The geography of the Anthropocene differs between the land and the sea

D.E. Bowler[1,2*], A.D. Bjorkman[3], M. Dornelas[4], I.H. Myers-Smith[5], L. M. Navarro[2,6], A. Niamir[1], S.R. Supp[7], C. Waldock[8], M. Vellend[9], S. A. Blowes[2,10], K. Böhning-Gaese[1], H. Bruelheide[6,2], R. Elahi[11], L.H. Antão[4,12], J. Hines[2,13], F. Isbell[14], H.P. Jones[15], A.E. Magurran[4], J. S. Cabral[2,16], M. Winter[2,17], & A.E. Bates[8,18]

[1]Senckenberg Biodiversity and Climate Research Centre, Senckenberganlage 25, D-60325 Frankfurt am Main, Germany.

[2]German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, Deutscher Platz 5e, 04103 Leipzig, Germany

[3]Section for Ecoinformatics & Biodiversity, Department of Bioscience, Aarhus University, DK-8000 Aarhus, Denmark.

[4]Centre for Biological Diversity, University of St Andrews, Sir Harold Mitchell Building, St Andrews, KY16 9TH Scotland, UK.

[5]School of GeoSciences, University of Edinburgh, Edinburgh EH9 3FF, UK

[6]Institute of Biology/Geobotany and Botanical Garden, Martin Luther University Halle–Wittenberg, Am Kirchtor 1, 06108 Halle, Germany.

[7]Denison University, Data Analytics Program, Granville, OH 43023 USA

[8]Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Waterfront Campus, European Way, Southampton, SO14 3ZH, United Kingdom

[9]Université de Sherbrooke, Sherbrooke, QC Canada J1K 2R1

[10]Department of Zoology, George S. Wise Faculty of Life Sciences, Tel Aviv University, Tel Aviv 69978, Israel

[11]Hopkins Marine Station, Stanford University, Pacific Grove, CA 93950, USA

[12]Department of Biology and CESAM, Universidade de Aveiro, Campus Universitário de Santiago, 3810-193, Aveiro, Portugal

[13]Institute of Biology, Leipzig University, Deutscher Platz 5e, 04103 Leipzig, Germany

[14]Department of Ecology, Evolution, and Behavior, University of Minnesota Twin Cities, Saint Paul, Minnesota 55108, USA

[15]Department of Biological Sciences and Institute for the Study of the Environment, Sustainability, and Energy. Northern Illinois University, DeKalb, IL 60115, USA.

[16]Ecosystem Modeling, Centre for Computational and Theoretical Biology, University of Würzburg, Würzburg, Germany

[17]Leipzig University, Ritterstraße, 26, 04109 Leipzig, Germany

[18]Department of Ocean Sciences, Memorial University of Newfoundland, St. John's A1C 5S7, Canada

*Correspondence to: diana.e.bowler@gmail.com

Abstract

1. Climate change and other anthropogenic drivers of biodiversity change are unequally distributed across the world. The geographic patterns of different drivers, and the spatial overlap among these drivers, have important implications for the direction and pace of biodiversity change, yet are not well documented. Moreover, it is unknown if the geographic patterns of drivers differ between the terrestrial and marine realm, as expected due to marked differences in how humans interact with the land and ocean.

2. We compiled global gridded datasets on climate change, land-use, resource exploitation, pollution, species invasions, and human population density. We used multivariate statistics to examine the spatial relationships among the datasets and to characterize the typical combinations of drivers experienced by different parts of the world.

3. We found stronger positive correlations among drivers in the terrestrial than in the marine realm, leading to areas of high intensities of multiple drivers on land. Climate change tended to be negatively correlated with other drivers in the terrestrial realm (e.g., in the tundra and boreal forest with high climate change but low human use and pollution) whereas the opposite was true in the marine realm (e.g., in the Indo-Pacific with high climate change and high fishing).

4. We show that different regions of the world can be defined by anthropogenic threat complexes (ATCs), distinguished by different sets of drivers with varying intensities. The ATCs can be used to test hypothesis about the pattern of biodiversity change, especially the joint effects of multiple drivers. More generally, our global analysis highlights the broad conservation priorities needed to mitigate the effects of anthropogenic change on

biodiversity responses, with different priorities emerging on land and in the ocean, and in different parts of the world.

63 ## Introduction

64 Human activities are reshaping biological communities and impacting ecosystem functioning
65 across the Earth (Pereira *et al.* 2010; Barnosky *et al.* 2011; Dornelas *et al.* 2014; Isbell *et al.*
66 2017). Meeting the global challenge of the conservation and sustainable use of nature requires
67 not only quantifying biodiversity change, but also identifying the underlying causes of change
68 (Tittensor *et al.* 2014; Isbell *et al.* 2017). Climate change, habitat change, exploitation, pollution
69 and alien species have been recognized as the most important and widespread causes (Butchart *et*
70 *al.* 2010; Pereira, Navarro & Martins 2012; IPCC 2013). However, the realized impacts of these
71 drivers on species' populations depend on the extent of exposure, which varies in space and time,
72 and species' sensitivity, which tends to be species-specific (Foden *et al.* 2013). Many studies
73 have examined species sensitivity and the role of functional traits in determining sensitivity
74 (Foden *et al.* 2013). By contrast, fewer studies have compared the exposure patterns of different
75 drivers or examined the overlap among them for different regions of the world. Hence, an
76 important, but so far missing, step towards understanding the global patterns of biodiversity
77 change is characterizing the exposure patterns of biological communities to environmental
78 change.

79 Global maps of pressures such as the terrestrial human footprint (Sanderson *et al.* 2002;
80 Venter *et al.* 2016), marine pressures (Halpern *et al.* 2008; Halpern *et al.* 2015a) and river threats
81 (Vorosmarty *et al.* 2010) highlight the geographic hotspots of anthropogenic threats to
82 biodiversity. These maps have estimated that at least 75% of terrestrial land has been exposed to
83 some sort of land-use change (Venter *et al.* 2016), while nearly the whole ocean is exposed to
84 multiple pressures including climate change (Halpern *et al.* 2015a). Supporting the significance
85 of these maps for biodiversity, they also explain variation in ecological patterns; for instance,

86 reduced animal movement was found in areas with a higher human footprint across different
87 species (Tucker *et al.* 2018).

88 The relative importance of different drivers for biodiversity change and ecosystem
89 services is a key component of both policy-oriented assessments such as IPBES framework
90 (Diaz *et al.* 2015) and conservation targets such as CBD Aichi Biodiversity Targets (Tittensor *et*
91 *al.* 2014). Yet, global maps, such as the human footprint, show the summed pressure of different
92 drivers related to human activities and ignore any relationships among them. Hence, areas of
93 high human pressure can be caused by different combinations of underlying drivers, each of
94 which may have contrasting impacts on biodiversity. Hence, unpacking the spatial patterns of
95 different drivers, and assessing the extent of their overlap, is essential for better understanding of
96 their impacts, in isolation and in combination, on biodiversity. For many drivers, it can be
97 hypothesized that exposure patterns maybe inter-linked due to related local or regional human
98 activities, driven by local human population density (Ellis *et al.* 2010). In contrast, climate
99 change is expected to be distributed differently than other variables because it is an outcome of
100 processes at regional and global scales (IPCC 2013).

101 Here, we present the spatial relationships among some of the main hypothesized drivers
102 of biodiversity change, and show how they overlap in different biogeographic regions, across the
103 entire surface of the world. We selected global spatial gridded datasets on variables that
104 characterize dimensions of different anthropogenic drivers (Tables 1 and S1–S2). We conducted
105 our analysis at the global scale to identify the most general patterns emerging across ecosystems.
106 Although the specific variables differ among realms, we aligned each variable to the dominant
107 drivers that are common across both realms (Table 1). We quantified the strengths of the
108 relationships among the intensities of the different variables related to climate change, habitat

conversion and exploitation (grouped together as 'human use'), pollution and species invasions. Based on these relationships, we defined 'anthropogenic threat complexes' that typify the combinations of drivers impacting different regions of the world. Studies mapping drivers of biodiversity change have so far considered the terrestrial and marine realms separately. By employing a standardized analysis for both the terrestrial and marine realms, out study highlights similarities and differences in anthropogenic environmental changes across the world, including across realms.

Methods

Approach to data selection

We selected variables included in previous studies on global drivers of change based on known impacts (Table 1) (Sanderson *et al.* 2002; Halpern *et al.* 2008). We further searched for data on other relevant variables following the IUCN threats categories (Table S1) (Salafsky *et al.* 2008). We focused on a land versus ocean comparison and thus did not specifically consider freshwater threats (Vorosmarty *et al.* 2010). Biodiversity change driver variables were obtained from publically available datasets and as much as possible were based on data between 1990 and 2010 (except climate change, and forest loss; see below). The terrestrial datasets came from various sources (Table S2). Most of the marine datasets came from the landmark study of Halpern et al. (Halpern *et al.* 2008). For interpretation and presentation purposes, variables were grouped by which global driver of change they were most directly related to, i.e., climate change, habitat conversion, exploitation, pollution or species invasions. Because habitat conversion and exploitation were difficult to classify separately across terrestrial and marine ecosystems, we combined both into a single "human use" category.

Climate change

Climate change has multiple components (IPCC 2013), hence we characterized climate change by several variables using global spatiotemporal gridded temperature data for the terrestrial (Harris *et al.* 2014) and marine realm (Rayner *et al.* 2003). We used data between 1950 and 2010, since 1950 has been proposed as the start of the Anthropocene (Waters *et al.* 2016). Temperature trends were estimated by fitting simple linear regression models to annual temperature means of each grid and extracting the coefficient for the effect of year. Temperature divergence, following ideas by (Nadeau & Fuller 2015), was inferred from the t-static of this linear regression and represents the significance of the trend, i.e., the trend after accounting for the degree of annual variability in temperature. Velocity of climate change (Loarie *et al.*, 2009) was calculated as the ratio between the temporal temperature trend and the local spatial gradient in temperature. Trends of extreme temperatures were calculated by whichever was largest of the temporal trends in mean temperature of the warmest or coolest month. To characterize further climate change trends, we also included aridity for the terrestrial realm and ocean acidification for the marine realm. Aridity trend was estimated by taking monthly and annual datasets on potential evapotranspiration and precipitation, and calculating their ratio (Zorner *et al.* 2008), and then the temporal trend of the annual monthly average of this ratio. Ocean acidification, from the Halpern layers, was based on the change in aragonite saturation state between 1870 and 2000–2009 (Halpern *et al.* 2008).

