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Habitat associations drive species vulnerability to climate change in boreal forests

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62	Abstract	Species climate change vulnerability, their predisposition to be adversely affected, has been assessed for a limited portion of biodiversity. Our knowledge of climate change impacts is often based only on exposure, the magnitude of climatic variation in the area occupied by the species, even if species sensitivity, the species ability to tolerate climatic variations determined by traits, plays a key role in determining vulnerability. We analyse the role of species' habitat associations, a proxy for sensitivity, in explaining vulnerability for two poorly-known but species-rich taxa in boreal forest, saproxylic beetles and fungi, using three IPCC emissions scenarios. Towards the end of the 21st century we projected an improvement in habitat quality associated with an increase of deadwood, an important resource for species, as a

consequence of increased tree growth under high emissions scenarios. However, climate change will potentially reduce habitat suitability for ~9–43 % of the threatened deadwood-associated species. This loss is likely caused by future increase in timber extraction and decomposition rates causing higher deadwood turnover, which have a strong negative effect on boreal forest biodiversity. Our results are species- and scenario-specific. Diversified forest management and restoration ensuring deadwood resources in the landscape would allow the persistence of species whose capacity of delivering important supporting ecosystem services can be undermined by climate change.

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Electronic supplementary material

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Habitat associations drive species vulnerability to climate change in boreal forests

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Abstract Species climate change vulnerability, their predisposition to be adversely affected, has been assessed for a limited portion of biodiversity. Our knowledge of climate change impacts is often based only on exposure, the magnitude of climatic variation in the area occupied by the species, even if species sensitivity, the species ability to tolerate climatic variations determined by traits, plays a key role in determining vulnerability. We analyse the role of species' habitat associations, a proxy for sensitivity, in explaining vulnerability for two

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can be undermined by climate change.   28

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1 Introduction   30

Assessing species climate change vulnerability requires an estimate of their exposure, sensi-   31
tivity and adaptive capacity (Dawson et al. 2011). Foden et al. (2013) carried out an evaluation   32
of well-studied taxonomic groups such as birds (≈9800 species, 35 % found susceptible to   33
climate change), amphibians (≈6200 species, 52 % susceptible) and important ecosystem   34
engineers such as corals (≈800 species, 70 % susceptible). Our knowledge of the impacts of   35
climate change on other poorly known but functionally important taxa, such as insects,   36
remains limited (Bush et al. 2014; Mair et al. 2014; Arribas et al. 2012; Bellard et al. 2012;   37
Wilson and Maclean 2011). For this neglected majority of species, vulnerability has often been   38
based only on their exposure to climate change. However it is well-established that sensitivity   39
and adaptive capacity also play a role in determining species vulnerability (Garcia et al. 2014;   40
Foden et al. 2013; Triviño et al. 2013; Arribas et al. 2012; Summers et al. 2012; Dawson et al.   41
2011). The knowledge of species characteristics affecting their sensitivity to climate change is   42
very limited for most species, and practically null concerning their adaptive capacity (Bush   43
et al. 2014; Arribas et al. 2012). Furthermore, species vulnerability critically depends on land   44
use change (Barbet-Massin et al. 2012; Ponce-Reyes et al. 2012; Brook et al. 2008).   45
Accounting for this important component of global change when predicting vulnerability   46
improves predictions about future species persistence (Fordham et al. 2013; Triviño et al.   47
2013; Ponce-Reyes et al. 2012).   48

    Here we analysed the role of species' habitat associations in affecting climate change   49
vulnerability for 129 Finnish threatened saproxylic (deadwood associated) beetles and fungi   50
(Tikkanen et al. 2006), two species-rich taxonomic groups in boreal forests. Both groups   51
depend on deadwood, the main habitat and food resource for 25 % of the species living in this   52
biome, and are functionally important in key processes like nutrient and carbon cycling and   53
soil formation (Harmon et al. 1986). For this assessment we used the SIMA forest simulator to   54
forecast the effects of climatic conditions on ecological processes (Kellomäki et al. 2008). The   55
simulator can translate forest changes driven by climatic scenarios and management regimes   56
into changes in habitat characteristics for saproxylic species (details in Supplementary   57
Methods 1–3, limitations in Supplementary Methods 6). In our simulations, the vulnerability   58
of species was measured as a combination of species sensitivity to changes in habitat   59
characteristics and exposure of forest stands to climate change.   60

