

List of changes: Changes incorporated in the version uploaded with our author comment include the corrected Figure 2, some in-text changes (see version uploaded with author comment), and the new fifth section.

Any additional changes are highlighted as mark-ups in the here provided revision. We read through the text again to eliminate unnecessarily aggressive expressions following the editor's suggestion, but we found little to change (see also below responses to reviewer's 2 2nd report). Surely, the tone alone cannot be a criterion for the publication of scientific manuscript that is "well written" and "clearly" presents and discusses its arguments (see comment of Reviewer 2).

If it is, we would appreciate that the problematic sentences/expressions are marked and suggestions are given how to rephrase/put it political correct.

Response to anonymous reviewer #2

In my first review, while acknowledging the in-depth description and criticism of the Coexistence Approach, I raised two major limitations of that paper: 1) the absence of a proper discussion and 2) a confrontational tone that did not deserve the paper.

The revised manuscript presented by Grimm and Potts has been seriously amended for the first point and the two authors integrated most of the remarks the other reviewer and myself rose. Section 3 has been largely expanded, now putting in evidence the advantages SDM may have. The new section "Where to go from here?" is interesting as the authors now discuss and put into perspective the results described in the previous sections and propose a list of criteria upon which to judge taxon-based methods. Altogether these modifications give more consistency to the discussion, hence to the paper itself.

Response: Thank you.

Considering the second major criticism, I still believe that the tone of the overall manuscript, particularly the tone of the abstract and introduction, is too aggressive. I'm convinced that toning down the most aggressive sentences would benefit to the paper greatly. That remark holds, however, a part of subjectivity.

Response: If our assessment is valid, we have to accept that Coexistence Approach is flawed. Thus, the conclusions of 15 years of research relying, uncritically (i.e. naïve), on the method are to be disregarded. How can we put this nicely without obscuring the message of the paper?

Given the gravitas of our conclusions, we find it difficult to relativize sentences which may appear overly aggressive to some of the readers (the reviewer notes that his remark holds a certain subjectivity). How to down-tone, for example, the fact that the Coexistence Approach (CA) can shoe-horn any NLR assemblage (random, artificial or real) into coexistence (abstract, l. 24) by implementing an elimination strategy that lacks *any* methodological or biological basis (recognition of "climatic outliers")? See also our earlier responses to both reviewers regarding the confrontational nature of the paper, which still stand.

Nevertheless, we went again through the text to see if some expressions can be replaced without changing the meaning of sentences. For instance, we deleted "naïve" throughout the

text, although this is the best word to describe how the Coexistence Approach has been used in the last 15 years, and still is used (see papers by Huang et al. 2015; Tang et al. 2015; Utescher et al. 2015), despite of known problems (Grimm & Denk 2012; Utescher et al. 2014).

As a conclusion, the paper is well written and the arguments are now clearly presented and discussed. I am not against the publication of this revised manuscript as it stands now, but I nevertheless recommend to the authors a modification of their most confrontational sentences.

Response: It would have been helpful to know which sentences are too confrontational for a doubtlessly (and necessarily) confrontational paper, one of the few that (dare to) discuss and criticise the Coexistence Approach. We appreciate the reviewer's sentiment that we should be more careful in stating the troublesome facts related to the Coexistence Approach. Please note that none of the authors is dependent on financial or logistic support by the Coexistence Approach syndicate, organised in the frame of NECLIME, and its main funding organisation, the German Science Foundation. Hence, we will not have to suffer the consequences of publishing this paper and any statement that may be taken personally by applicants of the Coexistence Approach (which may be the reason for the reviewer's worries).

- Grimm GW, Denk T. 2012. Reliability and resolution of the coexistence approach — A revalidation using modern-day data. *Review of Palaeobotany and Palynology* 172: 33–47.
- Huang Y-J, Chen W-Y, Jacques FMB, Liu Y-SC, Utescher T, Su T, Ferguson DK, Zhou Z-K. 2015. Late Pliocene temperatures and their spatial variation at the southeastern border of the Qinghai–Tibet Plateau. *Journal of Asian Earth Sciences* doi: 10.1016/j.jseaes.2015.1004.1048.
- Tang H, Eronen JT, Kaakinen A, Utescher T, Ahrens B, Fortelius M. 2015. Strong winter monsoon wind causes surface cooling over India and China in the Late Miocene. *Climates of the Past Discussions* 11: 63–93.
- Utescher T, Bondarenko OV, Mosbrugger V. 2015. The Cenozoic Cooling – continental signals from the Atlantic and Pacific side of Eurasia. *Earth and Planetary Science Letters* 415: 121–133.
- Utescher T, Bruch AA, Erdei B, François I, Ivanov D, Jacques FMB, Kern AK, Liu Y-SC, Mosbrugger V, Spicer RA. 2014. The Coexistence Approach—Theoretical background and practical considerations of using plant fossils for climate quantification. *Palaeogeography, Palaeoclimatology, Palaeoecology* 410: 58–73.