Human use

154 In the terrestrial realm, we used human use variables related to different types of land conversion
155 or use: cropland, pasture land, cattle density, urban land and forest loss. Data on crop land,
156 pasture land and urban/built land cover were taken from different databases, primarily based on
157 satellite imagery – crop land (Fritz *et al.* 2015), pasture land (Ramankutty *et al.* 2008) and urban
158 land (Friedl *et al.* 2010). We additionally included information on forest loss since deforestation
159 itself is a recognized threat (Barlow *et al.* 2016; Vijay *et al.* 2016). Forest loss, based on FAO
160 wood harvest statistics, was calculated as the loss of primary forest for the same time frame as
161 our climate change statistics, i.e., between 1950 and 2010 (Hurtt *et al.* 2011). We also included
162 data on cattle density, which was based on sub-national livestock data that were statistical
163 downscaled using multiple predictors (Robinson *et al.* 2014). In the marine realm, human use
164 variables were based on different commercial fishing activities separated by gear types (e.g.,
165 dredging or castnets), which determine their selectivity and impact on the surrounding seascape
166 (Halpern *et al.* 2008). These fishing types were pelagic low-bycatch, pelagic high-bycatch,
167 demersal habitat-modifying, demersal non-habitat-modifying low-bycatch, and demersal non-
168 habitat-modifying high bycatch. These data were based on FAO and other commercial catch data
169 sources and downscaled based on an ocean productivity model (Halpern *et al.* 2008).

170

171 *Pollution*

172 Nitrogen from both fossil fuel combustion and agriculture is one is the biggest pollutants
173 impacting biodiversity (De Schrijver *et al.* 2011; Erisman *et al.* 2013). We included data on
174 nitrogen pollution for the terrestrial realm in the form of atmospheric nitrogen (Dentener 2006)
175 and fertilizer use (Potter *et al.* 2010), and for the marine realm as fertilizer use (Halpern *et al.*
176 2008). We also included data on pesticide use in both realms (Halpern *et al.* 2008; Vorosmarty *et*

177 *al.* 2010), another important component of agricultural intensification that negatively affects
178 biodiversity (Geiger *et al.* 2010). Country-specific estimates of fertilizer use and pesticide were
179 downscaled to a raster grid by the data providers according to the crop land maps; thus, these
180 datasets were not fully independent of the cropland data. We also included a layer reflecting the
181 extent of ocean pollution, based on the distribution of shipping lanes (Halpern *et al.* 2008).
182 Finally, we included night-time light pollution detected by satellite imagery (Halpern *et al.*
183 2015a), which were also included in previous terrestrial and marine threat maps (Halpern *et al.*
184 2015a; Venter *et al.* 2016).

185

186 *Invasions*

187 There are no high-resolution gridded richness maps of alien species (Dyer *et al.* 2017; van
188 Kleunen *et al.* 2019); however, we used maps of human transport connectivity as a proxy of
189 human-mediated propagule pressure of alien species related to human movement and trade,
190 which is known to be an important determinant of invasion success (Hulme 2009; Seebens *et al.*
191 2015). We used spatial datasets of connectivity based on transport infrastructure (including data
192 on road and rail networks and navigable rivers) in the terrestrial realm and cargo volume at ports
193 in the marine realm (Table S1). For the terrestrial realm, information on alien species distribution
194 is available at a regional, sub-national and national levels for some taxonomic groups, including
195 birds (Dyer *et al.* 2017) and plants (van Kleunen *et al.* 2019). To assess the validity of our
196 connectivity proxy, we used these datasets, representing taxa with low and high mobility, to test
197 the correlation between alien species richness and mean connectivity at the spatial scale of the
198 distribution data. Since we found a significant rank correlation for both datasets (birds, ρ=0.42;
199 plants, ρ=0.46), our terrestrial proxy variable was reasonably well justified given the coarseness

of the distribution data (see Fig. S1 for more details). For the marine, there are no readily available spatial datasets on alien species. However, transportation infrastructure (via ships) is also regarded as an important factor for biological invasions in the marine realm, via ballast water, sediments and biofouling (Davidson *et al.* 2018). Moreover, cargo volume at ports was included as the proxy for invasion species in Halpern *et al.* (2008).

Human population

We also included "human population density" as a separate driver (CIESIN 2017) accounting for the effects of human activities not falling into the other categories, such as tourism/recreation activities (Salafsky *et al.* 2008). By including it, we could also assess the relationship between human population density and the other drivers.

Justification for layer exclusion

We did not use data for some variables that were previously included in the terrestrial human footprint or the Halpern layers. The human footprint includes data on roads, railways and navigable waterways (Venter *et al.* 2016). Although we did not separately include these data, these data were already included in our connectivity variable (for invasions). In the marine realm, we excluded a shipping lane variable since the ocean pollution variable was already based on the distribution of shipping lanes (Halpern *et al.* 2008). Additional available Halpern marine layers that we did not use were: UV radiation, oils rigs (based on night lights, already included), inorganic pollution (highly correlated with other land-based coastal pollutants that were already included) and artisanal fishing (data poor and mostly modelled) (Halpern *et al.* 2008).

222

223 *Geographic region data*

224 Data on the spatial distribution of terrestrial biomes were taken from WWF (Olson *et al.* 2001).
225 Marine regions were defined by combining coastal/shelf region polygon data – MEOW
226 (Spalding *et al.* 2007) and ocean polygon data (naturalearthdata.com). We did not use marine
227 ecosystem data as used by others (Halpern *et al.* 2015a) because the ecosystems spatially
228 overlapped in our coarse 2-D global raster grid, when, in reality, different ecosystems occur at
229 different depths in the water column.

230

231 *Data processing*

232 We harmonized each dataset to a standard global grid. The resolutions of the original datasets
233 were approximately at a 100 km square grid (or 1°) or finer resolution; hence, we aggregated all
234 datasets to a standard grid of 100 km square grid cells by taking the mean value of the grid cells.
235 Atmospheric nitrogen deposition was only available at a courser resolution (see Table S1);
236 however, we disaggregated this also to 100 km. Datasets were bound between latitudes of -58
237 and 78 to avoid edge effects. Datasets were re-projected onto a common equal-area map
238 projection (Eckert IV; ESPG = 54012). Missing values in some of the human activity datasets
239 were in remote regions (e.g., very high latitudes) with likely absent or low variable values and
240 were imputed as zero. Greenland was excluded due to missing data in several of the datasets.

241 Because each dataset comprised data in different units (e.g., temperature data in °C and
242 fertilizer data in kg/ha), it was not possible to directly compare their absolute values. Instead, we
243 ranked the values of each dataset and scaled them between 0 and 1 for ease of interpretation (Fig.

244 S2 show the distributions of the original values of each variable and Fig. S3 shows global maps
245 of the ranked and scaled data). This processing also reduced the large skew in the absolute values
246 of many of the datasets. For all datasets, larger values reflected a greater potential exposure of
247 that variable on biodiversity. Transformations were needed in only one case to achieve this – we
248 inverted terrestrial accessibility (i.e., $values^{-1}$).

249

250 *Data analysis*

251 To examine the relationships among the intensities of different variables, we calculated
252 Spearman's rank correlation coefficients (ρ) for each pairwise combination of variables across all
253 grid cells in each realm. We chose this statistic because it only uses the rankings of the data
254 values and is equivalent to the commonly used Pearson's correlation on ranked data. We used
255 Dutilleul's modified t-test to account for spatial autocorrelation in each dataset before testing the
256 significance of the correlations (Dutilleul, Pelletier & Alpargu 2008). We also used Moran's I
257 and correlograms to determine the extent of spatial autocorrelation within each variable
258 (Bjornstad, Ims & Lambin 1999). For the marine realm, correlations were also examined
259 separately for grid cells whose centroid overlapped with oceanic or coastal regions. To assess the
260 importance of the drivers in different parts of the world, we calculated the average drivers values
261 for each region. To do this, we first calculated the mean of the values for each driver for each
262 grid cell. We then plot the distribution of these mean values across all grid cells within each
263 terrestrial biome and marine region.

264 We used k-medoid clustering, with the partitioning around the medoids algorithm with
265 Manhattan distances (Maechler *et al.* 2018), for clustering grid cells according to their extent of
266 exposure of all the variables. We applied the cluster analysis to the dataset of all 16 variables for

267 each realm. We selected the number of clusters by comparing the changes in dissimilarly and
268 cluster silhouette width with increasing cluster number. However, we limited the cluster number
269 to <10. To slightly smooth the maps, we used a moving window to assign each cell the mode of
270 its 3 x 3 cell neighborhood. Although, driver combinations vary in a continuous manner, we
271 chose a clustering method that produces discrete grouping to provide the simplest description of
272 the main groupings in the data. Finally, to repack the datasets into cumulative driver maps across
273 the entire surface of the world, we summed the number of driver variables for which each grid
274 cell was in the upper 10% of values (based on all values greater than zero). Analyses were run in
275 R v. 3.4.1 (R Core Team 2018), mostly using the packages raster (Hijmans 2017), SpatialPack
276 (Vallejos, Osorio & Bevilacqua 2018) and cluster (Maechler *et al.* 2018).

