

39 potentially compromising its contribution to resilient provision of ecosystem functions and
40 services, such as biomass production and pollination, that underpin human wellbeing (4–7).
41 Species-removal experiments suggest that loss of ecosystem function accelerates with ongoing
42 species loss (5), implying there may be thresholds beyond which human intervention is needed to
43 ensure adequate local ecosystem function (8, 9). The loss of 20% of species – which affects
44 ecosystem productivity as strongly as other direct drivers (5) – is one possible threshold, but it is
45 unclear by which mechanism species richness affects ecosystem function, and whether there are
46 direct effects or only effects on resilience of function (6, 7). Whereas this proposed safe limit
47 comes from studies of local ecosystem health, the Planetary Boundaries framework (8, 9)
48 considers longer-term maintenance of function over much larger (biome to global) scales. At
49 these temporal and spatial scales, the maintenance of function depends on functional diversity –
50 the ranges and abundances of the functional traits of the species present (8, 10). As direct
51 functional trait data are lacking, the Biodiversity Intactness Index (BII: the average abundance of
52 originally present species across a broad range of species, relative to abundance in undisturbed
53 habitat; (11)) is suggested as the best metric (8, 9). The safe limit is placed at a precautionary
54 10% reduction in BII, but it might be as high as a 70% reduction (9).

55 A key uncertainty when estimating safe limits concerns the value of species not present in
56 the undisturbed ecosystem. Such species could benefit ecosystem functioning, have no effect (as
57 assumed by the BII), or even impair it (12–15). Most models estimating net human impacts on
58 biodiversity (3, 16) treat novel and originally-present species as functionally equivalent, whereas
59 experimental studies manipulate species originally present (17).

60 Given the possibly severe consequences of transgressing safe biodiversity limits, global
61 assessments of relevant metrics are needed urgently. Data limitations have hampered efforts to
62 date: BII has so far only been estimated, from expert opinion, for seven southern African
63 countries (11). More recently, we combined global models linking land-use pressures to local
64 biodiversity with global land-use maps. We estimated that net reductions in local species
65 richness exceeded 20% across 28% of the world's land surface by 2005, while 48.7% of land had
66 seen net reductions in total abundance of $\geq 10\%$ (3). However, our projections of net effects did
67 not account for any reductions of originally-present diversity that were offset by influx of novel
68 species (18), as well as being at too coarse a scale ($\sim 50 \text{ km}^2$) to be relevant for local ecosystem
69 functioning and decision making. Furthermore, we did not analyze the spatial distribution of the
70 transgression of proposed safe limits.

71 Here we present fine-scale ($\sim 1 \text{ km}^2$) global estimates of how land-use pressures have
72 affected the numbers of species and individuals found in samples from local terrestrial ecological
73 assemblages (19). To explore different assumptions about novel species, we estimate both
74 overall net change (correct if novel species contribute fully to ecosystems) and – using estimates
75 of species turnover among land uses to exclude novel species – change in species originally
76 present (correct if novel species play no role). We ask how much of the Earth's land surface is
77 already 'biotically compromised' (i.e. exceeds the boundaries of 10% loss of abundance or 20%
78 loss of species). We focus on results for the relative abundance of originally-present species
79 (BII), because this is the measure suggested in the Planetary Boundaries framework (9). We
80 estimate average losses per biome, because of the suggested importance of biomes for the
81 functioning of the whole Earth System (8, 9), and to assess possible consequences for people –
82 assuming that many biodiversity-regulated ecosystem services operate locally – we quantify the
83 geographical congruence between biodiversity reduction and human population. We also assess
84 the biotic integrity of areas identified as particularly important for conservation (although the

85 proposed planetary boundary in terms of BII may not always be relevant for areas much smaller
86 than biomes, and probably needs to vary depending on the sensitivity of the biota). First,
87 Conservation International's 'Biodiversity Hotspots' – areas rich in endemic species but with
88 high levels of habitat loss – have been suggested as urgent conservation priorities (20). Because
89 these areas were identified reactively (20) with a criterion of 70% loss of primary vegetation, we
90 expect them to have lower biodiversity intactness than average. For comparison, we also
91 estimate the biodiversity intactness of Conservation International's High Biodiversity Wilderness
92 Areas, which also meet the criterion of high species endemism, but which retain 70% of their
93 natural habitat and so present more opportunity for proactive conservation (20).