1 **Fallacies and Fantasies: the theoretical underpinnings of**
2 **the Coexistence Approach for palaeoclimate**
3 **reconstruction**

4

5 **Guido W. Grimm¹ and Alastair J. Potts²**

6 [1] University of Vienna, Department of Palaeontology, Vienna, Austria

7 [2] Nelson Mandela Metropolitan University, Centre of Coastal Palaeoscience, Port Elizabeth,
8 South Africa

9 **Abstract**

10 The Coexistence Approach has been used to infer palaeoclimates for many Eurasian fossil
11 plant assemblages. However, the theory that underpins the method has never been examined
12 in detail. Here we discuss acknowledged and implicit assumptions, and assess the statistical
13 nature and pseudo-logic of the method. We also compare the Coexistence Approach theory
14 with the active field of species distribution modelling. We argue that the assumptions will
15 inevitably be violated to some degree and that the method has no lacks any substantive means
16 to identify and quantify these violations. The lack absence of a statistical framework makes
17 the method highly vulnerable to the vagaries of statistical outliers and exotic elements. In
18 addition, we find numerous logical inconsistencies, such as how climate shifts are quantified
19 (the use of a “center value” of a coexistence interval) and the ability to reconstruct “extinct”
20 climates from modern plant distributions. Given the problems that have surfaced in species
21 distribution modelling, accurate and precise quantitative reconstructions of palaeoclimates (or
22 even climate shifts) using the nearest-living-relative principle and rectilinear niches (the basis
23 of the method) will not be possible. The Coexistence Approach can be summarised as an
24 exercise that shoe-horns a plant fossil assemblage into coexistence and then naively assumes
25 that this must be the climate. Given the theoretical issues, and methodological issues
26 highlighted elsewhere, we suggest that the method be discontinued and that all past
27 reconstructions be disregarded and revisited using less fallacious arbitrary and erroneous
28 methods. We outline six steps for (further) validation of available and future taxon-based

1 methods and advocate developing (semi-quantitative) methods that prioritise robustness over
2 precision.

3 **Keywords:** Cainozoic; Eurasia; mutual climate range; nearest-living-relative principle;
4 physiological uniformitarianism; species distribution modelling; theoretical problems;
5 univariate niche

6 **1 Introduction**

7 One of the most widely used methods to infer the palaeoclimates of Eurasia using fossil plant
8 assemblages is the ‘Coexistence Approach’ (Utescher et al., 2014). Conceptually, this
9 approach belongs to the family of mutual climate range techniques but also makes use of the
10 ‘nearest-living-relative’ principle; a nearest-living-relative (NLR) is a modern taxon (species,
11 group of species, genus, or higher) that is considered an analogue for the fossil taxon. Mutual
12 climate range methods use the climatic preferences of modern species (a set of nearest-living-
13 relatives), as defined by their current distribution, to infer the potential climatic niche for a
14 fossil assemblage. In the case of the Coexistence Approach, the climate niche is defined using
15 minimum and maximum climate values of an NLR, obtained from its present-day distribution.
16 Pure mutual climate range techniques are usually restricted to reconstructing palaeoclimates
17 of the recent past (i.e. Quaternary) where species in the fossil assemblages can be directly
18 linked to modern species (e.g. Elias, 1997, 2001; Thompson et al., 2012; Harbert and Nixon,
19 2015); the processes of extinction and speciation ~~are~~can be fairly ignored and niche
20 conservatism is considered to be the norm. However, to apply these palaeoclimate
21 reconstruction techniques to assemblages from older time periods requires the use of the
22 nearest-living-relative principle, which is linked to the concept of physiological
23 uniformitarianism (Tiffney and Manchester, 2001; Tiffney, 2008). The niche-space of an
24 NLR is used to represent that of the fossil taxon. Thus, one assumes that the climate niche of
25 the NLR (the modern species or species set) is identical to that of the associated fossil taxon
26 (an extinct sister or ancestral species) and the mutually shared climate range of the NLRs
27 enables the estimation of the climate conditions in which the fossil assemblage thrived (Fig.
28 1).