277

278 *Sensitivity analyses*

279 To examine the effect of the grain size of our global grid, we repeated the data processing steps
280 except harmonizing the datasets to a global grid of 500 km resolution and repeated the analysis
281 of correlations (similar results were obtained – see Fig. S4). To check the effects of ranking the
282 data values because of the skewed data distributions, we repeated the data processing steps by
283 logging the values (to the base 10) rather than ranking them, after bounding values above the
284 upper and lower 2.5% of quantiles to the values of the upper and lower 2.5% quantiles. This
285 alternative data transformation does not affect the correlation coefficients because Spearman's
286 correlations only uses the ranks of the data. We repeated our remaining analysis with this
287 alternative transformation, calculating the average variable intensities for different terrestrial and
288 marine regions, and the clustering analysis (generally similar results were obtained – see Fig. S5

and S6). Since the distributions are still skewed after logging, the patterns are strongly affected by extreme values with this approach, especially in the marine realm.

Results

We found that drivers of biodiversity change were more spatially coupled in the terrestrial than in the marine realm (Fig. 1, Fig. S7). On land, 40% of the possible pair-wise relationships between variables (excluding climate change-related variables) showed positive correlation strengths of at least 0.7. Thus, terrestrial areas with high intensities of one variable also tended to have high intensities of other variables. Moreover, correlations were found between different types of drivers. High crop land cover was associated with high pollution, high connectivity and high human population density. Of the terrestrial land cover trend variables, only urban land cover trend displayed any strong correlations with the other variables. Conversely, in the marine realm, we found fewer correlations – only 15% of the possible pair-wise relationships (excluding climate change-related variables) showed a strong positive correlation (> 0.7) – and these relationships were mostly within, rather than between, different driver types; for instance, among different types of human use (e.g., pelagic and demersal fishing; Fig. 1). Across all variables, oceanic regions showed fewer correlations compared to coastal regions (Fig. S8). Spatial autocorrelation was present in all variables and tended to reach greater distances in the marine human-uses and climate-change variables (Figs S9 and S10), and shorter distances in the coastal-based marine variables, but the correlations among drivers remained statistically significant (all $P<0.05$) after accounting for autocorrelation. In neither realm were there strong negative correlations among variables (Fig. S11 shows the full correlation matrix).

Strong correlations between climate change and other drivers were not observed in either realm (Fig. 1, Fig. S11), as expected based on the broader spatial scale at which carbon emissions affect climate. However, there were still significant weak correlations, with the direction of these correlations differing systematically between realms (Fig. 2). Temperature change was negatively associated with the average intensity of other variables in the terrestrial realm ($\rho = -0.26$, $P<0.01$, Fig. 2), but positively associated with the average intensity of other variables in the marine realm ($\rho = 0.21$, $P<0.05$; Fig. 2). Terrestrial biomes exposed to strong climate change, such as the tundra, boreal forest and deserts, have experienced relatively low human use (Fig. 3, Fig. S12) while terrestrial biomes, such as tropical dry broadleaf forest, with high intensities of human use, pollution and invasions have had lower intensities of climate change. In contrast, marine areas exposed to strong climate change have also been strongly exposed to other drivers, especially fishing (Fig. 3). The central and western Indo-Pacific emerged as regions particularly at risk by being exposed to both rapid climate change and multiple human uses. Overall, temperate broadleaf and mixed forest and the Central Indo-Pacific regions were most impacted by multiple drivers in the terrestrial and marine realms, respectively, while deserts and the South Pacific Ocean were the least impacted by multiple drivers.

The cluster analysis defined six terrestrial and six marine regions according to their similarity of exposure to the different driver variables (Fig. 4). These exposure patterns can be regarded as ‘anthropogenic threat complexes’ (ATC) that characterize the typical combinations of environmental change. ATCs I and VII represent terrestrial and marine areas ranked with higher exposure to climate change than to other drivers (dark orange regions in Fig. 4), while the reverse is true for ATCs V and XI (blue regions). ATCs III (terrestrial) and VII and IX (marine) are regions exposed to relatively high intensities of many variables (grey regions) while ATCs

334 VI and XII (light orange regions) represent areas generally exposed to lower intensities of most
335 variables. The largest terrestrial ATC was ATC 1 (29% of terrestrial grid cells), which defines
336 regions exposed to high climate change and lower intensities of other drivers. The largest marine
337 ATC was VIII (20% of marine grid cells), which defines regions exposed to high climate change
338 as well as high fishing activities.

339 The global maps (Fig. 5) show areas exposed to high intensities of multiple drivers and
340 connect the ATCs to previous cumulative human impact maps produced separately for the
341 terrestrial (Sanderson *et al.* 2002; Venter *et al.* 2016) and marine realms (Halpern *et al.* 2008;
342 Halpern *et al.* 2015a). Regions with the highest cumulative intensities across all variables tended
343 to be within ATCs III and V (terrestrial), areas with especially high pollution, human population
344 and connectivity, and VIII and IX (marine), areas with high intensities of almost all drivers. By
345 contrast, regions with the lowest cumulative intensities include ATCs I and VI (terrestrial) and X
346 and XII (marine), which have lower human uses, pollution and invasions, but still could have
347 high exposure to climate change.

348

349 **Discussion**

350 Spatial relationships between different land use changes in the terrestrial realm are likely based
351 on the land requirements to support proximal human populations (Ellis *et al.* 2010). Venter *et al*.
352 (2016) already linked spatial variation in the human footprint to land suitable for agriculture. In
353 the marine realm, different human uses (i.e., fisheries) largely occur in different areas, explaining
354 the weaker correlations. For instance, demersal fisheries mostly occur over the continental shelf,
355 whilst pelagic fisheries can be either continental or oceanic. Coastal regions were intermediate in

356 patterns between terrestrial and oceanic regions, suggesting that the prevalence of human
357 presence may contribute to the differences between the two realms (Halpern *et al.* 2015b).

358 Correlations among drivers have important implications because they indicate that
359 regional biological communities are often jointly impacted by different pressures. When multiple
360 drivers simultaneously act on a community, they could have additive, synergistic or antagonistic
361 effects (Travis 2003; Hof *et al.* 2011; Garcia-Valdes *et al.* 2015). Our analysis indicates where
362 interactive effects have most opportunity to occur. In fact, disentangling the independent
363 contributions of different drivers to biodiversity change may be difficult when multiple drivers
364 overlap, e.g., within temperate broadleaf and mixed forest. Although spatial heterogeneity at
365 smaller spatial scales (e.g., neighboring sites with different land cover) can be used to estimate
366 the local effect of drivers such as habitat conversion (Newbold *et al.* 2015) , correlated large-
367 scale drivers may affect regional species pools and hence still influence local community
368 dynamics (Harrison & Cornell 2008). As we found fewer strong correlations among different
369 driver variables in the marine realm (Fig. 1), separating the effects of different drivers may be
370 more feasible in marine, especially in open ocean, ecosystems.

371 Climate change emerged from our analysis as a spatially distinct driver of biodiversity
372 change. As climate change is only weakly associated with other drivers, there is considerable
373 opportunity to disentangle climate change impacts from those of other drivers. In areas where
374 other drivers are weak, climate change has the potential to be the dominant driver of change, for
375 instance in deserts, tundra and boreal forests. Consequently, climate change impacts on species
376 abundances, range limits and community compositions (Parmesan & Yohe 2003; Poloczanska *et*
377 *al.* 2013) may be easier to isolate than those of other drivers. Locations in which climate change
378 is the main driver of change in a community are likely to be especially common in the terrestrial

379 realm in which climate change was negatively correlated with other drivers. Indeed, high-latitude
380 regions that are experiencing pronounced climate change (IPCC 2013; Pithan & Mauritsen 2014)
381 have historically undergone less human settlement and agriculture. By contrast, the positive
382 correlation between climate change and other drivers in the marine realm indicates there may be
383 more opportunity for interactive effects. The Indo-Pacific and North Sea are areas with both
384 rapid temperature change and also intense fishing activity (Ramirez *et al.* 2017).

385 Given the strong spatial correlations among many drivers of biodiversity change,
386 attributing biodiversity change to human drivers may be most successful if focused on
387 complexes of environmental change, rather than on each variable individually. Our classification
388 of ATCs helps regard anthropogenic environmental change as a series of at least 12 natural
389 experiments across the globe. The differential associations of drivers, summarized by the
390 proposed ATCs, provide an informed baseline for studies aiming at understanding the joint
391 effects of multiple drivers on biodiversity and ecosystem services. Moreover, our approach could
392 be used to inform the design of quasi-experimental observatories that aim to test the additive and
393 joint effects of different drivers. Observatories could be selected along different driver gradients
394 (keeping all but one driver constant) or within different driver combinations. Study regions that
395 are most suitable to isolate the effects of a specific driver could be selected from within
396 geographic clusters dominated by the driver of interest, to reduce the confounding effects of
397 other drivers in the landscape. The ATCs could be further used in macroecological studies of
398 driver impacts. For example, examination of the relationships between the ATCs and the
399 distributions of threatened species or local/regional estimates of biodiversity change may help to
400 identify the most harmful combination of drivers.

401 Management at specific locations is clearly aided by assessing the local magnitudes of
402 different drivers. However, there are a number of advantages of having knowledge on the large-
403 scale driver patterns. First, these large-scale patterns allow local management to be modified
404 according to the wider anthropogenic land- or seascape context, which affects the regional
405 species pool and hence potentially biodiversity changes at smaller-scales (Harrison & Cornell
406 2008). Second, managers may only have access to partial data at local scales; thus, the typical
407 combinations of drivers that we identify can help managers predict the extent to which other
408 drivers should be of concern. Finally, by characterizing regions of the world in terms of the
409 nature of environmental change, the ATCs suggest how information and data might be pooled
410 and synthesized across regions, and even across realms. Regions exposed to the same ATC,
411 regardless of location, would benefit from exchanging knowledge about prioritization strategies
412 and management of the multiple drivers, as well as implementing cross-border strategies to
413 minimize their impact.

