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Fallacies and fantasies: the theoretical underpinnings of the Coexistence Approach for palaeoclimate reconstruction

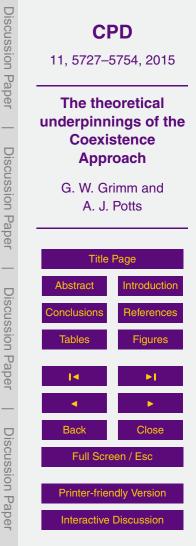
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Abstract

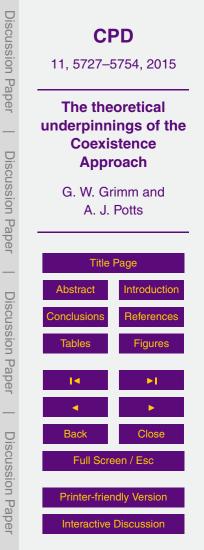
The Coexistence Approach has been used infer palaeoclimates for many Eurasian fossil plant assemblage. However, the theory that underpins the method has never been examined in detail. Here we discuss acknowledged and implicit assumptions, and assess the statistical nature and pseudo-logic of the method. We also compare the Coexistence Approach theory with the active field of species distribution modelling. We argue that the assumptions will inevitably be violated to some degree and that the method has no means to identify and quantify these violations. The lack of a statistical framework makes the method highly vulnerable to the vagaries of statistical outliers and exotic elements. In addition, we find numerous logical inconsistencies, such as how climate shifts are quantified (the use of a "center value" of a coexistence interval) and the ability to reconstruct "extinct" climates from modern plant distributions. Given the problems that have surfaced in species distribution modelling, accurate and precise quantitative reconstructions of palaeoclimates (or even climate shifts) using

the nearest-living-relative principle and rectilinear niches (the basis of the method) will not be possible. The Coexistence Approach can be summarised as an exercise that shoe-horns a plant fossil assemblages into coexistence and then naively assumes that this must be the climate. Given the theoretical issues, and methodological issues highlighted elsewhere, we suggest that the method be discontinued and that all past reconstructions be disregarded and revisited using less fallacious methods.

1 Introduction

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One of the most widely used methods to infer the palaeoclimates of Eurasia using fossil plant assemblages is the "Coexistence Approach" (Utescher et al., 2014). Conceptually, this approach belongs to the family of mutual climate range techniques but also makes use of the "nearest-living-relative" principle; a nearest-living-relative (NLR) is a modern taxon (species, group of species, genus, or higher) that is considered an



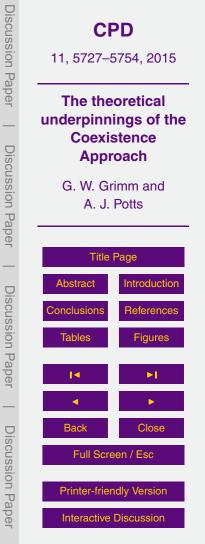


analogue for the fossil taxon. Mutual climate range methods use the climatic preferences of modern species (a set of nearest-living-relatives), as defined by their current distribution, to infer the potential climatic niche for a fossil assemblage. In the case of the Coexistence Approach, the climate niche is defined using minimum and maximum

- climate values of an NLR, obtained from its present-day distribution. Pure mutual climate range techniques are usually restricted to reconstructing palaeoclimates of the recent past (i.e. Quaternary) where species in the fossil assemblages can be directly linked to modern species (e.g. Elias, 1997, 2001; Thompson et al., 2012; Harbert and Nixon, 2015); the processes of extinction and speciation are ignored and niche con-
- ¹⁰ servatism is considered to be the norm. However, to apply these palaeoclimate reconstruction techniques to assemblages from older time periods requires the use of the nearest-living-relative principle, which is linked to the concept of physiological uniformitarianism (Tiffney and Manchester, 2001; Tiffney, 2008). The niche-space of an NLR is used to represent that of the fossil taxon. Thus, one assumes that the climate niche
- of the NLR (the modern species or species set) is identical to that of the associated fossil taxon (an extinct sister or ancestral species) and the mutually shared climate range of the NLRs enables the estimation of the climate conditions in which the fossil assemblage thrived (Fig. 1).

Despite the availability of alternative palaeoclimate reconstruction techniques using NLRs and the mutual climate range approach (e.g. Greenwood et al., 2005), the Coexistence Approach has become the de facto method for plant fossil assemblages of Eurasia for time periods spanning the Miocene to Late Cretaceous (Utescher et al., 2014). The cumulative citation count of studies using the Coexistence Approach is in excess of 10 000. On the surface, it reconstructs precise palaeoclimatic conditions

²⁵ (usually reported with a precision of 0.1 °C and 1 mm precipitation per month or year) based on a series of acknowledged and implicit basic assumptions (Table 1; Mosbrugger and Utescher, 1997; Utescher et al., 2014). These assumptions appear straightforward, but have theoretical and practical implications essentially ignored in the application of the Coexistence Approach (Mosbrugger and Utescher, 1997; Utescher et al.,





2014; Grimm et al., 2015). Furthermore, the Coexistence Approach avoids any statistical processing (Mosbrugger and Utescher, 1997; Utescher et al., 2014). It relies to some degree on hard-to-grasp pseudo-logic, some of which is advocated as strengths of the method, e.g. the ability to reconstruct extinct climates (Utescher et al., 2014).

⁵ The applicability of the nearest-living-relative principle for reconstructing past climates in a quantitative manner is never questioned. This is surprising in the light of ongoing discussions in the field of spatial distribution modelling, which shares a number of assumptions with mutual climate range and nearest-living-relatives methods. Below we discuss each of these issues in further detail.

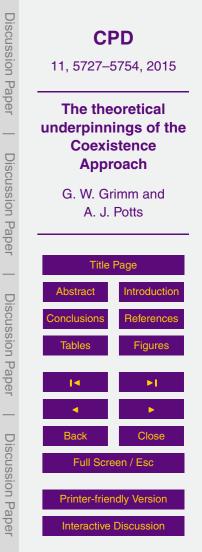
10 2 Theoretical background of the "Coexistence Approach"

2.1 Assumptions of the Coexistence Approach

Mosbrugger and Utescher (1997) list four basic assumptions that need to be fulfilled (Table 1). The first assumption has never been used in the application of the Coexistence Approach, and the three others superimpose additional uncertainty on the ¹⁵ method and are easily violated, particularly if the aim is high accuracy and precision. Notably, none of the assumptions have been tested and verified for taxa commonly used in the Coexistence Approach.

