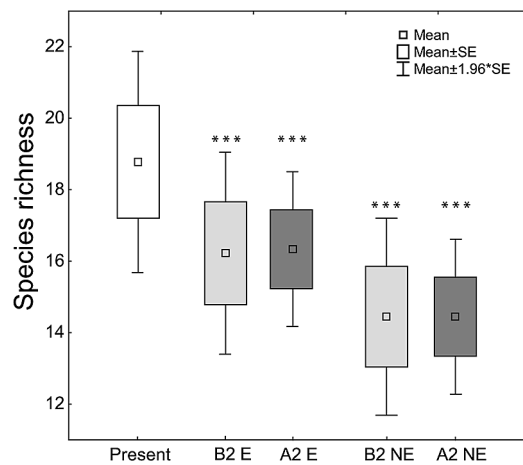
Both of these species have closely-related con-

Fig. 2. Species-richness scores for present bird communities within surveyed Norway spruce monocultures in southern Sweden, and the projected outcomes for B2 (light grey) and A2 (dark grey) climatic-change scenarios (see text for details), with establishment (E) or no establishment (N) of new bird species. Box plots are based on overall means; *P* values are obtained from paired *t* tests after FDR correction. *** = *P*<0.001.

geners which breed in spruce monocultures of southern Sweden, viz. the Goldcrest (*Regulus regulus*) and the Eurasian Treecreeper (*Certhia familiaris*). These congeneric pairs often co-occur within stands (Steverding & Leuschner 2002, de Warnaffe & Deconchat 2008). For our analysis, we therefore considered climate projections for the 36 bird species recorded to occur in the managed spruce monocultures of southern Sweden (Nilsson 1979a, 1979b, Felton *et al.* 2011), in combination with projections for the Firecrest and Short-Toed Treecreeper.

For both the B2 and A2 scenarios, the net impact of climatic change on bird species associated with spruce production forests was negative in terms of species richness. Stands were projected to have significantly lower than current species richness for both B2 and A2 scenarios (Fig. 2), regardless of whether the scenarios included the establishment of Firecrest and Short-Toed Treecreeper (B2: $t = 6.78$, df = 8, $P < 0.001$, $D = -0.54$; A2: $t = 4.05$, df = 8, $P < 0.001$, $D = -0.52$), or excluded their establishment (B2: $t = 13$, df = 8, $P < 0.001$, $D = -0.91$; A2: $t = 6.95$, df = 8, $P < 0.001$, $D = -0.91$).

Table 1. Bird species contributing ≥1% of relative abundance in spruce monocultures in southern Sweden. Characteristics of the two species projected to both find suitable climate and use spruce monocultures in the future are also included. Species are sorted according to their foraging and dietary ecology. Species are classified according to body mass (g), foraging and dietary ecology during the breeding season, migratory status (R = resident, PM = partial migrant, M = migrant), and the projected relative change in climatic suitability score from present to the A2 and B2 scenarios (Huntley *et al.* 2007, 2008) for each species as an average across the surveyed sites. Categories for climatic suitability change are; Substantial increase (SI) = >25% increase, Stable (S) = =10% change, Decrease (D) = >10-25% decline, Substantial decrease (SD) = >25% decline, but still present, Unsuitable (U) = unsuitable climate. C/B = conifer/broadleaf.

