Review

Do drivers of biodiversity change differ in importance across marine and terrestrial systems — Or is it just different research communities' perspectives?

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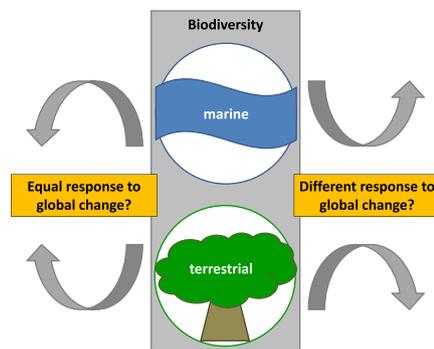[k] UFZ - Helmholtz-Centre for Environmental Research, Department Computational Landscape Ecology, Permoserstr. 15, 04318 Leipzig, Germany
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HIGHLIGHTS

- Global change affects biodiversity across the marine and terrestrial realm.
- We rate global change impacts by using expert questionnaires and literature review.
- Marine and terrestrial scientists largely differ in their judgement of impacts.
- Literature shows that terrestrial and marine ecosystems follow similar principles.
- Impacts on marine and terrestrial biodiversity will converge increasingly.

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Cross-system studies on the response of different ecosystems to global change will support our understanding of ecological changes. Synoptic views on the planet's two main realms, the marine and terrestrial, however, are rare, owing to the development of rather disparate research communities. We combined questionnaires and a literature review to investigate how the importance of anthropogenic drivers of biodiversity change differs among marine and terrestrial systems and whether differences perceived by marine vs. terrestrial researchers are reflected by the scientific literature. This included asking marine and terrestrial researchers to rate the relevance of

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different drivers of global change for either marine or terrestrial biodiversity. Land use and the associated loss of natural habitats were rated as most important in the terrestrial realm, while the exploitation of the sea by fishing was rated as most important in the marine realm. The relevance of chemicals, climate change and the increasing atmospheric concentration of CO_2 were rated differently for marine and terrestrial biodiversity respectively. Yet, our literature review provided less evidence for such differences leading to the conclusion that while the history of the use of land and sea differs, impacts of global change are likely to become increasingly similar.

Contents

1. Introduction

Global change affects ecosystems across the world from the deep seas (Hoegh-Guldberg and Bruno, 2010) to the high mountains (Pauli et al., 2012). Human existence crucially depends on the goods and services that both marine and terrestrial ecosystems provide (Millennium Ecosystem Assessment, 2005). However, for a sustainable provision of goods and services it is crucial to understand how global change affects different ecosystems, their biodiversity and associated ecosystem functions.

Webb (2012) stated that if ecosystems are defined in accordance with a specific research question, initially perceived differences between these systems can disappear. An example is the comparison of the community structure of coral reefs in the marine realm and tropical forests in the terrestrial realm. In contrast to Webb (2012), Sunday et al. (2012) suggested that even if ecological processes are similar in terrestrial and marine ecosystems, effects of global change can differ considerably between the two. Key questions are why such differences exist and how ecosystems respond to these differences.

The historic development and current state of biomass extraction – the oldest human impact on ecosystems (Table 1) – differs considerably between the terrestrial and marine realms and so might the response of biodiversity to biomass extraction. On land, a 12,000 year-old history of plant cultivation led to the dominance of artificial production systems at the level of primary producers. 34% of the earth's ice-free land surface has been converted to cropland (12%) and pastures (22%; Ramankutty et al., 2008). A considerable proportion of forests is not in a pristine state but heavily transformed by forestry (Food and Agriculture Organization of the United Nations, FAO, 2015). Fishing, collecting and cultivation of marine organisms started in an early stage of human existence as well, similar to hunting and gathering on land (Barrett et al., 2004). While the rate of increase in area used as cropland considerably decelerated within the last 50 years, the increase in the amount of marine aquaculture seems to stabilize (Fig. 1). According to FAO (2014), marine aquaculture had an average annual growth rate of 6.1% between 2002 and 2012. In contrast to terrestrial agricultural production, marine aquaculture is focussed on higher trophic levels such as finfish or crustaceans, albeit farmed marine plants account for approximately 18% of

Table 1
The history of the use of land and sea differs (numbers indicate the time period for which a certain practice has already been in use). Many kinds of use started later in the marine than in the terrestrial realm.

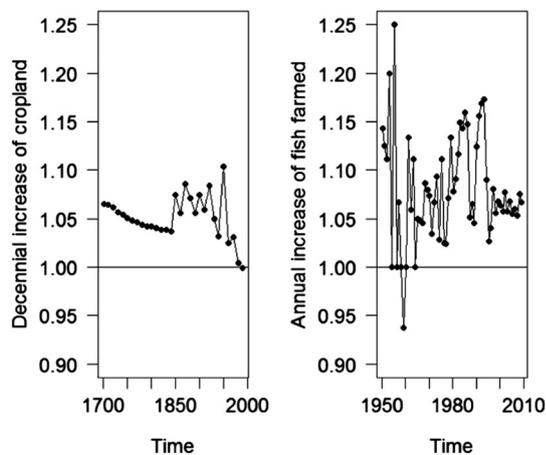| Land/sea use	Terrestrial biome	Marine biome	References
Hunting/fishing (referring to *Homo sapiens*)	200.000 years	200.000 years	Anton and Swisher (2004), Encyclopaedia Britannica (2016), Trinkaus (2005)
Food sampling (referring to *Homo sapiens*)	200.000 years	200.000 years	Anton and Swisher (2004), Encyclopaedia Britannica (2016), Trinkaus (2005)
Agriculture	11.000 to 12.000 years		Builth et al. (2008), Encyclopaedia Britannica (2016)
Aquaculture/mariculture (i.e. marine aquaculture)	Up to 10.000 years	ca. 500 years	Roberts (2007)
Share of total area agriculture/mariculture	38% of land cover	Marginal part of the marine biome	FAO; Statistics Division (2015)
Organisms used as human food resources	Primary producers (crop plants) and consumers (mainly herbivores)	Mainly consumers (fish, shellfish) and predators	FAO (2014), FAO; Statistics Division (2015)
Domestication of plants and animals	11.000 years	ca. 100 years	Duarte et al. (2007)

Fig. 1. Decennial increase of the area globally used as cropland (left panel; the y-axis shows the factor by which cropland area increased from one decade to the next based on one value per decade (black dots)) and annual increase of fish farmed, i.e. aquaculture (right panel; the y-axis shows the factor by which the production (in terms of biomass) of fish farmed increased from one year to the next based on one value per year (black dots)). The horizontal line indicates y = 1.0 (equal to no change).
Data taken from Seppelt et al. (2014) based on Costanza et al. (2007) for cropland and Brown (2012) for fish (here, data earlier than 1950 were not available).

total yield already (FAO, 2014). Despite the importance of aquaculture, humans still predominantly act as "hunters and gatherers" of marine organisms – much longer than this was the case in the terrestrial realm (in 2012, >60% of fish resource originated from caught fish; FAO, 2014). It seems likely that marine biomass extraction will shift from mainly fishing to mainly cultivation. Marine catches peaked in 1996 (at 130 Mio tonnes) and declined at a mean annual rate of −1.22 Mio tonnes ever since (Pauly and Zeller, 2016).