    We simulated forest ecosystem dynamics for 2816 sample plots (forest stands) of the   61
National Forest Inventory in Finland, evenly spanning across all vegetation subzones of the   62

boreal forest (Supplementary Methods 2). We selected a time horizon of 90 years (2010–2099), and evaluated the changes in habitat quality for deadwood species. We assumed no changes in land use and forest management during the time horizon, with 91 % of the forest area currently under intensive timber production (Yrjölä 2002) and 9 % set-aside. Even if management practices remain the same, shorter forest rotations will take place following faster tree growth caused by climate change (Kellomäki et al. 2008). To account for stochasticity in SIMA models (Supplementary Methods 3), we reran the simulations ten times and calculated the average values of the characteristics of the forest sample plots under three different IPCC emissions scenarios (B1, A1B, A2) downscaled for Finland (Jylhä 2009) (Supplementary Methods 1).

We evaluated the effects of climate change on species habitat availability by comparing these results with the outputs from simulations with current climatic conditions. Estimates of habitat availability for saproxylic species were based on the best available knowledge on their resources (tree species and diameter, deadwood decay stage) and micro-climatic niche axes (Kouki and Tikkanen 2007) (Supplementary Methods 4 and 6). For each species we calculated a climatic vulnerability value and identified *winner* (species experiencing improved habitat quality in the future), *loser* (reduced habitat quality) and *stable* species. We estimated the climate change vulnerability of the landscape by summing for each stand the species-specific vulnerability values. Finally, we used Generalized Linear Models (GLMs) for each IPCC scenario to assess the effects of sensitivity (species habitat association) vs. exposure (projected rate of climate change) on species climatic vulnerability.

2 Methods

Details concerning the climate data, the National Forest Inventory data modeling and simulation procedures applied in this manuscript are reported in Supplementary Methods 1–3. In the following sections we only report information about *threatened saproxylic species data*, the procedures to calculate *climate vulnerability* (*CV*), *and* the *GLMs* relating vulnerability with habitat associations and climate.

Threatened saproxylic species data We extracted records of threatened species from the Hertta database, a subset of the Environmental Information System of SYKE, the Finnish Environment Institute, based on the data updated to 2013 for 64 coleopteran and 65 fungal species (Tikkanen et al. 2006) (Supplementary Table 2). Threatened saproxylic species are considered good indicators of the quality of forests, being able to survive only with reasonably high amounts of deadwood in the stand ($\geq 20 \mathrm{m}^3$/ha); therefore favourable conditions for species survival in the stands can guarantee the persistence for many other saproxylic species inhabiting boreal forests.

Climate Vulnerability (CV) For each stand of the National Forest Inventory (NFI) we calculated Stand Conservation Capacity (SCC) as a weighted sum of species-specific habitat suitabilities (*HSIs*), the weights being the *HSI*s themselves (Supplementary Methods 4, 5 and 6). *CV* of forest stands is defined by subtracting the *SCC* calculated under three IPCC emissions scenarios ($s = B1, A1B, A2$), regionally downscaled for Finland (Jylhä 2009), from the *SCCs* calculated under baseline climatic conditions ($s = BC$). SCCs were averaged across

the last three simulated decades of the 21st century (2070–2099), when the effects of climate 105
change on forest dynamics are predicted to be the highest (Jylhä 2009): 106

$$CV_s = \Delta SCC = SCC_{BC} - SCC_{s=B1,A1B,A2}$$

Original SCC values vary between 0 and 1. To put more emphasis on changes in values in 109
the middle of the gradient (SCC values around 0.5 having more biological importance), we 110
transformed CV values as follows: 111

$$scaled\ CV_s = CV_s[SCC_{BC} \times (1 - SCC_{BC})].$$

This transformation accounts for the fact that a small change in habitat suitability induced 114
by climate change is expected to have less biological importance when the initial level of SCC 115
under stationary climate is either very low or very high, and the highest importance is for 116
intermediate SCC values. A negative sum of scaled CV values across the whole NFI corre- 117
sponds to an increase in SCC induced by climate change (improved landscape quality); a 118
positive sum of scaled CV values corresponds to a decrease in SCC under climate change 119
(landscape degradation). In the text, figures, tables and supplementary materials, when not 120
specified, the notation 'CV' always must be considered as an abbreviation for 'scaled CV' 121
values. CV depends both on the modifications of stand quality induced by climate change 122
(exposure) and on how species respond to these changes on the basis of their habitat 123
association (sensitivity) (Dawson et al. 2011). 124