Scientific name	Common name	"Present" relative abun- dance	Body mass (g)	Migra- tory status	Foraging and diet	B2 sce- nario	A2 sce- nario
Ficedula hypoleuca	European Pied Flycatcher	1%	13.2	M	Arboreal/aerial feeding insectivore	U	U
Pyrrhula pyrrhula	Eurasian Bullfinch	1%	31.1	PM	Arboreal/ground-feeding ominivore	S	S
Parus caeruleus	Blue Tit	1%	11.4	R	Broadleaf-preferring arboreal insectivoore	S	S
Parus major	Great Tit	5%	18.5	R	Broadleaf-preferring arboreal insectivoore	S	S
Phylloscopus trochilus	Willow Warbler	3%	8.9	M	Broadleaf-preferring arboreal insectivoore	U	U
Poecile palustris	Marsh Tit	1%	11.8	R	Broadleaf-preferring arboreal insectivoore	S	D
Sitta europaea	Eurasian Nuthatch	1%	23.9	R	Broadleaf-preferring arboreal insectivoore	S	S
Sylvia atricapilla	Blackcap	1%	19.4	M	Broadleaf-preferring arboreal insectivoore	S	S
Garrulus glandarius	Eurasian Jay	1%	180.9	R	Broadleaf-preferring arboreal omnivore	S	S
Certhia familiaris	Eurasian Tree-creeper	5%	8.9	R	C/B generalist arboreal insectivore	U	U
Fringilla coelebs	Chaffinch	21%	24.5	PM	C/B generalist arboreal insectivore	S	S
Dryocopus martius	Black Woodpecker	<1%	318	R	C/B generalist arboreal insectivore	U	U
Dendrocopos major	Great Spotted Woodpecker	<1%	87.5	R	C/B generalist arboreal insectivore	S	S
Carduelis spinus	Eurasian Siskin	10%	13.2	PM	Conifer-preferring arboreal granivore (nomadic)	U	U
Loxia curvirostra	Red Crossbill	1%	40.4	PM	Conifer-preferring arboreal granivore (nomadic)	U	SD
Parus cristatus	Crested Tit	1%	11.2	R	Conifer-preferring arboreal insectivore	SD	SD
Periparus ater	Coal Tit	5%	9.0	R	Conifer-preferring arboreal insectivore	S	S
Poecile montanus	Willow Tit	2%	11.2	R	Conifer-preferring arboreal insectivore	U	U
Regulus regulus	Goldcrest	7%	5.8	PM	Conifer-preferring arboreal insectivore	SD	SD
Columba palumbus	Common Wood-Pigeon	3%	509.6	M	Ground-feeding granivore	S	S
Anthus trivialis	Tree Pipit	1%	23.4	M	Ground-feeding insectivore	S	D
Erithacus rubecula	European Robin	15%	16.4	M	Ground-feeding insectivore	S	S
Prunella modularis	Dunnock	3%	19.0	M	Ground-feeding insectivore	SD	D
Troglodytes troglodytes	Winter Wren	4%	8.9	M	Ground-feeding insectivore	S	S
Turdus merula	Eurasian Blackbird	3%	93.2	R	Ground-feeding insectivore	S	S
Turdus philomelos	Song Thrush	5%	69.7	M	Ground-feeding insectivore	S	D
New arrivals							
Certhia brachydactyla	Short-toed Tree-Creeper	–	9.2		C/B generalist arboreal insectivore	SI	SI
Regulus ignicapilla	Firecrest	–	5.6		C/B generalist arboreal insectivore	SI	SI

3.2. Bird species ecology

Bird dietary guilds, foraging ecology, mass, and migratory status are provided in Table 1. As 12 of the 36 species recorded in cited studies (Nilsson 1979a, 1979b, Felton *et al.* 2011) occurred at extremely low densities (e.g., were rare visitors to these stands and absent from all but 1–2 of the surveyed stands) and thus were unlikely to play major roles in the bird-community composition, we restricted this aspect of assessment (but not the sta- tistical analysis) to those species that contributed at least 1% of total abundance (Table 1). The bird species excluded from this analysis thus were Common Chiffchaff (*Phylloscopus collybita*), Common Raven (*Corvus corax*), Eurasian Sparrowhawk (*Accipiter nisus*), European Greenfinch (*Carduelis chloris*), European Starling (*Sturnus vulgaris*), Long-Tailed Tit (*Aegithalos caudatus*), Mistle Thrush (*Turdus viscivorus*), Redwing (*Turdus iliacus*), Wood Warbler (*Phylloscopus sibilatrix*) and Yellowhammer (*Emberiza citri-*

nella). Despite similar occurrence at less than 1% of total abundance, we included Black Woodpecker (*Dryocopus martius*) and Great Spotted Woodpecker (*Dendrocopos major*) due to their potential ecological importance via their capacity to create reproduction habitat for cavity-nesting birds. None of the excluded species were projected to experience an increase in climate suitability under the considered climate-change scenarios. Of the species commonly found in spruce monocultures, five were projected to not occur due to a loss of climatic suitability in the region under both the B2 and A2 scenarios. These were Eurasian Tree Creeper (*Certhia familiaris*), Eurasian Siskin (*Carduelis spinus*), European Pied Flycatcher (*Ficedula hypoleuca*), Willow Tit (*Poecile montanus*), and Willow Warbler (*Phylloscopus trochilus*).