94 We modelled how sampled richness and abundance respond to land-use pressures using
95 data from the PREDICTS (Projecting Responses of Ecological Diversity in Changing Terrestrial
96 Systems) database (21). These data consisted of 2,382,624 records (Fig. S1; nearly twice as
97 many as our earlier, coarser-scale analyses (3)) of the abundance (1,888,784 records) or else
98 occurrence of 39,123 species at 18,659 sites. The hierarchical mixed-effects models we used
99 considered four pressure variables – land use, land-use intensity, human population density and
100 proximity to the nearest road – as fixed effects (Figs. S2-3), while random effects accounted for
101 among-study differences in sampling (methods, effort and focal taxonomic groups) and for the
102 spatial arrangement of sampled sites within studies (see Supplementary Methods). We had
103 insufficient data to fit separate models for each biome or clade. Responses may vary
104 taxonomically or geographically, although our earlier analyses (3) showed no significant
105 differences among plants, invertebrates and vertebrates, and suggested limited variation among
106 biomes. As more data become available, future analyses will be better able to reflect any
107 differences in response. We combined the models of species richness and total abundance with
108 models of species turnover among land uses (based on 24, but adapted to reflect asymmetric
109 differences among land uses), to discount the fraction of species absent in non-primary habitat
110 (see Methods for details). To map modelled responses, we used global pressure data for the year
111 2005 at a resolution of 30 arc seconds (approximately 1 km²). We used land-use estimates for
112 2005 (25), and estimated land-use intensity as in (3); human population (for the year 2000) came
113 from (22) and proximity to nearest road from (23). Values of the response variables are always
114 expressed relative to an intact assemblage undisturbed by humans, so do not rely on estimates of
115 absolute abundance or species richness, which vary widely among biomes and taxa.

116 Our map of terrestrial BII (Fig. 1A; Fig. S4) suggests that the average local abundance of
117 originally present species (11) globally has fallen to 84.6% (95% confidence interval: 82.2-
118 91.6%) of its value in the absence of human land-use effects, probably below the value (90%)
119 proposed as a safe limit (9). Considering net changes in abundance, as in (3), assuming that
120 novel species contribute fully to ecosystem function, global average abundance has fallen to
121 88.0% (95% CI: 83.5-94.8%) of its value before human effects.

122 Assuming that only originally present species contribute to ecosystem function, most of the
123 world's land surface is biotically compromised in terms of BII (58.1% of terrestrial area; 95% CI:
124 40.4-70.2%; Fig. 1A) and within-sample richness of originally present species (62.4%; 95% CI:
125 20.0-72.7%; Fig. 1B). If the proposed boundaries are broadly correct, ongoing human
126 intervention may be needed to ensure delivery of ecosystem functions across most of the world
127 (5). The proposed planetary boundary for BII (9) had uncertainty ranging from 30% to 90%; the
128 proportion of the land surface exceeding the boundary varies widely across this range (Fig. S5),
129 highlighting the urgent need for better understanding of how BII relates to Earth-system
130 functioning (9). Assuming that novel species contribute as much to ecosystems as originally

131 present species we estimate the safe limit for total abundance to have been crossed in 48.4%
132 (95% CI: 30.9-66.5%) of land (Fig. 1C) and that for within-sample species richness in 58.4%
133 (95% CI: 21.8-75.0%; Fig. 1D). Even assuming that novel species have no effect on ecosystem
134 function will be optimistic if they actually impair it, an important question to test in future. Most
135 people (71.4%) live in biotically compromised areas, as judged by BII (Fig. 2), although
136 uncertainty in this result was high (95% CI: 8.7-92.4%). There is growing evidence that access to
137 high-biodiversity areas benefits people's physical and psychological wellbeing (26, 27), although
138 uncertainty remains over which aspects of biodiversity are important.