The first assumption is anchored on the ability to define a "systematically close" NLR (Table 1). However, Mosbrugger and Utescher (1997) or Utescher et al. (2014) do not provide a framework on how to quantify "systematically close" and in what respect systematic closeness should be relevant for the identification of the NLR. A focus on "systematic closeness" can lead to conflict with the nearest-living-relative principle. This principle is based on overall morphological similarity and not necessarily linked to phylogenetic relatedness, which is the current basis of systematics. Thus, a fossil may

²⁵ be "systematically close" to a modern species (or group) that has undergone significant shifts in morphology and fundamental niche, and the best modern analogue may be

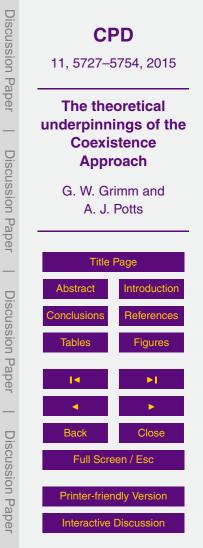




a more distantly related lineage that has been morphologically and ecologically stable (Fig. 2a). In addition, the degree of systematic relatedness of a fossil to an NLR requires the placement of fossils within a phylogenetic framework (i.e. a tree or network) and this has never been explored in any Coexistence Approach study.

- ⁵ There are further issues with Assumption 1 when considering the taxonomic affiliation of an NLR. Given the timespan separating ancient assemblages and modern day taxa, it has been agreed that defining an NLR at the species level is highly problematic (Grimm and Denk, 2012; Utescher et al., 2014). Thus, the Coexistence Approach usually defines a "systematically close" NLR as the genus or family to which the fossil can
- ¹⁰ be assigned, with rare instances of an intrageneric lineage or a modern species (Grimm and Denk, 2012; Utescher et al., 2014; Grimm et al., 2015). For example, the NLR of a fossil oak leaf would be genus *Quercus*, the NLR of a deciduous, convexly lobed oak leaf would be *Quercus* Group Quercus (the white oak clade), and the NLRs of a fagaceous fossil of unknown generic affinity would be all Fagaceae. Hence "system-
- atically close", as used in the Coexistence Approach and other nearest-living-relative approaches, translates into simply being a member of the same taxonomic rank (e.g. genus or family), and the actual phylogenetic (= systematic) distances between fossils and their NLRs is never established. Under this implementation of assigning NLRs to higher taxonomic ranks (above species) includes the taxonomic problems linked to
- ²⁰ paraphyly (exclusive common origin; Fig. 2b). Fossils of a paraphyletic group will have different systematic distances to the modern members of the specified taxonomic group of NLRs. However, this is not a problem for the combination of mutual climate range approaches and nearest-living-relative principle as long as the assumption of physiological uniformitarianism is fulfilled (Assumption 2). Thus, shared ancestry remains
- ²⁵ important, but the "systematic closeness" of Assumption 1 is entirely superfluous for the application of mutual climate range techniques making use of the nearest-livingrelative concept.

The second assumption (Table 1) is based upon the concept of physiological uniformitarianism (Tiffney and Manchester, 2001; Tiffney, 2008). Physiological uniformi-



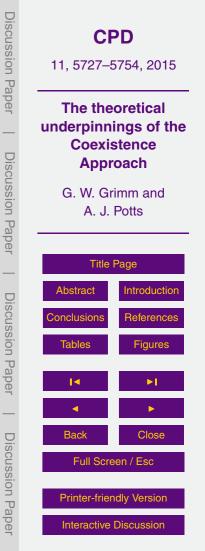


tarianism implies that as long as lineage stays within its environmental niche, it will not accumulate morphological changes. Hence, a modern species with the same, or very similar, morphological traits of a fossil of the same evolutionary lineage should share the same environmental niche. It also implies that members of the lineages that

- ⁵ have undergone niche shifts also experienced morphological changes. Assumption 2 is likely to be violated when morphological changes are evident between the fossil and modern members of an evolutionary lineage and an NLR of a fossil specimen should only be used if there is morphological, not mere taxonomic, similarity (ideally identical) and have a common origin. This would exclude the use of most modern plant genera and all familian as NLR on a three taxonomic and the second of morphological divergent.
- ¹⁰ and all families as NLRs as they are typically composed of morphologically divergent species.

In addition, the use of morphologically diverse taxonomic groups to represent an NLR usually means that the environmental niche of the NLR is large, likely encompassing the niche of the fossil, but is not "climatically similar" to that of the fossil; thus,

- directly violating Assumption 2. Novel procedures and methods are required that take cognisance of the fact that the NLR niche is likely to be far broader than can be expected for that of the fossil. The actual assumption, as used by Coexistence Approach practitioners, is that the climatic niche of a fossil taxon lies somewhere within the range of niches found within the species comprising the NLR. This has two major implications
- ²⁰ for the setup and interpretation of reconstructed palaeoclimates using the Coexistence Approach (and other mutual climate range techniques that use NLRs): (1) a high resolution climate reconstruction should not be possible, especially when only minimum and maximum NLR tolerances are used (Fig. 3a), and (2) mixed floras may not be identified as mutually exclusive species (or communities) can have overlapping climate
- ranges at higher taxonomic levels (Fig. 3b). Thus, highly precise and accurate climate reconstructions can only be obtained using the Coexistence Approach if the critical species within a palaeoassemblage occupied niches close to the minimum and maximum tolerances of their corresponding modern genus- or family level NLRs.



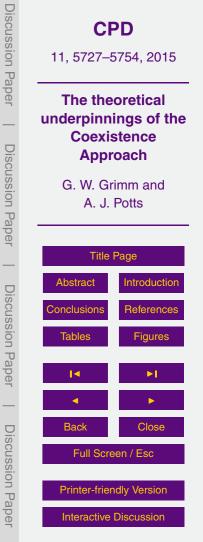


The third assumption (Table 1), that the distributions of extant species are in equilibrium with their climate, is a topic rich with discussions in the ecological and species distribution modelling literature (Araújo and Pearson, 2005; Bond et al., 2005; Sexton et al., 2009; Franklin, 2010). Species are often not in equilibrium with their climate for abiotic (e.g. soil, fire) or biotic (e.g. competition) reasons, and thus their realised niches do not span their fundamental niches. Thus species will be plastic in their expression of the realised niche depending on external factors, which would exclude the reconstruction of palaeoclimate with high accuracy. Any change in the abiotic or biotic parameters can affect the distribution of a species (i.e. its realised niche) even if the fundamental niche remains unchanged.

