## **REVIEW ARTICLE**



# The role of land use and land cover change in climate change vulnerability assessments of biodiversity: a systematic review

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## **Abstract**

Context For many organisms, responses to climate change (CC) will be affected by land-use and land-cover changes (LULCC). However, the extent to which LULCC is concurrently considered in climate change vulnerability assessments (CCVAs) is unclear. Objectives We identify trends in inclusion of LULCC and CC in vulnerability assessments of species and the direction and magnitude of their combined effect on biodiversity. Further, we examine

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A. B. Smith Center for Conservation and Sustainable Development, Missouri Botanical Garden, Saint Louis, Missouri, USA the effect size of LULCC and CC in driving changes in "currencies" of response to CC, such as distribution, abundance and survival.

*Methods* We conducted a systematic literature review of articles published in the last 30 years that focused on CCVA and accounted for impacts of both CC and LULCC.

Results Across 116 studies, 34% assumed CC and LULCC would act additively, while 66% allowed for interactive effects. The majority of CCVAs reported similar effect sizes for CC and LULCC, although they affected different CCVA currencies. Only 14% of the studies showed larger effects of CC than of LULCC. Another 14% showed larger effects of LULCC than CC, specifically for dispersal, population viability, and reproduction, which tend to be strongly affected by fragmentation and disturbance. Although most studies

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found that LULCC and CC had negative effects on species currencies, in some cases effects were neutral or even positive.

Conclusions CCVAs that incorporate LULCC provided a better account of drivers of vulnerability, and highlight aspects of drivers that are generally more amenable to on-the-ground management intervention than CCVAs that focus on CC alone.

**Keywords** Species · Climate change vulnerability assessment · Currencies · Methodologies · Impact and effect

## Introduction

Climate change (CC) is a major driver of biodiversity change, alongside concurrent impacts of land-use and land-cover change (LULCC), invasive species, pollution and overexploitation (IPBES 2019). CC and LULCC shape niches and geographical distributions of species, their persistence and extinction probability, and the processes through which species interact with their environment and with each other (Pacifici et al. 2017). Climate change vulnerability assessments (CCVAs) typically define vulnerability as a function of exposure, sensitivity, and adaptive capacity (Williams et al. 2008; Foden and Young 2016). CCVAs in general have been applied to many different areas (mountain ranges, biomes, countries, states, conservation areas, etc.), sectors (agriculture, water, energy, etc.), while varying in the level of biological and ecological detail considered (ecosystems,

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communities, species). For CCVAs focused on aspects of biodiversity, exposure is defined as the amount of environmental change the species could experience; sensitivity as the species' response when exposed to such change; and adaptive capacity as the ability of the species to adjust or cope with the impacts, for example through adaptive evolution, migration, or behavioral change (Watson et al. 2013).

Although CC is expected to become a major driver of species' endangerment, currently the most threat to species arises from LULCC (IPBES 2019). LULCC will likely continue to be a dominant driver of vulnerability into the future (Marques et al. 2019). LULCC can affect vulnerability independently of CC, but it can also interact with CC to exacerbate or ameliorate endangerment (Mantyka-Pringle et al. 2015). Indeed, a recent global analysis predicts that LULCC alone by 2070 could result in a loss of 8% of terrestrial vertebrates (Powers and Jetz 2019), and together with CC could lead to a cumulative loss of about 38% of terrestrial vertebrates (Newbold 2018). As a result, CCVAs that ignore current and anticipated LULCC risk mischaracterizing the vulnerability of species (Foden et al. 2013; Pacifici et al. 2015). LULCC can be incorporated into CCVAs under the assumption that it interacts with CC additively (CC + LULCC) or interactively (CC \* LULCC). For example, CC and LULCC each directly shape species' physiological tolerances in terrestrial (Chuine 2010) and aquatic environments (Thackerey et al. 2016), phenology (Blois et al. 2013), interspecific interactions, movement patterns (Tucker et al. 2018), resource availability (Walther et al. 2002), and energy requirements (Gallagher et al. 2017). Climate change and LULCC also interact to affect vulnerability. LULCC determines the incidence, type, and effectiveness of macro- and microclimatic refugia (Morelli et al. 2012, 2020; Stralberg et al. 2018), alters landscape connectivity important for climate-driven range shifts (Meier et al. 2012), and facilitates spread of invasive species that benefit from climate change.

Several factors may hinder the ease of inclusion of LULCC in CCVA: lack of data, difficulty in quantifying the manner in which CC and LULCC interact, and uncertainty (Sirami et al. 2017). Incorporating CC and LULCC requires data on both current and anticipated future states of both drivers, which are not often available (especially for LULCC). While the climate modeling community has self-organized to

produce widely-agreed upon sets of scenarios (e.g., the Intergovernmental Program on Climate Change's Representative Concentration Pathways), data sources for current and projected LULCC are more fragmented and less standardized (but see Schulp et al. 2019).