We also calculated the species-specific scaled CV values, i.e., the sum of differences across 125
stands in HSI for each species, between the current and future climate. In the assessment we 126
categorized species into winners if their average scaled CV across all stands belonged to the 127
lowest quartile of the range of CV values, and losers when CV was in the highest quartile; all 128
other species were considered stable typically having both negative and positive CV values 129
(Supplementary Table 2). To summarize the species-specific information we calculated the 130
average values of climate vulnerability for each species' habitat associations in terms of 131
resources and micro-climatic associations (Supplementary Table 1). 132

Generalized Linear Models (GLMs): the association between climate vulnerability (re- 133
sponse variable) and the joint and separate effects of sensitivity (i.e., species habitat association 134
in terms of resources and micro-climatic associations as a categorical predictor) and exposure 135
(i.e., climate change rate as a continuous predictor) were evaluated using GLMs for each IPCC 136
emissions scenario (Supplementary Table 3). Climate change rate was measured as the 137
difference between future and baseline emissions scenarios for the best combination (in terms 138
of the lowest AIC values and limited multicollinearity) of five climatic variables (temperature 139
sum, dry days, evaporation, evapotranspiration, precipitation) simulated for the end of the 21st 140
century (averaged across the period 2070–2099). For the response variable we assumed a 141
gamma distribution of errors (random part of the model) and a log link function (systematic 142
part) between the dependent variable and the predictors. The means of GLM regression 143
parameters for CV were calculated with the Wald test using robust standard errors. The 144
importance of habitat association and climate change in explaining CV in the full model was 145
evaluated by summing up for each ~~for~~ these two CV components the averaging sequential 146
sums of squares over all orderings of regressors proposed by Lindeman et al. (1980) (lmg 147
values) calculated for each variable related with these two components for the corresponding 148
linear models. The sum of lmg values for all the climate change-related variables (ΔTsum, 149
ΔDry days, etc) defined the effect of climate, and the corresponding sum of habitat association 150

variables (tree, decay stage, etc) measured the effect of habitat factors. The relative effect of the two predictors in the full model was then summarized as a percent share of the total sum of lmg values.

All statistical analyses were performed using SPSS 20.0 (IBM Corp. 2011). Lmg values to evaluate the importance of the predictors in the GLMs were calculated via the R package "relaimpo" (https://cran.r-project.org/web/packages/relaimpo/relaimpo.pdf, Grömping 2006).

3 Results

3.1 Response of forest landscape and species to climate change

Across all studied species we projected negative vulnerability values, i.e., improvement in habitat quality, for 53 % to 57 % of stands, depending on the IPCC scenario, and positive vulnerability, i.e., habitat degradation, for 38 % to 42 % of the stands (Fig. 1a). Even if there was an overall improvement in habitat quality losers were represented in the landscape depending on the emission scenario and in the case of the B1 and A1B scenario outperformed winners (Fig. 1b). Between 9 % and 43 % of the 129 deadwood-associated species can be considered losers and 10–26 % winners, while 45–70 % are stable in the face of climate
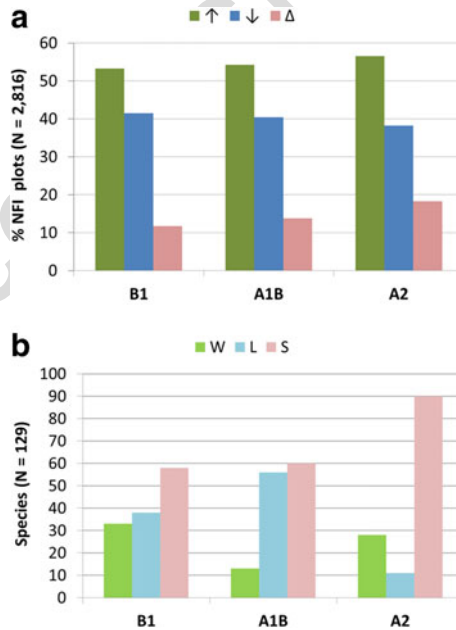