The extraction of other goods provided by ecosystems has reached a peak, too (such as peat or wood; Seppelt et al., 2014). Moreover, biomass extraction is by far not the only anthropogenic driver of biodiversity change. Various kinds of land use, nutrient inputs, chemical pollution, increasing mean and extreme temperatures, elevated CO_2 and biological invasions all affect biodiversity (Sala et al., 2000).

The ecology of terrestrial and marine ecosystems has been studied for over a hundred years and human utilization of both realms has been documented going back hundreds or even thousands of years. Nevertheless, mainstream ecology is dominated by terrestrial research (Raffaelli et al., 2005), joint studies are rare (Rotjan and Idjadi, 2013) and different research communities have developed (Stergiou and Browman, 2005). Marine and terrestrial ecologists even tend to ignore each other's work, with especially terrestrial ecologists hardly citing marine research (Menge et al., 2009). Marine and terrestrial ecosystems however, are not disconnected but they are linked with each other, and some functional principles may be similar. A disconnection of marine and terrestrial research can therefore hamper our understanding of the response of biodiversity to global change and consequently our efforts to protect and manage ecosystems and their biodiversity (Ruttenberg and Granek, 2011).

By combining review and expert consultation, we asked whether drivers of biodiversity change differ in importance across marine and terrestrial systems – or whether differences are just perceived as a result of the separation among the marine and terrestrial research community.

2. Material and methods

Going beyond conventional review procedures, we expanded a literature review by means of focus group discussions of both marine and terrestrial experts as well as a Delphi-assessment. The Delphi-technique (Dalkey and Helmer, 1963) is an expression of expert knowledge used

to achieve convergence of opinion among experts on a specified question. According to Hsu and Sandford (2007) it can be used to

1. explore individual assumptions or knowledge leading to different judgments;
2. seek out information that may generate a consensus within the respondent group;
3. correlate informed judgments on a topic spanning a wide range of disciplines;
4. educate the respondent group as to the diverse and interrelated aspects of a topic.

We tailored this method to our specific case, conducting two rounds of expert questioning: In the first round, we provided a questionnaire to a group of marine (N = 90) and terrestrial (N = 90) senior ecologists (hereafter called "experts"; working at our host institutions). Experts come from two different research institutes, reflecting different research communities but sharing an applied and socially relevant research focus. The two institutes are the largest of their kind in Germany; they both cover a range of ecological questions and investigate these questions internationally, with research sites across the world.

Experts were asked to rank the impact of selected anthropogenic drivers of biodiversity change for marine or terrestrial biodiversity (terrestrial experts ranked drivers of terrestrial biodiversity change; marine experts ranked drivers of marine biodiversity change). 23% of the terrestrial (N = 21) and 20% of the marine (N = 18) experts completed the Delphi-survey. Response rates thus followed the typical rates of online questionnaires, which on average range from 17.1% to 21.5% (Evans and Mathur, 2005; Sax et al., 2003).

The questionnaire contained the following definitions (Table 2):

- Definition of drivers (based on the Millennium Ecosystem Assessment, 2005):
  ○ Drivers are only anthropogenic drivers that lead to changes in biodiversity.
  ○ Effects are only direct effects of drivers (for example no indirect effect of CO_2 via temperature).

- Definition of biodiversity:
  ○ Biodiversity concerns all organisational levels from genes to species and populations, to communities (including taxonomic, functional and phylogenetic aspects), to entire ecosystems

- Definition of ecosystems:
  ○ Terrestrial: all terrestrial systems except freshwater systems and soil systems
  ○ Marine: all marine systems including coastal waters, offshore and deep sea areas

We focussed on the following main drivers (Table 2; adapted and extended from Sala et al., 2000): (i) land use/sea use, (ii) chemical inputs, (iii) climate change (with a focus on changing temperatures), (iv) increasing atmospheric concentration of CO_2, and (v) biological invasions. "Land/sea use" and "chemical inputs" were further divided into (ia) habitat loss, (ib) habitat degradation, (ic) habitat fragmentation, (id) hunting and fishing; and (iia) nutrients and (iib) pollutants. We defined habitat loss as a change in habitat conditions which leads to the replacement by another habitat (such as deforestation to create crop fields), while we define fragmentation as the breaking apart of habitat independent of habitat loss, i.e. increasing degree of isolation such as the separation of a forest into several pieces by road construction (Fahrig, 2003). Habitat degradation is defined here as a decline in habitat quality (Table 2).

We asked all experts to give a maximum score of 100 to the driver they considered most important and to rank all other drivers

Table 2

Anthropogenic drivers of biodiversity change (based on Sala et al., 2000) with their definitions and examples. For these drivers, we asked experts to score their impacts on biodiversity in a Delphi-assessment (Dalkey and Helmer, 1963).

Driver	Sub-category	Definition	Example
Biological invasions	–	Successful establishment of non-native species that spread vigorously within their non-native range and have the potential to cause ecological and/or socioeconomic impacts	Spread of the Harlequin ladybird (*Harmonia axyridis* Pallas), which is a pest in orchard crops in America, Africa and Europe and reduces the biodiversity of other aphidophages and non-pest insects (DAISIE European Invasive Alien Species Gateway, 2008)
Chemical inputs	Nutrients	Nutrients of artificial origin or natural origin but imported into the environment by human activities	Nitrogen
	Pollutants	Chemical substances that are potentially harmful to the environment/toxicants	Pesticides
Climate change	–	"A change in the state of the climate that can be identified […] by changes in the mean and/or the variability of its properties, and that persists for an extended period, typically decades or longer." – here: directly or indirectly caused by human activities (cf. United Nations Framework Convention on Climate Change)	Rise in global temperature due to anthropogenic CO_2-emissions
CO_2	–	Carbon dioxide and the increase of its concentration in the atmosphere	–
Land use/sea use	Habitat loss	A change in habitat conditions that is so strong that it results in the original habitat being replaced by another habitat	Deforestation to create agricultural production sites
	Habitat degradation	Decline in habitat quality	Changes of light availability or O_2-concentrations
	Habitat fragmentation	Breaking apart of habitat without decreasing the total size of available habitat (which would be habitat loss), i.e. increasing degree of isolation	Separation of a forest into several pieces by road construction
	Hunting, fishing	Killing animal species as food resource, thereby withdrawing individuals from the environment	–

accordingly between 0 (no impact) and 100. This was done for drivers i–v, ia–id and iia–iib separately. Different drivers were allowed to have the same score. The assessment was carried out for biodiversity changes up to the present day and the reference period of the questionnaire was restricted to the last 100 years. Experts were asked to only consider the effect size on biodiversity (i.e. large or small), not the direction of change (positive or negative). Moreover, we asked experts to score long-term and large-scale effects higher than short-term and small-scale effects. Importantly, for each driver, experts were asked to shortly explain their judgement and to provide key references.

In the second round (a crucial part in the Delphi process), experts who had taken part in the first round were provided with the median and range of scores from the first round and an aggregated version of the arguments for high or low scoring. Based on the anonymised arguments, the experts then had the possibility to adjust every single score. This aimed at a streamlined expert opinion. The final judgements together with explanations and key references were compared to a literature review on the effects of global change on terrestrial and marine biodiversity. In summary, our approach combines three key steps:

1) the Delphi assessment;
2) asking experts to name key publications for each type of global change (as part of Delphi);
3) a literature review focusing on key drivers and references (identified by (2) and by ourselves).

