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9 **The extent and predictability of the biodiversity-carbon correlation**
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13 MDM and OV designed the study; MDM performed the research; all authors discussed the
14 results and contributed to the writing.

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17 **Data accessibility statement**
18 All the data used in this study derive from published sources, cited in the Methods section.

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58 **Abstract**

59 Protecting biomass carbon stocks to mitigate climate change has direct implications for

60 biodiversity conservation. Yet, evidence that a positive association exists between carbon

61 density and species richness is contrasting. Here we test how this association varies i) across

62 spatial extents, and ii) as a function of how strongly carbon and species richness depend on

63 environmental variables. We found the correlation weakens when moving from larger

64 extents, e.g. realms, to narrower extents, e.g. ecoregions. For ecoregions, a positive

65 correlation emerges when both species richness and carbon density vary as functions of the

66 same environmental variables (climate, soil, elevation). In 20% of tropical ecoregions there

67 are opportunities to pursue carbon conservation with direct biodiversity co-benefits, while

68 other ecoregions require careful planning for both species and carbon to avoid potentially

69 perverse outcomes. The broad assumption of a linear relationship between carbon and

70 biodiversity can lead to undesired outcomes.

Introduction

The two greatest threats to life on Earth are anthropogenic climate change (Thomas *et al.* 2004; Scheffers *et al.* 2016) and land use change (Newbold *et al.* 2016; Venter *et al.* 2016), with ecological impacts spanning all scales of biological organisation, from genes to ecosystems (Scheffers *et al.* 2016). The interaction between these two threats and the management actions taken to ameliorate them is of primary conservation relevance, with rapid climate change expected to amplify the effect of land use change (Mantyka-Pringle *et al.* 2015; Visconti *et al.* 2016).

The establishment of protected areas in biologically diverse locations is the main strategy to minimize the impacts on biodiversity from land use change (Watson *et al.* 2014), while action to mitigate climate change focuses on the protection and restoration of high vegetative carbon stocks (Venter & Koh 2012). Protection of natural habitats that reduces land clearing can serve both the purpose of preserving carbon stocks and protecting ecosystems. This means that different environmental policy goals, such as climate change mitigation and biodiversity conservation, can be achieved simultaneously with the same investment (Di Marco *et al.* 2016). A much-debated example of carbon conservation schemes is the UN mechanism for Reducing Emissions from Deforestation and forest Degradation (REDD+), which is primarily aimed at reducing global greenhouse gas emissions but can have also direct implications for biodiversity conservation (Venter *et al.* 2009a; Thomas *et al.* 2013). Understanding the relationship between carbon and biodiversity, and their potential conservation synergies, is fundamental for achieving both goals under this scheme.

A dual benefit is expected when financial resources are mobilised towards the conservation of areas with high carbon and biodiversity content that are at high risk of deforestation (Venter *et al.* 2009a), but preventive carbon credits can also benefit highly forested countries with low current deforestation rates (Da Fonseca *et al.* 2007). However,

4

96   reducing deforestation in a carbon-rich area might also have negative implications for

97   biodiversity, if the deforestation is reallocated to areas with lower carbon but higher

98   biodiversity content (a phenomenon known as 'leakage'; Gan & Mccarl 2007). At the same

99   time, actions to prevent climate change have also raised concerns for biodiversity

100   conservation as they can result in the modification of natural habitats, such as biofuel

101   plantations replacing natural forests (Danielsen *et al.* 2009) or afforestation of areas rich in

102   non-forest biodiversity (Brockerhoff *et al.* 2008; Lindenmayer *et al.* 2012). Such perverse

103   outcomes at most likely when biodiversity and carbon density are weakly or even negatively

104   correlated (Paoli *et al.* 2010).

105   To date, the evidence of a positive correlation between biodiversity and carbon

106   density is mixed, with different studies reporting contrasting findings. Some authors have

107   found a positive correlation between the global variation of terrestrial carbon and the

108   variation of vertebrate species richness (Strassburg *et al.* 2010; Buchanan *et al.* 2011;

109   Siikamäki & Newbold 2012). Others have found a weak or moderate correlation in national

110   and sub-national analyses, for example using threatened mammals in Borneo (Venter *et al.*

111   2009b), terrestrial vertebrates in Colombia (Armenteras *et al.* 2015) and Costa-Rica

112   (Locatelli *et al.* 2013), and tree species in central Africa (Day *et al.* 2013). In contrast, several

113   analyses have revealed limited, or even negative, correspondence between species richness

114   and carbon in UK (Anderson *et al.* 2009), Indonesia (Paoli *et al.* 2010; Murray *et al.* 2015),

115   and Colombia at a sub-national extents (Armenteras *et al.* 2015). This was also observed

116   when analysing fine grain (plot-level) carbon data in tropical forests around the globe, with

117   no correlation found with vertebrate (Beaudrot *et al.* 2016) or plant (Sullivan *et al.* 2016)

118   biodiversity.

