

The theoretical underpinnings of the Coexistence Approach

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This discussion paper is/has been under review for the journal Climate of the Past (CP).
Please refer to the corresponding final paper in CP if available.

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

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Received: 18 November 2015 – Accepted: 6 December 2015 – Published: 18 December 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.

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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

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

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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 conservatism 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 (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.,

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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 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 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 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.

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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, 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 important 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 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 artificial 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 ($< 1^{\circ}\text{C}$ for temperature parameters, $< 100\text{ mm}$ precipitation per year, $< 10\text{ mm}$ 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

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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 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 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 Coexistence 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 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

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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 divergent 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 (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 elements 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 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.

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 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 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 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

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has completely bypassed the Coexistence Approach and many other nearest-living-relative 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 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.

4 Conclusions

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

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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 climate 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 applicability of the nearest-living-relative principle. Application of mutual climate range techniques 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 Coexistence Approach studies.

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 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

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

Acknowledgements. This study was funded by the Austrian Science Fund (FWF) with a grant to GWG, project number M1751-B16. AJP received support from the National Research Foundation (RCA13091944022).

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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 relatives (NLRs) can be identified.” | (a) Lack of a theoretical framework to define a systematically close relative, (b) Concept of physiological uniformitarianism assumes a common origin, but does not need quantification of phylogenetic closeness |
| Assumption 2: “The climatic requirements of a fossil taxon are similar to those of its nearest living relative.” | (a) Physiological uniformitarianism cannot be generally assumed, (b) Different taxonomic ranks of fossils 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 climate, 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 microfossils (pollen). (b) Fossils may not be strictly coeval (macrofossil lagerstätten usually cover substantial time periods) |
| Assumption 6: Absence of a fossil in a palaeoassemblage is evidence of true absence | The fossil record is incomplete |

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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 modern 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 parameters of the fossil taxon. Any coexistence interval 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 tolerances are unreliable. | If this is the case, then no coexistence interval is reliable and palaeoclimate reconstruction using modern analogues is impossible. |

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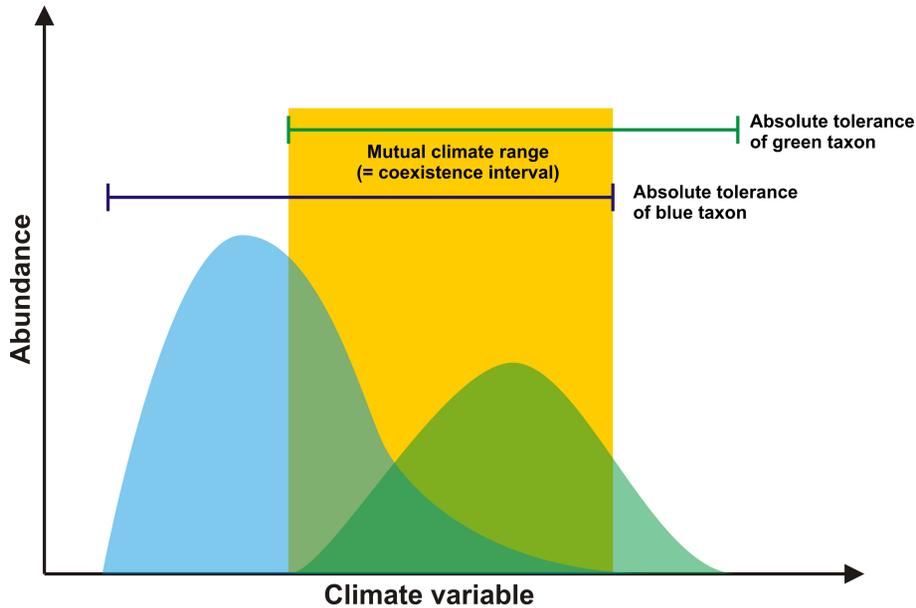


Figure 1. The concept of the mutual climate range as used in the Coexistence Approach.

