

1 Consumption-based biodiversity footprints – do different
2 indicators yield different results?
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4 Sandra Marquardt^{a*}, Michael Guindon^a, Harry Wilting^b, Zoran Steinmann^a, Sarah Sim^c, Michal
5 Kulak^c, Mark Huijbregts^a
6

7 ^a*Department of Environmental Science, Institute for Water and Wetland Research, Radboud*
8 *University Nijmegen, P.O. Box 9010, 6500 GL Nijmegen, The Netherlands*

9 ^b*PBL Netherlands Environmental Assessment Agency, P.O Box 30314, 2500 GH The Hague,*
10 *The Netherlands*

11 ^c*Safety and Environmental Assurance Center, Unilever, Colworth Science Park, Sharnbrook*
12 *MK44 1LQ, United Kingdom*
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23 ABSTRACT

24 Land use related to human consumption patterns leads to significant loss of biodiversity.
25 Here, the implications of using different indicators in the calculation of biodiversity footprints
26 caused by land use were analyzed. Footprints refer to the impacts related to the net consumption
27 in a region. We calculated biodiversity footprints for 140 regions in the world with an
28 environmentally-extended multi-regional input-output (EEMRIO) model. The EEMRIO links
29 economic activities from the Global Trade Analysis Project (GTAP) database with land use and
30 four indicators of biodiversity loss. We included three alpha diversity indicators (loss of mean
31 species abundance, relative abundance and relative species richness) and one indicator of
32 gamma diversity (vulnerability-weighted relative species richness loss). While the three alpha
33 diversity indicators reflect local diversity within a site, the gamma diversity indicator captures
34 global diversity by weighting regional species richness with species' extinction vulnerability in a
35 region. We found that the three alpha diversity footprints show close alignment ($r_s > 0.93$), while
36 there was limited convergence between alpha and gamma diversity footprints ($r_s < 0.22$). The
37 alpha diversity indicators identified a diverse set of regions with high per capita consumption-
38 based biodiversity footprints across the globe, while the gamma diversity indicator emphasized
39 human consumption patterns threatening particularly tropical biodiversity. Although all footprints
40 are positively related to rising household expenditure, this relationship was weaker and highly
41 uncertain for the gamma diversity footprints. The alpha-based footprints also showed a negative
42 relationship with population density, while the gamma-based footprint was not related to
43 population density. Our results highlight the relevance of including both alpha and gamma
44 diversity indicators in land-based biodiversity footprint calculations.

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47 Keywords (max 6): Biodiversity footprint; Multi-regional input-output analysis; Gamma diversity;
48 Alpha diversity; Consumption; GTAP

49 *Corresponding author e-mail address: s.marquardt@fnwi.ru.nl

50 1. Introduction

51 Biodiversity ultimately supports and stabilizes the provisioning of ecosystem services that are
52 necessary for maintaining the production of food and fiber and regulating earth systems such as
53 climate and freshwater (Cardinale et al., 2012; Isbell et al., 2017; Tilman et al., 2014). The impacts
54 of human consumption on biodiversity can be assessed with multi-regional input-output (MRIO)
55 analysis in which global industry transactions are translated into final demand for goods and
56 services in the global economy (Miller and Blair, 2009). The economic relationships can be linked
57 to environmental impacts to derive environmentally-extended (EE)MRIO models and compute
58 production-based and/or consumption-based environmental footprints (e.g. Hertwich and Peters,
59 2009; Kitzes et al., 2016; Steen-Olsen et al., 2012; Weinzettel et al., 2013).

60 While several biodiversity footprinting studies have been published, they have typically
61 focused on one dimension of biodiversity, such as number or composition of species (Chaudhary
62 et al., 2016a; Chaudhary and Kastner, 2016; Chaudhary and Brooks, 2017; Lenzen et al., 2012;
63 Moran et al., 2016; Moran and Kanemoto, 2017; Verones et al., 2017; Wilting et al., 2017).
64 Comprehensive assessments of biodiversity require consideration of different dimensions of
65 biodiversity and different spatial scales (Isbell et al., 2017; Marques et al., 2018; Purvis and
66 Hector, 2000; Santini et al., 2017, Schipper et al., 2016b). Although examples of comparing
67 different biodiversity indicators for specific products exist (Nishijima et al., 2016), systematic
68 evaluation of whether different biodiversity indicators provide additional insights in a global
69 footprint context covering all economic flows is currently lacking. Indicators reflecting different
70 biodiversity dimensions provide different insights: alpha diversity captures local biodiversity within
71 a site; beta diversity reflects structural differences between sites and gamma diversity is the total
72 species diversity in a landscape (Whittaker 1972).

73 In this study, we quantified and compared different biodiversity indicators to derive
74 consumption-based footprints of nations. We focused on land use as one of the key pressures on
75 biodiversity (Murphy and Romanuk, 2014). To this end, we linked an MRIO model, based on the
76 Global Trade Analysis Project (GTAP) database, with areas of land (forestry, pasture, cropland
77 and urban) and the intensity of its use (low, medium, high). Land use was subsequently linked to
78 three indicators of alpha diversity: loss of mean species abundance (Alkemade et al., 2009;
79 Schipper et al., 2016a), loss of relative abundance (Newbold et al., 2016, 2015) and loss of
80 relative species richness (Newbold et al., 2016, 2015) and one indicator of gamma diversity: loss
81 of vulnerability-weighted global relative species richness (Chaudhary et al., 2016a, 2016b, 2015).
82 All the chosen biodiversity indicators reflect long-term biodiversity effects of a specific land use
83 type relative to a reference land use state.

84 Rising incomes, as an indicator of increasing prosperity, typically result in increased levels of
 85 consumption and thus consumption expenditure (Varian 2006). To understand how the four
 86 biodiversity footprints were linked to levels of prosperity, we tested the responsiveness of each of
 87 the per capita biodiversity footprints to per capita household expenditure. With increasing
 88 population density, less land is available for resource use thus driving technological development
 89 for improved resource use efficiency (Wiedmann et al., 2015; Wilting et al., 2017). To test for a
 90 systematic relationship between population density and per capita biodiversity footprints, we also
 91 included population density as a second explanatory variable.

92 2. Methods

93 2.1. Biodiversity footprint

94 We calculated the biodiversity footprints following the approach employed by Wilting et al.
 95 (2017). The biodiversity footprint B of region j in the multi-regional context was defined as:

$$96 \quad B^j = i(M^{\circ}D) (I - A)^{-1} y^j + m^j d^j \quad (1)$$

97 with i being a vector of ones needed for the summation over all land use categories to arrive at
 98 the biodiversity footprint B of region j . M corresponds to the matrix of biodiversity loss factors (in
 99 percent of biodiversity loss per land use) per region and sector, and is linked to land use
 100 intensities, D , differentiated per region and sector, and land use category employed in this
 101 analysis. Both matrices, M and D , are defined for all regions and sectors per land use category;
 102 elementwise multiplication of matrix components is indicated by the matrix operator \circ . $(I-A)^{-1}$ is the
 103 standard Leontief inverse matrix depicting information on industry use of imported and domestic
 104 intermediate inputs (Leontief, 1936). Vector y depicts the final demand for goods and services in
 105 region j from domestic and foreign origin. The Leontief inverse and final demand vector y were
 106 derived using the procedure described by Peters et al. (2011) to construct an MRIO table from
 107 the GTAP database. To account for the direct linkage of land use to final demand the product $m^j d^j$
 108 is added. m corresponds to the vector of biodiversity loss factors linked to land use in region j and
 109 vector d to the direct land use pressures for all land use categories by final consumers in region
 110 j .

111 2.1.1 Biodiversity indicators

112 To link biodiversity indicators to the MRIO framework, the indicators need to be applicable at
 113 the global scale and have sufficient detail on the definition of the underlying land use categories.
 114 This limited the range of potential indicators to three alpha diversity indicators (loss of mean
 115 species abundance, relative abundance at the local scale and relative within-sample species
 116 richness) and one indicator of gamma diversity (vulnerability-weighted relative species richness

117 loss). Table 1 provides an overview on the definition, diversity classification (following Whittaker,
 118 1972), and characteristics of the respective biodiversity indicators.