119   Contrasting evidence on the correlation between biodiversity and carbon may reflect

120   the diversity of studies in terms of geographic location (including the natural variation of the

121 study areas), taxonomic groups analysed, and carbon measured (e.g. above- and/or below-

122 ground). At a global extent, wet tropical areas tend to be richer in biodiversity than temperate

123 areas (Gaston 2000), and also contain high stored carbon (Ruesch & Gibbs 2008). However,

124 at more local extents the potential for co-benefits can be much more limited, especially in

125 silvicultural and agroforestry landscapes in the tropics, where altering the composition of

126 natural ecosystems can result in relatively high carbon sequestration with a substantial

127 reduction of species diversity (Putz & Redford 2009; Kessler *et al.* 2012; Lindenmayer *et al.*

128 2012).

129   Overall, a pattern emerges from the literature, with global-extent analyses being more

130 likely to reveal a positive correlation (Strassburg *et al.* 2010) than regional- or local-extent

131 analyses (Buchanan *et al.* 2011; Armenteras *et al.* 2015). This may be related to the fact that

132 the spatial variation in the environmental drivers of biodiversity and carbon, such as climate,

133 is higher at larger spatial extents (Field *et al.* 2009). In fact, at the global extent, spatial

134 variation in species richness (Kreft & Jetz 2007; Belmaker & Jetz 2015), primary

135 productivity (Rosenzweig 1968; Cramer *et al.* 1999), and soil carbon (Cao & Woodward

136 1998), are all strongly correlated with climate. At regional or local extents the role of other

137 variables in driving these ecosystem properties can become predominant, species richness for

138 example may depend upon factors like topographic heterogeneity (Kerr & Packer 1997), soil

139 properties (Stevens *et al.* 2004), or Quaternary glacial history (Normand *et al.* 2011).

140 Regional carbon density may also deviate from that expected due to climate regimes, for

141 example when wildland fire disturbance is prevalent (Midgley *et al.* 2010). At narrower

142 extents, it is also expected that both carbon density and species richness show less variation

143 than at larger extents, and this in turn influences their correlation. The choice of an

144 appropriate spatial extent for analysing this relationship is thus of particular relevance to

145 making management and policy decisions (Blackburn & Gaston 2002; Rahbek 2005), with

146 the potential for contrasting findings to emerge at different extents (Armenteras *et al.* 2015).

147   Here we analyse how the correlation between species richness, one of the most

148 investigated measures of biodiversity (Field *et al.* 2009), and carbon density varies from

149 global to local extents, and what influences the correlation locally. We adopt the

150 biogeographical subdivision of the world produced by Olson and colleagues (2001) to

151 measure the correlation between carbon density and species richness among ecoregions,

152 biomes, realms, and the globe. Since we were specifically interested in the role of spatial

153 extent (i.e. the size of the study region; (Blackburn & Gaston 2002)), we employed a fixed

154 grain size in our analysis, after performing a sensitivity test (see also (Belmaker & Jetz 2011)

155 for a comprehensive analysis of grain size). We then use ecoregions, the smallest extent in

156 our analysis, to test the predictability of the biodiversity-carbon correlation. We hypothesize

157 that the correlation between biodiversity and carbon depends on (i) the spatial extent

158 considered, decreasing in strength when moving from a global to an ecoregional extent, and

159 (ii) the predictability of both species richness and carbon density from a suite of

160 environmental variables.

161

162

163 **Methods**

164 **Carbon and biodiversity data**

165 We represented carbon density (Fig. 1a) using a 1km map of the above-ground vegetation

166 biomass in tropical and subtropical regions worldwide (Avitabile *et al.* 2016). This is an up-

167 to-date pantropical map that combines two comprehensive recent estimates of carbon density

168 (Saatchi *et al.* 2011; Baccini *et al.* 2012). The two estimates of carbon density were built

169   using a similar methodology – based on a combination of Modis and LiDAR satellite images

170   – but adopted different calibration data, resulting in some significant differences. The

171   combined pantropical map resolves these inconsistencies using a fusion model calibrated on a

172   reference carbon dataset. We tested the sensitivity of our results to the carbon measure

173   adopted, by using a different 1km map (Fig. S1) representing the above- and below-ground

174   vegetation biomass for tropical and temperate areas of the entire globe (Ruesch & Gibbs

175   2008). This map, already used in previous studies (Strassburg *et al.* 2010), applied the

176   International Panel on Climate Change Tier-1 method (IPCC 2006) for estimating carbon

177   stocks of vegetation types in different ecoregions. Both carbon maps were resampled to a

178   resolution of 10 km using average pixel values (see below for a description of our grain size

179   choice).

180   We used species richness as our biodiversity metric for each grid cell. We defined

181   species richness maps (Fig. 1b) from the geographic ranges of terrestrial amphibians (n =

182   6,407), birds (n=10,424), and mammals (n=5,312) (Birdlife International & NatureServe

183   2015; IUCN 2016). We rasterised species ranges at a resolution of 10 km, which represents a

184   compromise between computational tractability and data accuracy (Di Marco *et al.* 2017).

