1   **The European functional tree of bird life in the face of global change**

2

3   Wilfried Thuiller[1], Samuel Pironon[1,2], Achilleas Psomas[3], Morgane Barbet-Massin[4],

4   Frédéric Jiguet[4], Sébastien Lavergne[1], Peter B. Pearman[3], Julien Renaud[1], Laure Zupan[1],

5   and Niklaus E. Zimmermann[3].

6   [1] Laboratoire d'Ecologie Alpine, UMR CNRS 5553, Univ. Joseph Fourier, BP 53, FR-38041 Grenoble Cedex 9,

7   France

8   [2] Instituto Pirenaico de Ecología (CSIC), 50080 Zaragoza, Spain.

9   [3] Landscape Dynamics, Swiss Federal Research Institute WSL, 8903 Birmensdorf, Switzerland

10   [4] Muséum National d'Histoire Naturelle, UMR 7204 MNHN-CNRS-UPMC, Centre de Recherches sur la Biologie

11   des Populations d'Oiseaux, CP 51, 55 Rue Buffon, 75005 Paris, France

12

13   Corresponding author: Wilfried Thuiller, wilfried.thuiller@ujf-grenoble.fr

14

Despite the recognized joint impact of climate and land cover change on facets of biodiversity and their associated functions, risk assessments have primarily evaluated impacts on species ranges and richness. Here we quantify the sensitivity of the functional structure of European avian assemblages to changes in both regional climate and land cover. We combine species range forecasts with functional trait information. We show that species sensitivity to environmental change is randomly distributed across the functional tree of the European avifauna and that functionally unique species are not disproportionately threatened by 2080. However, projected species range changes will modify the mean species richness and functional diversity of bird diets and feeding behaviours. This will unequally affect the spatial structure of functional diversity, leading to homogenization across Europe. Therefore, global changes may alter the functional structure of species assemblages in the future in ways that need to be accounted for in conservation planning.

25

Both climate and land cover change are major causes of the current unprecedented rates of global biodiversity loss that may, ultimately, deteriorate the structure of biota[1], ecosystem stability[2] and ecosystem service provisioning[3]. Indeed, the current and future response of species to climate and land use changes can substantially impact species assemblages and, therefore, alter phylogenetic and functional structures[4]. When evaluating how changes in land cover and regional climate might impinge on biodiversity, focus on facets of biological diversity that go beyond the commonly studied species richness or turnover is crucial[4]. Phylogenetic diversity (PD) in species assemblages is, for instance, important for explaining the role of species interactions and biogeographic histories in structuring communities[5]. Further, functional diversity (FD), reflecting the diversity of morphological, physiological and ecological traits within biological assemblages[6] better depicts ecosystem functions and associated services than simple patterns of species richness and turnover[7]. Beyond aesthetic, patrimonial and philosophical arguments, the maintenance of functional diversity is a powerful argument to halt the so-called 6th extinction[3]. Loss of functions provided by particular species, if these are forced to relocate or to become locally extinct due to changes in land cover or climate, likely jeopardizes important regional ecosystem processes[8]. This underscores the importance of quantifying how functional uniqueness and diversity of species assemblages relates to the projected sensitivity of species to environmental changes.

41   Not all species are equally influenced by changes in climate or land cover. Generalist species are often perceived as

42   being less sensitive to such changes than specialists that have traits adapted to a narrower range of conditions[9].

43   Indeed, a recent modelling study on Alpine plants indicates lower extinction risk for generalists compared to rare and

44   threatened plant species[10]. Increase in forests, agriculture and urban areas at the expense of semi-natural grasslands,

45   together with change in precipitation regimes and temperature increase, may influence the structure of avian

46   assemblages[11] and their associated functional diversity. Bird assemblages are interesting to study as they heavily

47   depend on both vegetation structure and climate, and have been shown to have important ecological role on

48   ecosystem functioning and associated services[12]. Through their mutualisms with plants, birds act as genetic linkers

49   by pollenating flowers and transporting seeds, thereby helping to maintain plant diversity by supporting gene flow[12,

50   13]. Scavengers on carcasses help limit disease spread while predators on vertebrates and insects play important roles

51   in the regulation of prey density[12, 13, 14]. As another example, cavity-drillers and nest-burrowers are recognized as

52   ecosystem engineers that provide shelter to additional species[13, 15, 16]. Beside these direct functions, birds also provide

53   important cultural services for nature enthusiasts and contribute to global nutrient dynamics[13]. Climate- or land

54   cover-induced modifications in bird assemblages could have cascading negative effects in trophic chains, and

55   strongly reduce the provision of some functions. For instance, a decline in top-predators could benefit prey species,

56   with radiating effects on all lower-trophic levels[17, 18]. Therefore, biological simplification of agricultural lands or

57   forests through land use intensification may decrease the provisioning of pest control and other ecosystem services

58   by birds if their taxonomic and functional diversity decline[15, 19].

59   Moreover, if global changes lead to more homogenous landscapes, then this naturally translates into more similar

60   animal assemblages[20]. Functionally diverse assemblages likely show greater complementarity in resource use and

61   thus provide enhanced ecosystem functioning[21]. Alternatively, assemblages with numerous similar species have a

62   greater chance to provide more functional insurance against environmental changes (e.g. pesticides or diseases) than

63   functionally diverse assemblages because redundancy buffers against loss of functions otherwise provided by single

64   species[22]. Although these specific threats are difficult to account for or predict, it is nevertheless crucial to project the

65   potential detrimental or beneficial effects on functional diversity by projected climate and land cover change at large

66   spatial scales[23].

67

68   Here we report impact analyses of changes in land cover and regional climate on the distribution of 402

69   European breeding bird species and the resulting effects on the functional diversity of bird assemblages. Functional

70   diversity is represented here by behavioural traits during feeding to reflect how species acquire resources from their

71   environment (feeding behaviour, feeding location and activity), and by body mass and diet traits to reflect the

72   resource use requirements of species. We consider these as effect traits that determine the impact of a given organism

73   on community structure and ecosystem functioning[24, 25], although the distinction between effect and response traits

74   (traits that stand for the response of organisms to environmental change) is not always straightforward for animals[14].

75   In order to project current and future suitable habitats for each species, we use consensus projections extracted from

76   multiple species distribution models, several up-to-date high-resolution regional climate models, and land cover

77   change scenarios, where the latter two originate from recently finished EU projects. First, we ask whether species

78   sensitivity to climate and land cover change is randomly distributed across a functional tree of the European

79   avifauna, depicted as a dendrogram based on inter-specific functional distances. Second, we test whether functionally

80   unique species (species bearing singular combination of traits) are projected to experience more-severe changes in

81   suitable climates and habitats than species bearing more common traits syndromes. Third, we ask whether changes in

82   species habitat suitability influence the richness (i.e. the number of species bearing each function) and functional

83   diversity of different guilds. To do so, we investigate species richness and functional diversity in diet, feeding

84   behaviour and location, and activity and body mass over Europe. By investigating whether the functional diversity in

85   feeding behaviour and location within each diet type (and similarly for the other trait types) responds to global

86   change, we identify the functions that will likely increase or decrease in frequency and diversity. Finally, we test for

87   spatial structure in expected change of functional diversity. To this end, we map current and future functional

88   diversity of bird assemblages, and we investigate spatial changes in regional functional diversity across Europe.

89   Under the assumptions that bird species will track their suitable climate and land cover, we showed that species

90   bearing unique trait combinations were not more sensitive than other species, and that the trait diversity of some

91   guilds was projected to change drastically (i.e. insectivores) while other guilds should not be strongly affected.