Here we report on a systematic literature review to assess biodiversity-focused CCVAs for their inclusion/integration of LULCC and CC, and evaluate how these factors affect the responses of biodiversity. CCVAs use many types of "responses" to characterize vulnerability (geographical distributions, survival rates, and other species traits), which, following a previous global review (Pacifici et al. 2015), we call "currencies." First, we assess trends in the use of various currencies in CCVAs that include both CC and LULCC. Second, we evaluate the frequency and manner in which LULCC is incorporated into historical and future (predictive) CCVAs. Then, we assess representation of taxonomic groups and type of impact of LULCC on currencies (positive/negative/neutral). Finally, we use this information to propose ways forward for enhanced integration of CC and LULCC in CCVA.

#### Methods

# Trends in CCVA currencies

CCVAs measure or estimate responses to a variety of currencies, including: 1) absolute changes in distribution or population size, 2) probability of extinction, or 3) indices or relative measurements of changes in distribution, population, or extinction risk (Pacifici et al. 2015). These currencies can be assessed by CCVA frameworks that rely on different methodological approaches (Pacifici et al. 2015; Wheatley et al. 2017). Many assessments (especially of large groups of species for which data availability is low) utilize a scoring-system based on species' auto-ecological and life-history traits expected to mediate climate impacts (Foden et al. 2013). Other assessments use statistical or mechanistic models to project future geographical distributions of species or population dynamics. Both approaches can be combined in "hybrid" assessments that score traits and use model projections for multidimensional assessment of the different currencies (Pacifici et al. 2015; Smith et al. 2016).

We performed a literature search to determine how are currencies utilized in CCVA assessments. Our systematic review examined whether or not 1) LULCC was assumed to act independently or interact with CC to determine vulnerability; 2) LULCC was assumed to be static or dynamic through time; 3) LULCC and CC affected the same or different currencies; and 4) LULCC and CC had the same or opposing effects on overall vulnerability, and their relative magnitude (positive or negative). We conducted the search on 27.03.2018 following recommendations for conducting systematic reviews (Gurevitch et al. 2018). Journal articles were located using Web of Science (WoS) and PubMed. In this initial step, no time restrictions were implemented for the search. For WoS, terms were searched under "Topic" (title, abstract, key terms, key terms plus). For PubMed terms were searched under "title." abstract, key terms". To define search terms that could correspond to currencies in CCVA, we did a screening of relevant texts in ecology, conservation biology, animal behavior, etc. (See Appendix I for a brief search on the importance of CCVA and the details on the search method). Acknowledging that some search terms or concepts do not necessarily correspond to a single currency (e.g., "species distribution" and "dispersal"), a quick scoping search using WoS and PubMed only for those concepts showed how often these cited are in the same papers or used interchangeably. We retrieved 86 search terms, which are found in Appendix I (Table I.2.). To simplify the search, we defined three search strings, i.e., sets of key terms (Table I.3), and the resulting records are displayed in Table I.4 in Appendix I (note that the search described in Sect. 2.1. is not included). We opted not to review the references within the papers that we retrieved from the search engines.

Papers were then filtered to retain studies directly related to CCVA. First, we excluded studies that (i) focused on vulnerability of human populations or human infrastructure and activities, (ii) examined climate impacts occurring outside the period 1900–2100, (iii) were reviews or meta-analyses, (iv) examined only effects of LULCC or of CC, or how CC affects LULCC but not biodiversity, (v) were context-specific or at fine spatial scales (i.e., very local studies or in very small study areas likely not representative of species' entire distributions), (vi) or did not clearly identify the studied types of impacts in the title or



abstract. A total of 131 papers were retained (Appendix I, Table I.3). A coding procedure was then implemented to extract relevant information from these papers. With this step, we systematically retrieved information on (i) taxonomic group, (ii) currency(ies) (distribution, abundance, survival, dispersal, composition, interactions, diversity, and reproduction; Pacifici et al. 2015), (iii) whether the impact was observed (historical) or projected (future), (iv) the aspect(s) of LULCC studied, (v) the aspect(s) of CC studied, (vi) the manner in which LULCC and CC are assumed to affect vulnerability (additively/independently: CC + LULCC, versus interactively: CC\*LULCC), (vii) methods for including LULCC and CC in CCVA, (viii) direction of the impact by CC and LULCC (negative when the combined drivers result in a decrease in the currency connoting increased vulnerability, positive when the combined drivers result in an increase in the currency connoting less vulnerability, mixed when the drivers have positive and negative effects together, or neutralizing when the positive or negative effects of the drivers counteract each other), and (ix) effect sizes and main findings.

