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REVIEW

Towards more integration of physiology, dispersal and land-use change to understand the responses of species to climate change

Christian Hof

ABSTRACT

The accelerating biodiversity crisis, for which climate change has become an important driver, urges the scientific community for answers to the question of whether and how species are capable of responding successfully to rapidly changing climatic conditions. For a better understanding and more realistic predictions of species' and biodiversity responses, the consideration of extrinsic (i.e. environment-related) and intrinsic (i.e. organism-related) factors is important, among which four appear to be particularly crucial: climate change and land-use change, as extrinsic factors, as well as physiology and dispersal capacity, as intrinsic factors. Here, I argue that these four factors should be considered in an integrative way, but that the scientific community has not yet been very successful in doing so. A quantitative literature review revealed a generally low level of integration within global change biology, with a pronounced gap especially between the field of physiology and other (sub)disciplines. After a discussion of potential reasons for this unfortunate lack of integration, some of which may relate to key deficits e.g. in the reward and incentive systems of academia, I suggest a few ideas that might help to overcome some of the barriers between separated research communities. Furthermore, I list several examples for promising research along the integration frontier, after which I outline some research questions that could become relevant if one is to push the boundary of integration among disciplines, of data and methods, and across scales even further – for a better understanding and more reliable predictions of species and biodiversity in a world of global change.

KEY WORDS: Global change biology, Habitat change, Thermal biology, Range shifts, Ecology, Biodiversity

Introduction

Whilst the acceleration of the two major environmental challenges of our planet – the climate crisis and the biodiversity crisis – calls for immediate, large-scale, transformative action (IPBES, 2019; Leclère et al., 2020; IPCC, 2014 at https://www.ipcc.ch/report/ar5/wg3/), we still strive to improve our understanding of whether and how species are successfully able to cope with these interacting threats. These efforts are perfectly justified, as profound knowledge on how species and thus biodiversity as a whole respond to climate and land-use change is the basic requirement for developing reliable predictions on future impacts of anthropogenic impacts and to allow implementation of sustainable conservation strategies (Urban et al., 2016). Numerous empirical and review papers as well as meta-analyses have accumulated over the past decades, assessing the impact of changing habitat and climate conditions on biodiversity and the pathways of organisms to respond to these changes. However, here I argue, based on a quantitative literature review as well as on selective (and by no means comprehensive) examples that the lack of integration of the scientific community that deals with biological climate-impact research has impeded progress towards a more comprehensive understanding and more reliable predictions of biodiversity in a changing world (Orr et al., 2020).

For a better understanding and more realistic predictions of biotic responses to climate change, it is important to consider both environmental conditions and species' characteristics (Dawson et al., 2011; Urban et al., 2016). Environmental conditions (extrinsic factors hereafter) include, most importantly, ambient climatic conditions and habitat availability as given by land cover or land-use (Mantyka-Pringle et al., 2012), with other extrinsic factors such as soil conditions, topography and other aspects also being potentially influential. Species' characteristics (henceforth referred to as intrinsic factors) include any trait or attribute of the studied species that is relevant for how it may respond to climate change; of prime importance are its physiology and dispersal capacity (even though morphological or life-history traits, adaptability, demographic traits and population dynamics etc. may be relevant, too) (Bellard et al., 2012; Berg et al., 2010; Huey et al., 2012). Williams et al. (2008) summarized these and other aspects important for understanding species' responses and vulnerability to climate change in an elegant and comprehensive framework, of which key elements are (i) the exposure to climatic changes (representing the extrinsic factors mentioned above) and (ii) species' sensitivity to changes in climatic conditions, which is mediated by its adaptive capacity and resilience (representing the intrinsic factors) (see Williams et al., 2008 for further details).

In a more simplified, but hopefully still instructive conceptual framework of climate change responses (which can be viewed as a subset of the framework of Williams et al., 2008), the four specific components – climate and habitat conditions (extrinsic factors), physiology and dispersal capacity (intrinsic factors) – may interact in the way depicted in Fig. 1. The current distribution of a species is assumed to be located in an area of suitable climate (see Soberón, 2007 for conceptual details). With climate change (Fig. 1A), i.e. a (potential) shift of the suitable climatic conditions away from the species' current distribution, the species may respond via different pathways to avoid extinction (Holt, 1990). The first pathway is to track the shift of the suitable climate via dispersal (which I understand here – again in a very simplified way – as the species' capacity or ability to change its distributional range in response to a changing climate). The second pathway is to respond via its physiology, i.e., broadly summarized, via tolerating or adapting to the changed climatic conditions within its current distributional range. This is obviously, and once more, a bold reduction of the multitude of factors involved, which may include features and

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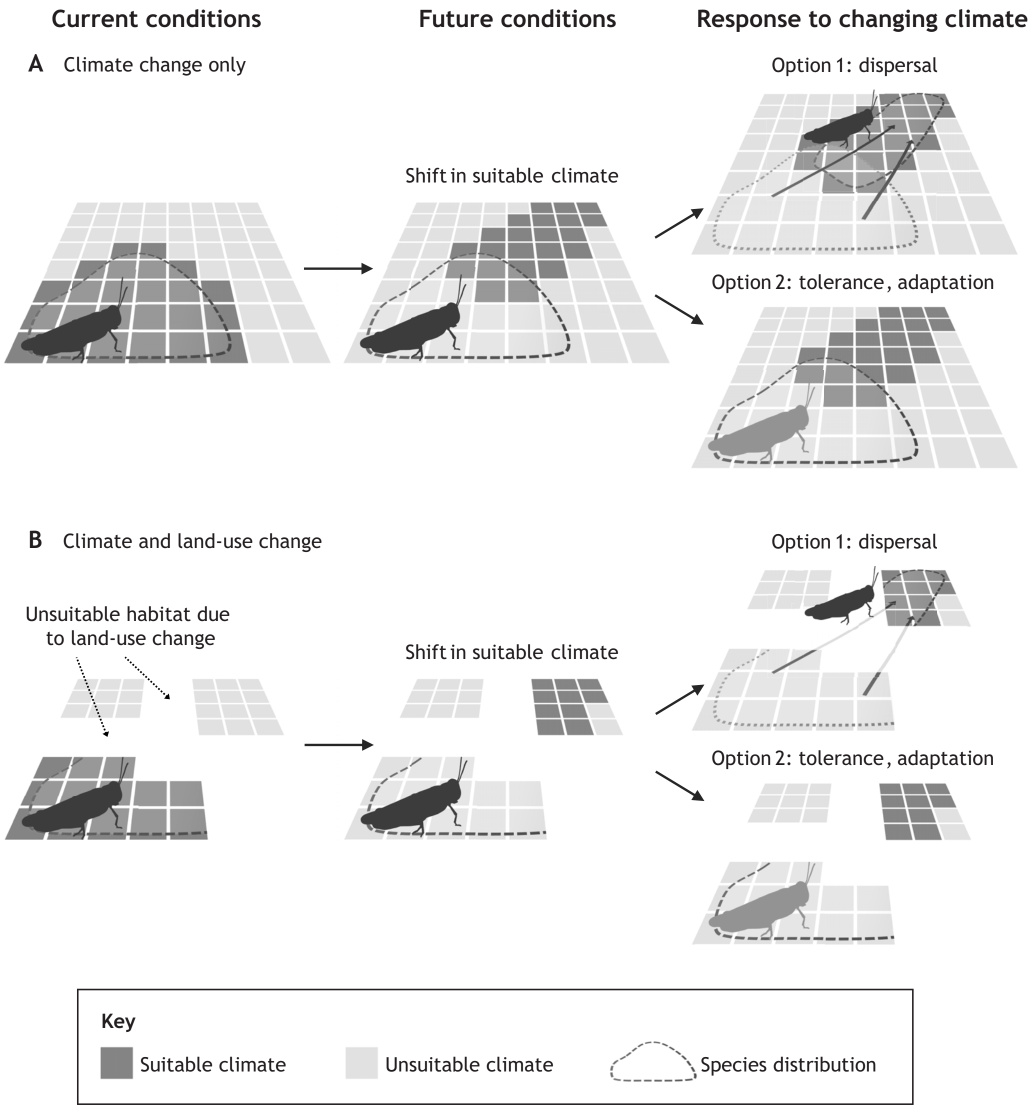