The climatic niche is solely represented by minimum and maximum values in the Coexistence Approach, which are independently compiled for climate parameters in a univariate manner. However, it has been long established that biological climate niches are multi-dimensional (Köppen, 1936; Hutchinson, 1957; Walter, 1973; Walter and Breckle,

- 15 1983–1991; Schroeder, 1998). Using minimum-maximum tolerances along univariate axes can only roughly approximate the multidimensional climatic niche, and may be misleading (Klotz, 1999; Thompson et al., 2012). For example, two *mutually exclusive* taxa, for which Assumption 3 applies, may still have an artificial mutual climate range regarding their minimum and maximum tolerances (Fig. 4a). In this context it is im-
- ²⁰ portant to note that species distribution modelling started with algorithms that used minimum and maximum values, but quickly moved on to methods that better represented the bioclimatic niche of a species (discussed further below). Thus, the use of range values for climatic parameters does not accurately capture the climatic requirements or tolerances of an NLR, which will affect the reconstructed palaeoclimate using the Coexistence Approach.

The fourth and last assumption has no apparent theoretical implications. Technical implications have been discussed in Grimm and Denk (2012), Thompson et al. (2012), Utescher et al. (2014), and Grimm et al. (2015). We do, however, wish to highlight that since local climate can substantially vary over short time scales, minimum and



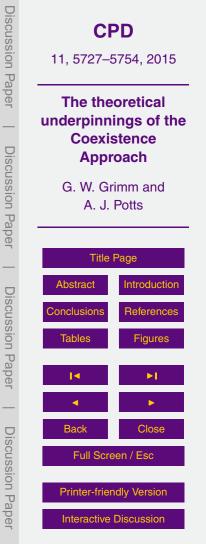


maximum tolerances may be unduly affected by the selected observation period of climate stations.

Not formally addressed by Mosbrugger and Utescher (1997) or Utescher et al. (2014) are two more fundamental assumptions in the application of the Coexistence Approach, which distinguish the method from mutual climate range techniques using modern-day species: (1) palaeoassemblages comprise only taxa that existed as actual communities (i.e. all fossil specimens are autochthonous and from the same point in time), (2) absence of a fossil taxon indicates true absence (i.e. each fossil plant assemblage comprehensively reflects the actual palaeocommunity). The Coexistence Approach implicitly assumes that only an autochthonous and strictly coeval palaeoassemblage will

- ¹⁰ plicitly assumes that only an autochthonous and strictly coeval palaeoassemblage will result in a single coexistence interval. However, given that two mutually exclusive taxa can share a climate range of minimum and maximum along univariate climate parameters, so too can allochthonous taxa in a fossil assemblage. In addition, the expansion of the climate niche using higher-level NLRs automatically increases the probability of ar-
- tificial coexistence. Thus, allochthonous assemblages (mixed floras) do not necessarily result in ambiguous intervals (Fig. 4b–d) and may very well be the reason for highly precise palaeoclimate estimates (< 1 °C for temperature parameters, < 100 mm precipitation per year, < 10 mm precipitation per month) observed in many studies using the Coexistence Approach (Grimm and Denk, 2012; Grimm et al., 2015). Thompson
- et al. (2012) suggest that a benefit of mutual climate range techniques, in comparison to indicator-species approaches, is that the reconstruction is only affected by the presence of taxa, not their absence. However, this does not apply to the Coexistence Approach, where the mere absence of a taxon can directly affect the outcome of the reconstruction (discussed further below). For instance, absence of a taxon may eliminate another NLR as "climatic outlier" rather than producing two "ambiguous" intervals.

We have outlined a range of probable and inevitable issues of the purported basic assumptions of the Coexistence Approach. These will all, to some unknown degree, decrease the precision and accuracy of any approach that attempts to reconstruct palaeoclimates. In this light, the Coexistence Approach is highly unlikely to reconstruct





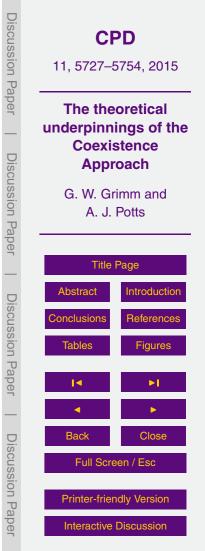
precise or accurate palaeoclimatic conditions. Utescher et al. (2014) state that it is impossible to test the accuracy of Coexistence Approach reconstructions (but see Grimm and Denk, 2012, for mean annual temperature estimates), but follow the original paper in assuming that violation of the basic assumptions will readily surface in the form of *"climatic outliers"*.

2.2 The statistical nature of the Coexistence Approach

According to Utescher et al. (2014) the "Coexistence Approach by Mosbrugger and Utescher (1997) is a nearest living relative method, which relies only on the presence/absence of a plant taxon within a fossil assemblage and the climatic requirements of its modern relatives. It avoids any statistical processing or further assumptions, ex-

- *cept those given in Mosbrugger and Utescher (1997)* [i.e. the four basic assumptions, see Table 1]". In the original paper, no means of statistical processing were proposed, hence, the Coexistence Approach defines an interval for a past climate parameter assuming that statistical effects do not exist or are negligible. The Coexistence Approach
- ¹⁵ ignores the majority of the community information because the reconstructed climate interval is always solely defined by the pair of the two most divergent, but putatively coexisting NLRs. Usually one member of the pair is an exotic element; here we define "exotic" as any NLR whose niche is at odds with the majority of the assemblage (e.g. Fig. 5). The Coexistence Approach lacks a statistical framework to account for potential
- oddities, errors or violations of assumptions, the likelihood of which increases with assemblage size or depositional age. The approach naively relies on the presumption that any violation will readily surface in the form of so-called "*climatic outliers*" (Mosbrugger and Utescher, 1997; Utescher et al., 2014). This exposes palaeoclimate reconstructions using this approach to the vagaries of statistical outliers and exotic elements (see Grimm and Denk, 2012; Grimm et al., 2015, for real-world data examples).