119

120 **Table 1**

121 Overview of indicators' classification, description and characteristics

Indicator	Diversity classification¹ / Description	Characteristics and limitations	Source
Mean species abundance (MSA) loss	<p>Classification: Alpha (local within-site diversity)</p> <p>Description: The mean original species abundance (A) in disturbed conditions relative to their presence in undisturbed conditions (A_{ref}):</p> $MSA_{loss} = 1 - \frac{1}{n_i} \sum_i \frac{A_i}{A_{ref,i}}$ <p>based on n species (n_i)</p>	<p>Characteristics: Generic factors for 16 land use categories</p> <p>Factors truncated at 1 (representing undisturbed habitat)</p> <p>Included taxa: mammals, birds, reptiles, amphibians, terrestrial invertebrates, vascular plants</p> <p>Limitations: Does not capture</p> <ul style="list-style-type: none"> - among site differences - species vulnerability 	Methodology: Alkemade et al. (2009) and Schipper et al. (2016a)
Relative abundance (RA) loss	<p>Classification: Alpha (local within-site diversity)</p> <p>Description: Sum of the measures of abundance of all taxa i at a site relative to abundance in undisturbed conditions.</p> $RA_{loss} = 1 - \frac{\sum_i A_i}{\sum_i A_{ref,i}}$	<p>Characteristics: Generic factors for 13 land use categories</p> <p>Factors not truncated at 1 (allowing for biodiversity gains compared to the undisturbed habitat)</p> <p>Included taxa: mammals, birds, amphibians, reptiles, anthropods, plants</p> <p>Limitations: Does not capture</p> <ul style="list-style-type: none"> - among site differences - species vulnerability 	Methodology: Newbold et al. (2015, 2016) ²
Relative within-sample species richness (RWSR) loss	<p>Classification: Alpha (local within-site diversity)</p> <p>Description: Number of taxa at a given site in a standardized sampling unit³ (S) relative to the number of taxa in an undisturbed habitat (S_{ref}).</p> $RWSR_{loss} = 1 - \frac{S}{S_{ref}}$	<p>Characteristics: Generic factors for 13 land use categories</p> <p>Included taxa: mammals, birds, amphibians, reptiles, anthropods, plants</p> <p>Limitations: Does not capture</p> <ul style="list-style-type: none"> - among site differences - species vulnerability - changes in species composition 	Methodology: Newbold et al. (2015, 2016)

Vulnerability-weighted global relative species (VGSR)⁴ loss	<p>Classification: Gamma (global across-site diversity)</p> <p>Description: Loss in global relative species richness associated with land use type (i) in country (c) per taxon (t). S_{loss} is the land use and country-specific species loss, $S_{w,t}$ is the global number of species of taxon t summed over all land use types and countries, VS_c⁵ is the country-specific vulnerability for global extinction based on IUCN⁶ and VS_w the world average vulnerability score of taxon t.</p> $VGSR_{loss_{i,c,t}} = \frac{S_{loss_{i,c,t}}}{S_{w,t}} \cdot \frac{VS_{c,t}}{VS_{w,t}}$	<p>Characteristics: Ecoregion-specific factors for six land use categories⁷</p> <p>Included taxa: mammals, birds, reptiles, amphibians, vascular plants</p> <p>Limitations: Does not capture - changes in species composition</p>	<p>Methodology: Chaudhary et al. (2015, 2016a, 2016b)</p>
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122 Notes:

123 ¹Following Whittaker (1972): alpha diversity captures biodiversity within a site and gamma diversity reflects

124 the total diversity.

125 ²We obtained the exact coefficients in log-transformed format through personal communication with Tim

126 Newbold in June 2017.

127 ³Calculated based on methodology in Gotelli and Colwell (2001)

128 ⁴The vulnerability-weighted relative species richness loss (expressed in potentially disappeared fraction

129 (PDF) per square meter) is obtained by a weighted average of the taxon-specific $VGSR_{loss}$ over all taxa

130 giving equal weighting to plants and animal taxa and equal weighting within the animal taxa.

131 ⁵Through vulnerability-weighting, actual species richness loss (in number of species lost) was weighted by

132 the vulnerability-weighted global species richness to arrive at a fraction of species lost (dimensionless).

133 Consequently, the gamma diversity indicator differs between countries due to (i) differences in species

134 richness between ecoregions and (ii) differences in vulnerability of the species occurring in different

135 ecoregions. This does not alter the spatial scale of the indicator but allows for inter-country comparisons

136 regarding country's contributions to global extinction. See Chaudhary et al. (2015, 2016b) for a more

137 detailed description of the calculation procedure.

138 ⁶IUCN - International Union for Conservation of Nature.

139 ⁷Factors are available at an ecoregion or country level and for five taxa. We used the country level factors

140 in our analysis. As our regional classification also includes aggregates composed of several countries, there

141 were cases where we needed to aggregate the supplied loss factors. This was done in compliance with

142 Chaudhary et al.'s (2015) geographical aggregation formula by computing area-weighted loss factors

143 (equation S8).

144

145 Consequently, there is, by definition, a high correlation between RWSR-based footprints

146 versus MSA- and RA-based footprints. For this reason, we chose to show the MSA- and RA-

147 based footprints in the main text and the RWSR-based footprints in the supporting information.

148 2.2. Data compilation

149 2.2.1. Specification of land use classes and derivation of region-specific land use areas

150 We harmonized the land use categorization from the different data sources to allow for a

151 consistent application of the biodiversity indicators. The land use categories reflect the type (e.g.

152 cropland) and intensity (e.g. low-input farming) or production system (e.g. reduced impact logging)
153 of the land use. Table A1 (Supplementary information) provides a detailed overview of the 19
154 different land use classes after harmonization, as well as corresponding nomenclature in the
155 different original sources.

156 Information on land use served as the link between biodiversity loss and global economic
157 relationships. To derive hectare values for land use differentiated according to our 19 land use
158 categories, we primarily used the country-specific land use data from the Food and Agriculture
159 Organization (FAO) database (FAO, 2017). As the FAO does not provide details about the
160 intensity of cropland or forest land use or stocking densities on pasture; we disaggregated the
161 FAO data according to other data sources. The Supplementary information (Section A2) provides
162 a detailed explanation of the individual steps associated with this data processing. These steps
163 are summarized below.

164 We used FAO data to derive arable land areas per crop and country. We then
165 distinguished arable land area per production system and crop based on country-specific relative
166 shares. Relative shares differentiate between the production systems 'irrigated high inputs', 'rain-
167 fed high input', 'rain-fed low input' and 'rain-fed subsistence' per crop and are based on the Spatial
168 Production Allocation Model (SPAM) (You et al., 2014).

169 Our pasture land use categories were derived using stocking densities and type of
170 vegetation as the main defining elements. FAO pasture areas were disaggregated using animal
171 density information contained in the Gridded Livestock of the World maps (Robinson et al., 2014)
172 and maps on global biomes (Olson et al., 2001).

173 For a differentiation between the different forest production systems, 'plantation forest',
174 'clear-cut forest', 'selectively logged forest' and 'reduced impact logging (RIL) forest', we used
175 area shares of these production systems as identified by Arets et al. (2011). As the FAO does not
176 provide explicit area information for urban areas, we chose to use values provided by the ESA
177 Climate Change Initiative (ESA CCI, 2017).

178 2.2.2. Allocation of region-specific land use areas per land use class to economic sectors

179 The GTAP databases represent the world economy for a single year, valued in US dollars.
180 They are based on the harmonization of national input-output tables, bilateral trade,
181 macroeconomic and protection data (Narayanan et al., 2015). The databases are typically used
182 to project the effects of economic shocks on the global economy using computable general
183 equilibrium (CGE) analysis; however, the databases can also be transformed into an MRIO table.

184 We used the GTAP Power Database, which is an extension to the standard GTAP database with
185 more detail in the energy sectors (Peters, 2016).

186 To construct an MRIO table using the GTAP Power-Database, we followed the methods
187 of Peters et al. (2011). The output was an MRIO table for 2011 with 140 regions (individual
188 countries and aggregate regions) and 68 economic sectors. Compared to other databases (e.g.
189 World Input-Output Database (WIOD) (Timmer et al., 2015), Eora (Lenzen et al., 2012) and
190 Exiobase (Wood et al., 2014)), GTAP provides higher regional detail for all continents and,
191 compared to WIOD and the harmonized Eora, a higher resolution in agricultural sectors (14
192 sectors in total, including eight crop sectors). Furthermore, the GTAP database is periodically
193 updated and expanded to include more regions and/or more sectors.

194 The GTAP database provides less regional and sectoral detail than the FAO statistics.
195 Therefore, we aggregated the relevant FAO crop-specific areas to the eight GTAP crop sectors
196 (Supplementary information, Table A3). As GTAP livestock sectors include different types of
197 livestock, pasture areas were allocated to the three livestock sectors using each sector's share of
198 land value-added. Following the approach by Wilting et al. (2017), we allocated urban areas to
199 final consumers (see Supplementary information Section A2 for further details).