92   Overall, the spatial distribution of trait diversity should change across Europe, leading to functional homogenization

93   of its avifauna.

94

Results

Species sensitivity to climate and land cover changes

Species sensitivity to both climate and land use change are estimated as the change in the amount of suitable habitat assuming that all species fully disperse to newly suitable habitats and track their shifting niche without any response lag. Most species are predicted to shift their range North- and up-ward[11], with a moderate increase in the amount of suitable habitat for most species under the A1B scenario (Fig. 1A, Supplementary Fig. 1 for the other regional climate and land cover scenarios). This implies that although several species are predicted to lose a substantial part of their current suitable habitat (Fig. 1B, Supplementary Fig. 1B), the majority is predicted to find larger extents of suitable habitat elsewhere in Europe under future conditions (Fig. 1A, Supplementary Fig. 1A).

Species sensitivity distribution along the functional tree

Among European bird species, we find only a weak, non-significant relationship between relative changes in the size of suitable habitat area following climate and land cover change and the position of species on the functional tree (Fig. 2, Supplementary Fig. 2 and Supplementary Table 1). This demonstrates that no group of functionally similar species is predicted particularly sensitive or insensitive to global change. This is surprising since large body mass and other life history traits usually predispose species to increased extinction risks[26]. Importantly, functionally unique species are unlikely more sensitive to environmental change than are functionally less unique species (Supplementary Table 2). The functional uniqueness of species is therefore not clustered on the phylogenetic tree of the European avifauna (Fig. 3).

Change in richness and diversity across functional groups

Interestingly, the projected species richness and functional diversity within each of the five groups of analysed traits (diet, feeding behaviour, feeding location, feeding activity, and body mass) show diverging patterns in response to environmental changes (Fig. 4 for diet, Fig. 5 for feeding behaviour and Supplementary Figs. 3, 4 and 5 for the other traits). Whereas mean and variance in body mass per pixel did not significantly change (Supplementary Fig. 5), there was a noticeable increase in the mean species richness of invertebrate diet and picking and pecking feeding

120   behaviour with environmental change. Interestingly, this increase of species richness for these two specific diet and

121   feeding behaviour groups is not followed by an increase in functional diversity (as measured by MFD), whether or

122   not we consider all traits or single traits. In other words, the increase in species richness for the invertebrate diet will

123   not result in a higher diversity in feeding behaviour or feeding locations. This is because all of these behaviours are

124   already represented within each pixel. In summary, our results reveal an increase in redundancy for invertebrate diet

125   and picking and pecking feeding behaviour. On the contrary, other diet groups are projected to experience an

126   increase in species richness per pixel, while their functional diversity is projected to decline at the same time (Fig. 4)

127   like, for instance, bird assemblages with a vertebrate diet. The diversity of feeding behaviours within the vertebrate

128   diet group is projected to slightly decrease, resulting in a decrease of complementarity. In contrast, the fish diet group

129   is projected to experience decreased functional diversity in feeding behaviours and locations, without an associated

130   change in species richness.

131   *Current and future trait diversity distribution*

132   The spatial distribution of the overall functional diversity (calculated as MFD with all traits included) was calculated

133   on a pixel basis among species that were projected to be present at each time period. Our analyses reveal that the

134   projected functional diversity of the avifauna is not homogenously structured across Europe under current conditions,

135   with northern regions and Atlantic coasts having the largest functional diversity and the European Alps and centre of

136   Iberian Peninsula the lowest. However, despite these projections, European biogeographic regions are not equally

137   affected (Fig. 6). Under current conditions, northern Europe and the northern UK currently exhibit markedly higher

138   bird functional diversity compared to central Europe (e.g. southern Germany), the center of the Iberian Peninsula and

139   the outer Alps (Fig. 6). Under projected global change, however, the marked difference between Northern and

140   central Europe tends to be reduced. In particular, mountainous regions of central and southern Europe are projected

141   to experience marked increase in functional diversity. For southern Scandinavia (i.e. nemoral and boreal regions) we

142   predict reduction in functional diversity in many parts. In other words, the expected upward shift of suitable habitats

143   for European birds in central European mountains may lead to a relative increase in functional diversity

144   (assemblages being functionally less redundant). In contrast, for northern latitudes we predict assemblages to

145   become functionally more redundant. The simulated differences between the various climate and land cover

146   scenarios are relatively small and do not greatly alter spatial patterns (Fig. 6). In general, under the A1b climatic

147   scenario and the associated GRAS land use scenario, the projected changes are the most marked, with stronger

148   relative increase in functional diversity in the Alps and centre of the Iberian Peninsula, and stronger relative decrease

149   in Northern UK and southern Scandinavia than under the A2 and B1 scenarios (Fig. 6).

150

151   **Discussion**

152   The analysis of joint climate and land cover change impact on the functional diversity of an entire species group over

153   large spatial scales is challenging. Our study addresses these challenges and presents a unique large-scale assessment

154   of the potential impacts of combined climate and land cover changes on the functional diversity and richness of

155   European avifaunal assemblages. Our study addresses important drawbacks of most existing global change risk

156   assessments. In methodological terms, our study is one of the first to model the response of species to both regional

157   climate and land use changes. For instance, Thuiller et al.[27] quantified the influence of climate change on the

158   phylogenetic diversity of European biota, but only focused on climate change as simulated from global (not regional)

159   circulation models and ignored potential additional effects of projected land cover change. As suggested by Barbet-

160   Massin[28], we estimate the climatic and land cover requirements of species for the whole Western Palearctic region

161   including Northern Africa. This allows us to account for species that may immigrate to Europe from North Africa,

162   and ensure that the ecological requirements of the modelled species were fully captured. These estimates are

163   consistent with recent analyses on the same group of species[28] and slightly less alarming than previous studies[29]. The

164   divergence from results of Huntley and colleagues[29] likely originates from inclusion of the southern and eastern

165   range limits of the modelled European bird species in North Africa and the Middle East[28]. In addition, we use the

166   latest release of regional climate models and also include land cover variables that certainly buffer the direct effects

167   of climate change. Finally, we have employed ensemble-forecasting methodologies by combining highly predictive

168   species distribution models (Supplementary Fig. 6) to generate robust projections and, thus, use four different

169   regional climate models and three socio-economic scenarios in order to incorporate into our projections all

170   recognized sources of uncertainty.

171   In summary, we show that although the overall functional avian diversity of Europe is expected to only weakly

172   change under projected climate and land cover change, some regions might experience increased functional

173   complementarity (e.g. the European Alps), or simply an increase of species richness per guild (e.g. Boreal and

7

174   Nemoral regions). Overall, this reshuffling should lead to a functional homogenisation of Europe, with most

175   combinations of traits occurring being available everywhere in the landscape. This result complements the current

176   opinion that the global avifauna is experiencing functional homogenization due to loss of specialist and proliferation

177   of generalist species[9]. In our case, the causal factors are slightly different as this homogenization is due to a spatial

178   re-structuring of assemblages and, notably, the arrival of species with new combinations of traits in specific regions

179   (i.e. artic and alpine) increasing their functional complementarity. Thus, assemblages with projected increases in

180   functional diversity may provide enhanced ecosystem functioning as a result of more efficient resource use, a

181   beneficial effect that is projected to occur primarily in mountain areas. In any case, we show that species richness in

182   a given guild is not predicted to dramatically drop meaning that no key functional groups (i.e. top predator) are

183   predicted to go locally extinct, which could have had importance consequences on trophic cascade.