4. Discussion

4.1. Projected climate-induced bird-community changes

Our assessment indicated a significant decrease in bird species richness for managed spruce monocultures of southern Sweden by the end of this century. We projected declines in species richness for both B2 and A2 SRES scenarios, regardless of the establishment alternative considered for newly-immigrating species. Notably, we found such declines in species richness despite the already depauperate nature of these stands, and the occupation of these stands by a bird fauna pre-selected to be tolerant of human disturbance. Below we discuss the specifics of our projections and potential caveats.

The species we projected to not occur, or to experience the most extensive decreases in climatic suitability for B2 and A2 scenarios (Table 1) included three of the most common species currently found in southern Swedish spruce monocultures, namely Eurasian Siskin, Goldcrest and Eurasian Treecreeper. Considered together, these species represent more than 20% of avian abundance presently encountered in these stands (Table 1). Furthermore, five of the six conifer-associated species were projected to not occur in the considered scenarios, or to experience substantial declines in cli-

matic suitability (with the exception of Coal Tit *Parus ater*; Table 1). The net result is a projected absence of all conifer-associated arboreal granivores and three of the four conifer-associated arboreal insectivores from these stands. This notably equates with a decline in both functional richness (the diversity and range of functional traits possessed by different species; Mayfield & Daily 2005, Wright *et al.* 2006) and functional redundancy (when a given function is fulfilled by multiple species; Walker 1992, 1995), which are important determinants of resilience of ecological systems (Peterson *et al.* 1998, Allen *et al.* 2005).

In contrast to the projected reductions of conifer specialists, among the six broadleaf-associated insectivores, we projected only Willow Warbler to decrease considerably according to the climatic suitability in the B2 and A2 scenarios (Table 1). The reason why a larger proportion of conifer-associated species was projected to be susceptible to climatic change may relate to the boreo-nemoral location of these coniferous stands. In southern Sweden, current management practices are promoting "borealised" forests (Emmer *et al.* 1998) within an increasingly "non-boreal" climatic zone (Koca *et al.* 2006). This has resulted in a managed-forest type inhabited by a significant number of boreal-forest-associated bird species, which appear to be more proximate to their limits of climatic tolerance, and generally less well suited to the direction the regional climate is projected to take than are their broadleaf-associated counterparts.

Any projected species loss in these managed forests may be compensated for by concomitant projected increases in newly-establishing birds from more temperate western European climates. However, only two bird species – the Short-Toed Treecreeper and the Firecrest – are likely to colonize spruce monocultures under the assessed scenarios (Table 1). Furthermore, even these two species are not specialized on these environments. Although they inhabit spruce production forests within their present range (Steverding & Leuschner 2002, Paquet *et al.* 2006, de Warnaffe & Deconchat 2008), neither of these species is a conifer specialist, nor are they particularly well adapted to structurally simplified stands (BWPi 2007). The Short-Toed Treecreeper is most commonly associated with tall rough-barked broadleaved tree species, whereas Firecrest prefers

mixed forests with a distinct understorey (BWPi 2007). These ecological requirements do not align with the environments found in spruce monocultures in southern Sweden. Furthermore, these ecological requirements are not characteristic of the Eurasian Treecreeper or Goldcrest. As a result, of all the species projected to newly encounter suitable climatic space within southern Sweden this century (Huntley *et al.* 2007, 2008), only two inhabit spruce monocultures, and neither are likely to be able to fulfill similar ecological roles to those occupied by their departing congeners, either with respect to abundance or ecological function. In short, if spruce monocultures in southern Sweden lose species due to climate change, replacement candidates among northward-shifting bird communities may not compensate this loss.