29 Despite the availability of alternative palaeoclimate reconstruction techniques using NLRs
30 and the mutual climate range approach (e.g. Greenwood et al., 2005), the Coexistence
31 Approach has become the *de facto* method for plant fossil assemblages of Eurasia for time

1 periods spanning the Miocene to Late Cretaceous (Utescher et al., 2014). The cumulative
2 citation count of studies using the Coexistence Approach is in excess of 10,000. On the
3 surface, it reconstructs precise palaeoclimatic conditions (usually reported with a precision of
4 0.1 °C and 1 mm precipitation per month or year) based on a series of acknowledged and
5 implicit basic assumptions (Table 1; Mosbrugger and Utescher, 1997; Utescher et al., 2014).
6 These assumptions appear straightforward, but have theoretical and practical implications
7 essentially ignored not addressed in the application of the Coexistence Approach (Mosbrugger
8 and Utescher, 1997; Utescher et al., 2014; Grimm et al., 2015). Furthermore, the Coexistence
9 Approach avoids any statistical processing (Mosbrugger and Utescher, 1997; Utescher et al.,
10 2014), hence, does not take into account most community information, which could help to
11 identify errors and exotic elements. It relies to some degree on hard-to-grasp pseudo-
12 logic illogical deductions, some of which is-are advocated as strengths of the method, e.g. the
13 ability to reconstruct extinct climates (Utescher et al., 2014). The applicability of the nearest-
14 living-relative principle for reconstructing past climates in a quantitative manner is-has never
15 been questioned. This is surprising in the light of ongoing discussions in the field of spatial
16 distribution modelling, which shares a number of assumptions with mutual climate range and
17 nearest-living-relatives methods. Below we discuss each of these issues in further detail.

18 **2 Theoretical background of the ‘Coexistence Approach’**

19 **2.1 Assumptions of the Coexistence Approach**

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

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

1 modern species (or group) that has undergone significant shifts in morphology and
2 fundamental niche, and the best modern analogue may be a more distantly related lineage that
3 has been morphologically and ecologically stable (Fig. 2A). In addition, the degree of
4 systematic relatedness of a fossil to an NLR requires the placement of fossils within a
5 phylogenetic framework (i.e. a tree or network) and this has never been explored in any
6 Coexistence Approach study.

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

28 The second assumption (Table 1) is based upon the concept of physiological
29 uniformitarianism (Tiffney and Manchester, 2001; Tiffney, 2008). Physiological
30 uniformitarianism implies that as long as lineage stays within its environmental niche, it will
31 not accumulate morphological changes. Hence, a modern species with the same, or very
32 similar, morphological traits of a fossil of the same evolutionary lineage should share the

1 same environmental niche. It also implies that members of the lineages that have undergone
2 niche shifts also experienced morphological changes. **Assumption 2** is likely to be violated
3 when morphological changes are evident between the fossil and modern members of an
4 evolutionary lineage and an NLR of a fossil specimen should only be used if there is
5 morphological, not mere taxonomic, similarity (ideally identical) and if both have a common
6 origin. This would exclude the use of most modern plant genera and all families as NLRs as
7 they are typically composed of morphologically divergent species.

8 In addition, the use of morphologically diverse taxonomic groups to represent an NLR usually
9 means that the environmental niche of the NLR is large, likely encompassing the niche of the
10 fossil, but is not “climatically similar” to that of the fossil; thus, directly violating
11 **Assumption 2**. Novel procedures and methods are required that take cognisance of the fact
12 that the NLR niche is likely to be far broader than can be expected for that of the fossil. The
13 actual assumption, as used by the Coexistence Approach practitioners and related mutual
14 climate range methods, is that *the climatic niche of a fossil taxon lies somewhere within the*
15 *range of niches found within the species comprising the NLR*. This has two major implications
16 for the setup and interpretation of reconstructed palaeoclimates using the Coexistence
17 Approach (and other mutual climate range techniques that use NLRs): 1) a high resolution
18 climate reconstruction should not be possible, especially when only minimum and maximum
19 NLR tolerances are used (Fig. 3A), and 2) mixed floras may not be identified as mutually
20 exclusive species (or communities) can have overlapping climate ranges at higher taxonomic
21 levels (Fig. 3B). Thus, highly precise *and* accurate climate reconstructions can only be
22 obtained using the Coexistence Approach if the critical species within a palaeoassemblage
23 occupied niches close to the minimum **and** maximum tolerances of their corresponding
24 modern genus- or family level NLRs.

25 The third assumption (Table 1), that the distributions of extant species are in equilibrium with
26 their climate, is a topic rich with discussions in the ecological and species distribution
27 modelling literature (Araújo and Pearson, 2005; Bond et al., 2005; Sexton et al., 2009;
28 Franklin, 2010). Species are often not in equilibrium with their climate for abiotic (e.g. soil,
29 fire) or biotic (e.g. competition) reasons, and thus their realised niches do not span their
30 fundamental niches. Thus species will be plastic in their expression of the realised niche
31 depending on external factors, which would exclude the reconstruction of palaeoclimate with

1 high accuracy. Any change in the abiotic or biotic parameters can affect the distribution of a
2 species (i.e. its realised niche) even if the fundamental niche remains unchanged.