184   Interestingly, our results demonstrating species with unique combinations of traits are not disproportionally sensitive

185   to climate and land cover change mirror a recent analysis carried out for 32 fish species in France[30]. This study

186   evaluates the potential impact of climate change on fish assemblages, and reports that those species at high risk of

187   local extinction are not necessarily those bearing the most unique combination of traits. Our results for European

188   birds show the same trend. Having used effect traits instead of response traits might explain this pattern, as there is

189   no *a priori* reason to believe that particular combinations of effect traits should negatively influence the response of

190   species to environmental change.

191   The projected changes we present may lead to an increase in richness of species with invertebrate diet and pick and

192   peck feeding behaviour, which, in turn, may impact human well-being through enhancement of natural pest control[31].

193   Indeed an increase in richness of species with invertebrate diets would likely benefit pest control and associated

194   ecosystem services, although the regions that need it most (southern European countries with economies that highly

195   dependent on agricultural yields) are projected to experience reductions in these services[32]. However, our results

196   need to be treated with caution as the overall functional diversity within the invertebrate diet group and, more

197   specifically, the diversity of feeding behaviours and locations are not projected to change. In other words, change in

198   the richness of species with an invertebrate diet will most likely result in an increase in predation but not in the

199   variety of predation behaviours and locations. More importantly, some diet groups (e.g. vertebrate diet) are likely to

200   experience an increase in mean species richness across Europe, together with a decrease in diversity of feeding

201   behaviour and location. Other groups, such as fish-eating diet, may experience a decrease in functional diversity that

202   is decoupled from changes in species richness. The outcome of such projected changes on complementarity require

203   additional analyses in order to deduce regional consequences on ecosystem services. Indeed, the link between traits,

204   ecosystem functioning and ecosystem services is far from trivial[14] and is influenced by quantity of other factors not

205   explicitly modelled here, such as community assembly rules and land use practices. Additionally, our modelling

206   framework does not explicitly account for inter-specific competition, which could impede the increase of species

207   richness in some groups. Projected change in species richness are thus likely to be the maximum change when

208   competition within a guild does not influence the pure effects of climate and land use change. However, this is also

209   important to note that at the resolution of our study (10 arc-minutes, roughly 19 km in Europe), the outcome of

210   competitive interactions might be moderate as the spatial heterogeneity and the area of a pixel might buffer

211   competitive exclusion within a guild.

212   Our study thus provides clear evidence that the repercussions of projected climate and land use change on functional

213   diversity of European avifauna assemblages is moderate, despite the likely negative impacts of these changes on

214   individual species ranges[11]. One major beneficial effect of environmental changes relates to the projected increase in

215   species with invertebrate diets, which could ultimately influence pest control, but which could also negatively

216   influence pollination services. These detrimental effects relate to a decrease in functional diversity in Northern

217   Scandinavia that might ultimately reflect reduced ecosystem functioning in an arctic region. However, relatively

218   small changes in functional diversity may be paralleled by high regional turnover of individual species that results in

219   substantial changes in trophic relationships that accompany altered species assemblages[4].

220

METHODS

Species distribution data

Presence-absence data for all European species were obtained from the EBCC atlas of European breeding birds[33],

that we further completed for Northern Africa and Eastern Europe using geo-referencing and digitizing breeding bird

distribution maps from the handbooks of the birds of the Western Palaearctic[34] at a 0.5° resolution. We did not

consider seabirds in our analysis as climate and land cover variables may not be the most relevant drivers of the

restricted terrestrial distribution of their breeding sites. Moreover, our spatial analysis has focused on projected

changes in Europe. Therefore, we considered only species that have their current breeding ranges at least partly

included in Europe and we removed species with less 20 occurrences for statistical modelling reasons. From the total

list of European breeding and resident bird species, we finally retained 402 species. For all modelled species, we

considered their whole Western Palaearctic range (including North Africa and the Middle East) in order to model the

full extent of their environmental niche[28].

Environmental data

Current climate was represented by five bioclimatic variables from the Worldclim database[35] at 0.5° resolution for

calibrating the models and 10' resolution for projecting them. These variables were: Temperature seasonality (intra-

annual standard deviation * 100), maximum temperature of the warmest month, minimum temperature of the coldest

month, precipitation of the wettest month and precipitation of the driest month (Supplementary Table 3).

Future climate by 2080 (2051–2080) was represented by a set of regional climate model (RCM) runs originating

from the ENSEMBLES EU project, which has physically downscaled global circulation model (GCM) data

generated for the 4th assessment report of the IPCC[36]. We used three available SRES scenarios[37] for these models,

namely A1b, A2 and B1. RCMs downscale the very coarse resolution climate model output of CGMs (usually 1 – 2 °

Lat/Lon per grid cell) to a much finer spatial resolution (usually 10 – 30 ' Lat/Lon) on a physical process basis. To

this end, an RCM is fed at the study area boundaries by the global output of GCMs in order to provide boundary

conditions and global weather input for the downscaling. We have used 3 different RCMs, namely HadRM3, RCA3

and RACMO2[38, 39, 40, 41], fed by three different GCMs (HadCM3, ECHAM5, and CCSM3) and resulting in 4

246   RCM/GCM combinations (Supplementary Table 4). All RCM scenarios were interpolated to the same 10' spatial

247   resolution for 30-year monthly mean values of temperature and precipitation. Based on these monthly values, our

248   five bioclimatic variables of the Worldclim database were calculated for future time steps.

249   Current land cover for the whole Palearctic was represented by GLOBCOVER 2009

250   (https://earth.esa.int/web/guest/pi-community) at 300m resolution. We up-scaled the data to the resolution of the

251   species distributions (0.5°) and 10' resolution for projection under current and future conditions by calculating the

252   area fraction of each land cover type within each pixel. We used the level 1 classification (i.e. built-up areas, arable

253   lands, permanent crops, grasslands, forests and others) that is consistent with the EU CORINE classification on

254   which the land cover scenarios were based.

255   Bird species distributions are also influenced by the structure of the vegetation. Despite the fact that it is difficult to

256   accurately represent the structure of the vegetation mosaic at 0.5° and 10' resolutions, we estimated the Simpson

257   diversity index using the fraction of each land cover class as a weighting scheme.

258   Future land cover data was taken from the EU funded ALARM and ECOCHANGE projects[42, 43, 44]. The ALARM

259   land cover change scenarios provide annual fractions of land use for 8 main land use/cover categories per 10'

260   resolution grid cell (i.e. % built-up, % cropland, % permanent crops, % grassland, % forest, % biofuels (liquid, non-

261   woody or woody), % land in succession) and for the period 2006-2080. We then retained the period 2051–2080 to be

262   consistent with the climatic data. The countries covered are those of the EU25 plus Switzerland and Norway. We

263   removed % of biofuel and % land in succession that were not available for calibrating the models (period 1961-

264   1990).

265   We retained three storylines that are consistent with the climate change scenarios: 1) GRAS - Growth Applied

266   Strategy, where deregulation, free trade, growth and globalisation will be policy objectives actively pursued by

267   governments. Environmental policies will focus on damage repair and limited prevention based on cost benefit-

268   calculations. There is no emphasis on biodiversity. This scenario is considered equivalent to A1b; 2) BAMBU –

269   Business-As-Might-Be-Usual, where policy decisions already made in the EU are implemented and enforced. At the

270   national level, deregulation and privatisation continue except in "strategic areas". Internationally, there is free trade.

271   Environmental policy is perceived as another technological challenge. This scenario is considered equivalent to A2;

272   and 3) SEDG – Sustainable European Development Goal, which enhances the sustainability of societal development

11

273   by integrated social, environmental and economic policy. The scenario aims for a competitive economy and a

274   healthy environment, gender equity and international cooperation. It represents a normative scenario with

275   stabilisation of GHG emissions. This scenario is considered equivalent to B1.