414 Data on global drivers of biodiversity change are still limited (Joppa *et al.* 2016). Many
415 of the recognized threats to biodiversity, such as by the IUCN (Salafsky *et al.* 2008), are not
416 available as high-resolution global datasets, such as the effects of energy production and mining,
417 hunting, and other forms of human disturbance (Salafsky *et al.* 2008). Rather than use proxy
418 variables, spatially-explicit maps of the number of alien species would have improved our
419 analysis. Ongoing projects, such as the Copernicus project (http://www.copernicus.eu/), will
420 greatly increase the availability of high resolution spatiotemporal datasets on different variables
421 (Skidmore *et al.* 2015) in the coming years for attribution of biodiversity change to the
422 underlying drivers.

423 Quantifying exposure to environmental change is the first step towards determining
424 which species, in which places, are most impacted by human activities. However, the realized
425 outcome of different drivers on biodiversity will ultimately depend on both a combination of the
426 magnitude of exposure to drivers and species' sensitivities to environmental change (Foden *et al.*
427 2013). We intentionally focused on exposure patterns, and as such our results are not species-
428 specific and are therefore potentially relevant for any taxa or ecosystem. Unlike exposure,
429 sensitivities vary among taxa according to characteristics such as their life history, traits and
430 niche breadth among others (Sunday *et al.* 2015) and therefore should be examined separately
431 for different taxa. Hence, despite similar exposure patterns, we can expect a diversity of
432 biodiversity responses within each ATC due to variation in species' sensitivities. We also
433 avoided making any complex assumptions about the relationships between the absolute values of
434 each driver variable and its impact on organisms. We rather assumed that all variables were
435 similarly important and that higher variable values would have a stronger impact on biodiversity.
436 Further work will need to integrate the role of species traits and consider the absolute magnitudes
437 of each driver to make species or community-level predictions.

438 Our macroecological approach to mapping the drivers of biodiversity change contributes
439 to the development of broad conservation policy targeted toward the mitigation of specific driver
440 complexes. A central focus of modern ecology is to understand global patterns of biodiversity
441 change. Yet, all too often, scientists and managers are reading, citing, and focusing on system
442 and realm-specific influences of global change drivers. By using a cross-realm approach, we
443 hope to encourage information exchange across regions of the world that are exposed to similar
444 suites of drivers, regardless of environmental realm, and the development of joined-up
445 conservation policies across the terrestrial-marine interface.

Data availability

Table S2 shows the sources of each dataset and links to where each dataset can be downloaded. Datasets produced during our analysis (raster layers shown in Figures 4 and 5) are available as georeferenced TIFF files in the SOM.

Code availability

R script to harmonize the raster to a standard grid is found here:

https://github.com/bowlerbear/harmonizeRasters

R script for the subsequent analysis is found here:

https://github.com/bowlerbear/geographyDrivers

Acknowledgments:

This paper arose from discussions at the sChange Workshop (www.idiv.de/schange), which was supported by sDiv, the synthesis centre of iDiv, the German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig. We thank all other participants of this workshop for the stimulating discussion and compilation of data that directly fed into this project. We also thank Suzanne Fritz, Mary O'Connor and Bob O'Hara for comments on a previous version of the manuscript. DB, JSC & MW were funded by the German Research Foundation (DB: Grant no BO 1221/23-1; JSC & MW: via iDiv: FZT 118). SRS was funded by the National Science Foundation, USA (NSF 1400911). LHA was supported by Fundação para a Ciência e Tecnologia, Portugal (POPH/FSE SFRH/BD/90469/2012). ADB was supported by The Danish Council for Independent Research - Natural Sciences (DFF 4181-00565). MD was funded by the Scottish Funding Council (MASTS, grant reference HR09011) and MD & AEM by the ERC project BioTIME (250189) and BioCHANGE (727440). CW was supported by the Natural Environmental Research Council (grant number NE/L002531/).

Author contributions

DB performed the analyses and wrote the first outline of the paper with AEB. All authors designed the study and helped draft the manuscript.

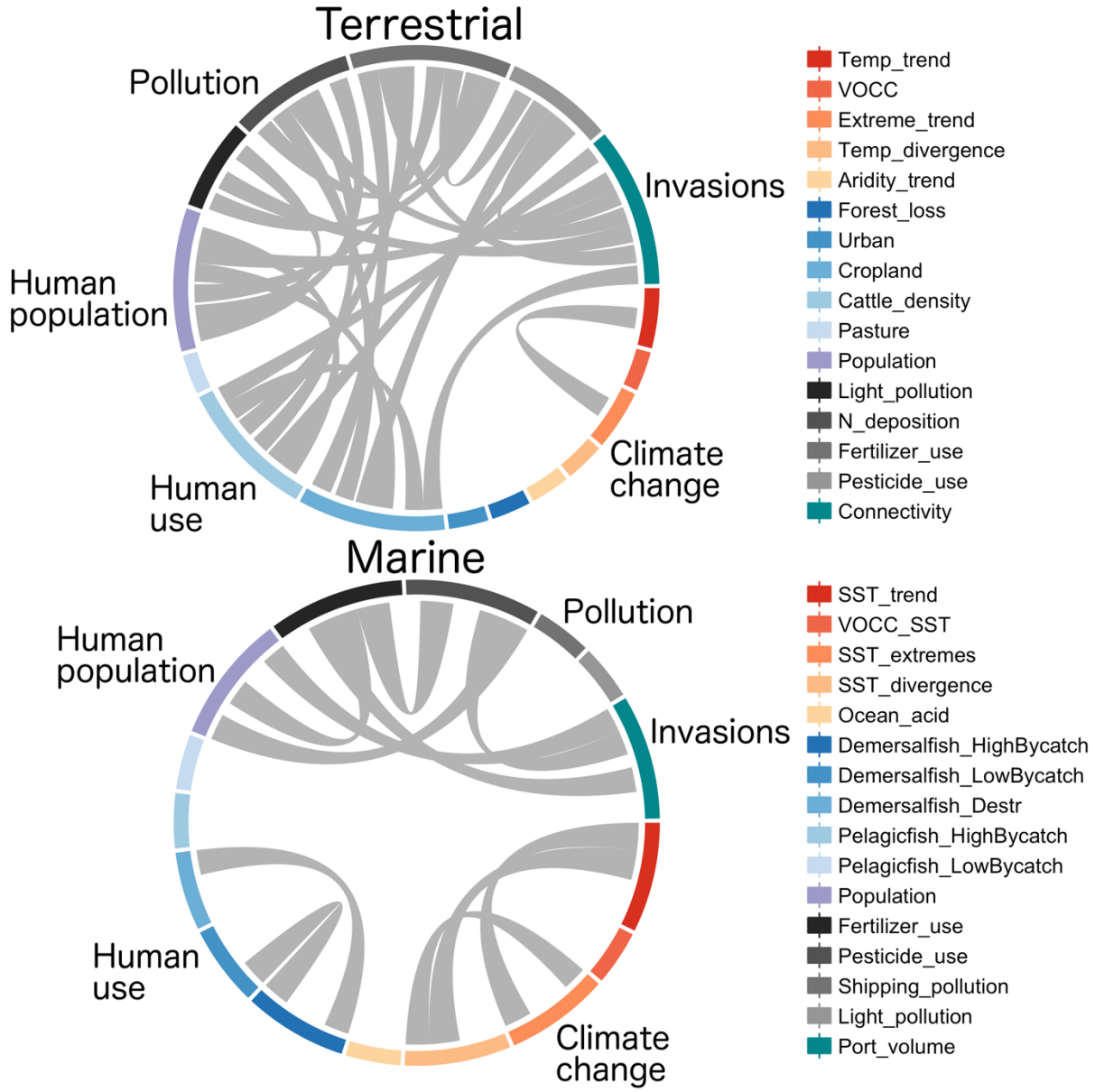

Fig. 1 Strong and positive relationships among anthropogenic drivers of biodiversity change. We find a higher number of correlations between drivers in the terrestrial versus the marine realm. Each link represents a significant and strong positive correlation with strength >0.7 between two variables across 100 square km grids covering the world.