#### Results

## Trends in CCVA currencies

Our systematic review identified 116 studies that formally included both LULCC and CC into assessments of climate change vulnerability (Fig. 1). Of these, 66% allowed for interactions between LULCC and CC (CC \* LULCC: n = 77), with the remainder (n = 39) assuming they acted independently of one another to affect vulnerability (CC + LULCC). Throughout the timeframe of the studies we analyzed, we found that potential interactions between LULCC and CC (CC \* LULCC) were considered more after ~ 2009 than before (33% before and 67% thereafter 2009). Sirami et al. (2017) also found a similar increase around 2007. LULCC was assumed to be static (i.e., unchanging with time) in 82% of the studies (n = 95) and dynamic in the rest. Most studies were attempting to predict future vulnerability, except for studies examining abundance, which tended to focus on historical trends. Plants were the most commonly studied taxonomic group, followed by

birds then mammals. The majority of studies reported negative impacts on currencies (increased vulnerability; 67%, n = 78), but for some currencies, such as survival and community composition, mixed impacts were frequently observed. CCVAs that incorporated LULCC used a diversity of inferential methods (e.g., traits, correlative and process-based modeling), but interpreting differences among the prevalence of methods was not straightforward because some of the currencies could only be estimated using specific inferential methodology (e.g., through correlative or mechanistic and process-based modeling).

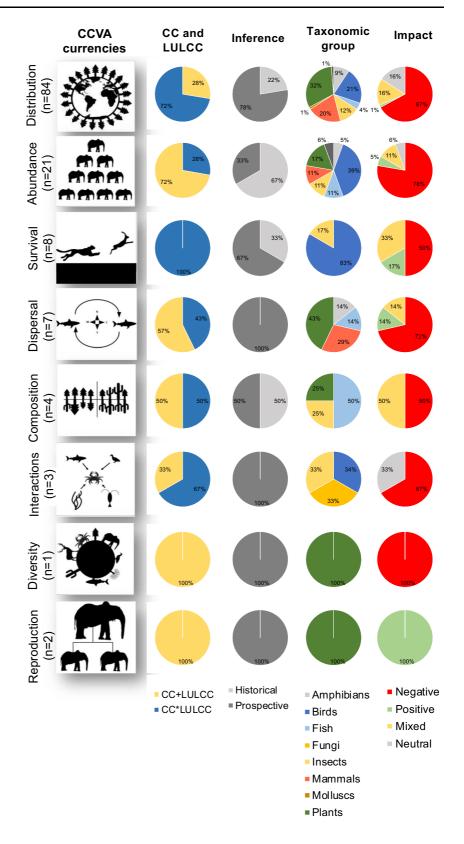
Distribution: Distributional changes were reported for all taxonomic groups, with a slightly higher number of studies focusing on plants, followed by birds and mammals. The reported distributional changes were mostly predictive; only 15% were historical (n = 17). The majority of the studies that reported distributional changes allowed for interactions between CC and LULCC (CC \* LULCC; n = 55). A few studies reported negative effects of either CC or LULCC on dispersal (n = 7), mostly assessed using distribution models of terrestrial plants and mammals. An almost even number of studies that reported on dispersal ability used CC + LULCC or CC \* LULCC (Fig. 1). The most frequently described distributional changes were range contractions and range shifts.

Population parameters: Most studies using abundance (including population growth rates) as a currency reported negative effects of exposure of CC and LULCC. These studies covered a wide range of taxonomic groups (Fig. 1). Contrary to studies focusing on distributional changes, population changes were more commonly the focus of historical CCVAs rather than predictive CCVAs. An even larger proportion of the studies using abundance currencies included CC \* LULCC. We find that 15% (n = 17) of the studies reported shifts in abundance. A few studies reported decreases in survival rates (n = 3), most of which were on birds and ascertained using either observations or models that assumed CC + LULCC.

Extinction probability: Surprisingly, none of the studies reported changes in extinction probability, likely because of the short time span of historical studies and the uncertainty with which future extinctions can be predicted. Nonetheless, some studies mentioned that range contractions coupled with



Fig. 1 Frequency of studies on CCVA currencies that included CC and LULCC additively or interactively (CC + LULCC), historical (empirical observations and modeled trends) and prospective analyses (model projections), per taxonomic group and with reported positive, negative, mixed and neutral impacts. (Graphic symbols designed by Dr. Dovi Kacev)





distribution shifts towards higher latitudes and elevations tend to result in high local extinctions.

Other ecological currencies: Eight percent (n = 9) of the papers considered the impact of CC and LULCC on other ecological processes, such as species interactions, community composition, and diversity. These studies focused on plants, fungi, insects, and fish, and included LULCC \* CC.