276   Given the land cover scenarios were only available for the EU25 plus Switzerland and Norway, species projections

277   into the future were only carried out over those 27 countries.

278   In summary, models were calibrated and projected in time using 5 bioclimatic variables, 5 land cover type variables,

279   and one land cover diversity variable under four regional climate models and three emission scenarios.

280

281   **Functional trait information**

282   Trait information for the 402 modelled birds were extracted from the Handbook of the Birds of the Western

283   Palaearctic[34]. Missing species and data were gathered from species publications and Internet websites treating

284   avifauna. The traits were: body mass, diet (invertebrates, vertebrates, vegetal, fish, carrion), feeding behaviour

285   (pursuit (air and/or aquatic), sally, foliage-gleaning, pouncing, grazing, picking/pecking/stabbing, digging,

286   overturning, probing), feeding location (water, mud, ground, canopy and air) and activity (nocturnal, crepuscular and

287   diurnal). For diet, feeding behaviour, and feeding location and activity, each sub-category was expressed as a binary

288   variable (0 or 1) to make sure a species could be assigned to several strategies. In our study, we did not consider

289   traits that can only be measured with reference to the surrounding environment, such as nesting habitats. We did so

290   because of the circularity in the methodology as changes in land cover (defining the surrounding environment) are

291   implicitly accounted for in our modelling framework. We preferred to constrain our analyses to a specific set of traits

292   that were relevant to understanding the implications of environmental change on community assembly [12].

293

294   **Species distribution modelling**

295   Species distribution models were calibrated over the whole western Palearctic biogeographic zone at a resolution of

296   0.5°, and then projected into the future over EU25 plus Switzerland and Norway at 10' resolution. By this, we

297   considered the whole Western Palaearctic range (including North Africa and the Middle East) to calibrate models for

298   the full extent of the niches of species[28] and to allow species that currently occur only around the margins of Europe

299   to potentially migrate into the EU25 as climate becomes suitable.

300   An ensemble of forecasts of species distributions models (SDM[45, 46]) was obtained for each of the 402 species. The

301   ensemble included projections with Generalized Additive Models, Boosting Regression Trees, Classification Tree

302   Analysis, Multiple Adaptive Regression Splines and Random Forest. Models were calibrated for the baseline period

303   using 65% random sample of the initial data and evaluated against the remaining 35% data, using the True Skill

304   Statistic (TSS[47]). This analysis was repeated 5 times, thus providing a 5-fold internal cross validation of the models

305   (*biomod* package[48] in R[49]) . The quality of the models was very high to excellent with an average AUC and TSS of

306   0.97 and 0.87 respectively (Supplementary Fig. 6), while for the least well-modelled species, the ensemble model

307   quality reached an AUC of 0.93 and a TSS of 0.7, which are traditionally considered as good predictive

308   performance[47].

309   For each species, we projected the probability of occurrence within each 10' resolution pixel under both current and

310   future conditions as a weighted sum of occurrence-probability projections made by the 5 modelling techniques run

311   over 5 sub-samples. This modest downscaling at a scale of 1:3, from models calibrated at 0.5° to 10' projections has

312   been shown well suitable at such spatial extent and resolution[50]. The weighting scheme for building ensembles was

313   proportional to the TSS statistics for each modelling technique and cross-validation (i.e. the techniques that delivered

314   the most accurate models had the highest weights). Probabilities of occurrence were further transformed into binary

315   maps using the value that maximized the TSS score as a threshold.

316

317   **Dispersal ability**

318   Not all species are expected to disperse at the same rate and distance. However, the information about natal dispersal

319   was not known for all 402 species. To estimate what could be the uncertainty associated to the non-inclusion of natal

320   dispersal, we gathered the information on natal dispersal for 74 species from Paradis et al. (1998)[51] and Barbet-

321   Massin et al. (2012)[11]. For these 74 species, we then estimated the projected change in habitat suitability accounting

322   for natal dispersal, and further compared them with the ones estimated assuming no dispersal constraints (CHS). The

323   results for these 74 species confirmed that the non-inclusion of natal dispersal into the modelling procedure for the

324   402 species should not change the outcome of the analyses (Supplementary Fig. 7). For the time considered (100

325   years), most species should be able to reach their suitable habitats in terms of climate and land cover change.

326

327   **Species sensitivity to climate and land use change**

328   Each ensemble of species projections for current and future conditions were converted into a metric of species

329   sensitivity[27]. Change in habitat suitability (CHS) measures the relative change in suitable climate and land use. It

330   corresponds to the total suitable area projected into the future under the assumption of unlimited dispersal minus the

331   total suitable area projected onto the current conditions, with the resulting quantity divided by the total suitable area

332   projected onto the current conditions. There was no relationship between CHS and the predictive performance of the

333   models (Supplementary Table 5).

334   The metric was averaged across Species x Model x Scenario x RCM combinations.

335

336   **Statistical analyses**

337   All analyses have been carried in the R environment[49] (specific functions within specific package are indicated in

338   brackets).

339

340   **Functional distance and the functional tree of bird life**

341

342   We first log-transformed and normalized body mass prior to all analyses. We used a mixed-variables coefficient of

343   distance that generalizes Gower's coefficient of distance to allow for the treatment of various types of variables when

344   calculating distances[52]. Euclidean distance was used for body mass, while the Sorensen distance[53] (S7 coefficient of

345   Gower and Legendre[54], function *dist.ktab* in *ade4*) was used for binary data types, e.g., for each sub-group of diet

346   and feeding behaviour trait. Then, we used hierarchical clustering to build the most reliable dendrogram of all

347   species in functional-trait space, employing an average agglomeration method (UPGMA, function *hclust*)[55]. The

348   functional dendrogram expressed 78% of the original distances between species (Mantel correlation between the

349   original distance matrix and the distance matrix from the dendrogram equaled 0.78, p-value < 0.001 with 9999

350   randomizations, function *Mantel* in *vegan*[56]).

351

352   **Functional uniqueness and link with species' sensitivity**

353   We adapted the Evolutionary Distinctiveness index[57], which measures the relative contributions of species to

354   phylogenetic diversity, for use in a functional context. First, for each branch of the functional dendrogram, we

355   estimated a value equal to its length divided by the number of species subtending the branch. The functional

356   uniqueness of a species is simply the sum of these values for all branches from which the species is descending, to

357   the root of the functional dendrogram (function *originality* in *ade4*[58]). We calculated the strength of the signal

358   between the functional tree and the measure of species sensitivity estimated for the range of climate and land use

359   projections. We used the robust measure proposed by Abouheif to test for serial independence to detect a functional

360   signal in species sensitivity[59] (function *abouheif.moran* in *ade4*). We tested the strength of the phylogenetic signal in

361   functional uniqueness using Pagel's lambda statistic and its associated likelihood ratio test[60, 61]. To test the link

362   between functional uniqueness and species sensitivity to climate and land use change, we calculated Pearson's

363   correlation between the functional uniqueness of species and their expected sensitivity to the range of climate and

364   land use projections.