These results raise important issues for forest-associated avian biodiversity in this region. Climate change appears likely to reduce the climatic suitability for a number of bird species found in these spruce monocultures over the forthcoming century (however see caveats below), primarily through the loss or decline of conifer-associated species. In contrast, broadleaf-associated species were projected to be relatively resilient to climatic change for the considered projections (Table 1). In combination, these findings indicate that climate change may exacerbate the differences in biodiversity value between spruce monocultures and mixed/broadleaved forests in this region during this century. As spruce monocultures are already associated with low ecological values in this region (Berg *et al.* 1994, Fridman 2000, Chapin *et al.* 2007, Felton *et al.* 2010b, Gärdenfors 2010), any further reduction in the capacity of these dominant production forests to provide suitable habitat for forest species is relevant to the future of Swedish avian biodiversity in general. Furthermore, these results highlight how existing biodiversity stressors (i.e., intensive forest management) may interact with climate change to escalate regional biodiversity loss (see Driscoll *et al.* 2011).

4.2. Caveats in the model predictions

The underlying assumption of bioclimatic projections is that if climatic conditions within all or parts of a species' present distribution are projected to shift outside the range experienced within that current distribution, then the species is unlikely to thrive in those areas. The processes that drive such induced declines in a species include habitat change (Warren *et al.* 2001, Julliard *et al.* 2004), physiological limitations (Angilletta *et al.* 2010, Fuller *et al.* 2010, Boyles *et al.* 2011, Oswald & Arnold 2012), species interactions (Van der Putten et al. 2010), diseases (LaPointe et al. 2005) and synergistic effects (Drake et al. 2005). However, the circumstance considered in our study is distinct, in that the climate is projected to change while the dominant vegetation cover – a key determinant of suitable habitat for terrestrial species – is artificially retained through human management. This disconnects two important components of a species' niche that are normally coupled during periods of relative climatic stasis. This fact has the potential to hamper the accuracy of our climate-induced projections. Specifically, if individuals of a species are capable of persisting under a wider range of climatic conditions than thee current distribution of the species indicates, then retention of the dominant vegetation may allow the species to persist in areas where climatic conditions for the scenarios considered shift outside the range experienced within the species' current distribution. Our projections may thus overestimate the extent to which the bird communities of these spruce monocultures will be affected by climatic change over the forthcoming century.

The accuracy of these projections may also be reduced if a species has been consistently eradicated (e.g., due to habitat loss or persecution) from areas experiencing a particular range of combinations of climatic conditions. In such cases a bioclimatic model will erroneously attribute the absence of the species to that particular combination of climatic conditions, whereas in fact the absence was due to non-climate-related human activity. In such cases, any resultant projections could mistakenly indicate a species' absence from locations where climatic conditions may in fact be suitable. We cannot rule out this possibility. However, the likelihood of this error is reduced by the fact that all of the species we considered are extensively distributed throughout much of Europe (Huntley *et al.* 2007), and therefore are less likely to have been consistently eradicated from all those locations overlapping with a particular suite of climatic conditions.

Recent observations of population declines for European bird species at the warmest edge of their distribution (Jiguet *et al.* 2010a) may be indicative of bird species experiencing temperature-related physiological stress (Jiguet *et al.* 2010b, Oswald & Arnold 2012). If this is the causal mechanism behind populations exhibiting the so-called trailing-edge retractions to their previous distribution (Maggini *et al.* 2011), then the habitat provided by mature spruce monocultures may buffer against some of the species losses indicated in our projections. As currently managed, the vegetation of Norway spruce monocultures is very dense during some periods of the rotation (Linder & Östlund 1998), with the resultant understorey microclimate capable of ameliorating local climatic extremes (Merklova & Bednarova 2007). If so, then the climate-change projections for these locations may diverge sufficiently from the microclimates actually experienced by birds within these stands to enable bird species to persist even when projections indicate they would not (Fuller *et al.* 2010). In addition, this could contribute to a lag in the response rate of bird communities to climatic change, as has recently been observed throughout Europe (Brommer *et al.* 2012, Devictor *et al.* 2012, Lindström *et al.* 2012b). The degree to which such processes would alter the outcomes of our projections requires further research and is primarily speculative at this stage.

