

*From tropical shelters to temperate defaunation: the relationship between agricultural transition stage and the distribution of threatened mammals*

Article

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1 **From tropical shelters to temperate defaunation: the relationship between agricultural**  
2 **transition stage and the distribution of threatened mammals**

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## 31 **Abstract**

### 32 ***Aim***

33 Agriculture is a key threat to biodiversity, however its relationship with biodiversity patterns is  
34 understudied. Here, we evaluate how the extent, intensity, and history of croplands relate to the  
35 global distribution of threatened mammals. We propose two hypotheses to explain these  
36 relationships: *shelter*, which predicts that threatened species concentrate in areas with low human  
37 land use; and *threat*, according to which threatened species should concentrate in areas of high  
38 human land use.

### 39 ***Location***

40 Global.

### 41 ***Time period***

42 c.B.C.6000 - 2014.

### 43 ***Major taxa studied***

44 Terrestrial mammals.

### 45 ***Methods***

46 We used boosted regression trees (BRT) that include spatial autocorrelation to investigate the  
47 relationship between the proportion of threatened terrestrial mammals (as defined by the IUCN Red  
48 List) and multiple metrics describing agricultural extent, intensity and history derived from remote  
49 sensing data and statistical projections. Data were analysed with a grain size of ~110 x 110 km at  
50 both global and biogeographic-realm scales.

### 51 ***Results***

52 Agricultural extent and intensity were the most relevant indicator types, with specific metrics  
53 important for each realm. Forest cover (extent) was identified as important in several regions.  
54 Tropical regions in early agricultural transition stages (e.g., frontier landscapes) were consistent  
55 with the *shelter* hypothesis, whereas patterns found for regions in later stages (e.g., intensified  
56 agricultural landscapes) were mostly found in temperate regions and agreed with the *threat*  
57 hypothesis.

### 58 ***Main conclusions***

59 These results highlight the need to consider multiple land-use indicators when addressing threats to  
60 biodiversity and to separately assess areas with divergent human and ecological histories in global-  
61 scale studies. Different relationships associated with different agricultural transition stages suggest  
62 that high concentrations of threatened species may have contrasting meanings in different regions  
63 worldwide. We propose a new unifying hypothesis following a cyclic relationship along agricultural  
64 transition stages resulting in alternating negative and positive relationships between agriculture and  
65 threatened species richness.

## 66 **Introduction**

67 The demand for agricultural resources (food, fodder, fibre, and bioenergy) is expected to increase  
68 rapidly due to human population growth and the rise in per-capita consumption (Kastner *et al.*,  
69 2012; UN, 2014). From the current 38% of land surface allocated to agriculture (~68% pastures and  
70 meadows, ~31% arable lands and permanent crops; FAOSTAT, 2011), projections predict a 10-  
71 25% increase (from 2005 levels) in global cropland extent by 2050 (Schmitz *et al.*, 2014), primarily  
72 in highly biodiverse areas of South America and sub-Saharan Africa. Simultaneously, further  
73 intensification is expected to occur in many developing regions (Dietrich *et al.*, 2012).

74 Agriculture is one of the main threats to terrestrial biodiversity (Salafsky *et al.*, 2008;  
75 González-Suárez *et al.*, 2013; Böhm *et al.*, 2016). The effects of agricultural expansion and  
76 intensification on biodiversity are varied and difficult to differentiate because both processes often  
77 occur simultaneously. Studies have shown that biodiversity decreases as agriculture expands into  
78 natural areas (e.g. Kerr & Deguise, 2004; Koh & Wilcove, 2008), mainly by means of habitat loss  
79 and fragmentation (Gasparri & Grau, 2009). However, some impacts on biodiversity may be  
80 detected only years later yet have significant consequences, such as the destabilization of ecological  
81 interactions and the establishment of non-native species (Kuussaari *et al.*, 2009; Vilà *et al.*, 2011;  
82 Fontúrbel *et al.*, 2015). In addition, increased intensification of existing agricultural land negatively  
83 affects species via habitat degradation (e.g. the addition of more chemicals increases pollution), by  
84 reducing geographical ranges (e.g. species may persist within extensive croplands, but not in  
85 intensively used ones), or by disrupting community composition (Flynn *et al.*, 2009; Kleijn *et al.*,  
86 2009). Given the potential for further expansion and intensification of croplands, understanding  
87 how biodiversity is distributed relative to different agricultural practices is crucial to safeguard  
88 remaining biodiversity.

89 Agricultural land use indicators can be classified into metrics of extent and intensity.  
90 When assessing the patterns and impacts of land use and biodiversity at the global scale, few studies  
91 assess both the extent and intensity of use (but see Phalan *et al.*, 2014; Kehoe *et al.*, 2015, 2016,  
92 2017; Shackelford *et al.*, 2015). There is also a temporal dimension that might be key to interpret  
93 the distribution of current extinction risk (Ellis *et al.*, 2013; Faurby & Svenning, 2015), but it is  
94 often overlooked. Past modifications in biotic and abiotic conditions caused by agriculture may  
95 have long-lasting indirect and lagged effects on ecosystems, which may continue even after  
96 agricultural uses cease (Foster *et al.*, 2003). Besides, areas with a history of profound land use  
97 might have already lost the most sensitive species and/or show sub-optimal habitat conditions.  
98 Conversely, where less intensive land uses have prevailed over longer time periods, species may  
99 have adapted to or even become dependent on low-intensity human land uses (Walker *et al.*, 2004).  
100 This difference in observed vulnerability mediated by past human pressures can be seen as a form

101 of extinction filter (Balmford, 1996). Biodiversity is inherently complex and cannot be reduced to  
102 one number, given the impracticability of assessing all components of biodiversity (genes, species,  
103 ecosystems, functionality, etc) and the difficulty of designing a valid metric for all species  
104 (Magurran, 2004; Santini *et al.*, 2016). When exploring human threats, it seems reasonable to use a  
105 metric that incorporates knowledge on the conservation status of species. Threatened species'  
106 richness is one of the metrics used to establish conservation priorities or biodiversity hotspots (e.g.  
107 Brooks *et al.*, 2006; Grenyer *et al.*, 2006). In these cases, preserving the maximum number of  
108 threatened species is a target in and of itself. High threatened species richness can also serve as a  
109 warning signal of higher concentrations of threatening activities.

110         Understanding which metrics of agricultural land-use change may best predict threatened  
111 species distribution is useful in interpreting global patterns of threatened biodiversity. Here, we  
112 evaluate multiple land use metrics under the framework of two hypothesized relationships. The first  
113 hypothesis (*threat*) is inspired by global studies relating land use and threatened species distribution  
114 (e.g. Lenzen *et al.*, 2009). This hypothesis proposes that in more heavily used areas, vulnerable  
115 species are exposed to more threats than in less modified environments and thus, predicts a positive  
116 relationship between agricultural extent, intensity and/or time of human use on the one hand, and  
117 the proportion of threatened species on the other. An alternative hypothesis, which we called  
118 *shelter*, proposes instead that vulnerable species in heavily used areas are likely to become locally  
119 extinct, with remaining populations largely persisting in areas less used by humans, where more  
120 quality habitat still persists (Sanderson *et al.*, 2002). Therefore, the *shelter* hypothesis predicts a  
121 negative relationship between agricultural extent, intensity and/or time of human use and the  
122 proportion of threatened species.

123         Our main goal is to explore the heterogeneous distribution of threatened species in relation  
124 to different levels of agricultural pressure. We focus on areas covered to some extent by croplands  
125 to compare gradients of extent and intensity within a single category of land use; and on terrestrial  
126 mammals because their conservation status is generally well defined by the IUCN Red List (IUCN,  
127 2014) and because many of them are affected by agriculture (González-Suárez & Revilla, 2014).  
128 Namely, we evaluate which of the three types of agricultural metrics: extent, intensity, or history,  
129 best predicts threatened mammals' current distributions; and explore the relationship between  
130 agricultural indicators and the proportion of threatened mammals to assess the degree of agreement  
131 with the two proposed hypotheses – *threat* and *shelter*. We completed analyses at both global and  
132 biogeographic-realm scales, given their noticeable differences in terms of land-use history and  
133 biodiversity.

134

## 135 **Methods**

## 136 *Data sources*

137 We obtained terrestrial mammals distribution maps from the International Union for Conservation  
138 of Nature (IUCN, 2014), selecting only native, extant, and probably extant areas. We intersected  
139 distribution data with a grid, and species were considered present in a particular grid-cell when any  
140 overlap existed. We used a Behrmann cylindrical, equal-area projection, where each grid-cell  
141 corresponded to 110 x 110 km ( $\sim 1^\circ \times 1^\circ$  at the Equator), as finer resolutions are not recommended at  
142 the global scale due to the overestimation of species' occurrences (Hurlbert & Jetz, 2007). We  
143 calculated the proportion of threatened mammals by grid-cell as the sum of overlapping species  
144 classified by the IUCN Red List (IUCN, 2014) as critically endangered, endangered, and vulnerable  
145 divided by overlapping total mammal richness. We preferred this measure over the total count of  
146 threatened species to account for the expected dependence on total richness and to control for the  
147 known environmental gradient in species richness (Torres-Romero & Olalla-Tárraga, 2014). For  
148 analyses, we selected cells that contain any level of cropland as defined by Erb et al. (2007)  
149 cropland extent map (see below), and that had a land area of at least 10,000 km<sup>2</sup> (to avoid  
150 comparing grids with very unequal land areas).

151 To describe agricultural land use, we considered three groups of metrics: land-use extent,  
152 land-use intensity, and land-use history (Table S1.1). We employed the global land-use/cover  
153 classification of Erb et al. (2007) to define different proportions of land use within each grid-cell  
154 including the categories: cropland, forest, grazing land, urban and infrastructure, and areas without  
155 land use (defined as the remaining surface not classified under any of the other categories). We  
156 chose this classification for three reasons: all categories sum up to 100% of the grid surface, it is  
157 coherent with national census data, and most of the intensity metrics we used are based on this  
158 cropland map.

159 We selected indicators of cropland intensity based on the conceptual framework of Erb et al.  
160 (2013) and Kuemmerle et al. (2013), including metrics of inputs (irrigated area and added  
161 fertilizers) and outputs (yields of maize, wheat and rice, as well as harvested areas of soy and oil  
162 palm; see Table S1.1. for full details on data sources). Input metrics reflect direct potential impacts  
163 on the environment, for example on nutrient and water cycles, and are often employed when  
164 assessing biodiversity responses to impacts of agriculture (e.g. García de Jalón et al., 2013). Output  
165 metrics measure productivity (e.g., yields, as the ratio of land and total production, or energy  
166 efficiency) and represent another important facet of the intensity of agriculture that includes indirect  
167 threats such as transport and on-site manipulation (Turner & Doolittle, 1978). We selected yields of  
168 maize, wheat and rice because these are the globally dominant cereal crops (Hafner, 2003).  
169 Representing each crop separately is important to capture regional differences in productivity  
170 among areas where one crop may be nearly absent but others are prevalent (Table S1.2). Finally,

soy and palm oil crops are increasingly relevant in the tropics, where they are expanding into primary forests where mammal biodiversity is high (Hecht, 2005; Gutiérrez-Vélez *et al.*, 2011). We used available data on harvested area of soybeans and palm oil rather than yields because they have been found to be more consistent across alternative data sources (Fitzherbert *et al.*, 2008; GAEZ, 2010). These are considered an intensity metric because these crops are normally associated to high inputs of fertilizers and overall yields (Fearnside, 2001; Koh & Wilcove, 2008).

To test the importance of agricultural history we included the categorical variable of time of first significant land use (hereafter, time of first use) following the KK10 model (Kaplan *et al.*, 2011), defined as the time at which >20% of a grid-cell is classified as dedicated for any human use (Ellis *et al.*, 2013). Temporal intervals considered in the KK10 model are B.C.6000, B.C.3000, B.C.1000, A.D.0, A.D.1000, A.D.1500, A.D.1750, A.D.1900, A.D.1950 and A.D.2000. The KK10 model includes estimations of area converted for any type of land use (e.g. settlements, grazing lands, etc.) based on population densities and per capita use of land, although it does not explicitly incorporate intensity metrics. This past land-use reconstruction is generally considered more realistic than others available (Ellis *et al.*, 2013; Boivin *et al.*, 2016).

A list of data sources is found in Appendix 1 and further described in Table S1.1. The original resolution of our datasets was varied, thus we recalculated mean values per grid-cell using the Zonal Statistics tool within the Spatial analyst extension in ArcGIS 10.3 (ESRI, 2011).

### *Statistical analyses*

We divided our grid-cells containing any level of cropland (>0) into biogeographic realms (based on a modified classification of Olson *et al.* (2001) including: Afrotropics (1463 grid-cells), Australasia (300 grid-cells), Indomalay (518 grid-cells), Nearctic (994 grid-cells) and Neotropics (1463 grid-cells). We further subdivided the Palearctic realm into Asia (2078 grid-cells) and Europe (including Morocco and northern Algeria; 926 grid-cells), given their marked differences in terms of human history. All grid-cells that were not fully included in any of the mentioned realms were assigned to the Ecotone category and included in the global model, but not analysed as a separate realm (N=210; grey areas in Fig.2). Madagascar was excluded from the Afrotropics' analysis (but not from the global) given its biogeographic particularities as an island, which situates it as a clear outlier in terms of threatened mammals due to small ranges sizes and high numbers of endemic species (Fig. S1.1A). Using these geographic units enhances our ability to detect patterns without confounding different processes, since the range of variation in land-use extent, intensity and history is specific to each biogeographic realm (e.g., the minimum cover of urban areas in Europe could be the maximum in areas of Australasia). Additionally, they may serve as a space-for-time substitution representing different stages in the agricultural development process.



206 We performed one global and seven realm-specific models to explore overall and regional  
207 relationships. Realm was included as a categorical variable in the global model to account for the  
208 expected differences among realms and to avoid pseudoreplication within realms. We used the  
209 mean portion of different land-use categories (proved to be equivalent to total proportion per grid-  
210 cell; Table S1.3), agricultural intensity metrics and time of first use by grid-cell as predictor  
211 variables, and the proportion of threatened mammals as the response, which we arcsine square-root  
212 transformed to achieve normality. We included an 'island' dummy explanatory variable for grid-  
213 cells included within an island territory ( $\geq 10,000 \text{ km}^2$ ) to account for potential island-specific  
214 vulnerability attributes. Australasia is entirely formed by islands, thus we did not include this  
215 dummy variable in that realm model. Conservatively, we excluded highly correlated predictors  
216 (Spearman's  $\rho \geq |0.7|$ ) to avoid interpretative errors (Olden *et al.*, 2008); we selected only one  
217 variable from each correlated pair, omitting the one that correlated with the greatest number of other  
218 predictors (Tables S1.5-S1.12).

219 To analyse data we used a machine-learning approach known as boosted regression trees  
220 (BRT). BRT differs from traditional regression methods that produce a single 'best' model by using  
221 the technique of boosting to combine large numbers of relatively simple tree models to optimize  
222 predictive performance. BRT allow for detecting nonlinear relationships and including variables of  
223 very different nature and units (Elith *et al.*, 2008). BRT were fitted using function 'gbm.step' in the  
224 *dismo* package (Hijmans *et al.*, 2013) in R version 3.0.3 (R Development Core Team & R Core  
225 Team, 2014). This function calculates the optimal number of boosting trees using 10-fold cross  
226 validation. We used a Gaussian error structure, a bagging fraction of 0.5, and a tree complexity of  
227 10 (up to 10-way interactions). Learning rate was 0.050 for the global model and 0.001 for the  
228 realm-specific models. These parameters were fixed according to the guidelines in Elith *et al.*  
229 (2008) to achieve a minimum of 1,000 trees.

230 We considered a particular predictor as relevant when its relative importance was greater  
231 than expected due to chance (total importance of 100% divided by the number of variables included  
232 in each model; Müller *et al.* 2013). To account for spatial autocorrelation, all models included a  
233 residuals-based autocovariate (RAC) that specified the relationship between residual values at each  
234 location to those at neighbouring locations (the 8 immediate grid-cells surrounding each cell,  
235 approximately within a 165 km distance in our case) from a model excluding spatial  
236 autocorrelation. Deriving the autocovariate from the residuals allows for the inclusion of only the  
237 unexplained deviance remaining after considering the explanatory variables, thus the actual  
238 influence of the predictors is better captured (Crase *et al.*, 2012). The explanatory power of each  
239 model was calculated as the percentage of deviance explained respect to a null model, defined as  
240 one without any splits – equivalent to an intercept only model in linear regression (Ferrier &

Watson, 1997). The effect of each predictor was described in relation to the fitted model in which all other predictors were set to their average by means of partial dependency plots (PDP).