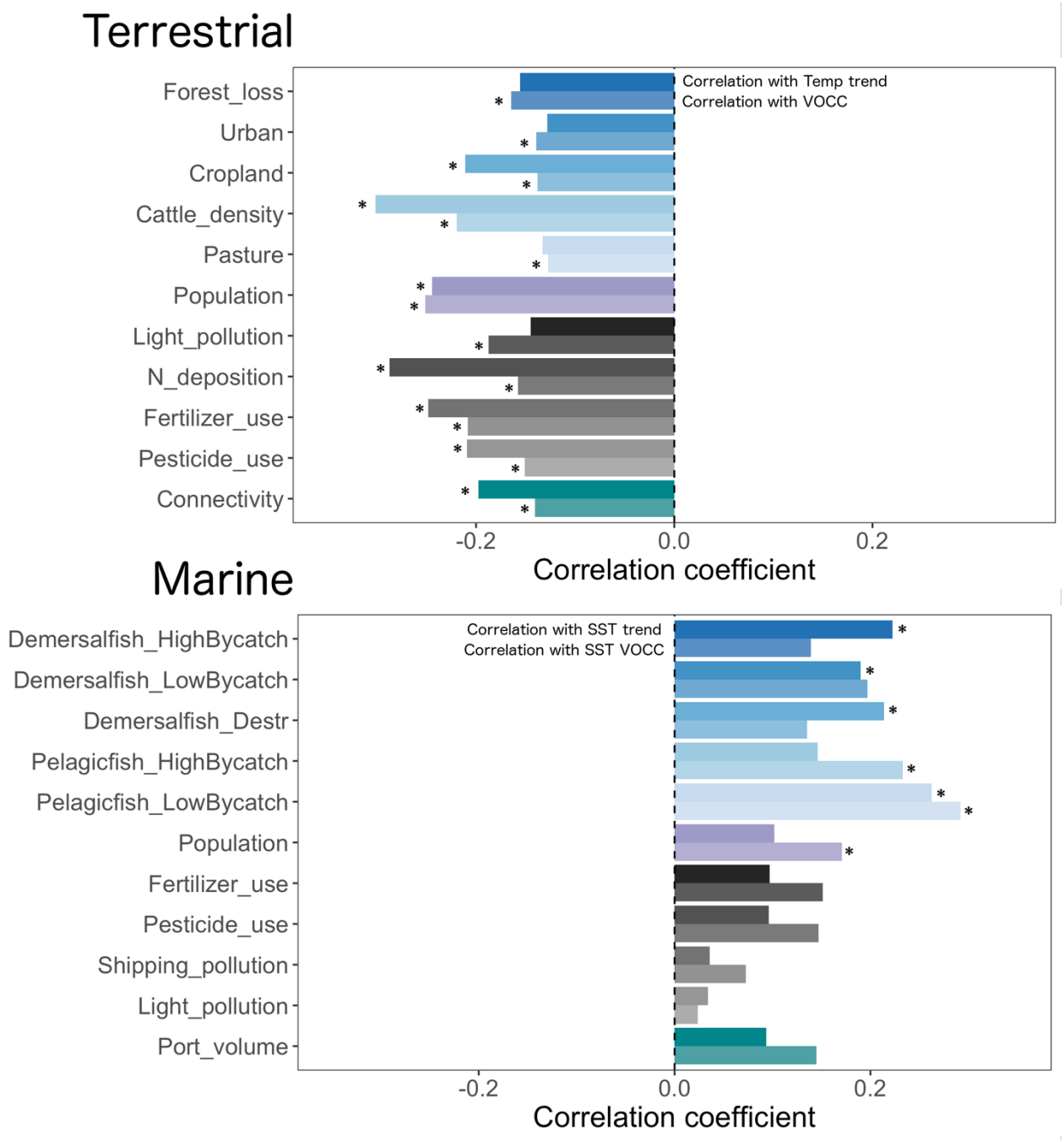

Fig. 2 Relationships between climate change and other drivers. Comparing the relationships between each variable and temperature change (air or sea surface temperature – SST) or the velocity of climate change (VOCC), we find weak negative (>-0.3) correlations in the terrestrial

realm and weak positive (<0.4) correlations in the marine realm. The length of each bar shows the correlation coefficient between temperature change (upper bar) or VOCC (lower bar) and each variable. * denotes statistical significance after accounting for spatial autocorrelation.

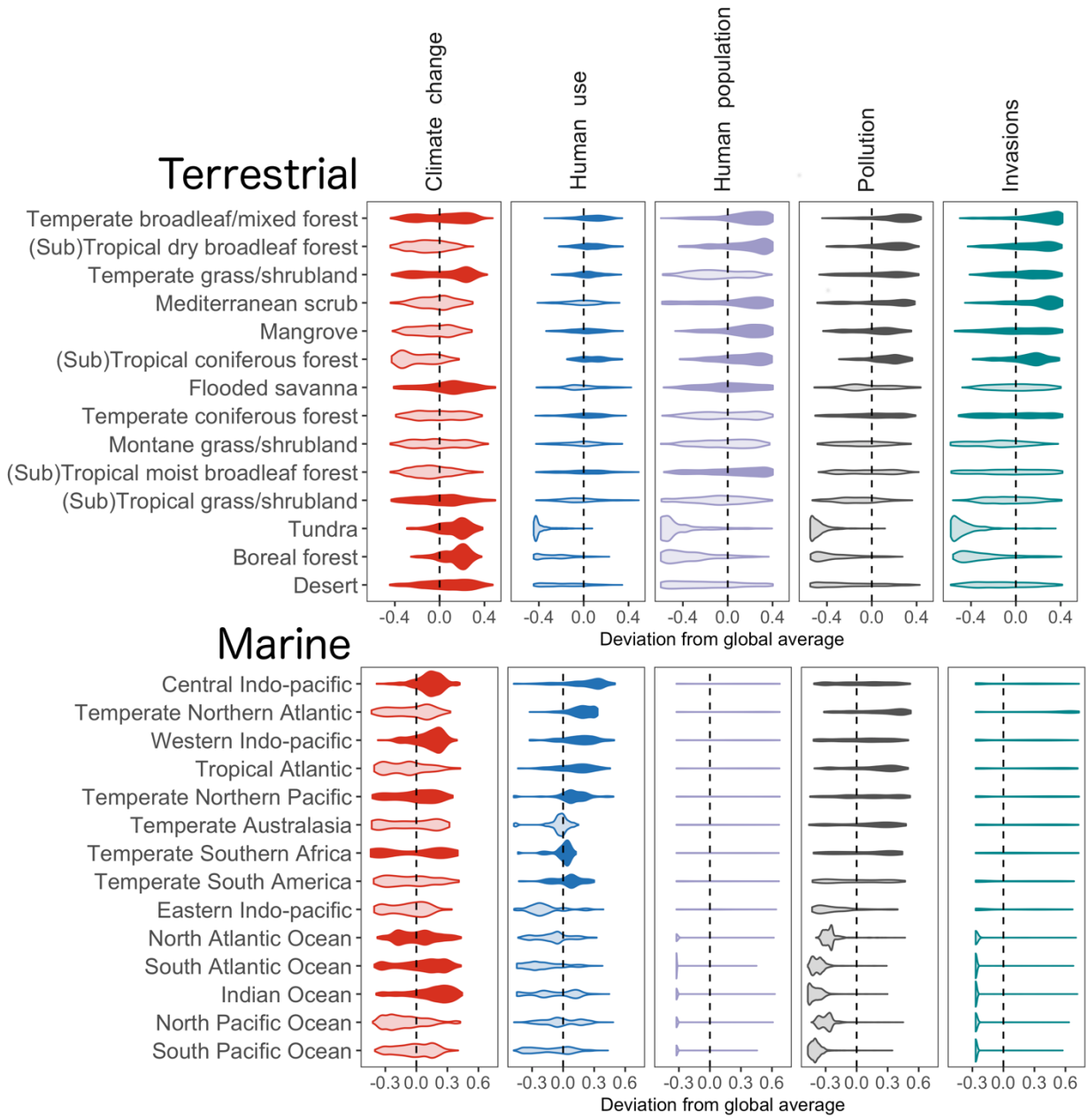

Fig. 3 Regions of the terrestrial and marine realms are exposed to distinct combinations of drivers. The violin plots show the distribution of values for each driver in each terrestrial and marine region. Violins with a median greater than the global median of each driver (centered on the dashed zero line) are colored in a darker color shade. Regions are presented in declining order of the sum of the driver means. Names of the terrestrial regions were shortened for

presentation purposes. Figure S12 shows the full distributions for each individual driver variable in each region as well as gives the full names of the terrestrial regions.

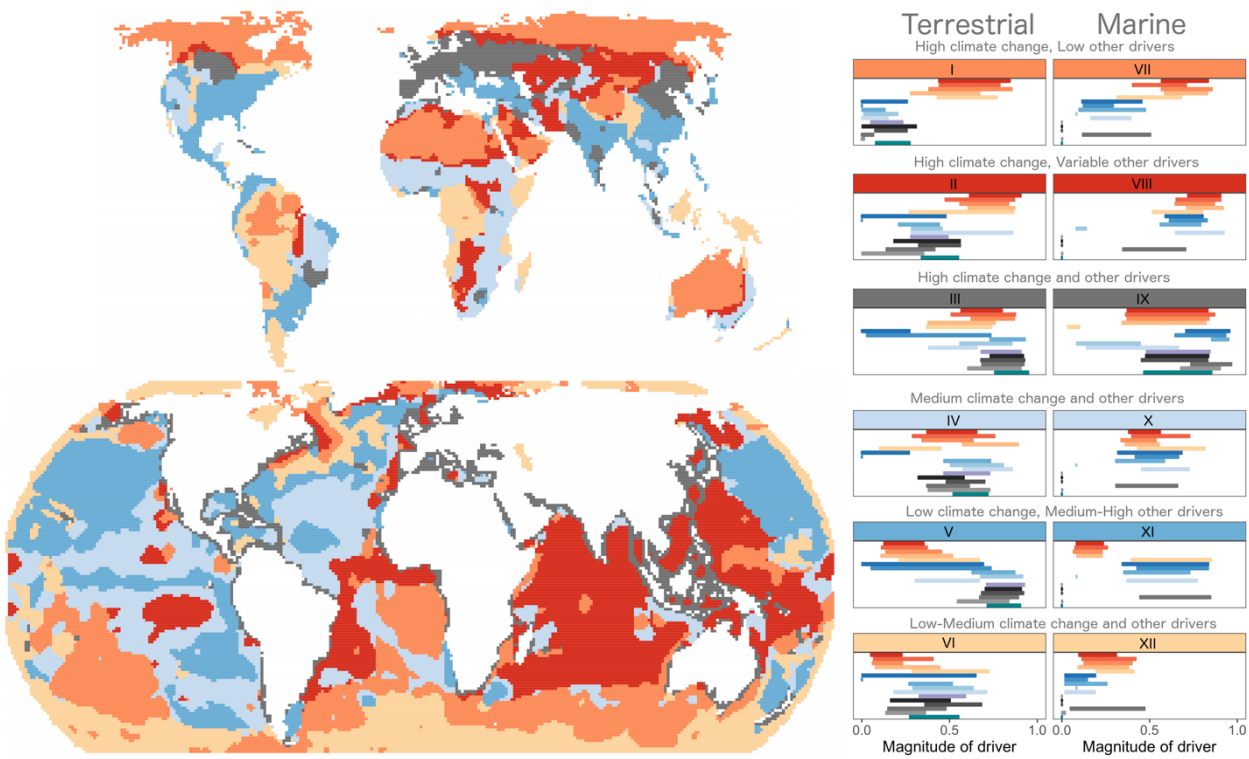

Fig. 4 Geography of the Anthropocene. Different geographic regions of the world are exposed to different Anthropogenic Threat Complexes (numbered I to XII). These regions were obtained by k-medoid clustering of their similarity of exposure to different drivers of biodiversity change. ATCs are colored to reflect a dominant variable and are harmonized across realms to facilitate comparison. The bars in the legend show the intensities (between the lower and upper quartiles) of each variable in each complex from 0 (no impact) to 1 (highest impact). White regions were not included in the analysis of each realm. Fig. S13 provides a larger plot of the legend.