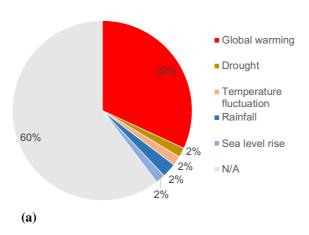
## CC and LULCC in CCVA

Most studies did not explicitly report the aspect of climate which was assumed to most affect vulnerability (e.g., drought, extreme storms, heat waves, rising temperatures, etc.), although studies included a range of variables that could reflect or could be correlated with specific climatic stressors (Fig. 2a). Similarly, several aspects of LULCC were utilized as "drivers" of potential change (Fig. 2b). Many proxies were used to describe land use, the most common one being a metric of land use change, followed by static descriptors of land cover type or of land use type or habitat quality. More infrequent proxies of LULCC were descriptors of fragmentation, connectivity and deforestation, or of human disturbance and population density.

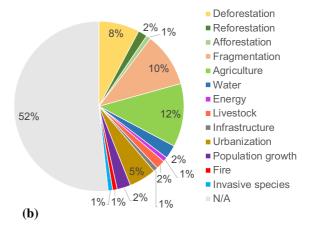
Inferential methodologies were varied (Fig. 3), with a greater variety of methods used to assess distribution and abundance as compared to other currencies. Species distribution modeling (SDM) was the most common method used, as geographic distribution changes were the most common types of studies, but also regression analyses were also common. Some studies proposed novel integration of methodologies, such as for example SDM and population viability analysis (Tian et al. 2014), metapopulation evaluation (García-Valdés et al. 2015) or demographic analysis (Hunt et al. 2017), SDM and graph theory (Giannini et al. 2015), environmental niche factor analysis and stochastic demographic models (Fordham et al. 2012), and even machine learning methods for assessing vulnerability (Heubes et al. 2013).

# Direction of impact and effect size

Most studies reported negative impacts (enhanced vulnerability; Fig. 4); it was not possible to determine whether they only assessed negative impacts or whether they contained a reporting bias against positive impacts. Negative impacts occurred irrespective of the taxonomic group. Several studies (19%)



**Fig. 2** CC and LULCC and CC phenomena addressed by the selected studies: **a** CC and **b** LULCC (SLR—sea level rise; N/A—not applicable i.e. when the study did not attribute the vulnerability to a specific phenomenon). Most studies do not make an attribution of changes in CCVA currencies with one or



more dimensions of LULCC or CC. For LULCC, deforestation, agriculture and fragmentation were the most common topics, with reforestation being only mentioned in the recent publications. For CC, the dominant dimension was global warming, and only very few recent studies addressed other dimensions



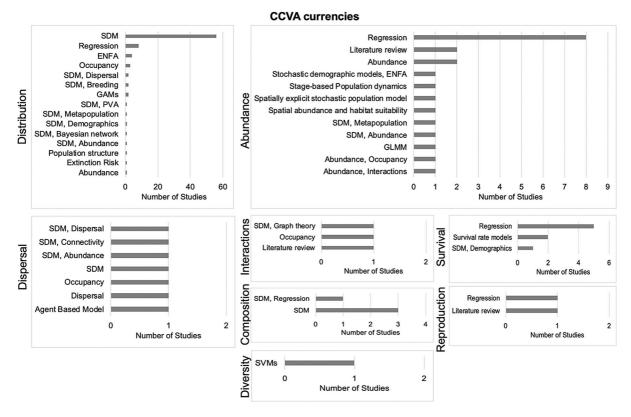


Fig. 3 Methodologies used to integrate LULCC into CCVA for each of the currencies. SDM—Species distribution models (includes Maxent, logistic regression, etc.), ENFA—Environmental Niche Factor Analysis, GAMs—Generalized Additive

Models, PVA—Population Viability Analysis, GLMM—Generlized Linear Mixed Models, SVMs—Support Vector Machines. When two methods are reported, the study integrated them

