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Evaluating the use of Biotic Interactions in Species Distribution Models

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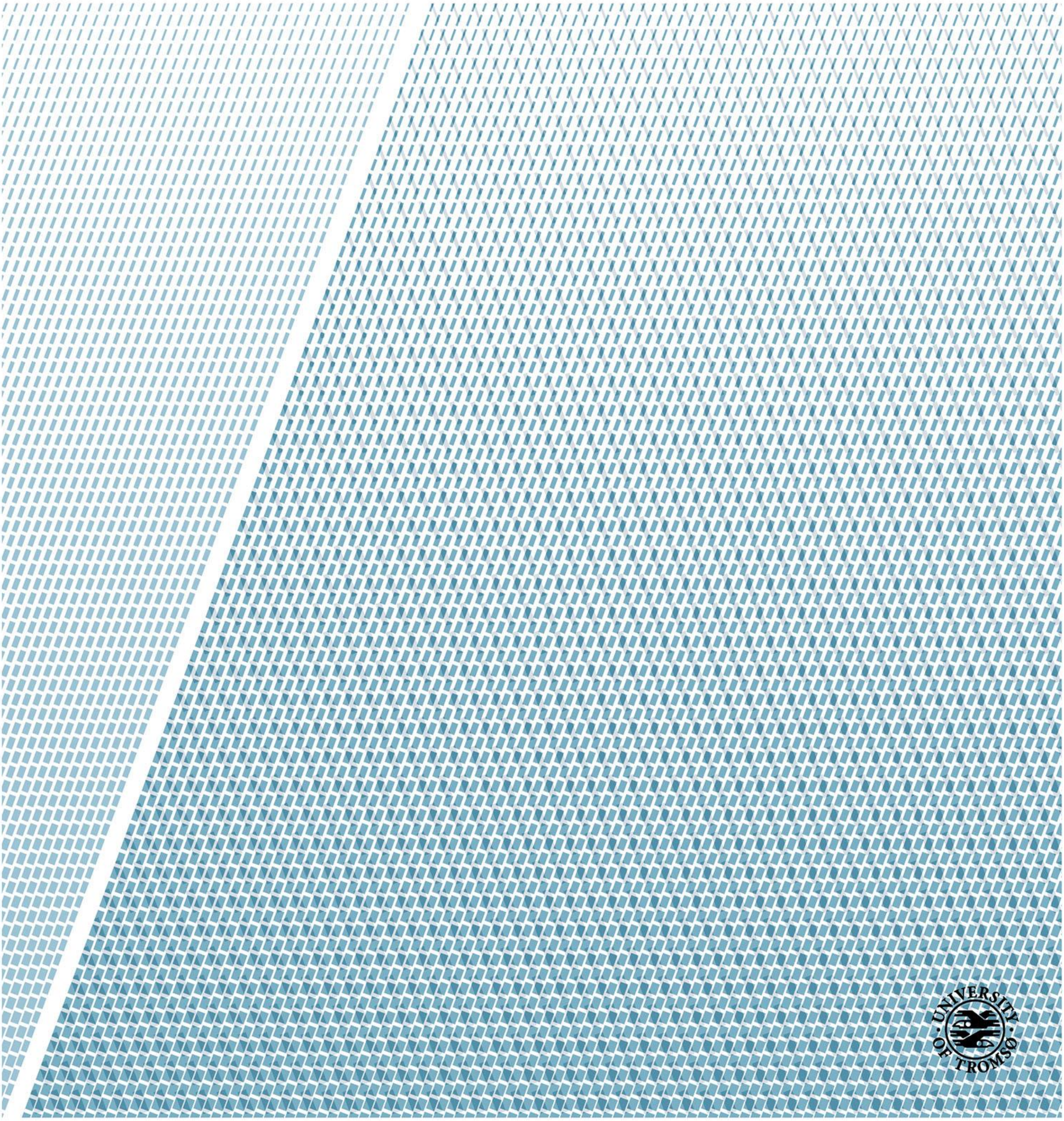

For my wife,

You know what you did

"That climate acts in main part indirectly by favouring other species we clearly see in the prodigious number of plants which in our gardens can perfectly well endure our climate, but which never become naturalised, for they cannot compete with our native plants nor resist destruction by our native animals."

- Charlies Darwin, On the Origin of Species (1859)

Abstract

Species distribution models are a key tool in predicting and projecting population changes in the past, present and future. In the past they have mostly focused on using abiotic interactions for their models. This may be inadequate however as biotic interactions play an important role in determining community composition. Climate change has created and will create many novel communities that have no modern analogue, understanding and predicting these is key to modern conservation and climate change mitigation. Through reviewing articles which use SDMs to project past, present and future distributions of species their level of biotic interaction will be evaluated. 122 articles were found using a set search criterion, of which 40 were found to be adequate. These articles were evaluated for biotic interaction and level of novelty they projected in their species compositions. It was found that though the number of articles finding novelty did decrease with the use of biotic interactions the level it decreased was not by much. Novel communities that were found with no biotic interaction did have biotic explanations found however. The significant threat of climate change means novelty is likely no matter the use of biotic interactions. Understand the full assemblages though requires the use of biotic interactions.

Evaluating the use of Biotic Interactions in Species Distribution Models

Every ecological community has a composition that is driven by abiotic and biotic processes. At every scale there are large numbers of mechanisms shaping communities (D’Amen *et al.*, 2017). Understanding and modelling these processes accurately is one of modern biology’s great challenges. Until recently the knowledge base was largely empirical and theoretical, while this provided insight there are still questions remaining about the spatial predictions of communities (D’Amen *et al.*, 2017).

Modelling of biological systems allows for the creation and analysis of vast amounts of data. The scientific communities’ reliance on different methods of modelling has only been increasing as the models themselves become more reliable and powerful. Environmental data is used increasingly in governmental policy (DEFRA, 2011), with models an important tool for delivering a dataset of the requisite quality for policy. The importance then of models being an accurate representation of the environment which they are based on, thus creating a projection of a real-world scenario, is clearly high (Poloczanska *et al.*, 2008).

Species distribution models (SDMs) extrapolate species distribution data spatially and temporally, based on a statistical model (Franklin, 2010). They have proven to be an effective tool within ecology for projections of the environment in the past, present and future for decades now. They are applicable at all scales, ecological niche models (ENMs) and community level models (CLMs) being examples of models used for prediction of the distribution of a species using its niche, or a model for predicting the biodiversity of a community (Poloczanska *et al.*, 2008). These models are fundamental to the management of landscapes, and the conservation of the species which interact within those landscapes (Franklin, 2010; Elith and Franklin, 2013; Lewis *et al.*, 2017)
SDMs are built on a framework of the relationship between a species’ distribution, or another biotic variable able to describe the ecology of a species, and the physical environment with any abiotic factors able to influence the distribution of the subject species (Elith and Franklin, 2013). Biotic data is defined as the living parts of the ecosystem, the organisms and their interactions within the ecosystem. It often takes the form of species occurrence data. Occurrence data, recorded through a form of survey, can be ordinal or binary (Franklin, 2010). The theory behind the relationship between a species and its environment stems from Hutchinson’s concept of fundamental and realised niches (Hutchinson, 1957). Hutchinson

(1957) wrote that multiple environmental factors were controlling the current and potential distribution of a species, and that these form the niche of the species (Colwell and Rangel, 2009; Veloz *et al.*, 2012).

Abiotic variables are defined as the non-living parts of the ecosystem, the chemical and physical aspects of the environment. Within SDMs abiotic variables are commonly represented as topography and climate (Kübler *et al.,* 2015; Maguire *et al.,* 2015). As the climate changes as a result of anthropogenic warming across all biomes the use of climate as an abiotic factor becomes more difficult. Models must now take into account the predicted changes in the climate, and how this will consequently impact the target species (Pearson and Dawson, 2003). The traditional system of species presence or abundance measured against environmental and climatic conditions is an excellent system for determining how a species may react to changes in its abiotic environment, however this is not a complete species distribution model. Climate change is a vital, evolving abiotic factor in SDMs but biotic factors have been heavily under-represented in detailed models (Pearson and Dawson, 2003; Poloczanska *et al.*, 2008; Lewis *et al.*, 2017).

Many studies have recorded the importance of biotic interactions to the distribution of a species, and its response to environmental changes (Araújo and Luoto, 2007; Pellissier *et al.*, 2010; Kissling *et al.*, 2012; Wisz *et al.*, 2013; Maguire *et al.*, 2015; Lewis *et al.*, 2017). These biotic interactions include facilitation (Cavieres *et al.*, 2014; Filazzola, Sotomayor and Lortie, 2018), competition (Poloczanska *et al.*, 2008), predation (Kammerle *et al.*, 2017), the culturally transmitted behaviours of individual populations (Keith *et al.*, 2009; Keith and Bull, 2017), interactions with soil microbes (Bueno de Mesquita *et al.*, 2016) and parasitism (Ebert, 2005). While different species will have different interactions with these biotic variables, and even individuals within that population (Keith *et al.*, 2009), it is clear that the ignorance of biotic interactions is limiting our ability to accurately predict how species will react to climate change, thus limiting the extent we can protect global biodiversity (Wisz *et al.*, 2013). Despite some success, especially at fine scales as local action is taken, the rate of biodiversity loss has not been slowed (Butchart, 2010). This suggests that the lack of incorporation of biotic variables into the majority of SDMs, ENMs and CLMs have not been able to forecast vulnerable species responses to climate change. Biotic interactions can be a powerful determinant of a species' range. Extremely positive interactions could allow a species to extend its range beyond its abiotic defined limits (Silva *et al.*, 2015). A mutualistic relationship, such as in the case of the grass species *Bromus laevipes,* has allowed the species to extend its range by 20% into areas thought to be too dry for the species to survive (Afkhami, McIntyre and Strauss, 2014). Extremely negative interactions may restrict species from areas which I thought to be environmentally favourable (Silva *et al.*, 2015). In the case of the wild sunflower (*Helianthus annuus* L.), its southern range meets the environmental requirements for this species to survive. This is proven by domesticated sunflowers growing in the areas the wild individuals are absent. However, insect herbivory from insects thriving in the more tropical southern range and competition from species occupying the same niche space are limiting the range of the wild sunflower (Lentz, Bye and Sánchez-Cordero, 2008). It will differ across species but in some cases biotic influences are stronger than their abiotic counterparts. This makes the absence of biotic interactions from SDMs even more glaring.

SDMs have traditionally been an individualistic endeavour. Under the impacts of climate change, fossil records have shown that when community structure remains the same there can still be changes in abundance and novel communities can even emerge (Williams, Shuman and Webb, 2001a). Although this is the case, and this study is not alone in giving evidence for individualistic responses to climate change (Simakova, 2006), the nature of biological communities means that if there is a change to one species then there is very likely a change to another in some capacity. Finding those links which tie species interactions together is fundamental to community level modelling.

Community level model’s are proving themselves to be effective tools for integrating biotic interactions into models which use the environmental variables which define the niche of a species (Ferrier and Guisan, 2006). CLMs are defined by Ferrier and Guisan (2006) as strategies which both combine data from multiple species during the analysis and produce spatial information about biodiversity at a community scale rather than at the level of an individual species. Although, like all models, CLMs have appropriate and inappropriate occasions to be applied, they are generally a more detailed method of combining biotic and abiotic interactions than typical ENMs. When rare or large numbers of species are involved CLMs are particularly useful, as they can use information from more common or easily investigated species to give further insight (Ferrier and Guisan, 2006; Nieto-Lugilde *et al.*, 2018).

CLM’s can be broadly separated into three strategies. The first is the ‘assemble first, predict later, method; the ‘predict first, assemble later’ method; and the ‘assemble and predict together method’ (Ferrier and Guisan, 2006; Nieto-Lugilde et al., 2018).