Fig. 1. Simplified depiction of the pathways of species' responses to changing climatic conditions. Shift in suitable climate under (A) climate change alone and (B) climate and land-use change (where land-use changes reduces the amount of suitable habitat). See Introduction for further explanations.

processes across the whole range of organismic scale levels, from mitochondria and cellular metabolic processes via anatomy or morphology to behavior (Somero, 2010). Furthermore, it is worth noting that the aspect of physiological toleration or adaptation is often looked at from the perspective of evolutionary biology, and the distinction between responses via plasticity (Seebacher et al., 2015) and those via evolutionary adaptive change (Bradshaw and Holzapfel, 2006) is as crucial as it is challenging (Chown et al., 2010). For instructive purposes, I avoid delving further into these issues here, notwithstanding the importance to more frequently and profoundly address this evolutionary dimension (Diamond, 2018; Diniz-Filho and Bini, 2019; Lavergne et al., 2010). Bringing together these three aspects – climate change, dispersal and physiology – requires conceptual, methodological and scale integration (i.e. integration across spatial and temporal scales as well as scales of biological organization), which is a challenge. However, this triplet still lacks the crucial extrinsic factor of habitat availability as given by data on land cover or land-use and their change.

Without the availability of suitable habitat (understood here *sensu lato* as any habitat-related aspect apart from climatic conditions), species will not be able to persist over time, even if the climate may be suitable. Thus, obviously, anthropogenic land-use change and its consequences of habitat destruction, degradation and fragmentation directly influence species' chances to persist over time and in space (Opdam and Wascher, 2004). However, in a climate change context, they also affect species' chances to successfully respond to changing climatic conditions via the pathways outlined above (Fig. 1B; Hof et al., 2011a; Travis, 2003). For instance, habitat fragmentation affects dispersal via increased distances that need to be covered by organisms from one suitable patch to the next. As another example, land-use change may alter habitats in a way that their (micro)climatic conditions change as well (e.g. changes from forests or wetlands to cropland), resulting in different physiological requirements for species to survive (Nowakowski et al., 2017). In summary, land-use change is a crucial extrinsic factor that needs to be considered if we really are to understand or even project species' responses to climate change (Hof et al., 2011b, 2018; Mantyka-Pringle et al., 2012; Titeux et al., 2016).

As mentioned already, this concept of two extrinsic and two intrinsic factors is a bold simplification and certainly not one able to comprise the real complexity of the interplay of processes and factors determining species' responses to environmental change (see, again, Williams et al., 2008 for a more comprehensive and also more general framework). However, even simplifications may be instructive for illustrating certain objectives. In fact, from the reductionist four-factor framework, the question arises: how often are these components looked at jointly in the enormous body of literature that has piled up over the past decades and that set out to study species or biodiversity responses to climate change?

Quantitative literature review

To get a better overview of the literature and to test my expectation of an overall rather low level of integration of the biological climate impact research community, I used the approach of a quantitative literature review. This was inspired by a similar analysis by Orr et al. (2020), which more generally assessed the research field of anthropogenic stressors on the environment and revealed a division into the fields of freshwater, marine and terrestrial ecology as well as ecotoxicology.

Methods

To assess the level of integration in the climate change response literature, I assessed climate change along with jointly considering land-use change, dispersal and physiology in a quantitative literature review and bibliographic analyses. To do so, I performed an extensive literature search within the Clarivate Web of Science database (https://apps.webofknowledge.com) applying different combinations of search terms (Table 1) in order to quantify the number of published studies with different degrees of integration. The terms were combined as title searches ('TI' in the advanced search of the Web of Science core collection) or topic searches ('TS') to vary the level of emphasis on the different factors. A topic search includes the search of the respective term in the publication's title, abstract, keywords given by the author and Web of Science's 'Keywords Plus', which are based on terms that are frequently appearing in the titles of the references cited in the publication (hereafter referred to as keywords). As the overall focus was on research in an explicit climate change context, the climate change search term (see Table 1) was held constant in all searches (either as title or topic search; see Fig. 2 for an overview of the search combinations). All searches included a term that helped restricting them to a biotic scope (see Table 1); furthermore, all searches were restricted to the Web of Science research areas Biodiversity Conservation, Biology, Ecology, Entomology, Evolutionary Biology, Marine and Freshwater Biology, Multidisciplinary Sciences, Ornithology, Physiology, Plant Sciences, and Zoology. All literature searches were performed on 5–9 January 2021 and included research papers, review papers, books and book chapters contained in the Web of Science database covering the years 1991–2020. 1991 was picked as the first year because it represents the year when the scientific literature on climate change and its impacts started to increase pronouncedly, with more than 100 papers published. To depict the results of the number of publications, I used the draw.triple.venn function in the VennDiagram package (https://cran.r-project.org/web/packages/VennDiagram/index.html) in R (https://www.r-project.org/).

Table 1. Search terms for the quantitative literature review, applied in different combinations in the advanced search of the Clarivate Web of Science (see Fig. 2)

Factor	Exact search term
Included in all searches	
Biodiversity, impact/ response	Topic=((impact* OR effect* OR threat* OR influenc* OR respon* OR react* OR driv* OR affect*) AND (species OR *diversity OR distribution* OR richness))
Climate change	Topic or Title=((climat* AND (chang* OR warm*)) OR warming OR (temperature* AND (increas* OR ris* OR warm*)))
Included as various combinations (see Fig. 2)	
Land-use	Topic or Title=(landuse* OR land-use* OR landcover* OR land-cover* OR ((habitat* OR landscap*) AND (change* OR loss* OR destruct* OR degrad* OR alter*)) OR fragment* OR deforest*)
Physiology	Topic or Title=(physiol* OR therm* OR ((respirat* OR metaboli*) AND (tolera* OR capacit* OR scope* OR performance* OR limit* OR adapt* OR rate*)) OR "aerobic scope*" OR acclim* OR (physiol* AND phenotypic* AND plastic*) OR ((freezing OR heat OR temperature OR cold) AND (tolerance*)) OR ctmax OR ctmin OR 'critical temperature*' OR (oxygen AND limit*))
Dispersal	Topic or Title=(dispers* OR coloni?*)