Fig. 1 Response of forest landscape (**a**) and species (**b**) to climate change. (**a**) Percentages of the National Forest Inventory (NFI) sample plots, which are predicted to have either an improvement (↑) or a reduction (↓) in habitat quality towards the end of the 21st century under different climate change scenario. The difference between improvement and reduction (Δ) qualifies the overall trend for the landscape. (**b**) Number of threatened species predicted to be either winners (W), i.e., experience an improvement in their habitat quality, losers (L), i.e., experience a reduction in habitat quality, or stable (S), i.e., experience constant habitat quality under climate change. For (**a**), (**b**) changes in habitat quality refer to climate vulnerability values for the three IPCC emissions scenarios (Jylhä 2009) (B1, A1B, A2) respect to the baseline scenario for Finland

change (Fig. 1b). The proportions of winners was the highest under a low emission scenario   166
(B1) while the losers were more represented under intermediate emissions (A1B) and the   167
proportion of stable species increased with emissions (from B1 to A2) (Fig. 1b). For winners   168
the average vulnerability was lower under low emissions (B1) than for higher emissions   169
scenarios (A1B, A2). For losers even if the highest average vulnerability was observed under   170
low (B1) emissions, the highest extreme values were observed under intermediate emissions   171
(A1B) (Fig. 2).   172

3.2 Response of forest species to climate change with regards to their habitat associations
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Winners and losers differed in terms of their habitat associations (Fig. 3, Supplementary   175
Tables 1 and 2). The losers under low (B1) and intermediate (A1B) emissions were   176
predominantly associated with deciduous trees (birch i.e., *Betula pendula* and   177
B. pubescens) (respectively 84 % and 57 % of the species) while under high (A2)   178
emissions losers were more often (91 %) associated with Scots pine. The winners were   179
associated with Scots pine under low (B1) emissions (61 %), with aspen (100 %) under   180
intermediate (A1B) and with other deciduous trees (71 %) under high (A2) emissions.   181
With concern to decay stage associations, losers were more frequently associated with   182
fresh deadwood (58 % under B1 scenario) or with well-decayed deadwood (61 % under   183
A1B and 100 % under A2 scenario) than winners. Association with large diameter   184
deadwood was not a crucial factor differentiating winners from losers. Under intermediate   185
(A1B) and high (A2) emissions a large proportion of winners (respectively 54 and 61 %)   186
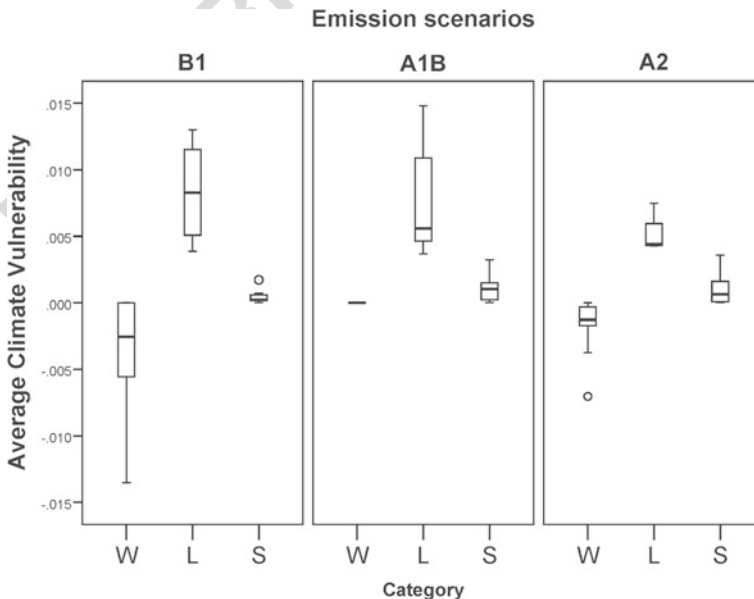were associated with sunny microclimate.   187