139 The biodiversity impact of land-use pressures varies among biomes (Fig. 3A; Table S2):
140 grasslands are most affected, and tundra and boreal forests least. Our BII estimates suggest 9 of
141 the 14 terrestrial biomes (95% CI: 4-12) have on average transgressed safe limits for biodiversity
142 (Fig. 3A), although this number drops to seven (95% CI: 1-12) if novel species are included. The
143 BII limit has been crossed in 22 of 34 terrestrial 'Biodiversity Hotspots' (28) (95% CI: 7-31; Fig.
144 3B; Table S3); this figure falls to 12 (95% CI: 5-32) if novel species are included, again
145 highlighting the need to understand their effects on ecosystem function. Given that Biodiversity
146 Hotspots were identified partly based on widespread historical habitat loss (20), their low
147 average BII is unsurprising, although our results suggest that at least some hotspots might stay
148 within safe ecological limits if future land conversion is reduced. In contrast, three out of the five
149 High Biodiversity Wilderness Areas, which were identified for conservation proactively because
150 the habitat is still relatively intact (20), have not experienced average losses of local biodiversity
151 (BII) that cross the planetary boundaries (95% CI: 2-4; Fig. 3C; Table S4; four out of five if
152 novel species are included; 95% CI: 2-5). Results concerning which areas have crossed proposed
153 planetary boundaries were generally consistent between the richness- and abundance-based
154 biodiversity measures (Figure 3; Tables S2-4).

155 Our models suggest generally smaller impacts of land use on BII than a previous study
156 (11). This might reflect differences in taxonomic coverage, but there are also two reasons why
157 our results may overestimate BII. First, we ignore lagged responses. Second, our models use sites
158 in primary vegetation as a baseline, because historical data are so rare (3, 11); these sites will
159 often have experienced some human impact. Nevertheless, it is important to note that since our
160 models are global, their baseline is not biome- or region-specific, and they do not rely on data
161 from minimally impacted land use from heavily modified landscapes, where such conditions do
162 not exist. Our data have good coverage of taxa and biomes (Fig. S1), but the density of sampling
163 is inevitably uneven. Biomes that are particularly underrepresented, relative to their global
164 ecosystem productivity, are boreal forests, tundra, flooded grasslands and savannas and
165 mangroves (Fig. S1), meaning that less confidence can be placed in the results for these biomes.
166 The data probably also under-represent soil and canopy species. The estimate of land area
167 biotically compromised in terms of species richness is much higher than our previous assessment
168 (58.4 vs. 28.4%, although the confidence intervals overlap), but the estimates based on total
169 abundance are almost identical (48.4% vs. 48.7%; 3). The discrepancy for species richness is
170 because of a stronger modelled interaction here between land use and human population density
171 (Fig. S3), and because we include the effect of roads and the interaction between roads and land
172 use, which were omitted from the projections in (3).

173 The Sustainable Development Goals adopted in September 2015 (29) aim to improve
174 human wellbeing while protecting, restoring and sustainably using terrestrial ecosystems. Our
175 results highlight the magnitude of the challenge. Exploitation of terrestrial systems has been vital
176 for human development throughout history (30), but the cost to biosphere integrity has been

177 high. Slowing or reversing the global loss of local biodiversity will require preserving the
 178 remaining areas of natural (primary) vegetation and, so far as possible, restoring human-used
 179 lands to natural (secondary) vegetation. Such an outcome would be beneficial for biodiversity,
 180 ecosystems and – at least in the long term – human wellbeing.

