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Plant- and micromammal-based paleoprecipitation proxies: Comparing results of the Coexistence and Climate-Diversity Approach

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ABSTRACT

Both plant and vertebrate communities have been used to reconstruct paleoprecipitation. However, direct stratigraphic comparisons between the two types of proxies have hardly been performed, which is due to the fact that plant and vertebrate fossils usually do not occur together in single geological beds. Here, we focus on a series of 18 sites from the Neogene of Europe and Anatolia that contain both types of fossils, and compare paleoprecipitation predictions produced by the Coexistence Approach (plants) and the Climate-Diversity approach (micromammals).

Most of the sites have overlapping uncertainty intervals for mean annual precipitation as generated by the two methods, pointing to a common precipitation-related signal in flora and fauna. Nevertheless, a systematic difference appears to characterize drier sites, for which micromammal richness-based estimates for annual precipitation tend to be lower than plant-based coexistence-based estimates. Driest-month precipitations are in agreement for drier sites, but strongly differ for wetter sites, with micromammal richness-based estimates being higher. Overlap is poor for estimates of wettest-month precipitation, which are higher when based on plant-based coexistence.

Possible sources for a bias towards higher annual values in plants are related to the inclusion of local, wetland elements in the analysis and/or to a lower taxonomic resolution for pollen and spores compared to macroflora. Micromammal-based annual estimates could be biased towards drier values, when smaller samples lack rare species that could be preferentially wet-adapted. Several of the higher driest- and lower wettest-month micromammal-based estimates could result from over-extrapolation beyond the calibration domain for arboreality as currently existing in the modern Western Old World. On the other hand, the use of several SE Asian reference taxa could add a high-precipitation (monsoonal) component to the plant-based predictions. In addition, wettest-month estimates for both plants and micromammals probably suffer from the poor performance of water excess as a limiting factor.

An attempt to further increase the predictive power of the micromammal-based prediction equations was performed by incorporating non-linear terms, and by using an extended calibration set including selected plant-based precipitation estimates for micromammal assemblages without modern analogue in the Western Old World ("proxy inter-calibration").

1. Introduction

Precipitation figures directly behind temperature as the second-most important climatic variable. Proxy development for paleoclimate reconstructions, however, has proven to be more difficult for precipitation than for temperature. The main reason is probably related to the fact that precipitation (and the hydrological cycle in general) is more variable spatially, and that more data points are needed to attain reliable larger-scale predictions. Nevertheless, various proxy methods have been developed that seem to perform well in estimating past rainfall levels. For instance, abiotic paleoprecipitation proxies have been formulated on the basis of soil features, such as element ratios reflecting weathering and horizon depth (Sheldon and Tabor, 2009). Another recent approach allows for the estimation of paleoprecipitation in C3 ecosystems on the basis of carbon isotopic ratios in fossil soil carbonate or organic material, plant tissue or animal skeletal parts (e.g., Kohn, 2010).

Most widely used, however, are biotic, paleocommunity-based approaches. For plants, these may incorporate morphological traits such as leaf shape (CLAMP, cf. Spicer, 2000) or wood anatomy (Wiemann et al., 1998). Alternatively, climatic tolerance limits from living taxa or from nearest living relatives of fossil taxa may be used, preferably across

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complete communities (e.g., Coexistence Approach and Climatic Amplitude method; Mosbrugger and Utescher, 1997; Fauquette et al., 1998).

Vertebrate communities constitute another source for paleo-precipitation reconstruction. Because extinction rates are generally higher than in plants, successful extrapolation of quantitative climatic preferences or requirements of nearest living relatives to fossil vertebrate taxa may not always be warranted, except for the youngest geological intervals. Whereas many mammal genera that lived in the Plio-Pleistocene are still living today, allowing relatively reliable paleoclimate predictions (e.g., Hernández Fernández et al., 2007), species richness-related approaches form an attractive alternative for older intervals. For instance, the number of species within some higher taxon such as a (sub)family can be linked to climatic variable using the modern geographic distribution of that taxon (e.g. for temperature, Montuire et al., 1997). However, for increasingly older periods, also the climatic range of a higher taxon will depart more and more from its modern values. For this reason, richness values of ecological categories of body size, diet, locomotion and physiology have been used, to predict levels of precipitation (Kay and Madden, 1997; Böhme et al., 2006; Van Dam, 2006). A complete "taxon-free" approach would be possible by using purely morphological variables. For example, the mean degree of molar hypsodonty across large-mammal herbivore communities has been used to predict larger-scale precipitation patterns for the Neogene (e.g., Eronen et al., 2010).