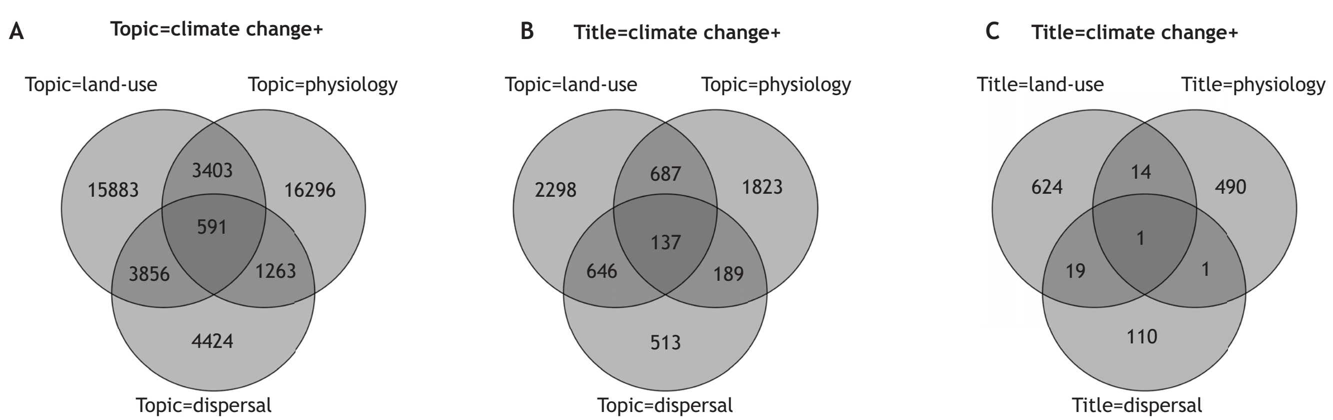

Fig. 2. Results of the quantitative literature review combining the different search terms given in Table 1 in a Clarivate Web of Science search on 5–9 January 2021. Numbers indicate the number of publications returned by the respective search terms where: (A) topic of the paper involves climate change plus combinations of three other topics; (B) title of the paper specifically mentions climate change plus combinations of the three other topics covered in the paper; (C) title of the paper includes climate change and combinations of the other three words.

To investigate the level of integration as well as the connectivity of research, I assessed the relationships among the studies returned by the literature search using cluster and ordination techniques. To do so, I used the bibliometrix package in R (https://cran.r-project.org/web/packages/bibliometrix/) which analyses the bibliographic information of specific sets of publications. As the two core sets for this analysis, I used the publication set for (i) the search term combination TI=climate change AND TS=(land-use OR physiology OR dispersal) (*n*=6212 publications; see also Fig. 2B for this combination, the slight differences in the exact numbers are due to searches on different days during the abovementioned search period) and (ii) the search term combination TI=(climate change) AND TS=(land-use AND physiology AND dispersal) (*n*=137 publications; depicted in the centre of Fig. 2A). To analyse the structure and relationships in the publications of these two sets, I used the conceptualStructure function in the bibliometrix package. This function applies an ordination technique to create maps of the conceptual structure or clustering dendrograms using the terms extracted from a given set of publications. Publications sharing similar sets of terms will cluster more closely together on the two-dimensional map or in the dendrogram. Specifically, multiple correspondence analysis was applied to the keywords of the papers in the abovementioned two publication datasets. For the cluster analysis, the automatic identification of the number of separate clusters was applied.

For the first dataset of 6212 publications (see above), the number of search terms was too large for a sensible depiction and interpretation of the data. For a compromise of consistency between the two dataset and feasibility for depiction and interpretation, I restricted the analyses to the top 90 terms (i.e. keywords). These 90 terms included keywords co-occurring in at least 74 out of the 6212 publications of the first dataset, and keywords with a minimum co-occurrence of three publications in the second dataset of 137 publications.

Results

As of the date of the literature search (5 January 2021), 79,157 publications were listed in the Web of Science core collection on the topic of climate change (in a biotic context; see Table 1 for the exact search phrase and specifications above regarding the included research areas). About 58% of those deal with at least one of the four extrinsic and intrinsic factors influencing species' climate change responses (45,716 studies having either of the three terms land-use, physiology or dispersal as their topic; Fig. 2A). This number can be split into those that include (1) only one of the factors (36,603 studies), two of the factors (8522 studies) or all three factors (591 studies) in addition to climate change. Thus, the vast majority, i.e. 80%, of the studies that combine climate change with any of the additional factors deal with only one of them, while 19% include two, and just a bit more than 1% include all three factors. Focussing more closely on the different factors, land-use is the dominant topic (52% out of 41,477 studies), followed by physiology (47%) and dispersal (22%) (percentages add up to more than 100% as studies that contain two or more factors are counted more than once; see Fig. 2A). Although having the second-largest share of all studies combining climate change with any of the additional factors, physiology is the least integrative field: 24% out of all physiology-related climate change studies also deal with at least with one other factor, whereas this number is higher for studies on land-use (33%) and particularly high for those on dispersal (56%).

When restricting the search to studies that list climate change in their titles, i.e. that focus on it more explicitly (10,361 studies overall), the number of studies addressing at least one additional factor out of those studies here reaches around 61% (6293 studies), and out of those the relative number including at least two additional factors increases to about 26% (Fig. 2B). Narrowing down the searches even more to a pure title search, i.e. searching only for publications having climate change as well as one of the other factors in their titles, gives a similar picture: out of a total of 1396 studies setting an emphasis on climate change and at least one more factor, just 35 or 2.5% focus on three or more, with only one study whose title comprises all factors (Fig. 2C, Table 2).

Overall, and not surprisingly, the highest levels of integration are reached between papers on land-use and dispersal. They are followed by those on land-use and physiology, whereas papers addressing physiology and dispersal showed the lowest levels of integration (Fig. 2).

Applying ordination and cluster analyses to the keywords of the publications datasets depicted (i) in Fig. 2B as a whole and (ii) in its centre underlines this picture of a stronger separation of the physiological climate change research community from the communities that address climate change in concert with land-use or in a dispersal context (Figs 3 and 4). For the 6212 publications contained in the first dataset, a map of the most frequently used keywords (where their proximity indicates co-occurrence in different publications) shows three distinct clusters (Fig. 3B). The first (green) cluster consists of physiology-related keywords such as thermal tolerance, acclimation or phenotypic plasticity, as well as of terms related to evolution, phenology and population biology. The second (red) cluster includes many terms related to spatial ecology, biogeography, and conservation such as species distribution, land-use, dispersal and extinction. A third (blue) cluster contains several keywords from the field of plant ecophysiology and ecosystem ecology (e.g. photosynthesis, CO_2, productivity or drought), but a set of rather heterogeneous and general terms such as communities, responses, variability or dynamics.