365

366   **Species richness per group and functional diversity**

367   We estimated the species richness for each category of each functional trait per pixel. We estimated the mean

368   assemblage body mass per pixel (instead of species richness) given that body mass is a continuous variable. To

369   calculate functional diversity, we used the mean pair-wise functional distance (MFD) between all species present in a

370   pixel. This index is a classic metric in community ecology[5], represents an unbiased estimate of the variance of the

371   trait considered, and is not correlated with species richness (function *mpd* in *picante*[62]). This was calculated for all

372   traits together (e.g. Fig. 4) and also within functional groups. For the latter, we re-calculated the functional distance

373   matrix without the trait considered (e.g. diet) and calculated the MFD for all remaining traits (Fig. 3B) and for single

374   trait (e.g. feeding MFD per diet type, Fig. 3C) within pixel. We analysed the variability to regional climate models

375   for MFD for diet and showed that the results were little sensitive to this variability (Supplementary Fig. 8).

376   For the spatial distribution of MFD, we simply mapped the MFD onto the geographic space. Relative change in

377   MFD between current and future conditions was estimated as equation 1:

378    $\Delta MFD = 100 * (MFD_{t+1} - MFD_t) / MFD_t$ (1)

379

Acknowledgments

Author contribution

389 WT designed the study, carried out the statistical analyses and wrote the initial draft of the paper, SP and WT

390 performed the species distribution modelling, PBP and LZ gathered the trait information for all species, MBM

391 created the observed distribution maps, JR created Figure 4 and worked out all GIS layers, NEZ and AP generated

392 the environmental layers. All authors substantially contributed to the writing of the paper.

Conflict of interest statement

394 The authors declare no competing financial interests.

395

396

397 1. Purvis A, Agapow P, Gittleman JL, Mace GM. Nonrandom extinction and loss of evolutionary history.
398   *Science* 2000, **288:** 328-330.

399
400 2. Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ. Linking biodiversity
401   to ecosystem function: implications for conservation ecology. *Oecologia* 2000, **122:** 297-305.

402
403 3. Díaz S, Fargione J, Chapin III FS, Tilman D. Biodiversity loss threatens human well-being. *Plos Biol* 2006,
404   **4**(8)**:** e277.

405
406 4. Bellard C, Bertelsmeier C, Leadley P, Thuiller W, Courchamp F. Impacts of climate change on the future of
407   biodiversity. *Ecol Lett* 2012, **15**(4)**:** 365-377.

408
409 5. Webb CO, Ackerly DD, McPeek MA, Donoghue MJ. Phylogenies and community ecology. *Annual Review*
410   *of Ecology and Systematics* 2002, **33:** 475-505.

411
412 6. Petchey OL, Gaston KJ. Functional diversity (FD), species richness and community composition. *Ecol Lett*
413   2002, **5:** 402-411.

414
415 7. Flynn DFB, Gogol-Prokurat M, Nogeire T, Molinari N, Richers BT, Lin BB*, et al.* Loss of functional
416   diversity under land use intensification across multiple taxa. *Ecol Lett* 2009, **12:** 22-33.

417
418 8. Hector A, Bagchi R. Biodiversity and ecosystem multifunctionality. *Nature* 2007, **448**(7150)**:** 188-U186.

419
420 9. Clavel J, Julliard R, Devictor V. Worldwide decline of specialist species: toward a global functional
421   homogenization? *Front Ecol Environ* 2010, **9**(4)**:** 222-228.

422
423 10. Dullinger S, Gattringer A, Thuiller W, Moser D, Zimmermann NE, Guisan A*, et al.* Extinction debt of high-
424   mountain plants under twenty-first-century climate change. *Nat Clim Change* 2012, **2:** 619-622.

425
426 11. Barbet-Massin M, Thuiller W, Jiguet F. The fate of European breeding birds under climate, land-use and
427   dispersal scenarios. *Glob Change Biol* 2012, **18:** 881-890.

428
429 12. Wenny DG, DeVault TL, Johnson MD, Kelly D, Sekercioglu CH, Tomback DF*, et al.* The Need to
430   Quantify Ecosystem Services Provided by Birds. *Auk* 2011, **128**(1)**:** 1-14.

431
432 13. Whelan CJ, Wenny DG, Marquis RJ. Ecosystem services provided by birds. *Year in Ecology and*
433   *Conservation Biology 2008*, vol. 1134, 2008, pp 25-60.

434
435 14. Luck GW, Lavorel S, McIntyre S, Lumb K. Improving the application of vertebrate trait-based frameworks
436   to the study of ecosystem services. *Journal of Animal Ecology* 2012, **81**(5)**:** 1065-1076.

437
438 15. Sekercioglu CH. Increasing awareness of avian ecological function. *Trends Ecol Evol* 2006, **21**(8)**:** 464-471.

439

440   16.   Sekercioglu CH, Daily GC, Ehrlich PR. Ecosystem consequences of bird declines. *Proc Natl Acad Sci USA*
441   2004, **101**(52)**:** 18042-18047.

442

443   17.   Lavergne S, Mouquet N, Thuiller W, Ronce O. Biodiversity and climate change: Integrating evolutionary
444   and ecological responses of species and communities. *Annual Review of Ecology, Evolution and Systematics*
445   2010, **41:** 321-350.

446

447   18.   Van der Putten WH, Macel M, Visser ME. Predicting species distribution and abundance responses to
448   climate change: why it is essential to include biotic interactions across trophic levels. *Philos T R Soc Lon B*
449   2010, **365**(1549)**:** 2025-2034.

450

451   19.   Sekercioglu CH. Functional Extinctions of Bird Pollinators Cause Plant Declines. *Science* 2011, **331**(6020)**:**
452   1019-1020.

453

454   20.   Jiguet F, Gadot AS, Julliard R, Newson SE, Couvet D. Climate envelope, life history traits and the
455   resilience of birds facing global change. *Glob Change Biol* 2007, **13**(8)**:** 1672-1684.

456

457   21.   Loreau M, Naeem S, Inchausti P, Grime JP, Hector A, Hooper DU*, et al.* Biodiversity and ecosystem
458   functioning: current knowledge and future challenges. *Science* 2001, **294:** 804-808.

459

460   22.   Naeem S. Species redundancy and ecosystem reliability. *Conserv Biol* 1998, **12**(1)**:** 39-45.

461

462   23.   Triplett S, Luck GW, Spooner P. The importance of managing the costs and benefits of bird activity for
463   agricultural sustainability. *International Journal of Agricultural Sustainability* 2012, **10**(4)**:** 268-288.

464

465   24.   Devictor V, Clavel J, Julliard R, Lavergne S, Mouillot D, Thuiller W*, et al.* Defining and measuring
466   ecological specialization. *Journal of Applied Ecology* 2010, **47:** 15–25.

467

468   25.   Lavorel S, Garnier E. Predicting changes in community composition and ecosystem functioning from plant
469   traits: revisiting the Holy Grail. *Functional Ecology* 2002, **16**(5)**:** 545-556.

470

471   26.   Bennett PM, Owens IPF. Variation in extinction risk among birds: chance or evolutionary predisposition?
472   *Proc R Soc Lon B* 1997, **264**(1380)**:** 401-408.

473

474   27.   Thuiller W, Lavergne S, Roquet C, Boulangeat I, Araujo MB. Consequences of climate change on the Tree
475   of Life in Europe. *Nature* 2011, **470:** 531-534.

476

477   28.   Barbet-Massin M, Thuiller W, Jiguet F. How much do we overestimate local extinction rates when
478   restricting the range of occurrence data in climate suitability models? . *Ecography* 2010, **33**(5)**:** 878-886.

479

480   29.   Huntley B, Green RE, Collingham YC, Willis SG. *A climatic atlas of European breeding birds*. Lynx
481   Edicions, 2007.

482

483   30.   Buisson L, Grenouillet G, Villéger S, Canal J, Laffaille P. Toward a loss of functional diversity in stream
484   fish assemblages under climate change. *Glob Change Biol* 2013, **19**(2)**:** 387-400.