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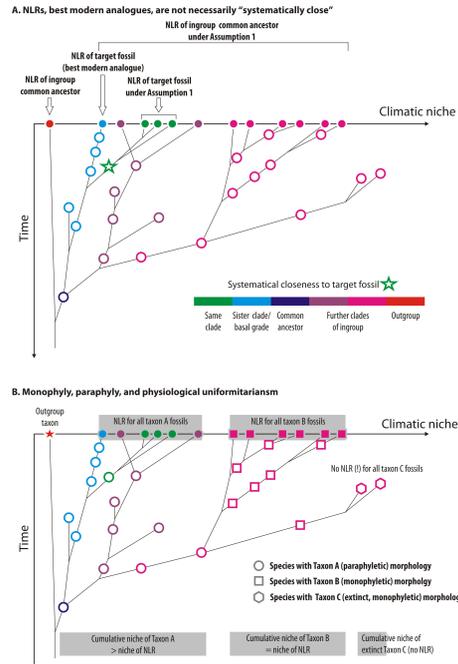


Figure 2. Difference between “systematically close” and nearest-living-relative (NLR, i.e. best modern analogues). Shown is a species phylogeny of a diversified ingroup; the outgroup in this example is a sister species of the ingroup. **(a)** Standard definition of nearest-living relative (best modern 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).

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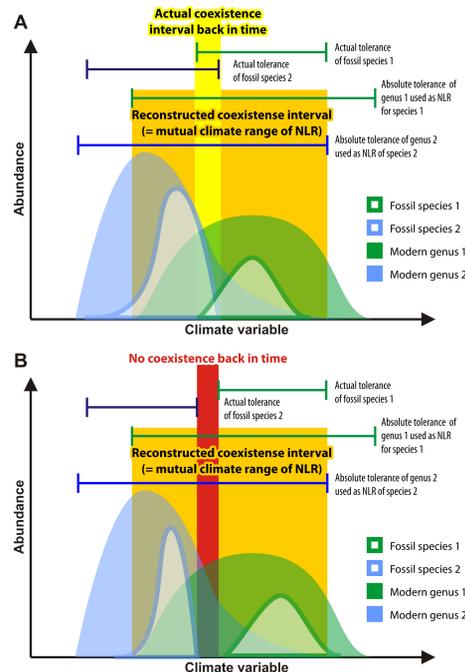


Figure 3. Issues related to the use higher-level taxonomic classification (e.g. genus or family) as nearest-living relatives (NLRs) of fossil species. In this example, two fossil species occupy a climate range within the modern climate range of their selected genus-level NLRs, fulfilling the principle 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).

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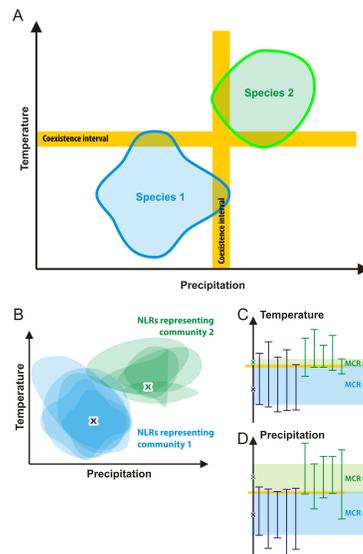


Figure 4. Pseudo-coexistence as a result of the representation of the climate niche using minimum and maximum tolerances. **(a)** Bivariate climate niches of two mutually exclusive species. These species have no overlapping climate space, but still reconstruct narrow coexistence intervals (orange bars) 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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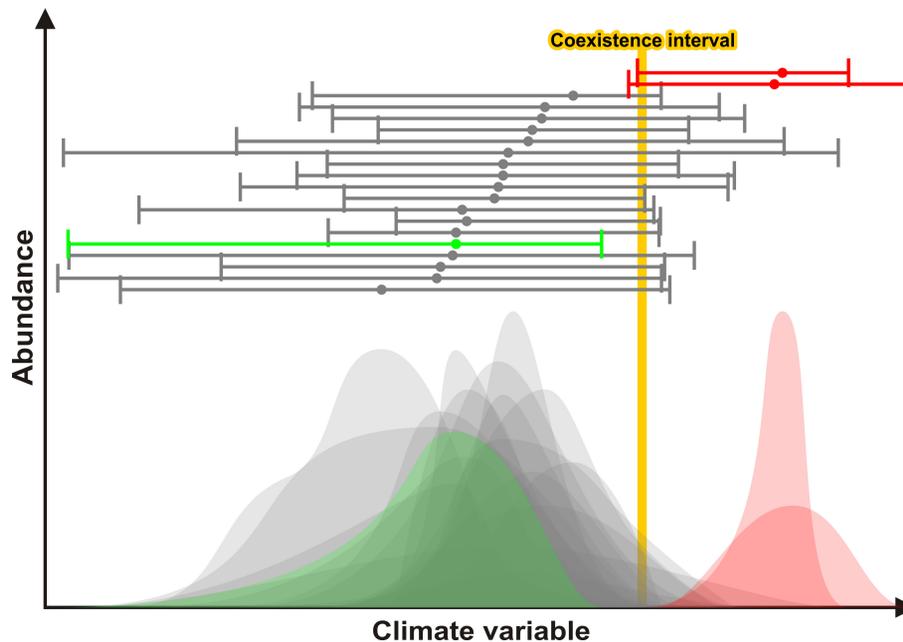