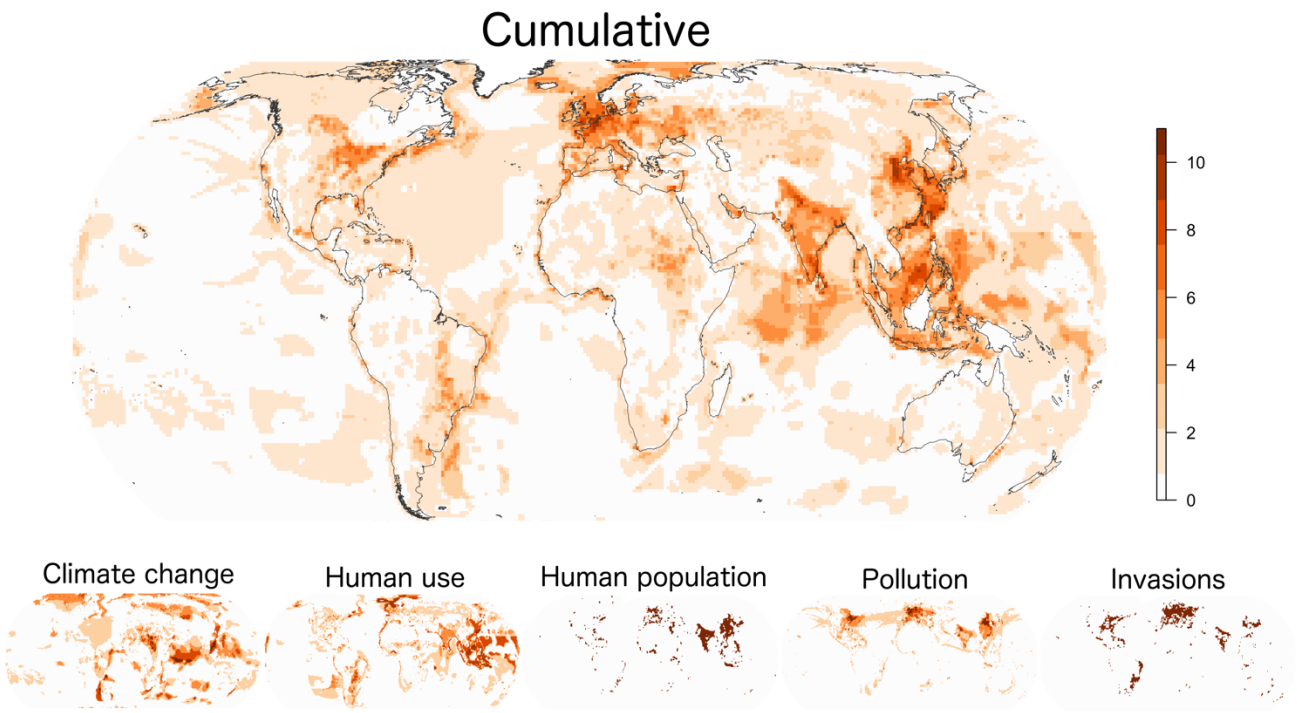

Fig. 5 Regions of the world exposed to high intensities of multiple drivers. The number of the 16 driver variables that each grid cell was in the highest 10% of values within each realm. Regions in the darkest orange are exposed to high intensities of multiple variables, while those in off-white are exposed to lower intensities (i.e., within the 90% quantile) of all. The same is shown for each of the separate drivers, i.e., the intensity of the color is scaled by the number of variables within each driver (Table 1) with a value in the highest 10%. Note: Greenland was not included in the analysis due to missing data in several of the datasets. Larger versions of the driver plots are presented in Fig. S14.

Table 1 Anthropogenic drivers of biodiversity change and their respective variables based on available global spatial datasets (Tables S1 and S2). Variables in the same line do not necessarily represent the equivalent variable in each realm.

Anthropogenic driver of biodiversity change	Associated variables	
	Terrestrial	**Marine**
Climate Change	Temperature trend Temperature divergence Change in climate extremes Velocity of climate change Aridity trend	Temperature trend Temperature divergence Change in climate extremes Velocity of climate change Ocean acidification
Human use (land/sea use or change, resource extraction, exploitation)	Crop cover Pasture cover Urban cover Forest loss Livestock density	Destructive demersal fishing Low by-catch demersal fishing High by-catch demersal fishing Low by-catch pelagic fishing High by-catch pelagic fishing
Human population density	Population density	Coastal population density
Pollution	Atmospheric nitrogen deposition Nitrogen fertilizer application Pesticide application Light pollution	Ocean pollution Fertilizer coastal pollution Pesticide coastal pollution Light pollution
Invasions	Connectivity (transport infrastructure)	Port cargo volume

References

Barlow, J., Lennox, G.D., Ferreira, J., Berenguer, E., Lees, A.C., Mac Nally, R., Thomson, J.R., Ferraz, S.F.D., Louzada, J., Oliveira, V.H.F., Parry, L., Solar, R.R.D., Vieira, I.C.G., Aragao, L., Begotti, R.A., Braga, R.F., Cardoso, T.M., de Oliveira, R.C., Souza, C.M., Moura, N.G., Nunes, S.S., Siqueira, J.V., Pardini, R., Silveira, J.M., Vaz-de-Mello, F.Z., Veiga, R.C.S., Venturieri, A. & Gardner, T.A. (2016) Anthropogenic disturbance in tropical forests can double biodiversity loss from deforestation. *Nature,* **535,** 144-+.

Barnosky, A.D., Matzke, N., Tomiya, S., Wogan, G.O.U., Swartz, B., Quental, T.B., Marshall, C., McGuire, J.L., Lindsey, E.L., Maguire, K.C., Mersey, B. & Ferrer, E.A. (2011) Has the Earth's sixth mass extinction already arrived? *Nature,* **471,** 51-57.

Bjornstad, O.N., Ims, R.A. & Lambin, X. (1999) Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution,* **14,** 427-432.

Butchart, S.H.M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J.P.W., Almond, R.E.A., Baillie, J.E.M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K.E., Carr, G.M., Chanson, J., Chenery, A.M., Csirke, J., Davidson, N.C., Dentener, F., Foster, M., Galli, A., Galloway, J.N., Genovesi, P., Gregory, R.D., Hockings, M., Kapos, V., Lamarque, J.F., Leverington, F., Loh, J., McGeoch, M.A., McRae, L., Minasyan, A., Morcillo, M.H., Oldfield, T.E.E., Pauly, D., Quader, S., Revenga, C., Sauer, J.R., Skolnik, B., Spear, D., Stanwell-Smith, D., Stuart, S.N., Symes, A., Tierney, M., Tyrrell, T.D., Vie, J.C. & Watson, R. (2010) Global Biodiversity: Indicators of Recent Declines. *Science,* **328,** 1164-1168.

CIESIN (2017) Gridded Population of the World, Version 4 (GPWv4): Population Density, Revision 10. Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). (ed. C.f.I.E.S.I.N.-C.-C. University).

Davidson, I.C., Scianni, C., Minton, M.S. & Ruiz, G.M. (2018) A history of ship specialization and consequences for marine invasions, management and policy. *Journal of Applied Ecology,* **55,** 1799-1811.

De Schrijver, A., De Frenne, P., Ampoorter, E., Van Nevel, L., Demey, A., Wuyts, K. & Verheyen, K. (2011) Cumulative nitrogen input drives species loss in terrestrial ecosystems. *Global Ecology and Biogeography,* **20,** 803-816.

Dentener, F.J. (2006) Global Maps of Atmospheric Nitrogen Deposition, 1860, 1993, and 2050. ORNL DAAC. Oak Ridge, Tennessee, USA.

Diaz, S., Demissew, S., Carabias, J., Joly, C., Lonsdale, M., Ash, N., Larigauderie, A., Adhikari, J.R., Arico, S., Baldi, A., Bartuska, A., Baste, I.A., Bilgin, A., Brondizio, E., Chan, K.M.A., Figueroa, V.E., Duraiappah, A., Fischer, M., Hill, R., Koetz, T., Leadley, P., Lyver, P., Mace, G.M., Martin-Lopez, B., Okumura, M., Pacheco, D., Pascual, U., Perez, E.S., Reyers, B., Roth, E., Saito, O., Scholes, R.J., Sharma, N., Tallis, H., Thaman, R., Watson, R., Yahara, T., Hamid, Z.A., Akosim, C., Al-Hafedh, Y., Allahverdiyev, R., Amankwah, E., Asah, S.T., Asfaw, Z., Bartus, G., Brooks, L.A., Caillaux, J., Dalle, G., Darnaedi, D., Driver, A., Erpul, G., Escobar-Eyzaguirre, P., Failler, P., Fouda, A.M.M., Fu, B., Gundimeda, H., Hashimoto, S., Homer, F., Lavorel, S., Lichtenstein, G., Mala, W.A., Mandivenyi, W., Matczak, P., Mbizvo, C., Mehrdadi, M., Metzger, J.P., Mikissa, J.B., Moller, H., Mooney, H.A., Mumby, P., Nagendra, H., Nesshover, C., Oteng-Yeboah, A.A., Pataki, G., Roue, M., Rubis, J., Schultz, M., Smith, P., Sumaila, R., Takeuchi, K., Thomas, S., Verma, M., Yeo-Chang, Y. & Zlatanova, D. (2015) The IPBES Conceptual Framework - connecting nature and people. *Current Opinion in Environmental Sustainability,* **14,** 1-16.

Dornelas, M., Gotelli, N.J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C. & Magurran, A.E. (2014) Assemblage Time Series Reveal Biodiversity Change but Not Systematic Loss. *Science,* **344,** 296-299.

Dutilleul, P., Pelletier, B. & Alpargu, G. (2008) Modified F tests for assessing the multiple correlation between one spatial process and several others. *Journal of Statistical Planning and Inference,* **138,** 1402-1415.