Finally, in order to improve the interpretability of our results, we tested whether consistency with the two hypotheses could be partially due to the correlation between agriculture and potential confounding factors not included in our analyses. We calculated simple correlations (Spearman's  $\rho$ ) between our predictors and a pool of environmental and non-land-use anthropogenic indicators typically assessed when exploring species distributions gradients at the global scale (Table S1.4; Torres-Romero & Olalla-Tárraga, 2014).

## Results

We completed the analyses on 7,962 grid-cells representing around 61% of the global terrestrial surface excluding Antarctica. A total of 4,780 terrestrial mammals overlapped the selected study area, 18% were classified as threatened, 69% as non-threatened, and 13% as data deficient. Regarding agricultural extent variables, our grid-cells included varying mean proportions of cropland, ranging from <0.01% to 98%, with the Indomalay realm having the highest mean value (40%), and the Neotropics the lowest (7.8%, Table S1.2). Other land-use extent components presented varying proportions: built-up areas represented the lowest extent (global average, 1.2%), and grazing lands the highest (global average, 40.5%). Globally, croplands tended to co-occur with built-up areas and heavily fertilized areas (Spearman's  $\rho=0.89$  and  $\rho=0.74$ , respectively) and were moderately disagreeing with non-used portions ( $\rho=-0.57$ ; Table S1.5), although these correlations varied among realms (Tables S1.6-S1.12). Agricultural intensity metrics also presented quite heterogeneous values among realms, with oil palm and soy presenting very low overall harvested areas (Table S1.2). Indomalay had on average the oldest and Australasia the youngest land-use history.

Model performance was relatively high, with 82.7% deviance explained by the global BRT model, and values ranging from 41.9% (Australasia) to 81.6% (Asia) for the realm-specific BRT models (Table 1). The inclusion of the spatial-autocorrelation term (RAC) improved these values and effectively corrected for spatial autocorrelation effects (as measured by Moran's I in the model residuals) in all models with the exception for Australasia (although even in this case the Moran's I parameter value was improved, Tables 1 vs. S2.1). The RAC was identified as relevant in all models, with an importance ranging from 26.5% (global) to 63.9% (Nearctic, Table 1). No relevant interactions among variables were found (Tables S2.2-S2.9).

### *Relevance of agricultural indicators*

275 We found differences among models regarding which type of agricultural indicators best predicted  
276 threatened mammals' distributions. In the global BRT, the variable contributing most to explain  
277 patterns of threatened mammals was realm (35.3% importance, Table 1). The highest proportion of  
278 threatened mammals was predicted in the Indomalay realm, followed by the Ecotone (grid-cells  
279 belonging to more than one biogeographic realm). The Afrotropics, the Neotropics, and Asia  
280 presented similar predicted values, while the Nearctic was predicted to have the lowest portion of  
281 threatened mammals (Fig. 1a). Only one land-use extent indicator was identified as relevant  
282 globally, forest coverage, with a 7.1% importance (Table 1), with slightly higher proportions of  
283 threatened species occurring in less-forested areas (Figs. 1b, S1.1, and S2.1).

284 In realm-specific BRTs, indicators of land-use extent were important in explaining the share  
285 of threatened mammals in Asia, Australasia, Europe, Indomalay, and the Neotropics; cropland  
286 intensity was important in the Indomalay and the Neotropics; while agricultural history presented a  
287 relevant contribution only in the Indomalay realm (Table 1). No agricultural land-use indicator  
288 appeared to explain threatened terrestrial mammals distribution in the Afrotropics and Nearctic  
289 realms.

290

#### 291 *Threat vs. shelter hypotheses*

292 Our results may be interpreted as consistent with both the *shelter* and the *threat* hypotheses varying  
293 across scales and realms. In the global model, the *threat* hypothesis seemed endorsed by the  
294 negative relationship between forest cover (relevant indicator) and proportion of threatened  
295 mammals, although this relationship was not very clear (Fig. 1). Realm-specific results served to  
296 disentangle part of this complexity.

297 Relationships in agreement with those predicted by the *shelter* hypothesis were observed in  
298 two realms: Australasia and Indomalay. In these areas higher portions of threatened mammals  
299 occurred where the extent and/or intensity of agriculture were relatively low. Namely, in  
300 Australasia and the Indomalay realms, areas with higher forest cover were associated with higher  
301 proportions of threatened mammals (Fig. 2; variable importance 26.8% and 27.0%, respectively). In  
302 the Indomalay realm, wheat yield was also found to be relevant (variable importance 14.4%), with  
303 more threatened species in areas of lower intensity (Fig. 2). The relationships predicted by the  
304 *threat* hypothesis were observed in Asia and Europe. The single most relevant indicator in both  
305 realms was the portion of forest per grid-cell (variable importance 17.0% and 20.2%, respectively),  
306 with higher proportions of threatened species found in cells with less forest (Fig. 2).

307 Finally, results from the Neotropics were consistent with both hypotheses. Relevant  
308 variables included maize yield (variable importance 14.5%) and forest area (13.5%), with more  
309 threatened mammals occurring in maize-intensive croplands (as expected from the *threat*

310 hypothesis; Fig. 2) and/or in areas with a greater cover of forest (as expected from the *shelter*  
311 hypothesis; Fig. 2).

312 The correlations between our relevant predictors and potential confounding factors  
313 (environmental and non-land-use anthropogenic) were high in some cases (Spearman's  $\rho \geq |0.7|$ ;  
314 Tables S1.5-1.12). In Australasia, where higher proportions of forest coincided with higher mean  
315 annual precipitation and mean annual actual evapotranspiration (AET, Table S1.8); and in the  
316 Indomalay realm, where more forested areas received also more mean annual precipitation, were  
317 less accessible, and had lower Human Footprint (HF) values; while intensive wheat croplands were  
318 associated with lower AET (Table S1.10).

319

## 320 **Discussion**

321 Agriculture is a key threat to global biodiversity, but our understanding of which aspects are more  
322 closely associated with threatened species distribution and how threat levels vary across the surface  
323 of the globe is partial. To our knowledge, our study is the first to systematically investigate the role  
324 of different facets of land use within croplands and how they predict the distribution of threatened  
325 mammals globally and by biogeographic realm.

326

### 327 *Relevance of agricultural indicators*

328 A land-use extent indicator, forest extent, was repeatedly associated with the distribution of  
329 threatened mammals. Alongside this, the inclusion of different indicators of agricultural intensity  
330 improved our ability to identify which types of croplands were more relevant predictors in each  
331 realm and added support to our proposed hypothesis.

332 Agricultural history was initially considered a promising indicator based on previous  
333 findings (Dullinger *et al.*, 2013). However, in our study it was only identified as relevant in the  
334 Indomalay realm and the relationship was intricate, with areas first modified in c.A.D. 0, 1900 and  
335 2000 having slightly higher proportions of threatened species (Fig. 2). These patterns are difficult to  
336 interpret probably because time since first use may be too simplistic to capture the complexities of  
337 land-use legacy at this scale. It would be desirable to know the particular type of land  
338 transformation at finer scales to provide a plausible explanation for this pattern. Importantly, in  
339 regions like Europe, which have experienced extinction filters (Turvey & Fritz, 2011) and where  
340 most sensitive mammals are likely to have already disappeared, the proportion of threatened  
341 mammals may be now largely independent from the time since first use and primarily related to  
342 relatively recent processes.

343

### 344 *Threat vs. shelter hypotheses*

345 Although global patterns were largely in agreement with predictions from the *threat* hypothesis,  
 346 when disaggregating our analyses by biogeographic realm, we uncovered realm-dependent  
 347 relationships. Patterns consistent with predictions from the *shelter* hypothesis were found in tropical  
 348 realms (Indomalay and Australasia, the latter is partially tropical in the current analysis; Fig. 2). In  
 349 some regions within these realms, like Papua New Guinea in Australasia (Fig. S1.4), or Indonesia  
 350 and Malaysia in the Indomalay (Fig. S1.6), the relatively large remaining tracts of forest were  
 351 associated with more threatened terrestrial mammals, as expected if these areas included the  
 352 remaining population of vulnerable species, as proposed by the *shelter* hypothesis. These forest  
 353 areas were positively correlated with higher precipitation and higher AET (Australasia,  $\rho_{\text{forest-prec.}}=0.82$  and  $\rho_{\text{forest-AET}}=0.86$ , Table S1.8, Indomalay,  $\rho_{\text{forest-prec.}}=0.74$ ), these environmental factors  
 354 may influence local species richness and presence of forest, but we do not expect they influence the  
 355 proportion of threatened mammals. In addition, in the Indomalay realm we found forested areas  
 356 generally were less accessible and had lower Human Footprint values ( $\rho_{\text{forest-acc.}}=0.74$  and  $\rho_{\text{forest-HF.}}=-$   
 357 0.78; Table S1.10), which provides additional hints for the potential *shelter* role of these areas.  
 358 Nevertheless, forest *shelter* areas are unlikely to be entirely free from threats, and may be affected  
 359 by wood extraction and other human activities like hunting (Fitzherbert et al., 2008), as well as  
 360 extinction debts (sensu Kuussaari et al., 2009).

362 We detected patterns consistent with the predictions from the *threat* hypothesis primarily  
 363 within temperate realms (Europe and Asia; Fig.2), where agriculture is so widespread that sensitive  
 364 species are often forced to co-occur within matrices of intensive agricultural land uses. This is the  
 365 case in Europe, where less forested lands coincided with higher numbers of threatened mammals  
 366 (Fig. S1.5); these areas are mainly located in southern Europe, where sensitive species remain. In  
 367 northern Europe, on the contrary, forested areas are mostly secondary species-poor forests, where  
 368 threatened mammals are absent (Polaina *et al.*, 2015). On the other hand, in Asia, lower forest cover  
 369 may coincide with a mixture of at least two contrasting types of landscapes: relatively unused lands  
 370 with a high level of endemism and threatened species, like the Tibetan Plateau (Fig. S1.3; Tang *et*  
 371 *al.*, 2006); and intensive croplands where species are more exposed to agricultural human pressures  
 372 (like wheat crops; Fig. S2.3). However, there was not a clear preponderance of any type of land use  
 373 and that may be why no additional indicator appeared as relevant in our models, leading to a weaker  
 374 overall agreement with the *threat* pattern.

375 Finally, a peculiar case in our results was the Neotropics, where higher proportions of  
 376 threatened terrestrial mammals tended to coincide with the large forested area of the Amazon, but  
 377 also with the Andean maize belt (Figs. S1.8 and S2.8), a region containing recognized hotspots of  
 378 endemism but also extensive agricultural lands (Leff *et al.*, 2004); thus showing patterns consistent  
 379 with predictions from both *shelter* and *threat* hypotheses. This may be a consequence of the size

380 and heterogeneity of this realm. In the Nearctic and the Afrotropics, agricultural land-use indicators  
381 were not associated with threatened species richness distribution and the spatial autocovariate  
382 showed high values, which suggests other factors not considered in the present study are associated  
383 with threatened mammals' distribution within croplands on this realm.

384

#### 385 *A unifying hypothesis?*

386 It is often assumed that threat levels, pressure from agriculture in our case, correspond to higher  
387 shares of threatened species. Our analyses show that this relationship might not be so  
388 straightforward and varies in important ways with the history of anthropogenic pressure in a  
389 territory. Even if agricultural land-use history by itself was not hugely relevant in our study,  
390 separating analyses by realm indirectly differentiates territories at different agricultural  
391 development stages and, accordingly, geographical differences consistent with predictions from  
392 both *threat* and *shelter* hypotheses were found. In light of these results, we propose a complex non-  
393 linear relationship between agricultural land use on the proportion of threatened species, described  
394 by dampening cycles, involving three broad stages (Fig. 3).

395 Under this hypothesis, expanding agricultural systems would initially generate patterns in  
396 line with the *threat* hypothesis; the proportion of threatened species would increase due to the rise  
397 in threatening activities. In this initial stage, extinction would be very limited, so total species  
398 richness would remain nearly constant, while the number of threatened species increases (Fig. 3a).  
399 Next, with further development, extinctions would occur, and threatened mammal richness will  
400 decrease more rapidly than the total species richness, resulting in an overall decrease in the  
401 proportion of threatened mammals. Only areas with at least partly suitable land use conditions  
402 would retain sensitive (threatened) species, thus showing patterns consistent with the *shelter*  
403 hypothesis (Fig. 3b). Finally, as development continues, the remaining sensitive species may be  
404 lost, causing a second wave of defaunation, while other species still present in the area may become  
405 threatened (due to persistent or new threats) leading to a rise in the proportion of threatened species  
406 and a new positive relationship consistent with the *threat* hypothesis. At this stage, differences in  
407 the proportion of threatened species would be less pronounced as overall richness would be reduced  
408 (sensitive species have already been lost) and persisting species would be expected to be more  
409 resistant/adapted to cohabit with humans (Fig. 3c).

410

#### 411 *Caveats and challenges*

412 The results and inferences presented here have some limitations. First, our study was too broad  
413 scale to assess the causal relationship between land use and biodiversity. Rather, we show what  
414 predictors are most strongly related to threatened species distributions. Finer scale work could delve

415 into our proposed hypotheses and better test their validity. For example, intra-realm variability  
416 could be explored at finer scales, particularly in large and heterogeneous realms. Second, the  
417 proposed continuous global hypothesis is based on assuming a valid space-for-time substitution in  
418 how land use influences biodiversity, since global time-series for the indicators presented here are  
419 not currently available and experimental manipulations are not possible. Finally, our study cannot  
420 account for lagged time effects or extinction debts or data quality limitations, but still can served to  
421 highlight areas where high concentrations of threatened species in apparent *shelter* regions exist.  
422 Global data describing distribution ranges and land use are likely to include heterogeneity in quality  
423 and precision (when data were captured and to what level of detail). Some areas in which we  
424 reported high proportions of threatened species may already have lost some species, but that  
425 information is not yet available. On the other hand, additional factors –likely environmental– may  
426 play a role in explaining distribution of threatened mammals worldwide (included in the RAC),  
427 however, the mechanism to influence threatened species is not expected to be straightforward and  
428 would require different analytical approaches. Together, these issues underline the challenges  
429 inherent in implying any form of causality between our predictor variables and our biodiversity  
430 distributions.

431 From a practical conservation perspective, our results present a challenge in that low  
432 proportions of threatened species may represent at least two distinct processes: few ongoing threats  
433 or past extinction of sensitive species, each leading to different conservation values and  
434 management implications (Polaina *et al.*, 2015). Our study aims to highlight the land-use attributes  
435 of areas where high proportions of threatened species still exist, and we considered the context of  
436 the different regions to interpret our results. However, more detailed studies that include data on  
437 local extinctions and that incorporate long-term time-series data would be necessary to disentangle  
438 these two processes. For example, multispecies long-term monitoring data or information on  
439 historical distributions within a particular site might offer the opportunity to evaluate the  
440 mechanisms behind our proposed continuous hypothesis, however these data are rarely available  
441 and may present quality issues (but see Boakes *et al.*, 2017).

## 443 *Conclusions*

444 This study provides a first global perspective of the complex relationships between agricultural land  
445 use, namely croplands, and threats to mammal biodiversity, in terms of agricultural extent, intensity  
446 and history. Arguably, the proposed unifying hypothesis could also be useful to contextualize the  
447 distribution of other important global threats for mammals, such as overexploitation or invasive  
448 species, in which non-linear relationships may also occur. In addition, our results open a way  
449 towards a better understanding of the potential consequences of future agricultural land-use changes

and the design of more context-specific conservation strategies. For example, areas where future cropland expansion is expected to occur, currently show vulnerable species remaining in potential *shelter* areas that may be further transformed, suggesting a high risk of biodiversity loss (Laurance *et al.*, 2014; Kehoe *et al.*, 2017a). Conservation actions to protect mammalian fauna in *shelter* areas would require to jointly considering croplands and forest patches, questioning traditional models of cropland expansion and intensification which could condemn numerous terrestrial mammal species. On the other hand, within the *threat* areas, remaining threatened species may require active conservation strategies to persist in highly modified environments. On the plus side, socioeconomic changes such as farmland abandonment due to emigration from rural areas, could bring region-specific opportunities for regeneration (Navarro & Pereira, 2012; Beilin *et al.*, 2014).

Our results suggest that understanding the stage of agricultural transition is key to correctly interpret biodiversity loss patterns. While useful in our study, the employed biogeographic realms may not be the most suitable assemble to understand different land-use transitions. Specific metrics that better characterize the transition stage of each region of the world are urgently needed in order to propose conservation actions adapted to the particularities of each region and to maximize biodiversity protection. Additionally, closer monitoring of long-term temporal trends within specific areas will improve the understanding of the fate of regional biodiversity.

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## Data accessibility

All data employed on the present work are public and can be downloaded from the original sources (Appendix 1).