Alternative approaches on the basis of micromammals have used relative abundances instead of richness to predict humidity (e.g., van der Meulen and Daams, 1992; van Dam and Weltje, 1999). Because of the quantitative nature of abundance data, environmental classifications of taxa may remain broad ("wet", "dry", etc.) in order to make predictions. Unfortunately, for the time being the lack of suitable modern calibrations is hampering the direct estimation of variables such as precipitation.

In this work we compare prediction results from a nearest-living-relative approach in plants (Coexistence Approach, CA) to that from a relative diversity-based approach in micromammals (Climate-Diversity Approach, CDA). In order to avoid bias due to a difference in spatio-temporal settings, we primarily focused on a restricted amount of fossil sites, for which it was known that plants and micromammals originated completely or partly from the same bed. Apart from these key sites, a second series of sites was selected for which the requirement of a common origin was not fulfilled, but for which it was known that micromammals and plants stemmed from beds stratigraphically separated maximally a few meters only.

2. Methods and material

2.1. Plants: Coexistence Approach

The Coexistence Approach (CA) employs climate requirements of extant relatives of fossil plant taxa, the so-called Nearest Living Relatives (NLRs), to reconstruct paleoclimate. Compared to other methods, CA has the advantage that it can be applied to all types of plant organs and that it does not require any information concerning the abundance of a component, thus avoiding an important source of taphonomic bias in the reconstructed climate signal. Here, we apply the method following the original procedure as described by Mosbrugger and Utescher (1997) and Utescher et al. (2014). Climate data for all known NLRs of a fossil flora are extracted from the Palaeoflora database (Utescher and Mosbrugger, 2014). The CLIMSTAT routine identifies the interval of a climate variable where a maximum number of taxa may coexist. This CA interval is then interpreted as the most probable paleoclimatic condition of the fossil flora considered. Applications towards mean annual precipitation (MAP), accompanied by estimates of monthly precipitation of the wettest (HMP), driest (LMP) and warmest month (WMP) (Utescher et al., 2000), have produced many details on rainfall throughout the Cenozoic of Eurasia (e.g., Utescher et al., 2000; Bruch et al., 2011;

Utescher et al., 2015). Furthermore, reconstructions based on the above variables have revealed Late Miocene and Pliocene climate cycles and have evidenced non-linear changes of the different precipitation variables studied, possibly related to orbital forcing (Utescher et al., 2012).

The quality of the paleoclimate reconstruction that CA provides depends on a variety of factors such as the taxonomic resolution of the fossils and the quality of the NLR data. Although the CA can work with a single taxon, it works better with diverse floras, because the climatic resolution increases with the number of taxa. For this reason, a minimum diversity of 10 taxa with climate data is needed (Mosbrugger and Utescher, 1997). Taxonomic resolution strongly depends on the organ type used (Mosbrugger and Utescher, 1997). Fruits, seeds, and leaves commonly allow for a more precise taxonomic allocation (species, genus) while NLR identification of pollen and spores is restricted to higher taxonomic levels (genus, family). Therefore, the climatic resolution obtained with the CA when applied on diverse macroflora is commonly better than the resolution obtained with pollen (Mosbrugger and Utescher, 1997). On the other hand, macrofloras (especially leaves) may reflect local climate conditions while pollen commonly provide a regional climate signal.