Fig. 2 Variability in the response of forest species to climate change. Boxplots of average levels of climate vulnerability for each response category to climate change (W = Winners, L = Losers; S = Stable) of the threatened species for IPCC scenarios of increasing emissions (Jylhä 2009)
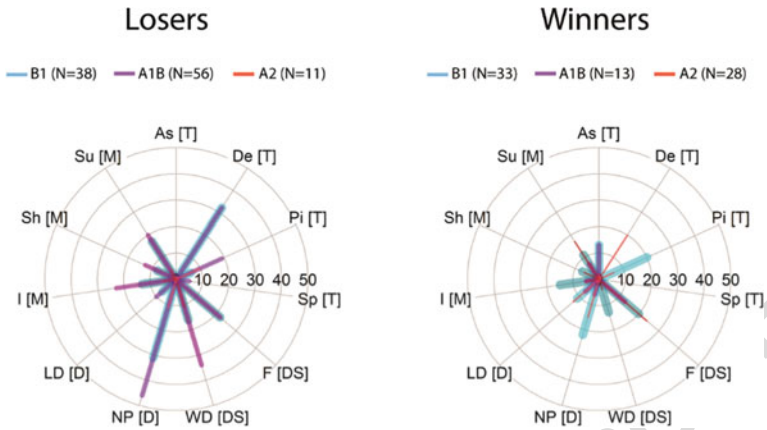
Fig. 3 Response of forest species to climate change with regards to their habitat associations. For each IPCC emissions scenario (Jylhä 2009) (B1, A1B, A2) numbers of threatened species, separated for their habitat associations, which experienced either a reduction (losers) or an improvement (winners) in their habitat quality. Explanations and abbreviations reported in the following footnotes. *Species habitat association*: evaluated in terms of tree species [T], decay stage of deadwood [DS], tree diameter [D], and microclimate [M]. The attribution of threatened species to each habitat association is based on the notes reported in Tikkanen et al. (2006). *Species response*: average climate vulnerability (CV) among the NFI sample plots. Species responses can be: winner (the species experiences an improvement in its habitat quality), loser (the species experiences a reduction in its habitat quality), or stable (species keeps constant habitat quality). Classification of response categories: W = Winners = (average CV value <25th percentile of CV range), L = Losers = (average CV value >75th percentile), S = Stable = (25th percentile < average CV value <75th percentile). Legend: As = Aspen. De = Deciduous; Pi = Pine; Sp = Spruce; F = Fresh deadwood. WD = Well-decayed deadwood. LD = association for large diameter deadwood (>30 cm). NP = No association for a certain diameter classes. Su = preferring sunny sites. Sh = Demanding shade. I = Indifferent to microclimate

3.3 The contribution of sensitivity and exposure to climate vulnerability

Species sensitivity, represented as habitat association, was a much stronger predictor of vulnerability across the landscape than climatic exposure, represented by the rate of projected climate change. In the full regression model where *CV* was explained both by habitat association (sensitivity) and climate change (exposure), predictors related with habitat association represented between 91 and 96 % of the explanatory power of the model (in terms of share of sum of lmg values) and only 4–9 % was explained by climatic exposure (Supplementary Table 3).

4 Discussion

In the present study we analyse the role of species' habitat associations in explaining climate change vulnerability for two poorly-known but species-rich taxa in boreal forest, saproxylic beetles and fungi, using three IPCC emissions scenarios. We found towards the end of the 21st century an improvement in their habitat quality associated with an increase of deadwood, an important resource for these species, as a consequence of increased tree growth but also a reduction of habitat suitability likely caused by future increase in timber extraction and decomposition rates.

In accordance with previous studies addressing species' climate change vulnerability (Garcia et al. 2014; Triviño et al. 2013; Foden et al. 2013; Summers et al. 2012), we projected

more losers than winners for both the low (B1) and intermediate (A1B) emission scenarios 205
while under high emission (A2) the winners increased dramatically respect to losers. Under 206
low-intermediate emissions, about 30–40 % of the threatened deadwood-associated species 207
were projected to face reduced habitat quality by the end of the 21st century, while habitat 208
quality improved for a smaller fraction of species. However, across all species we projected an 209
improvement in habitat quality for >50 % forest stands, most likely caused by increased 210
deadwood (Mazziotta et al. 2014) as a result of increased in-tree growth and mortality with 211
climate change (Mazziotta et al. 2014; Kellomäki et al. 2008). 212

The higher number of losers than winners for two emission scenarios, notwithstanding the 213
overall increase in habitat quality, highlights the importance of accounting for species-habitat 214
associations when evaluating vulnerability. This mismatch may be explained by the fact that, 215
even though global warming is expected to increase deadwood availability through increased 216
tree growth and mortality, the increased rate in deadwood turnover may ultimately limit 217
species persistence in the landscape. Nevertheless, the strong decrease in stand habitat quality 218
that we projected for about 40 % of stands reveals that climate change effects on habitat quality 219
vary with the current characteristics of localities. With increasing emissions, the higher 220
difference in the landscape's response to climate change among plots reflects the higher 221
proportion of stable species. Especially under high emission (A2), the stronger increase in 222
tree growth and mortality may outpace the increased rate in deadwood turnover overall 223
increasing deadwood habitats. However this increased habitat availability is still partly deter- 224
mined by the local landscape suitability. 225