‘Assemble first, predict later’ involves two separate stages. In the first stage biological data undergoes classification or ordination which has no reference to abiotic interactions. This is used to generate community types, species groups or compositional variation. Therefore, only locations with biological data, presence data, is applicable here. Second, the entity created first is then modelled as a function of environmental predictors. The second stage varies depending on the kind of community-level generated in the first step. It is possible to either model community types one at a time, by modelling presence/absence data about the community to the relevant environmental variables. This is notably similar to the traditional SDM method. However, the community is modelled rather than a singular species. This method can be achieved through generalised linear models (McCullagh and Nelder, 1989) or generalised additive modelling (Brown, 1994). An extrapolated distribution can be generated providing the probability of occurrence within grid cells. The other option is to fit a model to each community simultaneously through treating the community membership as a multinomial response. This is commonly fitted using classification and regression trees (Moore, Lees and Davey, 1991). As the name of the method suggests, ‘Assemble first, predict later’, the biological data is prepared for analysis before being modelled against abiotic variables. The output of this strategy a cumulative community attribute such as species richness or vegetation types (D’Amen *et al.*, 2017).

The second strategy is known as ‘predict first, classify later’ (Overton *et al.*, 2002) or ‘classification then modelling’ (Ferrier and Guisan, 2006). This strategy requires individual species to be modelled one at a time as a function of the relevant environmental variables, generating a separate species distribution map for individual species. A stack of species’ distributions is compiled and subjected to classification or ordination in order to derive the correct community-level output. This strategy follows similar analytical techniques to the previous strategy. Instead of applying the analytical techniques to biological data, this strategy applies them to individual cells containing predictions of species abundance. Each cell is its own survey plot containing predicted data for each species rather than direct observations. This strategy constructs community composition in a ‘bottom-up’ approach using predicted distribution to generate community composition. The method could potentially produce any property of a community or ecosystem, however the strategy is underused (Ferrier and Guisan, 2006).

The third and final strategy is known as ‘Assemble and predict together’. In the first two strategies there are two distinct steps. Both involve community-level entities or attributes, and the modelling of the biotic and abiotic environments. This strategy performs both functions simultaneously, all of the data is modelled in one integrated process (Ferrier *et al.*, 2002; Ferrier and Guisan, 2006; D'Amen *et al.*, 2017). In order to fit data to multiple species at the same time techniques traditionally used have been adapted. These adaptations include examples such as multi-response neural networks (Olden, 2003) and vector generalised additive models (Yee and Mackenzie, 2002). Overall species composition can be explained in detail through weighting the importance of environmental predictors, and their combinations. Final predictions are given for individual species, meaning community composition can be measured along with relative abundance of species. The recognition of interactions between species means that communities are known to be a fluid construct, not a fixed structure unable to change (D'Amen *et al.*, 2017).

Including biotic interactions, and creating increasingly complex CLMs cannot always be applied, especially in hindcasting studies. This may be because biotic interactions are inherently complex and it is not always simple to decide what information is pertinent for each species to identify their impact on the community composition (Godsoe, Franklin and Blanchet, 2017). When hindcasting, fossil records are used for data collection in many cases, species behaviour and individual responses are not easily interpreted from fossil records, they must be inferred rather than observed (Pearman *et al.*, 2008; Kuemmerle *et al.*, 2012). In other hindcasting SDM studies, the environmental requirements of the target species are applied to past climate datasets to model their potential range (Varela *et al.*, 2010; Levinsky *et al.*, 2013). These examples offer a presence-absence dataset modelled against past climate data, a classic climate envelope model of species distribution modelling (Poloczanska *et al.*, 2008; Urban, Zarnetske and Skelly, 2013).

When a model uses fossil records, it is possible to infer biotic interactions using fossil analysis. This can be found directly using presence of different species' fossils in the study site, competition, predation, parasitism have all been found by using fossil specimens (Poinar, 2002; Borszcz and Zatoń, 2013). Indirect methods of determining biotic interactions require inferring using modern analogues and any relevant morphological, geographical and ecological information that is gained from the fossil record (Liow *et al.*, 2016). Barry *et al* (2002), states that in a study using fossil records of a wide range of species types there was a noted disappearance of taxa across the study area. During this event the local climate saw no changes, therefore it has been theorised that biotic interactions had a greater effect on the community structure than the environment at that time (Barry *et al.*, 2002). Liow *et al* (2016) includes no abiotic interactions in determining the competitive ability of bryozoans, and does not use a different biotic interaction as a proxy for competition. The author states that each interspecific encounter must have a winner or loser, by using decades of previous research into bryozoans, and other communities. The study attempts to measure competitiveness using a method as direct and close to observation as possible, though it is noted that by not measuring biotic interactions which may impact species survival the question of inferring biotic interactions, and of competitive ability, is not fully answered.

When species data is applied as a function of modern environmental suitability, behaviour can only be inferred from modern counterparts. With the Anthropocene presently supplying threats unknown to Holocene communities (Steffen, Crutzen and McNeill, 2007), assuming a species' response to climate change will be the same in both time periods is unlikely to be accurate.

The Anthropocene is defined as an epoch that is shaped by humans. Human driven change of the planet has altered the biological fabric of Earth, causing interruptions in flows of nitrogen, carbon, silicon and phosphorous (Steffen, Crutzen and McNeill, 2007). The Earth's balance of energy is also imbalanced, absorbing more energy than it is able to emit (Hansen *et al.*, 2005), these are all symptoms of man-made climate change and the main reason the Anthropocene has been accepted as our present timeframe.

There have been five previously recorded 'mass extinctions' in Earth's history, characterised by a loss of more than 75% of species in a short geological interval (Barnosky *et al.*, 2011). Current extinction rates are comparable to the rates estimated during the five extinction events, this had led to the belief that we are currently experiencing a 'sixth extinction wave' (Dirzo *et al.*, 2014).

The natural geological state, the Holocene, has been left behind as we have entered the Anthropocene. A state whereby, should humans cease all harmful action against the planet, the effects of human activity(Steffen, Crutzen and McNeill, 2007) would not recover without a very long timeframe. It is largely agreed upon that human activity is responsible for the change in the planet however, discussion differs on the exact timeframe when anthropogenic disturbance became most harmful, but approximately 100-500 years ago is where discussion has settled (Steffen, Crutzen and McNeill, 2007; Dirzo *et al.*, 2014; Lewis and Maslin, 2015). This ignores the fact that *Homo sapiens* and ancestors have been successful colonisers and hunters ever since the Pleistocene (Carrión, Rose and Stringer, 2011). Many studies which include hindcasting will measure back to the LGM (21ka), when *Homo sapiens* were widely spread across the planet. However, when these studies model interactions, biotic or abiotic, any anthropogenic influences are rarely considered. The impact of modern humans on the environment is widely documented (Steffen, Crutzen and McNeill, 2007; Dirzo *et al.*, 2014; Lewis and Maslin, 2015) but the interactions of humans 20,000 years ago on the communities which they lived in could be important to the study of no-analog ecosystems. Hindcasting articles that have not included biotic interactions, or anthropogenic influences may be incorrectly labelling their resulting modelled environments as having no modern analogue.

A no-analog community, or novel community, can be defined as one that has a composition unlike any found in the modern day (Williams and Jackson, 2007; Radeloff *et al.*, 2015). Whether hindcasting or forecasting, this phenomenon may appear. Research is heavily indebted to our personal observations and experiences, what we know now can provide an accurate benchmark for all further study. As we move further from the present, the present becomes a less effective tool for modelling past and future systems (Williams and Jackson, 2007). Often, individual responses to biotic and abiotic interactions will result in range and abundance shifts. The last Ice Age was no exception to this and caused massive shifts and fragmentations in communities across all ecosystems (Bonaccorso, Koch and Peterson, 2006; Normand *et al.*, 2011). Individual species may have adapted by shifting their niche rather than their range (Jezkova, Olah-Hemmings and Riddle, 2011), or through shifting ranges (Sommer *et al.*, 2011). These changes mainly took place in the late glacial and early Holocene periods from 15 ka to 9 ka (Sommer *et al.*, 2011). These massive shifts may have created a host of no-analog communities through the unique conditions that the end of the ice age left across the Earth. Lyons (2003) argues that through the limited space that any one species can inhabit, especially within its own means of dispersal (Normand *et al.*, 2011; Blois *et al.*, 2014), mammals are restricted in what movements and range shifts they can make. Unless a species can change its niche at the same time as its range, it is likely that when environmental conditions become more favourable they will return to their original range, or they will adapt. The prediction that individualistic responses to climate change have resulted in a mass of non-analogous communities is an oversimplification, there will be communities with no modern analogue but not all of them (Lyons, 2003).

When forecasting to the future in SDMs, no-analog will refer to a current climate or community with no future analogue, these are known as disappearing climates or communities (Williams and Jackson, 2007). Being able to accurately locate novel communities in the future requires being able to detect ecological “surprises” (Lindenmayer *et al.*, 2010). The detection of “surprises” allows for conservation policy and action to alter to alleviate negative ecological “surprises”, and potentially to prevent no-analog communities from forming (Lindenmayer *et al.*, 2010). Novel communities and climates could negatively impact the work of conservation as climate change mitigation has to change methods to suit the future, of which there is no modern equivalent. Individual species rarely fulfil their own fundamental niche to its full extent due to biotic interactions and dispersal/range limitations (Williams and Jackson, 2007), with environmental conditions moving into unknown levels the ability of niche models to accurately represent a species response to climate change will decrease. The inability to predict individual responses to climate change means that at the community level there will be great uncertainty. Species exiting in a novel community may find their biotic interactions change, making not just the community structure a "novelty" but even the individuals themselves (Williams and Jackson, 2007). Increases in atmospheric CO_2 will likely increase the temperature optimum for photosynthesis, reducing sensitivity of moisture stress (Sage and Coleman, 2001). The present foundations of plant-climate relationships and their application in predicting species' responses to climate change will be weakened. When all we know is that behavioural responses will change, all that can be predicted for certain is that there will be novel communities, and there will be ecological surprises (Williams and Jackson, 2007; Lindenmayer *et al.*, 2010). Current models are not suited to this challenge, and must be made more robust. As we forecast futures that are further and further from the present, temporally, spatially, and observationally, it is possible that models need to rely less on the idea of analogues to become more robust. Climate change is going to be changing the world to a devastating degree only matched by anthropogenic disturbance. Land use change will feed into climate change as emissions increase (Searchinger *et al.*, 2008), both climate change and land use change will then cause habitat fragmentation, biodiversity loss and extinctions (Jetz, Wilcove and Dobson, 2007), all species are then forced to adapt to their new world through changing their biotic interactions. Current research reveals that the current trajectory of climate change is pushing toward a threshold that, if crossed, prevents a return to what models would consider to be the modern analogue (Steffen and et al., 2018). Such a destabilisation of the climate and environment would impact all walks of life, leading to what could be considered a "No-Analogue Earth". Lyons (2003) stated that the overuse of novel communities is incorrect, but with the current trajectory of the planet one of the only certainties is that whatever happens, it will be a novelty.

Humans have been influencing the climate for much longer than articles on the Anthropocene suggest, widespread forest clearance can be dated back 8000 years and rice irrigation by 5000 years (Ruddiman, 2003). At each of these historic moments climate anomalies have been recorded, CO_2 first registering anomalous increases at 8000 years and CH_4 5000 years ago. Paleoclimatic evidence rules out the possibility that these changes were naturally driven, the timings of widespread anthropogenic disturbance with this climate change argue that humans have been influencing the climate for much longer than previously thought (Ruddiman, 2003). Studies that hindcast back to periods of widespread human activity, and through use of SDMs determine that a community with no modern analogue has been found, may not consider anthropogenic biotic interactions.

Neolithic people were known to clear forests to create pastures and arable farms, approximately 5500 years ago a mass expansion in *Picea abies* was facilitated by anthropogenic disturbance (Schwörer *et al.*, 2015). Use of fire, grazing, and logging meant that *Abies alba* suffered an irreversible decline. *Abies alba* existed in the same habitats as *Picea abies* but thrived under warmer, dryer conditions such as would have been naturally found with no anthropogenic disturbance (Schwörer *et al.*, 2015). This is the type of scenario that could cause an incorrect novel community to be found in another study. An examination of the fossil and pollen records of this study site would reveal the dominance of *Picea abies*. In a study purely focused on the impact of climate and climate change this dominance would look out of place as the warm climates of 5500 years ago and the present should suit the growth of *Abies alba* over *Picea abies*. The *P. abies* dominant landscape would be labelled as having no modern analogue, not considering that it could have under the same biotic and abiotic interactions. In a study mapping past and present vegetation Pearman *et al* (2008) showed that the range of *Picea abies* was smaller than the modern range of the species across Europe during the mid-Holocene, exactly when Neolithic people were using their land clearance methods to promote the growth of *A. alba*. The article modelled the current range of *P. abies* and used pollen records to map *P. abies*' presence/absence during the mid-Holocene. The difference in the distribution of *P. abies* from the past and present was given an abiotic explanation in the form of rapid climate change (Pearman *et al.*, 2008). Schwörer *et al* (2015) shows that anthropogenic disturbance in the mid-Holocene in Europe, crucially through the use of fire, led to the widespread removal of *Abies alba*. This then facilitated the expansion of *Picea abies*. This is just one example of how SDMs using only abiotic interactions may not be presenting the whole relevant picture, and that biotic interactions from the natural environment or anthropogenic disturbance can have impacts greater than their abiotic counterparts.