This clear cluster triplet is also shown by the dendrogram for which the automatic cluster identification of the conceptualStructure function divided the keywords into these three groups (Fig. 3A), with the green cluster (terms on physiology, population and evolutionary biology) being most distinct from the other two clusters. Within the green cluster, the terms specifically related to thermal physiology (physiology, thermal tolerance and acclimation) represent a subcluster which appears to be separate from the terms of the other fields. Within the red cluster (spatial ecology, biogeography, conservation), the factors land-use and dispersal appear relatively close together.

It may be worth noting again that the keyword map and the cluster dendrogram are based on co-occurrences of keywords in 6212 publications with a common focus on climate change, but with different levels of joint consideration of the other factors land-use, physiology and dispersal. What becomes apparent is a complex relationship structure, but also, especially when focussing on the first axes of Fig. 3B, a relatively clear gradient from the factor of physiology (be it animal- or plant-focused) at the one end and the factors dispersal and land-use towards the other end.

This depiction of the (sub)divisions of (sub)disciplines of a large, heterogeneous publication dataset whose only unifying theme is the focus on climate change (Fig. 4) can be compared with a supposedly highly integrative set of publications as it is shown in the centre of Fig. 2B. The latter combines climate change in the title and all three additional focus factors in the topic fields, which unsurprisingly leads to a conceptual map and a dendrogram of the publication keywords that show a much less pronounced division among the

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Table 2. List of some of the most integrative publications indicated numerically in the overlapping areas of Fig. 2C and the respective title-based literature search

Reference	Article title	Factors explicitly considered in addition to climate change		
		Physiology	Dispersal	Land-use change
Sánchez-Fernández et al., 2016	Thermal niche estimators and the capability of poor dispersal species to cope with climate change	✓	✓	
Nakano et al., 1996	Potential fragmentation and loss of thermal habitats for charrs in the Japanese archipelago due to climatic warming	✓		✓
Isaak et al., 2010	Effects of climate change and wildfire on stream temperatures and salmonid thermal habitat in a mountain river network	✓		✓
Abdul-Aziz et al., 2011	Potential climate change impacts on thermal habitats of Pacific salmon (*Oncorhynchus* spp.) in the North Pacific Ocean and adjacent seas	✓		✓
Sears et al., 2011	The world is not flat: Defining relevant thermal landscapes in the context of climate change	✓		✓
Cline et al., 2013	Climate change expands the spatial extent and duration of preferred thermal habitat for Lake Superior fishes	✓		✓
Shackell et al., 2014	Thermal habitat index of many northwest Atlantic temperate species stays neutral under warming projected for 2030 but changes radically by 2060	✓		✓
Cascella et al., 2015	Diversification, evolution and sub-functionalization of 70 kDa heat-shock proteins in two sister species of Antarctic krill: Differences in thermal habitats, responses and implications under climate change	✓		✓
Snyder et al., 2015	Accounting for groundwater in stream fish thermal habitat responses to climate change	✓		✓
Nowakowski et al., 2017	Tropical amphibians in shifting thermal landscapes under land–use and climate change	✓		✓
Principe et al., 2018	Differential effects of water loss and temperature increase on the physiology of fiddler crabs from distinct habitats	✓		✓
Sedighkia et al., 2019	Modelling of thermal habitat loss of brown trout (*Salmo trutta*) due to the impact of climate warming	✓		✓
Núñez-Riboni et al., 2019	Spatially resolved past and projected changes of the suitable thermal habitat of North Sea cod (*Gadus morhua*) under climate change	✓		✓
González-del-Pliego et al., 2020	Thermal tolerance and the importance of microhabitats for Andean frogs in the context of land use and climate change	✓		✓
Wagner et al., 2020	Climate change drives habitat contraction of a nocturnal arboreal marsupial at its physiological limits	✓		✓
Iverson et al., 2004	Potential colonization of newly available tree-species habitat under climate change: an analysis for five eastern US species		✓	✓
Pearson and Dawson, 2005	Long-distance plant dispersal and habitat fragmentation: identifying conservation targets for spatial landscape planning under climate change		✓	✓
Crossman et al., 2011	An invasive plant and climate change threat index for weed risk management: Integrating habitat distribution pattern and dispersal process		✓	✓
Iverson et al., 2011	Lessons learned while integrating habitat, dispersal, disturbance, and life-history traits into species habitat models under climate change		✓	✓
Hof et al., 2012	Habitat stability affects dispersal and the ability to track climate change		✓	✓
Feeley and Rehm, 2012	Amazon's vulnerability to climate change heightened by deforestation and man-made dispersal barriers		✓	✓
Horak et al., 2013	Changing roles of propagule, climate, and land use during extralimital colonization of a rose chafer beetle		✓	✓
Imbach et al., 2013	Climate change and plant dispersal along corridors in fragmented landscapes of Mesoamerica		✓	✓
Coristine et al., 2016	Dispersal limitation, climate change, and practical tools for butterfly conservation in intensively used landscapes		✓	✓
Prasad et al., 2016	A multistage decision support framework to guide tree species management under climate change via habitat suitability and colonization models, and a knowledge-based scoring system		✓	✓
Ellis-Soto et al., 2017	Plant species dispersed by Galapagos tortoises surf the wave of habitat suitability under anthropogenic climate change		✓	✓
Ofori et al., 2017	Combining dispersal, landscape connectivity and habitat suitability to assess climate-induced changes in the distribution of Cunningham's skink, *Egernia cunninghami*		✓	✓
Radinger et al., 2017	The future distribution of river fish: the complex interplay of climate and land use changes, species dispersal and movement barriers		✓	✓
Yalcin and Leroux, 2018	An empirical test of the relative and combined effects of land-cover and climate change on local colonization and extinction		✓	✓
Årevall et al., 2018	Conditions for successful range shifts under climate change: The role of species dispersal and landscape configuration		✓	✓
Della Rocca and Milanesi, 2020	Combining climate, land use change and dispersal to predict the distribution of endangered species with limited vagility		✓	✓
Methorst et al., 2017	A framework integrating physiology, dispersal and land-use to project species ranges under climate change	✓	✓	✓

To be listed here, at least two of the three factors 'physiology', 'dispersal' and 'land-use change' had to be mentioned in the title, in addition to climate change (see Table 1 for the exact search phrases).

main term clusters (with the exception of very few rather specific terms). In fact, the automatic cluster definition option grouped the three factors physiology, dispersal and land-use into one large cluster. Thus, from an analytical perspective, this publication dataset appears to do indeed a good job integrating the different factors. However, an optical inspection of the subcluster structure reveals some interesting patterns (Fig. 4A). For instance, the factor of land-use appears relatively far from the factor of dispersal, in