Normally, when making reconstructions for microfloras, evidence from a single palynomorph grain is not considered, in order to reduce errors such as those caused by exotic elements (e.g., Utescher et al., 2000). In the present study, however, we consider all taxa listed, because some of our sources do not provide any information on quantity of palynomorph grains. In addition, taphonomic factors may affect the spatial scale to which the climatic predictions apply. While leaf floras are known to represent primarily local vegetation (e.g., Kovar-Eder et al., 2008), palynofloras reflect regional conditions as well. In general, the latter also holds for fruit and seed floras as contained in channel lags or as point bar deposits (Vassio and Martinetto, 2012). To overcome interpretational difficulties (see: Mosbrugger and Utescher, 1997; Hoorn et al., 2012), attempts have been made to classify floristic components as local/extrazonal or regional/zonal (Kovar-Eder et al., 2008). Such a procedure is not without controversy, because taxonomic resolution is often too poor to unambiguously assign a fossil taxon to one of the groups. Moreover, many plant species may occur in both extrazonal and zonal stands. Hence, the differentiation is not used in the standard application of the CA (Mosbrugger and Utescher, 1997). As a result, the presence of local wetland elements within a surrounding drier zone could bias reconstructions towards wetter conditions.

Any actualistic approach suffers from errors caused by changed requirements of taxa across earth history. For plants, errors will be minor for Neogene floras compared to Paleogene ones (Mosbrugger and Utescher, 1997). On the other hand, present-day relics from the Neogene do pose a problem, as their distribution area does not cover the real climatic space in which the taxon could exist. This flaw, which is inherent to an actualistic approach, cannot be overcome, but in CA analysis these taxa are frequently identifiable as "outliers" (cf. Mosbrugger and Utescher, 1997). According to our experience in numerous CA analyses of the Neogene paleobotanical record we therefore exclude here the following taxa: *Sciadopitys, Tetraclinis,* and *Cathaya* (cf. Utescher et al., 2014). Furthermore, climate data for various (sub-)cosmopolitan taxa were not at our disposal (cf. Appendix A), but would not affect the reconstruction due to their wide ecological range. For the tropical fern *Pronephrium* no adequate chorological data were available to define its climatic tolerances, and for the invasive taxon *Arundo* (cane) the natural distribution is unclear.

2.2. Micromammals: the Climate-Diversity Approach (CDA)

Here we apply the Climate-Diversity Approach (CDA, term introduced here) to fossil micromammal assemblages. The studied assemblages typically consist of screen-washed collections of teeth from rodents (Rodentia), insectivores (Lipotyphla) and hares and rabbits

(Lagomorpha). Although absolute numbers of species bear a relation to local precipitation as well (see Van Dam, 2006), in the context of fossil sites we prefer the use of relative species richness numbers, which are more robust against differential sampling effort. Specifically, we use the relative species richness of invertivore and arboreal species in fossil communities (Kay and Madden, 1997; Van Dam, 2006) as precipitation proxies. This approach of taking ecological richness values of extends on earlier work dealing with diversity spectra in fossil mammal communities (Andrews et al., 1979). The following indices are used for micromammal assemblages, after excluding aerial species (bats) and (semi-)aquatic species:

$$PI = 100 * NI/N \qquad (1)$$

with:

PI   invertivory index
NI   number of invertivore species
N   total number of species

$$PA = 100 * NA/N \qquad (2)$$

with:

PA   arboreality index
NA   number of arboreal species
N   total number of species

We follow earlier work (Van Dam, 2006) in excluding (semi-) aquatic taxa (Table 1) from the micromammal sum, because their presence may be at least partly determined by very local conditions, e.g., a water body, the presence of which could be more related to topography than to local rainfall. The total number of remaining specimens should be minimally ~100 to have a sufficiently large amount of species.

Both invertivory and arboreality are useful categories with regard to precipitation prediction. Invertivory (i.e., the feeding on small invertebrates) is related to the abundance of prey such as insects, arthropods, earthworms etc., and via these to plant richness and humid (soil) conditions. Invertivorous species are characterized by the possession of molars with a strong relief formed by sharp, pointed cusps and deep valleys in order to manipulate and pierce parts of insect exoskeletons or slice soft-bodied invertebrates such as grubs and worms. Lipotyphla (Insectivora) are the typical representatives, but similar adaptations may occur in rodents. For instance, on the basis of its jaw and teeth the extinct rodent genus *Melissiodon* can be assumed to have been invertivorous (Hordijk et al., 2015).