185   This resolution is in line with that adopted in previous national-extent analyses using similar

186   data (Armenteras *et al.* 2015), but is finer than the resolution previously adopted for global-

187   extent analyses (Strassburg *et al.* 2010). Employing a 10 km resolution, when measuring

188   species richness from IUCN range maps, can lead to overestimation of richness due to

189   commission errors in the maps, i.e. areas included as part of the geographic range of a species

190   even if the species is actually absent (Hurlbert & Jetz 2007; Jetz *et al.* 2008). Employing

191   coarser analytical resolutions can reduce the effect of commission errors, but also reduces

192   statistical power by reducing the number of available grid cells. Coarsening the resolution

193   also leads to more area having to be selected in spatial prioritisation analyses, making the

194 selection less cost-efficient without significantly altering the overall results (Montesino

195 Pouzols *et al.* 2014; Di Marco *et al.* 2017). To measure the sensitivity of our results to the

196 spatial resolution adopted, we repeated our test of the first hypothesis after changing the

197 resolution from 10 km to 100 km. In this case we used the global carbon map (Ruesch &

198 Gibbs 2008), as opposed to the pantropical one, to include as many ecoregions and biomes as

199 possible (using a cut-off rule of at least 10 grid cells each).

200

201 **Testing hypothesis 1: the correlation between species richness and carbon density**

202 **deteriorates when spatial extent decreases**

203 We used the hierarchical subdivisions of the world produced by Olson and colleagues (2001)

204 – globe, realms, biomes within realms, and ecoregions – to test the correlation between

205 species richness and carbon density at different spatial extents. We estimated the correlation

206 between carbon and species richness across all grid cells in each analytical region, using the

207 Spearman's rank correlation coefficient (r_s; Strassburg *et al.* 2010; Armenteras *et al.* 2015).

208 We first calculated the correlation value at a global extent, and then calculated the mean

209 correlation value, and 95% credible interval, at each geographic extent (realms, biomes, and

210 ecoregions). We tested whether the correlation values observed at a given biogeographical

211 extent were significantly lower than the values observed at broader extents (one sided t-test).

212 We calculated these correlations both for total species richness, aggregated across the three

213 vertebrate classes, and for the species richness in individual classes.

214   We verified whether our estimates of the species-carbon correlation were influenced

215 by the presence of human-modified environments, where the natural distribution of both

216 species and carbon is expected to be substantially altered. To do this, we repeated our

217 analyses after excluding areas of high human pressure, as identified by values of Human

218 Footprint of ≥ 4 (in a 0-50 range; Venter *et al.* 2016; Watson *et al.* 2016). We also verified

219 whether our results were influenced by the coarse distribution data used in our analyses,

220 repeating the analyses for mammals using habitat suitability models available from Rondinini

221 *et al.* (2011). These models derive from a systematic classification of the species' habitat

222 preferences reported in the IUCN Red List, and represent refined species distribution that

223 exclude areas of unsuitable habitat from each species' range. Using these models we were

224 also able to identify ecoregions where the use of IUCN species ranges lead to an

225 overestimation of species richness (Rondinini *et al.* 2011), thereby generating uncertainty in

226 the estimation of species-carbon correlation. Finally, we repeated our analysis using only

227 threatened species, as classified in the IUCN Red List, since these are the species of highest

228 immediate conservation concern.

229   We excluded from the analyses ecoregions with an area smaller than 5,000 km^2,

230 which have low statistical power (Watson *et al.* 2016). We also excluded ecoregions in which

231 carbon data were available for less than 50% of their area.

232

233 **Testing hypothesis 2: the correlation between species richness and carbon density**

234 **depends on how strongly each is related to environmental variables**

235

236 **Modelling carbon density and species richness**

237 We hypothesized that the strength of the species richness-carbon density correlation is a

238 function of how strongly each is related to environmental variables. We used individual

239 ecoregions as our analytical units, because these represented the finest biogeographical extent

240 in our hierarchal analyses. We ran two separate models within each ecoregion, one relating

241 carbon density to environmental variables, and one relating species richness to those

242   variables. We retained all areas in this analysis, but tested the role of disturbance factors in

243   altering the species-carbon correlation in ecoregions (see next section). The main focus of our

244   work is to identify general patterns and drivers of the species richness-carbon density

245   correlation, rather than testing several alternative hypotheses behind the distribution of the

246   two variables. We thus employed relatively simple, and consistent, model structures to

247   predict both species richness and carbon density as functions of climate, soil characteristics,

248   and altitude.

249   Following previous approaches (Iwamura *et al.* 2013), we selected six bioclimatic

250   variables from the WorldClim dataset (Hijmans *et al.* 2005) to represent ecoregions' climatic

251   profiles: annual mean temperature, mean diurnal temperature range, temperature annual

252   range, annual precipitation, precipitation seasonality, precipitation of the driest quarter. We

253   also included potential evapotranspiration (Trabucco & Zomer 2009). In order to prevent

254   potential collinearity issues among the bioclimatic variables, we ran a principal component

255   analysis on the variables and extracted the two principal axes (representing 79% of the

256   variance). We also selected seven descriptors of soil characteristics (Global Soil Data Task

257   Group 2000): bulk density, field capacity, profile available water capacity, thermal capacity,

258   total nitrogen density, wilting point. Similar to climate data, we ran a principal component

259   analysis on the soil variables (Sullivan *et al.* 2016) and used the two principal axes as

260   predictors (representing 77% of the variance). In addition to climatic and soil variables, we

261   also included elevation above sea level (USGS 2006) as an environmental predictor.