In this review the use of biotic interactions will be reviewed. A focus is given to models which hindcast or forecast the presence of novel/no-analog communities. The results of these studies will be further evaluated to determine the role of biotic interactions in this novel community, and how their inclusion might explain the identified analogous community. It is hypothesised that the discovery of no-analog systems is more likely when biotic interactions are not used. Using biotic interactions in SDMs increases the chance that the model's findings are explainable, and have a modern analog. Relevant literature will be searched for and reviewed under a specified set of parameters. The accepted literature will be graded in regards to their use of biotic interactions. The literature that has found novelty in its modelled environments will be evaluated and explanations will be found for novel communities that have arisen (Nieto-Lugilde *et al.*, 2018).

Methodology

Objective of this review

The primary aim of this review is to evaluate the use of biotic interactions in species distribution models (SDMs), with a focus on models used to identify novel communities through forecasting or hindcasting. The results of models using only abiotic factors adequately will be investigated to determine whether inclusion of biotic factors could potentially affect their outcome, and any subsequent novel communities that were found.

Primary Question

Have biotic interactions been sufficiently considered in SDMs to identify novel communities, and could biotic interactions change or explain the outcome of studies which did not include them?

Defining the primary question:

Subject (Novel communities): Novelty is defined here as a form of dissimilarity in a biological system within its own reference baseline, normally the present. If a particular association in a system is hindcasted or forecasted which has no currently existing precedence then it is considered novel (Radeloff *et al.*, 2015). This term is used interchangeably with 'No-analog communities'.

Exposure (Biotic interactions): Biotic interactions are defined here as interactions between biological organisms. These can be short-term interactions, such as predation. They can also be long-term interactions, such as competition, mutualism and facilitation (Wisz et al., 2013).

Comparator (Species distribution models (SDMs)): A statistically based model combining information regarding the distribution and ecology of relevant species, with their physical and chemical environment in order to create a predictive map of the subject species' distribution temporally and spatially (Franklin, 2010).

Outcome: Solving a novel community's presence.

Search Terms

Subject: Hindcasting; No-analog; Novel communit*

Exposure: Biotic interaction*; Competition; Predation

Comparator: Species distribution model*

An asterisk (*) denotes that a 'wildcard' truncation was used. As 'No-analog' and 'Novel Communities' are used synonymously with each other in this study, any search involving these terms uses the Boolean function 'OR' to search for results including either of the two terms. The Boolean operator 'AND' was used to combine search terms within this list. Each search term under '*Subject*' was individually combined with the '*Comparator'* term using the 'AND' operator. For example,

Hindcasting AND Species Distribution Model*

No-analog OR Novel communit* AND Species Distribution Model*

The framework was applied to searching using the '*Subject*' and the '*Exposure*' terms. For example,

Hindcasting AND Biotic interaction*

No-analog OR Novel communit* AND Competition

No language, time, or type of document restrictions will be applied in this review. The exposure term *'Biotic Interaction*'* encompassed most available information when applied to another search term which was deemed relevant. Specific examples of biotic interactions, competition and predation, were included to search for studies which could not be found using just the '*Biotic Interaction**' term. However, inclusion of these terms was rarely useful. Increasing specificity would either restrict the number of results or provide nothing that hadn't been found using a wider search term.

Publication Database

Web of Science is the sole database to which the search has been applied. The nature of the study provides very limited results; therefore, every result will be judged to be included in this review.

Other Literature Searches

Relevant literature will also be searched for in bibliographies of other literature reviews which have explored similar topics, such as Wisz *et al*., 2013 and Maguire *et al*., 2015.

Study Inclusion/Exclusion Criteria

All results that have come from the search framework defined above will be evaluated at two levels. The initial level is at the title and abstract, which are assessed for their relevance for inclusion. If the title and abstract are considered relevant, they will be assessed at the second level. The text of the articles will be studied to assess if the articles are appropriate for inclusion. When either of these levels leads to a case of uncertainty, the benefit of the doubt will be given towards the paper and will be included. Due to a lack of appropriate articles surrounding this topic of investigation it is important not to exclude any data unless it is certain to be inappropriate.

In order to be included in either of the search levels each study must pass the following criteria:

- *Relevant subject(s)*: Hindcasting or forecasting, and the subsequent location of novel communities. There are no restrictions on subject species.
- *Relevant types of exposure*: Use of either abiotic or biotic interactions as a variable in models attempted.
- *Relevant types of study*: Species distribution models. This term is being used as an umbrella term for several related models, this includes community level models and ecological niche modelling.

Study Quality Assessment

As the purpose of the study is to analyse the results of modelled communities and climates, with regards to how biotic interactions have been factored into models once every article which meets the acceptable criteria it is then graded on a scale of the articles use of biotic interactions in their modelling. The grading is on the following scale (Figure 1):

- *0* – Only abiotic interactions have been utilised in the article’s analysis. Such as how Harris *et al* (2018) only uses climate variables to perform a hindcasting study.

- *1* – Biotic interactions have been included, however at a level not considered detailed enough. Dobrowski *et al* (2011) includes species traits in SDMs as a method of categorising vegetation species. The focus of the SDMs used is still climate as a function of species presence, so while biotic interactions are a part of this study they are not accurately represented in the results.
- *2* – Biotic interactions play a primary role in the study and any results can be, at least, partially attributed to biotic interactions. Poloczanska *et al* (2008) uses competition as a variable along with abiotic interactions to perform a SDM.

There is the potential for subjectivity in this grading system, to mitigate for this the determinant for grading articles is found within the methodology. The models used for analysis will be studied. If biotic interactions are specifically used in the article's modelling, and the outcome of the model is a distribution map which displays the impact of biotic interactions then the article is graded as a 2. Any use of biotic interactions which has less of the aforementioned impact will be graded as a 1.

Variables which are considered useful to this review were identified and included. These are the subjects of each study, mostly the species type. It may be important to recognise how different subjects have been modelled, and how biotic interactions differently affect a range of species.

The location of the study, along with its scale, are important in how the articles models are critically analysed. At different scales, the biotic interactions which can be measured accurately are altered (Menge and Olson, 1990). Dispersal may be identified through a nationwide or continental survey. However, predation and competition require a finer scale of analysis. Community level models act at a community scale, providing a very fine yet detailed overview of interactions at that level (Maguire *et al.*, 2015).

The temporal state of each article is identified, whether it has been hindcasted, forecasted or exists in the present. This may reveal differences in applying biotic interactions depending on the temporal state of the model.

If a biotic interaction was applied, to any degree, in the article in question then exact nature of the interaction is noted. As has been mentioned previously, some biotic interactions can only be measured in certain contexts (Menge and Olson, 1990). It is therefore important to determine which interactions are applied at which scales and contexts, when critical examination takes place then this knowledge will be important.

Novel/no-analog communities should be recognised if they have been identified by the article. This is done in a similar method as the study inclusion criteria, the abstract is read however the methodology is not considered useful. The discussion and results can be read for mentions of no-analog or novel communities. Failing specific mentions of these keywords then the discussion should be read for instances where the model produces a result which is analogous to the present day.

There has been no limit placed on the subject, location or scale of studies which are deemed acceptable for this study. This is both to make sure all available data is compiled, and to receive a wider view of how biotic interactions impact community structure.

Identifying novel communities

The definition of a novel or no-analog community has been covered, it being a community or assemblage that has no modern, known equivalent. When actually identifying these communities in the literature it becomes challenging as the exact terminology used here is not always applied in SDM studies. If the study concludes that the species it has been modelling present an assemblage that does not exist in modern examples then it is noted as novel. There are cases when the species responds to an interaction in a novel way, this will then alter the range of the species outside of what was thought to be the potential niche. This novel individual response will then lead to novel communities being formed.

Through following these examples of how a novel community may be represented in an article, all of the studies being used in this review have been examined and any novel communities identified. The given explanations for these novel communities are noted. Using this information evidence can be gathered to determine whether there are biotic interactions, if they were not already applied sufficiently, that can possibly be applied to provide alternate explanations for novel communities or remove the novel factors involved.

Evaluating novelty

Each article that finds a novel community or assemblage of species provides an explanation using the criteria they have applied through their modelling. Studies which have used only abiotic criteria to perform their models will attempt to discuss any novelty found in regards to how abiotic variables may be responsible, with mentions of biotic interactions coming in concluding remarks. The purpose here then is to look at the interactions applied, or not applied, by each individual study which has found a no-analog community. When an article has found novelty, literature around their subject species and study site is compiled in order to fully form what interactions may occur which the article have not considered. For instance, an article covering the Eurasian otter (*Lutra lutra*) during the Last Glacial Maximum (LGM) concluding that mammal assemblages during this time period were in a non-analog state (Řičánková, Robovský and Riegert, 2014). This article explains that due to glaciation and climate change, an abiotic interaction, many species were forced to seek refugia thus creating assemblages of species that do not naturally occur in modern day. However, the article does not attempt to use biotic interactions to explain its results. Climate is undeniably a major driving force of a species' range, but if the niche of potential prey of this species are modelled then it could be possible to determine a biotic explanation behind the realised niche currently modelled using only abiotic interactions.

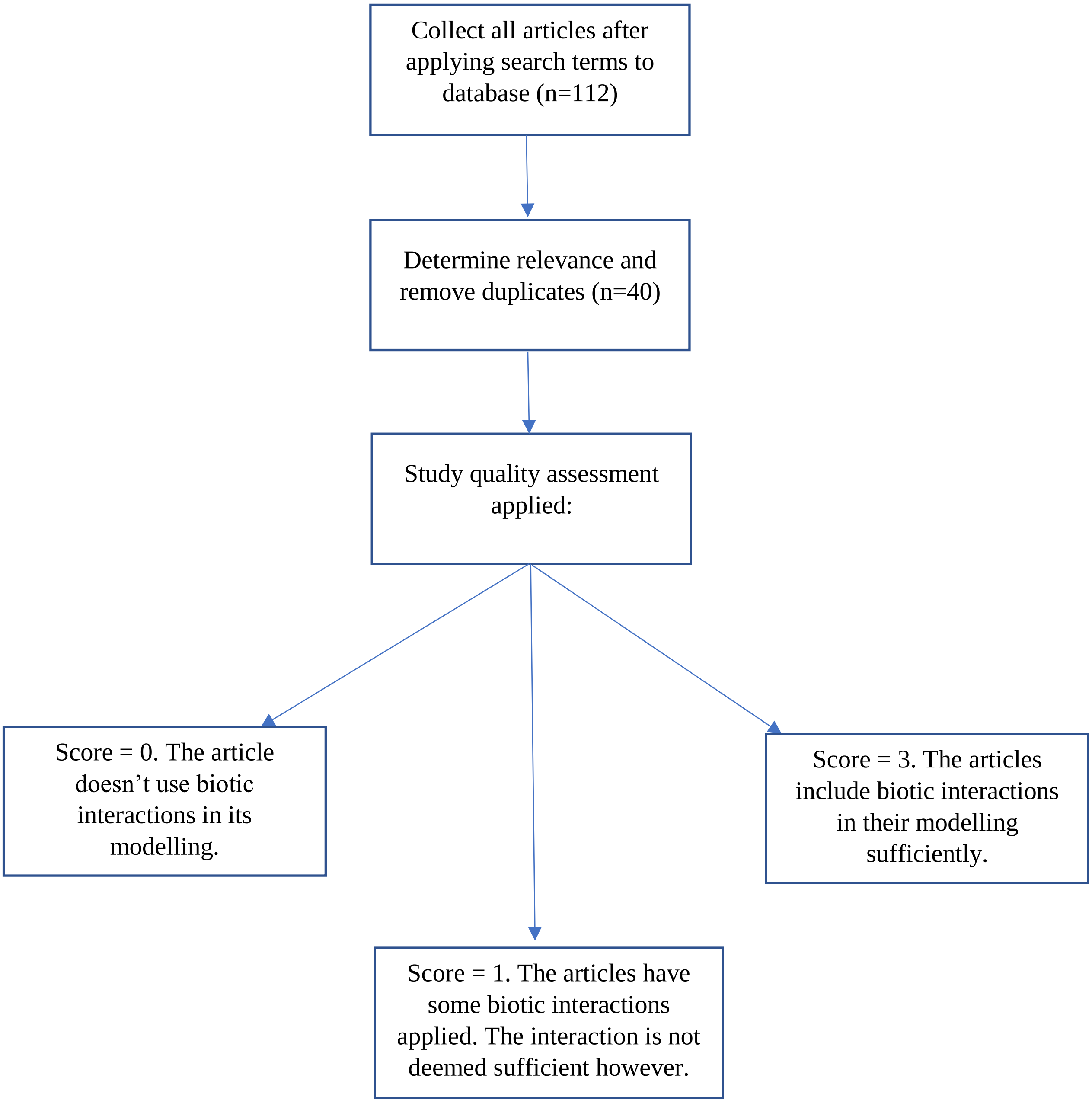

Figure 1: A flowchart displaying the methodology behind the selection and subsequent grading of articles for this literature review.