3 The climatic niche is solely represented by minimum and maximum values in the Coexistence
4 Approach, which are independently compiled for climate parameters in a univariate manner.
5 However, it has been long established that biological climate niches are multi-dimensional
6 (Köppen, 1936; Hutchinson, 1957; Walter, 1973; Walter and Breckle, 1983–1991; Schroeder,
7 1998). Using minimum-maximum tolerances along univariate axes can only roughly
8 approximate the multidimensional climatic niche, and may be misleading (Klotz, 1999;
9 Thompson et al., 2012). For example, two *mutually exclusive* taxa, for which **Assumption 3**
10 applies, may still have an artificial mutual climate range regarding their minimum and
11 maximum tolerances (Fig. 4A). In this context it is important to note that species distribution
12 modelling started with algorithms that used minimum and maximum values, but quickly
13 moved on to methods that better represented the bioclimatic niche of a species (discussed
14 further below). Thus, the use of range values for climatic parameters does not accurately
15 capture the climatic requirements or tolerances of an NLR (Table 1), which will affect the
16 reconstructed palaeoclimate using the Coexistence Approach.

17 The fourth and last assumption has no apparent theoretical implications. Technical
18 implications have been discussed in Grimm and Denk (2012), Thompson et al. (2012),
19 Utescher et al. (2014), and Grimm et al. (2015). We do, however, wish to highlight that since
20 local climate can substantially vary over short time scales, minimum and maximum tolerances
21 may be unduly affected by the selected observation period of climate stations.

22 Not formally addressed by Mosbrugger and Utescher (1997) or Utescher et al. (2014) are two
23 more fundamental assumptions of the Coexistence Approach, which distinguish the method
24 from mutual climate range techniques using modern-day species: 1) palaeoassemblages
25 comprise only taxa that existed as actual communities (i.e. all fossil specimens are
26 autochthonous and from the same point in time); 2) absence of a fossil taxon indicates true
27 absence (i.e. each fossil plant assemblage comprehensively reflects the actual
28 palaeocommunity; Table 1). The Coexistence Approach implicitly assumes that only an
29 autochthonous and strictly coeval palaeoassemblage will result in a single coexistence
30 interval. However, given that two mutually exclusive taxa can share a climate range of
31 minimum and maximum along univariate climate parameters, so too can allochthonous taxa
32 in a fossil assemblage. In addition, the expansion of the climate niche using higher-level

1 NLRs automatically increases the probability of artificial coexistence. Thus, allochthonous
2 assemblages (mixed floras) do not necessarily result in ambiguous intervals (Fig. 4B-D) and
3 may very well be the reason for highly precise palaeoclimate estimates (< 1 °C for
4 temperature parameters, < 100 mm precipitation per year, < 10 mm precipitation per month)
5 observed in many studies using the Coexistence Approach (Denk et al., 2012; Grimm et al.,
6 2015). Thompson et al. (2012) suggest that a benefit of mutual climate range techniques, in
7 comparison to indicator-species approaches, is that the reconstruction is only affected by the
8 presence of taxa, not their absence. However, this does not apply to the Coexistence
9 Approach, where the mere absence of a taxon can directly affect the outcome of the
10 reconstruction (discussed further below). For instance, absence of a taxon may eliminate
11 another NLR as “climatic outlier” rather than producing two “ambiguous” intervals.

12 We have outlined a range of probable and inevitable issues of the purported basic assumptions
13 of the Coexistence Approach. These will all, to some unknown degree, decrease the precision
14 and accuracy of any approach that attempts to reconstruct palaeoclimates. In this light, the
15 Coexistence Approach is highly unlikely to reconstruct precise or accurate palaeoclimatic
16 conditions. Utescher et al. (2014) state that it is impossible to test the accuracy of Coexistence
17 Approach reconstructions (but see Grimm and Denk, 2012, for mean annual temperature
18 estimates), but follow the original paper in assuming that violation of the basic assumptions
19 will readily surface in the form of “*climatic outliers*”.

20

21 **2.2 The statistical nature of the Coexistence Approach**

22 According to Utescher et al. (2014) the “*Coexistence Approach by Mosbrugger and Utescher*
23 (*1997*) is a nearest living relative method, which relies only on the presence/absence of a
24 plant taxon within a fossil assemblage and the climatic requirements of its modern relatives.
25 It avoids any statistical processing or further assumptions, except those given in Mosbrugger
26 and Utescher (1997) [i.e. the four basic assumptions, see Table 1]”. In the original paper, no
27 means of statistical processing were proposed, hence, the Coexistence Approach defines an
28 interval for a past climate parameter assuming that statistical effects do not exist or are
29 negligible. The Coexistence Approach ignores discounts the majority of the community
30 information because the reconstructed climate interval is always solely defined by the pair of
31 the two most divergent, but putatively coexisting NLRs. Usually one member of the pair is an

