Biodiversity responses to climate and land-use change: A historical perspective
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Species distributions, ecological niches and the impacts of climate and land-use changes on species range limits

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Where and how biodiversity is distributed around the globe has been investigated for centuries (Darwin, 1859; Patterson, 1994; Shaffer et al., 1998; Wallace, 1869). This research field has produced a wealth of information and insight on the factors determining species distributions and the functions species carry out in ecosystems (e.g. Gamfeldt et al., 2013; Nelson et al., 2009). Moreover, research on the distribution of biodiversity locally and globally has proven directly applicable for nature conservation actions (e.g. Rodrigues et al., 2004).

One of the main problems in studying species distributions is the lack of detailed distribution data and even more from old time periods (e.g. before 1950). Collecting such data requires enormous effort and has only been done for some iconic or local species, often only in part of their full distribution. Novel techniques have been applied to these historical species distribution data for investigating changes in biodiversity across time, as for instance in the work of Carvalheiro et al. (2013), however, this only renders a partial picture of these biodiversity changes. Consequently, methods that can robustly predict (global) species distributions based on a limited amount of species locations data as input are very important in this field. These methods should be able to capture, in an accurate manner, the environmental characteristics that limit species distributions (Chapter 2). These methods can then be used for a variety of applications including detection of current species distributions within protected areas (Bagchi et al., 2013; Hannah, 2008), analysis of the pathways and impact of alien species invasions (Buckland et al., 2014; Giovanelli et al., 2008), investigating ecosystem services delivery under climate change scenarios (Polce et al. 2013; polce et al. 2014) or the investigation of differences in the ecological niches of closely-related taxa (e.g. Chapter 3).

In the following sections, I will summarize how the biodiversity responses to environmental change from past to present presented in this thesis contribute to the field of biodiversity conservation, and how this can help predict future biodiversity distributions in a context of global environmental change. Lastly I will present the implications of my results in the context of biodiversity conservation and discuss some of the future research prospects within the field.
Predicting species distributions across time

Since the beginning of the decade there has been a great investment in the development of approaches that can estimate where species are distributed and how their ranges are delimited by biotic and abiotic conditions. This has led to a boom in novel methods and frameworks to which we refer to as “Species distribution models”, "Ecological Niche models" or “Habitat suitability models” (Franklin et al., 2009; Peterson et al., 2011). From these methods we have to decide on the modelling algorithm and framework. How or on what should we, as conservation biologists and ecologists, base our selection? Are all algorithms rendering the same answers? The decisions taken at this stage determine the results we get and thus the conclusions we draw.

In this thesis, I show that the performance of different modelling algorithms for predicting the distribution of a set of systematically selected data of species occurrences (rare to common and narrow to widespread species) varies significantly (Chapter 2). Some of these algorithms present significantly more accurate results than others, particularly MaxEnt or an ensemble of model predictions (Chapter 2). I show that these differences in outputs are maintained even when analysing landscapes across different spatial scales, and that algorithms also differ in how they attribute the importance of environmental drivers when delimiting the species distributions (Chapter 2). The differences in attribution of the drivers’ importance is of main concern as it can lead to different conclusions on how drivers of change define the distribution of each species and thus on how different species (groups) can be protected. We should ideally opt for algorithms that are consistent in their predictions across modelling repetitions (low within algorithm variability) and spatial scales, and that have high accuracy in their predictions without being constrained by the species data characteristics (number of records and their spatial distribution).

Furthermore, I show that algorithms such as MaxEnt and an ensemble of model predictions are among the best options for modelling species distributions as they render high model fit and are consistent in their outputs (Chapter 2). However, although the ensemble of models often renders projections with high accuracy, these are also often difficult to interpret in
regard to the assessment of how important are the environmental variables for delimiting species range limits given that they are an ensemble of predictions from different algorithm. Although the study presented in Chapter 2 focuses on the Netherlands, which has a relatively small area and homogeneous landscape characteristics, the results obtained are in line with others carried out in different locations and with different environmental conditions (e.g. Elith et al., 2006). The high performance of species distribution models constructed with the MaxEnt algorithm for the Mexican white pines in the American continent (Chapter 3) also confirms our findings. Besides MaxEnt, an ensemble of model predictions has become appealing in recent years as it can capture the variability presented by the different algorithms into a more robust prediction (Thuiller, 2014). However, the construction of model ensemble also implies the selection of the method to obtain the final projection, e.g. average of predictions across modelling algorithms, median of predictions, consensus approach, mean of predictions weighted by the model accuracy, among others, which also needs an in-depth evaluation as different model ensemble methods may vary in their final output.