Figure 5. “Climatic outliers” and the bias of the Coexistence Approach towards exotic nearest-living relatives (NLRs). Shown are the niche response curves for 20 potential NLRs, of which 18 (grey and green) show a general overlap in their climatic preference. The two red NLRs are exotic elements with strongly differing climatic preferences. Bars indicate the minimum and maximum tolerances of each NLR, the dots highlight each NLR’s optimal climate value. 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).

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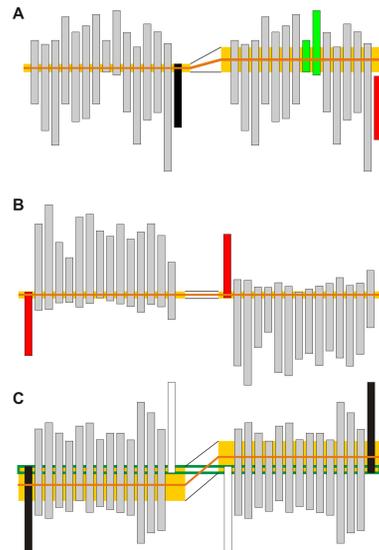


Figure 6. Logical inconsistencies in the application and theory of the Coexistence Approach. Shown are coexistence intervals (orange bars) based on slightly (**a, c**) or extremely (**b**) different sets of nearest-living relatives (NLRs). (**a**) Use of the “center value” to determine climate shifts. 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.

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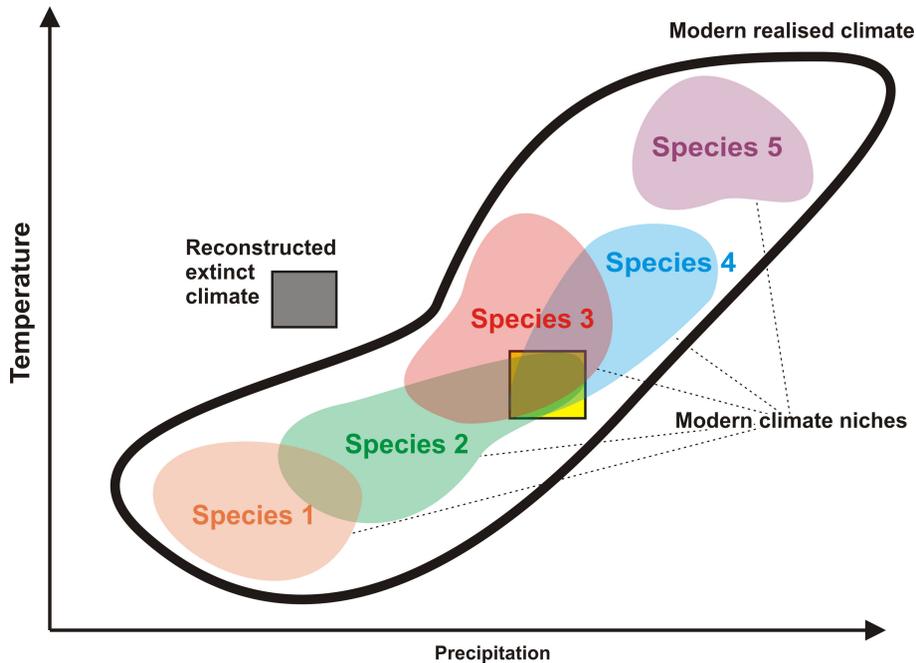


Figure 7. Impossibility of reconstructing extinct climates with the nearest-living-relative (NLR) principle. Shown are the (realised) climate niches of five modern species, which, inevitably have to lie within the frame of the modern climate space. Any coexistence space (yellow square, showing the coexistence 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.

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