181

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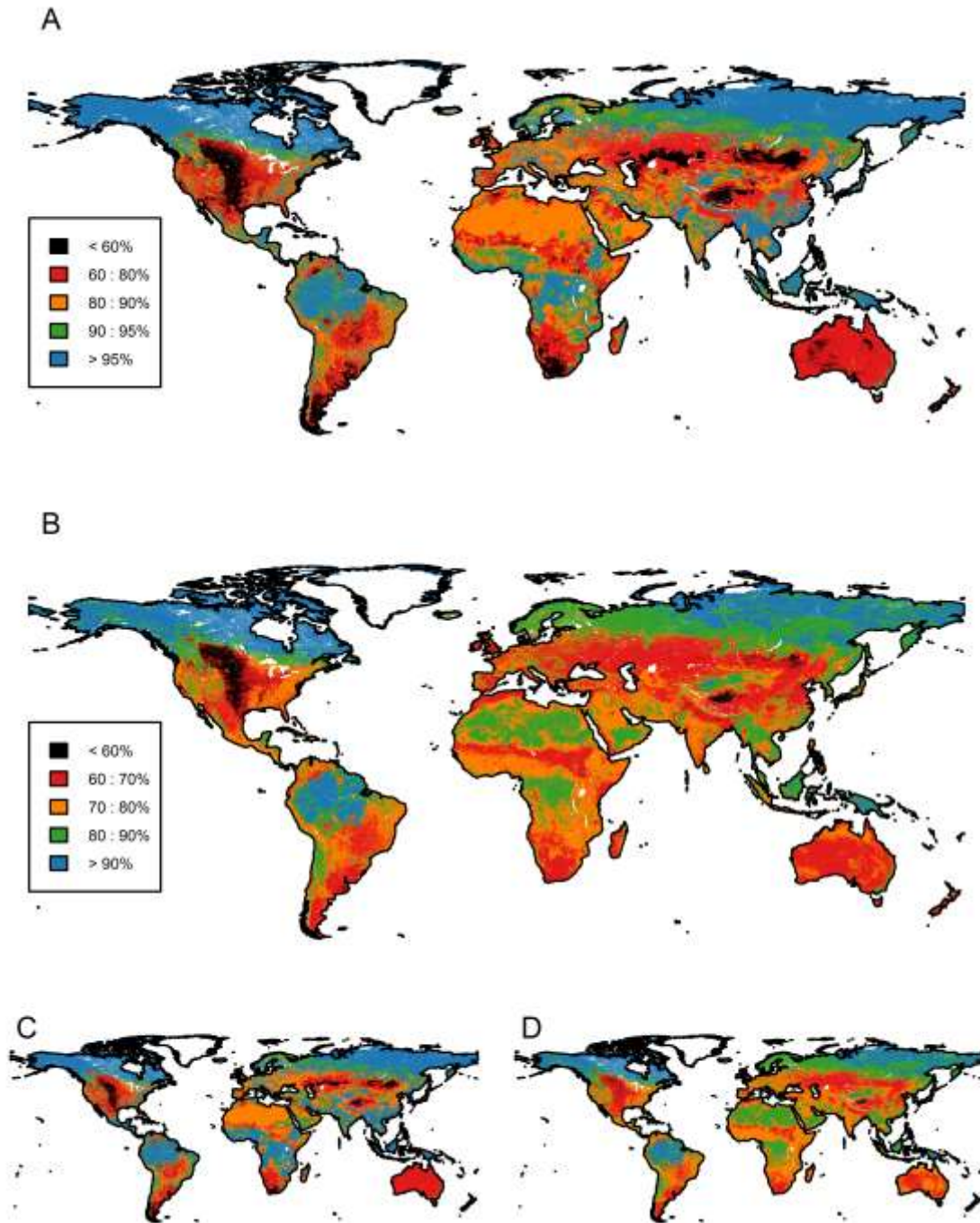
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Fig. 1. Biodiversity intactness of ecological assemblages, in terms of (A) total abundance of