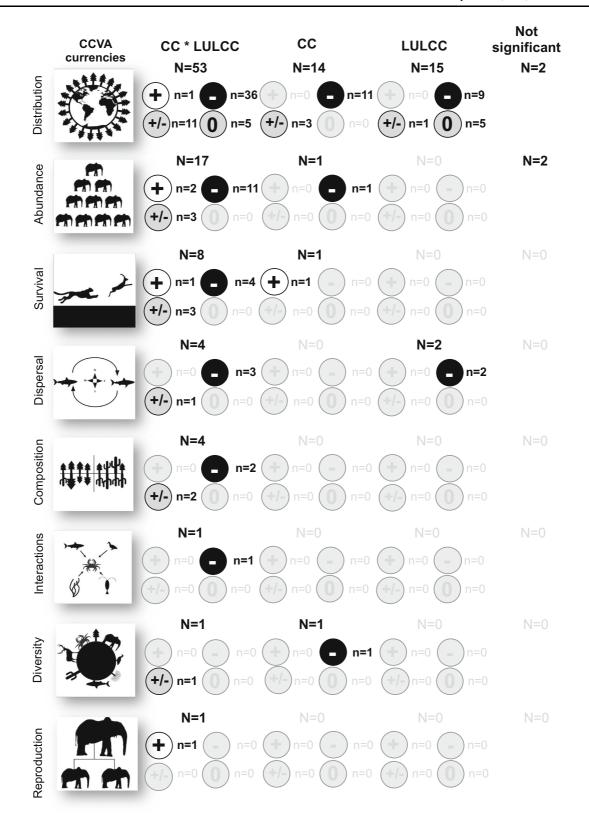
modeled or conceptualized a hierarchical interaction between LULCC and CC to assess whether LULCC had an effect on the ability of species to occupy potential ranges predicted on the basis of climate. The majority of studies (66%; 77 out of 116) reported negative effects of LULCC, which frequently exacerbated the negative effects of CC (n = 43, CC\* LULCC). LULCC and CC tended to either affect different currencies or operated at different spatial and temporal scales, with CC being longer-term and broader-scale than LULCC. In 34% of cases LULCC and CC affected currencies in opposing directions, which led to a zero-sum net effect of LULCC and CC for 12% of studies. Finally, we found that a small fraction of studies (14%; 16 out of 116 studies) reported that CC had a markedly greater effect than LULCC when examining distribution or abundance, while a similar fraction of studies reported the opposite with a greater effect from LULCC than CC for both distribution and dispersal. Inclusion of

LULCC became unimportant in two particular cases: at high latitudes where much LULCC has yet to occur (Kéry et al. 2006) and in extremely built-up places where additional LULCC was predicted to be restricted (Bombin and Reed 2016) or where most of it had already occurred in the past (Argent et al. 2018).

# Discussion

We set out to find the degree to which LULCC acted independently or interactively with CC in climate change vulnerability assessments, how each affects different currencies, and whether or not the inclusion of LULCC exacerbates or opposes effects of CC. Two-thirds of the studies allowed for interactive effects (CC\*LULCC), with proportionately more studies doing so since 2009 that before (Oliver and Morecroft 2014; Sirami et al. 2017), perhaps because of the growing awareness of LULCC as the strongest







▼Fig. 4 CC and LULCC impacts and effect sizes on the different currencies. Effect sizes for studies by currency (N at the top for each currency), Plus sign indicates a positive effect, negative sign indicates a negative effect, plus/minus indicate drivers in different directions and 0 indicates no net effect. Greyed out symbols indicate no studies. (Graphic symbols designed by Dr. Dovi Kacev)

driver of current biodiversity loss (IPBES 2019). Most studies (66%) found (or assumed) only negative effects of LULCC on vulnerability, although in 12% of studies their opposing impacts effectively neutralized one another. The number of studies in which the effects of CC overshadowed the effects of LULCC or vice versa was the same (14% in both cases). LULCC and CC were generally assumed to affect different currencies, and the diversity of currencies considered broadened through time. All together, we see these trends as promising signs because they likely reflect the real manner in which CC and LULCC affect biodiversity (i.e., interactively and in a multi-faceted manner). Nonetheless, our results highlight areas of potential improvement; the diversity of currencies used and the various ways in which LULCC was assumed to interact (or not) with CC suggests, that we have yet to develop a comprehensive understanding of how LULCC and CC act together to affect facets of vulnerability.

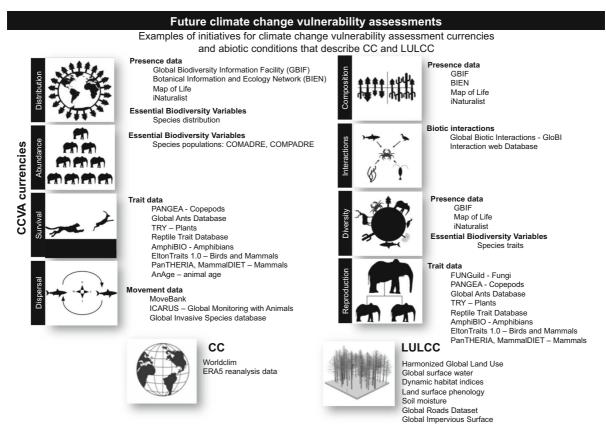
# LULCC and CC effects on vulnerability

CC and LULCC are widely acknowledged to influence vulnerability, so accounting for both in the same assessment will likely lead to a higher estimated vulnerability. We found this indeed to be the case for most studies. We also found that most studies showed notable effects of both drivers, with no systematic differences in the magnitude or sign of effect. However, despite the fact that including LULCC enhanced estimated vulnerability, we did find that including LULCC could have mixed effects on CCVA currencies, i.e., positive, negative, or neutralizing effects, irrespective of taxonomic group. For example, one of the most commonly reported positive synergies was an increase in range size due to expansion of suitable habitat conditions arising from both CC and LULCC (we note that a "positive" impact at the species level is not necessarily a positive effect at other levels, if range shifts cause community reorganization or enhance invasiveness).