Table 1: The full literature table used to find and evaluate biotic interactions and novel communities or assemblages. Legend for 'Interaction Score': 2 = Biotic interactions used sufficiently; 1 = Biotic interactions used insufficiently; 0 = No biotic interactions applied.

Keywords Used	*Authors*	*Subject*	*Subject type*	*Location*	*Temporal state*	*Biotic Interactions*	*Interaction Score*	*Novel Community? (Y/N)*
Hindcasting, Biotic Interactions	(Poloczanska *et al.*, 2008)	Modelling the response of competing species to climate change	Aquatic mollusc	England	Up to 2050	Intraspecific Competition	2	N
Hindcasting, Competition	**Nothing relevant or original**	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Hindcasting, Predation	**Nothing relevant or original**	N/A	N/A	N/A	N/A	N/A	N/A	N/A
Hindcasting, Species Distribution Model	(Harris, Taylor and White, 2017)	Forecasting species richness of breeding birds using different techniques	Birds	United States	1981-2050	Species interactions considered	1	N
	(Iannella, Cerasoli and Biondi, 2017)	Measuring climate influences of the distribution of newts	Amphibians	Italy	Last Glacial Max/Holocene - Present	Only Abiotic Factors	0	Y
	(Theodoridis *et al.*, 2017)	How do cold-adapted plants respond to Climatic cycles	Forbs	Europe	72ka	Only Abiotic Factors	0	Y
	(Veloz *et al.*, 2012)	How have past no analog climates and shifting niches impacted modern SDMs	Plants	North America	21-15ka	Only Abiotic Factors	0	Y
	(Pearman *et al.*, 2008)	Prediction of plant species over 6000 years	Plants	Europe	6ka	Only Abiotic Factors	0	Y
	(Dobrowski *et al.*, 2011)	Modelling plant ranges of 75 years of climate change in California	Plants	United States	1930	Dispersal	1	Y
	(Espíndola *et al.*, 2012)	Predicting present and future intra-specific genetic structure through niche hindcasting	Forbs	Europe	24ka	Only Abiotic Factors	0	N
	(Flojgaard *et al.*, 2011)	Understand historic mammal species richness in Europe	Mammals	Europe	Present	Human influence	1	N
	(Varela *et al.*, 2010)	Hindcasting the Spotted hyena to determine reasons for its absence	Mammals	Europe	126ka	Only Abiotic Factors	0	N
	(Levinsky *et al.*, 2013)	Envelope models suggest co-occurrence of refugia of African birds and mammals	Birds/ Mammals	Africa	LGM	Only Abiotic Factors	0	Y
	(Kuemmerle *et al.*, 2012)	Range dynamics and fragmentation of bison over 8000 years	Mammals	Europe	8ka	Human influence	1	N

	(Pelletier *et al.*, 2015)	Historical SDMs predict species limits in Western Salamanders	Amphibians	North America	21ka	Only Abiotic Factors	0	N
	(Lambert *et al.*, 2014)	Cetacean range in NE Atlantic, future predictions	Cetaceans	Europe	2099	Only Abiotic Factors	0	N
No-analog OR Novel Communities, Species Distribution Model	(Stralberg *et al.*, 2009)	A no-analog future for Californian birds?	Birds	North America	2070	Only Abiotic Factors	0	Y
	(Buisson *et al.*, 2013)	Toward a loss of functional diversity in stream fish under climate change	Fish	Europe	Present	Functional Diversity	2	N
	(Maguire *et al.*, 2016)	Comparison of SDM and CLM across novel communities	Plants	North America	21ka	Species Co-Occurance (Competition, Predation, Mutualism…)	1	Y
	(Brown *et al.*, 2015)	Predicting Plant Diversity in Madagascar	Plants	Africa	2080	Only Abiotic Factors	0	Y?
	(Latif *et al.*, 2013)	Predict habitat suitability for a large-scale disturbance specialist	Birds	North America	Present	Only Abiotic Factors	0	Y
	(García-López and Allué, 2013)	Modelling no analog climate distributions	Just climate	World	2080	Only Abiotic Factors	0	Y
	(Graham *et al.*, 2017)	Future geographic patterns of hummingbirds	Birds	South America	2070	Only Abiotic Factors	0	Y
	(Uribe-Rivera *et al.*, 2017)	Dispersal and extrapolation on temporal predictions for Darwin's Frog	Amphibians	South America	Present	Dispersal	2	N
	(Miller and McGill, 2018)	Land use and life history limit migration of tree species	Plants	North America	2100	Dispersal, Human influence	2 (Dispersal), 1 (Human)	Y
	(Hein, Öhlund and Englund, 2012)	Future distribution of Arctic char under climate change in Sweden	Fish	Europe	2100	Competition	2	Y
No-analog OR Novel Communities, Biotic Interactions	(Garciá Molinos *et al.*, 2016)	Climate velocity and the future global distribution of marine biodiversity	Marine	World	2100	Only Abiotic Factors	0	Y
	(Blois *et al.*, 2014)	Evaluating the influence of climate, dispersal and biotic interactions using fossil pollen	Plants	North America	16ka	Species Co-Occurance; Dispersal	2	Y
	(Buckley, 2013)	Putting models of climate change and species interactions into practice	Lizards	Caribbean	Present	Competition	2	N

	(Williams, Shuman and Webb, 2001b)	Analysis of novel communities in late quaternary vegetation	Plants	North America	21ka	Only Abiotic Factors	0	Y
	(Rehfeldt *et al.*, 2012)	North American model for land use planning in a changing climate	Plants	North America	2090	Only Abiotic Factors	0	Y
	(Bartlein, Whitlock and Shafer, 1997)	Climate and the future of vegetation in Yellowstone National Park	Plants	North America	2x CO2	Only Abiotic Factors	0	Y
	(Roberts and Hamann, 2012)	Paleoecological perspective of climate based SDMs	Plants	North America	21ka	Only Abiotic Factors	0	Y
	(Reu *et al.*, 2014)	Future no-analog vegetation produced by temperature and insolation	Plants	World	2100	Model accounts for ecophysical traits in plant growth and survival	1	Y
	(Boiffin, Badeau and Bréda, 2017)	SDMs may misdirect assisted migration	Plants	World	Present	Only Abiotic Factors	0	Y
	(Rafferty, 2017)	Effects of global change on insect pollinators	Insects	World	Present	Invasive species	2	Y
	(Bauer, Farrell and Goldblum, 2016)	Forest diversity under future climate conditions	Plants	North America	Future climate scenarios	Only Abiotic Factors	0	Y
	(Wainwright *et al.*, 2016)	Outcomes of species interactions in a plant community	Plants	Australia	Present	Invasive species	2	Y
	(Stuble *et al.*, 2017)	Rare events disrupt the relationship between climate and interactions	Plants	North America	Present	Invasive species	1	N
No-analog OR Novel Communities, Competition	(Urban, Tewksbury and Sheldon, 2012)	Competition and dispersal differences create no-analog communities and cause extinctions	No focus	No focus	Present	Competition; Dispersal	2	Y
	(Krosby *et al.*, 2015)	Climate induced range overlap among closely related species	Birds; Mammals; Amphibians	North America; South America	2100	Only Abiotic Factors	0	Y
No-analog OR Novel Communities, Predation	(Benito-Garzón, Leadley and Fernández-Manjarrés, 2014)	Assessing global exposure to climate change	Terrestrial climate	World	6ka; 2100	Only Abiotic Factors	0	Y

Results

Number of studies found and applied

Using the defined search criteria there were 112 articles found. When duplicates were removed and appropriateness was determined there were 40 articles left. On these 40 articles biotic interaction level was scored and novelty was searched for.

Compare use of biotic and abiotic interactions vs the generation of novel communities.

Table 2: A table displaying the relationship between biotic interaction score of the studies articles, and whether they found novelty to be present in their analysis.

Biotic interaction score	Novelty present (Y/N)	Proportion of novelty per score
0	19 Y	83%
0	4 N	17%
1	3 Y	50%
1	3 N	50%
2	6 Y	60%
2	4 N	40%

Table 2, shows that when biotic interactions are not used in analysis the chance of a novel community or ecosystem being found is much higher. When biotic interactions are used, even to a degree which is not deemed suitable, the proportion of studies which show novelty in their target area is more even. The first conclusion to be made from this is supporting of the hypothesis, that inclusion of biotic interactions in SDMs increases the chance that the results of any models will have a modern analogue.

Novelty when biotic interactions are not applied

Biotic interaction grade, 0; Novel community identified, Y

What follows is a wide selection of articles covering hindcasting, forecasting, use and non-use of biotic interactions in their modelling, the methodology of the study and a description of any novelty that arose during the study.

Ianella et al.*, (2017)*

Species Distribution Models are used to understand the current distributions of two species of newt, *Lissotriton vulgaris meridionalis* and *L. italicus*, and how they have been influenced by climatic conditions. The analysis of this study is focused on climatic conditions, in particular temperature and precipitation. These variables are focused upon due to their noted influence on amphibian life history traits (Ficetola and Maiorano, 2016). SDM’s were built using two modelling techniques, Boosted Regression Trees (BRT) and Maxent. The resulting models were then hindcasted to past climatic conditions in order to reveal historical habitat suitability, and to hypothesise how the Last Glacial Maximum and subsequent climate changes have influenced the two target species distributions.

The target species are endemic to peninsular Italy, the scale of the study is nationwide. Certain regions of Italy where the species is present were excluded due to introgression from other species or a lack of a parapatric zone between the two species.

The climate data was sourced from Worldclim. The only predictor variables considered were bioclimatic variables from the present, the Mid-Holocene (~6000 years ago), and the Last Glacial Maximum (~22,000 years ago), and three topographic variables. There are no biotic interactions included in the models applied.

Novelty has been found in this study, the smooth newt (*Lissotriton vulgaris meridionalis)* showed a range during the LGM that stretched further south than was thought possible. It had been thought that glacial water retention had restricted the fundamental niche of species. The article provides a possible abiotic explanation through possible increased humidity in the southern range which would facilitate the species’ move south.

Theodoris et al.*, (2017)*

Primula farinosa is a cold adapted forb located in the high-altitude flora of Southern Europe, occurring between 400 and 2900m above sea level. In northern Europe, *P. farinosa* occurs in flat, lowland areas between 0 and 400m above sea level. In this article the responses of *P.*

farinosa to past climate fluctuations are modelled by hindcasting SDMs across the last 72ka. The predictors used in the modelling are entirely environmental, 17 different environmental variables were calculated on the basis that they are a dominant driver of species boundaries. Especially on large scales and for cold adapted plants. These 17 variables were evaluated and the retained variables were the ones with the highest contribution to variation. Five of the 17 variables were retained, all being some form of temperature or precipitation control. They were then used to project past and present distribution of *P. farinosa* under past and present climatic conditions.