200 2.3. Footprint analysis and comparison

201 2.3.1. Biodiversity footprint comparison

202 We calculated the biodiversity footprints according to Eq. 1. Subsequently, we compared the
203 ranking of the 140 GTAP-regions' alpha and gamma footprints using spearman rank correlations.
204 A high spearman rank correlation between two biodiversity footprints implies low added value of
205 including these two indicators separately; low correlation shows that the two indicators provide
206 additional regional insights for a biodiversity assessment.

207 Additionally, testing for correlation between the generic alpha diversity loss factors revealed
208 high correlation between each of the abundance-based alpha diversity loss factors ($r = 0.88$ for
209 MSA and $r = 0.8$ for RA) and the species richness-based alpha diversity loss factors (RWSR);
210 correlation between the abundance-based factors is, however, limited ($r = 0.62$) (compare
211 Supplementary information, Section A4.2). For this reason, we show the results of the MSA- and
212 RA-based footprints in the main text and the RWSR-based footprints in the supporting
213 information.

214

215 2.3.2. Prosperity and population density as drivers of biodiversity footprints

216 We tested the responsiveness of each of the per capita footprints to per capita household
217 expenditure and population density allowing for linear and quadratic terms. The quadratic terms
218 in the regression account for the possibility of a non-linear relationship with expenditure and/or
219 population density and were only included if the linear term of the variable was retained in the
220 final model. Values for 2011 household expenditure (in purchasing power parity (PPP) corrected
221 US dollars) and population were taken from the World Bank World Development Indicators
222 database (World Bank, 2018). The corrected Akaike Information Criterion (AICc) was used to
223 select the best model among all possible combinations (see Section A5).

224 Following Wilting et al. (2017), we calculated the sensitivity towards changes in expenditure
225 and population density for each biodiversity footprint. The sensitivity was summarized by the
226 relative difference d , calculated as:

$$227 \quad d = \frac{|B_1 - B_2|}{\frac{B_1 + B_2}{2}} \quad (2)$$

228 With B_1 and B_2 corresponding to the biodiversity footprints calculated using the minimum and
229 maximum, respectively, of the explanatory variable of interest and the mean of the remaining
230 explanatory variable in the regression equation.

231 2.3.3. Uncertainty analysis

232 To test the variation in our footprint results due to uncertainty in biodiversity loss factors, we
233 conducted a Monte Carlo simulation (10,000 iterations). The uncertainty in the alpha loss factors
234 was reflected by a normal distribution, as derived from Newbold et al. (2016) for RA and RWSR
235 loss and Alkemade et al. (2009) for MSA loss. The uncertainty in the gamma loss factors was
236 reflected by a beta pert distribution, as derived from Chaudhary et al. (2016b). Further details of
237 deriving the uncertainty distributions are described in the Supplementary information, Section
238 A4.4.

239 2.3.4 Comparison with land footprint

240 Finally, we tested the added value of biodiversity footprints compared to land footprints
241 (Supplementary information, Section A4.3). Land footprints represent the total amount of land
242 area required for per capita consumption in a country without considering biodiversity loss factors.
243 These were calculated using Eq. 1 without including the biodiversity loss factors.

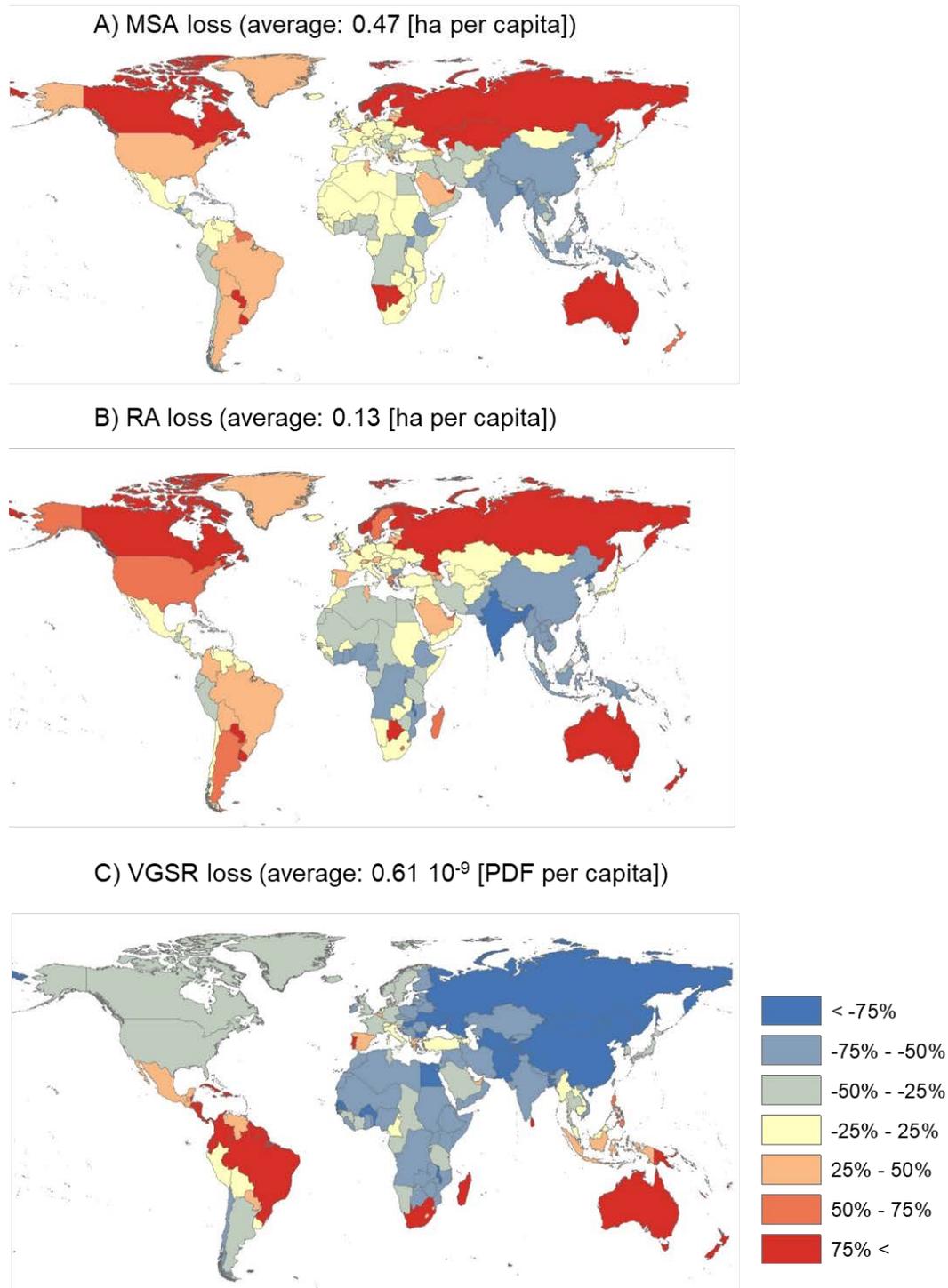
244 We compared the biodiversity and land footprint ranking of the 140 GTAP-regions with
245 spearman rank correlation. A high spearman rank correlation between biodiversity and land
246 footprint indicators implies low added value of including biodiversity as a separate indicator, while
247 low correlation shows that biodiversity indicators indeed provide additional regional insights.

248 3. Results

249 3.1. Footprints of nations

250 Alpha diversity-based results showed close regional alignment (Fig. 1). Australia,
251 Botswana, Canada and Russia ranked among the top ten countries, while India, China,
252 Bangladesh had the lowest per capita biodiversity footprints. Note that among the alpha diversity
253 footprints, MSA-based footprints of Uruguay and Paraguay were relatively low compared to RA-
254 based footprints (Fig. 2A). For Kazakhstan the situation was reversed. Compared to loss factors
255 for RA, loss factors for MSA are relatively high for cropland compared to pasture (compare
256 Supplementary information, Table A4). This explains why Kazakhstan, with a relatively high crop
257 consumption, has a relatively high MSA-based biodiversity footprint. The average uncertainty was
258 +/- 20% for MSA footprints, +/- 40% for RA footprints and +/- 16% for RWSR footprints (for
259 country-specific values see Supplementary data, Tables B1-B3).