Although much research has been carried out in the field of species distribution modelling, more is needed to better understand how factors such as biotic interactions (Giannini et al., 2013), species dispersal capacity (Boulangeat et al., 2012), and their plasticity for adapting to changing environments (instead of modifying their distributions) (Eckhart et al., 2011) may impact the model predictions. Incorporating this information in a satisfactory manner into the species distribution modelling protocol would enhance our knowledge of how biodiversity may respond to future environmental changes.

**Climate and land use change set the limits of species distributions across time**

Climatic and land-use changes are two of the main drivers of species distribution changes globally (Newbold et al., 2015; Wu et al., 2011). Modifications in each of these drivers can cause the extinction of species at local and global scales (Jetz et al., 2007; Sala et al., 2000; Thomas et al., 2004;
Thuiller et al., 2005). These drivers rarely change independently as the modification of one tends to impact the other, which may create a cascade effect that will ultimately effect the species distributions. The results of Chapter 5 show that in face of these environmental changes, species can adapt to the new conditions or, depending on their trait characteristics (e.g. pollinator wing size which is linked to dispersal ability), shift their ranges towards more suitable areas. Given the observed species geographic shifts, and their areal range changes within the study area, it is imperative to investigate how this may impact the protection status of these species as well as if, how and to what extent the ecosystem functions (i.e. pollination of wild plants) and services (i.e. pollination of crops) they provide may have been disrupted in the past or are likely to be disrupted in the future.

Studies on the effects that climate change can have on biodiversity are highly relevant given the predictions of changing temperature and precipitation patterns, as well as increases in extreme weather events, that are occurring around the world (Kirtman et al., 2013). In this thesis I show that although land use conditions are often highlighted as some of the most important drivers of species occurrences, climatic drivers are also highly important determinants of range limits for species. In Chapter 4, in a study carried out for three pollinator groups in the Netherlands, I specifically show that the importance of climatic drivers for determining species range limits, especially those related to temperature, has significantly increased during recent decades now reaching that of land use. The results suggest that for the Netherlands the influence of these climatic drivers will continue increasing and will probably surpass the importance of land use impacts on species distribution, especially given that land use related drivers have mostly stabilized during these last decades (Bouma et al., 1998; Knol et al., 2004). These results are most likely transferable to other highly industrialized countries in temperate regions. However, a more in depth research in tropical regions, where strong land use changes are still ongoing, is still needed to investigate the applicability of our results to these regions.

One of the main challenges when investigating biodiversity responses to past climatic and land use changes is the lack of historical data on species occurrences and environmental conditions. Given this lack of data most studies apply a space-for-time substitution approach. In this set-up a series of
landscapes differing in climatic and land use conditions are analysed as representatives of the modifications that could have occurred in a single landscape across time (e.g. Brosi et al., 2008; Uehara-prado et al., 2007). This may not always be fully representative of the responses to changes, as the original state of the landscape could also be guiding the responses of the remaining biodiversity (Kuussaari et al., 2009). In Chapter 6 I ask if recent landscape modifications (partially) drive current species distributions and whether historical landscape conditions are also responsible for the distribution patterns we see at present. I show that for most of the pollinator groups I analysed, the historical landscape state (i.e. before changes occurred) significantly constrains subsequent species responses to landscape changes. This means that many of the species distribution patterns that we see at present may actually be constrained by past landscape characteristics, pointing out to a possible extinction debt (delayed loss of biodiversity after habitat loss and/or fragmentation events) (Tilman et al., 1994), but also to possible “colonization debts” (as it may take time for species to colonize newly suitable areas). While my study provides new insights into this issue, more research is needed to disentangle what the time lags are for the effects of past landscape characteristics on current species distribution patterns, and what underlying ecological/evolutionary mechanisms cause this delayed time-effect.