It is expected that during postglacial periods the distribution of cold adapted plants remains fragmented, a scenario supported by many studies (Darwin, 1859; Dalen *et al.*, 2007; Stewart *et al.*, 2010; Espíndola *et al.*, 2012). Not only plants but all species to seek refugia are commonly understood to expand their range during postglacial periods, the cold adapted species which had taken over their niche then shrinking in response (Stewart *et al.*, 2010). This study however, shows that in contrast to the hypothesised response, *P. farinosa* undergoes a significant Holocene expansion. The suggested reasonings for this postglacial expansion are that the species has a tolerance for a wider array of environmental conditions than other cold tolerant plants, and in fact during glaciation its range had declined before a postglacial expansion.

Veloz et al.*, (2012)*

SDMs are tested to measure how well modern pollen-based taxon distributions are projected using environmental data from the late Quaternary. Fossil pollen data is collected from North America and combined with paleoclimate simulations from the late Quaternary. The paleoclimate simulations contain largely no-analog climates, the purpose of the study is to monitor the relationship of a wide range of plant species to changing climates. Through this method some novel communities and distributions have been found. *Fraxinus nigra* and *Ostrya/Carpinus* in particular showed higher abundances, and responses to climate change, different to what is expected from modern communities. *F. nigra* was, from 21ka to 15ka, a key and abundant species under highly seasonal climates. Under modern climates in the same locations *F. nigra* is still common but a minor component of the modern community composition. *Ostrya/Carpinus* also displays unusually high pollen abundances in areas at 15ka. The species that are associated with no-analog climates are the species which display the biggest difference in their past realised niche to their modern distribution. This suggests that the ability to exploit the kind of open spaces that no-analog climates, and the devastating impacts of glaciation, can open up.

Pearman et al.*, (2008)*

SDMs are tested on current and past climates going back 6ka to the mid-Holocene. Current plant distribution data is taken from plant atlas databases, past plant data is estimated from pollen core data from European databases and the environmental data which is used as the predictor in the models used is from a Global Circulation Model (GCM). Niche shifts and how species track climate can be tracked using models that take place between past periods and the present. In this study seven tree taxa are distributed across Europe and depending on the species the effectiveness of the modelling technique varies. *Picea abies* and *Juniperus communis* are two species in this study that stand out as not occupying the niche space they are potentially able to. Their realised niche is very restricted when compared to their realised niche.

Williams, Shuman and Webb (2001)

Plant formations during the last deglaciation were widely novel in comparison to extant plant assemblages. Dissimilarity analysis of up to 21ka of pollen data from eastern North America is used to reveal the extent of this dissimilarity. Distributions were projected across the last 21ka and compared to their modern counterparts. Climate simulations were used to model the distribution of the plants. Dissimilarity peaks in the late glacial period before declining rapidly immediately after 11ka. The results agree with Pearman *et al*., (2008) with ash and hornbeam showing markedly high levels of abundance not observed today. As the glacial period moved to the Holocene spruce began to fall while pine took its place. In North America rates of vegetation change were low, and stayed low until European settlement took place, then the anthropogenic disturbance began to severely impact the community composition of North American vegetation.

Levinsky et al.*, (2013)*

SDMs are applied to locate potential refugia of African birds and mammals during the LGM. 537 mammals and 1265 bird species were modelled, using current distributions, climate reconstructions of the LGM as a predictor variable and enveloping them to project predicted past distributions. Refugia were identified as areas “with a higher overlap of climatically suitable ranges (i.e. levels of species richness) than expected”.

Climate refugia are a classic example of no-analog communities, many assemblages which exist due to severe climate change (Stewart *et al.*, 2010) will have no modern analog. Six African areas were particularly novel, with high concentrations even beyond what resource availability could be predicted. This presence vs resource problem presented may be linked to a biotic interaction. The climate refugia itself may only exist due to abiotic interactions, but the assemblages themselves will be under significant influence from biotic interactions.

Stralberg et al., *(2009)*

Current and future distributions of Californian birds are predicted based on presence data and forecasting climate models of California. This study was specifically looking for communities without a modern analogue, it found that up to 57% of California could have novel assemblages. Areas with the most novel communities tended to be concentrated at the coast and in northern California. It is assumed in this study that biotic interactions do not affect current or future distributions of bird assemblages.

Brown et al.*, (2015)*

In Madagascar SDMs are applied to 2186 plant species. The models are constructed using occurrence records for the plants and three different environmental predictor scenarios based on current and future land cover variables. The impact of land cover and environmental changes is then projected onto the future of Madagascan plants. Large scale land cover and climate changes were predicted, the land cover itself an indirectly anthropogenic interaction. The novelty predicted is the massive loss of plant species due to land cover and climate changes, each scenario showed different levels of biodiversity loss depending on whether the focus was on climate or land use change. Though a combination of the two showed the sharpest declines. Dispersal was not factored in the models applied but it will undoubtably play a big role in the future of Madagascan vegetation and its ability to survive and recover from climate and land use changes.

Latif et al.*, (2013)*

Habitat suitability is predicted for black-backed woodpeckers in NW USA into the near future. Environmental variables are used as the sole predictors in the modelling used. The species is a disturbance specialist, settling in areas that have been recently disturbed. In this case, the species is a burned forest specialist. The habitat suitability of the study site was 40% across all models used. Due to the stochastic nature of fire novelty can arise in areas not normally vulnerable to fire. Climate change will only increase the number of areas vulnerable to fire so it is likely novel environments and communities will follow. The woodpecker moves to these areas for the purposes of nesting and foraging. The lack of competitors following a fire opens up areas normally unavailable to the woodpecker. Only modelling on the basis of fire ignores the main driver for the presence of the woodpecker.

García-López and Allué (2013)

By projecting worldwide climate into 2080 the future of no-analog zones is investigated. Climate is the sole prediction in this study. It is predicted that by 2080 between 3.5% and 17.5% of the surface of the earth will be under novel climates, depending on low and high climate change scenarios. >80% of this will be in the northern hemisphere. Temperature is the variable affecting the climate the most, with 32/34 biodiversity hotspots affected by temperature changes. 6.8% of the area of hotspots will develop a no-analog climate. These areas are likely to develop novel assemblages as individual species each react to this climate change.

Graham et al.*, (2017)*

SDMs are applied to hummingbird distribution in Ecuador, projecting climate and distribution up to 2070. The degree of disappearance and novelty of the species composition will be evaluated under the impact of climate change. As hummingbirds have a mutualistic relationship with local flora and they have physiological constraints, their potential range is considered to correlate well with environmental features. No assemblages were forecasted as disappearing fully but there was a great degree of novelty found in the eastern Andes. It was found nationwide that novelty was found mostly at high altitudes above 1000m. Disappearance was also of a greater degree at these high altitudes. This may indicate that hummingbird emigration is creating the novelty in these areas, whether the climate is less suitable at high altitudes or there is another interaction causing this change.

Novelty when biotic interactions are applied

Biotic interaction grade, 2; Novel community identified, Y

Miller and McGill (2017)

The migration capacity of trees across eastern US is assessed from the present until 2100. Temperate tree species are more likely to migrate rather than adapt to climate change. While many studies have focused on past distributions and responses to climate change the lack of anthropogenic impact means that using past results for our future is unlikely to be accurate. Here dispersal of 15 common species over 100 years is simulated, real world anthropogenic land use and species-specific life history is considered to create the most realistic representation of dispersal rates as possible. Results show that species dispersal rates will slow by 12-40%, with species the most impacted by anthropogenic land use having their habitat shifted the most. A slower dispersal coupled with effective barriers to dispersal created by humans will lead to species being unable to adapt to climate change quick enough to maintain biodiversity levels. The species which show a novel level of habitat change are sweetgum, loblolly pine, red oak and willow oak. The level of potential habitat for these species increases, however dispersal barriers mean the ability to fulfil this potential is low.

Hein, Öhlund and Englund (2012)

Arctic char is an ecologically and socially important species to northern countries, being the only species present in many alpine and Arctic waterbodies. The study aims to predict the future distribution of Artic char in Sweden while influenced by climate change. Fish occurrence and environmental data is applied to 1309 lakes across Sweden with the results then projected over 9430 lakes. Pike and brown trout are also modelled to provide additional variables to the distribution of Arctic char. The char are expected to lose approximately 73% of range across Sweden but should retain presence in lakes of a sufficient size. As expected, pike will cause extinctions of char but there is novelty to be found in brown trout having a facilitative effect on char though there is no known mutualistic relationship.

Urban, Tewksbury and Sheldon (2012)

Climate change predictions tend to omit species interactions and interspecific variation in dispersal. A model of competing species is applied here along a warming climate gradient, including biotic interactions along with environmental variables. Novel communities were created when competition and dispersal differences decreased diversity. Species with narrow niches were found to suffer the worst impacts of climate change, being unable to track climate change means they are vulnerable to a change in their environmental conditions. If the species is unable to either migrate or adapt it is unlikely they will survive. On the other hand, a species with a wide niche that is able to track climate change and has high interspecific dispersal variance will out-compete slower dispersers and ultimately cause their extinction. Current forecasts that neglect competition and dispersal differences are underestimating the impact of climate change and the extinction rates that will surely expand.

Discussion

The relationship between novelty and biotic interactions

When biotic interactions are not applied to SDMs there is evidence to suggest that the models and projections provided are not entirely accurate. The levels of novelty that arise during studies that do not apply biotic interactions could suggest information missing, it is possible that a species with an abnormally large range may have a more restricted range when under the influence of biotic interactions. Iannella *et al*., (2017) measures the impact of climate in the past on the smooth newt and notes that the southern range expands further than is expected. Maura *et al*., (2014) however, provides evidence of a biotic interaction. This study shows that the smooth newt did not recolonise its northernmost potential range during the post glaciation period by moving from the southern refugia. If climate was the most powerful driving force behind the smooth newts distribution then it stands to reason that during the post glaciation period, the newt would return to the pre-glaciation niche that it had realised (Maura *et al.,* 2014).

Theodoris *et al*., (2017) measures how the cold adapted *P.farinosa* adapted to climate change across Europe. The study shows that the species showed an atypical response to climate change, expanding its range unlike the normal response from a cold adapted species during the post glacial period. McKee and Richards (1998) show that *P. farinosa* is a species which responds negatively to warming temperatures, the seeds germinating least well at warmer temperatures. Increasing temperatures therefore may not be facilitating the expansion of *P. farinosa*, during the post glaciation period when many species are emerging from their refugia and beginning to expand dispersal is key to the composition of the community assemblages that form. This sudden expansion of potential niches creates new communities and coexistence of multiple species is promoted, while competitive exclusion reduces (Hewitt, 1999; Mohd *et al.,* 2017). These new communities that form may lack the kind of competitor that previously would have excluded *P. farinosa* from environmentally suitable areas. During the glaciated period the dominating vegetation type was steppe in the alps, a dry, grassy plain where the lack of competitors and somewhat favourable environmental conditions favoured the growth of *P. farinosa* (Huntley, 1990). During the post glacial period the vegetation type changed to mixed deciduous and coniferous forests over the next several thousand years, creating assemblages that may have been novel but were better suited to *P. farinosa* (Huntley, 1990; Lienert and Fischer, 2003). These facilitative assemblages are the kind which need further study in SDMs as they can assist in explanations of novel communities.

Pearman *et al*., (2008) and Veloz *et al*., (2012) simulate the response of European and North American plants, respectively to climate change from the Pleistocene and Holocene. Pearman *et al*., (2008) reveals that *Picea abies* and *Juniperus communis* both occupy a small realised niche when compared to their potential niche habitat. Schwörer *et al*., (2015) shows the impact that early humans had on plant communities in Europe and how they may have restricted the dispersal of some species while facilitating others, as was discussed earlier. The latter shows that *Fraxinus nigra* and *Ostrya/Carpinus* both have a much higher abundance than is expected and on levels not seen in modern assemblages. Gill *et al*., (2009) shows that the formation of novel plant communities in the time period of the deglaciation don't account for the massive megafaunal decline that occurred simultaneously. The loss of important, keystone herbivores will have released many plant species from herbivory pressure. This would have also created fuel accumulation and resulted in enhanced fire regimes across North America. The correlation between megafaunal decline and the rise of plant communities that have no analog is very high. Over 50% of large mammal species were extirpated, with climate change and anthropogenic influence (Gill *et al*., 2009; Schwörer *et al*., 2015) playing a significant role in this decline. The debate between these two impacts is not settled but both were key in the megafaunal collapse. While climate does play a vital role in the life history of North American and European plant communities, the impact of other species of plants, herbivores and humans should not be discounted. Due to the potential impact they may have, by not including them in modelling there are wide implications.