A "climatic outlier" is identified as an NLR or small number of NLRs that do not share the climate space for a given parameter with a slightly higher number of other NLRs (Fig. 5). In those cases where there are more than one interval that can be



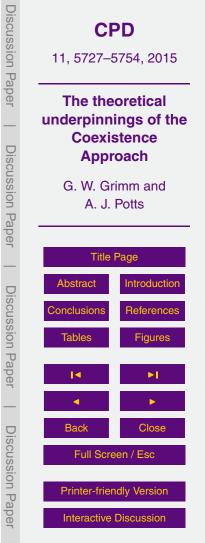
reconstructed using the same maximum possible number of NLRs, then alternative *"ambiguous"* intervals are reported; each of these intervals recognises a different set of climatic outliers. Ambiguous intervals are interpreted by Utescher et al. (2014) as the only evidence for mixed floras rather than a violation of any the assumptions discussed
 ⁵ above. Taxa identified as climatic outliers are typically removed from a Coexistence

Approach analysis for a given palaeoassemblage and parameter. We wish to highlight that a climatic outlier is simply an NLR that is seemingly at odds with a few other NLRs and must not to be confused with a statistical outlier (Fig. 5).

There are two paramount problems with the current outlier elimination strategy used

- ¹⁰ by the Coexistence Approach. First, *two* taxa *violating* the assumptions behind the Coexistence Approach may eliminate *one* taxon that is not. A typical situation is illustrated in Fig. 5, where an NLR occupying a climate range that is in general agreement with the rest of the flora would be identified and eliminated as a climatic outlier because of presence of two deviant taxa that are at odds with the overall NLR community. Second,
- taxa identified as climatic outliers for one parameter and therefore removed from the assemblage for estimating that parameter are still, in most cases, kept for analysing other parameters for the same assemblage. In some cases, these climatic outliers even define the coexistence interval in another parameter (Grimm et al., 2015). If we follow the logic that climatic outliers represent violations of the basic assumptions of the Coexis-
- tence Approach (Utescher et al., 2014), then it is imperative that they are removed from all reconstructions for a given assemblage or in general (Table 2). This has been rarely applied in any study that has identified climatic outliers in the Coexistence Approach, mainly to avoid wide, and thus uninformative, coexistence intervals (Grimm and Denk, 2012; Grimm et al., 2015). It could be argued that any palaeoassemblage represented by mutually avaluative. We have a should be imported until the reason for the pan epsylictence.
- ²⁵ by mutually exclusive NLRs should be ignored until the reason for the non-coexistence can be identified and corrected for.

Any mutual climate range approach needs a framework to identify statistical outliers as the assumptions will inevitably be violated, and establishing the degree of violation (e.g. degree of niche shifts) is not feasible based on current knowledge. Many



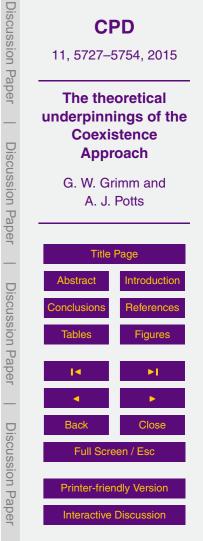


palaeoassemblages will comprise mixed floras with elements from different climate niches, and this would need to be explicitly addressed before reconstructing coexistence intervals. As stated above, the Coexistence Approach lacks any framework to identify exotic elements or allochthonous assemblages, unless they are sufficiently di-

- ⁵ vergent to generate climatic outliers. Allochthonous assemblages comprising mutually exclusive species can share a climate interval (Fig. 4b), and this problem of pseudo-coexistence is exacerbated by the use of *higher-level taxa* (genera, families) as NLRs of a fossil *species/morphotypes*. Any slightly conflicting, but exotic, element in an assemblage will have a disproportionally high influence on the palaeoclimate estimates
- ¹⁰ (Fig. 5). It is clear that not only "climatic outliers" and "ambiguous intervals" should be indicative of mixed floras, errors in the data, or violations in the assumptions, but also *any* narrow coexistence interval (see Grimm and Denk, 2012; Grimm et al., 2015, for real-world examples).

Mutual climate range techniques that apply simple statistics to filter exotic taxa, such as the Bioclimatic Approach (Greenwood et al., 2005), will be less susceptible to the presence and absence of a few exotic taxa, but will also usually fail to recognise mixed floras. The problem of mixed floras can only be overcome, to some degree, by using alternative mutual climate range techniques that make use of the full spectrum of distributional information, and thus include the climatic preference of all constituent el-

- ements of a palaeoassemblage (e.g. using the niche curves in Fig. 5). This includes methods such as the weighted mutual climate range approach (Thompson et al., 2012), the probability density function method (Chevalier et al., 2014), and the coexistence likelihood estimation method (Harbert and Nixon, 2015). However, these methods will probably begin to break down when the nearest-living-relative principle is needed to
- ²⁵ link fossils with extant lineages (Thompson et al., 2012; Harbert and Nixon, 2015), and may explain why their application has been limited to Quaternary assemblages.



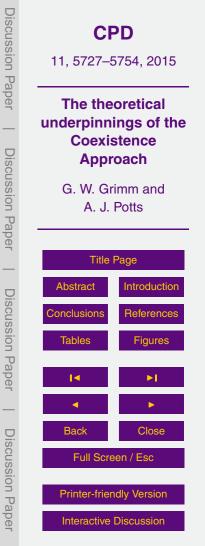
2.3 Pseudo-logic of the Coexistence Approach

We wish to highlight four additional points regarding the use of the Coexistence Approach that lack any (bio)logical basis, specifically: (1) the use of the "center value" to identify and quantify climatic shifts, (2) that the reconstructed climate is based on only two nominally coexisting elements, (3) that the reconstructed climate is highly dependent on the presence or absence of a single or few taxa (the "Heisenberg effect"), and

(4) the reconstruction of "extinct" climates. We elaborate on each of these points below. The conclusions of most Coexistence Approach studies rely on shifts observed in the so-called "center value". This value is simply the arithmetic mean of the upper and

- ¹⁰ lower boundary of the coexistence interval. Practical tests have shown that there is little correlation between the actual climate and the "center value" (Klotz, 1999; Grimm and Denk, 2012). The use of this value highlights a fundamental misunderstanding of the niche concept. If we imagine the coexistence interval to be correct, then *all* values within the interval should be equally probable as no other information is incorporated re-
- ¹⁵ garding the probabilities of occurrence of the assemblage. Selecting the "center value" as an indicator of a shift in climate makes no statistical or biological sense. For example, Fig. 6a shows two plant assemblages that differ only by the climatic preference of a single NLR. The replacement of one NLR by another with a preference towards *lower* values gives rise to a reconstructed climate shift towards *higher* values using the "center value".