262   In order to account for spatial autocorrelation in model residuals, we used spatial

263   simultaneous autoregressive error models (SAR; Kissling & Carl 2007). For each ecoregion

264   we selected the neighbourhood distance resulting in the lowest AIC value for the SAR

265   models, testing carbon models and species richness models separately. The tested distances

266   (15, 50, 100 km) span the magnitude of values found to be significant in other similar studies

267 (Tognelli & Kelt 2004; Kissling & Carl 2008). We measured the variance explained by the

268 environmental variables in each SAR model as the square of the correlation between

269 observed response (either carbon or species richness) and predicted response. Since we were

270 interested in the relative contribution of environmental characteristics, we only considered the

271 proportion of variance explained by the models' variables and excluded the portion of

272 variance explained by the spatial autocorrelation (Faurby & Svenning 2015; Santini et al.

273 2017). The explained variance measured that way is typically lower than the variance

274 explained by the full model, and we report both values for comparison.

275

276 **Determining the drivers of the correlation between species richness and carbon density**

277 For each ecoregion, we coupled the outcome of environmental models (their R^2 values

278 excluding the contribution of spatial autocorrelation) with the following variables: biome and

279 realm where the ecoregion is found, area of the ecoregion, fractal dimension of the ecoregion

280 (e.g. to account for different shapes between coastal vs inland ecoregions), standard deviation

281 of carbon density and species richness within the ecoregion. Accounting for standard

282 deviation is necessary to control for the effect that natural variation in species richness and

283 carbon have in determining high or low correlation between the two. We also accounted for

284 three disturbance factors in our models. The first factor is the proportion of the ecoregion

285 surface where Human Footprint is ≥ 4 (on a 0-50 range), which is considered a value of

286 significant human pressure (Venter *et al.* 2016; Watson *et al.* 2016). The second factor is the

287 average year in which the first human alteration of land use in the ecoregion was registered,

288 as derived from the KK10 model of historical land-use intensity, spanning 6,000 BC to 2,000

289 AD (Ellis et al., 2013). The third factor is wildland fire, which plays a key role in shaping

290 carbon density and biodiversity in some ecosystem (Midgley *et al.* 2010); we measured fire

291   extent as the average area burnt per year (over the period 1996-2016) using the GFED4

292   dataset (Giglio *et al.* 2013).

293   We ran a random forest regression model (Breiman 2001) to identify the most

294   important predictors of the spatial variation in the species richness-carbon correlation among

295   ecoregions, as a function of the above-listed variables (R^2 of environmental models, biome

296   and realm, size and fractal dimension of the ecoregion, SD of species richness and carbon,

297   disturbance). We then used partial dependence plots to represent the marginal effect of each

298   numerical variable on the correlation between species richness and carbon. We also repeated

299   the analyses within individual realms to represent the relative contribution of fire regimes in

300   different systems.

301   All analyses were run using freely available software. Spatial data preparation was

302   done in GrassGIS (GRASS Development Team 2016). Statistical analyses were done in R (R

303   Core Team 2015), using the packages 'spdep'(Bivand & Piras 2015), 'randomForest' (Liaw

304   & Wiener 2002), and 'party' (Strobl *et al.* 2009).

305

306

307   **Results**

308   **Testing hypothesis 1: the correlation between species richness and carbon density**

309   **deteriorates when spatial extent decreases**

310   When using the pan-tropical above-ground carbon map, we identified 437 ecoregions with a

311   total area size of at least 5,000 km^2 and >50% of their area covered by carbon data. We found

312   a moderate positive correlation between vertebrate species richness and carbon density at the

313   global extent ($r_s = 0.48$), and a slightly higher mean correlation at the extent of realms (mean

314    $r_s = 0.55$, sd = 0.26). The correlation was much weaker within biomes (mean $r_s = 0.31$, sd =

315   0.27) and even more so within ecoregions (mean r_s = 0.22, sd = 0.30) (Fig. 2a). With the

316   exception of `realms *vs* the globe`, the correlation values observed at a given biogeographical

317   extent were always lower than those observed at larger extents with a significance level of

318   0.05 or below (Table S1). This exception is removed when excluding areas with high human

319   pressure from the analysis (Table S2), and when looking at the global distribution of above-

320   and below-ground carbon (Table S3).

321   We plotted the values of the correlation in each tropical and sub-tropical ecoregion to

322   show areas where investments in carbon conservation are most likely to deliver biodiversity

323   co-benefits (Fig. 3). The map shows high variation in correlation values among ecoregions,

324   from very negative (r_s = -0.64) to very positive (r_s = 0.84). We observed high correlation

325   values in Madagascar, continental Southeast Asia, northern and eastern Australia, and part of

326   South America.

327   Similar to the all-species analysis, the correlation between species richness and carbon

328   become on average weaker from global to narrower extents when looking at individual

329   vertebrate classes (Fig. 2b-d). This pattern was qualitatively confirmed, and was even

330   stronger, when repeating the analyses only on areas not affected by high levels of human

331   pressure (Fig. S2). Our sensitivity testing on resolution also showed consistent results when

332   employing a 100 km grid instead of 10 km (Fig. S3), but in this case half of the ecoregions

333   were removed from analyses due to having fewer than 10 grid cells. When using habitat

334   suitability models to represent the distribution of terrestrial mammal species, we obtained

335   almost identical correlations as when we used IUCN range maps (Fig. S4). We were also able

336   to identify areas where the use of IUCN maps could lead to potential uncertainty in our

337   spatial results (Fig S5). We found most ecoregions (>80%) had a very similar level of species

338   richness when using habitat suitability models or IUCN ranges (average similarity of 90% or

339   more) but there were exceptions, especially in central Asia, where the species richness

340   measured from habitat models represented only 60% of the richness measured from IUCN

341   ranges. In those regions, the interpretation of our spatial results requires caution. Finally,

342   when only considering threatened species the correlation with carbon density was generally

343   lower than when all species were considered (Fig. S6).