Suitable habitat conditions will increase in the future for winners species. However, even if 226
habitat becomes available, many of these species may be unable to colonize this new space 227
because of limited dispersal ability (Menéndez et al. 2006; Devictor et al. 2008). This is 228
specially the case for poor dispersers like saproxylic species. Moreover, climate change is 229
predicted to create novel communities from the new associations of species able to track their 230
habitat and climatic niche (Williams and Jackson 2007). Species that are able to reach these 231 Q4
new suitable species space might not be able to survive in these novel communities because 232
they are not competitive enough, ultimately resulting in extinction events difficult to predict 233
(Urban et al. 2012). Many species may continue to persist at local scale as an effect of 234
extinction debt even after many decades of unfavorable environmental changes, ultimately 235
maintaining high local levels of species richness, but their populations might become extinct in 236
the long run (Hyvärinen et al. 2006; Berglund and Jonsson 2005). 237

We forecasted a positive trend in species associated with Scots pine and deciduous trees as a 238
consequence of the predicted enhancement in annual growth of these tree species with 239
increasing emissions (Mazziotta et al. 2014; Kellomäki et al. 2008). We also projected a 240
decline of species preferring well-decayed deadwood. This stems from the fact that with 241
climate change the retention time of the deadwood stock will be reduced by increased 242
decomposition rates (Tuomi et al. 2011) making their habitats more temporary. Climate change 243
also results in more frequent final harvest and subsequent harrowing (Kellomäki et al. 2008), 244
further shortening deadwood retention times (Rabinowitsch-Jokinen et al. 2010). On the other 245
hand, fresh deadwood will become more available, favoring species associated with this 246
resource. 247

Earlier research has suggested that the relative importance that climatic exposure and 248
ecological sensitivity have in determining vulnerability depends on the spatial scale. 249
Exposure has more importance than sensitivity at the landscape or regional scale, while the 250
opposite tends to be true at the local scale (Bradshaw et al. 2014; Garcia et al. 2014; Arribas 251

et al. 2012; Summers et al. 2012). In our regional-scale analysis, we projected that sensitivity, 252
i.e., habitat associations, accounted for a much larger proportion of the variance in vulnera- 253
bility than exposure. Evidently, whether exposure or sensitivity is driving vulnerability varies 254
not only with spatial scale, but also among taxa and perhaps within their ecological niches. 255
Earlier work has shown that the abundance, diversity and community composition of wood- 256
decaying fungi are more dependent on the amount and diversity of resources than on 257
macroclimate (Bässler et al. 2010). In other words, coarse (>10 cm) woody debris may create 258
local microclimatic conditions that effectively isolate saproxylic species from the direct effects 259
of macroclimate, and consequently climate change, at the landscape level (Bradford et al. 260
2014). This mismatch between micro- and macroclimatic conditions may explain why we 261
projected strong effect of habitat associations (sensitivity) and very weak effect of 262
macroclimate (exposure) on the vulnerability of saproxylic species. 263

5 Conclusions and implications 264

Many poorly known threatened species that are vitally important for supporting ecosystem 265
services may be negatively influenced by climate change (Wilson and Maclean 2011; Mooney 266
et al. 2009). This calls for action by policymakers and forest managers in establishing 267
management and restoration measures to make the most of the positive effects of climate 268
change for species, while alleviating the negative effects at the landscape level (see e.g. the 269
decision framework for species conservation management in Shoo et al. (2013) and its critics 270
in Ahteensuu et al. (2015)). Factors making some species losers vary among emissions 271
scenarios to some extent. This uncertainty calls for management decisions providing large 272
enough variability in forest structures, e.g. in terms of tree species composition, forest rotation 273
lengths and amount of retained forest biomass. As habitat association is so important for 274
explaining species climate vulnerability, management and restoration actions should aim at 275
increasing habitat diversity and maximizing resources for deadwood species (Mazziotta et al. 276
2014; Halme et al. 2013; Mönkkönen 1999) to support their persistence in production 277
landscapes in the face of climate change. These actions can be achieved with relatively low 278
opportunity costs for society if carefully planned (Mönkkönen et al. 2014). The preservation of 279 **Q5**
biodiversity under climate change may be in conflict with other societal interests. For example, 280
European level policy incentives for more renewable climate-friendly energy (Stupak et al. 281
2007) has already resulted in increasing forest fuel harvesting, which in turn will reduce 282
resource availability of deadwood-associated species and further cause species endangerment 283
(Eräjää et al. 2010). More comprehensive forest management planning is needed for recon- 284
ciling ecosystem services and the protection of biodiversity simultaneously (Mönkkönen et al. 285
2014). Enhanced biomass accumulation due to climate change may help to compensate the 286
costs (i.e., declined land area for biomass production) of habitat improvement for saproxylic 287
species. 288

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Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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