Many Coexistence Approach reconstructions rely on the presence of NLRs that nominally coexist, even if these elements have climate tolerances that are at odds with the rest of the assemblage (Fig. 5; cf. Grimm and Denk, 2012; Grimm et al., 2015). In extreme cases the same coexistence interval can be reconstructed based on plant assemblages with contrary climate tolerances (Fig. 6b). In Fig. 6b, the elements of two plant assemblages have contrary climate tolerances and it is the two exotic taxa in each assemblage that ensure that the reconstructed coexistence intervals are the same. Thus, the precision of the reconstructed palaeoclimates is often entirely depen-





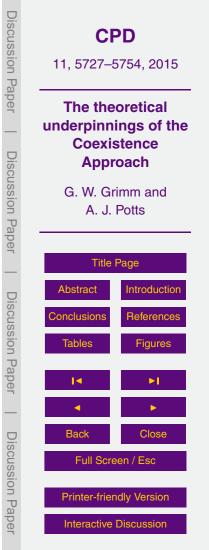
dent on the presence or absence of specific, usually exotic NLRs. Across Coexistence Approach studies, a handful of NLRs that occur towards the tolerance margins over the *entirety* of all palaeofloras usually determine the coexistence intervals; it is these few NLRs that give rise to the praised precision of the technique (Grimm and Denk, 2012; Grimm et al., 2015).

The presence or absence of individual NLRs are generally at the base of reconstruction uncertainty in coexistence interval – we term this the "Heisenberg" effect. Figure 6c shows two very similar assemblages where the presence or absence of the two highlighted taxa changes the coexistence interval reconstructed by the Coexistence 10 Approach in a degree that would be interpreted as a trend towards higher values. The Heisenberg effect renders palaeoclimate estimates obtained with the Coexistence Approach protocol highly susceptible to taxon-bias effects. The reconstructed climate is exceedingly dependent on what fraction of the actual vegetation has been captured by the fossil assemblages (note that in Fig. 6c all NLRs have a mutually shared climate 15 range). Thus, even if all assumptions needed for a mutual climate range approach that

range). Thus, even if all assumptions needed for a mutual climate range approach that also uses the nearest-living-relative principle are fulfilled, the Heisenberg effect will lead to unstable, even random, climate reconstructions.

Utescher et al. (2014) explicitly state that, as each parameter is independently reconstructed, the Coexistence Approach has the potential to reconstruct a climate that

- does not exist today: an "extinct climate". It is hard to grasp how this can be logically accommodated with the basic assumptions of the Coexistence Approach and the actuo-palaeontological nearest-living-relative principle in general (Fig. 7). An extinct climate for a palaeoassemblage would indicate that the present-day niches of the NLRs are not representative of the fossils, and therefore would indicate direct violations of the coexistence of the fossils.
- Assumptions 2 and 3 discussed above (Table 1). In addition, it is not possible to construct an extinct climate using species that are restricted to present-day climates if the principle of physiological uniformitarianism applies. Reasons why extinct climates are reconstructed using the Coexistence Approach include violations of basic assumptions, pseudo-coexistence, the inconsistent identification of climatic outliers within an



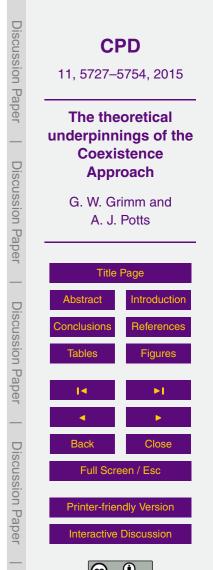


assemblage across climate variables, and the single-dimension effect where climate parameters are analysed in isolation and are assumed to be unlinked. The reconstruction of an extinct climate should be seen as a direct indication of error, and not lauded as a benefit of the method.

Ignoring these logical inconsistencies in the conception and application of the method, the Coexistence Approach still cannot be expected to reproduce a robust quantitative reconstruction of the palaeoclimate, as (1) assumptions are likely to be violated but cannot be detected, (2) one cannot avoid using higher-level taxa to represent fossil species or morphotypes, and (3) the fossil record will always be incomplete to different degrees, and this will affect the calculated coexistence interval.

3 Applicability of the nearest-living-relative principle: lessons to be learnt from species distribution modelling

Species distribution modelling (SDM) is an exceptionally active field which aims to empirically model the species-environment relationships and thereby quantify the realised niche of a given taxon (Franklin, 2010; Peterson et al., 2011) or, in some cases, commu-15 nities (e.g. Potts et al., 2013). The dawn of the field was the BIOCLIM software package (Nix, 1986), which is comparable to the Coexistence Approach as it used the range (or percentile range) of climatic variables in a rectilinear fashion. Booth et al. (2014) describe the roots of the field and highlight that one of the most active areas of SDM development has been of methods that trim the rectilinear climate envelopes of BIO-20 CLIM. This was driven by the early realisation that the relationships between climate variables was poorly captured by the rectilinear approach; for example, a rectilinear niche may suggest that a species could survive in a situation where it is both hot and dry, but the actual climate niche is that it only occurs where it is hot and wet. More advanced methods have refined the *n* dimensional hyperniche (Hutchinson, 1957) where response curves are used to capture the suitability of different conditions for species occurrence. This revolution in the multidimensional guantification of the niche



has completely bypassed the Coexistence Approach and many other nearest-livingrelative methods. BIOCLIM performed poorly in comparison to more recent methods in a comparison of more recent SDM methods (Elith et al., 2006) indicating that the simplistic use of range values for climatic variables, as used by the Coexistence Approach, is a poor representation of the realised niche of species or NLR.