Dyer, E.E., Cassey, P., Redding, D.W., Collen, B., Franks, V., Gaston, K.J., Jones, K.E., Kark, S., Orme, C.D.L. & Blackburn, T.M. (2017) The Global Distribution and Drivers of Alien Bird Species Richness. *Plos Biology,* **15**.

Ellis, E.C., Goldewijk, K.K., Siebert, S., Lightman, D. & Ramankutty, N. (2010) Anthropogenic transformation of the biomes, 1700 to 2000. *Global Ecology and Biogeography,* **19,** 589-606.

Erisman, J.W., Galloway, J.N., Seitzinger, S., Bleeker, A., Dise, N.B., Petrescu, A.M.R., Leach, A.M. & de Vries, W. (2013) Consequences of human modification of the global nitrogen cycle. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **368**.

Foden, W.B., Butchart, S.H.M., Stuart, S.N., Vie, J.C., Akcakaya, H.R., Angulo, A., DeVantier, L.M., Gutsche, A., Turak, E., Cao, L., Donner, S.D., Katariya, V., Bernard, R., Holland, R.A., Hughes, A.F., O'Hanlon, S.E., Garnett, S.T., Sekercioglu, C.H. & Mace, G.M. (2013) Identifying the World's Most Climate Change

Vulnerable Species: A Systematic Trait-Based Assessment of all Birds, Amphibians and Corals. *Plos One,* **8**.

Friedl, M.A., Sulla-Menashe, D., Tan, B., Schneider, A., Ramankutty, N., Sibley, A. & Huang, X. (2010) MODIS Collection 5 global land cover: Algorithm refinements and characterization of new datasets, 2001-2012, Collection 5.1 IGBP Land Cover. Boston University, Boston, MA, USA.

Fritz, S., See, L., McCallum, I., You, L.Z., Bun, A., Moltchanova, E., Duerauer, M., Albrecht, F., Schill, C., Perger, C., Havlik, P., Mosnier, A., Thornton, P., Wood-Sichra, U., Herrero, M., Becker-Reshef, I., Justice, C., Hansen, M., Gong, P., Aziz, S.A., Cipriani, A., Cumani, R., Cecchi, G., Conchedda, G., Ferreira, S., Gomez, A., Haffani, M., Kayitakire, F., Malanding, J., Mueller, R., Newby, T., Nonguierma, A., Olusegun, A., Ortner, S., Rajak, D.R., Rocha, J., Schepaschenko, D., Schepaschenko, M., Terekhov, A., Tiangwa, A., Vancutsem, C., Vintrou, E., Wu, W.B., van der Velde, M., Dunwoody, A., Kraxner, F. & Obersteiner, M. (2015) Mapping global cropland and field size. *Global Change Biology,* **21,** 1980-1992.

Garcia-Valdes, R., Svenning, J.C., Zavala, M.A., Purves, D.W. & Araujo, M.B. (2015) Evaluating the combined effects of climate and land-use change on tree species distributions. *Journal of Applied Ecology,* **52,** 902-912.

Geiger, F., Bengtsson, J., Berendse, F., Weisser, W.W., Emmerson, M., Morales, M.B., Ceryngier, P., Liira, J., Tscharntke, T., Winqvist, C., Eggers, S., Bommarco, R., Part, T., Bretagnolle, V., Plantegenest, M., Clement, L.W., Dennis, C., Palmer, C., Onate, J.J., Guerrero, I., Hawro, V., Aavik, T., Thies, C., Flohre, A., Hanke, S., Fischer, C., Goedhart, P.W. & Inchausti, P. (2010) Persistent negative effects of pesticides on biodiversity and biological control potential on European farmland. *Basic and Applied Ecology,* **11,** 97-105.

Halpern, B.S., Frazier, M., Potapenko, J., Casey, K.S., Koenig, K., Longo, C., Lowndes, J.S., Rockwood, R.C., Selig, E.R., Selkoe, K.A. & Walbridge, S. (2015a) Spatial and temporal changes in cumulative human impacts on the world's ocean. *Nature Communications,* **6**.

Halpern, B.S., Longo, C., Lowndes, J.S.S., Best, B.D., Frazier, M., Katona, S.K., Kleisner, K.M., Rosenberg, A.A., Scarborough, C. & Selig, E.R. (2015b) Patterns and Emerging Trends in Global Ocean Health. *Plos One,* **10**.

Halpern, B.S., Walbridge, S., Selkoe, K.A., Kappel, C.V., Micheli, F., D'Agrosa, C., Bruno, J.F., Casey, K.S., Ebert, C., Fox, H.E., Fujita, R., Heinemann, D., Lenihan, H.S., Madin, E.M.P., Perry, M.T., Selig, E.R., Spalding, M., Steneck, R. & Watson, R. (2008) A global map of human impact on marine ecosystems. *Science,* **319,** 948-952.

Harris, I., Jones, P.D., Osborn, T.J. & Lister, D.H. (2014) Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *International Journal of Climatology,* **34,** 623-642.

Harrison, S. & Cornell, H. (2008) Toward a better understanding of the regional causes of local community richness. *Ecology Letters,* **11,** 969-979.

Hijmans, R.J. (2017) raster: Geographic Data Analysis and Modeling. R package version 2.6-7. https://CRAN.R-project.org/package=raster.

Hof, C., Araujo, M.B., Jetz, W. & Rahbek, C. (2011) Additive threats from pathogens, climate and land-use change for global amphibian diversity. *Nature,* **480,** 516-U137.

Hulme, P.E. (2009) Trade, transport and trouble: managing invasive species pathways in an era of globalization. *Journal of Applied Ecology,* **46,** 10-18.

Hurtt, G.C., Chini, L.P., Frolking, S., Betts, R.A., Feddema, J., Fischer, G., Fisk, J.P., Hibbard, K., Houghton, R.A., Janetos, A., Jones, C.D., Kindermann, G., Kinoshita, T., Goldewijk, K.K., Riahi, K., Shevliakova, E., Smith, S., Stehfest, E., Thomson, A., Thornton, P., van Vuuren, D.P. & Wang, Y.P. (2011) Harmonization of land-use scenarios for the period 1500-2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Climatic Change,* **109,** 117-161.

IPCC (2013) *Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change* Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA.

Isbell, F., Gonzalez, A., Loreau, M., Cowles, J., Diaz, S., Hector, A., Mace, G.M., Wardle, D.A., O'Connor, M.I., Duffy, J.E., Turnbull, L.A., Thompson, P.L. & Larigauderie, A. (2017) Linking the influence and dependence of people on biodiversity across scales. *Nature,* **546,** 65-72.

Joppa, L.N., O'Connor, B., Visconti, P., Smith, C., Geldmann, J., Mann, M.H., Watson, J.E.M., Butchart, S.H.M., Virah-Sawmy, M., Halpern, B.S., Ahmed, S.E., Balmford, A., Sutherland, W.J., Harfoot, M., Hilton-Taylor, C., Foden, W., Di Minin, E., Pagad, S., Genovesi, P., Hutton, J. & Burgess, N.D. (2016) Filling in biodiversity threat gaps. *Science,* **352,** 416-418.

Loarie, S.R., Duffy, P.B., Hamilton, H., Asner, G.P., Field, C.B. & Ackerly, D.D. (2009) The velocity of climate change. *Nature,* **462,** 1052-U1111.

Maechler, M., Rousseeuw, P., Struyf, A., Hubert, M. & Hornik, K. (2018) cluster: Cluster Analysis Basics and Extensions. R package version 2.0.7-1.

Nadeau, C.P. & Fuller, A.K. (2015) Accounting for multiple climate components when estimating climate change exposure and velocity. *Methods in Ecology and Evolution,* **6,** 697-705.

Newbold, T., Hudson, L.N., Hill, S.L.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L.K., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D.L.P., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R.P., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G.M., Scharlemann, J.P.W. & Purvis, A. (2015) Global effects of land use on local terrestrial biodiversity. *Nature,* **520,** 45-+.

Olson, D.M., Dinerstein, E., Wikramanayake, E.D., Burgess, N.D., Powell, G.V.N., Underwood, E.C., D'Amico, J.A., Itoua, I., Strand, H.E., Morrison, J.C., Loucks, C.J., Allnutt, T.F., Ricketts, T.H., Kura, Y., Lamoreux, J.F., Wettengel, W.W., Hedao, P. & Kassem, K.R. (2001) Terrestrial ecoregions of the worlds: A new map of life on Earth. *Bioscience,* **51,** 933-938.

Parmesan, C. & Yohe, G. (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature,* **421,** 37-42.

Pereira, H.M., Leadley, P.W., Proenca, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarres, J.F., Araujo, M.B., Balvanera, P., Biggs, R., Cheung, W.W.L., Chini, L., Cooper, H.D., Gilman, E.L., Guenette, S., Hurtt, G.C., Huntington, H.P., Mace, G.M., Oberdorff, T., Revenga, C., Rodrigues, P., Scholes, R.J., Sumaila, U.R. & Walpole, M. (2010) Scenarios for Global Biodiversity in the 21st Century. *Science,* **330,** 1496-1501.

Pereira, H.M., Navarro, L.M. & Martins, I.S. (2012) Global Biodiversity Change: The Bad, the Good, and the Unknown. *Annual Review of Environment and Resources, Vol 37* (eds A. Gadgil & D.M. Liverman), pp. 25-+.

Pithan, F. & Mauritsen, T. (2014) Arctic amplification dominated by temperature feedbacks in contemporary climate models. *Nature Geoscience,* **7,** 181-184.

Poloczanska, E.S., Brown, C.J., Sydeman, W.J., Kiessling, W., Schoeman, D.S., Moore, P.J., Brander, K., Bruno, J.F., Buckley, L.B., Burrows, M.T., Duarte, C.M., Halpern, B.S., Holding, J., Kappel, C.V., O'Connor, M.I., Pandolfi, J.M., Parmesan, C., Schwing, F., Thompson, S.A. & Richardson, A.J. (2013) Global imprint of climate change on marine life. *Nature Climate Change,* **3,** 919-925.