344   These results overall provide support for our first hypothesis that the biodiversity-

345   carbon correlation is on average higher at broad spatial extent and lower at smaller extents,

346   and demonstrate the finding is robust to data uncertainty and the analytical settings.

347

348   **Testing hypothesis 2: the correlation between species richness and carbon density**

349   **depends on how strongly each is related to environmental variables**

350

351   **Modelling carbon density and species richness**

352   We tested the ability of environmental variables to account for the spatial variation of

353   both carbon density and species richness within each ecoregion. The performance of the two

354   sets of SAR models was quite variable among ecoregions, with a strong effect of spatial

355   autocorrelation, especially for species richness (Fig. 4). The overall performance of species

356   richness models (mean R^2 = 0.92, sd R^2 = 0.13) was higher than carbon models (mean R^2 =

357   0.72, sd R^2 = 0.15). However, this was not the case when only considering the contribution of

358   environmental variables to the models (excluding the spatial autocorrelation component), with

359   both sets of models having similar performances (species richness models: mean R^2 = 0.29, sd

360   R^2 = 0.25; carbon models: mean R^2 = 0.27, sd R^2 = 0.21).

361

Determining the drivers of the correlation between species richness and carbon density

The most important predictors of the correlation between species richness and carbon density was the predictability of carbon from environmental variables (Fig. 5). Other important predictors were the standard deviation of species richness, the predictability of species richness from environmental variables, and the average year of first human land use in the ecoregion. We represented the marginal effect of each predictor on the species-carbon correlation using partial dependence plots (Fig. S7), and found that higher correlation values were observed with higher performance of the environmental prediction models, higher SD of carbon and species richness, and higher levels of disturbance (human impact, and fire extent). We represented the relative contribution of fire regimes in different realms, and found the species-carbon correlation in the Afrotropics and the Neotropics was negatively associated with high fire extents, while Australasia had a positive association and the Indomalay region had high correlation observed at both low and high levels of fire extents (Fig. S8). Finally, a bivariate plot showed that that the species-carbon correlation value was particularly high in those ecoregions where both carbon and species richness had strong relationships with environmental variables (Fig. 6).

These results are overall consistent with our second hypothesis that the correlation between species richness and carbon density is higher in those ecoregions where both variables can be successfully predicted from environmental conditions (climate, soil, altitude).

Discussion

Years of debate on whether it is possible simultaneously to conserve biodiversity and stored carbon (Venter *et al.* 2009a; Gardner *et al.* 2012; Thomas *et al.* 2013; Armenteras *et al.* 2015)

386   have failed to give an unambiguous answer. Yet this question has significant practical

387   implications for carbon policies and site-based conservation actions. Here we provide a

388   comprehensive multi-extent analysis of where a positive correlation is most likely to occur,

389   and discuss two general findings. First, we found the correlation is lower when moving from

390   a larger to a narrower extent (e.g. global/realms to biomes/ecoregions). This result was robust

391   to variations in the group of species analysed, the use of refined species distributions, the

392   removal of human modified areas, and the analytical resolution employed, demonstrating the

393   general validity of the finding. This is consistent with previous findings that the association

394   between species richness and environmental variables is weaker in studies performed over

395   smaller scales, i.e. small extents and small grain sizes (Field *et al.* 2009; Belmaker & Jetz

396   2011). Second, we found a positive correlation is more likely in geographic domains in which

397   both species richness and carbon density vary as predictable functions of environment

398   characteristics. We showed that this is not simply related to the natural variability in species

399   richness and carbon density. When controlling for standard deviation in carbon and species

400   richness, and for disturbance factors operating in each ecoregion, we still found the species-

401   carbon correlation was positively associated with the predictability of the two variables from

402   environmental characteristics. In fact, the ability of environmental models to predict carbon

403   density was the most important driver of the species-carbon correlation.

404   We found high heterogeneity in the species richness-carbon correlation among

405   ecoregions, but showed that there are still opportunities to pursue local carbon conservation

406   with high biodiversity co-benefits. In tropical and subtropical areas, 20% of ecoregions have

407   a high correlation value ($r_s \geq 0.5$), while 34% have very low or even negative values ($r_s \leq$

408   0.1). This means that it is important to be strategic in planning carbon and biodiversity

409   investments. Efforts to protect carbon will likely deliver direct and important biodiversity

410   benefits in ecoregions with high positive correlation values. However this focus is not a

411   panacea, and a mixed strategy will be necessary elsewhere, where actions directly aimed at

412   protecting biodiversity need to be complemented with carbon schemes to obtain a double

413   benefit (Venter *et al.* 2009a; Thomas *et al.* 2013). This is especially relevant in areas that are

414   rich in biodiversity, have a low or negative carbon-biodiversity correlation, and are at

415   potential risk of habitat loss displacement (e.g. deforestation being stopped in one place but

416   reallocated in another). In these areas it is fundamental to couple the protection of carbon-

417   dense sites with the protection of important sites for biodiversity, to avoid potential

418   detrimental effects of carbon schemes on biodiversity. Biodiversity conservation, including

419   the global reduction of extinction rates, relies largely on local actions (Boyd *et al.* 2008) and

420   many sites are irreplaceable due to the unique biodiversity they host. On the contrary, there

421   are typically several options to achieve climate change mitigation through carbon

422   sequestration. Hence, there may be a case for giving priority to biodiversity conservation at

423   local extents where trade-offs with carbon conservation emerge, particularly in ecoregions in

424   which the absolute amount of carbon storage is low.