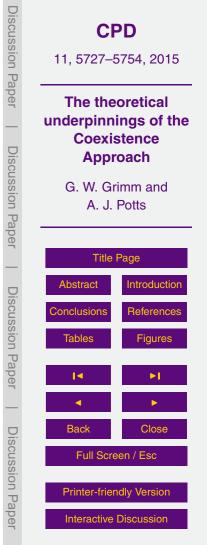
The assumption of niche conservatism (linked to the principle of physiological uniformitarianism) has generated considerable debate in the SDM literature as it has been used as justification for projecting models into altered climate states (past or future) and to predict the establishment and spread of invasive species (reviewed in Pearman

- et al., 2008a). These discussions have centred firstly on whether the current distribution for a given species, i.e. the realised niche, adequately represents the fundamental niche; and secondly, how quickly the fundamental niche might be able to shift? Such concerns are absent in the theoretical underpinnings of Coexistence Approach (Mosbrugger and Utescher, 1997; Utescher et al., 2014). Unfortunately, niche shifts have
 been documented for a wide range of plant species both through space (Broennimann
- ¹⁵ been documented for a wide range of plant species both through space (Broennimann et al., 2007; Pearman et al., 2008a) and even over relatively short time scales (Pearman et al., 2008b; Veloz et al., 2011). Therefore the assumption of physiological uniformitarianism has limited applicability to reconstruct precise and accurate palaeoclimates, especially with increasing age of an assemblage.

20 4 Conclusions

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Using best-possible climate data for modern North American woody plants, Thompson et al. (2012) were unable to reconstruct the climatic shifts from the Last Glacial Maximum to the present-day using an unweighted mutual climatic range method (which represents the niche using range values and is equivalent with the Coexistence Approach save for the use of NLRs). This is in stark contrast to the beliefs of Coexistence Approach practitioners that the method can reconstruct climate shifts at high-precision, despite the additional error and uncertainty associated with the nearest-living-relative

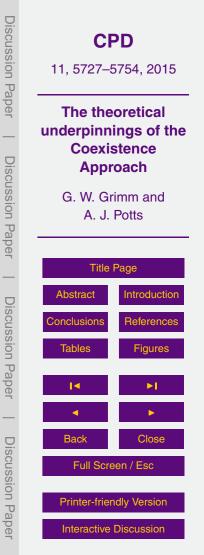


principle. The purported high precision in Coexistence Approach studies is dependent on phenomena such as pseudo-coexistence and the lack of a sound statistical framework.

- We argue that the Coexistence Approach, as conceived by Mosbrugger and Utescher (1997), violates the basic concepts behind mutual climate range techniques and the nearest-living-relative principle. It imposes a number of assumptions that will inevitably be violated and has no ability to detect violations and generally lacks any safeguards against the reconstruction of artificial coexistence intervals and thus erroneous palaeoclimate estimates. We conclude that using more elaborate mutual climate range techniques (e.g. point density function: Punyasena, 2008; weighted mutual cli-
- 10 mate range: Thompson et al., 2012; coexistence likelihood estimation: Harbert and Nixon, 2015) will, to some degree, counter these problems. Ultimately, the limitations of mutual climate range techniques for palaeoclimate reconstruction do not lie in the methodological framework to estimate the coexistence space, but rather the applica-
- bility of the nearest-living-relative principle. Application of mutual climate range tech-15 niques on palaeofloras will always depend on thoughtful filtering a fossil assemblage for elements that have proven to show niche conservatism. Fossil-NLR associations should be carefully selected to ensure that the principle of physiological uniformitarianism applies, in contrast to the current practise of data-naive bulk analyses in Coexis-
- tence Approach studies. 20

Given the theoretical problems outlined here, and the practical problems highlighted by Grimm et al. (2015) – for example, that any random real-world flora will eventually produce a "statistically significant" coexistence interval with a high number (> 20) of NLRs – we suggest that all palaeoclimate reconstruction studies using the Coexistence

Approach be disregarded and that the palaeoassemblages be revisited with improved 25 methods and careful, well-documented, and well-investigated NLR-associations. We suspect that quantitative palaeoclimate estimates at a high precision and accuracy is an impossible goal when the nearest-living-relative principle has to be applied, and





that semi-quantitative approaches may prove to be more robust, such as the Köppen signature approach proposed by Denk et al. (2013).

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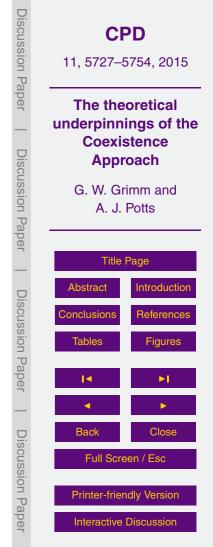
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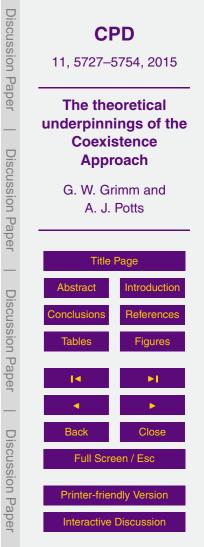
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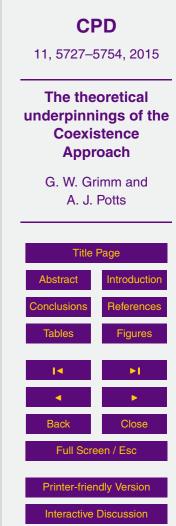
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Discussion

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Table 1. The assumptions of the Coexistence Approach (quotations from Utescher et al., 2014).