Table 1
Neogene fossil taxa (Western Eurasia) with assumed (semi-)aquatic locomotion, arboreal feeding habitat and invertivorous diet (modified after Van Dam, 2006).

(Semi-)aquatic (excluded taxa)	Invertivorous	Arboreal
Desmaninae	Lipotyphla	Pteromyinae
Asoriculus	*Melissiodon*	Ratufini
Neomys		"*Sciurus*" *giganteus*
Macroneomys		*Sciurus*
Castoridae		Glirinae
Mimomys hassiacus–savini lineage		Bransatoglirinae
Arvicola		*Glirulus*
Dolomys nehringi–milleri		*Paraglirulus*
Kislangia		*Microdyromys complicatus,*
		M. koenigswaldi,
		M. praemurinus, M. remmerti
		Vasseuromys
		Ramys
		Pseudotheridomys
		Eomyodon
		Eomyops
		Keramidomys
		Neocometes

By definition arboreality requires the presence of forests, which need humid conditions at least during a significant part of the year. We use the term 'arboreal' in the broad sense of a dominant feeding habitat consisting of trees. This category in fact combines the two locomotion-based categories "arboreal" (moving across the canopy) and "scansorial" (moving along the trunk and lower branches). Explicit arboreal adaptations such as gliding membranes have only rarely been preserved as fossils (Storch et al., 1996). As a consequence, the classification of arboreality in fossil micromammals is for an important part based on the life style of nearest living relatives. In addition, workers have observed a correlation between dental complexity and habitat, with forest dwellers characterized by more complex occlusal surfaces. For example, it has been observed that hamsters characterized by five ridges (pentalophodont) tend to live in forests, whereas open country dwellers have more simplified, four-ridged (tetralophodont) crowns (Hershkovitz, 1967). The latter crowns are often also more hypsodont, thus allowing the consumption of larger amounts of (lower-nutritional) food.

Here, we use dental complexity for distinguishing arboreal from non-arboreal forms in Gliridae and Eomyidae. For glirids (dormice), we follow earlier work (van der Meulen and De Bruijn, 1982; de Bruijn, 1998), in considering seven or more transverse ridges in the M12 as indicative for an arboreal lifestyle. For the extinct eomyids no control by recent forms is possible. Thanks to exceptional preservation circumstances it could be demonstrated that at least one Oligocene species was a glider (Storch et al., 1996), but probably not all eomyids were arboreal (Engesser, 1999). Here we follow an earlier proposal (Van Dam, 2006) to classify forms with five or more transverse ridges (*Pseudotheridomys*, *Eomyodon*, *Keramidomys*, *Eomyops*) as arboreal, and species with four or less ridges (*Rhodanomys*, *Ritteneria*, *Pentabuneomys*, *Ligerimys*, *Estramomys*) as terrestrial. This classification criterion should not be regarded as final and should be subjected to ongoing evaluation, e.g., by confronting eomyid-based habitat inferences with other types of available evidence (e.g., from other micromammal taxa in the same fauna). This may or may not lead to a modification of the used criterion in the future (see discussion).

Table 1 shows the (Neogene) taxa with assumed (semi-)aquatic, arboreal and insectivorous habits relevant to this work. *Neocometes* and "*Sciurus*" *giganteus* were not included in the fossil data set of Van Dam (2006). Here we assume that the feeding habitat of *Neocometes* was arboreal, i.e., similar to that of its closely living relatives *Platacanthomys* and *Typhlomys* (Fejfar, 1999; Nowak, 1999), and that "*Sciurus*" *giganteus* was an arboreal squirrel belonging to the Ratufini (de Bruijn, 1999).

For the modern Western Old World, a series of linear calibration equations using PI, PA to predict the precipitation variables MAP, LMP, HMP were inferred (Van Dam, 2006). Because of the importance of region- and continent-specific effects on richness related to unique tectonic and climatic histories (e.g., Qian and Rickleffs, 2008), only data points from the Western Old World were used to generate these equations, despite the fact that fossil faunas with higher relative richness values (especially PA) than today existed (see discussion in Section 4).