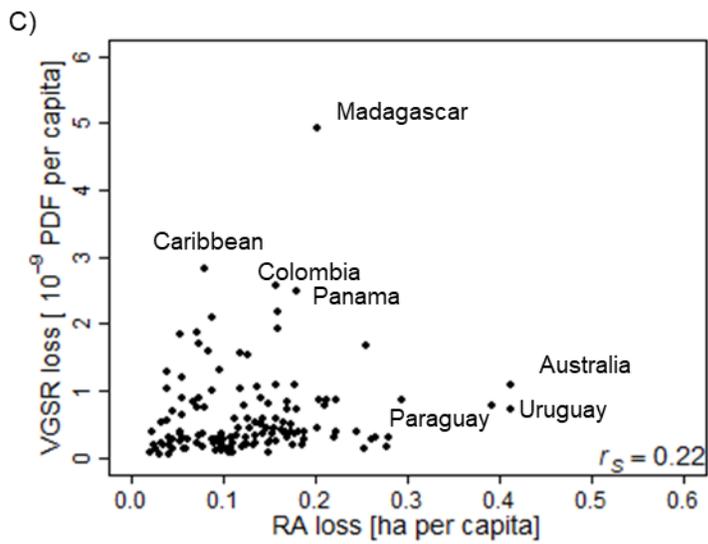
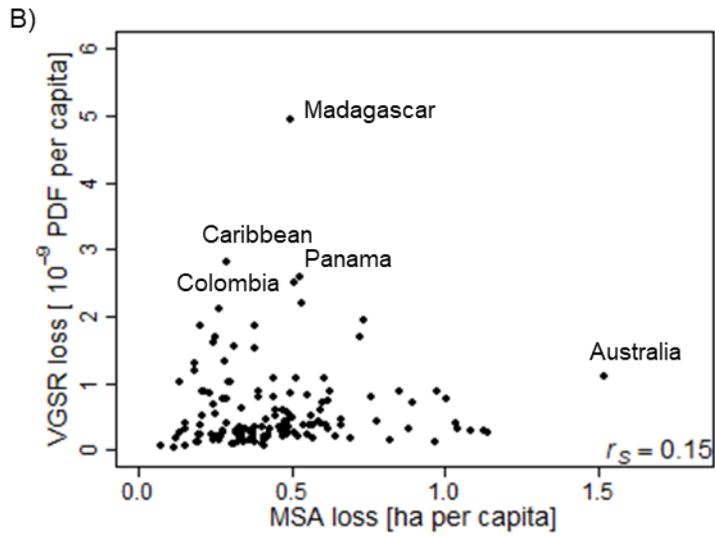
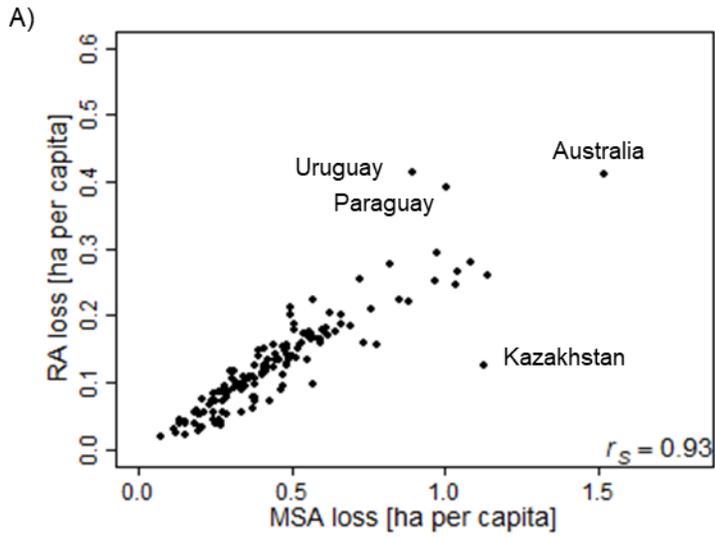
260 Contrastingly, the gamma diversity results identified primarily tropical regions, such as
261 Madagascar, the Caribbean and Brazil, as having high per capita footprints (Fig. 1; Fig. 2B, C).
262 Pakistan, Mongolia and Bangladesh were among the countries with the lowest per capita gamma
263 diversity footprints. The average uncertainty was -60 to +85% (for country-specific values see
264 Supplementary data, Tables B4).



265
 266 **Fig. 1.** Region-specific differences (in %) in biodiversity footprints per capita compared to the average per
 267 capita footprint for (A) mean species abundance loss, (B) relative abundance loss, and (C) vulnerability-
 268 weighted global relative species richness loss. PDF = potentially disappeared fraction of species.

269 **3.2. Comparison of biodiversity footprints**

270 Fig. 2 indicates high (Spearman rank) correlations between the alpha diversity footprints
271 ($r_s > 0.93$), while the (Spearman rank) correlation between the gamma and the alpha diversity
272 footprints was relatively low ($r_s < 0.22$). Alpha diversity loss factors do not depend on the regional
273 context, while regional differences are prominent in gamma diversity loss factors. Consequently,
274 we found limited convergence of the gamma diversity footprints with any of the alpha diversity
275 footprints. The same findings were obtained for individual consumption categories (see
276 Supplementary information, Table A7a).

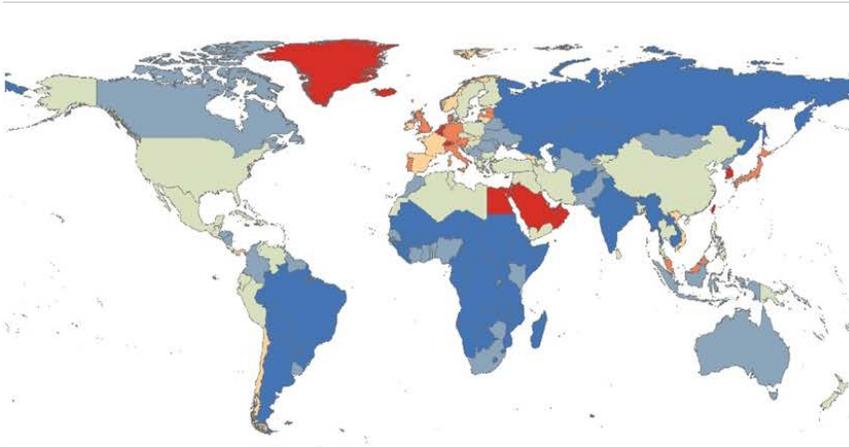


278 **Fig. 2.** Pairwise comparison of consumption-based per capita biodiversity footprints (A) relative abundance
279 (RA) and mean species abundance (MSA) footprints, (B) vulnerability-weighted global relative species
280 richness (VGSR) and mean species abundance footprints, (C) vulnerability-weighted global relative species
281 richness and relative abundance footprints. PDF = potentially disappeared fraction of species, r_s =
282 Spearman rank correlation.

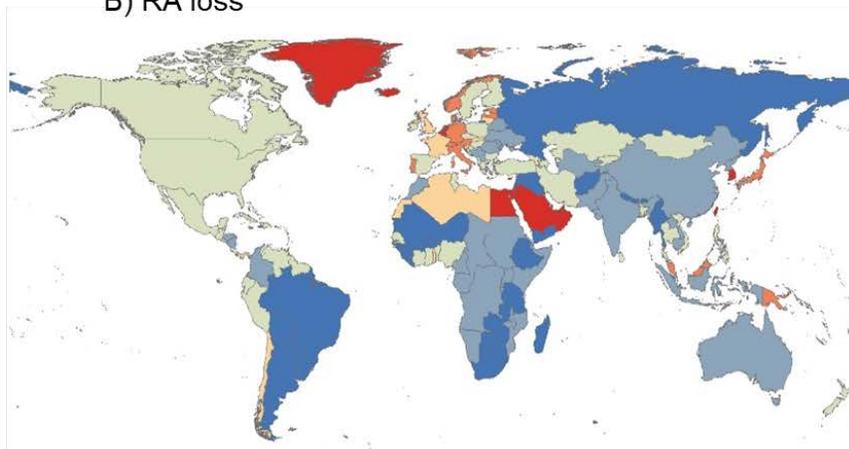
283 3.3. Footprints and trade

284 Alpha diversity footprints showed high shares of imported biodiversity loss for developed and
285 densely populated regions (e.g. Europe, Japan, South Korea) or regions with natural conditions
286 limiting the potential for agricultural land use (e.g. Saudi Arabia). In contrast, the gamma diversity-
287 based footprints were largely influenced by the initial threat of species' extinction, as captured by
288 the specific loss factors of the country in question, or the relevance of trade relationships with
289 countries with a high threat level (Fig. 3.; Supplementary data, Tables B1-B4). For instance, the
290 gamma diversity footprints also indicated high imported biodiversity loss shares for countries such
291 as Russia (68% for gamma diversity vs 9% for alpha diversity footprints), the US (71% for gamma
292 diversity vs 33% for alpha diversity footprints) and Canada (88% for gamma diversity vs 24% for
293 alpha diversity footprints).