Potter, P., Ramankutty, N., Bennett, E.M. & Donner, S.D. (2010) Characterizing the Spatial Patterns of Global Fertilizer Application and Manure Production. *Earth Interactions,* **14,** 1-22.

R Core Team (2018) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Ramankutty, N., Evan, A.T., Monfreda, C. & Foley, J.A. (2008) Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles,* **22**.

Ramirez, F., Afan, I., Davis, L.S. & Chiaradia, A. (2017) Climate impacts on global hot spots of marine biodiversity. *Science Advances,* **3**.

Rayner, N.A., Parker, D.E., Horton, E.B., Folland, C.K., Alexander, L.V., Rowell, D.P., Kent, E.C. & Kaplan, A. (2003) Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *Journal of Geophysical Research-Atmospheres,* **108**.

Robinson, T.P., Wint, G.R.W., Conchedda, G., Van Boeckel, T.P., Ercoli, V., Palamara, E., Cinardi, G., D'Aietti, L., Hay, S.I. & Gilbert, M. (2014) Mapping the Global Distribution of Livestock. *Plos One,* **9**.

Salafsky, N., Salzer, D., Stattersfield, A.J., Hilton-Taylor, C., Neugarten, R., Butchart, S.H.M., Collen, B., Cox, N., Master, L.L., O'Connor, S. & Wilkie, D. (2008) A standard lexicon for biodiversity conservation: Unified classifications of threats and actions. *Conservation Biology,* **22,** 897-911.

Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V. & Woolmer, G. (2002) The human footprint and the last of the wild. *Bioscience,* **52,** 891-904.

Seebens, H., Essl, F., Dawson, W., Fuentes, N., Moser, D., Pergl, J., Pysek, P., van Kleunen, M., Weber, E., Winter, M. & Blasius, B. (2015) Global trade will accelerate plant invasions in emerging economies under climate change. *Global Change Biology,* **21,** 4128-4140.

Skidmore, A.K., Pettorelli, N., Coops, N.C., Geller, G.N., Hansen, M., Lucas, R., Mucher, C.A., O'Connor, B., Paganini, M., Pereira, H.M., Schaepman, M.E., Turner, W., Wang, T.J. & Wegmann, M. (2015) Agree on biodiversity metrics to track from space. *Nature,* **523,** 403-405.

Spalding, M.D., Fox, H.E., Halpern, B.S., McManus, M.A., Molnar, J., Allen, G.R., Davidson, N., Jorge, Z.A., Lombana, A.L., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. & Robertson, J. (2007) Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *Bioscience,* **57,** 573-583.

Sunday, J.M., Pecl, G.T., Frusher, S., Hobday, A.J., Hill, N., Holbrook, N.J., Edgar, G.J., Stuart-Smith, R., Barrett, N., Wernberg, T., Watson, R.A., Smale, D.A., Fulton, E.A., Slawinski, D., Feng, M., Radford, B.T., Thompson, P.A. & Bates, A.E. (2015) Species traits and climate velocity explain geographic range shifts in an ocean-warming hotspot. *Ecology Letters,* **18,** 944-953.

Tittensor, D.P., Walpole, M., Hill, S.L.L., Boyce, D.G., Britten, G.L., Burgess, N.D., Butchart, S.H.M., Leadley, P.W., Regan, E.C., Alkemade, R., Baumung, R., Bellard, C., Bouwman, L., Bowles-Newark, N.J., Chenery, A.M., Cheung, W.W.L., Christensen, V., Cooper, H.D., Crowther, A.R., Dixon, M.J.R., Galli, A., Gaveau, V., Gregory, R.D., Gutierrez, N.L., Hirsch, T.L., Hoft, R., Januchowski-Hartley, S.R., Karmann, M., Krug, C.B., Leverington, F.J., Loh, J., Lojenga, R.K., Malsch, K., Marques, A., Morgan, D.H.W., Mumby, P.J., Newbold, T., Noonan-Mooney, K., Pagad, S.N., Parks, B.C., Pereira, H.M., Robertson, T., Rondinini, C., Santini, L., Scharlemann, J.P.W., Schindler, S., Sumaila, U.R., Teh, L.S.L., van Kolck, J., Visconti, P. & Ye, Y.M. (2014) A mid-term analysis of progress toward international biodiversity targets. *Science,* **346,** 241-244.

Travis, J.M.J. (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proceedings of the Royal Society B-Biological Sciences,* **270,** 467-473.

Tucker, M.A., Bohning-Gaese, K., Fagan, W.F., Fryxell, J.M., Van Moorter, B., Alberts, S.C., Ali, A.H., Allen, A.M., Attias, N., Avgar, T., Bartlam-Brooks, H., Bayarbaatar, B., Belant, J.L., Bertassoni, A., Beyer, D., Bidner, L., van Beest, F.M., Blake, S., Blaum, N., Bracis, C., Brown, D., de Bruyn, P.J.N., Cagnacci, F., Calabrese, J.M., Camilo-Alves, C., Chamaille-Jammes, S., Chiaradia, A., Davidson, S.C., Dennis, T., DeStefano, S., Diefenbach, D., Douglas-Hamilton, I., Fennessy, J., Fichtel, C., Fiedler, W., Fischer, C., Fischhoff, I., Fleming, C.H., Ford, A.T., Fritz, S.A., Gehr, B., Goheen, J.R., Gurarie, E., Hebblewhite, M., Heurich, M., Hewison, A.J.M., Hof, C., Hurme, E., Isbell, L.A., Janssen, R., Jeltsch, F., Kaczensky, P., Kane, A., Kappeler, P.M., Kauffman, M., Kays, R., Kimuyu, D., Koch, F., Kranstauber, B., LaPoint, S., Leimgruber, P., Linnell, J.D.C., Lopez-Lopez, P., Markham, A.C., Mattisson, J., Medici, E.P., Mellone, U., Merrill, E., Mourao, G.D., Morato, R.G., Morellet, N., Morrison, T.A., Diaz-Munoz, S.L., Mysterud, A., Nandintsetseg, D., Nathan, R., Niamir, A., Odden, J., O'Hara, R.B., Oliveira-Santos, L.G.R., Olson, K.A., Patterson, B.D., de Paula, R.C., Pedrotti, L., Reineking, B., Rimmler, M., Rogers, T.L., Rolandsen, C.M., Rosenberry, C.S., Rubenstein, D.I., Safi, K., Said, S., Sapir, N., Sawyer, H., Schmidt, N.M., Selva, N., Sergiel, A., Shiilegdamba, E., Silva, J.P., Singh, N., Solberg, E.J., Spiegel, O., Strand, O., Sundaresan, S., Ullmann, W., Voigt, U., Wall, J., Wattles, D., Wikelski, M., Wilmers, C.C., Wilson, J.W., Wittemyer, G., Zieba, F., Zwijacz-Kozica, T. & Mueller, T. (2018) Moving in the Anthropocene: Global reductions in terrestrial mammalian movements. *Science,* **359,** 466-469.

Vallejos, R., Osorio, F. & Bevilacqua, M. (2018) *Spatial Relationships Between Two Georeferenced Variables: with Applications in R*. Springer, New York.

van Kleunen, M., Pysek, P., Dawson, W., Essl, F., Kreft, H., Pergl, J., Weigelt, P., Stein, A., Dullinger, S., Konig, C., Lenzner, B., Maurel, N., Moser, D., Seebens, H., Kartesz, J., Nishino, M., Aleksanyan, A., Ansong, M., Antonova, L.A., Barcelona, J.F., Breckle, S.W., Brundu, G., Cabezas, F.J., Cardenas, D., Cardenas-Toro, J., Castano, N., Chacon, E., Chatelain, C., Conn, B., de Sa Dechoum, M., Dufour-Dror, J.M., Ebel, A.L., Figueiredo, E., Fragman-Sapir, O., Fuentes, N., Groom, Q.J., Henderson, L., Inderjit, Jogan, N., Krestov, P., Kupriyanov, A., Masciadri, S., Meerman, J., Morozova, O., Nickrent, D., Nowak, A., Patzelt, A., Pelser, P.B., Shu, W.S., Thomas, J., Uludag, A., Velayos, M., Verkhosina, A., Villasenor, J.L., Weber, E., Wieringa, J.J., Yazlik, A., Zeddam, A., Zykova, E. & Winter, M. (2019) The Global Naturalized Alien Flora (GloNAF) database. *Ecology,* **100**.

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A. & Watson, J.E.M. (2016) Sixteen years of change in the global terrestrial human footprint and implications for biodiversity conservation. *Nature Communications,* **7**.

Vijay, V., Pimm, S.L., Jenkins, C.N. & Smith, S.J. (2016) The Impacts of Oil Palm on Recent Deforestation and Biodiversity Loss. *Plos One,* **11**.

Vorosmarty, C.J., McIntyre, P.B., Gessner, M.O., Dudgeon, D., Prusevich, A., Green, P., Glidden, S., Bunn, S.E., Sullivan, C.A., Liermann, C.R. & Davies, P.M. (2010) Global threats to human water security and river biodiversity. *Nature,* **467,** 555-561.

Waters, C.N., Zalasiewicz, J., Summerhayes, C., Barnosky, A.D., Poirier, C., Galuszka, A., Cearreta, A., Edgeworth, M., Ellis, E.C., Ellis, M., Jeandel, C., Leinfelder, R., McNeill, J.R., Richter, D.D., Steffen, W., Syvitski, J., Vidas, D., Wagreich, M., Williams, M., An, Z.S., Grinevald, J., Odada, E., Oreskes, N. & Wolfe, A.P. (2016) The Anthropocene is functionally and stratigraphically distinct from the Holocene. *Science,* **351,** 137-+.

Zorner, R.J., Trabucco, A., Bossio, D.A. & Verchot, L.V. (2008) Climate change mitigation: A spatial analysis of global land suitability for clean development mechanism afforestation and reforestation. *Agriculture Ecosystems & Environment,* **126,** 67-80.