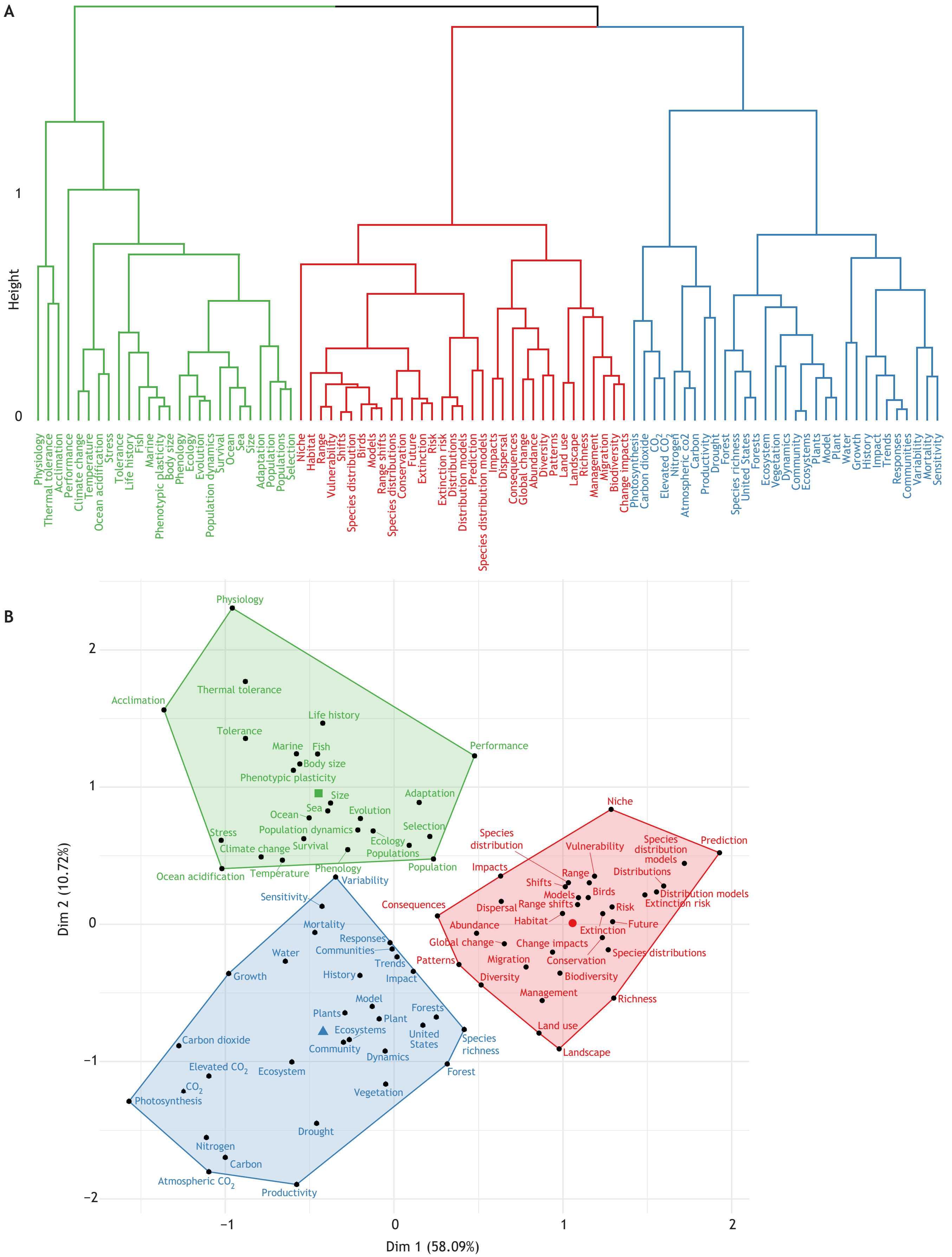

Fig. 3. See next page for legend.

Fig. 3. Conceptual structure of the keywords (Web of Science 'Keywords Plus') of the publication dataset returned by the literature search with the search term combination depicted in Fig. 2B, containing 6212 publications. (A) Dendrogram shows the results of a cluster analyses of the 90 most frequently co-occurring keywords, with keywords co-occurring in larger numbers of publications showing closer proximity. (B) A conceptual map depicting this co-occurrence-based proximity of the same keywords in two-dimensional ordination space as given by a multiple correspondence analysis. The three separate keyword groups in A and B are based on an automatic cluster selection. See text for further details.

contrast to several physiological terms. However, a gradient from more specific keywords related to thermal physiology via population dynamics towards biogeography and conservation can be inferred from the red subcluster in Fig. 4B. Interestingly, the field of plant ecophysiology has disappeared from this more integrative publication dataset. Even though the topic has not been an explicit focus of this analyses, the observation that apparently no studies from this important field of ecological climate-impact research have been published in relation to any of this paper's focus factors underlines its somewhat unfortunate separation.

Reasons for the lack of integration

From the quantitative literature review, two major observations are emerging. First, relatively low proportions of the studies published on species responses to climate change try to integrate more than one additional extrinsic or intrinsic factor relevant for a better understanding of biotic responses to environmental changes. The only exception to this pattern is the factor of dispersal, which showed relatively high levels of integration with the factor of land-use. Second, while many publications including at least one of the investigated key factors have a physiological focus, the research field of physiology appears to be more separated from the other studies than those dealing with dispersal and land-use change.

There are several reasons why higher levels of integration across subdisciplines are not observed (see e.g. Leitão et al., 2019 for examples and references). For instance, cutting-edge research keeping up to date with the state of the art of a specific field requires, obviously, the development of in-depth expertise, which profits from a high degree of disciplinary focus. Furthermore, even though higher education curricula – at least of European universities – are changing and integrative graduate schools and inter-disciplinary study programs of PhD centres are growing, disciplinary training is still widespread. This may be, in turn, partly driven by the trend of mono-disciplinary studies having a higher chance for being published, also because the largest part of the 'classic' publication market is still organized disciplinarily – with a growing number of exceptions, however, such as the glamorous and/or prestigious multi-disciplinary journals or outlets from the open-access publication world such as *PeerJ*, *PLoS ONE* and the like. As a third point, the majority of the well-known and prestigious scientific conferences are still organized along very disciplinary lines. And even within large and by definition rather integrative academic organisations such as (just to name the three largest ecological societies) the Ecological Society of America (ESA), the British Ecological Society (BES) or the Ecological Society of Germany, Austria and Switzerland (GfÖ), the disciplinary imprint still dominates, as mirrored for example, by their conference programs or their line-up of specialist groups. Finally, the larger funding organisations still tend to set emphasis on supporting disciplinary proposals for which one of the reasons is, again, the rather disciplinary structure of decision panels (Bromham et al., 2016). And even large-scale projects with overarching goals that strive to tackle current research challenges from a multi-disciplinary or multi-approach perspective often fail to live up to their ambitions, owing to their often predominantly disciplinary internal structures and hierarchies and missing incentives for cross-disciplinary exchange even within the same institution.

These five observations which largely relate to the organisation of the scientific system and namely its training, publication, conference and funding sub-systems are, of course, just examples for potential drivers of the rather low levels of integration among scientific (sub)disciplines in general. Several of them inherently relate to a scientific reward system that appears to encourage low-risk, (mono)disciplinary focus along established research tracks, such as in funding initiatives or academic career pathways. Consequently, such a system tends to discourage cross-disciplinary, ambitious, and thus risky, avenues, which may, however, be more promising to successfully tackle the most exciting, but also most challenging scientific questions. Fortunately, the number of exceptions to these rather bold and certainly to some degree subjective observations is growing, and more and more examples for cross-disciplinary training and research initiatives accumulate. Nevertheless, the demand for answers to some of the most important research questions related to the great planetary challenges appears to grow faster than the increase in integrative studies that may deliver contributions to these answers. Below, I mention some promising examples for systemic improvements.