Despite the general consensus that CC and LULCC make species more vulnerable, a few CCVAs did not find any clear negative or positive effects. Similarly, negative effects on one currency could diminish positive effects in another. For example, for population parameter currencies, one of the studies we reviewed showed that due to rising temperatures, the mosquito Aedes notoscriptus may experience increased predation but, concurrently, shorter life cycles, which could therefore buffer higher mortality rates (Hunt et al. 2017). Surprisingly, only a small fraction (14%) of the studies reported a much stronger effect of CC, and an equivalent fraction (14%) reported a stronger effect of LULCC. Across studies, LULCC tended to be relatively unimportant in two cases: in landscapes where anthropogenic LULCC has yet to occur (Kéry et al. 2006) and in extremely builtup places where future LULCC is predicted to be restricted or have little additional impact (Argent et al. 2018).

We also found that CCVAs tend to incorporate LULCC such that it operates at different spatial and temporal scales than CC. This likely follows from the theoretical understanding that, in general, LULCC operates at local, shorter time scales and CC on broader and longer scales (Soberón 2007). In some cases, these differences in scale are reflected in the hierarchical nature of the framework used to assess impacts in which LULCC is used as a "filter" to assess whether species can, for instance, colonize newly climatically suitable habitat. Despite a general consensus that effects of CC operate at broader scales (Soberón 2007), comparisons are somewhat compromised when the spatial and temporal resolutions of land use and climate data are mismatched, which we found to be common in the studies we reviewed. Similarly, LULCC datasets with high thematic resolution (e.g., number of land cover classes) and broad temporal coverage are rare, making it more difficult to include LULCC in CCVAs. Relatedly, many potentially important aspects of LULCC are not reflected in available data sets, including habitat-relevant land cover classes, land use (versus simply cover), density of roads, power lines, etc.





**Fig. 5** Example of currently available initiatives that could be used in or improved by CCVA (see appendix II for a list of the references included in this figure, hyperlinks to data, extent, resolution and data type). This process is not without challenges

relating to data collection and scenarios to be modelled in CCVA for the different currencies. (Graphic symbols designed by Dr. Dovi Kacev)

## LULCC and CC effects on currencies

The compounding effect of LULCC on impacts predicted from CC alone arises because LULCC and CC tend to affect different currencies (Thuiller et al. 2004), which occurs because they operate at different spatial and temporal scales. Most studies we reviewed report CC's influence on distribution while LULCC tended to be assumed to affect dispersal, reproductive output, and population viability. If true, these differences could arise because changes in geographical distribution usually require longer time periods to respond to external drivers, making CC more suitable "predictor" of distributional shifts and thus more informative (Taheri et al. 2021). On the other hand, LULCC tends to have more immediate effects on survival—species loss with deforestation for instance, and dispersal-effects of barriers like roads, and thus LULCC affects aspects usually considered when assessing extinction probability. It is also possible that the immediate effects of CC are less straightforward to observe (but see Blois et al. 2013, and the emerging field of conservation physiology e.g., Thackerey et al. 2016). While some CCVA currencies may be more informative than others, our results echo conclusions by Pacifici et al. (2015), who also found that the use of more informative currencies is still relatively rare among CCVAs. For example, the focus on geographic distribution is warranted for understanding the potential future impacts of climate change on species' ranges (Taheri et al. 2021). However, realization of projected changes in geographical distribution is dependent on assumptions about dispersal, establishment, successful reproduction, and biotic interactions, which are less commonly assessed in CCVAs – but those that do indeed tend to frame



LULCC and CC in a multi-tiered approach. We found studies that incorporated LULCC were more likely use the latter set of currencies. However, these currencies are difficult to assess because data on demographic parameters are less available than on broad-scale distribution.

We found that there is not only a diversity of methods used to include both LULCC and CC on the studies of the impacts of these global change drivers on CCVA currencies, but also that the type of proxy for LULCC (i.e., the "agent" of LULCC that was expected to affect vulnerability) was extremely diverse. This may be a strength—LULCC can manifest itself in multiple dimensions and is expected to affect many different aspects of ecological systems. However, this diversity of formulations of LULCC proxies can also be a weakness as it makes comparison between studies difficult and may reflect lack of knowledge about the most important drivers of changes induced by LULCC.