## Biosketch



485 Ester Polaina works to understand current distribution of biodiversity and how human activities  
486 influence that spatial configuration. She is interested in finding a balance between socioeconomic  
487 development and natural systems' conservation at different scales and using different approaches.  
488

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673

674 **Appendix 1 – Data sources**

675 *Land-use extent*

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708 **Tables**

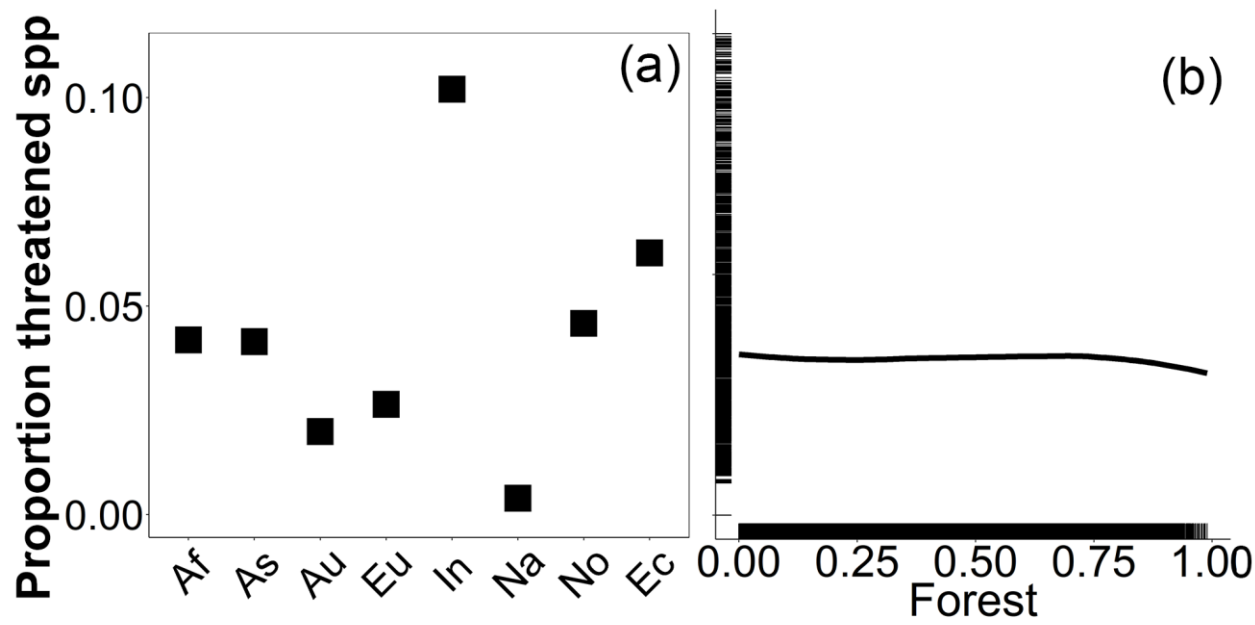
709 **Table 1.** Results of the BRT models, global and by realm. *Afro.* = Afrotropics; *Austr.* = Australasia;  
710 *Indo.* = Indomalay; *Neotrop.* = Neotropics. *Moran's I* was calculated for the residuals of each cell  
711 and the grid-cells surrounding it (all adjacent neighbours; max=8). *RAC*, residuals spatial  
712 autocovariate. Bold numbers indicate variables considered as relevant (i.e. their importance is  
713 greater than the expected under uniformity; thresholds are indicated in the last row).

	Global	Afro.	Asia	Austr.	Europe	Indo.	Nearctic	Neotrop.
No. trees	1400	8000	6300	3300	6350	4850	4300	4650
Residuals Moran's I	-0.04	-0.05	-0.04	0.12***	-0.05	-0.01	-0.03	-0.05
% Deviance explained	82.68	61.95	81.62	41.86	79.76	76.37	65.25	63.15
Variables (importance, %)								
<b>Land-use extent</b>								
Built-up	~	~	~	3.86	~	~	~	~
Cropland	3.12	5.69	4.55	~	1.79	~	6.13	6.93
Forest	<b>7.14</b>	4.58	<b>17.06</b>	<b>26.82</b>	<b>20.25</b>	<b>27.05</b>	3.33	<b>13.50</b>
Grazing land	2.77	~	2.85	5.65	2.53	2.55	2.81	7.50
Not used	2.15	6.32	2.16	3.79	3.14	~	2.76	2.40
<b>Land-use intensity</b>								
Fertilizer	~	4.67	~	4.39	6.09	5.22	~	~
Irrigated area	2.32	2.75	~	4.04	8.93	~	2.57	2.44
Maize	2.52	5	~	4.19	~	2.62	2.54	<b>14.53</b>
Rice	5.99	8.15	~	0.97	5.50	4.34	0	1.52
Wheat	2.94	5.94	8.08	~	~	<b>14.39</b>	7.25	3.25
Oil palm	0.48	4.91	-	0.72	-	2.33	-	0.08
Soy	1.21	1.83	1.96	0.19	6.42	6.98	2.92	6.78
<b>Land-use history</b>								
Time of first use	4.7	6.22	8.9	5.62	9.02	<b>12.76</b>	5.71	2.23
<b>Island</b>	2.77	-	0.01	-	0.14	0.58	-	0
<b>Realm</b>	<b>35.33</b>	-	-	-	-	-	-	-
<b>RAC</b>	<b>26.55</b>	<b>43.95</b>	<b>54.44</b>	<b>39.76</b>	<b>36.19</b>	<b>21.18</b>	<b>63.98</b>	<b>38.84</b>
<i>Relevance threshold</i>	<i>7.14</i>	<i>8.33</i>	<i>11.11</i>	<i>8.33</i>	<i>9.09</i>	<i>9.09</i>	<i>9.09</i>	<i>7.69</i>

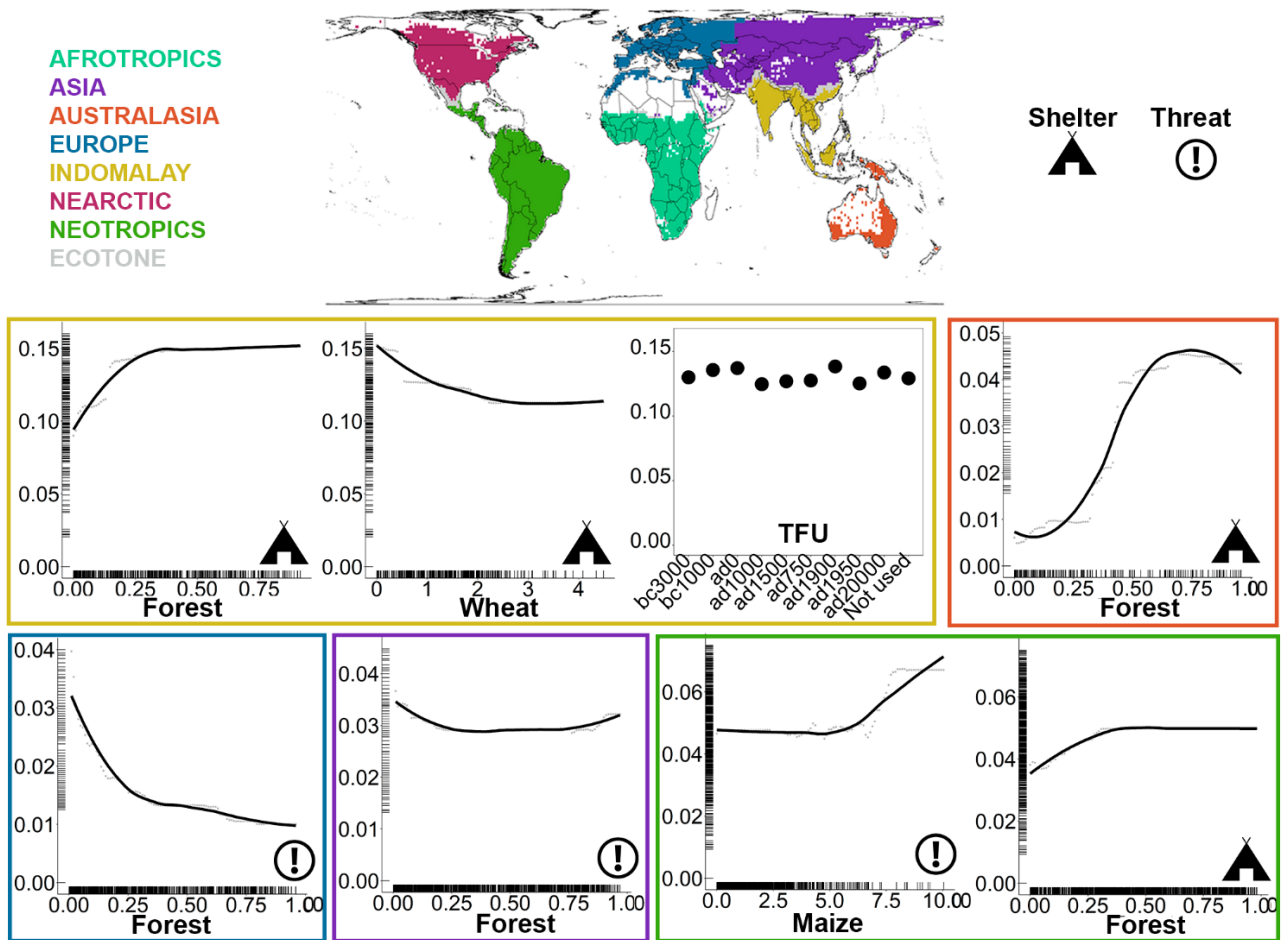
714 \*\*\* p<0.001, spatial autocorrelation exists; -, not existent/applicable; ~, variable excluded because its correlation with  
715 other/s was  $\geq |0.7|$  (Spearman's  $\rho$ ).

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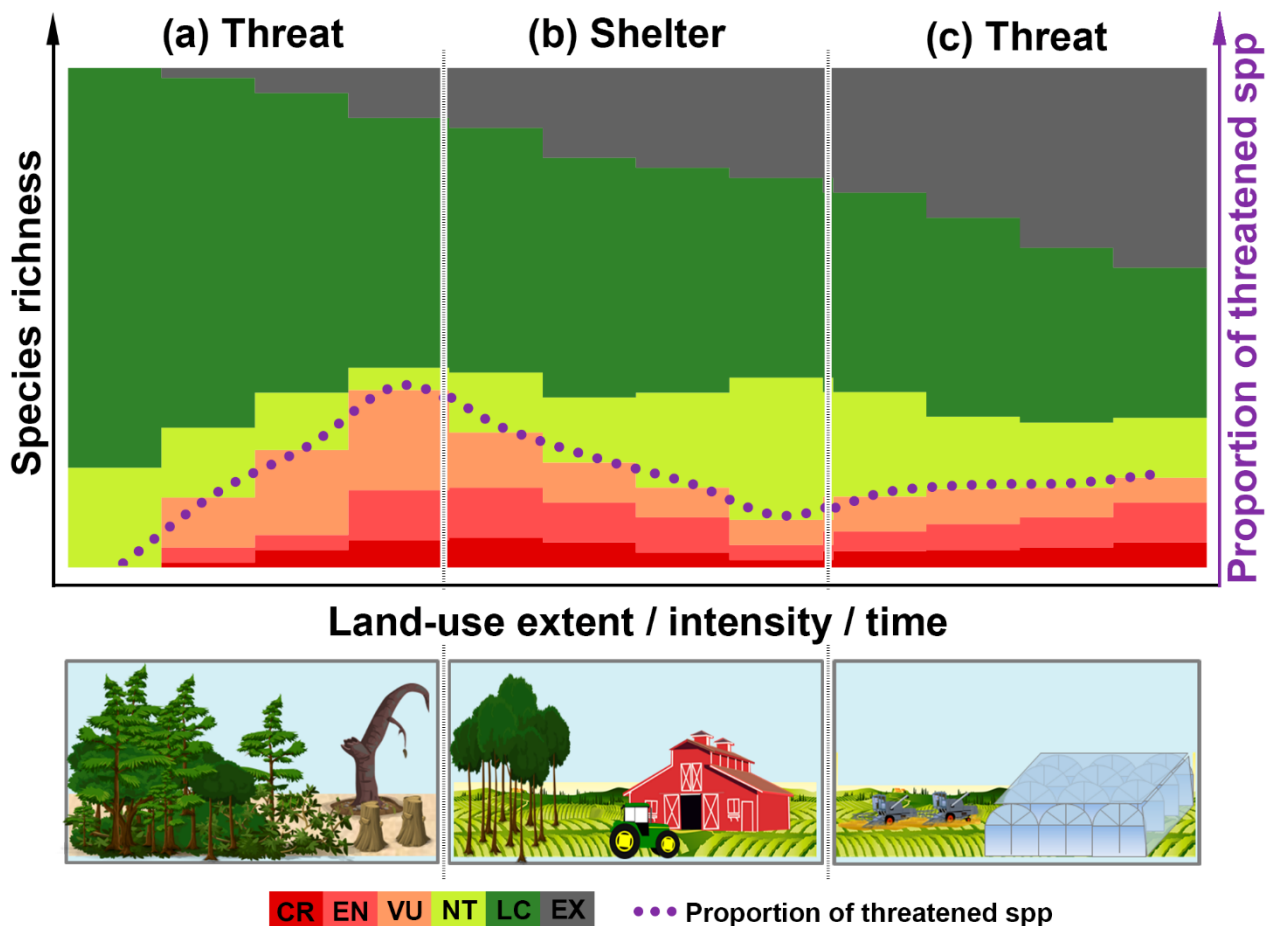




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719 **Figure 1.** Partial dependency plots of relevant predictors in the global BRT model; (a)  
720 biogeographic realm (35.33% importance) and (b) forest extent (7.14% importance). *Af* =  
721 Afrotropics; *As* = Asia; *Au* = Australasia; *Eu* = Europe; *In* = Indomalay; *Na* = Nearctic; *No* =  
722 Neotropics; *Ec* = Ecotone.  
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**Figure 2.** Partial dependency plots (PDP) of relevant predictors of the realms BRT models. Colour legend matches realms' names, map and PDPs' borders. Y-axis in all plots represents predicted proportion of threatened mammals. Symbols illustrate the matching hypothesis for each predictor (*threat* or *shelter*). *TFU* refers to the time period of first significant land use.



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**Figure 3.** Schematic representation of the continuous hypothesis proposed. The X-axis represents land-use extent, intensity or time since first use within a certain area. The Y-axis (left) represents species richness where each colour indicates the number of species in each category; greenish colours represent non-threat categories, reddish colours mark threat categories. Legend: *CR*, critically endangered; *EN*, endangered; *VU*, vulnerable; *NT*, near threatened; *LC*, least concern; *EX*, extinct. The Y-axis (right) represents the proportion of threatened species, marked by the purple dotted line.

## Supporting Information

### Appendix S1. SUPPLEMENTARY DATA DESCRIPTION

**Table S1.1.** Description and sources of indicators of land use extent, intensity and history. Short name is used in the main manuscript.

Indicators						
<i>Long name</i>	<i>Short name</i>	Units, description	Year	Original resolution	Data sources	Reference
<b>Land-use extent</b>						
Urban and infrastructure	Built-up	% grid-cell	2000	5 min	Eurostat, national inventories, GLC2000	Erb <i>et al.</i> (2007)
Cropland	Cropland	% grid-cell	2000	5 min	Ramankutty & Foley (1999), FAO	Erb <i>et al.</i> (2007)
Forest	Forest	% grid-cell	2000	5 min	FRA2000, GLC2000	Erb <i>et al.</i> (2007)
Grazing land	Grazing land	% grid-cell	2000	5 min	GLC2000	Erb <i>et al.</i> (2007)
Areas without land use	Not used	% grid-cell	2000	5 min	Human footprint (Sanderson et al. 2002), GLC 2000	Erb <i>et al.</i> (2007)
<b>Land-use intensity</b>						
<i>Inputs</i>						
Industrial and manure fertilizer application rates (N, P)	Fertilizer	kg/ha	1994 - 2001	10 km	FAO “Fertilizer Use by Crop 2002” combined with harvested area for 175 crops (Monfreda et al. 2008).	Potter <i>et al.</i> (2010)
Land equipped for irrigation	Irrigated area	% grid-cell	2000	5 min	FAO, World Bank and other international organizations, USGC-GLCC-2.0 and JRC-GLC2000	Siebert <i>et al.</i> , (2015)
<i>Outputs</i>						
Yields for rice, wheat and maize	Maize, rice and wheat	tons/ha	2000	5 min	Combining census statistics with global cropland area (Ramankutty et al. 2008)	Monfreda <i>et al.</i> (2008)
Harvested area for soy and oil palm	Soy and oil palm	% grid-cell	2000	5 min	Combining census statistics with global cropland area (Ramankutty et al. 2008)	Monfreda <i>et al.</i> (2008)
<b>Land-use history</b>						
Time period of first significant land use <sup>1</sup>	Time of first use	year (categorical)	-	5 min	KK10 model (Kaplan et al. 2011)	Ellis <i>et al.</i> (2013)

<sup>1</sup> Categories: BC6000, BC3000, BC1000, AD0, AD1000, AD1500, AD1750, AD1900, AD1950, AD2000, Not used.