Advancement via cross-disciplinary integration and collaboration is particularly important in biological climate-impact research, due to the interacting factors and processes influencing species responses to changes in ambient climatic conditions (Berg et al., 2010; Brook et al., 2008). Therefore, especially the apparent separation of the field of physiology from the other fields is unfortunate because physiological traits and processes are the key to understand the survival of organisms and thereby populations, species and communities under varying climatic conditions (Chown and Gaston, 2008; Evans et al., 2015; Khaliq et al., 2014; Pörtner and Farrell, 2008).

There may be various reasons for the gap between physiological research and research focussing on dispersal and on land-use change (Fig. 3A,B). One of the main factors probably relates to the differences in methodological approaches and, consequently, in spatial scope. The field of thermal physiology is, naturally, a predominantly experimental one, with a focus on sophisticated lab work, especially when studying the physiological mechanisms of organismic responses to varying ambient climates. Owing to the field's requirements for resources and time in order to generate in-depth knowledge on the thermal characteristics of organisms, there is an inherent limitation to the possibilities of covering larger spatial, temporal and taxonomic scales (for a related discussion on potential trade-offs between data quality and inclusiveness, see McKechnie and Wolf, 2004; McNab, 2009). This tendency is further pronounced if, as often the case, the focus is set on the cellular, biochemical and genetic mechanisms that determine physiological pathways or characteristics of organisms. Only few studies try to establish connections from the molecules, cells or genes via the organismic level to its spatial and environmental context (e.g. Dahlke et al., 2020; Pörtner, 2001; Pörtner, 2002; Somero, 2010).

By contrast, research on dispersal or land-use change is spatial by definition. Furthermore, land-use change impacts on the configuration of habitats most prominently influence dispersal pathways and processes (Thomas, 2000); thus, a rather high level of integration between these two factors is rather unsurprising. While there is, overall, a gap between physiology and the other fields

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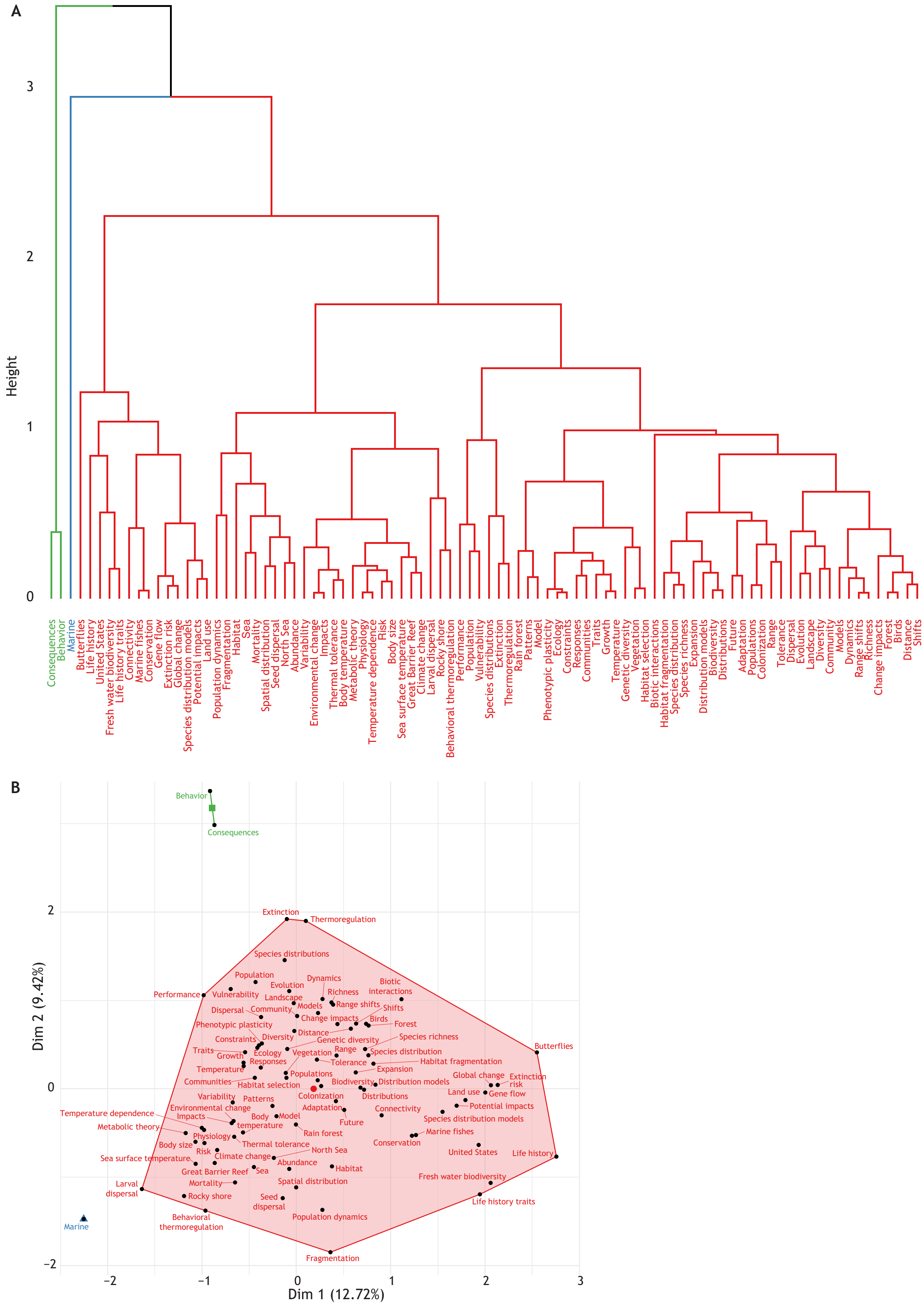

Fig. 4. See next page for legend.

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Fig. 4. Conceptual structure of the keywords (Web of Science 'Keywords Plus') of the publication dataset returned by the literature search with the search term combination depicted in the three-way-overlap area in the centre of Fig. 2B, containing 137 publications. (A) Dendrogram shows the results of a cluster analysis of the 90 most frequently co-occurring keywords, with keywords co-occurring in larger numbers of publications showing closer proximity. (B) A conceptual map depicting this co-occurrence-based proximity of the same keywords in two-dimensional ordination space as given by a multiple correspondence analysis. The three separate keyword groups in A and B are based on an automatic cluster selection. See text for further details.

(Fig. 3A,B), the field of thermal physiology has stronger links to research on land-use and habitat change than to the intrinsic factor of dispersal, as indicated by the bibliometric analysis (Fig. 2 and Fig. 3A,B). Even though the integration of physiology with land-use and habitat change is challenging, as methods and study systems appear to be very far apart, the small but growing number of studies combining these two fields is promising, as a better understanding not only of the 'if', but also of the 'how' of species' survival under land-use change is urgently needed, especially in the context of climate change (Cooke et al., 2013). Indeed, the journal *Conservation Physiology* thus stands out as a pioneer here, promoting work at an interface which is timely and important to study if one is to understand the multiple interacting drivers of global change that species are confronted with. The particularly low level of integration between physiology and dispersal is somewhat surprising, because for studies that focus on the organism's perspective – on species' intrinsic characteristics relevant for responses to a changing climate or, following the framework of Williams et al. (2008), on the organism's sensitivity and adaptive capacity – physiological and dispersal capacities should be among the most relevant factors (Berg et al., 2010). However, the extent to which there are trade-offs among them or whether they are inter-related is an interesting, but rarely addressed question (see below).