We solely focused on species associated with a managed habitat type (i.e., Norway spruce monocultures) that is currently actively created (planted) and maintained, and expected to remain in this region over the course of this century. By so doing we attempted to account for one of the primary limitations to species tracking climate change, viz. the availability of suitable habitat (Barbet-Massin *et al.* 2012, Barnagaud *et al.* 2012). However, other studies have emphasised the capacity of extensive land-use change to override observed impacts on bird-species populations (Julliard *et al.* 2004, Eglington & Pearce-Higgins 2012). We therefore acknowledge that, even accepting that Norway spruce monocultures will remain in southern Sweden throughout this century, substantial changes to management approaches would have implications for these bird species communities that to some extent could rival those due to climatic change. These include, for instance, rotation length, fertilization intensity, or thinning regimes (Nilsson *et al.* 2011). At this stage, such potential changes to Norway spruce management remain experimental, and due to the slow rate at which production forestry operations can shift direction (Felton *et al.* 2010a), they probably only alter a small percentage of production stands in the time period considered.

4.3. Conclusions

Although there is increasing empirical support for spatial responses being a predominant adaptation strategy among terrestrial species to climatic change (Parmesan & Yohe 2003, Root *et al.* 2003, Devictor *et al.* 2008, Green *et al.* 2008, Gregory *et al.* 2009, Jiguet et al. 2010a, Thomas 2010, Brommer *et al.* 2012, Devictor *et al.* 2012, Lindström *et al.* 2012b), our results should not be conflated with predictions. The response of any species to climate change represents a complex interplay of vulnerabilities and opportunities (Williams *et al.* 2008), with the net result being species specific. As such, our results are best considered as indications of the direction and potential extent to which climatic change alters these bird communities, limited for the scenarios, locations and habitat type considered. Accepting the caveats and limitations specific to our approach (see above), and that all bioclimate projections will be to some extent inaccurate, our results indicate that climate change reduces the avian diversity of Norway spruce monocultures in southern Sweden. We emphasize that Norway spruce monocultures are the most prevalent forest type in southern Sweden, and also one of the most prevalent production forest types in Europe (Forest Europe 2011). Our results thus appear relevant to European conservation biologists, forest managers and policy makers concerned about the capacity of such plantations – proximate to their recent natural low-latitude range boundaries – to maintain their avian diversity this century.

Conservation biologists need to consider the projected forest-dependent species pool, if biodiversity is to be maintained over the forthcoming century within dominant land-uses, such as production forestry. For southern Sweden, further studies are needed to confirm whether this requires

a shift towards managed forests with a higher share of broad-leaved trees better suited to the habitat requirements of both present and colonizing bird species in the region.

Inverkan av antropogen klimatförändring på sydsvenska fåglesamhällen i monokulturer av gran: kommer det artfattiga att ytterligare utarmas?

Forskare har nyligen modellerat hur europeiska fågelarters utbredning kan komma att påverkas av eventuella klimatförändringar under detta århundrade. Resultaten visar att många arters utbredning sannolikt kommer att förskjutas norrut med hundratals kilometer. Vi presenterar här en analys av vilka konsekvenser sådana förskjutningar kan ha för fågelfaunan i södra Sveriges monokulturer av gran (*Picea abies*), en skogstyp som med människans hjälp sannolikt kommer att bestå även under ett förändrat klimat.

Vår analys ger tre viktiga slutsatser. För det första, är det endast två arter med monokulturer av gran som lämplig livsmiljö som kan tänkas "vandra norrut" och etablera sig i södra Sverige under detta århundrade. För det andra, beräknas antalet arter i denna skogstyp minska totalt sett, vilket i så fall ytterligare utarmar mångfalden i dessa bestånd. För det tredje, förväntas alla fröätande arter kopplade till barrskog försvinna från denna skogstyp i södra Sverige, liksom tre av fyra insektsätare, vilket leder till en nedgång i både funktionell diversitet och redundans.

Vi diskuterar flera källor för osäkerhet i våra resultat, bland annat att bioklimatiska förutsägelser kan minska i precision när den dominerande vegetationstypen behålls artificiellt. Vi diskuterar vidare vilka implikationer våra resultat kan ha för fågelfaunan i brukade granskogar, som är den vanligaste skogstypen i Sverige och i många andra regioner i Europa.

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