425   Many ecoregions with negative correlation between species richness and carbon

426   values hosts dry savannah and grassland environments with low variation in carbon content,

427   such as the Somali Acacia-Commiphora bushlands and thickets, the Western Australia Mulga

428   shrublands, and the Patagonian Steppe. These are fire- and browse-driven systems where

429   diversity is related to lower carbon density, where species diversity might not be necessarily

430   associated with the presence of trees, which explains the lack of a positive association with

431   carbon storage. However, a recent study (Bastin *et al.* 2017), using visual interpretation of

432   very-high resolution satellite imagery, suggests that tree density in dryland biomes might be

433   underestimated when using medium-resolution satellite imagery, and this might also affect

434   the measure of species-carbon correlation in these environments. Other regions where

435   negative correlations were observed are characterised by low variation in species richness,

436   which was either consistently high throughout the ecoregion, such as the Purus-Madeira

437   moist forest in the Amazon, or relatively low throughout, such as in some deserts. We also

438   observed negative correlation in ecoregions which were almost entirely converted to

439   anthropogenic uses, such as the Southern Korean Evergreen Forests and the Guizhou Plateau

440   broadleaf and mixed forests in China. However ecoregions with a long history of human land

441   use were characterised by relatively higher carbon-richness correlation. This is likely related

442   to the alteration of natural habitat, which reduces the space available for the manifestation of

443   key ecosystem properties (such as carbon storage and species diversity). This also implies

444   that the protection of remaining natural habitats in ecoregions with a long history of human

445   land use is likely to serve both biodiversity and carbon conservation purposes.

446   Carbon density is known to be affected by fire regimes associated with seasonal

447   climates in the subtropics (Midgley *et al.* 2010), while high biodiversity can exist in those

448   areas due to specific fire adaptations (Bond & Parr 2010). When considering all ecoregions,

449   we found relatively little influence of fire extent on the species-carbon correlation (Fig S7).

450   However, when separating the effect for individual realms (Fig S8), we found that fire extent

451   in the Neotropics and particularly in the Afrotropics were negatively associated with the

452   species-carbon correlation. This highlights the importance of considering the trade-offs

453   between carbon sequestration policies and conservation of biodiversity in fire-driven systems

454   (Midgley & Bond 2015).

455   The correlation between species richness and carbon was weaker if only considering

456   species threatened with extinction, especially when looking at broader spatial extents

457   (biomes, realms, or the globe). This was already discussed by Strassburg et al. (2010), and is

458   not surprising: while the global variation in both carbon storage and species richness is

459   primarily climate-dependent, the richness in threatened species is more influenced by

460   anthropogenic pressures. However, there are still ecoregions (18% of all pantropical

461 ecoregions) in which the correlation of threatened species richness with carbon value is high

462 ($r_s \geq 0.5$). These ecoregions represent important opportunities for using carbon conservation

463 schemes to conserve areas with high concentration of threatened species, contributing to two

464 of the most important challenges for global biodiversity conservation.

465   Mitigating climate change and halting biodiversity loss represent key objectives for

466 achieving sustainable development (United Nations General Assembly 2015). Evidence for

467 the existence of a positive correlation between biodiversity and carbon is mixed, and many

468 have argued that action to mitigating climate change might have a negative impact on

469 biodiversity. Thereby, acting on the presumption of a linear positive relationship between

470 carbon and biodiversity can lead to perverse outcomes in the many areas where this

471 assumption does not hold. Carbon policies applied at large spatial extents (i.e. encompassing

472 multiple biomes within a realm, or the globe) are likely to have positive effects on species

473 conservation. Management interventions planned within individual ecoregions can lead to

474 trade-offs, and requires considering the environmental factors that drive the correlation

475 between carbon and species. Areas with high species-carbon correlation represent immediate

476 opportunity for achieving both objectives. Areas with low, or even negative, correlation

477 should be approached with caution in carbon conservation schemes. In these regions, it is

478 essential that biodiversity monitoring and conservation measures are put in place to avoid

479 potentially perverse outcomes, such as natural habitat alteration or displacement of habitat

480 loss into high biodiversity areas.