**Table S1.2.** Global and realm-specific summary of indicators of land-use extent, intensity and history, and mammal diversity. All values represent the mean proportion value within each grid-cell of ~110x110 km. Time of first use was converted to continuous for this purpose.

Indicators	Mean values per grid-cell							
	Global	Afrotropics	Asia	Australasia	Europe	Indomalay	Nearctic	Neotropics
<b>Land-use extent (portion of grid-cell)</b>								
Built-up <sup>1</sup>	0.012	0.005	0.008	0.004	0.032	0.018	0.025	0.003
Cropland <sup>1</sup>	0.141	0.095	0.088	0.126	0.255	0.400	0.178	0.078
Forest <sup>1</sup>	0.319	0.300	0.254	0.239	0.319	0.326	0.325	0.447
Grazing land <sup>1</sup>	0.405	0.558	0.432	0.460	0.304	0.245	0.328	0.375
Not used <sup>1</sup>	0.123	0.042	0.218	0.171	0.091	0.011	0.145	0.096
<b>Land-use intensity</b>								
<i>Inputs</i>								
Fertilizer <sup>2</sup> (kg/ha)	6.167	0.552	6.351	2.452	10.915	18.622	8.767	1.927
Irrigated area <sup>3</sup> (portion of grid-cell)	2.470	0.312	2.628	0.496	2.810	12.516	2.326	0.624
<i>Outputs</i>								
Maize <sup>4</sup> (tons/ha)	1.703	0.820	1.226	1.568	2.445	1.831	3.419	1.663
Rice <sup>4</sup> (tons/ha)	1.103	1.002	1.129	0.801	0.678	2.712	0.130	1.411
Wheat <sup>4</sup> (tons/ha)	1.052	0.965	0.884	0.514	1.732	1.045	1.709	0.521
Oil palm <sup>4</sup> (portion of grid-cell)	0.001	0.002	-	<0.001	-	0.005	-	<0.001
Soy <sup>4</sup> (portion of grid-cell)	0.007	0.000	0.003	0.000	0.001	0.011	0.024	0.014
<b>Land-use history</b>								
Time of first use <sup>5</sup> (years)	626	1185	329	1374	120	-315 <sup>6</sup>	1127	651
<b>Mammal diversity</b>								
Total richness	78.1	106.4	45.5	42.5	49.0	95.0	58.3	130.8
Threatened spp. (%)	4.1 5%	4.4 4%	2.4 5%	1.5 3%	1.5 3%	14.3 15%	0.4 1%	6.8 5%

<sup>1</sup>Erb et al. (2007); <sup>2</sup>Potter et al. (2010); <sup>3</sup>Siebert et al. (2015); <sup>4</sup>Monfreda et al. (2008); <sup>5</sup>Ellis et al. (2013); <sup>6</sup>B.C.315

**Table S1.3.** Correlations (Spearman's rank coefficient,  $\rho$ ) between mean portion and total portion per grid of the land-use categories included in the analyses.

	<b>Spearman's <math>\rho</math></b>
<b>Built-up</b>	0.99
<b>Cropland</b>	0.99
<b>Forest</b>	0.97
<b>Grazing land</b>	0.96
<b>Not used</b>	0.99

**Table S1.4.** Description and sources of environmental and non-land-use anthropogenic indicators tested for correlation with our land-use predictors.

Indicators		Units, description	Year	Original resolution		References
<i>Long name</i>	<i>Short name</i>			<i>Spatial</i>	<i>Temporal</i>	
<b>Environmental</b>						
Mean annual actual evapotranspiration	AET	mm, accumulated	2000	1 degree	month	Zhang <i>et al.</i> (2010, 2015)
Mean annual temperature	Temperature	°C, average	1970-2000	10 arc minutes	month	Fick & Hijmans (2017)
Mean annual precipitation	Precipitation	mm, average	1970-2000	10 arc minutes	month	Fick & Hijmans (2017)
Global digital elevation model	Elevation	m	1996	30 arc seconds	-	LP DAAC (2004)
Crop suitability index for high input level rain-fed cereals	Crop suitability	index [0-10,000]	1961-1990	5 arc minutes	-	Fischer <i>et al.</i> (2012)
<b>Non-land-use anthropogenic</b>						
Travel time to major cities (≥50,000 people)	Accessibility	minutes	2000	30 arc seconds	-	Nelson (2008)
Global Human Footprint	Human footprint	index [0-10]	1995-2004	1 km	-	Sanderson <i>et al.</i> , (2002)

**Table S1.5.** Spearman's rank coefficient of correlation ( $\rho$ ) for all pairs of variables included in the global BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
<b>Cropland</b>	0.89																	
<b>Forest</b>	0.07	-0.01																
<b>Grazing land</b>	-0.01	0.03	-0.55															
<b>Not used</b>	-0.55	-0.57	-0.22	-0.10														
<b>Irrigated area</b>	0.61	0.62	-0.21	0.19	-0.39													
<b>Fertilizer*</b>	0.69	0.74	-0.09	0.09	-0.49	0.76												
<b>Wheat yield</b>	0.51	0.49	-0.18	0.21	-0.37	0.57	0.63											
<b>Maize yield</b>	0.57	0.60	-0.02	0.14	-0.45	0.61	0.74	0.63										
<b>Rice yield</b>	0.23	0.34	0.06	0.12	-0.29	0.37	0.42	0.22	0.45									
<b>Oil palm</b>	-0.03	0.01	0.22	-0.01	-0.17	-0.10	0.00	-0.14	0.03	0.27								
<b>Soy</b>	0.48	0.52	0.07	-0.03	-0.40	0.45	0.58	0.43	0.59	0.34	-0.02							
<b>AET</b>	0.13	0.22	0.47	-0.19	-0.26	0.00	0.18	0.02	0.29	0.41	0.38	0.22						
<b>Temperature</b>	-0.07	0.14	0.03	0.11	-0.22	0.06	0.14	-0.10	0.12	0.44	0.31	0.01	0.50					
<b>Precipitation</b>	0.17	0.23	0.63	-0.32	-0.30	-0.02	0.17	-0.05	0.22	0.41	0.40	0.24	0.82	0.47				
<b>Elevation</b>	-0.15	-0.19	-0.18	0.26	0.13	0.06	-0.07	0.18	0.04	0.02	-0.01	-0.12	-0.17	-0.22	-0.23			
<b>Human Footprint</b>	0.72	0.76	-0.06	0.19	-0.62	0.71	0.77	0.57	0.65	0.43	0.09	0.51	0.21	0.19	0.21	-0.07		
<b>Accessibility</b>	-0.68	-0.69	0.11	-0.19	0.56	-0.68	-0.70	-0.52	-0.58	-0.20	0.07	-0.46	-0.07	-0.13	-0.06	0.16	-0.84	
<b>Crop suitability</b>	0.37	0.46	0.27	-0.06	-0.46	0.10	0.31	0.23	0.36	0.22	0.15	0.33	0.54	0.39	0.52	-0.39	0.43	-0.42

\*excluded predictors in the BRT model.

**Table S1.6.** Spearman's rank coefficient of correlation ( $\rho$ ) for all pairs of variables included in the Afrotropics BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
<b>Cropland</b>	0.84																	
<b>Forest</b>	-0.01	-0.09																
<b>Grazing land</b>	-0.09	-0.08	-0.75															

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
No used	-0.15	-0.10	-0.42	0.29														
Irrigated area	0.46	0.46	-0.28	0.16														
Fertilizer	0.53	0.62	-0.34	0.23	-0.01	0.58												
Wheat yield	0.15	0.13	-0.12	0.16	-0.03	0.16	0.21											
Maize yield	0.53	0.55	-0.14	0.12	-0.06	0.45	0.63	0.31										
Rice yield	0.41	0.45	-0.01	0.07	-0.09	0.30	0.52	0.11	0.61									
Oil palm	0.05	0.02	0.49	-0.45	-0.31	-0.15	-0.20	-0.20	-0.07	0.05								
Soy	0.32	0.36	0.03	-0.13	-0.14	0.29	0.41	0.28	0.32	0.20	0.11							
AET	0.03	-0.10	0.76	-0.59	-0.25	-0.28	-0.40	-0.08	-0.14	-0.10	0.43	0.08						
Temperature	-0.18	0.02	-0.16	0.13	-0.06	-0.07	-0.01	-0.44	-0.23	0.01	0.00	-0.23	-0.37					
Precipitation	0.04	0.04	0.77	-0.64	-0.32	-0.25	-0.28	-0.26	-0.07	0.02	0.60	0.11	0.83	-0.12				
Elevation	0.12	-0.02	-0.05	0.06	0.14	-0.01	-0.01	0.44	0.16	-0.07	-0.14	0.08	0.17	-0.84	-0.04			
Human Footprint	0.59	0.64	0.04	-0.06	-0.28	0.45	0.50	0.03	0.37	0.39	0.13	0.29	-0.03	0.10	0.15	-0.09		
Accessibility	-0.50	-0.50	0.10	-0.08	0.23	-0.50	-0.50	-0.04	-0.37	-0.32	-0.06	-0.35	0.16	-0.09	0.06	0.13	-0.70	
Crop suitability	0.15	0.25	0.44	-0.29	-0.13	-0.08	0.03	0.01	0.14	0.23	0.09	0.05	0.39	0.05	0.42	-0.11	0.23	-0.10

\*excluded predictors in the BRT model.

**Table S1.7.** Spearman's rank coefficient of correlation ( $\rho$ ) for all pairs of variables included in the Asia BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area*	Fertilizer*	Wheat yield	Maize yield*	Rice yield*	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland	0.95																
Forest	0.37	0.28															
Grazing land	0.11	0.16	-0.50														
Not used	-0.65	-0.66	-0.20	-0.46													
Irrigated area*	0.54	0.61	-0.18	0.32	-0.47												
Fertilizer*	0.59	0.65	-0.09	0.27	-0.56	0.82											
Wheat yield	0.45	0.51	-0.18	0.33	-0.46	0.73	0.86										



	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area*	Fertilizer*	Wheat yield	Maize yield*	Rice yield*	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Maize yield*	0.52	0.57	-0.05	0.17	-0.46	0.74	0.87	0.83									
Rice yield*	0.39	0.44	-0.13	0.20	-0.39	0.69	0.73	0.73	0.82								
Soy	0.54	0.59	0.14	0.10	-0.54	0.63	0.78	0.69	0.75	0.59							
AET	0.40	0.37	0.35	-0.16	-0.23	0.22	0.35	0.38	0.36	0.26	0.43						
Temperature	0.32	0.43	-0.47	0.37	-0.39	0.67	0.67	0.51	0.54	0.53	0.41	-0.06					
Precipitation	0.51	0.47	0.69	-0.27	-0.31	0.10	0.22	0.18	0.24	0.18	0.39	0.59	-0.17				
Elevation	-0.24	-0.20	-0.30	0.15	0.16	0.11	0.09	0.28	0.15	0.17	0.01	0.00	0.00	-0.20			
Human Footprint	0.62	0.68	-0.10	0.40	-0.67	0.83	0.86	0.75	0.74	0.64	0.69	0.31	0.68	0.17	0.03		
Accessibility	-0.62	-0.66	0.08	-0.34	0.65	-0.70	-0.72	-0.51	-0.58	-0.47	-0.57	-0.16	-0.72	-0.11	0.21	-0.84	
Crop suitability	0.62	0.60	0.25	0.14	-0.60	0.38	0.53	0.37	0.46	0.27	0.47	0.39	0.34	0.39	-0.35	0.53	-0.61

\*excluded predictors in the BRT model.

**Table S1.8.** Spearman's rank coefficient of correlation ( $\rho$ ) for all pairs of variables included in the Australasia BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up	Cropland*	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield*	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland*	0.90																	
Forest	0.26	0.12																
Grazing land	-0.11	0.02	-0.45															
No used	-0.67	-0.53	-0.58	0.19														
Irrigated area	0.61	0.62	0.17	0.08	-0.47													
Fertilizer	0.65	0.71	0.17	0.10	-0.46	0.58												
Wheat yield*	0.68	0.77	0.08	0.10	-0.36	0.70	0.76											
Maize yield	0.57	0.51	0.55	-0.30	-0.61	0.53	0.48	0.51										
Rice yield	0.34	0.19	0.42	-0.42	-0.54	0.13	0.13	-0.04	0.54									
Oil palm	0.04	-0.17	0.60	-0.48	-0.40	-0.30	-0.17	-0.46	0.32	0.66								
Soy	0.34	0.38	0.19	0.03	-0.31	0.57	0.49	0.40	0.46	0.22	-0.12							
AET	0.38	0.22	0.86	-0.45	-0.60	0.28	0.28	0.12	0.70	0.53	0.62	0.25						
Temperature	-0.56	-0.62	0.11	-0.24	0.36	-0.45	-0.47	-0.64	-0.21	0.00	0.36	-0.23	0.14					

	Built-up	Cropland*	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield*	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Precipitation	0.31	0.16	0.82	-0.52	-0.54	0.24	0.20	0.06	0.65	0.49	0.63	0.19	0.95	0.26				
Elevation	0.02	0.00	0.36	-0.22	-0.15	-0.10	-0.06	-0.05	0.21	0.03	0.23	-0.03	0.34	0.00	0.34			
Human Footprint	0.78	0.66	0.30	0.06	-0.78	0.61	0.55	0.56	0.57	0.39	0.13	0.32	0.40	-0.57	0.31	0.00		
Accessibility	-0.58	-0.65	0.08	-0.31	0.29	-0.74	-0.65	-0.81	-0.29	0.20	0.58	-0.40	0.00	0.58	0.06	0.14	-0.57	
Crop suitability	0.40	0.33	0.49	-0.16	-0.45	0.46	0.50	0.48	0.50	0.16	0.10	0.27	0.63	0.02	0.62	-0.05	0.42	-0.42

\*excluded predictors in the BRT model.

**Table S1.9.** Spearman's rank coefficient of correlation ( $\rho$ ) for all pairs of variables included in the Europe BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	No used	Irrigated area	Fertilizer	Wheat yield*	Maize yield*	Rice yield	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland	0.77																
Forest	0.07	-0.12															
Grazing land	0.02	0.05	-0.50														
Not used	-0.43	-0.49	-0.43	0.27													
Irrigated area	0.48	0.63	-0.33	0.35	-0.15												
Fertilizer	0.73	0.70	-0.05	0.13	-0.31	0.63											
Wheat yield*	0.83	0.74	0.01	0.09	-0.38	0.55	0.87										
Maize yield*	0.73	0.71	-0.01	0.09	-0.36	0.60	0.78	0.82									
Rice yield	0.23	0.45	-0.25	0.19	-0.05	0.55	0.30	0.27	0.38								
Soy	0.41	0.43	0.08	-0.01	-0.30	0.31	0.23	0.39	0.45	0.21							
AET	0.68	0.64	0.04	0.07	-0.30	0.52	0.63	0.71	0.71	0.40	0.46						
Temperature	0.09	0.27	-0.68	0.27	0.14	0.54	0.35	0.24	0.27	0.39	-0.07	0.21					
Precipitation	0.40	0.17	0.63	-0.22	-0.35	-0.02	0.39	0.45	0.32	-0.09	0.10	0.35	-0.33				
Elevation	-0.18	-0.06	-0.07	0.17	0.09	0.17	0.10	-0.01	0.14	0.17	-0.15	-0.05	0.28	0.10			
Human Footprint	0.85	0.81	-0.07	0.18	-0.38	0.62	0.82	0.86	0.76	0.31	0.37	0.71	0.27	0.34	-0.03		
Accessibility	-0.78	-0.74	0.04	-0.09	0.44	-0.53	-0.75	-0.79	-0.64	-0.18	-0.28	-0.58	-0.27	-0.31	0.15	-0.86	
Crop suitability	0.61	0.64	0.22	-0.13	-0.58	0.18	0.37	0.53	0.47	0.03	0.54	0.42	-0.19	0.25	-0.39	0.55	-0.59

\*excluded predictors in the BRT model.