The way forward: towards more and better integration

To avoid any misunderstanding: this paper's aim is by no means to criticize specific, in-depth studies on whatever aspect related to climate or land-use change, dispersal or physiology. Such work is still needed in order to improve our understanding of patterns, processes and mechanisms for specific species or across taxa, and across scales of space and time. What I intend to make the case for here is, in addition to these valuable contributions, a broadening of research horizons that better acknowledge the interplay of different intrinsic and extrinsic factors. Broadening the horizon in this way may in turn even further improve our knowledge base to understand species responses to climate change, also by identifying knowledge gaps which to fill more specialized projects are needed for. Tackling this challenge requires the active search for opportunities to integrate data and approaches across disciplines and scales. Here, I first outline how some of the systemic obstacles mentioned further above can be overcome. Second, based on some of the most integrative papers returned by the quantitative literature review (Table 2) and on several other publications and lines of previous work I will give examples for promising ways of how previous work has successfully integrated different aspects related to the four intrinsic and extrinsic factors that are the focus of this paper. Third, and finally, I list a few research questions as a perspective for future scientific endeavours that may contribute to pursuing a more integrative agenda in global change biology.

Overcoming systemic obstacles to integration

Successful integration across (sub)disciplines requires constructive exchange and collaboration. While integrative studies sometimes appear to lack scientific rigor (Boyles et al., 2019) and to misunderstand fundamental concepts, valid criticism towards such studies can by joined by arguments partly fuelled by a failure of communication or of acknowledging the validity of approaches of other fields (see discussion in Hof et al., 2017a,b; McKechnie et al., 2017; Mitchell et al., 2018; Wolf et al., 2017, debating data and results of Buckley et al., 2018; Fristoe et al., 2015; Khaliq et al., 2014, 2015). To achieve more and especially better integration, we need critical, but at the same time constructive and encouraging feedback and scientific exchange, as well as a general openness for concepts, approaches and standards common in other research areas (Campbell, 2005).

While disciplinary education and training remains crucial to gain the expertise and skills required for cutting-edge research, it is also vital to re-shape study programs and training curricula in ways that keep researchers' minds open for unconventional pathways and approaches that may differ from their own pet systems and method portfolios. Obviously, on the one hand setting too much and too early emphasis on inter-, multi- or even transdisciplinarity bears a certain risk of producing scientists that know bits of everything, but lack the scientific profoundness and rigor needed to advance science in general. On the other hand, getting researchers of late career stages excited enough to leave their comfort zones and community bubbles in order to engage in communication and collaboration with colleagues from rather distant scientific communities may present a challenge as well. Thus, balancing these trade-offs and difficulties requires careful thought and a diverse set of strategies, for which the general promotion of scientific and epistemic openness may be an underlying thread.

With their publishing policies and strategies, journals have a responsibility for encouraging or discouraging integrative studies. Many journals – those that are multi-disciplinary by definition as well as those that still have a more specific focus – have started acknowledging the value of integrative papers (as documented in the broad range of publication outlets that have published the most integrative studies found in the quantitative literature review; data not shown). This development should be further encouraged if more and better integration is to be achieved.

Because of the accelerating progress of each research field, it is barely possible for an individual researcher to pursue the integration of very different approaches from various fields. Therefore, collaboration is the key pathway to bring together data, methods and expertise from different disciplines. More and deeper collaboration requires exchange and communication, which may be fostered by more cross-disciplinary exchange formats; these may range from incentives or funding opportunities for small-scale collaboration networks (consisting of a few collaborators) within and between universities and research institutions via funding programs for workshops and working groups (such as the sDiv program of the German Centre for Integrative Biodiversity Research) to interdisciplinary symposia and conference formats such as the Species On the Move Conference Series (http://www.speciesonthemove.com/) or the Gordon Research Conferences (https://www.grc.org/unifying-ecology-across-scales-conference/).

Not least, reward and funding systems need to break out of some of their established pathways and habits, and should acknowledge the value of novel, cross-disciplinary studies that integrate knowledge and ideas from various fields. Here, changing the system's implicit mechanisms on how research and their protagonists are acknowledged and rewarded requires longer time lines than incentivizing integrative initiatives via financial resources (e.g. in funding programs), staff management or career pathways. However, the funding agencies must also rethink their internal

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structures, which are all too often organized in a disciplinary way, in order to sustainably support more interdisciplinary projects (Bromham et al., 2016; Leitão et al., 2019).

Promising examples for more integration in biological climate impact research

My quantitative literature review highlights the need for more studies that integrate more than two of the environment- and organism-related factors which are crucial to assess biotic responses to climate change. However, this Review also reveals examples (including conceptual, empirical and review articles) for promising work that brings together different types of concepts, data and methods covering three or more of the relevant factors (see Table 2 for the most integrative results, also depicted by the overlapping areas in Fig. 2C). Based on these examples, as well as the results of additional selective scans of the literature, several promising lines of research are emerging.

The importance of jointly assessing the intrinsic factors physiology (often looked at from a thermal tolerance perspective) and dispersal has been emphasized especially by studies focussing on aquatic systems. Among them, water beetles have served as a rewarding study system (Arribas et al., 2012; Calosi et al., 2010). For instance, recent work on troglobitic (cave-dwelling) beetles showed that thermal tolerances that were experimentally measured were larger than those estimated by correlative species distribution models, suggesting that just using the latter would underestimate the capability of these rather poorly dispersing species to cope with temperature increases (Sánchez-Fernández et al., 2016).

Even though the bibliometric analyses (Fig. 3) suggests that linking species' thermal physiology with the effects of land-use change in a climate change context presents a challenge, efforts that try to pursue this avenue are probably one of the most important and promising emerging fields in global change ecology. An increasing number of studies have shown that integration is possible for these usually disparate fields (Table 2), namely via the concept of 'thermal landscapes', which stresses that the fine-scale variation of thermal conditions provides opportunities for behavioural thermoregulation of many species, even under global warming (González-del-Pliego et al., 2020; Sears et al., 2011). However, that climate change in combination with land-use-driven habitat change may render potentially suitable thermal landscapes unsuitable (Fig. 1) has also been shown frequently. Nowakowski et al. (2017) measured critical thermal maxima of various frog species as well as the variation of microclimates of different land-cover types at the landscape scale to quantify the amount of thermally suitable habitat. Using future land-use change simulations and climate change projections, as well as biophysical modelling (see below), they projected changes in suitable habitat for the different land-cover types. Their results suggested that climate-change-driven future decreases in thermally suitable habitat may be larger than the sole impacts of habitat loss; based on this, they concluded that conservation strategies should take into account such changing thermal landscapes, especially for ectotherm species (Nowakowski et al., 2017). Involving several case studies and a meta-analysis, another study (Nowakowski et al., 2018a) emphasized the need to consider species' thermal biology when investigating community changes, namely because habitat modification leads to alterations in microclimatic conditions (see also Nowakowski et al., 2018b, for a review).