Only by combining these three steps were we able to efficiently identify the most important effects of global change on biodiversity in both realms. This extends the classical review approaches that could not have identified the current research gaps.

3. Results: the Delphi-assessment

In both rounds of our Delphi-assessment, 21 terrestrial and 18 marine expert judgements were obtained. While the second Delphi assessment led to a slight reduction in the variability of the range of expert opinion, no major changes in the ranking of importance occurred (Table S1 in Supplementary information).

For marine systems (Fig. 2), sea use and climate change produced the highest scores in both rounds. The scoring of the impacts of biological invasions, chemical inputs and enhanced CO_2 changed in variance but not in median or order.

For terrestrial systems (Fig. 2), land use was rated highest with no variance in either round. Chemical inputs were rated second with higher median weight than in the first round. Climate change was given the same median weight as in the first round but ranked third now. Biological invasions had a lower median weight than in the first round but stayed in fourth place. Increasing atmospheric concentrations of CO_2 were ranked least important, as in the first round.

Neither for marine nor terrestrial systems (Fig. 3) did the order or median weights of habitat loss, degradation, fragmentation and hunting/fishing change from the first to the second round (Table S1). Similarly, the importance of nutrients for changes in biodiversity was rated higher than for chemical pollutants in both rounds and for both marine and terrestrial (Fig. 4) systems.

4. Discussion: drivers of biodiversity change in terrestrial and marine ecosystems – differences and similarities

4.1. Does the importance of harvesting (hunting and fishing) differ for marine versus terrestrial biodiversity?

Keeping in mind that our Delphi-assessment focussed on the last 100 years and thus omitted earlier developments such as late Quaternary terrestrial megafauna extinctions linked to hunting (Sandom et al., 2014) experts perceived hunting as least important in terrestrial ecosystems. In contrast, fishing was ranked as the most important driver of marine biodiversity change. This might be explained by major differences in hunting and fishing.

In many terrestrial regions, hunting is strongly regulated today and restricted to certain target species, whose populations are regularly monitored and managed accordingly. An example is the European directive on the conservation of wild birds (European Commission, 2016). However, it was only adopted in 1979 at a time when hunting had already decimated species numbers, for example the number of migratory birds (Mcculloch et al., 1992). However, hunting is far more unspecific in other regions of the world and has led to serious population declines, for instance in large-sized mammals and birds in the tropics (Harrison, 2011). Growing demands for bush meat are discussed as the greatest threat to wildlife in some regions of the world, such as Africa (Cawthorn and Hoffman, 2015).

In contrast to hunting, many fishing methods (such as bottom trawling) are either unspecific with multiple target species or yield significant amounts of non-target bycatch (Davies et al., 2009). Therefore,
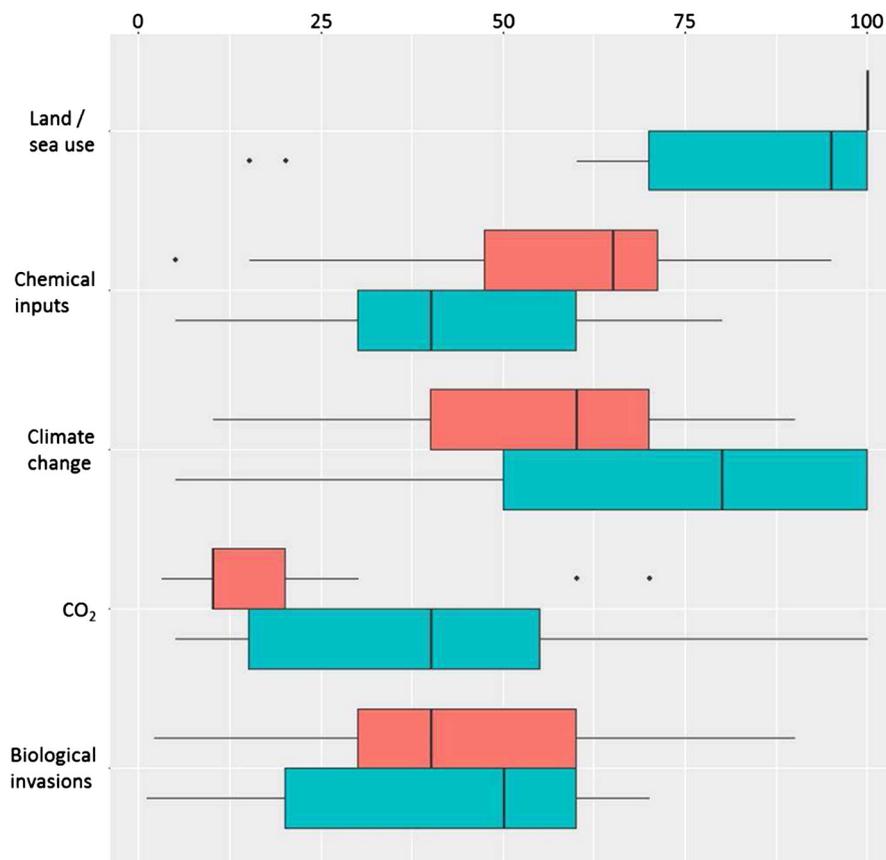
Fig. 2. Comparison of the relative impact of the main drivers of global change on biodiversity in terrestrial (red) and marine (blue) ecosystems covering the last 100 years (Delphi-assessment, 2nd round). Experts rated the most important impact = 100; all other impacts were rated relative to the most important one. Boxplots represent median (line) and 25–75% quartiles (boxes); upper/lower whiskers extend from the box to the highest/lowest value that is within 1.5 ∗ the interquartile range; outliers are represented by circles (see R-package 'ggplot2'; Wickham, 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

commercial fishing practices have detrimental effects on a range of organisms, including endangered species (Table 3). The regulation of most fisheries in the marine realm is to date, despite considerable efforts over many decades, insufficient in preventing the overexploitation of fish stocks (Boonstra and Österblom, 2014). Despite well-aligned conservation and fisheries metrics (Davies and Baum, 2012) 28.8% of assessed global fish stocks are fished at a biologically unsustainable level (FAO, 2014) with an accelerating trend (Worm et al., 2006). Cascading effects from lower to higher trophic levels are very likely since smaller fish provide food for the larger. Vice versa, the radical diminishing of higher trophic level populations can cause a consecutive shift in fishing effort to smaller species. This shift ('fishing down the food web'), although debated (Branch et al., 2010), was both experimentally proven (Pauly, 1998) and observed, for instance the shift in Antarctic fishing from marine mammals to groundfish to krill (Ainley and Pauly, 2014).

Irrespective of these differences in hunting and fishing, the fundamental consequences for marine and terrestrial biodiversity are very similar. Overexploitation diminishes the abundances of both marine and terrestrial species and can cause extinctions as well as shifts in species and functional trait composition (Table 3). However, the fact that most hunting-related species extinctions (Day, 1981; Sandom et al., 2014), took place > 100 years ago, explains why hunting was perceived as least important for today's terrestrial biodiversity.

Another similarity is that both hunting and fishing affect almost all trophic levels – but to a different extent. Today, hunting focusses on primary and secondary consumers such as deer or wild boar in Central Europe (Krostitz, 1996) or Herpestidae in Africa (Doughty et al., 2015). In terms of trophic position, this is comparable to smaller fish and crustaceans feeding on microalgae. Anchovy, horse mackerel,

sandeel and krill are caught mainly to produce fishmeal as feed for stock farming and aquaculture. Terrestrial predators are rarely hunted for human nutrition (but for other reasons such as trophy hunting; Di Minin et al., 2016). In contrast, in the oceans, the yield of edible predatory fish is approximately 75% of total catches (FAO, 2014).