485
486   31.   Wilby A, Thomas MB. Natural enemy diversity and pest control: patterns of pest emergence with
487   agricultural intensification. *Ecol Lett* 2002, **5**(3)**:** 353-360.

488
489   32.   Civantos E, Thuiller W, Maiorano L, Guisan A, Araujo MB. Potential impacts of climate change on
490   ecosystem services in Europe: the case of pest control by vertebrates. *BioScience* 2012, **62**(7)**:** 658-666.

491
492   33.   Hagemeijer WJM, Blair MJ. *The EBCC atlas of European breeding birds, their distribution and
493   abundance*. Poyser: London, 1997.

494
495   34.   BWPi. *Birds of the Western Palearctic Interactive 2.0*. BirdGuides: Oxford, UK, 2006.

496
497   35.   Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A. Very high resolution interpolated climate surfaces
498   for global land areas. *International Journal of Climatology* 2005, **25:** 1965-1978.

499
500   36.   IPCC. *The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the
501   Intergovernmental Panel on Climate Change*. Cambridge University Press: Cambridge, UK and New York,
502   NY, USA, 2007.

503
504   37.   Nakicenovic N, Swart R (eds). *Emissions Scenarios: A Special Report of Working Group III of the
505   Intergovernmental Panel on Climate Change*. Cambridge University Press: Cambridge, 2000.

506
507   38.   Collins M, Booth BBB, Harris GR, Murphy JM, Sexton DMH, Webb MJ. Towards quantifying uncertainty
508   in transient climate change. *Climate Dynamics* 2006, **27**(2-3)**:** 127-147.

509
510   39.   Jones CG, Willen U, Ullerstig A, Hansson U. The Rossby Centre Regional Atmospheric Climate Model
511   part 1: Model climatology and performance for the present climate over Europe. *Ambio* 2004, **33**(4-5)**:** 199-
512   210.

513
514   40.   Jones CG, Wyser K, Ullerstig A, Willen U. The Rossby Centre regional atmospheric climate model part II:
515   Application to the Arctic climate. *Ambio* 2004, **33**(4-5)**:** 211-220.

516
517   41.   Meijgaard E, van Ulft LH, van de Berg WJ, Bosveld FC, van den Hurk BJJM, Lenderink G*, et al.* The
518   KNMI regional atmospheric climate model RACMO, version 2.1: KNMI, Postbus 201, 3730 AE, De Bilt,
519   The Netherlands; 2008.

520
521   42.   Dendoncker N, Bogaert P, Rounsevell M. A statistical method to downscale aggregated land use data and
522   scenarios. *Journal of Land Use Science* 2006, **1:** 63-82.

523
524   43.   Rounsevell MDA, Reginster I, Araújo MB, Carter TR, Dendoncker N, Ewert F*, et al.* A coherent set of
525   future land use change scenarios for Europe. *Agriculture, Ecosystems & Environment* 2006, **114**(1)**:** 57-68.

526

527 44. Dendoncker N, Schmit C, Rounsevell M. Exploring spatial data uncertainties in land-use change scenarios.
528   *International Journal of Geographical Information Science* 2008, **22**(9)**:** 1013-1030.

529
530 45. Araújo MB, New M. Ensemble forecasting of species distributions. *Trends Ecol Evol* 2007, **22:** 42-47.

531
532 46. Marmion M, Hjort J, Thuiller W, Luoto M. Statistical consensus methods for improving predictive
533   geomorphology maps. *Computers and Geosciences* 2009, **35:** 615– 625.

534
535 47. Allouche O, Tsoar A, Kadmon R. Assessing the accuracy of species distribution models: prevalence, kappa
536   and the true skill statistic (TSS). *Journal of Applied Ecology* 2006, **43:** 1223-1232.

537
538 48. Thuiller W, Lafourcade B, Engler R, Araujo MB. BIOMOD – A platform for ensemble forecasting of
539   species distributions. *Ecography* 2009, **32:** 369-373.

540
541 49. R Development Core Team (ed). *R: A Language and Environment for Statistical Computing.* R Foundation
542   for Statistical Computing: Vienna, Austria, 2013.

543
544 50. Araújo MB, Thuiller W, Williams PH, Reginster I. Downscaling European species atlas distributions to a
545   finer resolution: implications for conservation planning. *Global Ecology and Biogeography* 2005, **14:** 17-
546   30.

547
548 51. Paradis E, Baillie S, Sutherland WJ, Gregory RD. Patterns of natal and breeding dispersal in birds. *Journal
549   of Animal Ecology* 1998, **67:** 518-536.

550
551 52. Pavoine S, Vallet J, Dufour AB, Gachet S, Daniel H. On the challenge of treating various types of variables:
552   application for improving the measurement of functional diversity. *Oikos* 2009, **118**(3)**:** 391-402.

553
554 53. Dray S, Chessel D, Thioulouse J. Co-inertia analysis and the linking of ecological data tables. *Ecology*
555   2003, **84**(11)**:** 3078–3089.

556
557 54. Gower JC, Legendre P. Metric and Euclidean properties of dissimilarity coefficients. *Journal of
558   Classification* 1986, **3:** 5-48.

559
560 55. Mouchet M, Guilhaumon F, Villeger S, Mason NWH, Tomasini JA, Mouillot D. Towards a consensus for
561   calculating dendrogram-based functional diversity indices. *Oikos* 2008, **117**(5)**:** 794-800.

562
563 56. Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB*, et al.* vegan: Community Ecology
564   Package. R package version 2.0-7. http://CRANR-projectorg/package=vegan 2013.

565
566 57. Isaac NJB, Turvey ST, Collen B, Waterman C, Baillie JEM. Mammals on the EDGE: conservation
567   priorities based on threat and phylogeny. *PloS One* 2007, **2:** e296.

568
569 58. Chessel D, Dufour A-B, Thioulouse J. The ade4 package-I - one-table methods. *R News* 2004, **4:** 5-10.

570
571   59.   Abouheif E. A method for testing the assumption of phylogenetic independence in comparative data. *Evol*
572   *Ecol Res* 1999, **1:** 895–909.

573
574   60.   Münkemüller T, Lavergne S, Bzeznik B, Dray S, Jombart T, Schiffers K*, et al.* How to measure and test
575   phylogenetic signal. *Methods in Ecology and Evolution* 2012, **3**(4)**:** 743-756.

576
577   61.   Pagel M. Inferring the historical patterns of biological evolution. *Nature* 1999, **401:** 877-884.

578
579   62.   Kembel SW, Cowan PD, Helmus MR, Cornwell WK, Morlon H, Ackerly DD*, et al.* Picante: R tools for
580   integrating phylogenies and ecology. *Bioinformatics* 2010, **26:** 1463-1464.

581
582   63.   Roquet C, Thuiller W, Lavergne S. Building megaphylogenies for macroecology: taking up the challenge.
583   *Ecography* 2013, **36**(1)**:** 13-26.

584

585

586

Figure captions

Figure 1 – Distribution of changes in suitable habitats and loss in currently suitable habitats. Histograms representing the projected relative change in suitable habitats (a) and loss in currently suitable habitats (b) (in percentage) under the A1b emission scenarios by 2080, using the RCA30 regional climate model driven by the ECHAM5 global circulation model and ensembles of five species distribution models. The Y-axis represents the number of species for each class of projected change in suitable habitats. In (a), most of species are projected to experience between -2% and +5% of change in suitable habitats (with negative values standing for a loss in suitable habitat while positive values are a gain).