**Table S1.10.** Spearman's rank coefficient of correlation ( $\rho$ ) for all pairs of variables included in the Indomalay BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland*	Forest	Grazing land	Not used*	Irrigated area*	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
<b>Cropland*</b>	0.91																	
<b>Forest</b>	-0.65	-0.72																
<b>Grazing land</b>	-0.42	-0.49	-0.04															
<b>Not used*</b>	-0.38	-0.43	0.04	0.73														
<b>Irrigated area*</b>	0.77	0.79	-0.73	-0.25	-0.25													
<b>Fertilizer</b>	0.71	0.66	-0.56	-0.20	-0.15	0.72												
<b>Wheat yield</b>	0.46	0.46	-0.48	-0.27	-0.29	0.61	0.47											
<b>Maize yield</b>	-0.09	-0.10	0.12	0.25	0.24	-0.10	0.03	-0.37										
<b>Rice yield</b>	0.13	0.01	0.08	0.06	0.08	0.10	0.25	-0.13	0.50									
<b>Oil palm</b>	-0.42	-0.31	0.34	0.14	0.19	-0.51	-0.26	-0.59	0.31	0.01								
<b>Soy</b>	0.18	0.13	0.00	0.01	-0.08	0.17	0.21	0.18	0.17	0.06	-0.16							
<b>AET</b>	-0.48	-0.50	0.62	0.13	0.21	-0.60	-0.37	-0.72	0.33	0.29	0.65	-0.18						
<b>Temperature</b>	0.09	0.24	-0.37	0.06	0.04	0.10	-0.06	-0.15	-0.11	-0.34	0.22	-0.24	-0.13					
<b>Precipitation</b>	-0.41	-0.52	0.74	0.02	0.12	-0.64	-0.30	-0.58	0.15	0.19	0.51	-0.06	0.78	-0.27				
<b>Elevation</b>	-0.27	-0.30	0.40	0.03	-0.03	-0.25	-0.33	-0.11	0.13	0.07	-0.12	0.18	0.05	-0.63	0.08			
<b>Human Footprint</b>	0.81	0.82	-0.78	-0.18	-0.21	0.85	0.71	0.50	-0.08	0.00	-0.44	0.13	-0.57	0.22	-0.59	-0.31		
<b>Accessibility</b>	-0.79	-0.78	0.74	0.21	0.26	-0.82	-0.63	-0.56	0.08	-0.04	0.58	-0.15	0.62	-0.13	0.63	0.21	-0.89	
<b>Crop suitability</b>	0.58	0.69	-0.51	-0.25	-0.31	0.51	0.32	0.16	-0.10	-0.19	-0.15	0.05	-0.30	0.52	-0.36	-0.37	0.65	-0.62

\*excluded predictors in the BRT model.

**Table S1.11.** Spearman's rank coefficient of correlation ( $\rho$ ) for all pairs of variables included in the Nearctic BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
<b>Cropland</b>	0.96																
<b>Forest</b>	-0.21	-0.25															

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Grazing land	0.16	0.15	-0.49														
Not used	-0.72	-0.69	0.01	-0.25													
Irrigated area	0.49	0.48	-0.29	0.61	-0.51												
Fertilizer*	0.86	0.88	-0.34	0.29	-0.62	0.57											
Wheat yield	0.62	0.61	-0.24	0.45	-0.53	0.65	0.71										
Maize yield	0.66	0.64	-0.36	0.42	-0.61	0.60	0.69	0.68									
Rice yield	0.15	0.14	0.10	-0.02	-0.19	0.22	0.15	0.09	0.14								
Soy	0.71	0.68	-0.13	-0.02	-0.60	0.27	0.63	0.48	0.62	0.18							
AET	0.72	0.70	0.13	-0.16	-0.60	0.20	0.58	0.40	0.44	0.26	0.73						
Temperature	0.44	0.43	-0.18	0.57	-0.58	0.66	0.43	0.56	0.54	0.26	0.39	0.33					
Precipitation	0.31	0.27	0.45	-0.52	-0.26	-0.17	0.12	0.02	0.06	0.23	0.55	0.62	0.08				
Elevation	-0.35	-0.32	-0.09	0.42	0.17	0.23	-0.21	-0.07	-0.12	-0.23	-0.53	-0.62	-0.05	-0.61			
Human Footprint	0.84	0.79	-0.04	0.22	-0.80	0.55	0.75	0.67	0.69	0.21	0.74	0.72	0.65	0.42	-0.34		
Accessibility	-0.78	-0.73	0.14	-0.35	0.73	-0.59	-0.71	-0.65	-0.66	-0.21	-0.63	-0.62	-0.72	-0.28	0.29	-0.90	
Crop suitability	0.74	0.73	-0.05	-0.14	-0.52	0.12	0.66	0.41	0.47	0.15	0.74	0.76	0.22	0.46	-0.60	0.64	-0.58

\*excluded predictors in the BRT model.

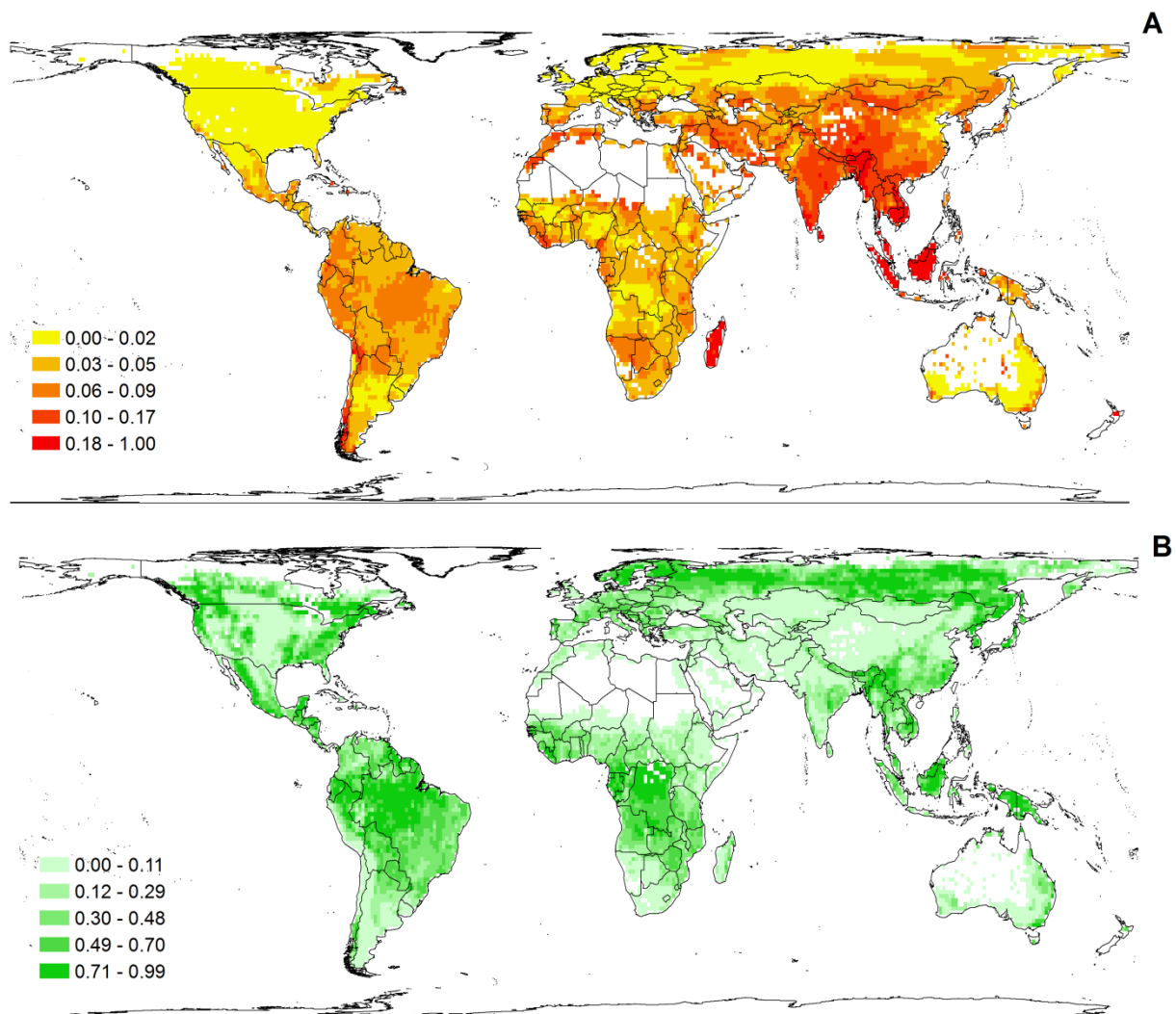
**Table S1.12.** Spearman's rank coefficient of correlation ( $\rho$ ) for all pairs of variables included in the Neotropics BRT (white background) and for additional environmental and non-land-use anthropogenic indicators (grey background).

	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Cropland	0.85																	
Forest	-0.18	-0.23																
Grazing land	0.35	0.38	-0.77															
Not used	-0.56	-0.59	-0.06	-0.31														
Irrigated area	0.59	0.54	-0.40	0.59	-0.49													
Fertilizer*	0.61	0.53	-0.19	0.37	-0.51	0.71												
Wheat yield	0.27	0.30	-0.37	0.45	-0.20	0.45	0.45											

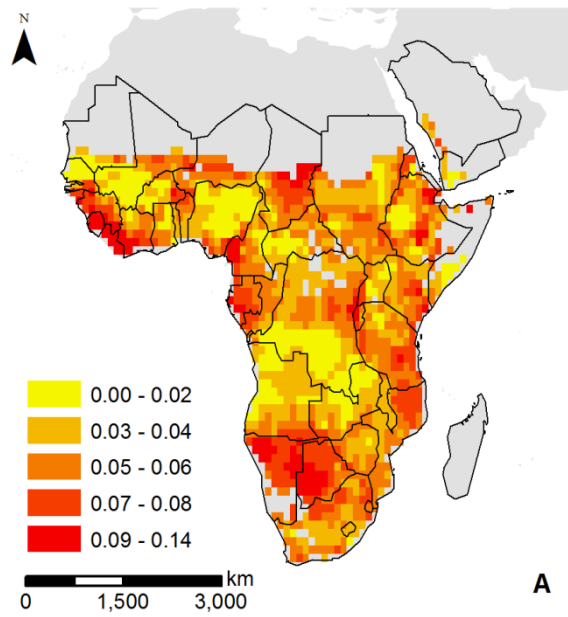
	Built-up*	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer*	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	AET	Temperature	Precipitation	Elevation	Human Footprint	Accessibility
Maize yield	0.46	0.46	-0.35	0.50	-0.35	0.53	0.64	0.61										
Rice yield	0.48	0.35	-0.05	0.24	-0.34	0.45	0.62	0.37	0.53									
Oil palm	0.30	0.06	-0.07	0.14	-0.15	0.21	0.37	0.13	0.08	0.34								
Soy	0.35	0.49	-0.12	0.21	-0.34	0.31	0.48	0.40	0.59	0.42	-0.04							
AET	-0.37	-0.40	0.64	-0.78	0.29	-0.55	-0.39	-0.42	-0.61	-0.23	-0.04	-0.30						
Temperature	-0.36	-0.44	0.57	-0.57	0.21	-0.57	-0.43	-0.59	-0.57	-0.21	-0.01	-0.31	0.63					
Precipitation	-0.28	-0.42	0.54	-0.66	0.28	-0.52	-0.33	-0.38	-0.55	-0.17	0.14	-0.25	0.71	0.64	1.00	-0.41		
Elevation	0.31	0.20	-0.35	0.34	-0.09	0.43	0.29	0.31	0.37	0.16	0.13	0.06	-0.50	-0.65	-0.41	1.00		
Human Footprint	0.66	0.62	-0.38	0.62	-0.61	0.80	0.84	0.45	0.64	0.54	0.30	0.42	-0.51	-0.51	-0.49	0.33		
Accessibility	-0.59	-0.63	0.44	-0.65	0.57	-0.74	-0.74	-0.36	-0.67	-0.43	-0.07	-0.50	0.59	0.49	0.61	-0.27	-0.89	
Crop suitability	-0.08	0.07	0.01	0.03	-0.07	-0.13	0.06	0.09	0.17	0.15	-0.12	0.42	0.04	0.25	-0.01	-0.50	0.06	-0.16

\*excluded predictors in the BRT model.

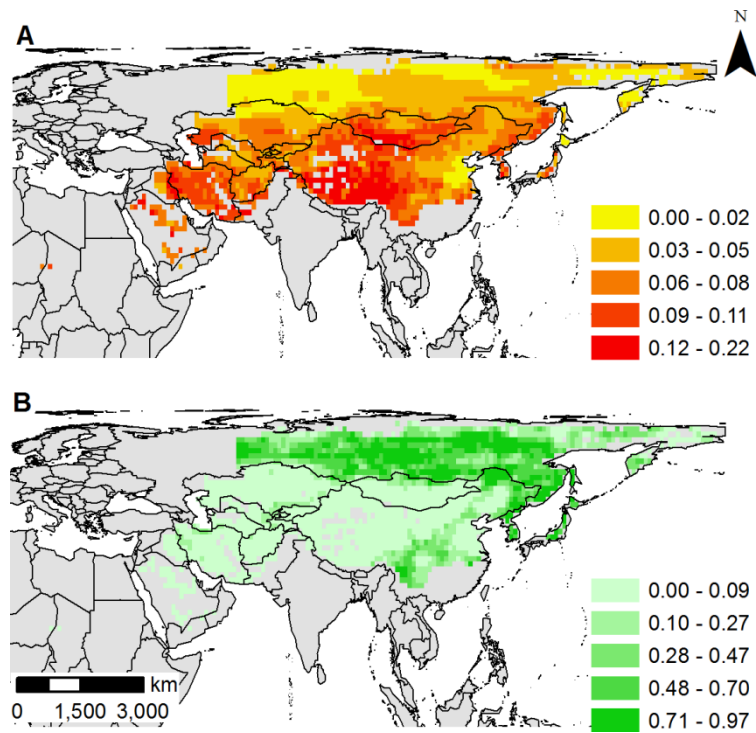
*Maps of proportion of threatened mammals and relevant indicators globally, and by biogeographic realm*



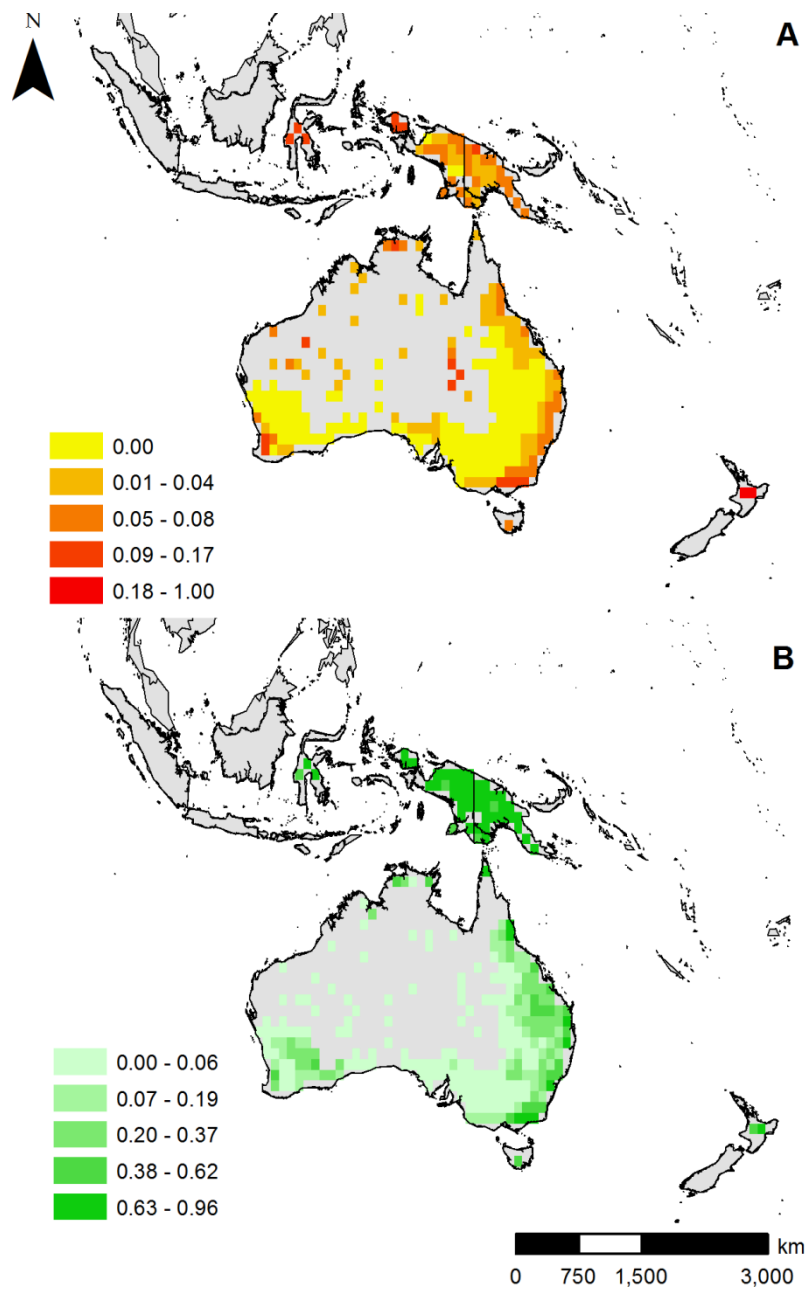
**Figure S1.1.** Proportion of threatened mammals (A) and proportion of forested area per grid-cell (tons/ha; B).