In summary, while hunting drove a number of terrestrial species to extinction > 100 years ago (Day, 1981; Sandom et al., 2014), a combination of technological progress, already reduced stocks and insufficient governance (among other factors) today threatens many marine species (Boonstra and Österblom, 2014). Thus, the importance of harvesting for biodiversity change is similar in marine and terrestrial systems. Still, the lag in the historical development of fishing as compared to hunting makes the changes in marine biodiversity lag behind those in terrestrial biodiversity.

4.2. Does the importance of habitat loss, degradation and fragmentation differ for marine versus terrestrial biodiversity?

While the experts listed the use of both land and sea as most important driver of biodiversity change, habitat loss, degradation, and fragmentation were rated differently.

In the marine realm, annual loss of global habitat area has been estimated to be 1–9% for coral reefs (Bellwood et al., 2004; Gardner et al., 2003) and 1.8% for mangroves (Valiela et al., 2001). Seagrass beds in North America, Europe and Australia have disappeared at an annual net rate of 110 km^2 since 1980 and have suffered a loss of a total of 29% since their initial recording in 1879 (Waycott et al., 2009). In the terrestrial realm, loss of tropical forest has been estimated to be similar in scale to losses of coral reefs and seagrass beds (Waycott et al., 2009). The degree of habitat loss and degradation by bottom trawling in the
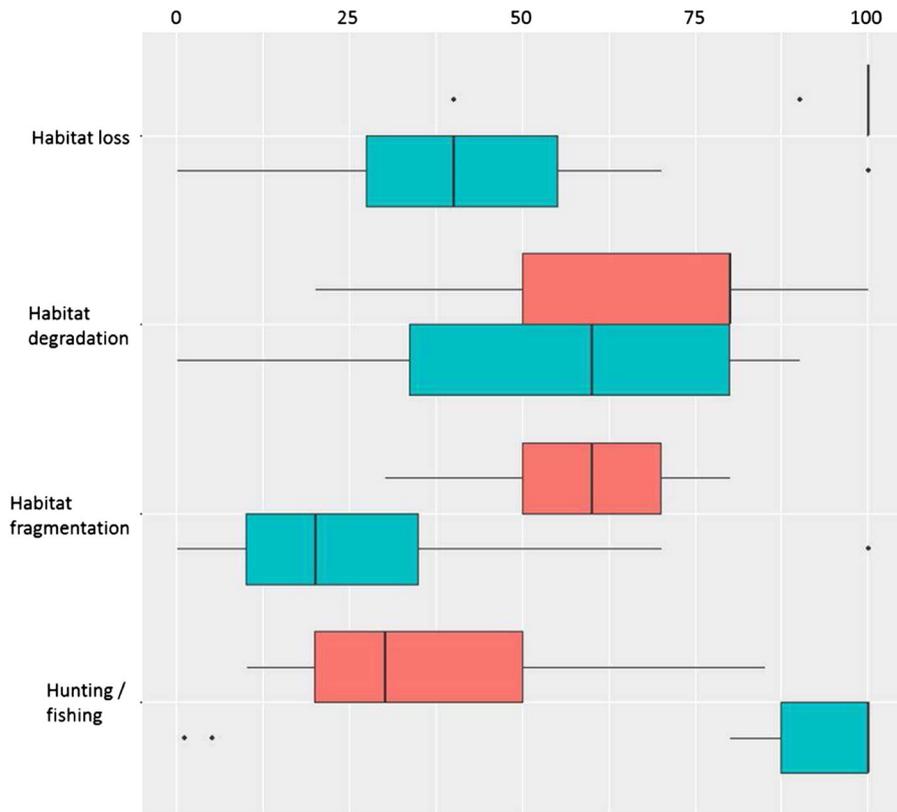
Fig. 3. Comparison of the relative impact of subcategories of anthropogenic use of land (red) and sea (blue) on biodiversity covering the last 100 years (Delphi-assessment, 2nd round). Experts rated the most important impact = 100; all other impacts were rated relative to the most important one. Boxplots represent median (line) and 25–75% quartiles (boxes); upper/lower whiskers extend from the box to the highest/lowest value that is within 1.5 ∗ the interquartile range; outliers are represented by circles (see R-package 'ggplot2'; Wickham, 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

marine realm have been estimated to be 150-times greater than the terrestrial area affected by clear-felling of forests (Dulvy et al., 2003). However, while terrestrial habitat loss occurs on large scales, in the marine realm it is mainly restricted to coastal areas, where sea use has a long tradition (Barrett and Orton, 2016). However intensive utilization even in coastal areas started centuries later than in the terrestrial realm (Duarte et al., 2007), as shown for harvesting. We suggest that the differences in scales of observation and in the time period for which a certain practice has already been in use (Table 1) add to the difference in perception of habitat loss in marine and terrestrial systems.

Generally, habitat degradation alters the quality and quantity of biodiversity and their related goods and services. In marine systems, changes in sediment structure, hydrodynamics, and river run-off result in changes in light availability and O_2-concentrations (De'ath and Fabricius, 2010; Duarte, 1991) so that species composition can change dramatically, for example from seagrass to macroalgae (McGlathery, 2001). Similarly, in terrestrial systems, changes in nutrient supply (especially nitrogen-loads) and related changes in light availability cause changes in species composition (cf. chapter 4.3 "Nutrients"). These similarities are reflected in the responses of both expert groups in the Delphi-assessment.

The impacts of habitat fragmentation on biodiversity can vary considerably among species. While fragmentation such as by roads increases isolation among habitat patches, it can also increase edge effects. In terrestrial ecosystems, edge effects foster some but disadvantage other species, even within one taxon such as different bird guilds (Batary et al., 2014). Similar to roads in the terrestrial realm, pipelines, coastal defences or pylons of wind turbines form stepping-stones or dispersal corridors for marine settling larvae. Increasing artificial coastal constructions, for example are increasingly cited as one reason for the explosive growth of jellyfish in some geographic areas, which depend on the sessile polyps living on hard substrata (Duarte et al., 2013).

Dispersal potential is basic to the ability of species to cope with isolation in both marine and terrestrial systems. While humans have created dispersal barriers across large parts of the terrestrial world, anthropogenic dispersal barriers in the oceans are mainly restricted to coasts. Moreover, dispersal potential has often been assumed to be higher in marine than terrestrial species (Kinlan and Gaines, 2003). The dispersal potential of sessile and sedentary marine species, for example was estimated to be 1.5 orders of magnitude higher than for terrestrial plants (Kinlan and Gaines, 2003). However, dispersal is often passive in marine organisms in contrast to terrestrial organisms, which are mostly adapted to active dispersal (Burgess et al., 2016). The fact that extinction rates are pretty similar for marine and non-marine taxa also suggest that marine species do not profit from higher dispersal potential (Webb and Mindel, 2015).

Overall, evidence suggests that the importance of habitat loss, degradation and fragmentation is similar in marine and terrestrial systems. The large differences in the experts' perceptions of habitat loss and fragmentation indicate knowledge gaps, especially for marine species, which are harder to detect and to monitor than terrestrial species.