Past glaciation, which forms the temporal state of many studies in this review, created a series of no-analog climates which led to no-analog communities forming. The community composition of populations under a no-analog climate is not itself a useful tool for mitigating modern climate change and environmental changes. The individual responses to a changing climate are where conservationists and policy makers should focus, it is unlikely the no-analog climates of the Pleistocene and Holocene will reappear but it is species may respond to climate change similarly.

According to Table 1, when biotic interactions are applied the chance of a novel community appearing in the study is less. The number is still higher than no novel community found though. It is likely that under climate change novel communities will be formed no matter the level of biotic interaction modelling. However, the assemblages and communities that form during climate change must be understood fully to be able to mitigate any negative impacts, this is where the importance of biotic interactions is fully realised.

Challenges species distribution models face and the future of their application

Environmental variables and abiotic interactions are applied alone without biotic interactions in many cases in this review (Table 1). Inferring biotic interactions from the results of applying only abiotic interactions is possible. Species dispersal can be calculated from the potential and realised niche space a species occupies under climate change. Invasive species could be predicted by estimating when environmental variables alter to the point where potential habitats crosses boundaries into separate communities (Hellmann *et al.*, 2008). This is not a reliable method though. Predicting a species response to an environmental change should include direct information of the species (Baselga and Araújo, 2009).

Invasive species are rarely accounted for in SDMs but their impact on the environments that they invade can be severely detrimental to native biodiversity (Hellmann *et al.*, 2008; Lewis *et al.*, 2017). They are a primary driver of negative impacts to ecosystems across the globe and due to their nature of being a successful invader, they are tolerant to environmental changes. Invasive species are well suited to a climate changing world and due to changes in migration (Black *et al.*, 2011) as a form of adaptation there will be many new invasive species entering vulnerable ecosystems around the planet. Invasive species are another challenge SDMs face when predicting the future of global biodiversity.

Humans have had a well-documented negative impact on the planet, climate and biodiversity (Steffen, Crutzen and McNeill, 2007; Dirzo *et al.*, 2014; Lewis and Maslin, 2015) and with nearly every modern environmental study including climate change as a variable this is reflected. However, in SDMs the inclusion of land use change is still lacking. Land use change is attributed to increases in climate change (Kalnay and Cai, 2003; Searchinger *et al.*, 2008) and a decrease in global biodiversity (Reidsma *et al.*, 2006). The articles in this review which used land use change found it to be a serious threat to the ability of species to adapt and track climate change (Miller and McGill, 2018). The future of the planet is likely to be more and more urbanised and human encroachment will only increase upon natural habitats. Including land use change as a barrier to dispersal should be a key part of SDMs that project into the future.

It is common for projections into the future to use past climate responses as a platform to understand how future populations might respond to climate change. Even when early humans were causing extirpations and influencing their environment in a climate changing world, the anthropogenic impact they may have had pales in comparison to the epoch altering impact of modern humans. It is inaccurate to assume a species will respond in kind to past and present climate change.

Climate refugia played a crucial role in maintaining levels of biodiversity during the late Ice Age (Stewart *et al.*, 2010). Refugia present an interesting case of a no-analog community as they may become important to maintaining modern biodiversity in the case of extreme climate change causing widespread devastation to the planet. Modern refugia should be identified and have conservation efforts focused there in order to preserve biodiversity as much as possible in the future (Keppel *et al.*, 2012). Refugia play a role both during climate change and afterward. This is where understanding past responses to climate change will be necessary. The mass dispersal of species post climate event will create a planet wide novel assemblage of species, understanding and predicting this will help maintain modern life.

Due to time constraints the number of articles could only be limited, though the amount of literature on this topic is small enough that this review covered a large proportion of what is available.

Conservation efforts need to apply more biotic interactions into their SDMs, applying CLMs into future projections of climate change will create a reliable set of projections that allow for conservation efforts to focus on where species are predicted to habituate in future climate scenarios.

Conclusion

This study attempted to review species distribution models, their use of biotic interactions, and their identification of novel communities.

112 articles were found using a pre-defined set of criteria, from this 40 were used and evaluated. They were graded based on level of biotic interaction and investigated for novel communities. It was found that the use of biotic interactions in SDMs may play some role in determining novel communities, but it is likely they will form with only abiotic interaction due to the significant threat of climate change. In many articles where novelty was found, biotic explanations were found but the community compositions remained novel.

Future conservation must understand the need for fully understanding community assemblages and any potential refugia that plants and animals may migrate to. These are two major challenges that will make preparing for protection of biodiversity an easier task.

Afkhami, M. E., McIntyre, P. J. and Strauss, S. Y. (2014) ‘Mutualist-mediated effects on species’ range limits across large geographic scales’, *Ecology Letters*. Edited by W. van der Putten. Wiley/Blackwell (10.1111), 17(10), pp. 1265–1273. doi: 10.1111/ele.12332.

Araújo, M. B. and Luoto, M. (2007) ‘The importance of biotic interactions for modelling species distributions under climate change’, *Global Ecology and Biogeography*, 16(6), pp. 743–753. doi: 10.1111/j.1466-8238.2007.00359.x.

Barnosky, A. D. *et al.* (2011) ‘Has the Earth’s sixth mass extinction already arrived?’, *Nature*. Nature Publishing Group, pp. 51–57. doi: 10.1038/nature09678.

Barry, J. C. *et al.* (2002) ‘Paleontological Society Faunal and Environmental Change in the Late Miocene Siwaliks of Northern Pakistan Faunal and environmental change in the late Miocene Siwaliks of northern Pakistan’, *Paleobiology*. Cambridge University Press, 28(2), pp. 1–71. doi: 10.1666/0094-8373(2002)28[1:faecit]2.0.co;2.

Bartlein, P. J., Whitlock, C. and Shafer, S. L. (1997) ‘Future climate in the Yellowstone National Park region and its potential impact on vegetation’, *Conservation Biology*. Wiley/Blackwell (10.1111), 11(3), pp. 782–792. doi: 10.1046/j.1523-1739.1997.95383.x.

Baselga, A. and Araújo, M. B. (2009) ‘Individualistic vs community modelling of species distributions under climate change’, *Ecography*. Wiley/Blackwell (10.1111), 32(1), pp. 55–65. doi: 10.1111/j.1600-0587.2009.05856.x.

Bauer, A., Farrell, R. and Goldblum, D. (2016) ‘The Geography of Forest Diversity and Community Changes under Future Climate Conditions in the Eastern United States’, *Ecoscience*. Taylor & Francis, 23(1–2), pp. 41–53. doi: 10.1080/11956860.2016.1213107.

Benito-Garzón, M., Leadley, P. W. and Fernández-Manjarrés, J. F. (2014) ‘Assessing global biome exposure to climate change through the Holocene-Anthropocene transition’, *Global Ecology and Biogeography*. Wiley/Blackwell (10.1111), 23(2), pp. 235–244. doi: 10.1111/geb.12097.

Black, R. *et al.* (2011) ‘Migration as adaptation’, *Nature*, 478(7370), pp. 447–449. doi: 10.1038/478477a.

Blois, J. L. *et al.* (2014) ‘A framework for evaluating the influence of climate, dispersal limitation, and biotic interactions using fossil pollen associations across the late Quaternary’, *Ecography*. Wiley/Blackwell (10.1111), 37(11), pp. 1095–1108. doi: 10.1111/ecog.00779.

Boiffin, J., Badeau, V. and Bréda, N. (2017) ‘Species distribution models may misdirect assisted migration: Insights from the introduction of Douglas-fir to Europe: Insights’, *Ecological Applications*, pp. 446–457. doi: 10.1002/eap.1448.

Bonaccorso, E., Koch, I. and Peterson, A. T. (2006) ‘Pleistocene fragmentation of Amazon species' ranges', *Diversity and Distributions*. Wiley/Blackwell (10.1111), 12(2), pp. 157–164. doi: 10.1111/j.1366-9516.2005.00212.x.

Borszcz, T. and Zatoń, M. (2013) 'The oldest record of predation on echinoids: Evidence from the Middle Jurassic of Poland', *Lethaia*. Wiley/Blackwell (10.1111), 46(2), pp. 141–145. doi: 10.1111/let.12007.

Brown, D. G. (1994) 'Predicting vegetation types at treeline using topography and biophysical disturbance variables', *Journal of Vegetation Science*. Wiley/Blackwell (10.1111), 5(5), pp. 641–656. doi: 10.2307/3235880.

Brown, K. A. *et al.* (2015) 'Predicting plant diversity patterns in madagascar: Understanding the effects of climate and land cover change in a biodiversity hotspot', *PLoS ONE*. Edited by L. Kumar. Public Library of Science, 10(4), p. e0122721. doi: 10.1371/journal.pone.0122721.

Buckley, L. B. (2013) 'Get real: putting models of climate change and species interactions in practice', *Annals of the New York Academy of Sciences*. Wiley/Blackwell (10.1111), 1297(1), p. n/a-n/a. doi: 10.1111/nyas.12175.

Bueno de Mesquita, C. P. *et al.* (2016) 'Incorporating biotic factors in species distribution modeling: are interactions with soil microbes important?', *Ecography*, 39(10), pp. 970–980. doi: 10.1111/ecog.01797.

Buisson, L. *et al.* (2013) 'Toward a loss of functional diversity in stream fish assemblages under climate change', *Global Change Biology*. Wiley/Blackwell (10.1111), 19(2), pp. 387–400. doi: 10.1111/gcb.12056.

Butchart, S. H. M. (2010) 'Global Biodiversity : Indicators of', *Science*, 1164(May), pp. 1164–1169. doi: 10.1126/science.1187512.

Carrión, J. S., Rose, J. and Stringer, C. (2011) 'Early Human Evolution in the Western Palaearctic: Ecological Scenarios', *Quaternary Science Reviews*. Pergamon, 30(11–12), pp. 1281–1295. doi: 10.1016/J.QUASCIREV.2011.04.003.

Cavieres, L. A. *et al.* (2014) 'Facilitative plant interactions and climate simultaneously drive alpine plant diversity', *Ecology Letters*, 17(2), pp. 193–202. doi: 10.1111/ele.12217.

Colwell, R. K. and Rangel, T. F. (2009) 'Hutchinson's duality: the once and future niche.', *Proceedings of the National Academy of Sciences of the United States of America*, 106 Suppl(Supplement 2), pp. 19651–8. doi: 10.1073/pnas.0901650106.

D'Amen, M. *et al.* (2017) 'Spatial predictions at the community level: from current approaches to future frameworks', *Biological Reviews*. Wiley/Blackwell (10.1111), 92(1), pp. 169–187. doi: 10.1111/brv.12222.

Dalen, L. *et al.* (2007) 'Ancient DNA reveals lack of postglacial habitat tracking in the arctic fox', *Proceedings of the National Academy of Sciences*. National Academy of Sciences, 104(16), pp. 6726–6729. doi: 10.1073/pnas.0701341104.

Darwin, C. R. (1859) *On the origin of species by means of natural selection, or the preservation of favoured races in the struggle for life*. 1st edn. London: John Murray.

DEFRA (2011) *The Natural Choice: securing the value of nature, English*. Available at: http://www.official-documents.gov.uk/document/cm80/8082/8082.pdf.

Dirzo, R. *et al.* (2014) 'Defaunation in the Anthropocene', *Science*. American Association for the Advancement of Science, pp. 401–406. doi: 10.1126/science.1251817.

Dobrowski, S. Z. *et al.* (2011) 'Modeling plant ranges over 75 years of climate change in California, USA: temporal transferability and species traits', *Ecological Monographs*. Wiley-Blackwell, 81(2), pp. 241–257. doi: 10.1890/10-1325.1.

Ebert, D. (2005) '9 . Population Dynamics and Community Ecology', *Community Ecology*, (May 1974), pp. 1–8.

Elith, J. and Franklin, J. (2013) 'Species Distribution Modeling', *Encyclopedia of Biodiversity: Second Edition*, 6, pp. 692–705. doi: 10.1016/B978-0-12-384719-5.00318-X.