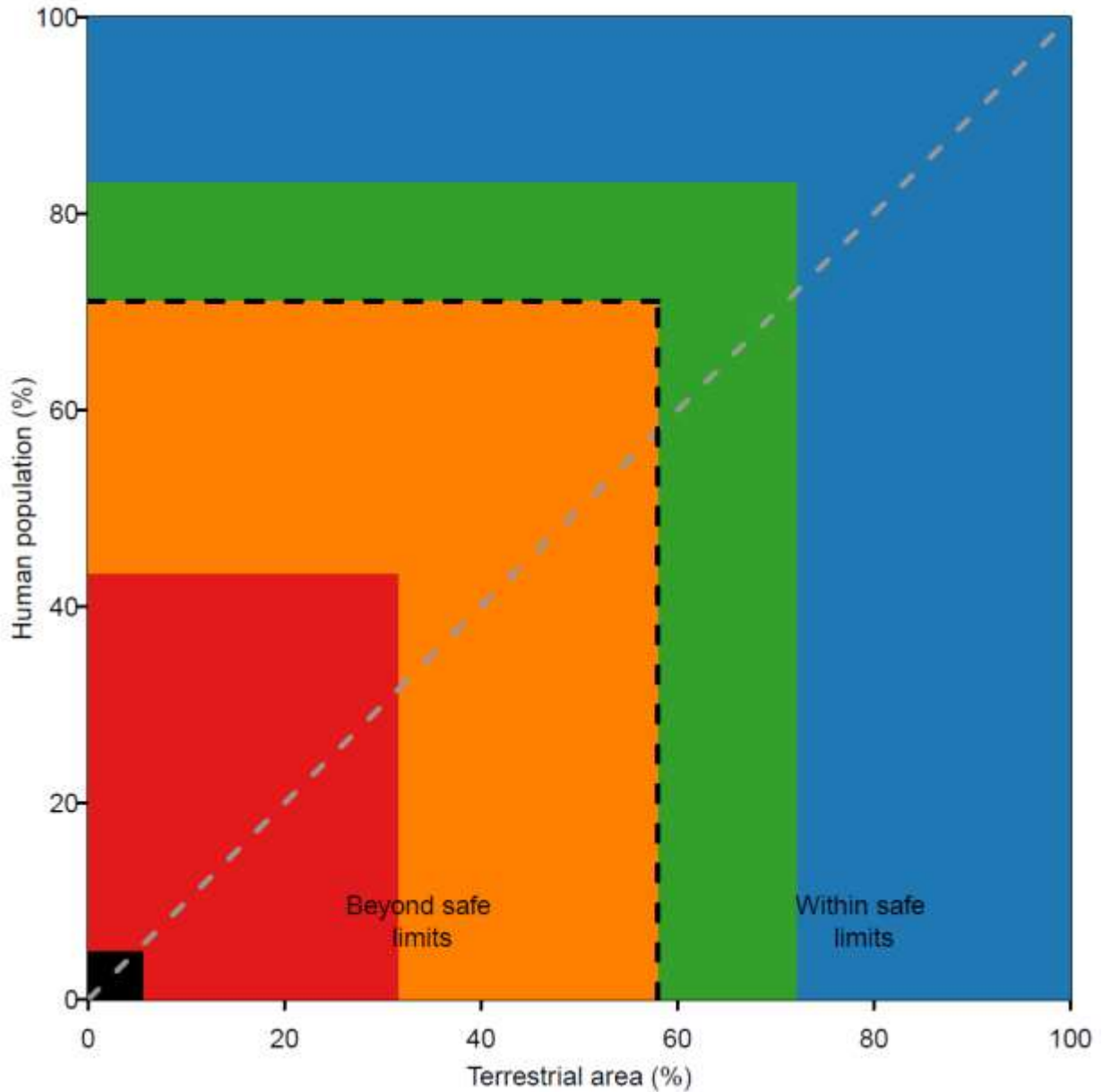
species occurring in primary vegetation (i.e. BII), (B) richness of species occurring in primary

vegetation. Panels C and D correspond to A and B, respectively, and have the same legend

values, but including species not present in primary vegetation.

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1314 **Fig. 2. Terrestrial area and human population at different levels of the Biodiversity**1315 **Intactness Index (BII).** Biodiversity intactness increases from bottom-left to top-right, and has

1316 the same colour scheme as Fig. 1. The dashed black line shows the position of the planetary

1317 boundary (9): only areas to the right and human population above this line (shaded green and