Figure 2. Link between the European functional tree of bird life and species sensitivity to climate change. Species sensitivity measured as change in suitable habitat and mapped onto the functional tree of the avifauna for one emission scenario (A1B) by 2080, using the RCA30 regional climate model driven by the ECHAM5 global circulation model and ensembles of five species distribution models. Species sensitivity was log transformed (log(CHS-1-min(CHS))) for this analysis.

Figure 3. Functional uniqueness of the European avifauna mapped onto the phylogenetic tree [63]. There was no significant phylogenetic signal of functional uniqueness (Pagel's lambda likelihood ratio test p>0.05[61]). Functionally unique species were not more closely related to each other than if sampled randomly along the phylogeny.

Figure 4. Species richness and functional diversity per diet type across Europe under current and three future climate and land cover scenarios. Each bar of the boxplot (sample size = 402 species) represents the median, first and third quartiles (defining the filled box) and minimum and maximum values (error bars excluding outliers) of the distributions of: species richness (a), MFD (mean pair-wise functional distance) considering all remaining traits except diet (b), MFD considering feeding behaviour only (c), and MFD considering feeding location only (d) mapped over Europe. The Y-axis represents the number of species (a) and the MFD values per functional group (b-c-d). Colour code is indicated in panel a. Species number per feeding behaviour is indicated in panel d. Only projections for climatic scenarios by 2080 and modelled under the RCA30 regional climate model are represented. The influence of regional climate models is represented in Supplementary Fig. 8.
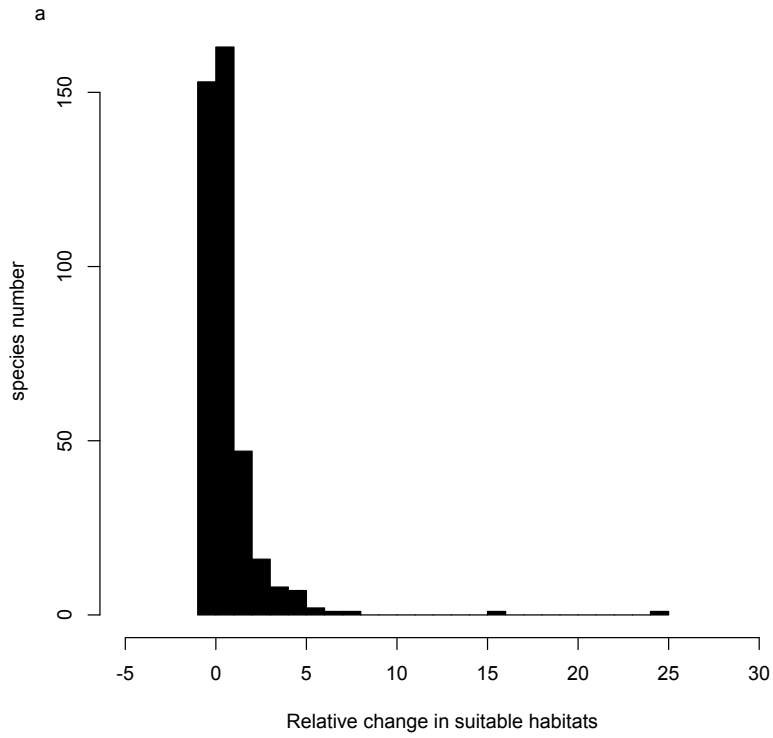
613

Figure 5. Species richness and functional diversity per feeding behaviour type across Europe under current and three future climate and land cover scenarios. Each bar of the boxplot (sample size = 402 species) represents the median, first and third quartiles (defining the filled box) and minimum and maximum values (error bars excluding outliers) of the distributions of: species richness (a), MFD (mean pair-wise functional distance) considering all remaining traits except feeding behaviour (b), MFD considering diet only (c), and MFD considering feeding location only (d) mapped over Europe. Y-axis represents the number of species (a) and the MFD values per functional group (b-c-d). Colour code is indicated in panel a. Species number per feeding behaviour is indicated in panel d. Only projections for climatic scenarios by 2080 and modelled under the RCA30 regional climate model are represented. Abbreviations for feeding behaviour type are: dig=digging, Gle=foliage gleaning, Graz=grazing, Turn=overturning, Pick= picking/pecking/stabbing, Poun=pouncing, Sally=sally. The influence of regional climate models is represented in Supplementary Fig. 8
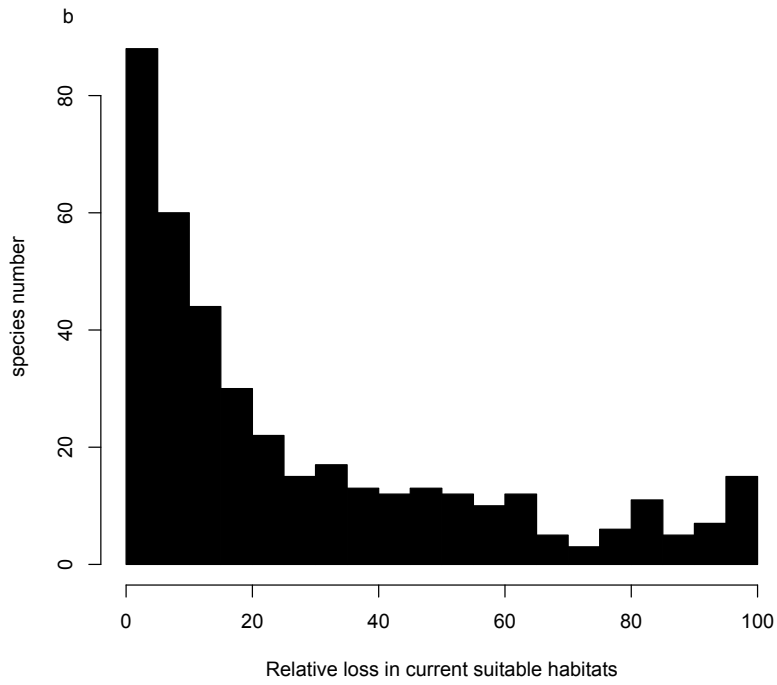
625