The finding of this thesis and other recent studies have shown that both climate and land use characteristics define biodiversity distributions locally and globally (Newbold et al., 2015; Wu et al., 2011). However, the relative importance of each of these drivers for setting species range limits may, however, not be equal and constant over time. In Chapter 4, by analysing the importance that different land use characteristics have for setting species range limits, I show that habitat composition, fragmentation and spillover potential have constantly been major drivers of pollinator species distributions over the last half century in the Netherlands. Especially habitat composition, which I analyse as the amount of each land use type in the landscape and the variety of the land use classes, has been a highly important driver over time; even more so than fragmentation and spillover potential.

I have shown that land use is a major driver of species distributions and that although both past and present landscape characteristics are
important, for the Netherlands, the historical land use characteristics have
constrained the present biodiversity of pollinators even more than the
landscape changes (Chapter 6). Still, as shown in Chapter 5, the way in which
different pollinator groups respond to these changes (also to climatic changes)
in terms of range modifications and geographical shifts greatly depend on
their functional traits and the pollinator group identity (Chapter 5).

Implications for conservation and concluding remarks

Biodiversity conservation actions are increasingly based on analysis made
with tools such as SDMs (Franklin, 2010; Guisan et al., 2013). The results of
this thesis show that the selection of the methodological details when fitting
SDMs should not be done haphazardly, as the outputs of different methods
may render diverse and sometimes even contrasting results. As shown in
Chapter 2, no single algorithm will be best under all circumstances. I therefore
suggest selecting the preferable modeling tool for the aim (e.g. determining
the range of spatially restricted species, environmental variables profiling)
and data characteristics (e.g. number and spatial distribution of species
presence records) in a given study via a calibration-evaluation procedure.
Chapter 2 provides a template for such a calibration-evaluation procedure.

Biodiversity conservation actions tend to focus on single groups that
may represent the effects that climatic and land use changes have on general
species within bigger biodiversity groups (Fleishman et al., 2000; Ozaki et al.,
2006), e.g. butterflies are often used to represent insect biodiversity. Based on
these groups, conservation actions are then proposed. This approach has been
recently challenged by studies that favour a multi-group approach for
biodiversity conservation (Gerlach et al., 2013; Maes & Dyck, 2005). The
reason is that different (pollinator) groups are often impacted by different
drivers (climate or land use) or by the same driver in a different manner or
intensity. The results obtained in this thesis show that, although the pollinator
groups present synergies in their responses to climatic and land use impacts,
their responses cannot be generalized (see for example chapters 4 to 6). Given
the diversity of responses observed between pollinator groups, I suggest that
multi-group approaches that account for the different responses of
biodiversity to these drivers of change should be considered when planning
future conservation actions. The findings of this thesis further emphasize the limited value of one-size-fits-all type of biodiversity conservation measures and suggest that including historical and present climatic and land use information when planning future biodiversity conservation programmes is of critical importance.

The findings of this thesis suggest future challenges as in the field of biodiversity conservation and applied ecology. The inclusion of multi-species responses to climatic and land use changes and of historical climatic and land use information in future conservation plans are definitely two with high importance. Moreover, including multi-species interaction information in the modelling framework is a challenge that deserves much attention given that species distributions and persistence clearly depend on them. This is of main concern as most research for biodiversity conservation purposes is carried out with multiple species which makes this process more complex than when modelling only few species. Lastly, the coupling of new technologies as remote sensing techniques, e.g. LiDAR (light detection and ranging) and (hyper)spectral data, with the modelling of species distributions should be more deeply explored as new research suggest this could be highly advantageous for the field of conservation biology and in our case for investigating more in depth and at high spatial resolution how the landscape context, e.g. landscape structure, defines species range limits at high spatial resolution.
References