Espíndola, A. *et al.* (2012) 'Predicting present and future intra-specific genetic structure through niche hindcasting across 24 millennia', *Ecology Letters*. Wiley/Blackwell (10.1111), 15(7), pp. 649–657. doi: 10.1111/j.1461-0248.2012.01779.x.

Ferrier, S. *et al.* (2002) 'Extended statistical approaches to modelling spatial pattern in biodiversity in northeast New South Wales. II. Community-level modelling', *Biodiversity and Conservation*. Kluwer Academic Publishers, 11(12), pp. 2309–2338. doi: 10.1023/A:1021374009951.

Ferrier, S. and Guisan, A. (2006) 'Spatial modelling of biodiversity at the community level', *Journal of Applied Ecology*. Wiley/Blackwell (10.1111), pp. 393–404. doi: 10.1111/j.1365-2664.2006.01149.x.

Ficetola, G. F. and Maiorano, L. (2016) 'Contrasting effects of temperature and precipitation change on amphibian phenology, abundance and performance', *Oecologia*, 181(3), pp. 683–693. doi: 10.1007/s00442-016-3610-9.

Filazzola, A., Sotomayor, D. A. and Lortie, C. J. (2018) 'Modelling the niche space of desert annuals needs to include positive interactions', *Oikos*, 127(2), pp. 264–273. doi: 10.1111/oik.04688.

Flojgaard, C. *et al.* (2011) 'Deconstructing the mammal species richness pattern in Europe - towards an understanding of the relative importance of climate, biogeographic history, habitat heterogeneity and humans', *Global Ecology and Biogeography*. Wiley/Blackwell (10.1111), 20(2), pp. 218–230. doi: 10.1111/j.1466-8238.2010.00604.x.

Franklin, J. (2010) *Mapping species distributions*. Cambridge: Cambridge University Press. doi: 10.1017/CBO9780511810602.

García-López, J. M. and Allué, C. (2013) ‘Modelling future no-analogue climate distributions: A world-wide phytoclimatic niche-based survey’, *Global and Planetary Change*. Elsevier, 101, pp. 1–11. doi: 10.1016/j.gloplacha.2012.12.001.

Garciá Molinos, J. *et al.* (2016) ‘Climate velocity and the future global redistribution of marine biodiversity’, *Nature Climate Change*. Nature Publishing Group, 6(1), pp. 83–88. doi: 10.1038/nclimate2769.

Gill, J. L. *et al.* (2009) ‘Pleistocene megafaunal collapse, novel plant communities, and enhanced fire regimes in North America’, *Science*. American Association for the Advancement of Science, 326(5956), pp. 1100–1103. doi: 10.1126/science.1179504.

Godsoe, W., Franklin, J. and Blanchet, F. G. (2017) ‘Effects of biotic interactions on modeled species’ distribution can be masked by environmental gradients’, *Ecology and Evolution*. Wiley-Blackwell, 7(2), pp. 654–664. doi: 10.1002/ece3.2657.

Graham, L. J. *et al.* (2017) ‘Future geographic patterns of novel and disappearing assemblages across three dimensions of diversity: A case study with Ecuadorian hummingbirds’, *Diversity and Distributions*. Edited by J. Austin. Wiley/Blackwell (10.1111), 23(8), pp. 944–954. doi: 10.1111/ddi.12587.

Hansen, J. *et al.* (2005) ‘Climate Change: Earth’s energy imbalance: Confirmation and implications’, *Science*, 308(5727), pp. 1431–1435. doi: 10.1126/science.1110252.

Harris, D. J., Taylor, S. and White, E. P. (2017) ‘Forecasting biodiversity in breeding birds using best practices’, *bioRxiv*, pp. 1–27. doi: 10.1101/191130.

Hein, C. L., Öhlund, G. and Englund, G. (2012) ‘Future distribution of arctic char Salvelinus alpinus in Sweden under climate change: Effects of temperature, lake size and species interactions’, *Ambio*. Springer Netherlands, 41(SUPPL.3), pp. 303–312. doi: 10.1007/s13280-012-0308-z.

Hellmann, J. J. *et al.* (2008) ‘Five potential consequences of climate change for invasive species’, *Conservation Biology*. Wiley/Blackwell (10.1111), pp. 534–543. doi: 10.1111/j.1523-1739.2008.00951.x.

Hewitt, G. M. (1999) ‘Post-glacial re-colonization of European biota’, in *Biological Journal of the Linnean Society*. No longer published by Elsevier, pp. 87–112. doi: 10.1006/bijl.1999.0332.

Huntley, B. (1990) ‘European post-glacial forests: compositional changes in response to climatic change', *Journal of Vegetation Science*. Wiley/Blackwell (10.1111), 1(4), pp. 507–518. doi: 10.2307/3235785.

Hutchinson, G. E. (1957) 'Concluding Remarks', *Cold Spring Harbor Symposia on Quantitative Biology*, 22(0), pp. 415–427. doi: 10.1101/SQB.1957.022.01.039.

Iannella, M., Cerasoli, F. and Biondi, M. (2017) 'Unraveling climate influences on the distribution of the parapatric newts Lissotriton vulgaris meridionalis and L. italicus', *Frontiers in Zoology*, 14. doi: 10.1186/s12983-017-0239-4.

Jetz, W., Wilcove, D. S. and Dobson, A. P. (2007) 'Projected impacts of climate and land-use change on the global diversity of birds', *PLoS Biology*. Edited by G. M. Mace. Public Library of Science, 5(6), pp. 1211–1219. doi: 10.1371/journal.pbio.0050157.

Jezkova, T., Olah-Hemmings, V. and Riddle, B. R. (2011) 'Niche shifting in response to warming climate after the last glacial maximum: inference from genetic data and niche assessments in the chisel-toothed kangaroo rat (Dipodomys microps)', *Global Change Biology*. Wiley/Blackwell (10.1111), 17(11), pp. 3486–3502. doi: 10.1111/j.1365-2486.2011.02508.x.

Kalnay, E. and Cai, M. (2003) 'Impact of urbanization and land-use change on climate', *Nature*. Nature Publishing Group, 423(6939), pp. 528–531. doi: 10.1038/nature01675.

Kammerle, J. L. *et al.* (2017) 'Range loss of a threatened grouse species is related to the relative abundance of a mesopredator', *Ecosphere*, 8(9). doi: 10.1002/ecs2.1934.

Keith, S. A. *et al.* (2009) 'Non-analogous community formation in response to climate change', *Journal for Nature Conservation*. Elsevier, 17(4), pp. 228–235. doi: 10.1016/j.jnc.2009.04.003.

Keith, S. A. and Bull, J. W. (2017) 'Animal culture impacts species' capacity to realise climate-driven range shifts', *Ecography*, 40(2), pp. 296–304. doi: 10.1111/ecog.02481.

Keppel, G. *et al.* (2012) 'Refugia: identifying and understanding safe havens for biodiversity under climate change', *Global Ecology and Biogeography*. Wiley/Blackwell (10.1111), 21(4), pp. 393–404. doi: 10.1111/j.1466-8238.2011.00686.x.

Kissling, W. D. *et al.* (2012) 'Towards novel approaches to modelling biotic interactions in multispecies assemblages at large spatial extents', *Journal of Biogeography*, 39(12), pp. 2163–2178. doi: 10.1111/j.1365-2699.2011.02663.x.

Krosby, M. *et al.* (2015) 'Climate-induced range overlap among closely related species', *Nature Climate Change*. Nature Publishing Group, 5(9), pp. 883–886. doi: 10.1038/nclimate2699.

Kübler, D. *et al.* (2015) 'Assessing the importance of topographic variables for the spatial distribution of tree species in a tropical mountain forest', *Erdkunde*, 70(1), pp. 19–47. doi: 10.3112/erdkunde.2016.01.03.

Kuemmerle, T. *et al.* (2012) 'Reconstructing range dynamics and range fragmentation of European bison for the last 8000years', *Diversity and Distributions*. Wiley/Blackwell (10.1111), 18(1), pp. 47–59. doi: 10.1111/j.1472-4642.2011.00849.x.

Lambert, E. *et al.* (2014) 'Cetacean range and climate in the eastern North Atlantic: Future predictions and implications for conservation', *Global Change Biology*. Wiley/Blackwell (10.1111), 20(6), pp. 1782–1793. doi: 10.1111/gcb.12560.

Latif, Q. S. *et al.* (2013) 'Ensemble modeling to predict habitat suitability for a large-scale disturbance specialist', *Ecology and Evolution*, 3(13), pp. 4348–4364. doi: 10.1002/ece3.790.

Lentz, D. L., Bye, R. and Sánchez-Cordero, V. (2008) 'Ecological Niche Modeling and Distribution of Wild Sunflower (Helianthus annuus L.) in Mexico', *International Journal of Plant Sciences*. The University of Chicago Press, 169(4), pp. 541–549. doi: 10.1086/528754.

Levinsky, I. *et al.* (2013) 'Climate envelope models suggest spatio-temporal co-occurrence of refugia of African birds and mammals', *Global Ecology and Biogeography*. Wiley/Blackwell (10.1111), 22(3), pp. 351–363. doi: 10.1111/geb.12045.

Lewis, J. S. *et al.* (2017) 'Biotic and abiotic factors predicting the global distribution and population density of an invasive large mammal', *Scientific Reports*. Nature Publishing Group, 7(March), pp. 1–12. doi: 10.1038/srep44152.

Lewis, S. L. and Maslin, M. A. (2015) 'Defining the Anthropocene', *Nature*. Nature Publishing Group, 519(7542), pp. 171–180. doi: 10.1038/nature14258.

Lienert, J. and Fischer, M. (2003) 'Habitat fragmentation affects the common wetland specialist Primula farinosa in north-east Switzerland', *Journal of Ecology*. Wiley/Blackwell (10.1111), 91(4), pp. 587–599. doi: 10.1046/j.1365-2745.2003.00793.x.

Lindenmayer, D. B. *et al.* (2010) 'Improved probability of detection of ecological "surprises"', *Proceedings of the National Academy of Sciences*. National Academy of Sciences, 107(51), pp. 21957–21962. doi: 10.1073/pnas.1015696107.

Liow, L. H. *et al.* (2016) 'Interspecific interactions through 2 million years: Are competitive outcomes predictable?', *Proceedings of the Royal Society B: Biological Sciences*. The Royal Society, 283(1837), p. 20160981. doi: 10.1098/rspb.2016.0981.

Lyons, S. K. (2003) 'A QUANTITATIVE ASSESSMENT OF THE RANGE SHIFTS OF PLEISTOCENE MAMMALS', *Journal of Mammalogy*. Oxford University Press, 84(2), pp. 385–402. doi: 10.1644/1545-1542(2003)084<0385:AQAOTR>2.0.CO;2.

Maguire, K. C. *et al.* (2015) 'Modeling Species and Community Responses to Past, Present, and Future Episodes of Climatic and Ecological Change’, *Annual Review of Ecology, Evolution, and Systematics*, 46(1), pp. 343–368. doi: 10.1146/annurev-ecolsys-112414-054441.

Maguire, K. C. *et al.* (2016) ‘Controlled comparison of species- and community-level models across novel climates and communities’, *Proceedings of the Royal Philosophical Society - B*, 283, p. 20152817. doi: 10.1098/rspb.2015.2817.

Maura, M. *et al.* (2014) ‘Northern richness and cryptic refugia: Phylogeography of the Italian smooth newt Lissotriton vulgaris meridionalis’, *Biological Journal of the Linnean Society*. Wiley/Blackwell (10.1111), 113(2), pp. 590–603. doi: 10.1111/bij.12360.

McCullagh, P. (Peter) and Nelder, J. A. (1989) *Generalized linear models*. Chapman and Hall. Available at: https://www.crcpress.com/Generalized-Linear-Models-Second-Edition/McCullagh-Nelder/p/book/9780412317606 (Accessed: 23 May 2018).

McKee, J. and Richards, A. J. (1998) ‘The effect of temperature on reproduction in five Primula species’, *Annals of Botany*. Oxford University Press, 82(3), pp. 359–374. doi: 10.1006/anbo.1998.0697.

Menge, B. A. and Olson, A. M. (1990) ‘Role of scale and environmental factors in regulation of community structure’, *Trends in Ecology & Evolution*. Elsevier Current Trends, 5(2), pp. 52–57. doi: 10.1016/0169-5347(90)90048-I.