4.3. Does the importance of nutrients differ for marine versus terrestrial biodiversity?

Anthropogenic nutrient inputs were regarded as highly important in both terrestrial and marine ecosystems. This might reflect the fact that they have been studied extensively in both realms for over a hundred years and that their impacts are closely linked to human well-being (Anton et al., 2011).

Nutrients, in particular nitrogen and phosphorus emerge from various anthropogenic sources. In 2010 global anthropogenic nitrogen fixation from fertilizer production, fossil fuel combustion and agricultural biogenic fixation even exceeded natural nitrogen fixation
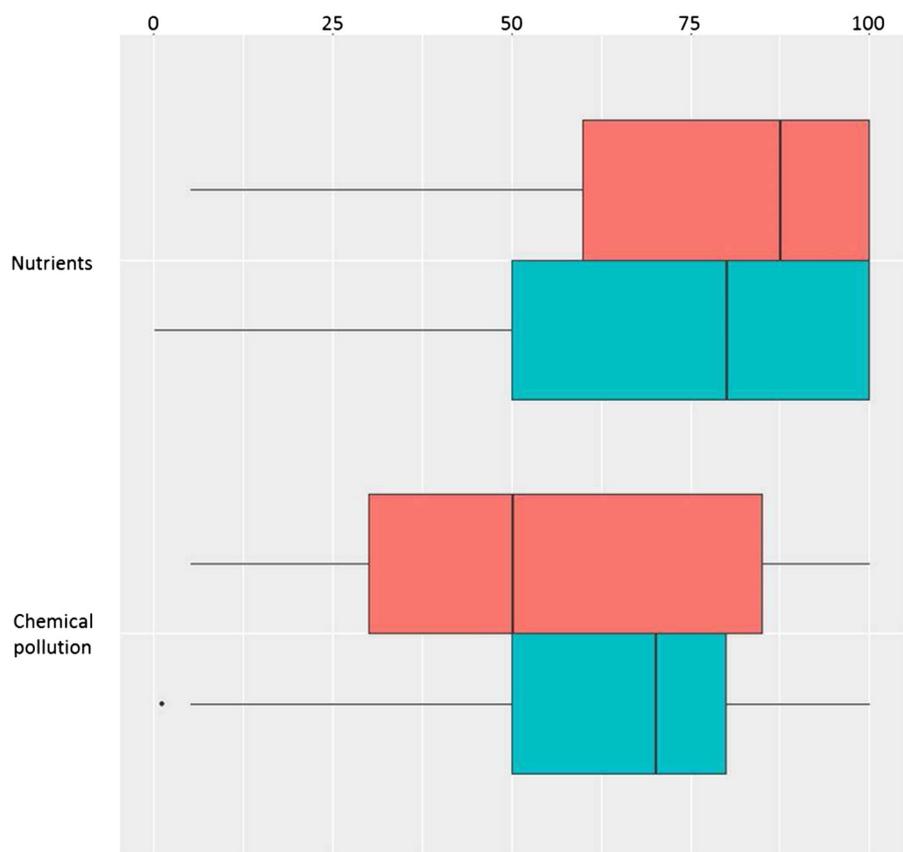
Fig. 4. Comparison of the relative impact of subcategories of chemical inputs on biodiversity in terrestrial (red) and marine (blue) ecosystems covering the last 100 years (Delphi-assessment, 2nd round). Experts rated the most important impact = 100; all other impacts were rated relative to the most important one. Boxplots represent median (line) and 25–75% quartiles (boxes); upper/lower whiskers extend from the box to the highest/lowest value that is within 1.5 * the interquartile range; outliers are represented by circles (see R-package 'ggplot2'; Wickham, 2009). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(210 Tg N yr^{-1} vs. 203 Tg N yr^{-1}; Fowler et al., 2013). Large-scale atmospheric deposition of human-induced nutrients affects both terrestrial and marine ecosystems (Meyer et al., 2013; Troost et al., 2013). Additionally, terrestrial ecosystems (especially those used agriculturally) are directly affected through fertilizer application. In the marine realm, coastal regions and estuaries are affected the most, with nutrient inputs occurring principally via rivers whose nutrient levels have increased as a result of land use change and which have been polluted at least since the mid-19th century (Meybeck and Helmer, 1989). This is of course not a universal phenomenon. Efforts to restrict nutrients in effluents reaching rivers and ultimately the sea mean that many coastal areas are not seeing eutrophication to the extent that might otherwise have occurred. However enclosed, badly mixed areas (possibly in regions with a lack of appropriate legislation) might be more adversely affected.

Although nutrients are essential for plant growth and thus for ecosystem functions and services such as human nutrition their excessive input into terrestrial and marine ecosystems has profound ecological consequences. In marine systems, excess nutrients, especially phosphorous and nitrogen boost phytoplankton production and can shift the whole system from an oligotrophic towards a eutrophic state, including changes in species composition and food web structure (Prins et al., 2012; Xie et al., 2015). Microbial decomposition of large algal blooms can cause hypoxic areas with negative consequences for all biota and ultimately for human food production. In summary, effects of eutrophication cascade through marine ecosystems from primary producers to top predators and may change species assemblages at all levels, from macrofauna (Schückel and Kröncke, 2013; Snickars et al., 2015) to fish communities (Nixon, 1982) and waterbirds (Møller et al., 2015).

In terrestrial ecosystems, enhanced nitrogen supply generally accelerates plant growth but may lead to growth reductions, foliar damage or decreased stress resistance if concentrations exceed species-specific tolerances (Krupa, 2003). Akin to marine systems, changes in species composition towards more nitrogen-tolerant communities represent the most significant impact of excess nutrients and have been reported for plants in grasslands (Dise et al., 2011), arable lands (Meyer et al., 2013), forests (Dirnböck et al., 2014) and urban ecosystems (Knapp et al., 2010). This process may go along with a reduction in species richness, particularly in species rich, nutrient-poor habitats (Gerstner et al., 2014; Stevens et al., 2010). Still, it is not necessarily the total amount of nitrogen but the exceedance of the ecosystem-specific critical load that results in changes of community composition and species richness (Dirnböck et al., 2014). Knowledge of the effects of nitrogen on higher trophic levels is limited in terrestrial systems (Dise et al., 2011). Animals might be indirectly affected by nitrogen-mediated vegetation changes, habitat structure or food quality as shown by Öckinger et al. (2006) for butterflies – similar to marine food webs.

In summary, although agriculture affects terrestrial ecosystems more directly than marine ecosystems, evidence suggests that the effects of human-induced nutrient dynamics (at least for nitrogen and phosphorus) on marine and terrestrial biodiversity are similar.

4.4. Does the importance of chemical pollutants differ for marine versus terrestrial biodiversity?

The relevance of chemical pollutants for biodiversity change was given a medium score in both realms, with a high variance of assumed impact.