1 exotic element; here we define ‘exotic’ as any NLR whose niche is at odds with the majority
2 of the assemblage (e.g. Fig. 5). The ~~Coexistence Approach lacks a statistical framework to~~
3 ~~account for potential oddities, errors or violations of assumptions, the likelihood of potential~~
4 ~~oddities, errors or violations of assumptions which~~ increases with assemblage size or
5 depositional age. The ~~approach Coexistence Approach naively~~ relies, however, on the
6 presumption that any violation will readily surface in the form of so-called “*climatic outliers*”
7 (Mosbrugger and Utescher, 1997; Utescher et al., 2014). This exposes palaeoclimate
8 reconstructions using this approach to the vagaries of statistical outliers and exotic elements
9 (see Grimm and Denk, 2012; Grimm et al., 2015, for real-world data examples).

10 A ‘climatic outlier’ is identified as an NLR or small number of NLRs that do not share the
11 climate space for a given parameter with a slightly higher number of other NLRs (Fig. 5). In
12 those cases where there are more than one interval that can be reconstructed using the same
13 maximum possible number of NLRs, then alternative ‘*ambiguous*’ intervals are reported; each
14 of these intervals recognises a different set of climatic outliers. Ambiguous intervals are
15 interpreted by Utescher et al. (2014) as the only evidence for mixed floras rather than a
16 violation of any the assumptions discussed above. Taxa identified as climatic outliers are
17 typically removed from a Coexistence Approach analysis for a given palaeoassemblage and
18 parameter. We wish to highlight that a climatic outlier is simply an NLR that is seemingly at
19 odds with a few other NLRs and must not to be confused with a statistical outlier (Fig. 5).

20 There are two paramount problems with the ~~current~~-outlier elimination strategy used by the
21 Coexistence Approach. First, *two* taxa *violating* the assumptions behind the Coexistence
22 Approach may eliminate *one* taxon that is not. A typical situation is illustrated in Figure 5,
23 where an NLR occupying a climate range that is in general agreement with the rest of the
24 flora would be identified and eliminated as a climatic outlier because of presence of two
25 deviant taxa that are at odds with the overall NLR community. Second, taxa identified as
26 climatic outliers for one climatic parameter and therefore removed from the assemblage for
27 estimating that parameter are still, in most cases, kept for analysing other parameters for the
28 same assemblage. In some cases, these climatic outliers even define the coexistence interval
29 in another parameter (Grimm et al., 2015). If we follow the logic that climatic outliers
30 represent violations of the basic assumptions of the Coexistence Approach (Utescher et al.,
31 2014), then it is imperative that they are removed from all reconstructions for a given
32 assemblage or in general (Table 2). This has been rarely applied in any study that has

1 identified climatic outliers in the Coexistence Approach, mainly to avoid wide, and thus
2 uninformative, coexistence intervals (Grimm and Denk, 2012; Grimm et al., 2015). It could
3 be argued that any palaeoassemblage represented by mutually exclusive NLRs should be
4 ignored until the reason for the non-coexistence can be identified and corrected for.

5 Any mutual climate range approach needs a framework to identify statistical outliers as the
6 assumptions will inevitably be violated, and establishing the degree of violation (e.g. degree
7 of niche shifts) is not feasible based on current knowledge. Many palaeoassemblages will
8 comprise mixed floras with elements from different climate niches, and this would need to be
9 explicitly addressed before reconstructing coexistence intervals. As stated above, the
10 Coexistence Approach lacks any framework to identify exotic elements or allochthonous
11 assemblages, unless they are sufficiently divergent to generate climatic outliers.
12 Allochthonous assemblages comprising mutually exclusive species can share a climate
13 interval (Fig. 4B), and this problem of pseudo-coexistence is exacerbated by the use of
14 *higher-level taxa* (genera, families) as NLRs of a fossil *species/morphotypes*. Any slightly
15 conflicting, but exotic, element in an assemblage will have a disproportionately high influence
16 on the palaeoclimate estimates (Fig. 5). It is clear that not only ‘climatic outliers’ and
17 ‘ambiguous intervals’ should be indicative of mixed floras, errors in the data, or violations in
18 the assumptions, but also *any* narrow coexistence interval (see Grimm and Denk, 2012;
19 Grimm et al., 2015, for real-world examples).