Miller, K. M. and McGill, B. J. (2018) ‘Land use and life history limit migration capacity of eastern tree species’, *Global Ecology and Biogeography*, 27(1), pp. 57–67. doi: 10.1111/geb.12671.

Mohd, M. H. *et al.* (2017) ‘Effects of biotic interactions and dispersal on the presence-absence of multiple species’, *Chaos, Solitons and Fractals*. Pergamon, 99, pp. 185–194. doi: 10.1016/j.chaos.2017.04.012.

Moore, D. M., Lees, B. G. and Davey, S. M. (1991) ‘A new method for predicting vegetation distributions using decision tree analysis in a geographic information system’, *Environmental Management*. Springer-Verlag, 15(1), pp. 59–71. doi: 10.1007/BF02393838.

Nieto-Lugilde, D. *et al.* (2018) ‘Multiresponse algorithms for community-level modelling: Review of theory, applications, and comparison to species distribution models’, *Methods in Ecology and Evolution*. Edited by P. Peres-Neto. Wiley/Blackwell (10.1111), 9(4), pp. 834–848. doi: 10.1111/2041-210X.12936.

Normand, S. *et al.* (2011) ‘Postglacial migration supplements climate in determining plant species ranges in Europe’, *Proceedings of the Royal Society B: Biological Sciences*. The Royal Society, 278(1725), pp. 3644–3653. doi: 10.1098/rspb.2010.2769.

Olden, J. D. (2003) ‘A Species-Specific Approach to Modeling Biological Communities and Its Potential for Conservation’, *Conservation Biology*. Wiley/Blackwell (10.1111), 17(3), pp. 854–863. doi: 10.1046/j.1523-1739.2003.01280.x.

Overton, J. M. *et al.* (2002) ‘Information pyramids for informed biodiversity conservation’, *Biodiversity and Conservation*. Kluwer Academic Publishers, 11(12), pp. 2093–2116. doi: 10.1023/A:1021386426790.

Pearman, P. B. *et al.* (2008) ‘Prediction of plant species distributions across six millennia’, *Ecology Letters*. Wiley/Blackwell (10.1111), 11(4), pp. 357–369. doi: 10.1111/j.1461-0248.2007.01150.x.

Pearson, R. G. and Dawson, T. P. (2003) ‘Predicting the impacts of climate change on the distribution of species: Are bioclimate envelope models useful?’, *Global Ecology and Biogeography*, 12(5), pp. 361–371. doi: 10.1046/j.1466-822X.2003.00042.x.

Pelletier, T. A. *et al.* (2015) ‘Historical species distribution models predict species limits in western plethodon salamanders’, in *Systematic Biology*, pp. 909–925. doi: 10.1093/sysbio/syu090.

Pellissier, L. *et al.* (2010) ‘Species distribution models reveal apparent competitive and facilitative effects of a dominant species on the distribution of tundra plants’, *Ecography*, 33(6), pp. 1004–1014. doi: 10.1111/j.1600-0587.2010.06386.x.

Poinar, G. (2002) ‘First fossil record of nematode parasitism of ants; a 40 million year tale’, *Parasitology*. Cambridge University Press, 125(5), pp. 457–459. doi: 10.1017/S0031182002002287.

Poloczanska, E. S. E. S. *et al.* (2008) ‘Modeling the Response of Populations of Competing Species To Climate Change’, *Ecology*, 89(11), pp. 3138–3149. doi: 10.1890/07-1169.1.

Radeloff, V. C. *et al.* (2015) ‘The rise of novelty in ecosystems’, *Ecological Applications*, 25(8), pp. 2051–2068. Available at: https://pdfs.semanticscholar.org/f345/3d82d3488edbed1f8570fac5fae2fb2af1f4.pdf (Accessed: 17 April 2018).

Rafferty, N. E. (2017) ‘Effects of global change on insect pollinators: multiple drivers lead to novel communities’, *Current Opinion in Insect Science*. Elsevier, pp. 22–27. doi: 10.1016/j.cois.2017.06.009.

Rehfeldt, G. E. *et al.* (2012) ‘North American vegetation model for land-use planning in a changing climate: A solution to large classification problems’, *Ecological Applications*. Wiley-Blackwell, 22(1), pp. 119–141. doi: 10.1890/11-0495.1.

Reidsma, P. *et al.* (2006) ‘Impacts of land-use change on biodiversity: An assessment of agricultural biodiversity in the European Union', *Agriculture, Ecosystems & Environment*. Elsevier, 114(1), pp. 86–102. doi: 10.1016/J.AGEE.2005.11.026.

Reu, B. *et al.* (2014) 'Future no-analogue vegetation produced by no-analogue combinations of temperature and insolation', *Global Ecology and Biogeography*. Wiley/Blackwell (10.1111), 23(2), pp. 156–167. doi: 10.1111/geb.12110.

Ričánková, V. P., Robovský, J. and Riegert, J. (2014) 'Ecological structure of recent and last glacial mammalian faunas in northern Eurasia: The case of Altai-Sayan refugium', *PLoS ONE*. Edited by M. Hofreiter. Public Library of Science, 9(1), p. e85056. doi: 10.1371/journal.pone.0085056.

Roberts, D. R. and Hamann, A. (2012) 'Predicting potential climate change impacts with bioclimate envelope models: A palaeoecological perspective', *Global Ecology and Biogeography*. Wiley/Blackwell (10.1111), 21(2), pp. 121–133. doi: 10.1111/j.1466-8238.2011.00657.x.

Ruddiman, W. F. (2003) 'The Anthropogenic Greenhouse Era Began Thousands of Years Ago', *Climatic Change*. Kluwer Academic Publishers, 61(3), pp. 261–293. doi: 10.1023/B:CLIM.0000004577.17928.fa.

Sage, R. F. and Coleman, J. R. (2001) 'Effects of low atmospheric CO2on plants: More than a thing of the past', *Trends in Plant Science*. Elsevier Current Trends, pp. 18–24. doi: 10.1016/S1360-1385(00)01813-6.

Schwörer, C. *et al.* (2015) 'Early human impact (5000-3000 BC) affects mountain forest dynamics in the Alps', *Journal of Ecology*. Edited by A. Austin. Wiley/Blackwell (10.1111), 103(2), pp. 281–295. doi: 10.1111/1365-2745.12354.

Searchinger, T. *et al.* (2008) 'Use of U.S. croplands for biofuels increases greenhouse gases through emissions from land-use change', *Science*. American Association for the Advancement of Science, 319(5867), pp. 1238–1240. doi: 10.1126/science.1151861.

Silva, D. P. *et al.* (2015) 'Adding Biotic Interactions into Paleodistribution Models: A Host-Cleptoparasite Complex of Neotropical Orchid Bees', *PLOS ONE*. Edited by H. T. Lumbsch. Public Library of Science, 10(6), p. e0129890. doi: 10.1371/journal.pone.0129890.

Simakova, A. N. (2006) 'The vegetation of the Russian Plain during the second part of the Late Pleistocene (33–18 ka)', *Quaternary International*. Pergamon, 149(1), pp. 110–114. doi: 10.1016/J.QUAINT.2005.11.024.

Sommer, R. S. *et al.* (2011) 'When the pond turtle followed the reindeer: Effect of the last extreme global warming event on the timing of faunal change in Northern Europe', *Global Change Biology*. Wiley/Blackwell (10.1111), 17(6), pp. 2049–2053. doi: 10.1111/j.1365-

2486.2011.02388.x.

Steffen, W., Crutzen, P. J. and McNeill, J. R. (2007) ‘The Anthropocene: Are Humans Now Overwhelming the Great Forces of Nature’, *AMBIO: A Journal of the Human Environment*. The Royal Swedish Academy of Sciences, 36(8), pp. 614–621. doi: 10.1579/0044-7447(2007)36[614:TAAHNO]2.0.CO;2.

Steffen, W. and et al. (2018) ‘Trajectories of the Earth System in the Anthropocene’, *Proceedings of the National Academy of Sciences of the United States of America*. National Academy of Sciences, in review, pp. 1–45. doi: 10.1073/pnas.1810141115.

Stewart, J. R. *et al.* (2010) ‘Refugia revisited: Individualistic responses of species in space and time’, *Proceedings of the Royal Society B: Biological Sciences*. The Royal Society, pp. 661–671. doi: 10.1098/rspb.2009.1272.

Stralberg, D. *et al.* (2009) ‘Re-shuffling of species with climate disruption: A no-analog future for California birds?’, *PLoS ONE*. Edited by R. DeSalle. Public Library of Science, 4(9), p. e6825. doi: 10.1371/journal.pone.0006825.

Stuble, K. L. *et al.* (2017) ‘Outside the envelope: rare events disrupt the relationshipbetween climate factors and species interactions’, *Ecology*. Wiley-Blackwell, 98(6), pp. 1623–1630. doi: 10.1002/ecy.1820.

Theodoridis, S. *et al.* (2017) ‘How Do Cold-Adapted Plants Respond to Climatic Cycles? Interglacial Expansion Explains Current Distribution and Genomic Diversity in Primula farinosa L.’, *Systematic Biology*. Oxford University Press, 66(5), pp. 715–736. doi: 10.1093/sysbio/syw114.

Urban, M. C., Tewksbury, J. J. and Sheldon, K. S. (2012) ‘On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during climate change’, *Proceedings of the Royal Society B: Biological Sciences*, 279(1735), pp. 2072–2080. doi: 10.1098/rspb.2011.2367.

Urban, M. C., Zarnetske, P. L. and Skelly, D. K. (2013) ‘Moving forward: dispersal and species interactions determine biotic responses to climate change’, *Annals of the New York Academy of Sciences*. Wiley/Blackwell (10.1111), 1297(1), p. n/a-n/a. doi: 10.1111/nyas.12184.

Uribe-Rivera, D. E. *et al.* (2017) ‘Dispersal and extrapolation on the accuracy of temporal predictions from distribution models for the Darwin’s frog:’, *Ecological Applications*. Wiley-Blackwell, 27(5), pp. 1633–1645. doi: 10.1002/eap.1556.

Varela, S. *et al.* (2010) ‘Were the Late Pleistocene climatic changes responsible for the disappearance of the European spotted hyena populations? Hindcasting a species geographic distribution across time', *Quaternary Science Reviews*. Pergamon, 29(17–18), pp. 2027–2035. doi: 10.1016/J.QUASCIREV.2010.04.017.

Veloz, S. D. *et al.* (2012) 'No-analog climates and shifting realized niches during the late quaternary: Implications for 21st-century predictions by species distribution models', *Global Change Biology*, 18(5), pp. 1698–1713. doi: 10.1111/j.1365-2486.2011.02635.x.

Wainwright, C. E. *et al.* (2016) 'Diverse outcomes of species interactions in an invaded annual plant community', *Journal of Plant Ecology*. Oxford University Press, 10(6), p. rtw102. doi: 10.1093/jpe/rtw102.

Williams, J. W. and Jackson, S. T. (2007) 'Novel climates, no-analog communities, and ecological surprises', *Frontiers in Ecology and the Environment*, 5(9), pp. 475–482. doi: 10.1890/1540-9295(2007)5[475:NCNCAE]2.0.CO;2.

Williams, J. W., Shuman, B. N. and Webb, T. (2001a) 'Dissimilarity analysis of late-Quaternary vegetation and climate in eastern North America', *Ecology*. Wiley-Blackwell, 82(12), pp. 3346–3362. doi: 10.1890/0012-9658(2001)082[3346:DAOLQV]2.0.CO;2.

Williams, J. W., Shuman, B. N. and Webb, T. (2001b) 'Dissimilarity analysis of late-Quaternary vegetation and climate in eastern North America', *Ecology*, 82(12), pp. 3346–3362. doi: 10.1890/0012-9658(2001)082[3346:DAOLQV]2.0.CO;2.

Wisz, M. S. *et al.* (2013) 'The role of biotic interactions in shaping distributions and realised assemblages of species: Implications for species distribution modelling', *Biological Reviews*, 88(1), pp. 15–30. doi: 10.1111/j.1469-185X.2012.00235.x.

Yee, T. W. and Mackenzie, M. (2002) 'Vector generalized additive models in plant ecology', *Ecological Modelling*. Elsevier, 157(2–3), pp. 141–156. doi: 10.1016/S0304-3800(02)00192-8.