Perhaps the ecologically most relevant exposure to toxicants originates from agricultural pesticides. At the global scale an estimated $4 * 10^6$ tons of pesticides are applied to agricultural land annually (Sánchez-Bayo, 2011). This amount is equivalent to an annual application of 0.27 kg of pesticide per hectare of land worldwide. The nature of application of these substances is fundamentally different from those of other chemicals, as pesticides are intentionally designed and released into the environment to have widespread ecological effects – to kill pests and weeds. This application leads to a widespread contamination with highly effective substances. Consequently, pesticides are a major threat to both marine and terrestrial biodiversity and ecosystem functioning (Mineau and Whiteside, 2013; Oehlmann et al., 2007; Rundlof et al., 2015). Generally, pesticide contamination reduces freshwater biodiversity in streams alongside agricultural fields (Beketov et al., 2013). This contamination later affects coastal ecosystems such as coral reefs as well as life across trophic levels (Kroon et al., 2015). Neonicotinoids, for example, reduce the survival of terrestrial non-target insect species (Scholer and Krischik, 2014), an effect that might propagate to higher trophic levels such as birds (Hallmann et al., 2014). In marine systems, organochlorine compounds (OC) that originate from pesticides (such as DDT) or from industrial chemicals (such as PCBs) are present in all oceans. OC tend to accumulate in marine organisms through the food web (Borgå et al., 2001; Vieweg et al., 2012) and thus can affect sensitive early development stages of invertebrates (Bellas et al., 2005) and in particular higher level predators (Jepson and Law, 2016).

In addition to pesticides, thousands of toxicants from anthropogenic sources such as oil extraction, industrial processes, traffic, waste incineration or terrestrial and deep sea mining are released to the air, water bodies and soils (e.g. Ellis et al., 2012; Manzetti and van der Spoel, 2015). Their environmental effects vary greatly, depending on their characteristics, concentration and spatial distribution. Many effects of pollutants on the genetic makeup, species, communities and ecosystems have been documented (see Table 3 for examples). This diversity of compounds and their effects might be the reason behind the high variance of assumed importance in the Delphi-assessment.

Both marine and terrestrial ecosystems are exposed to toxicants and the impacts of pesticides and their derivatives affect marine and terrestrial biodiversity across trophic levels. Due to dilution processes, which are often highly relevant in marine environments, it seems necessary to develop strategies that enable assessing ecological effects of low level but persistent contamination. Management approaches need to include cascading routes of sublethal effects, trans-generation effects and multigenerational culmination of low-dose effects (Liess et al., 2013).

4.5. Does the importance of climate change (increasing temperatures) differ for marine versus terrestrial biodiversity?

The importance of climate change, in particular increasing temperatures, for changes in biodiversity was ranked higher for marine than terrestrial ecosystems, likely due to the pervasive impacts of climate change across all oceans, from surface to deep seas. Experts stressed that climate change causes shifts in community composition, species distribution, biotic interactions or phenology and even drives evolutionary processes and species extinctions. Both marine and terrestrial experts agreed that climate change will become more relevant in the

Table 3
Examples for effects of anthropogenic drivers of biodiversity in marine versus terrestrial ecosystems.

Driver → effect	Marine biodiversity	Terrestrial biodiversity
Harvesting (hunting/fishing) → Declining species abundances	→ Population decline of dolphins as a result of yellowfin tuna purse-seine fishery (Cramer et al., 2008)	→ Data from tropical countries suggest that mammal densities decline in hunted areas (Cawthorn and Hoffman, 2015)
→ Shifts in life-history traits	→ Shifts in migration of sockeye salmon (*Oncorhynchus nerka*) to earlier dates (Quinn et al., 2007) as a result of being fished during migration and thus before being able to reproduce.	→ Average horn length of bighorn sheep (*Ovis canadensis*) decreased by 20 cm in 30 years because large-horned individuals were preferably hunted (reviewed by Allendorf et al., 2008).
Use of land/sea → Threatened species	→ Declines in corals threaten fish communities living in coral reefs (Jones et al., 2004)	→ 40% of the world's terrestrial mammal species are threatened by habitat loss and habitat degradation (Schipper et al., 2008)
Nutrient inputs → Shifts in species composition	→ Seagrass beds and coral reefs suffer from eutrophication by strong growth of epiphytes (Burkholder et al., 2007), macroalgae or turf algae (Naumann et al., 2015).	→ Increased soil phosphorous contents favoured exotic annual grasses and forbs over native perennial geophytes, ferns and shrubs in Australian livestock systems (Dorrough and Scroggie, 2008)
Chemical pollutants → Changes in fitness and reproduction	→ Organotins such as TBT, used as biocides and resulting from *anti*-fouling paint, resulted in endocrine disruption, imposex and intersex in molluscs (Oehlmann et al., 2007).	→ Neonicotinoid insecticides reduced the growth rate of bumble bee colonies of the species *Bombus terrestris* and reduced their production of queen bees by 85% (Whitehorn et al., 2012).
Climate change (increasing temperatures) → Local species extirpations	→ Mass mortality of corals (coral bleaching; Ash, 2016)	→ Projected local loss of 15–19% of the German flora until 1080, depending on the scenario applied (Pompe et al., 2008).
→ Shifts in species composition	→ Increase in oxygen minimum zones damages or displaces large, active oxygen-depending organisms at the sea-floor close to continental margins (Diaz and Rosenberg, 2008) in favor of small metazoans with low metabolic rates and high anaerobic capacity as well as anaerobic microbes.	→ Upward shift of plant species along alpine summits increased alpha-diversity but decreased beta-diversity among summits (Jurasinski and Kreyling, 2007).
Elevated CO_2 → Changes in trophic interactions	→ Reduction in the ability of sharks to locate food through olfaction, resulting from ocean acidification (Pistevos et al., 2015)	→ Increasing consumption rates and development times of herbivorous insects resulting from changes in the C/N-ratio of plant tissue are likely (Cornelissen, 2011)
Biological invasions → Changes in food webs	→ Introduction of the pacific oyster (*Crassostrea gigas*) to the European Wadden Sea significantly altered the local food web (Baird et al., 2012).	→ Exotic plant species were less visited by native pollinator insects than native plant species in Great Britain, probably as a result of lacking coevolution (Corbet et al., 2001).

future. Terrestrial experts argued that plastic or evolutionary responses of species might buffer climate change effects.

In the oceans, sea-surface temperature changes between 1901 and 2012 reached up to $+2.5$ K (IPCC, 2014a). The warming rate over land is approximately twice that of the warming rate over the oceans since 1979 (IPCC, 2013). The response of organisms to warming is simple: When ambient temperature moves towards and beyond the physiological limits of a particular organism, individual performance will suffer and the corresponding population will decline once tolerated temperature extremes or the time-limits of tolerance are surpassed (Pörtner, 2010; Pörtner and Knust, 2007). Mechanisms that enable organisms to cope with increasing temperatures are the shift of their biogeographic ranges and a shift in phenology (see Burrows et al., 2011 and references therein).

In the absence of barriers, species may follow the moving isotherms and abandon their original distribution range (Stenseth et al., 2002). The potential for range shifts in the oceans is generally high in relation to the actual climate velocity (Pinsky et al., 2013) and has been estimated between 1.4 and 28 km per decade (Burrows et al., 2011). This range of estimates illustrates that the potential for range shifts depends on the organism's mobility (Poloczanska et al., 2013) – with a range of marine organisms not being adapted to active (and thus directed) dispersal (Burgess et al., 2016). Marine dispersal can be further limited by substrate availability, light regime, oxygen saturation, pollution, ocean-use or the opportunity to escape poleward (Gutt et al., 2015) – parallel to terrestrial organisms that are restricted to high-altitude mountains or polar regions (Jurasinski and Kreyling, 2007; Table 3). Range shifts in the terrestrial realm have been estimated to be 1.5 to 5 times lower than in the oceans (Burrows et al., 2011), e.g. 16.9 km/decade poleward across birds, mammals, arthropods, reptiles and plants (Chen et al., 2011). On the one hand, temperatures are more homogeneous across ocean than land surfaces – a difference that might explain different velocities of marine versus terrestrial organisms (Burrows et al., 2011); on the other hand, anthropogenic barriers, such as agricultural and built-up areas are mainly terrestrial. However, to which extent such barriers slow down species migration remains largely open (Mendenhall et al., 2012). Generally, the capacity to move depends on the degree of warming which in turn defines the velocity of temperature change. In flat landscapes, for example, the risk is high that most trees, herbs, primates and rodents cannot keep up with the moving isotherms beyond $+2$ K warming above pre-industrial values (IPCC, 2014b).