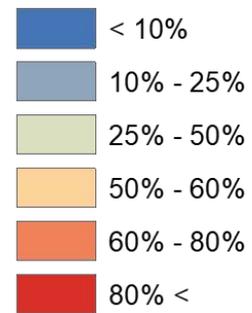
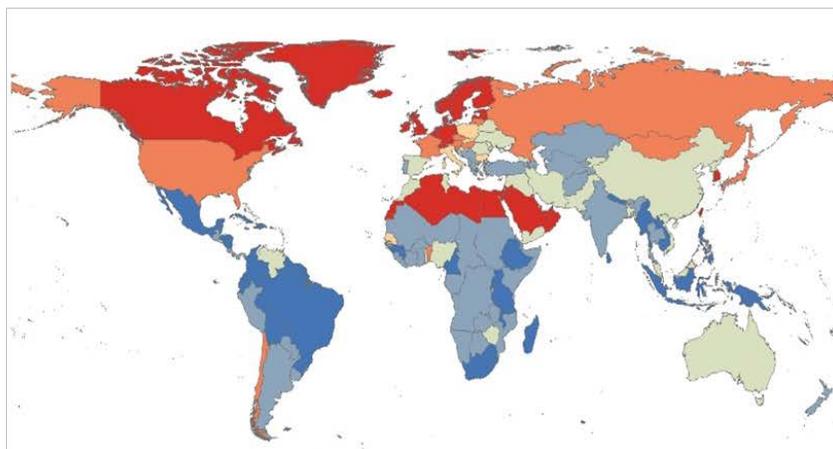
A) MSA loss



B) RA loss



C) VGSR loss



294

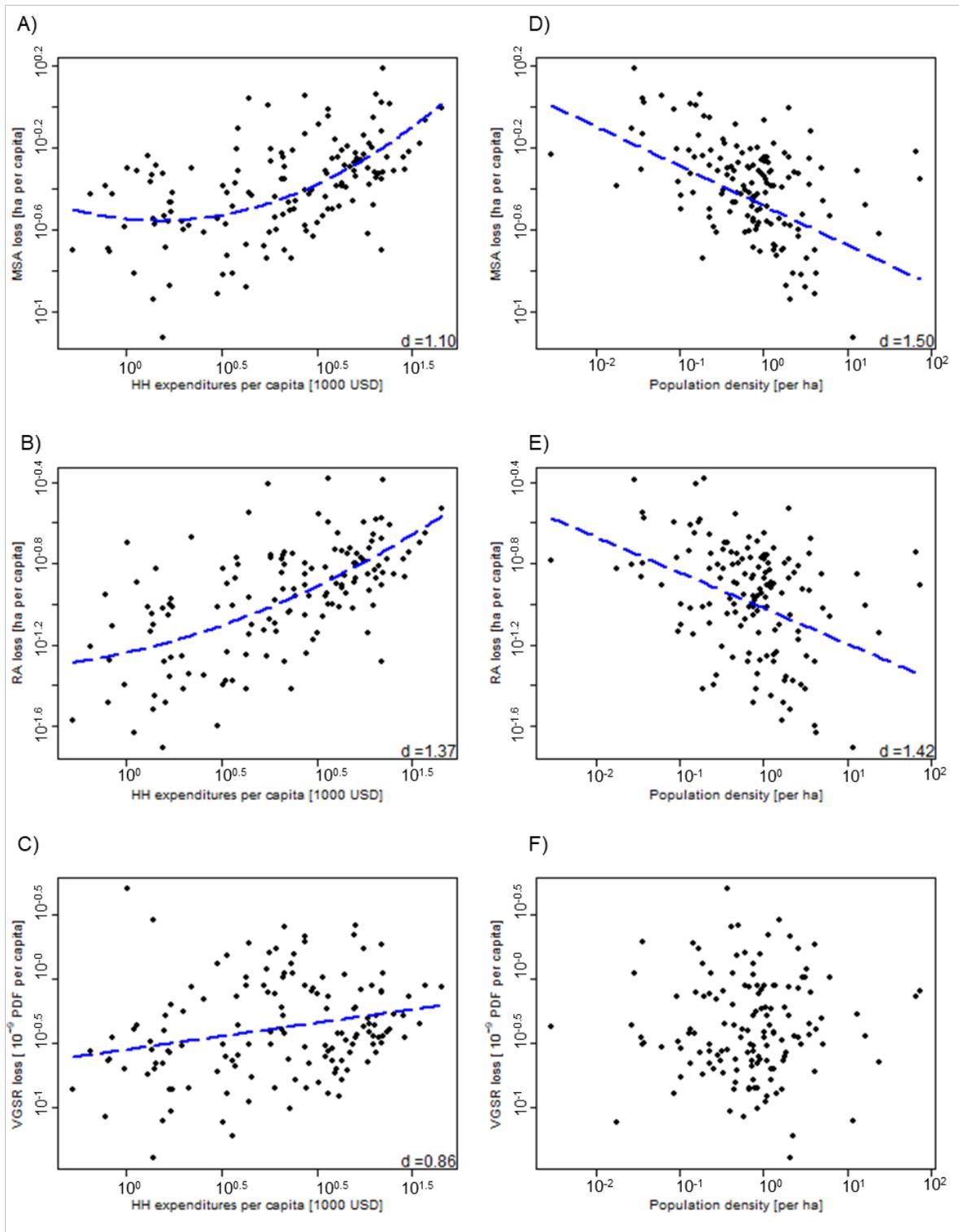
295 **Fig. 3.** Shares of imported biodiversity loss (A) mean species abundance, (B) relative abundance, (C)

296 vulnerability-weighted global relative species richness.

297 3.4. Footprints, prosperity and population density

298 Household expenditure and population density explain 52% to 55% of the variance for the
299 alpha diversity footprints and considerably less for the gamma diversity footprints with an
300 explained variance of 5%. The alpha diversity-based footprints showed a distinct positive
301 relationship with household expenditure and negative relationship with population density (Fig.
302 4). For these relationships, the alpha based footprints were less sensitive to household
303 expenditure ($d = 1.10-1.37$) compared to population density ($d = 1.42-1.50$). The gamma diversity
304 footprint showed a relatively weak responsiveness to household expenditure ($d = 0.87$) and no
305 relationship for population density, as population density was not selected as variable in the best
306 model (Supplementary information, Section A5).

307



308

309 **Fig. 4.** Partial response plots of per capita biodiversity footprints related to per capita household
 310 (HH) expenditure (A) mean species abundance, (B) relative abundance, (C) vulnerability-
 311 weighted global relative species richness; and related to population density (D) mean species
 312 abundance, (E) relative abundance, (F) vulnerability-weighted global relative species richness.

313 Relative differences, d , were calculated according to equation (3). PDF = potentially
314 disappeared fraction of species.

315 3.5. Comparison with land footprints

316 Comparing the alpha diversity footprints with land footprints showed close alignment ($r_s =$
317 0.69 – 0.82) implying low added value of alpha biodiversity indicators compared to a simple
318 summation of land requirements. There are, however, noteworthy outliers (Supplementary
319 information, Section A4.3). Countries, such as Mongolia and Botswana, have large shares of low-
320 intensity grazing areas and consequently large land footprints. These areas have – according to
321 the definition of the alpha biodiversity loss factors (Supplementary information, Table A4) – no
322 biodiversity impacts. Thus, using a land footprint assessment as a proxy for alpha diversity
323 footprints could overestimate countries' biodiversity impacts. For gamma footprints we found only
324 a limited relationship to land footprints ($r_s = 0.16$) showing that land footprints cannot be used as
325 a proxy for gamma diversity.

326 4. Discussion

327 4.1. Interpretation

328 Our novel inter-indicator comparison of linking a common land use and MRIO framework with
329 different biodiversity indicators, shows that employing alpha diversity indicators results in a
330 different selection of countries with relatively high biodiversity footprints compared to the gamma
331 diversity indicator. For alpha diversity footprints, regional differences were partly driven by the
332 generic loss factors allocated to different land use types (compare Supporting information, Table
333 A4). For gamma diversity, loss factors are given by region as well as land use types, giving more
334 emphasis to the location of biodiversity loss. The regional component reflects threat levels to
335 global biodiversity, as per the IUCN red list classification (IUCN 2018) (see Supplementary
336 information, Section A7). Compared to a purely land based footprint assessment, biodiversity
337 footprints capture the quality of biodiversity. While there was close alignment between countries'
338 ranking of alpha footprints and land footprints, the identified outliers showed the additional insights
339 gained from incorporating alpha diversity indicators for some countries. Land footprints treat land
340 areas equally and would thus overestimate the biodiversity impact of countries with large shares
341 of low-intensity grazing areas, such as Mongolia and Botswana. Furthermore, as indicated by our
342 findings, land footprints are not able to serve as a proxy for gamma diversity footprints.