20 Mutual climate range techniques that apply simple statistics to filter exotic taxa, such as the
21 Bioclimatic Approach (Greenwood et al., 2005), will be less susceptible to the presence and
22 absence of a few exotic taxa, but will also usually fail to recognise mixed floras. The problem
23 of mixed floras can only be overcome, to some degree, by using alternative mutual climate
24 range techniques that make use of the full spectrum of distributional information, and thus
25 include the climatic preference of all constituent elements of a palaeoassemblage (e.g. using
26 the niche curves in Fig. 5). This includes methods such as the weighted mutual climate range
27 approach (Thompson et al., 2012), the probability density function method (Chevalier et al.,
28 2014), and the coexistence likelihood estimation method (Harbert and Nixon, 2015).
29 However, these methods will probably begin to break down when the nearest-living-relative
30 principle is needed to link fossils with extant lineages (Thompson et al., 2012; Harbert and
31 Nixon, 2015), and may explain why their application has been limited to Quaternary
32 assemblages.

2.3 Pseudo-logical inconsistencies 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 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 regarding 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, Figure 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 Figure 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 dependent 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).

1 The presence or absence of individual NLRs are generally at the base of reconstruction
2 uncertainty in coexistence interval - we term this the “Heisenberg” effect. Figure 6C shows
3 two very similar assemblages where the presence or absence of the two highlighted taxa
4 changes the coexistence interval reconstructed by the Coexistence Approach in a degree that
5 would be interpreted as a trend towards higher values. The Heisenberg effect renders
6 palaeoclimate estimates obtained with the Coexistence Approach protocol highly susceptible
7 to taxon-bias effects. The reconstructed climate is exceedingly dependent on what fraction of
8 the actual vegetation has been captured by the fossil assemblages (note that in Fig. 6C all
9 NLRs have a mutually shared climate range). Thus, even if all assumptions needed for a
10 mutual climate range approach that also uses the nearest-living-relative principle are fulfilled,
11 the Heisenberg effect will lead to unstable, even random, climate reconstructions when the
12 Coexistence Approach is used.

13 Utescher et al. (2014) explicitly state that, as each parameter is independently reconstructed,
14 the Coexistence Approach has the potential to reconstruct a climate that does not exist today:
15 an “extinct climate”. It is hard to grasp how this can be logically accommodated with the
16 basic assumptions of the Coexistence Approach and the actuo-palaeontological nearest-living-
17 relative principle in general (Fig. 7). An extinct climate for a palaeoassemblage would
18 indicate that the present-day niches of the NLRs are **not** representative of the fossils, and
19 therefore would indicate direct violations of Assumptions 2 and 3 discussed above (Table 1).
20 In addition, it is not possible to construct an extinct climate using species that are restricted to
21 present-day climates if the principle of physiological uniformitarianism applies. Reasons why
22 extinct climates are reconstructed using the Coexistence Approach include violations of basic
23 assumptions, pseudo-coexistence, the inconsistent identification of climatic outliers within an
24 assemblage across climate variables, and the single-dimension effect where climate
25 parameters are analysed in isolation and are assumed to be unlinked. The reconstruction of an
26 extinct climate should be seen as a direct indication of error, and not lauded as a benefit of the
27 method.

28 Ignoring Left aside, these logical inconsistencies in the conception and application of the
29 method, the Coexistence Approach still cannot be expected to reproduce a robust quantitative
30 reconstruction of the palaeoclimate, as 1) assumptions are likely to be violated but cannot be
31 detected, 2) one cannot avoid using higher-level taxa to represent fossil species or

1 morphotypes, and 3) the fossil record will always be incomplete to different degrees, and this
2 will affect the calculated coexistence interval.

3 **3 Lessons to be learnt from species distribution modelling**

4 Species distribution modelling (SDM) is an exceptionally active field which aims to
5 empirically model the species-environment relationships and thereby quantify the realised
6 niche of a given taxon (Franklin, 2010; Peterson et al., 2011) or, in some cases, communities
7 (e.g. Potts et al., 2013). The dawn of the field was the BIOCLIM software package (Nix,
8 1986), which is comparable to the Coexistence Approach as it used the range (or percentile
9 range) of climatic variables in a rectilinear fashion. Booth et al. (2014) describe the roots of
10 the field and highlight that one of the most active areas of SDM development has been of
11 methods that trim the rectilinear climate envelopes of BIOCLIM. This was driven by the early
12 realisation that the relationships between climate variables were poorly captured by the
13 rectilinear approach; for example, a rectilinear niche may suggest that a species could survive
14 in a situation where it is both hot and dry, but the actual climate niche is that it only occurs
15 where it is hot and wet. More advanced methods have refined the n -dimensional hyperniche
16 (Hutchinson, 1957) where response curves are used to capture the suitability of different
17 conditions for species occurrence. BIOCLIM performed poorly in comparison to more recent
18 methods in a comparison of more recent SDM methods (Elith et al., 2006) indicating that the
19 simplistic use of range values for climatic variables, as used by the Coexistence Approach, is
20 a poor representation of the realised niche of species or NLR.