During the past decade or so, the field of biophysical or mechanistic niche modelling has especially experienced a tremendous development towards ever more sophisticated models (Briscoe et al., 2016; Buckley et al., 2010; Kearney and Porter, 2009; Kearney et al., 2014b; Mathewson et al., 2016). These models 'characterise the fundamental niche of an organism by determining thermodynamic constraints on its heat, water and nutritional budget, and the consequences of this for growth, development and reproduction. They can thus quantify constraints on survival, activity and, ultimately, the vital rates that determine population growth, given a sequence of environmental conditions and the key morphological, physiological and behavioural functional traits' (Kearney and Porter, 2020, p.85). Together with a better availability of climatic datasets at high spatio-temporal resolution (e.g. Karger et al., 2017; Kearney et al., 2014a; see also Wüest et al., 2019), they become usable for a broad range of scientists from different fields and may partly help in overcoming the experimental limitations inherent to the field of thermal physiology (see above). Applying this kind of model to an ever-more growing number of organisms, regions and ecosystems across spatial and temporal scales, also in combinations with novel datasets from different disciplines, will be crucial to enhance the integration I am arguing for in this paper.

In contrast to most of the other factor combinations, the joint consideration of dispersal, land-use change and climate change has started early. Dyer (1994) investigated the potential responses of forest species to climate change with simulation models that incorporated the pattern of land-use and dispersal types (wind- and bird-mediated dispersal). His model results suggested that many species were not able to follow changes in climatic conditions, 'resulting in widespread disequilibrium between vegetation and climate' (Dyer, 1994, p. 77). About a decade later, Pearson and Dawson (2005) showed, again based on simulations, that the influence of landscape structure in migration ability strongly depends on the probability of long-distance dispersal. More recent studies have used surrogates for dispersal distances, such as eco-morphological traits (see e.g. Sheard et al., 2020; Tobias et al., 2020): an exemplary study on river fish (Radinger et al., 2017) combined estimates of fish dispersal ability based on morphological measurements such as body size and fin lengths with species distribution models and the presence of movement barriers to assess the potential future distributions of different species. They found that shifts in suitable habitats are likely to be faster than species are able to disperse. Furthermore, smaller-bodied fish species appeared to be mainly restricted by their intrinsic dispersal ability, while dispersal of large-bodied species was rather restricted by anthropogenic movement barriers, such as river dams (Radinger et al., 2017). While data on empirically measured dispersal distances or capacities do remain scarce (which may be one of the reasons for the overall low number of dispersal-related studies in this analyses, Fig. 2), studies have started to use them for projections of species distributions under climate change (for a rather rare example from the world of insects, see Jaeschke et al., 2013). Very recently, Della Rocca and Milanesi (2020) also took into account land-use change in addition to climate change alone and used species-specific dispersal information to predict the potential distribution of six different species of saproxylic (i.e. deadwood-adapted) beetles in Europe. They found that the species would only profit from climate change in the unlikely case of unlimited dispersal, whereas with realistic dispersal information, species' future distributions were mainly limited by land-use change (Della Rocca and Milanesi, 2020). As long as empirical data on species' dispersal ability remain fragmented, trait-based approaches such as the one presented above (Radinger et al., 2017) present a promising pathway for integrating dispersal with other factors such as land-use, but also physiology. That said, establishing valid links between the (eco)morphological traits measured or used and the dispersal capacities (e.g. Dawideit et al., 2009) is as important as it is challenging.

As a final example, the analytical framework proposed by Methorst et al. (2017) aimed to combine all four extrinsic and intrinsic factors – climate and land-use change, physiology and dispersal – and assessed their relative importance for future projections of the distribution of an endangered European songbird species. The framework is based on a species distribution model supplemented with data on the species' thermal tolerance which is then combined with empirical data on dispersal ability as well as land-use projections. While use of only climate and physiological data resulted in projected increases in the distribution of this warm-adapted species, accounting for dispersal and land-use change altered these projections strongly, turning the increase into a decrease if dispersal is assumed to be minimal. Although it is not surprising that projections become more restricted when restricted by dispersal or land-use, the results underline the importance of taking into account multiple factors for assessing climate change impacts on species (Methorst et al., 2017).

All these examples are by no means supposed to give a comprehensive representation of the many studies compiling at the integration frontier, striving for improved assessments of how biodiversity responds to climate change. Instead, these exemplary studies are intended to highlight what is already possible along the lines of the integration of the four factors that are the focus of this paper. That said, numerous aspects also relevant for understanding and predicting biotic responses to climate change have consciously been ignored here; among these aspects are (and I just list a very subjective selection of examples): phenology (Hassall et al., 2007; Thorup et al., 2007), population dynamics and demography (Bowler et al., 2017; Fordham et al., 2013a,b), biotic interactions (Engelhardt et al., 2020; Schleuning et al., 2016, 2020) and evolutionary adaptation (Diamond, 2018; Diniz-Filho and Bini, 2019).

To push the integration frontier even further, it may be interesting to address many research questions; here, I list a few of them, again without any ambition or claim to be comprehensive: (1) How do trade-offs or correlations between sets of intrinsic factors, e.g. related to physiology and dispersal, but also to morphology, reproduction, or behaviour, enable or disable organisms to respond to extrinsic factors, and does this influence differ between land-use and climate change? To which extent do the relationships among intrinsic factors vary within and between species along spatial and environmental gradients? (2) How do extrinsic factors such as climate and land-use (as well as their changes) influence the evolutionary and ecological interplay of organismic traits (e.g. related to the intrinsic factors dispersal and physiology) and biotic interactions and thereby the spatio-temporal variation of species distributions, biotic community structure and biodiversity patterns at different geographical and temporal scales? (3) How do historical environmental dynamics – over shorter and longer time scales – still shape current distributions and, via the evolutionary (or phylogenetic) conservatism of intrinsic factors such as dispersal or physiological capacities, species' potential to respond to current and future climate and land-use change? (4) How is the variation of physiological traits, e.g. of thermal limits or optima reflected in biogeographical characteristics, such as mean, size and limits of geographic ranges, bioclimatic niches as inferred from correlations between distributions and ambient climate? What is the influence of spatial extent and resolution on these relationships, and how do the relationships vary between different taxonomic groups and why?

A concluding remark

With this paper I aim to highlight the challenges of and the opportunities for more and better integration of some of the factors that are assumed to be crucial for a more holistic understanding of species' responses to anthropogenic environmental change. I argue that change is required in our established systems of research, education and training, of scientific exchange and of research funding, as well as in how we reward and incentivize scientific work. This change is supposed to foster ambitious, certainly risky, but often highly promising integrative research. As illustrated by several examples for studies that have taken up the challenge, integration across disciplines and scales is rewarding and, importantly, possible. Continuing along these promising lines of research and pushing the boundary of scientific integration even further may be a key contribution to tackling one of the most urgent and important scientific and planetary challenges of our times – the biodiversity crisis in an age of global change.

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