# Moving forward on CCVAs

We believe that the first step necessary to improve the implementation CCVA is to better understand how currencies relate to each aspect of CC and LULCC. There are several initiatives for collecting data that could support better assessments of CCVA currencies and improve our understanding of the interacting effects of LULCC and CC (Fig. 5; Hudson et al. 2014). For reliable CCVAs we need long-term, largearea studies, but we generally have short-term, smallarea data. For example, data relevant to biotic interactions (i.e., prey resources, competitive regimes, phenological timing, refugia, etc.) require detailed studies, often at local scales, focusing on a few selected target species, typically require a long timeframe and large teams to collect data. Movement data (i.e., activity time, movement patterns, phenology, prevailing winds, connectivity, introductions) also require detailed studies, which are costly, time consuming and logistically demanding, and therefore usually limited to a single species in a single region at a time. While tracking studies have a long tradition in ecology, systematic collection of such data is only now taking place, and will allow determining general patterns about activity times (Gaynor et al. 2018) and movement patterns (Tucker et al. 2018). Likewise, initiatives like the IUCN's Global Invasive Species database (http://www.iucngisd.org/gisd), movement by certain classes of organisms. Alternatively, coupled model/empirical efforts may help bridge this gap. For example, Gallagher et al. (2017) illustrate how to derive an "energy landscape" that serves as a proxy for prey resources which could in turn be modeled as a function of land cover and climate. Similarly, advances in understanding and measuring landscape thermal signatures may provide future data on landscape characteristics as a proxy for refugia (Meerdink et al. 2019). Other efforts such as GEOBON Essential Biodiversity Variables (https:// geobon.org/ebvs/what-are-ebvs/) can serve to monitor many of the currencies over larger areas, in a systematic and consistent way. Finally, initiatives like NEON (https://www.neonscience.org/) or LTER (https://lternet.edu/) in the US are now working on operationalizing a workflow to link repeat satellite or airborne imagery with time-series plot data to track biodiversity and habitat conditions. Thus, there are many efforts underway that will allow for improved CCVAs relatively soon. Within the plethora of data sources and types that are available or soon will be available, we foresee two challenges. First, not all data are collected or available at the spatial or temporal scales most relevant to CCVAs or at which management action occurs. Second, data often reflect land cover, but not land use. A step forward could be to develop a common platform to address issues related to data availability; define a common set of modeling conventions for predicting future LULCC; document and database responses of species to CC (like the PREDICTS database for LULCC; Hudson et al. 2014); and share knowledge to increase efficiency and effectiveness.

For inferring the effects of CC and LULCC on biodiversity it is necessary to rely on models that relate individual species or community characteristics (e.g., species richness or turnover) to particular environmental factors, which can be projected into future scenarios of LULCC and CC. These models, however, face many challenges, which relate to the quality and availability of (species and environmental) data and to the modelling approach used (Faurby and Araújo, 2018). Modelling changes in distributions due to climate change is founded on the assumption that species occupy a specific niche, which for many species, include land cover characteristics (e.g., Hunt et al. 2017; Santos et al. 2017). Hence, appropriate



assessment of changes in the amount of area where niche requirements are met needs to include both CC and LULCC. However, the predictors used in species distribution modelling are often represented by simplified data that lack ecological realism (Leitão and Santos, 2019). For example, many LULCC products are categorical in nature (e.g., agriculture/forest) so do not differentiate within categories (e.g., kind of crop, primary vs. secondary forest, type or intensity of use, etc.). Nevertheless, animals and plants respond to differences in the same general type of habitat, and we lack information on LULCC that can be linked to the relevant biological processes rather than anthropocentric perspectives of land cover classes (but see Moeslund et al. 2019). We also lack longitudinal data going back in time to reconstruct LULCC over more than a couple of decades. Projects like HYDE (Goldewijk et al. 2017) aim at reconstructing past LULCC with historical and anthropological accounts and can serve as data sources that span longer time periods, albeit at coarse resolution.