21 The revolution in the multidimensional quantification of the niche has completely bypassed
22 the Coexistence Approach. Measuring ecological niche overlap between species in
23 multivariate space is an active area of investigation (Rödder and Engler, 2011; Broennimann
24 et al., 2012), which can be used to determine the shared niche within a set of species.
25 However, measuring the niche in such a manner also requires that all the variables selected
26 are, in fact, significant in limiting the niche. Establishing the contribution and importance of
27 different environmental variables (i.e. variable selection) in setting the bounds of a taxon's
28 niche is a theoretical issue (Araújo and Guisan, 2006) where advances are also being made
29 (Austin and Van Niel, 2011). In comparison, the Coexistence Approach blindly uses a wide
30 range of environmental parameters in a univariate manner assuming that they are all important
31 in determining a taxon's niche.

1 Furthermore, the assumption of niche conservatism (linked to the principle of physiological
2 uniformitarianism) has generated considerable debate in the SDM literature as it has been
3 used as justification for projecting models into altered climate states (past or future) and to
4 predict the establishment and spread of invasive species (reviewed in Pearman et al., 2008a).
5 These discussions have centred firstly on whether the current distribution for a given species,
6 i.e. the realised niche, adequately represents the fundamental niche; and secondly, how
7 quickly the fundamental niche might be able to shift? Such concerns are absent in the
8 theoretical underpinnings of Coexistence Approach (Mosbrugger and Utescher, 1997;
9 Utescher et al., 2014). Unfortunately, niche shifts have been documented for a wide range of
10 plant species through space (Broennimann et al., 2007; Pearman et al., 2008a) and even over
11 relatively short time scales (Pearman et al., 2008b; Veloz et al., 2011). Therefore the
12 assumption of physiological uniformitarianism has limited applicability to reconstruct precise
13 and accurate palaeoclimates, especially with increasing age of an assemblage.

14 **4 Conclusions**

15 Using best-possible climate data for modern North American woody plants, Thompson et al.
16 (2012) were unable to reconstruct the climatic shifts from the Last Glacial Maximum to the
17 present-day using an unweighted mutual climatic range method (which represents the niche
18 using range values and is equivalent with the Coexistence Approach save for the use of NLRs
19 and recognition of climatic outliers). This is in stark contrast to the beliefs of Coexistence
20 Approach practitioners that the method can reliably reconstruct climate shifts at high-
21 precision (e.g. Huang et al., 2015; Utescher et al., 2015), despite the additional error and
22 uncertainty associated with the nearest-living-relative principle. The purported high precision
23 in Coexistence Approach studies is dependent on phenomena such as pseudo-coexistence and
24 the lack of a sound-statistical framework.

25 We argue that the Coexistence Approach, as conceived by Mosbrugger and Utescher (1997),
26 violates the basic concepts behind mutual climate range techniques and the nearest-living-
27 relative principle. It imposes a number of assumptions that will inevitably be violated and has
28 no ability to detect violations and generally lacks any safeguards against the reconstruction of
29 artificial coexistence intervals and thus erroneous palaeoclimate estimates.

30 Given the theoretical problems outlined here, and the practical problems highlighted by
31 Grimm et al. (2015) – for example, that any random real-world flora will eventually produce a

1 “statistically significant” (according Mosbrugger and Utescher, 1997) coexistence interval
2 with a high number (>20) of NLRs – we suggest that all palaeoclimate reconstruction studies
3 using the Coexistence Approach be disregarded and that the palaeoassemblages be revisited
4 with other methods and careful, well-documented, and well-investigated NLR-associations.

5 **5 Where to go from here?**

6 There are already a range of potential methods available for palaeoclimate reconstruction
7 using plant fossils as proxies in a univariate manner that have been rarely used or recently
8 proposed (e.g. Greenwood et al., 2005; Boyle et al., 2008; Thompson et al., 2012; Chevalier
9 et al., 2014; Harbert and Nixon, 2015), and there are avenues ripe for exploration (e.g.
10 Broennimann et al., 2012; Denk et al., 2013). However, all of these methods require (further)
11 testing, and then careful, well-documented usage when reconstructing palaeoclimates. The
12 development of the physiognomic approach (CLAMP) within the last two decades may serve
13 as an example regarding validation, advancement, and, most importantly, documentation and
14 transparency. The various publications demonstrate a constant thrive to reach higher precision
15 and counter known problems (e.g. Kovach and Spicer, 1995; Herman and Spicer, 1997;
16 Spicer et al., 2009; Yang et al., 2015; Li et al., 2016). All primary data is made freely
17 accessible and means are implemented allowing for quick application (CLAMP online; Yang
18 et al., 2011). CLAMP online does not only provide data, guidelines and templates for
19 application, but also pinpoints shortcomings and ideas how to deal with them. No method is
20 or will be ‘perfect’. Nevertheless, it is crucial to define the principal accuracy and precision of
21 any quantitative method. If this is not possible, as in the case of the Coexistence Approach
22 (Utescher et al., 2014: 61), it must not be used. Therefore, we suggest that any current or
23 future taxon-based method be:

- 24 1. Tested against the modern flora (e.g. Boyle et al., 2008; Thompson et al., 2012;
25 Chevalier et al., 2014; Harbert and Nixon, 2015).
- 26 2. Tested with randomised and unlikely communities of modern flora. A robust (taxon-
27 based) method that is to be applied to micro-, meso- and macrofossil assemblages
28 must detect possible allochthonous elements/mixed floras.
- 29 3. First applied to the ‘better-understood’ palaeoclimates of the most recent past (e.g.
30 present to the Last Glacial Maximum) and compared with available relevant proxies
31 (e.g. Thompson et al., 2012).

4. Explored using both species-level and taxonomic levels of potential or probable
- nearest-living relatives (e.g. Boyle et al., 2008).
5. Examined using a jackknifing or similar procedure to ensure that results remain
- accurate and establish the actual precision that can be expected with fossil floras.
- Fossil floras will always only provide a fraction of the actual flora, and may include
- incorrectly determined taxa. The accuracy of a result must not change due to the
- presence or absence of specific taxa in the assemblage, although precision can, and is
- likely to, decline.
6. Finally, tested in a stepwise fashion further and further into the past using available,
- well-studied and dated, more or less continuous records, such as the recently revised
- Icelandic record covering the last 15 million years ranging from subtropical lowland to
- ice age conditions (Denk et al., 2011; Denk et al., 2013)

After such a series of tests, the method can be considered an alternative means to reconstruct past climates for further exploration. However, the ultimate limitations of mutual climate range techniques or other nearest-living-relative methods for palaeoclimate reconstruction do not lie in the methodological framework to estimate, for example, the coexistence space, but rather the applicability of the nearest-living-relative principle. When it comes to application into the more distant past, the basic assumption of any method must be that the nearest-living-relative principle will be violated to an unknown degree. The degree of violation will likely increase with time, and may not necessarily surface during application or testing phase. Bivariate or multivariate approaches, which can tackle the problem of pseudo-coexistence (e.g. Fig. 4), will be more sensible in this respect. The capability to accurately and precisely predict palaeoclimate will not only deteriorate with increasing age, but also with compositional change of the fossil plant assemblages relative to the modern-day situation. Precise, highly sophisticated methods (e.g. Punyasena, 2008; Harbert and Nixon, 2015) or methods using few, overly precise, values to characterise the niche space of the NLR (e.g. Greenwood et al., 2005) run a higher risk of being affected by violations of the nearest-living-relative principle than methods that use semi-quantitative approximations of the niche (e.g. Thompson et al., 2012; Denk et al., 2013).

Taking into account all theoretical and practical issues involved, 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. Therefore, our opinion is that method

1 development should not focus on high (or higher) precision, as the basis of this precision is
2 undermined as the temporal difference between fossil and NLR increases, but rather on
3 establishing climate change trends in a robust and reproducible manner. Semi-quantitative
4 approaches can detect such changes and may prove to be more robust (e.g. the Köppen
5 signature approach proposed by Denk et al., 2013). Furthermore, the application of any
6 nearest-living-relative method on palaeofloras will always depend on thoughtful filtering a
7 fossil assemblage for elements that have been shown to have a high likelihood of niche
8 conservatism. Fossil-NLR associations must be carefully selected to ensure that the principle
9 of physiological uniformitarianism applies, in contrast to the current practise of seemingly
10 data-naive bulk analyses.

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34 **Figure legends**

- 35 **Figure 1. The concept of the mutual climate range as used in the Coexistence Approach.**
- 36 **Figure 2. Difference between ‘systematically close’ and nearest-living-relative (NLR, i.e.
 37 best modern analogues).** Shown is a species phylogeny of a diversified ingroup; the
 38 outgroup in this example is a sister species of the ingroup. **A.** Standard definition of
 39 nearest-living relative (best modern analogue) vs. definition if Assumption 1 of the
 40 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.

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).

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

1 interval is the same. **C.** Two floras that only differ by the absence (white bars) or presence
2 (black bars) of each a single taxon. The resulting coexistence intervals would be
3 interpreted as a shift towards higher values. The green box shows the coexistence interval
4 of a flora in which both taxa are represented.

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

13

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 & 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

1 **Table 2: The consequences of identifying a ‘climatic outlier’ in a palaeoassemblage**
 2 **supposing that these represent violations of one or more of the four basic**
 3 **assumptions.**

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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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