The following equations were inferred by Van Dam (2006):
Mean annual precipitation (MAP):

$$MAP = 0.179 + 14.134\, PI + 18.066\, PA, \qquad (3)$$

$$\left(R^2 = 0.69\right).$$

Precipitation in the driest month (LMP):

$$LMP = 2.567 + 1.978\, PA, \qquad (4)$$

$$\left(R^2 = 0.72\right).$$

Precipitation in the wettest month (HMP):

$$HMP = 0.609 + 2.716 \, PI, \qquad (5)$$

$$\left(R^2 = 0.51 \right).$$

Because the fit to HMP was only moderately strong, it was not used for fossil predictions before. However, in the present context of plant–mammal comparison, it is included.

Obviously, taphonomic factors play a role in interpreting the paleoclimatic results inferred from the micromammal assemblages. Most small-mammal fossils end up in sediments via the droppings of predators, such as owls, diurnal avian predators and small mammalian carnivores (Andrews, 1990). This mechanism implies that the fossil site may not correspond to the place where the micromammals were residing, and may even be a few km distant of it. Although some predators are selective and others just randomly catch what comes across, it has been observed that fossil micromammal assemblages in local sequences or time-equivalent assemblages within basins are often surprisingly similar, even in their species relative abundances. Also over larger distances, composition and abundance patterns appear to vary predictably (van Dam and Weltje, 1999; Peláez-Campomanes et al., 2003; Furió et al., 2011). These observations point to the presence of a strong regional signal in fossil micromammal assemblages. In this respect micromammal faunas may partly differ from fossil floras, for which the local signal may be stronger. (Note that although (semi-)aquatic small mammals were excluded from our analyses because of their supposedly local significance, also their distributions require larger, regional pools of individuals that allow local populations to persist. For instance, the presence of beavers corresponds well with the presence/absence of other indicators of more closed/open vegetation (see for example van der Meulen and Daams, 1992)).

The application of actualistic principles constitutes another source of prediction bias. This applies both to the autecology of individual species (see above) and richness patterns as a whole. By using richness variables as proxies for climate, it is in fact assumed that richness patterns reflect environmental conditions at the approximate time of death. This assumption may be wrong: for example, the "evolutionary time hypothesis", holds that, in the absence of major perturbations, richness grows intrinsically by the continuous creation of new niches (Margalef, 1963). If richness may indeed increase without any change in climate, CDA predictions could be biased.

In this work, we compare precipitation estimates based on CA and CDA, discuss discrepancies, and try to identify potential sources of bias. Finally, we will also offer some alternative micromammal-based equations that take into account non-linearities in the calibration data set, and include explicit inter-calibrations to the plant-based results by incorporating CA predictions for no-analogue, high-precipitation micromammal sites. The generation of optimal non-linear fits was performed with the curve fitting program Datafit (version 9.1.32, Oakdale Engineering, 1995–2008). All further regression statistics were produced using IBM SPSS Statistics (version 22).

2.3. Description of the fossil sites

Our search across the literature resulted in twelve Neogene sites for which it could be assumed that plant and micromammal collections originated at least partly from the same bed(s), and which at the same time provided sufficient plant and small-mammal material to make reliable predictions. Another series of six sites was selected, for which plant- and micromammal-containing levels differed only maximally a few meters stratigraphically. Because environmental conditions may vary significantly at the scale of individual beds (for instance in the case of Milankovitch climate oscillations), we kept these sites separate from the first twelve. The complete data set includes six sites from Anatolia, seven from Central Europe (Austria, Germany), four from France and one from Spain (for all 18 sites: see Fig. 1, Table 2). Ages range from the Oligocene–Miocene transition to the Early Pliocene. Paleoenvironments include both forest and open-country ecosystems.

All floral lists and plant reference taxa with their precipitation ranges are given in Appendix A. Appendix B includes the micromammal lists with the arboreal, insectivorous and excluded (semi-)aquatic taxa indicated. A summary of the micromammal diversity statistics is given in Table 3. Below we first present a short description of the sites, ordered from east to west. When two names are given, the first refers to the name given to the flora, and the second to the name given to the fauna (see also Table 2).