Our second suggestion for advancing the implementation of CCVAs is to further include interactions, especially dynamic interactions, between LULCC and CC. Many CCVA assume a static environmental context where vulnerability is assessed at a single point in time with data or model projections from one or more periods, within which no change is assumed (or mean values are used-effectively assuming no change). In reality, the environment is constantly changing and so vulnerability estimates should, as well. However, so far, process-based biodiversity models are mostly only possible for functional types (Hickler et al. 2012). Likewise, the integration of process-based modeling related to dispersal, ecophysiology (Thackerey et al. 2016), population dynamics (Zurell et al. 2016), biotic interactions (van der Putten et al. 2010) and ecological traits (Brown et al. 2014), although still uncommon approaches, constitute promising avenues for the improvement of predictions on the effects of LULCC and CC on biodiversity. Some of the studies we reviewed reported or accounted for interactions between LULCC and CC effects. Increasingly, regional and global circulation models incorporate feedbacks between LULCC and climate (e.g., the Advanced Canopy-Atmosphere-Soil Algorithm ACASA; Marras et al. 2008). Land use type affects albedo and sensible and latent heat fluxes, which in turn could alter land cover or use. Despite advances, not all relevant feedbacks between LULCC and CC have been incorporated into regional and global circulation models, as for example effects of deforestation and fire on water cycling and changes in temperature and albedo, effects of wetland removal on evapotranspiration and cooling, or effects of agricultural irrigation or urbanization on changes in albedo and cooling (Massad et al. 2018). At the global scale, integrated assessment models have been used to model development scenarios and simulate future LULCC (Doelman et al. 2018). In such models, the main drivers of LULCC are land use for agriculture, bioenergy, and carbon storage (Leclère et al. 2020). At the regional level several general LULCC models also allow for dynamic land cover types. Regional models include a set of rules to attribute which land use type will more likely be found in a grid cell at a given point in time. Many of these models have been used to assess future scenarios for energy and commodity development, as well as encroachment on ecologically valuable land (e.g., Verstegen et al. 2019). We do note opportunities for incorporating thematically-focused LULCC models into regional and global circulation models (e.g., Sleeter et al. 2019). For example, urban growth models could be better integrated into regional climate models to account for urban heat island effects and related effects of development on albedo and latent heat flux.

Third, we suggest we need to better include aspects of LULCC that are currently missing from CCVAs, such as land use intensity and ecological restoration. LULCC models need to better reflect disturbance (natural or anthropogenic), land use intensity, abandonment, and rejuvenation or restoration. Although most LULCC models do not explicitly account for abandonment or land use intensity, or for encroachment (legal or illegal) on natural ecosystems, some models do allow reversion to earlier states (e.g., forest becomes cropland which then later becomes forest again). However, intentional restoration is also typically ignored, likely because it would fit into the



sensitivity and adaptive capacity component of a CCVA or be recommended in response to the outcome of a CCVA. Restoration should always be carefully considered to mediate or reduce LULCC and CC effects in CCVA studies (Strassburg et al. 2019). However, given the structural and functional losses found in restored ecosystems compared to undisturbed ecosystems (Moreno-Mateos et al. 2017), restoration should be incorporated into CCVAs since restored ecosystems may translate to reduced exposure and enhance adaptive capacity.

Finally, there is also a need to better assess all components of vulnerability, i.e., exposure, sensitivity and adaptive capacity. We find that the direct inclusion of LULCC on CCVA provides a more comprehensive picture of threats to species (as suggested by the wider diversity of currencies used by studies incorporating LULCC; Fig. 4). CC is typically assumed to affect exposure, whereas sensitivity and adaptive capacity to CC are presumed to be "inherent" to the species. In contrast, LULCC can interact with sensitivity and adaptive capacity (as well as affect exposure). Studies that use CC and LULCC in combination bring a broader understanding of the factors making species vulnerable. Surprisingly, only a small fraction of studies (12%) reported that CC is a stronger driver of change than LULCC. Incorporating LULCC in CCVA brings additional understanding as CC and LULCC mostly have compound effects, as different CCVA currencies are impacted by CC and LULCC. Although joint effects of LULCC and CC can be additive, multiplicative, or ameliorative, we found that most CCVAs concluded greater negative effects on biodiversity when LULCC was included. This is particularly important as it suggests that there will be a systematic bias towards underestimating these effects when LULCC is excluded. Additionally, LULCC and CC operate at different scales in space and time, which can help defining better conservation actions and management plans alongside with rethinking or optimizing the way CCVAs are currently implemented (Fig. 5).

Many CCVAs to date result from government-led initiatives and some of the academic literature has no explicit link to ongoing government programs or even to NGO lead initiatives (for example the IUCN; Foden and Young 2016). A better integration of these three types of institutional ways of addressing CCVAs may help streamline their content, comparability and the

synthesis we aim to achieve about how species respond to and are impacted by global change drivers. For example, some locations are better at implementing CCVAs than others, e.g. California has just finished its fourth CCVA and in many European countries similar initiatives are ongoing at different paces. LULCC and CC are also hard to measure and model together, thus more and better data and methodological advances are necessary which can again benefit from a better integration across agencies that implement or study biological vulnerability. Further, part of this work will necessitate better understanding of biophysical feedbacks between CC and LULCC, and how these feedbacks affect biodiversity and responses of species to LULCC and CC (Williams and Newbold 2019), and herein we outline ongoing efforts and provide a roadmap and recommendations for improvement of CCVAs in the future.

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