**Figure S1.2.** Proportion of threatened mammals (A) in the Afrotropics realm.

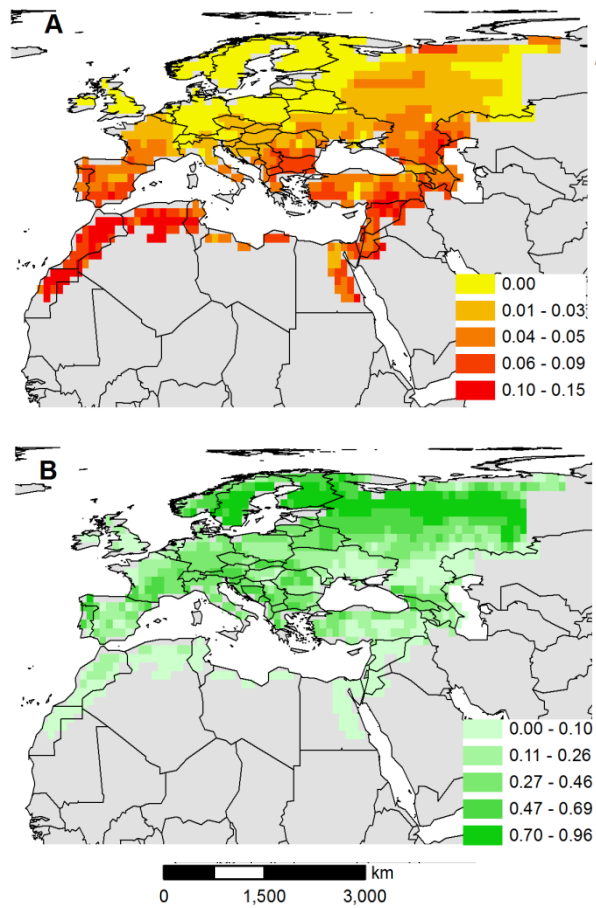


**Figure S1.3.** Proportion of threatened mammals (A) and proportion of forested area per grid-cell (B) in the Asia region (Palearctic realm).

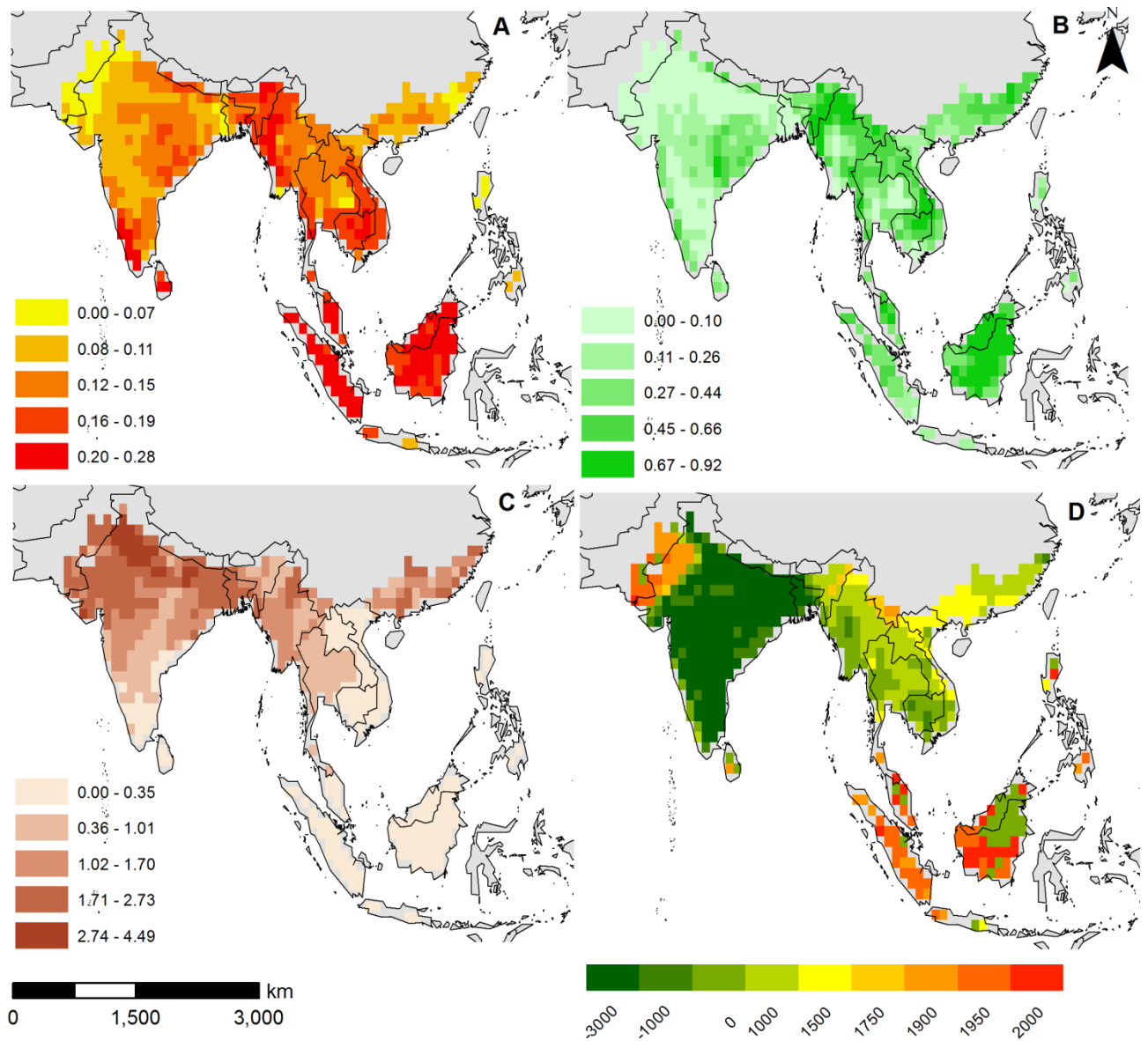


**Figure S1.4.** Proportion of threatened mammals (A) and forested area per grid-cell (B) in the Australasia realm.

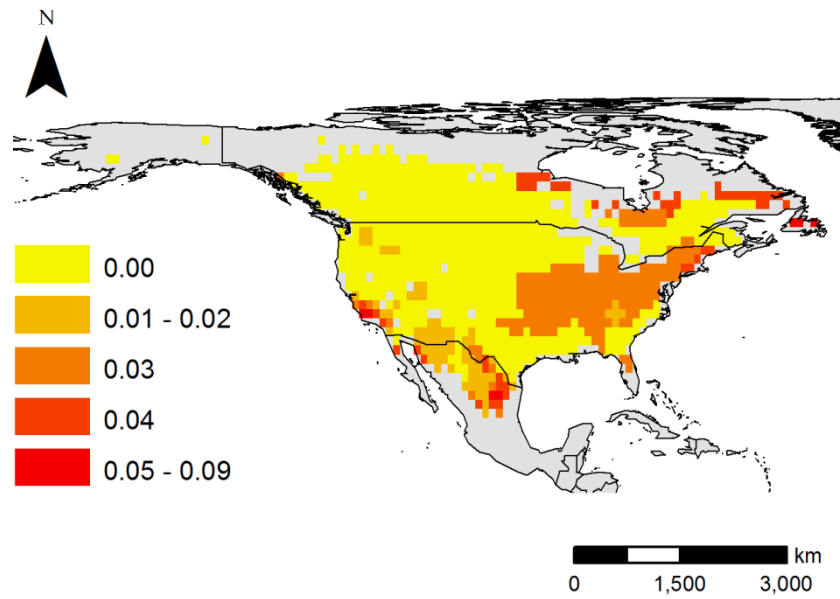




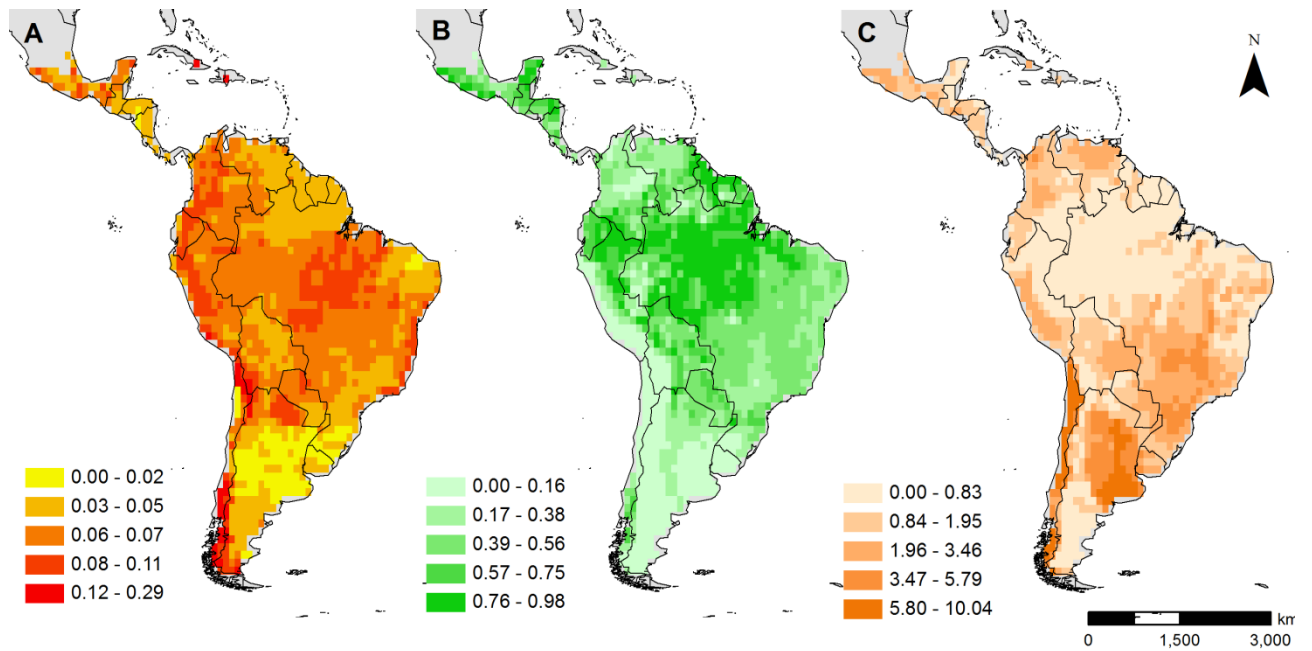
**Figure S1.5.** Proportion of threatened mammals (A) and proportion of forested area per grid-cell (B) in the Europe region (Palearctic realm).



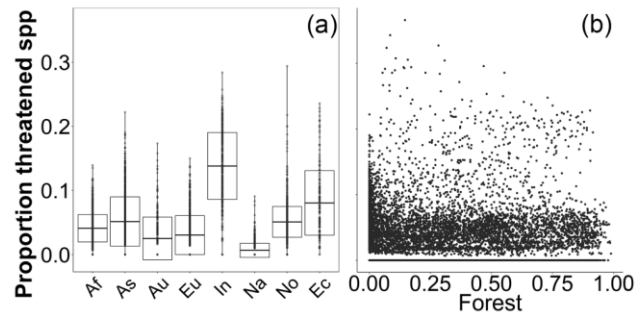
**Figure S1.6.** Proportion of threatened mammals (A), forested area (B), average wheat yields per grid-cell (tons/ha; C) and time of first use (D) in the Indomalay realm.



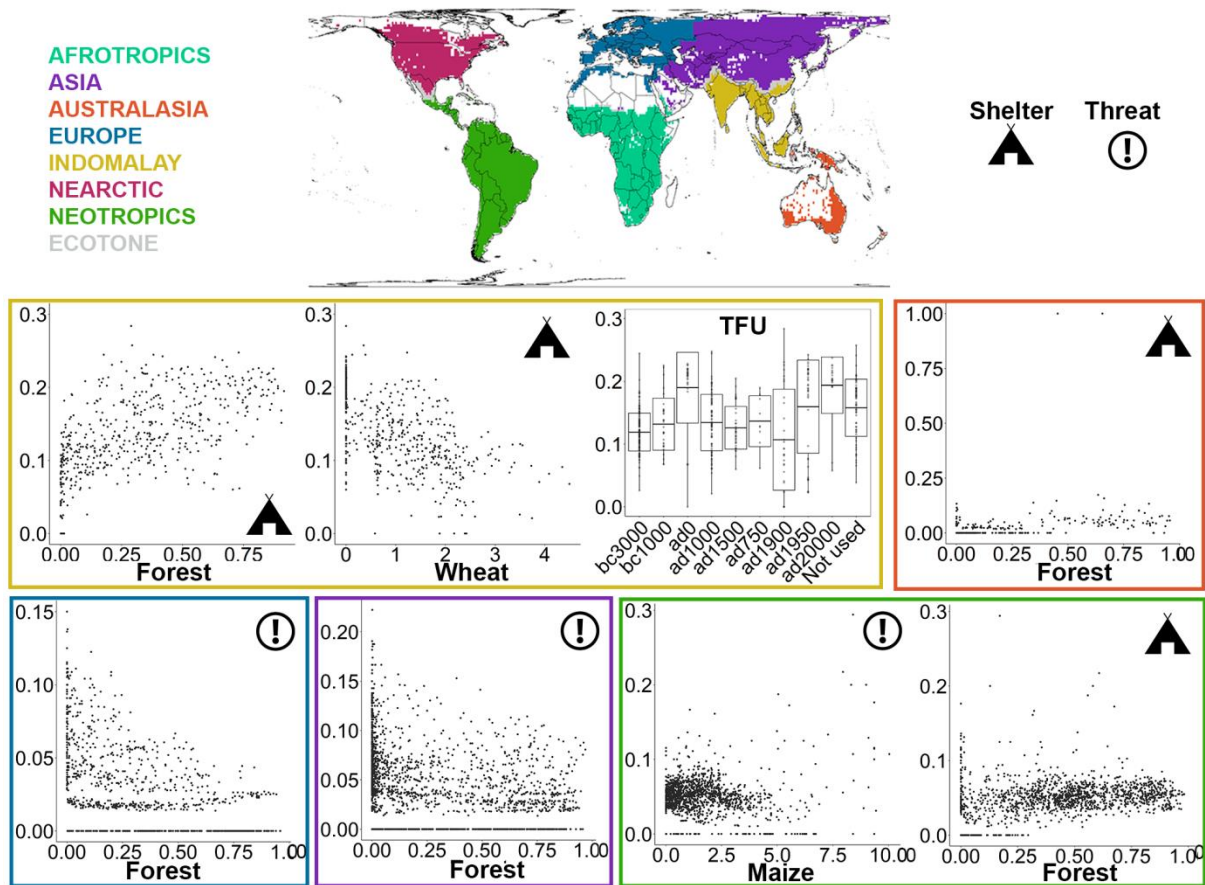
**Figure S1.7.** Proportion of threatened mammals in the Nearctic realm.



**Figure S1.8.** Proportion of threatened mammals (A), forested area per grid-cell (B) and maize yields (tons/ha; C) in the Neotropics realm.



**Figure S1.9.** Boxplot and scatter plot showing the relationships between the relevant predictors in the global BRT model and the proportion of threatened species (raw data); (a) biogeographic realm (38.12% importance) and (b) forest extent (7.16% importance). *Afr* = Afrotropics; *As* = Asia; *Au* = Australasia; *Eu* = Europe; *In* = Indomalay; *Na* = Nearctic; *No* = Neotropics; *Ec* = Ecotone.