Description	Issues
Assumption 1: "For fossil taxa systematically closely related nearest living rel- atives (NLRs) can be identified."	(a) Lack of a theoretical framework to define a sys- tematically close relative, (b) Concept of physiologi- cal uniformitarianism assumes a common origin, bu does not need quantification of phylogenetic close- ness
Assumption 2: "The climatic requirements of a fossil taxon are similar to those of its nearest living relative."	(a) Physiological uniformitarianism cannot be gener- ally assumed, (b) Different taxonomic ranks of fos- sils and their nearest-living relatives
Assumption 3: "The climatic requirements or tolerances of a nearest living relative" [i.e. minimum and maximum tolerances regarding single parameters that are considered per se to be independent from each other] "can be derived from its" [current] "area of distribution"	(a) Distribution is not necessarily a function of cli- mate, but also other biotic and abiotic parameters: the realised niche < fundamental niche (b) Minimum and maximum tolerances are poor estimates for the climatic niche of a taxon (c) Climate parameters are not independent from each other (d) There are no working frameworks to test if a potential nearest- living-relative fulfils Assumption 3
Assumption 4: "The modern climatic data used are reliable and of good quality"	More or less violated in all studies that applied the Coexistence Approach (see Grimm and Denk 2012)
Assumption 5: Palaeoassemblages represent actual communities	(a) Fossils may be allochthonous, in particular mi- crofossils (pollen). (b) Fossils may not be strictly coeval (macrofossil lagerstätten usually cover sub- stantial time periods)
Assumption 6: Absence of a fossil in a palaeoassemblage is evidence of true absence	The fossil record is incomplete

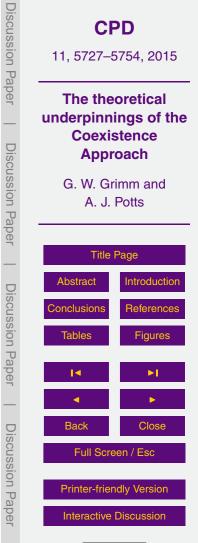
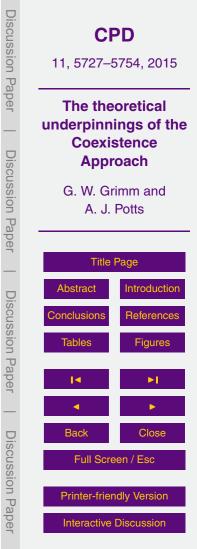




Table 2. The consequences of identifying a "climatic outlier" in a palaeoassemblage supposing that these represent violations of one or more of the four basic assumptions.

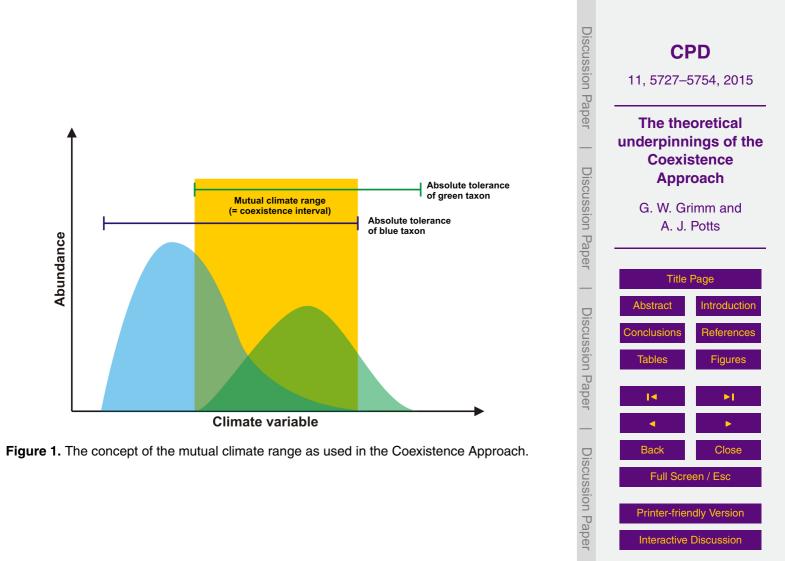
Violation of basic assumption	Consequence
1: The nearest-living-relative (NLR) is not a close relative of a fossil taxon	There is no consequence as long as the NLR shares the same lineage and is a good physiological mod- ern analogue.
2: The climatic requirements of the fossil taxon are different from the NLR	If different for one climate parameter, the NLR may be equally non-representative for other climate pa- rameters of the fossil taxon. Any coexistence inter- val including this fossil taxon may be misinformed.
3: The NLR's distribution is not representative for its climatic requirements (relict distribution)	Coexistence intervals delimited by the NLR are likely to be misinformed in any study using the NLR.
4: The modern climate data to estimate NLR minimum and maximum toler- ances are unreliable.	If this is the case, then no coexistence interval is re- liable and palaeoclimate reconstruction using mod- ern analogues is impossible.



Discussion Paper

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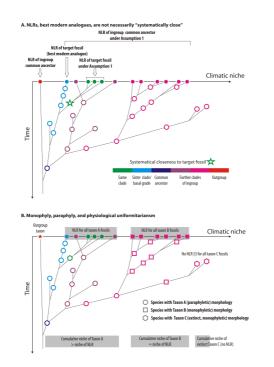
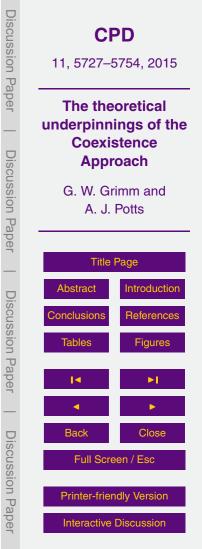


Figure 2. Difference between "systematically close" and nearest-living-relative (NLR, i.e. best modern analogues). Shown is a species phylogeny of a diversified ingroup; the outgroup in this example is a sister species of the ingroup. **(a)** Standard definition of nearest-living relative (best modern analogue) vs. definition if Assumption 1 of the Coexistence Approach should be fulfilled. **(b)** Same tree as in A, only that each species is categorised as a member of a distinct morphotaxon that can be distinguished in the fossil record. Note that all morphotaxa are mutually exclusive regarding their climatic niche, but there is no strict correlation between systematic closeness (phylogeny) and the climatic niche of the fossils and their nearest-living relatives (modern species of the same morphotypes as the fossils).





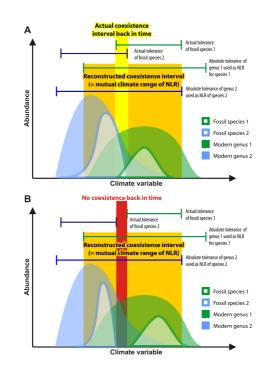
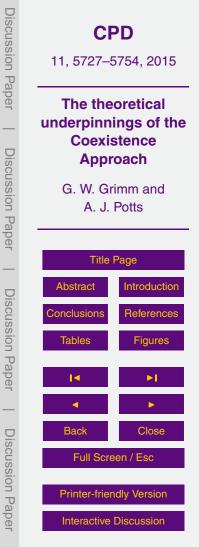


Figure 3. Issues related to the use higher-level taxonomic classification (e.g. genus or family) as nearest-living relatives (NLRs) of fossil species. In this example, two fossil species occupy a climate range within the modern climate range of their selected genus-level NLRs, fulfilling the principle of physiological uniformitarianism. (a) The fossil species have a narrow shared climate range and coexisted in the past. The use of higher-level taxonomic ranks as NLRs will lead, in most cases, to a much broader and less precise reconstructed coexistence interval. (b) The fossil species are mutually exclusive, but the expansion of the niche space – due to the use of genera as NLRs – results in a coexistence interval (i.e. pseudo-coexistence).