481

485   Rome for providing mammal species distribution models used in the sensitivity analyses.

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729   **Figure 1**
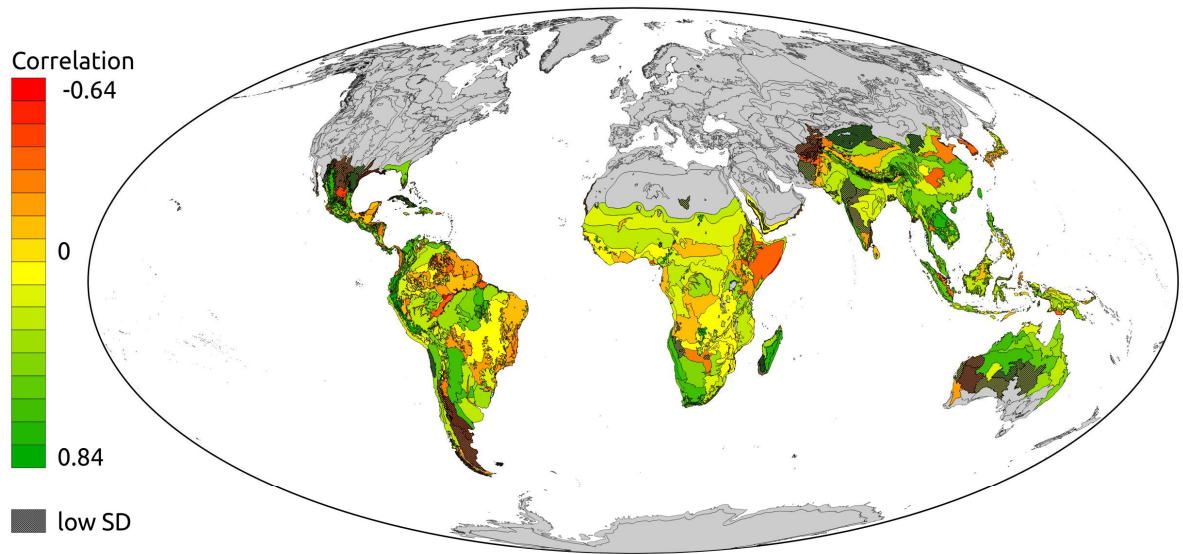730