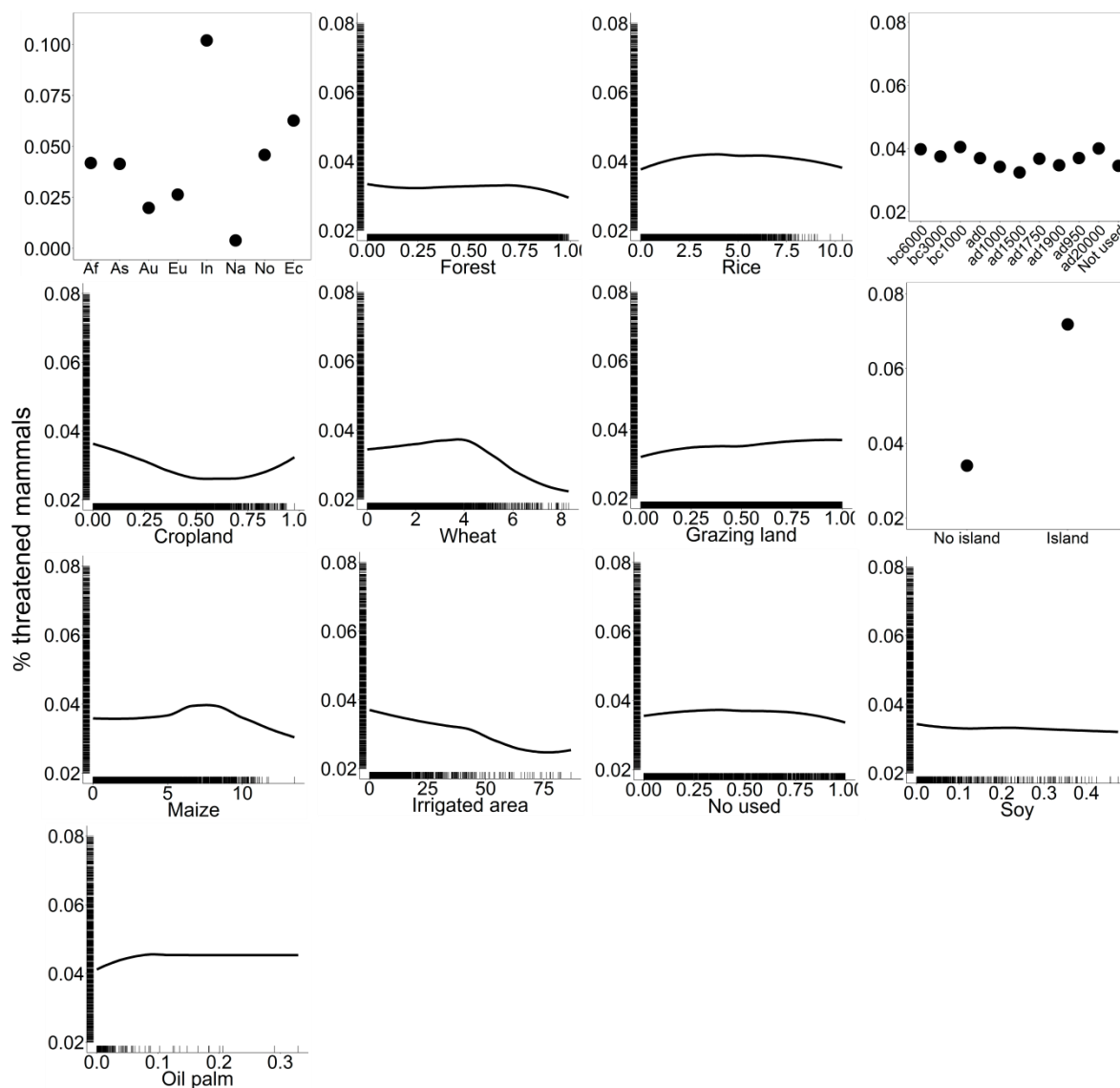
**Figure S1.10.** Scatter plots (continuous variables) and boxplot (categorical variable) showing the relationships between relevant predictors of the realms' BRTs and the proportion of threatened species (raw data). Colour legend matches realms' names, map and PDPs' borders. Y-axis in all plots represents observed proportion of threatened mammals. Symbols illustrate the hypothesis supported by each predictor (*threat* or *shelter*). *TFU* refers to the time period of first significant land use.

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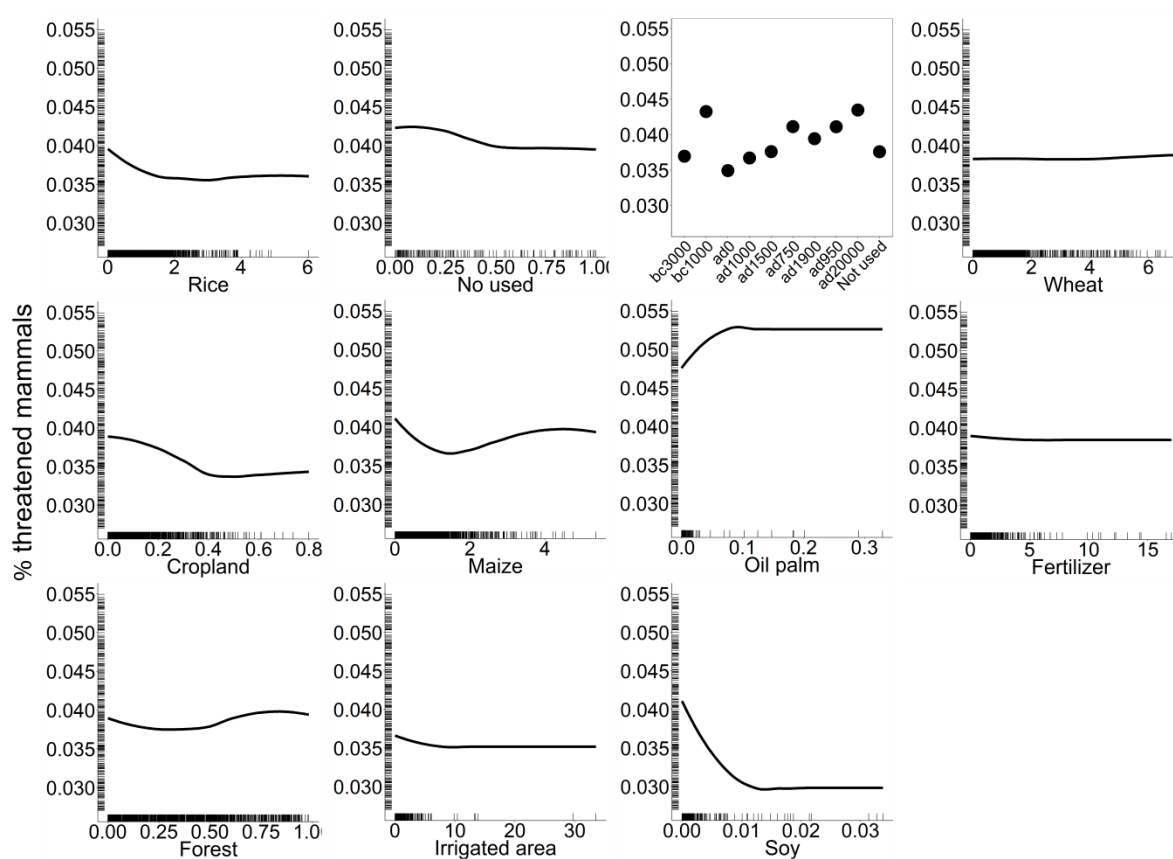
## Appendix S2. SUPPLEMENTARY RESULTS: BOOSTED REGRESSION TREES

*Global:*



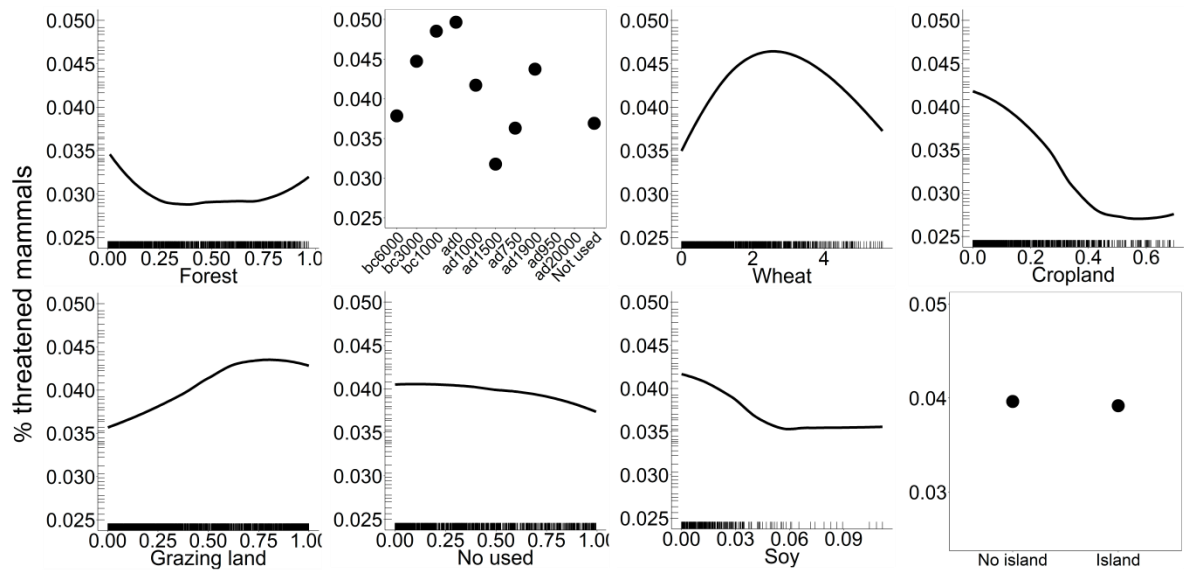
**Figure S2.1.** Partial dependence plots (PDPs) of all variables included in the Global BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

# *Afrotropics:*



**Figure S2.2.** Partial dependence plots (PDPs) of all variables included in the Afrotropics BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).G

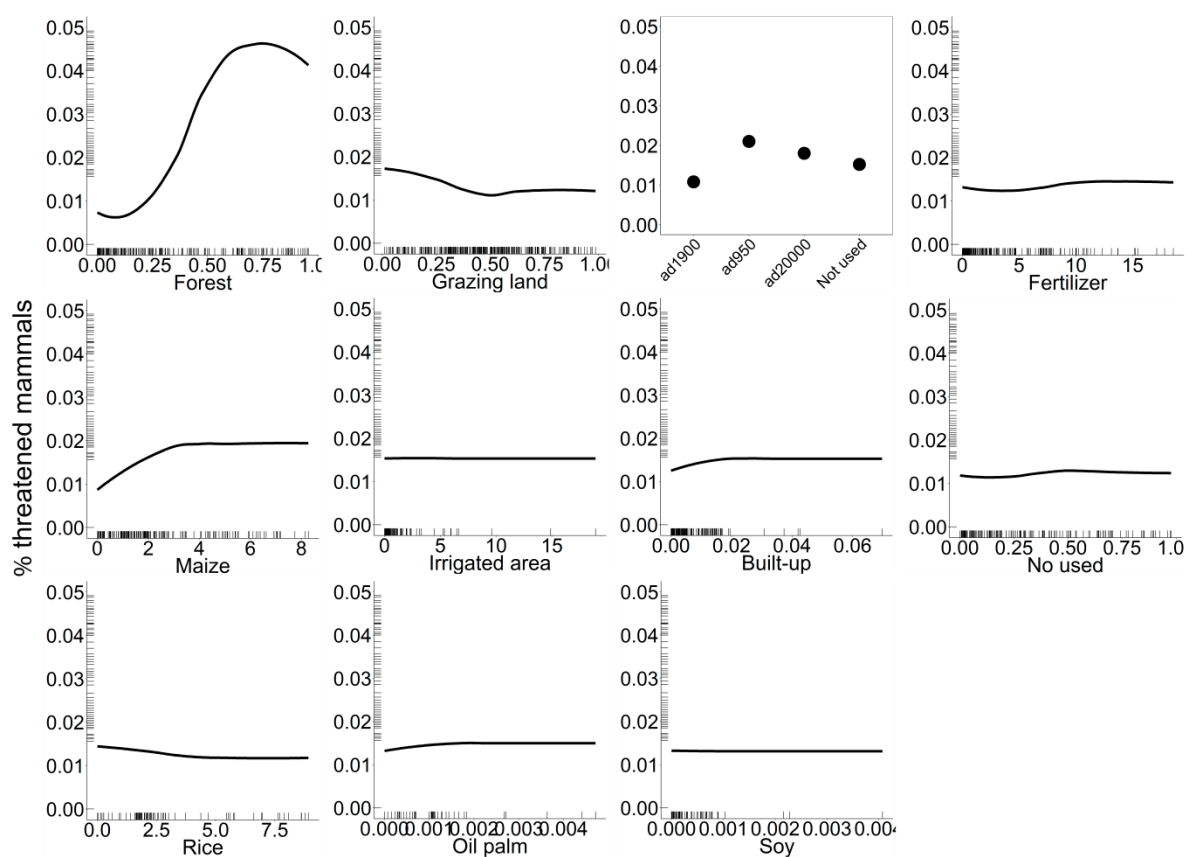
*Asia (Palearctic):*



**Figure S2.3.** Partial dependence plots (PDPs) of all variables included in the Asia BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

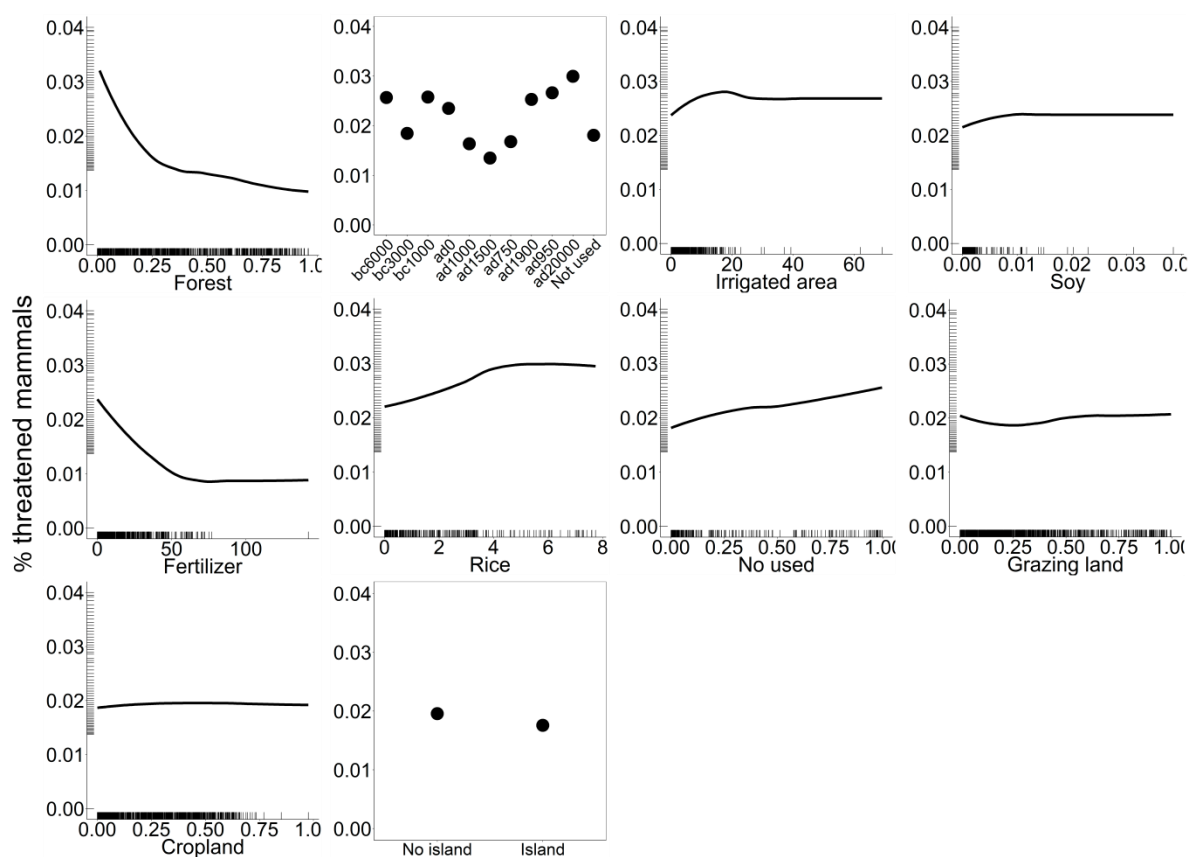


# *Australasia:*



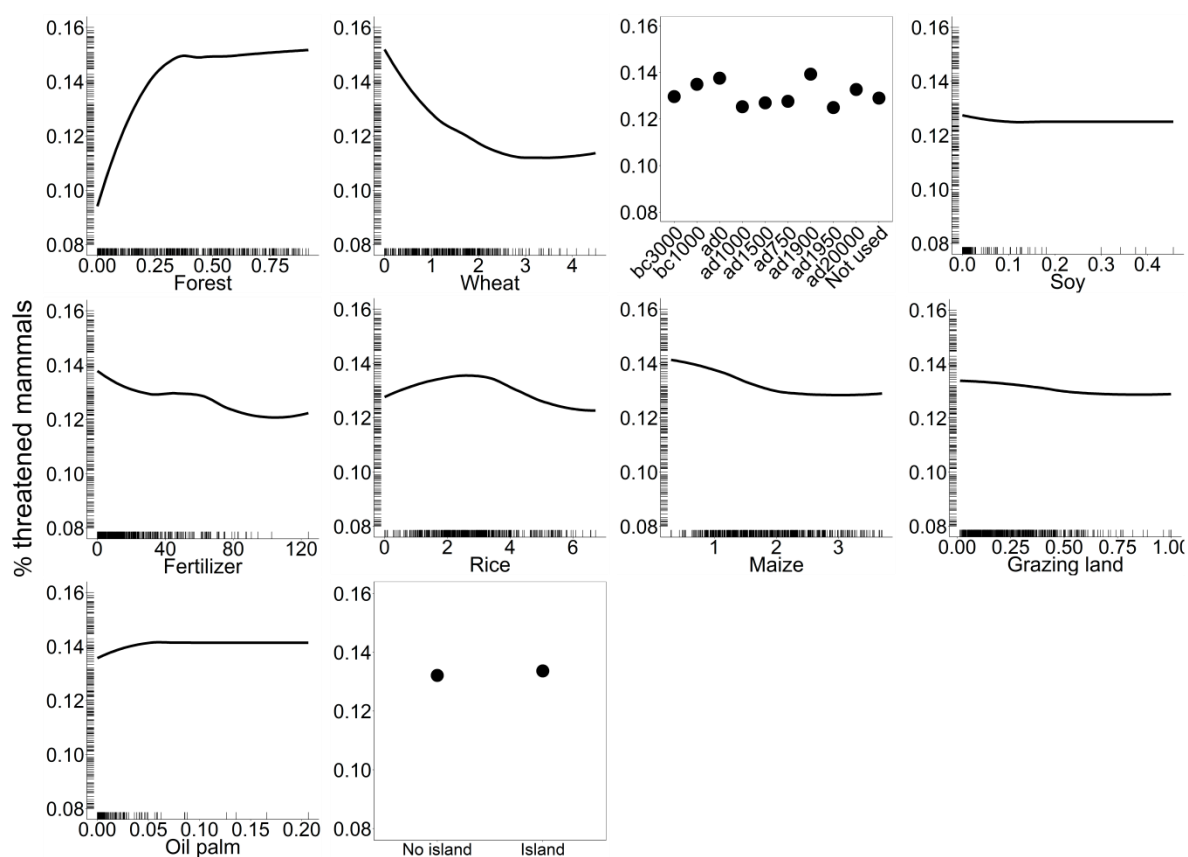
**Figure S2.4.** Partial dependence plots (PDPs) of all variables included in the Australasia BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