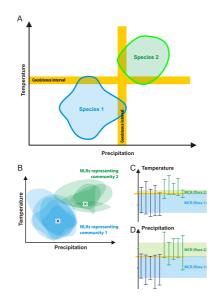
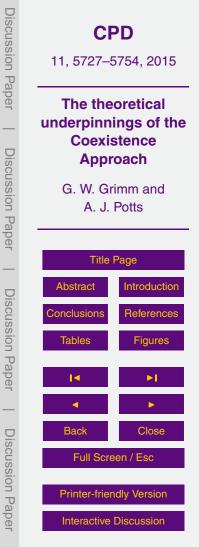
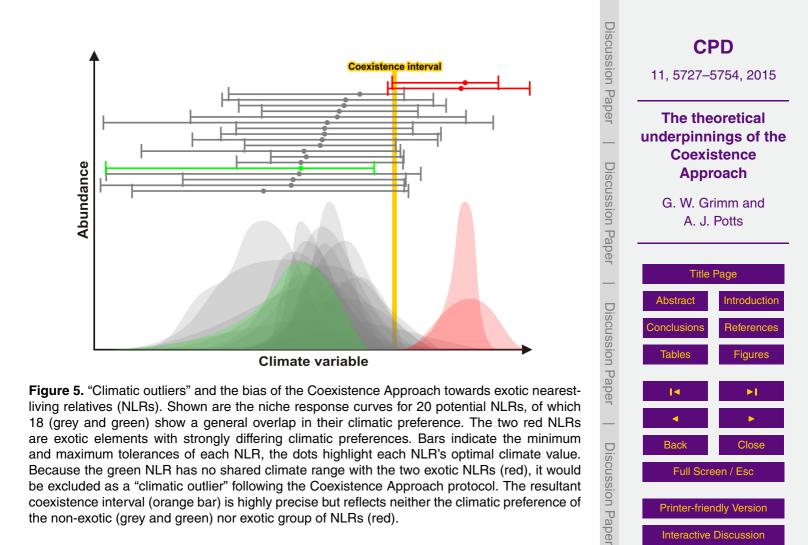


Figure 4. Pseudo-coexistence as a result of the representation of the climate niche using minimum and maximum tolerances. **(a)** Bivariate climate niches of two mutually exclusive species. These species have no overlapping climate space, but still reconstruct narrow coexistence intervals (orange bars) along univariate axes. **(b)** Bivariate climate niches of NLRs of two floras growing under substantially different climates (indicated "x"s). Note that only the niches of three of the Community 1 species overlap with one or two of the Community 2 species. **(c, d)** Univariate mutual climate ranges (MCR) of both communities; the overlap of the two MCR result in highly precise coexistence intervals for the artificially mixed communities including all elements from Community 1 and Community 2.







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Interactive Discussion

Because the green NLR has no shared climate range with the two exotic NLRs (red), it would

be excluded as a "climatic outlier" following the Coexistence Approach protocol. The resultant coexistence interval (orange bar) is highly precise but reflects neither the climatic preference of

the non-exotic (grey and green) nor exotic group of NLRs (red).

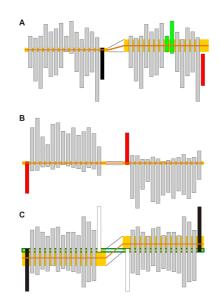
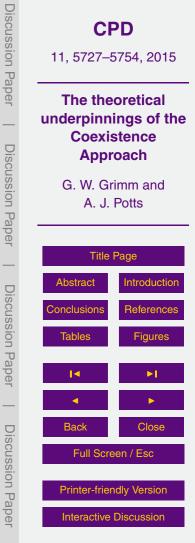


Figure 6. Logical inconsistencies in the application and theory of the Coexistence Approach. Shown are coexistences intervals (orange bars) based on slightly **(a, c)** or extremely **(b)** different sets of nearest-living relatives (NLRs). **(a)** Use of the "center value" to determine climate shifts. A single NLR (black) is replaced by a NLR tolerant to *lower* values (red), which would be eliminated as a "climatic outlier" by the two green NLRs; thus leading to a *higher* "center value": **(b)** all NLRs have contrasting climate tolerances, the exotic taxa in both floras (red) ensure that the reconstructed coexistence interval is the same. **(c)** Two floras that only differ by the absence (white bars) or presence (black bars) of each a single taxon. The resulting coexistence intervals would be interpreted as a shift towards higher values. The green box shows the coexistence interval of a flora in which both taxa are represented.





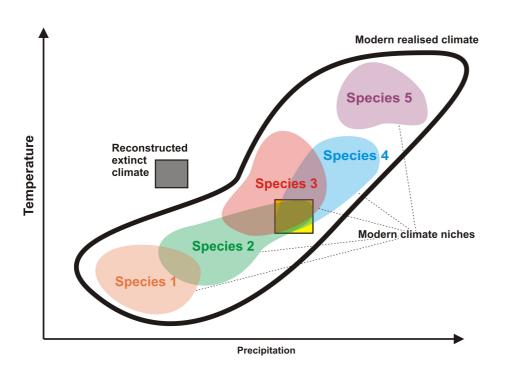


Figure 7. Impossibility of reconstructing extinct climates with the nearest-living-relative (NLR) principle. Shown are the (realised) climate niches of five modern species, which, inevitably have to lie within the frame of the modern climate space. Any coexistence space (yellow square, showing the coexistence space of species 2, 3, and 4 using their minimum and maximum tolerances) must reflect a climate situation also found today. Any extinct climate (grey square) could only be defined by the coexistence of species with *different* climate niches than found in modern species, species with no living NLR or species belonging to lineages that underwent niche shift.