343 There is close agreement between our alpha diversity-based (particularly MSA) results and
344 those of Wilting et al. (2017), who employed an EEMRIO based on the WIOD economic database
345 to link land use, greenhouse gas (GHG) emissions and MSA. For example, both studies showed

346 relatively high per capita biodiversity footprints for Australia and Russia, as well as North
347 American and European countries. Wilting et al. (2017) identified food consumption as
348 contributing 50% of global land-related biodiversity loss; we report an aggregated contribution of
349 59% for the consumption of 'grains, other crops', 'meat, dairy, fish' and 'processed foods,
350 beverages, tobacco' for our MSA-based assessment (see Supplementary information, Table
351 A7a). The land-related biodiversity footprint in Wilting et al. (2017) also includes biodiversity
352 losses from infrastructure and encroachment that are not directly caused by the consumption of
353 food. Furthermore, Wilting et al. (2017) have a limited representation of developing nations,
354 particularly in Africa. Our results show high biodiversity footprints for several African countries
355 (e.g. Botswana, Namibia), illustrating the importance of greater regional detail for comprehensive
356 analysis of consumption-based biodiversity footprints.

357 Our relatively high per capita biodiversity footprints of Australia, Botswana and Kazakhstan
358 are in line with the analysis of Kitzes et al. (2016). They employed the GTAP database and used
359 the same methodology as Peters et al. (2011) for their MRIO model construction. To assess
360 biodiversity impacts, they related land use impacts to bird loss (measured as 'missing individual
361 birds'). Thus, by focusing on one taxon, they employed a narrower focus of the implications of
362 biodiversity loss, which possibly causes the comparatively low relevance of Europe and Central
363 America in their analysis. Kitzes et al. (2016) also identified food consumption as the largest cause
364 of biodiversity loss and attributed a lesser relevance to sectors with limited connection to land use
365 (such as 'transport, communication' and 'services').

366 Comparing analyses by Lenzen et al. (2012) and Chaudhary and Kastner (2016) to our
367 gamma diversity results, we find a similar emphasis on losses in tropical biodiversity. Lenzen et
368 al. (2012) used an MRIO model based on the Eora database (Lenzen et al., 2013) and directly
369 linked its sectors to IUCN red-list species, establishing a focus on globally endangered species.
370 Using IUCN species information to reflect global biodiversity impacts is also intrinsic to the gamma
371 indicator used in our analysis. Based on the IUCN data, species extinction threat levels are
372 particularly high in tropical regions. Similar to our findings, Lenzen et al. (2013) identified North
373 American and European countries and Japan as having high imported shares of biodiversity loss;
374 countries in tropical regions with endangered biodiversity, (e.g. Madagascar) were primary
375 exporters of biodiversity loss. Chaudhary and Kastner (2016) did not employ an EEMRIO, but
376 linked land use maps with physical trade data from the FAO and biodiversity loss factors to
377 analyze global biodiversity footprints. Countries in Central America and the Caribbean were
378 shown to have high per capita footprints. They also found high shares of imported biodiversity
379 loss for developed and small countries, such as European countries, Bahrain and Qatar.

380 The relationship between biodiversity footprints and household expenditure levels and
381 population density observed for our alpha diversity indicators was also found by Wilting et al
382 (2017). However, in our study, the relationship between gamma diversity footprints and household
383 expenditure was much weaker and the relationship between gamma diversity footprints and
384 population density is not statistically significant. Thus, the strength of the link between the
385 biodiversity loss drivers, household expenditure levels and population density, and biodiversity
386 impacts is influenced by the choice of biodiversity indicator.

387 4.2. Limitations

388 By connecting various biodiversity indicators to land use information, we provide a method to
389 calculate consumption-based biodiversity footprints globally. However, this approach also has
390 several limitations and constraints.

391 Although using the GTAP database allows for a greater level of regional detail, our method
392 does not overcome key weaknesses of using MRIO in biodiversity footprint assessments, namely
393 the high level of geographic aggregation (country-level) and the reliance on monetary flows to
394 capture global dynamics (for further discussion of MRIO weaknesses in the biodiversity context
395 see Kjaer et al. (2015) and Kitzes et al. (2016)). Biodiversity contributes to local life-supporting
396 functions and thus assessment based on country-level aggregation might obscure threats to local
397 ecosystem function.

398 Furthermore, our assessment is limited to biodiversity loss related to land use. Excluding other
399 drivers, such as climate change, clearly results in an underestimation of biodiversity footprints for
400 consumption categories that are less reliant on land use, such as 'transport, communication'. For
401 this consumption category, our MSA-based assessment indicates a contribution of 2% to overall
402 biodiversity footprints, whereas Wilting et al. (2017) report a contribution of 11% (47% of which
403 resulted from GHG emissions).

404 Other constraining factors are that only a limited number of biodiversity indicators have
405 sufficient global coverage to be linked to our calculations and the potential influence of the
406 underlying land use classification scheme on the results. In the present analysis we were
407 restricted to using biodiversity indicators that can be used in global assessments, have a well-
408 documented methodological basis and which employ data that is publicly available. The
409 indicators' methodology needed to be documented such that it enabled easy aggregation and
410 provided sufficient detail on the definition of the underlying land use categories, to allow for a
411 mapping with our country and land use classification. For land use classification, we faced the
412 challenge of harmonizing aggregate classification schemes (e.g. Chaudhary et al. (2015, 2016a,

413 2016b) rely on six categories) and relatively disaggregated schemes (Newbold et al. (2016) and
414 Schipper et al. (2016a) that rely on 13 and 16 categories, respectively) to facilitate allocation of
415 physical areas from the FAO without losing information contained in the biodiversity loss factors.

416 Furthermore, the choice of land use areas included in the assessment can influence the list
417 of countries identified as having high biodiversity footprints (see Supplementary information,
418 Section A8 for an extensive analysis). For instance, setting the loss factors connected to the land
419 use category 'other forest' to zero, substantially lowered the per capita footprints for several
420 developing countries (e.g. Botswana, Namibia, Zambia) and developed nations (e.g. Finland,
421 Russia, Australia) (Supplementary information, Fig. A12). The (Spearman rank) correlation
422 analysis, however, still showed high correlations between alpha diversity indicators and limited
423 convergence between alpha and gamma diversity indicators (compare Supplementary
424 information, Table A7a and Table A7b).

425 4.3. Implications – relevance and outlook

426 Our methodology allows for a comprehensive assessment of the main consumption patterns
427 causing biodiversity loss. We demonstrate that using different biodiversity indicators (alpha vs.
428 gamma) has implications on the countries and regions identified as key contributors to global
429 biodiversity loss. Assessing and mitigating global environmental impacts requires targeted action
430 by producers and changes in consumption patterns (Poore and Nemecek, 2018). Biodiversity
431 footprinting can facilitate decision-makers to assess the implications of behavior change, ranging
432 from changes in diets to shifts towards low impact agricultural production (see Wilting et al. (2017)
433 for an extensive list). By extending these analyses across different dimensions of biodiversity, the
434 scope of results can be broadened. Alpha diversity footprints are particularly linked to ecosystems'
435 capacity to provide local ecosystem services (Newbold et al., 2015). Gamma diversity footprints
436 compliment alpha diversity footprints, by capturing implications of consumption on, for example,
437 endangered tropical diversity. According to our comparison, no single indicator would have been
438 able to capture both aspects. Comprehensive biodiversity assessment should also include
439 functional or structural aspects of biodiversity (beta diversity) (Balvanera et al., 2014; Isbell et al.,
440 2017; Marques et al., 2018). However, there is currently no indicator capturing these features of
441 biodiversity with a regional and sectoral coverage and connection to land use that could be linked
442 to our EEMRIO framework. The flexibility of our EEMRIO structure allows for a future widening of
443 the scope of analyses, should relevant indicators become available.