Phenological shifts have been observed across marine and terrestrial organisms (IPCC, 2014a) and are estimated to be 30 to 40% faster in the marine than in the terrestrial realm (Burrows et al., 2011). In both marine and terrestrial systems, both phenological and range shifts may also alter species interactions (Pörtner et al., 2014). Examples are temporal mismatches (like in the hatching of larvae at a time favorable for their predators) and spatial mismatches (such as butterflies and their host plants shifting their ranges at different pace; Schweiger et al., 2008).

Moreover, in marine systems, the sinking of warmer and saltier water masses as a result of thermohaline convection alters deep-sea conditions. Atmospheric warming also causes increased stratification of the upper ocean layer, which in turn expands oxygen minimum zones in the water column (Johnson et al., 2008) and, combined with enhanced eutrophication, leads to changes in species composition (Table 3). Stratification also blocks the flux of nutrients from deeper water layers to the surface, causing "desertification" of ocean gyres. As a consequence of a thinner and more stable surface layer, lower primary production (Sarmiento et al., 2004) and a shift from larger to less diverse smaller organisms is expected for all oceans. This is the case at least in the pelagial (Pörtner et al., 2014; Sarmiento et al., 2004; Smith et al., 2008) but polar regions show both increases (such as in the Arctic; Boetius et al., 2013) and decreases in primary productivity, demonstrating that basic biological processes depend on a variety of environmental factors (Gutt et al., 2015; Montes-Hugo et al., 2009). In areas of retreating sea-ice cover, diversity is shifting towards temperate

communities (Wassmann et al., 2011), parallel to the loss of permafrost, which changes terrestrial species richness, abundance and community composition (Rosbakh et al., 2014).

In summary, while temperature changes are faster in the terrestrial realm, range shifts and phenological shifts are faster in the marine realm. In addition, the interaction of rising temperatures with thermohaline convection and ocean stratification lacks an analogy in terrestrial systems. These differences, together with the manifold effects of climate change, the time-lag in the response of biodiversity to climate change and the uncertainties with respect to individual organism's responses (such as dispersal capacity) might explain the uncertainties in experts' judgements and also the higher rating of the importance of climate change for marine versus terrestrial biodiversity.

4.6. Does the importance of elevated CO_2 differ for marine versus terrestrial biodiversity?

Elevated CO_2 was considered to be of least concern in both realms but more important in marine than terrestrial systems.

In terrestrial systems, CO_2 mainly affects plant growth, water fluxes and trophic interactions. The analysis of satellite observations revealed an increase in foliage cover across global arid zones between 1982 and 2010 which can be attributed to the increase of atmospheric CO_2 during that period (Donohue et al., 2013). Free air CO_2-enrichment experiments showed that elevated CO_2 enhances photosynthesis and decreases transpiration of terrestrial plants with marked differences among species and photosynthetic systems (Leakey et al., 2009). Moreover, changes in the chemical composition of plant tissues, like increases in C/N-ratio as a result of increased C-availability, affect higher trophic levels (Sardans et al., 2012) by decreasing the nutritious value of plant tissues (Cornelissen, 2011; Table 3). However, terrestrial animals generally appear less sensitive to the anthropogenic CO_2-enrichment in the atmosphere than marine animals due to the inherently higher CO_2 partial pressures in their body fluids (Ishimatsu et al., 2005).

In marine systems, elevated atmospheric CO_2-levels cause an increased uptake of CO_2 into sea surface waters and thereby ocean acidification. The biological carbon drawdown transfers CO_2 from surface to deeper waters (Hauck and Völker, 2015). Ocean acidification affects marine organisms in multiple ways ranging from metabolic activity of calcifiers and non-calcifiers (Liu and He, 2012; Wittmann and Pörtner, 2013) to calcification (Kroeker et al., 2013) and habitat shifts as well as changes in trophic interactions (Table 3) and species abundance (Nagelkerken et al., 2016). Most effects are mediated by CO_2 accumulating inside different organisms (Pörtner et al., 2014). Among species engineering ecosystems such as warm and cold water corals as well as species of commercial interest such as crustaceans, echinoderms and molluscs CO_2 dependent effects reflect differential sensitivities. Impacts are mostly negative and exacerbated by rising ambient CO_2 levels (Wittmann and Pörtner, 2013). How these effects will add up at the system level potentially affecting biodiversity is not yet well understood (Clements and Hunt, 2015).

Another aspect of concern in marine systems is the upward shift of the calcium carbonate compensation depth below which aragonite and calcite dissolve. This impacts especially on existing carbonate structures such as reefs or mounds. By 2100, almost the entire Southern and subarctic Pacific Oceans are predicted to be undersaturated (Orr et al., 2005). It is further expected that species compositions will shift from losers to winners of ocean acidification. Marine biodiversity will decrease in some important hotspots and food web-interactions will be affected. Still, the scale of these impacts is unknown due to insufficient data. Generally, combined warming and acidification enhance the risks of strong impacts between $+1.5$ K and $+2$ K warming above pre-industrial values as >20 to 50% of corals, echinoderms and molluscs become affected (IPCC, 2014b).

Elevated CO_2 is likely to drive changes in the physiological and morphological traits and in the composition of both marine and

terrestrial species. Present knowledge suggests that extinctions are more likely in marine systems, which is reflected in our Delphi-assessment.

4.7. Does the importance of biological invasions differ for marine versus terrestrial biodiversity?

The relevance of biological invasions was rated similar for both realms, with medium impacts but large uncertainties. Experts who stressed the relevance of invasions focused on the characteristics of invasive species, for example competitive ability. Special focus was placed here on the diversity of responses to species invasions from individuals to ecosystem level, such as effects on genetic diversity and trophic interactions or the potentially global spread of pathogens. In contrast, experts who stressed that invasions have rather low impacts focused on the small extent of their impacts, such as invasions being most relevant on islands. They argued that there is a lack of evidence of invasions affecting ecosystem functioning, implying that invasive species being rather passengers than drivers of change, pointing towards the context-dependency of their impacts.

We conclude from these diverging views that these different perceptions result from the lack of a widely accepted research definition of "invasion" (cf. Table 2 for the definition we adopted), on differences in spatial and temporal study scales, on taxonomic biases (Heger et al., 2013) and on the variety of potential reasons for the success of invasive species. For a number of alien species, their success is discussed as a result of the combination of climate change, its effect on relative performance capacity and fitness (Pörtner et al., 2014) and man as the vector for their invasion.