*Europe (Palearctic):*



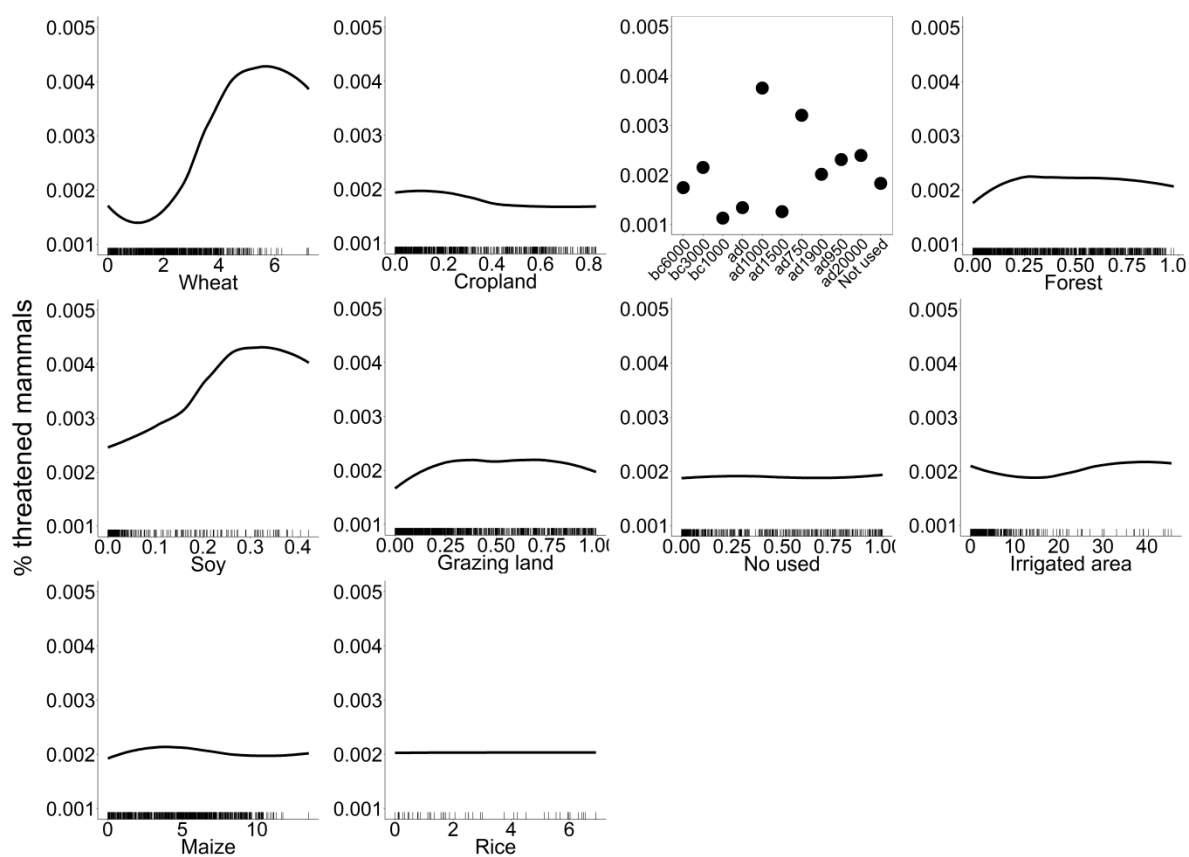
**Figure S2.5.** Partial dependence plots (PDPs) of all variables included in the Europe BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

*Indomalay:*



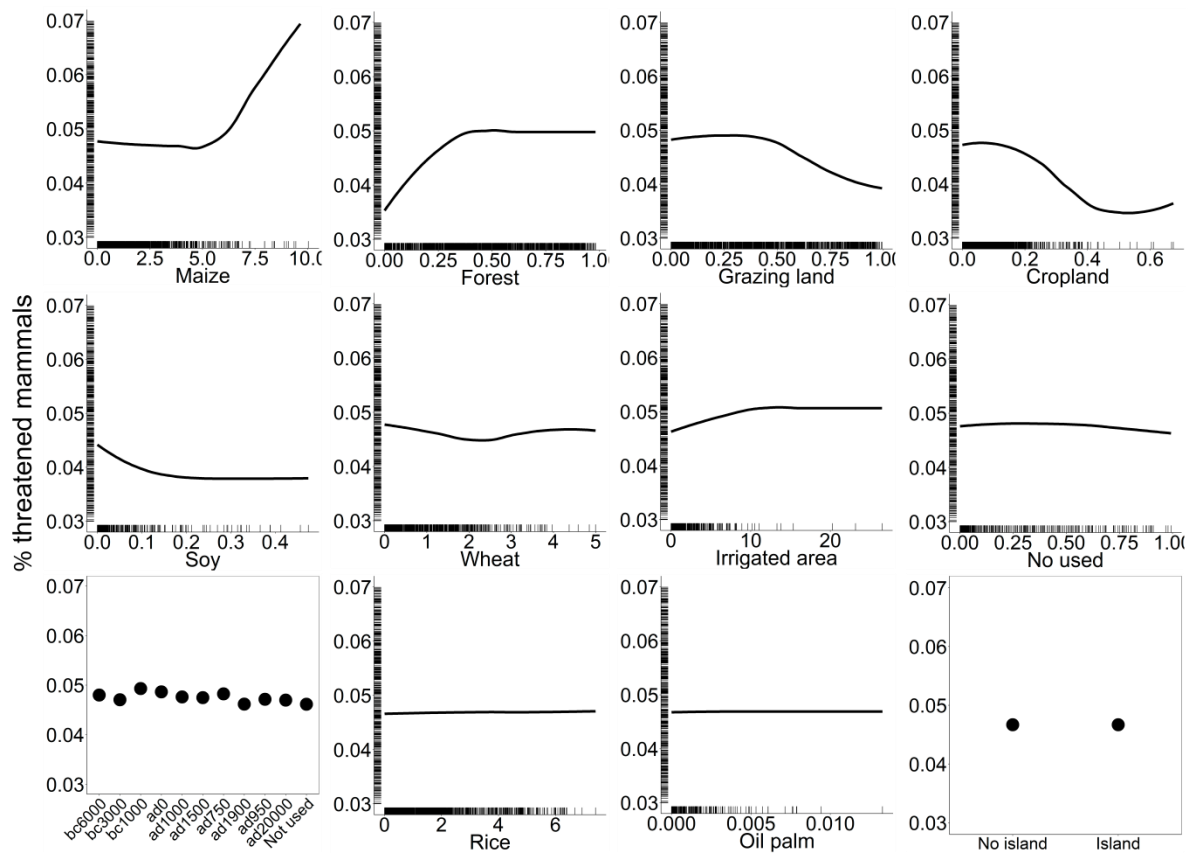
**Figure S2.6.** Partial dependence plots (PDPs) of all variables included in the Indomalay BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

*Nearctic:*



**Figure S2.7.** Partial dependence plots (PDPs) of all variables included in the Nearctic BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

*Neotropics:*



**Figure S2.8.** Partial dependence plots (PDPs) of all variables included in the global BRT. Individual plots are ordered according to their relative importance in the BRT (Table 1, main manuscript).

**Table S2.1.** Parameters and results of the BRTs, global and by realm, excluding the residual autocovariate (RAC). *Afro.* = Afrotropics; *Austr.* = Australasia; *Indo.* = Indomalay; *Neotrop.* = Neotropics. *Moran's I* was calculated for the residuals of each cell and the grid-cells surrounding it (all adjacent neighbours; max=8). *RAC*, residuals spatial autocovariate. Bold numbers indicate variables considered as relevant (i.e. their importance is greater than the expected under uniformity; thresholds are indicated in the last row).

	Global	Afro.	Asia	Austr.	Europe	Indo.	Nearctic	Neotrop.
No. trees	1500	13500	8600	2700	7500	7700	6500	7900
Residuals Moran's I	0.37***	0.28***	0.52***	0.19***	0.33***	0.18***	0.32***	0.37***
% Deviance explained	71.71	48.04	56.68	33.6	68.1	71.14	36.15	43.55
Variables (importance, %)								
<b>Land-use extent</b>								
Built-up	~	~	~	7.22	~	~	~	~
Cropland	6.55	<b>10.7</b>	<b>12.65</b>	~	4.62	~	<b>18.18</b>	8.03
Forest	<b>10.71</b>	8.02	<b>29.77</b>	<b>39.15</b>	<b>26.24</b>	<b>29.13</b>	9.82	<b>18.29</b>
Grazing land	6.19	~	9.14	<b>11.86</b>	6.4	5.67	9.5	<b>11.12</b>
Not used	5.27	<b>9.86</b>	7.65	5.46	7.01	~	8.84	5.5
<b>Land-use intensity</b>								
Fertilizer	~	<b>9.65</b>	~	<b>11.94</b>	9.93	8.67	~	~
Irrigated area	4.53	6.4	~	8.1	<b>17.18</b>	~	8.73	7.05
Maize	4.25	<b>10.27</b>	~	4.61	~	5.24	8.76	<b>17.84</b>
Rice	6	<b>14.57</b>	~	2.09	5.24	5.79	0.34	3.77
Wheat	5.47	<b>11.4</b>	<b>13.74</b>	~	~	<b>14.66</b>	<b>14.49</b>	<b>9.3</b>
Oil palm	0.76	6.85	-	1	-	3.31	-	1.72
Soy	2.09	2.86	5.41	0.92	<b>10.33</b>	8.03	8.11	<b>10.92</b>
<b>Land-use history</b>								
Time of first use	6.81	<b>9.42</b>	<b>21.61</b>	7.66	<b>12.53</b>	<b>19.26</b>	<b>13.23</b>	6.46
<b>Island</b>	3.05	-	0.04	-	0.51	0.22	-	0
<b>Realm</b>	<b>38.33</b>	-	-	-	-	-	-	-
<i>Relevance threshold</i>	7.69	9.09	12.5	9.09	10	10	10	8.33

\*\*\*  $p < 0.001$ , spatial autocorrelation exists; -, not existent/applicable; ~, variable excluded because its correlation with other/s one was  $\geq |0.7|$  (Spearman's  $\rho$ ).

**Table S2.2.** Interactions table for the global BRT.

	Cropland	Forest	Grazing land	Not used	Irrigated area	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	Island	Realm	RAC
<b>Cropland</b>	0.00	0.01	0.01	0.00	0.03	0.02	0.00	0.00	0.00	0.01	0.04	0.00	0.01	0.02
<b>Forest</b>	0.00	0.00	0.00	0.02	0.00	0.01	0.02	0.02	0.00	0.00	0.02	0.16	0.17	0.04
<b>Grazing land</b>	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.01	0.00	0.00	0.01	0.00	0.05	0.04
<b>Not used</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.03	0.05
<b>Irrigated area</b>	0.00	0.00	0.00	0.00	0.00	0.01	0.02	0.00	0.00	0.00	0.02	0.01	0.01	0.01
<b>Wheat yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.02	0.00	0.00	0.05	0.00	0.02	0.03
<b>Maize yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.00	0.05	0.10
<b>Rice yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.11	0.04	0.02
<b>Oil palm</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Soy</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Time of 1st use</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08	0.04	0.74
<b>Island</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.69	1.11
<b>Realm</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	1.40
<b>RAC</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

**Table S2.3.** Interactions table for the Afrotropics BRT.

	Cropland	Forest	Not used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	RAC
<b>Cropland</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
<b>Forest</b>	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.01
<b>Not used</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Irrigated area</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Fertilizer</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Wheat yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Maize yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Rice yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Oil palm</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<b>Soy</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

	Cropland	Forest	Not used	Irrigated area	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	RAC
Time of 1st use	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
RAC	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

**Table S2.4.** Interactions table for the Asia BRT.

	Cropland	Forest	Grazing land	Not used	Wheat yield	Soy	Time of 1st use	Island	RAC	
Cropland	0.00	0.00	0.00	0.00	0.02		0.00	0.03	0.00	0.02
Forest	0.00	0.00	0.01	0.01	0.03		0.00	0.01	0.00	0.02
Grazing land	0.00	0.00	0.00	0.00	0.01		0.00	0.00	0.00	0.02
Not used	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.01
Wheat yield	0.00	0.00	0.00	0.00	0.00		0.01	0.06	0.00	0.04
Soy	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
Time of 1st use	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.10
Island	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00
RAC	0.00	0.00	0.00	0.00	0.00		0.00	0.00	0.00	0.00

**Table S2.5.** Interactions table for the Australasia BRT.

	Built-up	Forest	Grazing land	Not used	Irrigated area	Fertilizer	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	RAC
Built-up		0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Forest			0.00	0.00	0.01	0.00	0.02	0.00	0.00	0.00	0.00	0.02
Grazing land				0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.02
Not used					0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
Irrigated area						0.00	0.00	0.00	0.00	0.00	0.00	0.00
Fertilizer							0.00	0.00	0.00	0.00	0.00	0.00
Maize yield								0.00	0.00	0.00	0.00	0.03
Rice yield									0.00	0.00	0.00	0.00
Oil palm										0.00	0.00	0.00
Soy											0.00	0.00
Time of 1st use												0.02
RAC												0.00



**Table S2.6.** Interactions table for the Europe BRT.

	Cropland	Forest	Grazing land	Not used	Irrigated area	Fertilizer	Rice yield	Soy	Time of 1st use	Island	RAC
<b>Cropland</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Forest</b>	0.00	0.00	0.00	0.00	0.01	0.02	0.00	0.01	0.03	0.00	0.02
<b>Grazing land</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Not used</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Irrigated area</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.01
<b>Fertilizer</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.00	0.01
<b>Rice yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.03
<b>Soy</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Time of 1st use</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03
<b>Island</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>RAC</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

**Table S2.7.** Interactions table for the Indomalay BRT.

	Forest	Grazing land	Fertilizer	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	Island	RAC
<b>Forest</b>	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.01	0.04	0.00	0.02
<b>Grazing land</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Fertilizer</b>	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.01
<b>Wheat yield</b>	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.01	0.00	0.00
<b>Maize yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Rice yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<b>Oil palm</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Soy</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<b>Time of 1st use</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<b>Island</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>RAC</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

**Table S2.8.** Interactions table for the Nearctic BRT.

	Cropland	Forest	Grazing land	Not used	Irrigated area	Wheat yield	Maize yield	Rice yield	Soy	Time of 1st use	Island	RAC
<b>Cropland</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<b>Forest</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<b>Grazing land</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Not used</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Irrigated area</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Wheat yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.07
<b>Maize yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Rice yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Soy</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<b>Time of 1st use</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.04
<b>Island</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>RAC</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

**Table S2.9.** Interactions table for the Neotropics BRT.

	Cropland	Forest	Grazing land	Not used	Irrigated area	Wheat yield	Maize yield	Rice yield	Oil palm	Soy	Time of 1st use	Island	RAC
<b>Cropland</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.11
<b>Forest</b>	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01	0.00	0.00	0.05
<b>Grazing land</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.08
<b>Not used</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Irrigated area</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Wheat yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.00	0.00	0.00	0.00
<b>Maize yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.00	0.13
<b>Rice yield</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Oil palm</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Soy</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.01
<b>Time of 1st use</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>Island</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
<b>RAC</b>	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00