444 Our work also provides the basis for future scenario analyses. With these analyses, public
445 and private sector decision-makers could gain additional insights into the biodiversity implications

446 of future global production and consumption patterns – e.g. cross-industry changes in product
447 composition or raw material sourcing strategies, shifts in dietary preferences, conservation
448 activities and changes in policy environments. By employing at least a two-dimensional view on
449 biodiversity, future actions can be designed that safeguard against a loss of diversity with high
450 risks of species extinction (gamma diversity) as well as losses that are relevant for local
451 ecosystem functioning (alpha diversity).
452

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459 [Appendix A. Supplementary information \(DOCX file\)](#)

460 [Appendix B. Supplementary data \(XLS file\)](#)

461

- 463 Alkemade, R., Oorschot, M. van, Miles, L., Nellemann, C., Bakkenes, M., Brink, B. ten, 2009.
464 GLOBIO3: A Framework to Investigate Options for Reducing Global Terrestrial
465 Biodiversity Loss. *Ecosystems* 12, 374–390. <https://doi.org/10.1007/s10021-009-9229-5>
- 466 Arets, E., Van der Meer, P., Verwer, C., Hegeveld, G., Tolcamp, G., Nabuurs, G., Van Oorschot,
467 M., 2011. Global wood production: assessment of industrial wood supply from
468 forest management systems in different global regions (No. 1808). Alterra Wageningen
469 UR, Wageningen.
- 470 Balvanera, P., Siddique, I., Dee, L., Paquette, A., Isbell, F., Gonzalez, A., Byrnes, J., O'Connor,
471 M.I., Hungate, B.A., Griffin, J.N., 2014. Linking Biodiversity and Ecosystem Services:
472 Current Uncertainties and the Necessary Next Steps. *BioScience* 64, 49–57.
473 <https://doi.org/10.1093/biosci/bit003>
- 474 Cardinale, B.J., Duffy, J.E., Gonzalez, A., Hooper, D.U., Perrings, C., Venail, P., Narwani, A.,
475 Mace, G.M., Tilman, D., Wardle, D.A., Kinzig, A.P., Daily, G.C., Loreau, M., Grace, J.B.,
476 Larigauderie, A., Srivastava, D.S., Naeem, S., 2012. Biodiversity loss and its impact on
477 humanity. *Nature* 486, 59–67. <https://doi.org/10.1038/nature11148>
- 478 Chaudhary, A., Brooks, T.M., 2017. National Consumption and Global Trade Impacts on
479 Biodiversity. *World Development*. <https://doi.org/10.1016/j.worlddev.2017.10.012>
- 480 Chaudhary, A., Kastner, T., 2016. Land use biodiversity impacts embodied in international food
481 trade. *Global Environmental Change* 38, 195–204.
- 482 Chaudhary, A., Pfister, S., Hellweg, S., 2016a. Spatially Explicit Analysis of Biodiversity Loss
483 Due to Global Agriculture, Pasture and Forest Land Use from a Producer and Consumer
484 Perspective. *Environ. Sci. Technol.* 50, 3928–3936.
485 <https://doi.org/10.1021/acs.est.5b06153>
- 486 Chaudhary, A., Verones, F., de Baan, L., Hellweg, S., 2015. Quantifying Land Use Impacts on
487 Biodiversity: Combining Species–Area Models and Vulnerability Indicators. *Environ. Sci.*
488 *Technol.* 49, 9987–9995. <https://doi.org/10.1021/acs.est.5b02507>
- 489 Chaudhary, A., Verones, F., de Baan, L., Pfister, S., Hellweg, S., 2016b. 11. Land stress:
490 Potential species loss from land use (global; PSSRg), in: LC-IMPACT Report.
- 491 ESA CCI, 2017. Land Cover Climate Change Initiative - Product User Guide Version 2.0. UCL-
492 Geomatics, Belgium.
- 493 FAO, 2017. FAO Statistical Database.
- 494 FAO, 2010. Global Forest Resources Assessment 2010 Main report, FAO Forestry Paper. FAO,
495 Rome.
- 496 Gotelli, N.J., Colwell, R.K., 2001. Quantifying biodiversity: procedures and pitfalls in the
497 measurement and comparison of species richness. *Ecology Letters* 4, 379–391.
498 <https://doi.org/10.1046/j.1461-0248.2001.00230.x>
- 499 Hertwich, E.G., Peters, G.P., 2009. Carbon Footprint of Nations: A Global, Trade-Linked
500 Analysis. *Environ. Sci. Technol.* 43, 6414–6420. <https://doi.org/10.1021/es803496a>
- 501 Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Díaz, S., Hector, A., Mace, G.M., Wardle, D.A.,
502 O'Connor, M.I., Duffy, J.E., Turnbull, L.A., Thompson, P.L., Larigauderie, A., 2017.
503 Linking the influence and dependence of people on biodiversity across scales. *Nature*
504 546, 65–72. <https://doi.org/10.1038/nature22899>
- 505 IUCN, 2018. IUCN Red List of Threatened Species. Version 2017-3. <http://www.iucnredlist.org>
- 506 Kitzes, J., Berlow, E., Conlisk, E., Erb, K., Iha, K., Martinez, N., Newman, E.A., Plutzer, C.,
507 Smith, A.B., Harte, J., 2016. Consumption-Based Conservation Targeting: Linking
508 Biodiversity Loss to Upstream Demand through a Global Wildlife Footprint.
509 *CONSERVATION LETTERS* n/a-n/a. <https://doi.org/10.1111/con4.12321>

510 Kjaer, L.L., Høst-Madsen, N.K., Schmidt, J.H., McAlloone, T.C., 2015. Application of
511 Environmental Input-Output Analysis for Corporate and Product Environmental
512 Footprints—Learnings from Three Cases. *Sustainability* 7, 11438–11461.
513 <https://doi.org/10.3390/su70911438>

514 Kuiper, M., Bartelings, H., Kavallari, A., 2013. Data manipulations in MAGNET User guide. LEI,
515 The Hague.

516 Lee, H., 2005. The GTAP Land Use Data Base and the GTAPE-AEZ Model: Incorporating Agro-
517 Ecologically Zoned Land Use Data and Land-based Greenhouse Gases Emissions into
518 the GTAP Framework. Presented at the 8th Annual Conference on Global Economic
519 Analysis, Purdue University Global Trade Analysis Project, West Lafayette, IN.

520 Lenzen, M., Kanemoto, K., Moran, D., Geschke, A., 2012. Mapping the Structure of the World
521 Economy. *Environ. Sci. Technol.* 46, 8374–8381. <https://doi.org/10.1021/es300171x>

522 Lenzen, M., Moran, D., Kanemoto, K., Foran, B., Lobefaro, L., Geschke, A., 2012. International
523 trade drives biodiversity threats in developing nations. *Nature* 486, 109–112.
524 <https://doi.org/10.1038/nature11145>

525 Lenzen, M., Moran, D., Kanemoto, K., Geschke, A., 2013. Building Eora: A Global Multi-Region
526 Input–Output Database at High Country and Sector Resolution. *Economic Systems
527 Research* 25, 20–49. <https://doi.org/10.1080/09535314.2013.769938>

528 Leontief, W., 1936. Quantitative input and output realtions in the economic systems of the
529 United States, in: *The Review of Economic Statistics*. pp. 105–125.

530 Marques, A., Verones, F., Kok, M.T., Huijbregts, M.A., Pereira, H.M., 2017. How to quantify
531 biodiversity footprints of consumption? A review of multi-regional input–output analysis
532 and life cycle assessment. *Current Opinion in Environmental Sustainability*, Part A:
533 Environmental change issues. Part B: Open Issue, Part III 29, 75–81.
534 <https://doi.org/10.1016/j.cosust.2018.01.005>

535 McLeod, M., Gerber, P., Mottet, A., Tempio, G., Falcucci, A., Opio, C., Vellinga, T., Henderson,
536 B., Steinfeld, H., 2013. Greenhouse gas emissions from pig and chicken supply chains
537 - A global life cycle assessment. FAO, Rome.

538 Miller, R., Blair, P., 2009. *Input-output analysis: foundations and extensions*. Cambridge Univ.
539 Press, Cambridge.

540 Moran, D., Kanemoto, K., 2017. Identifying species threat hotspots from global supply chains.
541 *Nature Ecology & Evolution* 1, 0023. <https://doi.org/10.1038/s41559-016-0023>

542 Moran, D., Petersone, M., Verones, F., 2016. On the suitability of input–output analysis for
543 calculating product-specific biodiversity footprints. *Ecological Indicators* 60, 192–201.
544 <https://doi.org/10.1016/j.ecolind.2015.06.015>

545 Murphy, G.E.P., Romanuk, T.N., 2014. A meta-analysis of declines in local species richness
546 from human disturbances. *Ecol Evol* 4, 91–103. doi:10.1002/ece3.909

547 Narayanan, B., Aguiar, A., McDougall, R., 2015. *Global Trade, Assistance and Production: The
548 GTAP 9 Data Base*. Center for Global Trade Analysis, Purdue University, West
549 Lafayette, IN.