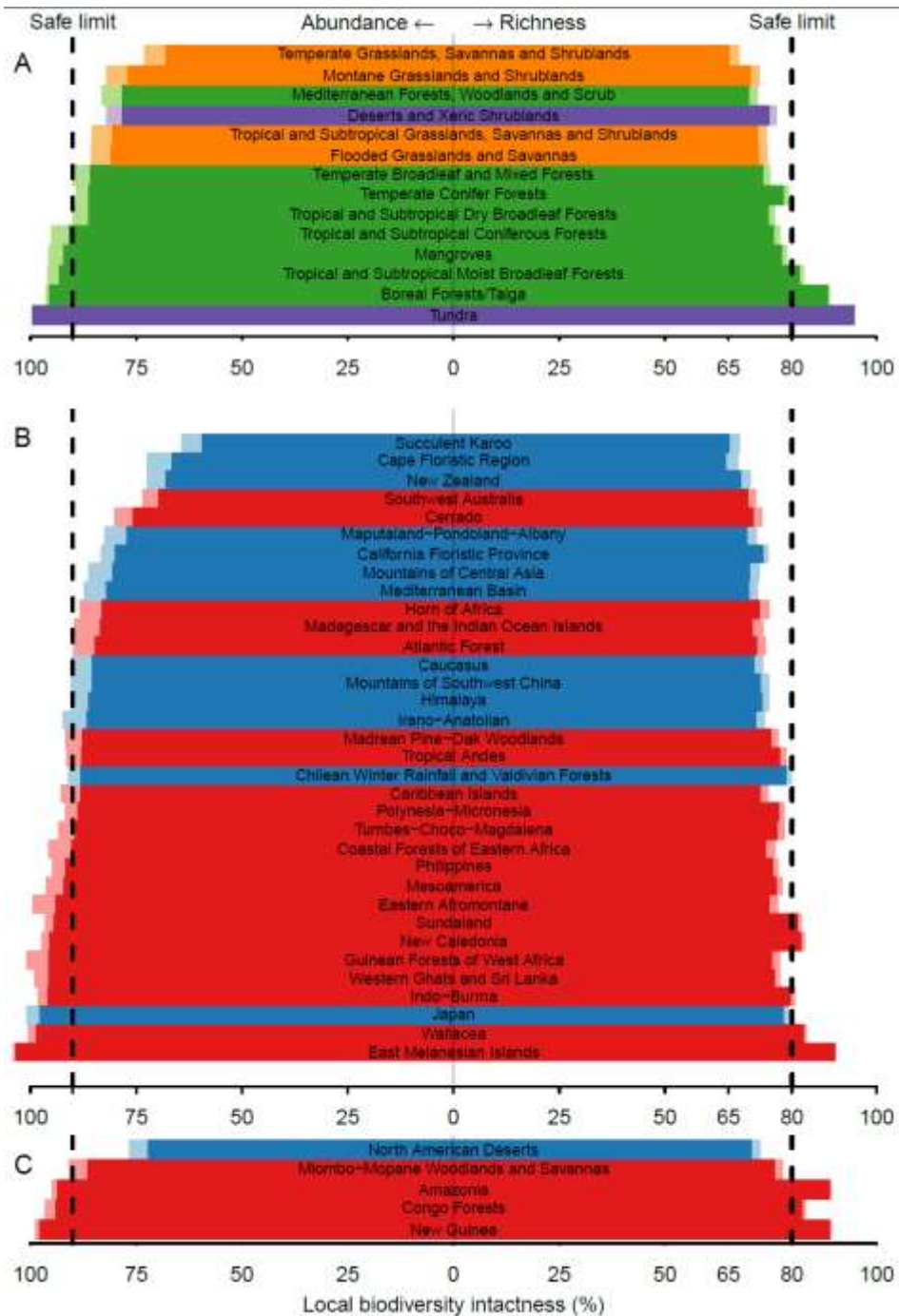
1318 blue) are within the proposed safe operating space. If human population were distributed

1319 randomly with respect to BII, the corners of the boxes would align with the dashed grey line; the

1320 extent to which the corners lie above this line indicates the strength of the bias in human

1321 populations toward less intact areas.

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1325 **Fig. 3. Biodiversity intactness for biomes, Biodiversity Hotspots and High Biodiversity**1326 **Wilderness Areas.** Biodiversity intactness in terms of total abundance (BII; solid bars on left)

1327 and species richness (solid bars on right) in each of 14 terrestrial biomes (A), 34 Biodiversity

1328 Hotspots (B), and five High Biodiversity Wilderness Areas (C). Translucent bars show the

1329 corresponding relative biodiversity values if novel species are treated as equivalent to those

1330 originally present (these numbers can surpass 100% because gains may outnumber losses). Bars

1331 in (A) are coloured by major biome type (orange = grasslands, green = forests, purple = other),

1332 while bars in (B) and (C) are coloured according to whether they are in the temperate (blue) or

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1335 **Supplementary Materials:**

1336 Materials and Methods

1337 Figures S1-S7

1338 Tables S1-S7

1339 References (31-457)