(a) carbon density: min — max

(b) species richness: min — max
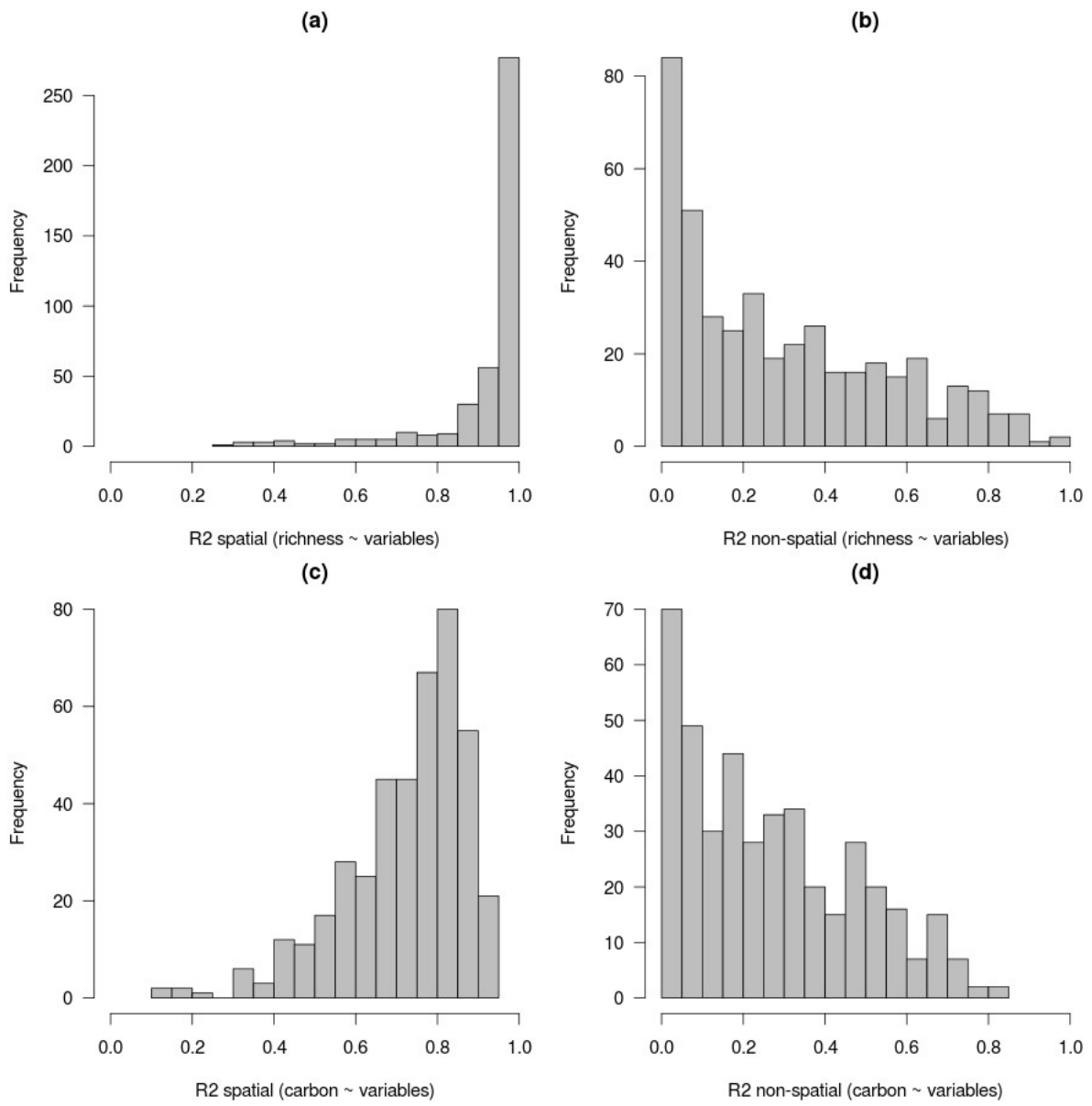
731

732 **Figure 2**
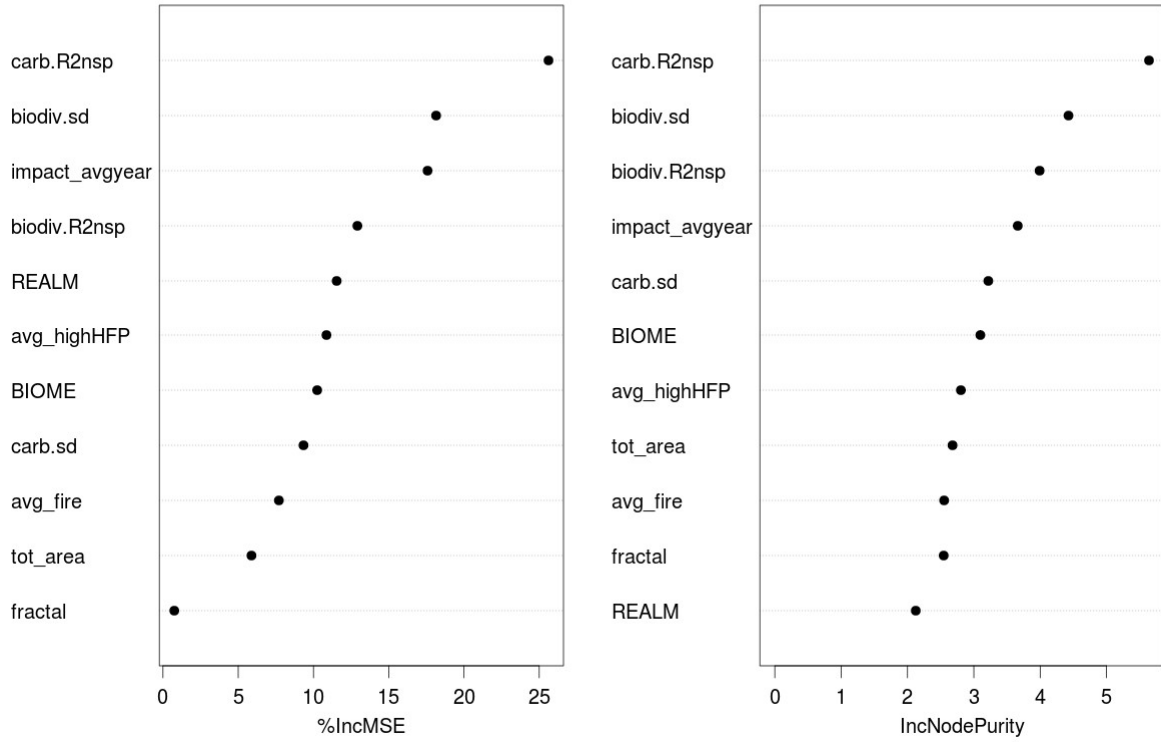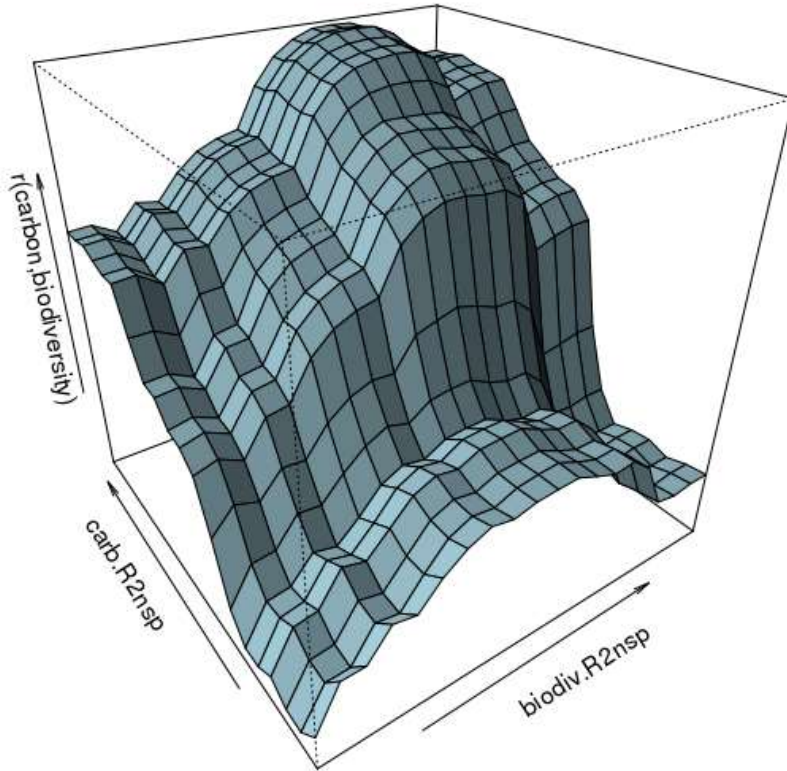733

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Figure 3

738 **Figure 4**

741   **Figure 5**

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744   **Figure 6**
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