550 Newbold, T., Hudson, L.N., Arnell, A.P., Contu, S., Palma, A.D., Ferrier, S., Hill, S.L.L., Hoskins,
551 A.J., Lysenko, I., Phillips, H.R.P., Burton, V.J., Chng, C.W.T., Emerson, S., Gao, D.,
552 Pask-Hale, G., Hutton, J., Jung, M., Sanchez-Ortiz, K., Simmons, B.I., Whitmee, S.,
553 Zhang, H., Scharlemann, J.P.W., Purvis, A., 2016. Has land use pushed terrestrial
554 biodiversity beyond the planetary boundary? A global assessment. *Science* 353, 288–
555 291. <https://doi.org/10.1126/science.aaf2201>

556 Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Börger, L., Bennett,
557 D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S.,
558 Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J.,
559 Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D.,
560 Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson,

561 J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W.,
562 Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. *Nature* 520,
563 45–50. <https://doi.org/10.1038/nature14324>

564 Nishijima, S., Furukawa, T., Kadoya, T., Ishihama, F., Kastner, T., Matsuda, H., Kaneko, N.,
565 2016. Evaluating the impacts of wood production and trade on bird extinction risks.
566 *Ecological Indicators* 71, 368–376. <https://doi.org/10.1016/j.ecolind.2016.07.008>

567 Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood,
568 E.C., D'amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F.,
569 Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P., Kassem, K.R.,
570 2001. Terrestrial Ecoregions of the World: A New Map of Life on Earth A new global map
571 of terrestrial ecoregions provides an innovative tool for conserving biodiversity.
572 *BioScience* 51, 933–938. [https://doi.org/10.1641/0006-](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)
573 [3568\(2001\)051\[0933:TEOTWA\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2001)051[0933:TEOTWA]2.0.CO;2)

574 Otte, J., Costales, A., Dijkman, J., Pica-Ciamarra, U., Robinson, T., Ahuja, V., Ly, C., Roland-
575 Holst, D., 2012. Livestock sector development for poverty reduction: an economic and
576 policy perspective. FAO, Rome.

577 Pereira, H.M., Navarro, L.M., Martins, I.S., 2012. Global Biodiversity Change: The Bad, the
578 Good, and the Unknown. *Annual Review of Environment and Resources* 37, 25–50.

579 Peters, G.P., Andrew, R., Lennox, J., 2011. Constructing an Environmentally-Extended Multi-
580 Regional Input–Output Table Using the Gtap Database. *Economic Systems Research*
581 23, 131–152. <https://doi.org/10.1080/09535314.2011.563234>

582 Peters, J.C., 2016. The GTAP-Power Data Base: Disaggregating the Electricity Sector in the
583 GTAP Data Base. *Journal of Global Economic Analysis* 1, 209–250.
584 <https://doi.org/10.21642/JGEA.010104AF>

585 Poore, J., Nemecek, T., 2018. Reducing food's environmental impacts through producers and
586 consumers. *Science* 360, 987–992. <https://doi.org/10.1126/science.aag0216>

587 Pouillot, R., Delignette-Mueller, M.L., 2010. Evaluating variability and uncertainty separately in
588 microbial quantitative risk assessment using two R packages. *International Journal of*
589 *Food Microbiology* 142, 330–340. <https://doi.org/10.1016/j.ijfoodmicro.2010.07.011>

590 Purvis, A., Hector, A., 2000. Getting the measure of biodiversity. *Nature* 405, 212–219.
591 <https://doi.org/10.1038/35012221>

592 Robinson, T.P., Wint, G.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E.,
593 Cinardi, G., D'Aiotti, L., Hay, S.I., Gilbert, M., 2014. Mapping the Global Distribution of
594 Livestock. *PLoS One* 9. <https://doi.org/10.1371/journal.pone.0096084>

595 Santini, L., Belmaker, J., Costello, M.J., Pereira, H.M., Rossberg, A.G., Schipper, A.M., Ceașu,
596 S., Dornelas, M., Hilbers, J.P., Hortal, J., Huijbregts, M.A.J., Navarro, L.M., Schippers,
597 K.H., Visconti, P., Rondinini, C., 2017. Assessing the suitability of diversity metrics to
598 detect biodiversity change. *Biological Conservation*, SI:Measures of biodiversity 213,
599 Part B, 341–350. <https://doi.org/10.1016/j.biocon.2016.08.024>

600 Schipper, A., Bakkenes, M., Meijer, J., Alkemade, R., Huijbregts, M., 2016a. GLOBIO 3.5
601 technical model description - PBL Netherlands Environmental Assessment Agency, PBL
602 publication number: 2369. PBL Netherlands Environmental Assessment Agency, The
603 Hague.

604 Schipper, A.M., Belmaker, J., de Miranda, M.D., Navarro, L.M., Böhning-Gaese, K., Costello,
605 M.J., Dornelas, M., Foppen, R., Hortal, J., Huijbregts, M.A.J., Martín-López, B.,
606 Pettorelli, N., Queiroz, C., Rossberg, A.G., Santini, L., Schippers, K., Steinmann, Z.J.N.,
607 Visconti, P., Rondinini, C., Pereira, H.M., 2016b. Contrasting changes in the abundance
608 and diversity of North American bird assemblages from 1971 to 2010. *Glob Change Biol*
609 22, 3948–3959. <https://doi.org/10.1111/gcb.13292>

610 Spangenberg, J.H., 2007. Biodiversity pressure and the driving forces behind. *Ecological*
611 *Economics* 61, 146–158. <https://doi.org/10.1016/j.ecolecon.2006.02.021>

612 Steen-Olsen, K., Weinzettel, J., Cranston, G., Ercin, A.E., Hertwich, E.G., 2012. Carbon, Land,
613 and Water Footprint Accounts for the European Union: Consumption, Production, and
614 Displacements through International Trade. *Environ. Sci. Technol.* 46, 10883–10891.
615 <https://doi.org/10.1021/es301949t>

616 Tilman, D., Isbell, F., Cowles, J.M., 2014. Biodiversity and Ecosystem Functioning. *Annual*
617 *Review of Ecology, Evolution, and Systematics* 45, 471–493.
618 <https://doi.org/10.1146/annurev-ecolsys-120213-091917>

619 Timmer, M.P., Dietzenbacher, E., Los, B., Stehrer, R., de Vries, G.J., 2015. An Illustrated User
620 Guide to the World Input–Output Database: the Case of Global Automotive Production.
621 *Review of International Economics* 23, 575–605. <https://doi.org/10.1111/roie.12178>

622 Varian, H. 2006. *Intermediate Microeconomics (International Student Edition)*. Seventh Edition.
623 New York: W.W. Norton.

624 Veronesi, F., Moran, D., Stadler, K., Kanemoto, K., Wood, R., 2017. Resource footprints and
625 their ecosystem consequences. *Scientific Reports* 7, 40743.
626 <https://doi.org/10.1038/srep40743>

627 Weinzettel, J., Hertwich, E.G., Peters, G.P., Steen-Olsen, K., Galli, A., 2013. Affluence drives
628 the global displacement of land use. *Global Environmental Change* 23, 433–438.
629 <https://doi.org/10.1016/j.gloenvcha.2012.12.010>

630 Whittaker, R.H., 1972. Evolution and Measurement of Species Diversity. *Taxon* 21, 213–251.
631 <https://doi.org/10.2307/1218190>

632 Wiedmann, T.O., Schandl, H., Lenzen, M., Moran, D., Suh, S., West, J., Kanemoto, K., 2015.
633 The material footprint of nations. *PNAS* 112, 6271–6276. <https://doi.org/10.1073/pnas.1220362110>

634

635 Wilting, H.C., Schipper, A.M., Bakkenes, M., Meijer, J.R., Huijbregts, M.A.J., 2017. Quantifying
636 Biodiversity Losses Due to Human Consumption: A Global-Scale Footprint Analysis.
637 *Environ. Sci. Technol.* 51, 3298–3306. <https://doi.org/10.1021/acs.est.6b05296>

638 Wood, R., Stadler, K., Bulavskaya, T., Lutter, S., Giljum, S., de Koning, A., Kuenen, J., Schütz,
639 H., Acosta-Fernández, J., Usubiaga, A., Simas, M., Ivanova, O., Weinzettel, J., Schmidt,
640 J.H., Merciai, S., Tukker, A., 2014. Global Sustainability Accounting—Developing
641 EXIOBASE for Multi-Regional Footprint Analysis. *Sustainability* 7, 138–163.
642 <https://doi.org/10.3390/su7010138>

643 World Bank. 2018. *World Development Indicators*. Washington, D.C.: The World Bank.

644 World Programme for the Census of Agriculture 2020 - Volume 1: Programme, concepts and
645 definitions, 2015. , *FAO Statistical Development Series*. FAO.

646 You, L., Wood-Sichra, S., Fritz, Z., Guo, L., See, L., Koo, J., 2014. Spatial Production Allocation
647 Model (SPAM) 2005 v2.0.

648

649