Despite the apparent lack of an all-encompassing definition of invasion, the same mechanisms related to biological invasions are studied in marine and terrestrial systems such as introduction pathways. In Europe, 52.2% of alien terrestrial vascular plants were introduced as ornamental or horticultural species (Lambdon et al., 2008), while 86% of terrestrial alien arthropods were introduced unintentionally (Rabitsch, 2010). For the marine realm, 1369 alien species have been identified in Europe. About half of them were introduced unintentionally by shipping, either in ballast water or as hull-fouling organisms (Katsanevakis et al., 2013). Other marine introduction pathways are aquaculture, aquarium trade, artificial canals and scientific in situ experiments.

Where invaders threaten biodiversity, this often results from a combination of factors such as the traits of the invader itself and disturbances in the recipient system. In the Mediterranean, the macroalgae *Caulerpa taxifolia* and *C. ramosa* (accidentally released by aquarium managers) have displaced large areas of native seagrass meadows (*Posidonia oceanica*). Healthy seagrass meadows confine *Caulerpa* to the periphery of the mats, but exposure of *Posidonia* to high levels of anthropogenically induced stress (such as wastewater discharges and fish farm effluents) increases invasibility (Occhipinti-Ambrogi and Savini, 2003). A terrestrial example is *Splanchnonema platani*, a parasite fungus of plane trees originating from the Mediterranean. Heat and drought promote its impact on plane in Central Europe, i.e. branch dieback (Kehr and Krauthausen, 2004). Other cconsequences of biological invasions for biodiversity in terrestrial systems involve the hybridization of alien and native species that threatens rare native species (Bleeke et al., 2007) as well as biotic homogenization (Winter et al., 2009). However, extinctions of terrestrial native species by invasive species are mainly restricted to islands, where alien vertebrate predators extirpated many native birds (Blackburn et al., 2004). As for terrestrial systems, there is poor evidence of biological invasions causing local species extinctions. Nevertheless, marine invaders can considerably impact biodiversity as competitors or predators of local species or by degrading native species' habitat (Le Pape et al., 2004). As in terrestrial systems, it is expected that biological invasions - particularly by thermophilic species - will lead to biotic homogenization (Occhipinti-Ambrogi and Galil, 2010).

In conclusion, a multitude of biotic introductions have been observed in both realms and there does not seem to be much difference in the response of marine versus terrestrial biodiversity to invasions. Despite differences in the definition of invasiveness by different authors, it is clear that most introduced species do not become invasive (Richardson and Pyšek, 2006). However, the few that do so can have devastating ecological effects (Molnar et al., 2008). These contrasts can explain the large uncertainties associated with both marine and terrestrial invasions in the Delphi-assessment.

5. Conclusions

We found asymmetries in the experts' perceptions of the importance of different anthropogenic drivers of biodiversity change in marine versus terrestrial systems. Based on the review, we conclude that this asymmetry roots in the differences of (i) how and how intensely humans use land and sea, (ii) the possibilities to investigate the biodiversity in marine versus terrestrial ecosystems and (iii) in time-lags of the response of biodiversity to global changes. However, differences in time lags as well as in human use are diminishing. On the one hand, the degree and scope of human exploitation of the sea is increasing drastically (for example with respect to aquaculture; FAO, 2014); on the other hand, human-induced environmental changes today have global and cross-system impacts rather than "just" regional ones. We are currently facing a major change in the use of the sea reflecting the historic transition from hunters/gatherers to farmers on land. This, together with the other drivers of global change will cause problems for marine ecosystems that will likely be similar to those experienced in terrestrial ecosystems already. Still, we have the chance not to repeat mistakes, such as focusing on aquaculture only when most of the huntable marine organisms have been reduced below levels of commercial efficiency or even went extinct. We argue that, even if drivers of biodiversity differ in their relative importance for marine versus terrestrial biodiversity, the protection of marine biodiversity will at least partly benefit from the same approaches as does terrestrial biodiversity:

- With respect to harvesting, regulations need to become more effective, especially for marine organisms but also in some terrestrial areas of the world. Additionally, special forms of hunting and fishing should be used to create benefits for the protection of wildlife. An example from Namibia shows that the abundance of wildlife species can increase when local communities economically benefit from trophy hunting tourism (Di Minin et al., 2016).
- The use of marine areas lags behind land use. Nevertheless, types of use that have been restricted to the terrestrial realm are now increasingly applied in the marine realm, with aquaculture as the pendant to agriculture being one example and also marine urbanization (construction of artificial structures in marine environments) not only being debated but already having ecological consequences (Dafforn et al., 2015). The relevance of marine habitat loss should thus not be underestimated.
- The application of nutrients and chemicals generally needs stronger regulation. While in Europe and the USA there is a will to mitigate eutrophication, most fertilizers are now produced in Asia and environmental problems related to eutrophication are increasingly reported there (Li et al., 2015).
- Humanity needs to halt climate change in order to reduce negative effects in both marine and terrestrial systems.
- Similarly, biological invasions are driven by trade and traffic, no matter whether marine or terrestrial (Hulme, 2009). Thus, pathways of species introductions need to be regulated.

From a systems perspective, terrestrial and marine biodiversity changes follow similar principles. Cross-system synthesis (surveys, in situ experiments and analytical as well as predictive models) is the

only way to understand differences and similarities between marine and terrestrial biodiversity change and whether these are driven by the history of human use or inherent to the respective system.

Acknowledgements

Appendix A. Appendix

Table S1

Delphi-assessment of global change drivers of biodiversity. The Delphi technique (Dalkey and Helmer, 1963) is an expression of expert knowledge used to achieve convergence of opinion among experts on a specified question. The table shows the aggregated results of the Delphi-assessment, 1st and 2nd round, performed by 18 marine and 21 terrestrial senior science ecologists from Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research (AWI) and Helmholtz Centre for Environmental Research – UFZ. Originally, 90 marine and 90 terrestrial scientists at AWI and UFZ were asked to participate in the assessment. We asked all experts to score the driver which they identified as most important with 100 and to rank all other drivers accordingly between 0 (no impact) and 100. This was done for drivers i–v, ia–id and iia–iib separately.

Dalkey N. and Helmer O. (1963). An experimental application of the Delphi method to the use of experts. *Management Science*, 9, 458–467.

Driver	Median score				Minimum score				Maximum score			
	Marine 1st	Marine 2nd	Terrestrial 1st	Terrestrial 2nd	Marine 1st	Marine 2nd	Terrestrial 1st	Terrestrial 2nd	Marine 1st	Marine 2nd	Terrestrial 1st	Terrestrial 2nd
(i) Land/sea use	92.5	95	100	100	15	15	100	100	100	100	100	100
(ii) Chemical inputs	40	40	60	65	5	5	5	5	80	80	95	95
(iii) Climate Change	75	80	60	60	5	5	10	10	100	100	95	90
(iv) CO_2	40	40	10	10	5	5	3	3	100	100	90	70
(v) Biological invasions	50	50	50	40	5	1	2	2	70	70	90	90
(ia) Habitat loss	40	40	100	100	0	0	40	40	100	100	100	100
(ib) Habitat degradation	60	60	80	80	0	0	30	20	100	90	100	100
(ic) Habitat fragmentation	20	20	60	60	0	0	20	30	100	100	90	80
(id) Hunting/fishing	100	100	30	30	0	1	10	10	100	100	85	85
(iia) Nutrients	80	80	90	87.5	0	0	5	5	100	100	100	100
(iib) Pollutants	70	70	60	50	0	1	10	5	100	100	100	100

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