Figure 6. Mean pair-wise functional distance and its projected changes across Europe under current and future conditions. Large panels represent the per-pixel functional diversity of European avifauna. Small panels show the relative change in functional diversity between future and current conditions.
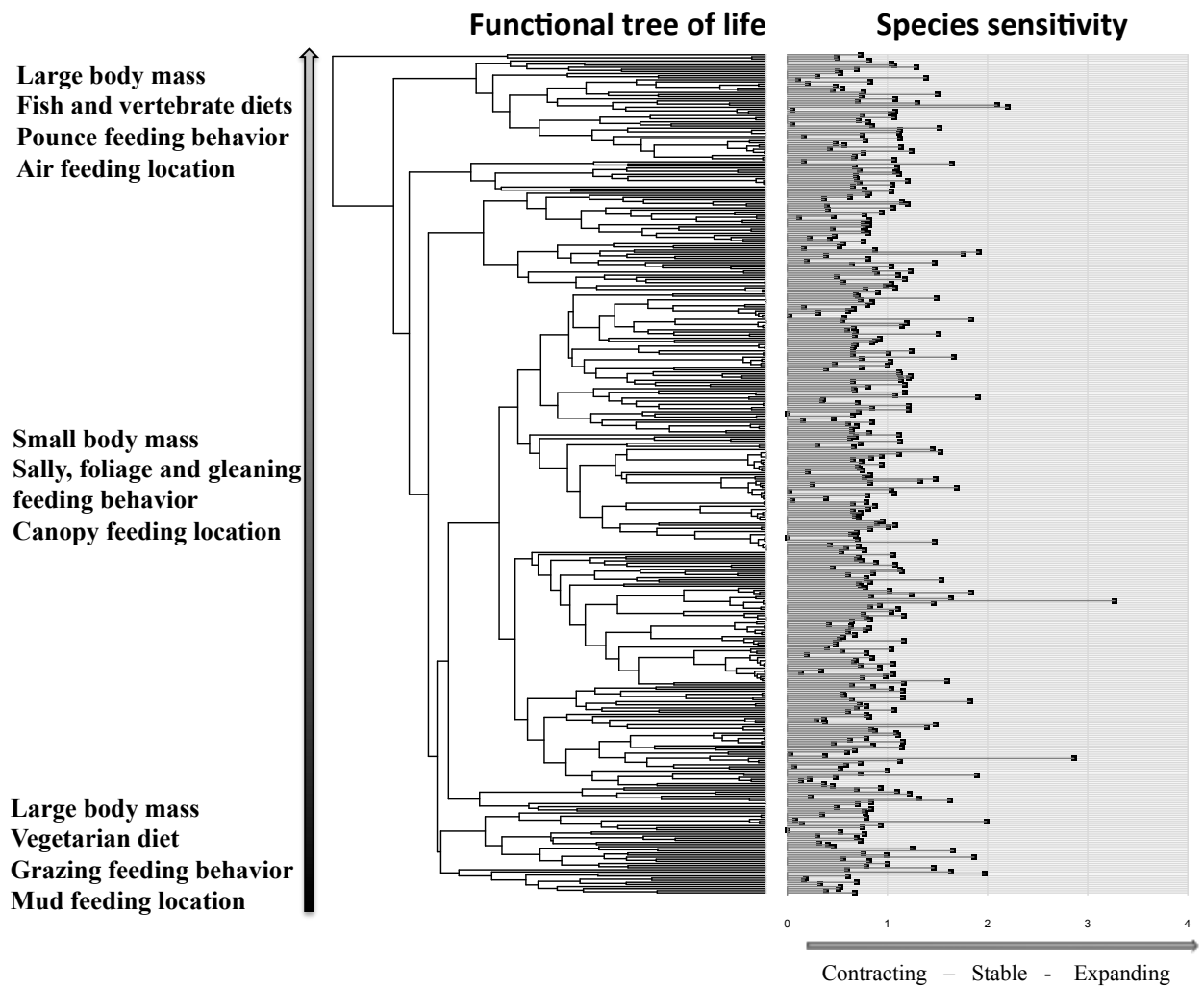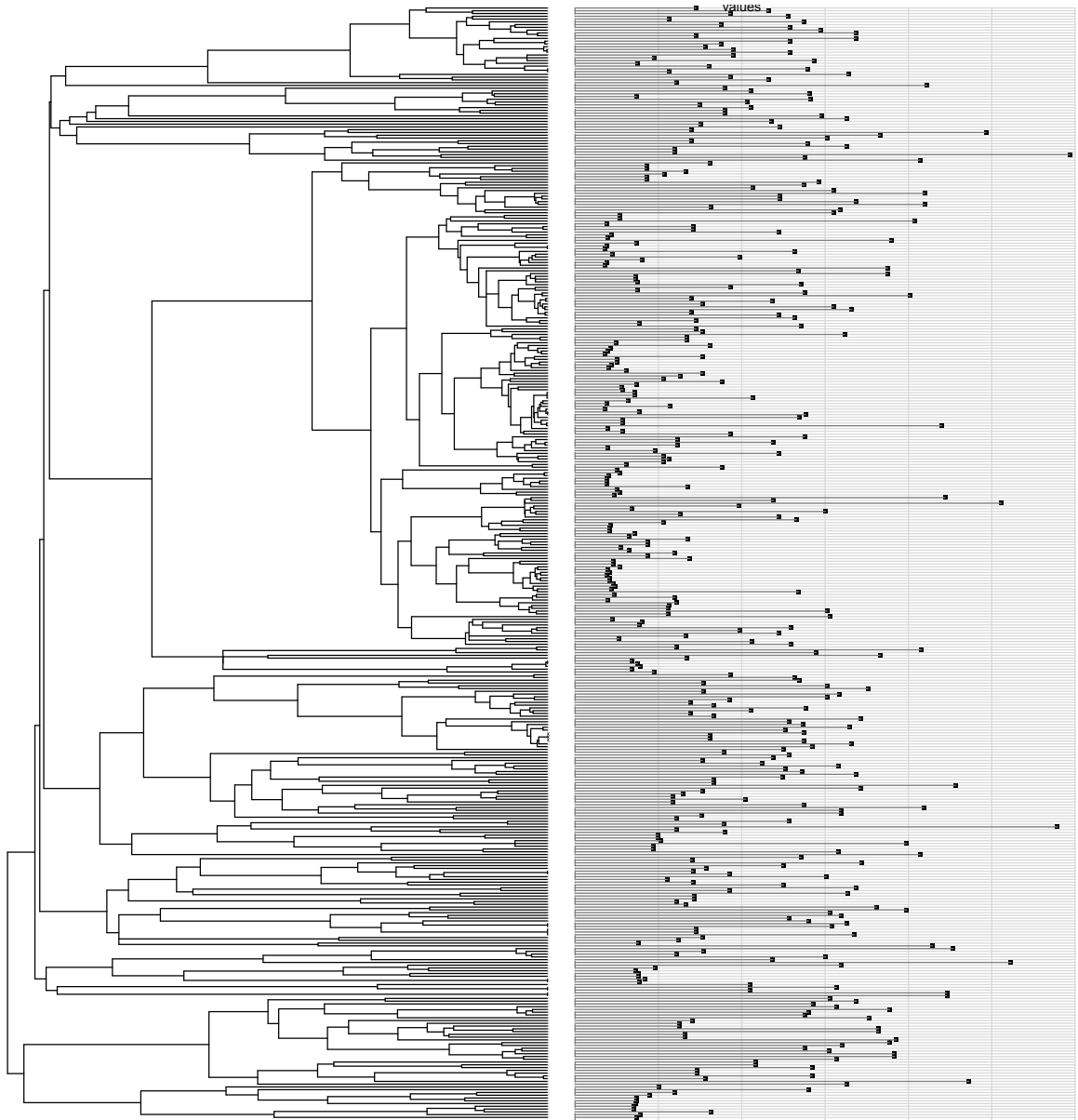
629

630

631

632   Figure 1

633

634

Functional tree of life   **Species sensitivity**

Large body mass
Fish and vertebrate diets
Pounce feeding behavior
Air feeding location

Small body mass
Sally, foliage and gleaning
feeding behavior
Canopy feeding location

Large body mass
Vegetarian diet
Grazing feeding behavior
Mud feeding location

0   1   2   3   4

Contracting – Stable - Expanding

635

636   Figure 2

637

26

638

Figure 3

640

Species richness per diet type

a

Mean functional distance per diet type

b

Mean functional distance in feeding behavior per diet type

c

Mean functional distance in feeding location per diet type

d

641

642   Figure 4

643

Species richness per feeding behavior type

a

Mean functional distance per feeding behavior type

b

Mean functional distance in diet per feeding behavior type

c

Mean functional distance in feeding location per feeding behavior type

d

644

645

646   Figure 5

Current conditions

A1b climatic scenario
GRAS land use scenario

A2 climatic scenario
BAMBU land use scenario

B1 climatic scenario
SEDG land use scenario

Mean functional distance
0.52   0.62

Change in mean functional distance (%)
-7   10

647

648

649

650   Figure 6

651

652