2.3.1. Sivas Karaözü/Karaözü

The late Miocene site Karaözü is included in a clastic sedimentary series (Eğerci Formation) in the Gemerek area in the Kayseri-Sivas basin, Central Anatolia (Sümengen et al., 1989). The fossil level is a ~1 m thick grey homogeneous silty clay (Hans de Bruijn, pers. comm.). Small mammal identifications are after the original publication (Sümengen et al., 1989) with subsequent modifications (Saraç, 2003; Suata-Alpaslan, 2004). The number of insectivore species has been counted by one of us personally (JvD). The palynomorph record is a combination of two consecutive samples (Yavuz-Işik et al., 2011).

The spectra are characterized by an overall low species richness of woody plants (<5%). The palyno-record points to a dominantly herbaceous vegetation. Except *Ulmus* sp., woody angiosperms are represented by a few grains only. Even Pinaceae pollen, which commonly are frequently encountered in the spectra as allochthonous background component, do not exceed 5%, thus pointing to the absence of a source relatively close to the deposition area (e.g., conifer forest of the higher altitudes). The presence of *Ulmus* points to alluvial wetlands, as today in Central Anatolia (Woldring and Cappers, 2001). No (semi)-aquatic micromammal species are recorded that could indicate the permanent nature of wetlands. Only one micromammal species was recorded that is associated with an arboreal feeding habitat (the eomyid *Keramidomys*).

2.3.2. Kargı 2

The terminal Oligocene (or possibly basal Miocene) site Kargı 2 is situated in a lignite mine in the Osmancik–Dudurga Basin in Anatolia, about 200 km northeast of Ankara. The lignitic level has yielded both micromammals and pollen.

With a ca. 70% relative richness of the arboreal component, the Kargı 2 palynomorph sample points to a forested environment. High percentages of *Engelhardia* and other "megamesothermic" elements (Yavuz-Işik et al., 2011) underline the warm temperate character of the flora that according to its taxonomic composition can be regarded as mixed mesophytic (see also Utescher et al., 2007). The micromammal fauna (van den Hoek Ostende, 2001a; Saraç, 2003; Ünay et al., 2003; de Bruijn et al., 2013), however, is not confirming the inference of a dense forest, because for only one out of twenty recorded species an arboreal habitat is assumed (*Paraglirulus* sp.). No (semi-)aquatic species are recorded.

Fig. 1. Google Earth landsat image (2014) with studied sites. For codes and full names: see Table 2.

Table 2
Studied localities with details on type of plant fossils, geography and chronology. P: pollen and spores; B: leaves; F: fruits and seeds; M: unspecified macroflora.

Code	Name flora	Flora type	Country	Longitude	Latitude	Biochronology	References flora
Ka	Sivas Karaözü	P	Turkey	35.93	39.17	MN10	Yavuz-Işik et al. (2011)
K2	Kargı 2	P	Turkey	34.87	40.87	MP30?	Yavuz-Işik et al. (2011)
Ke	Keseköy	P	Turkey	32.68	40.66	MN3	Yavuz-Işik et al. (2011)
Ak	Afyon Akçaköy	P	Turkey	30.26	38.12	MN14	Yavuz-Işik et al. (2011)
Ko	Koçgazi	P	Turkey	30.11	38.41	MN7–8	Yavuz-Işik et al. (2011)
Ye	Yeni Eskihisar	P	Turkey	28.08	37.32	MN7–8	Yavuz-Işik et al. (2011)
Gd	Götzendorf	P	Austria	16.58	48.01	MN9	Rögl et al. (1993)
Ob	Oberdorf mine (M)	M	Austria	15.15	47.08	MN4	Meller et al. (1999)
Ma	Massendorf	M	Germany	12.46	48.60	MN5	Jung (1963); Spitzlberger (1986)
Am/AS3	Ambérieu S3 (=125–141 m)	P	France	4.73	45.92	MN10	Farjanel and Mein (1984)
Am/A1	Ambérieu S2 (=143–147 m)	P	France	4.73	45.92	MN10	Farjanel and Mein (1984)
Am/A2C	Ambérieu S4 (=117–124 m)	P	France	4.73	45.92	MN10	Farjanel and Mein (1984)
Ru	Rudabanya	B	Hungary	20.63	48.72	MN9	Kretzoi et al. (1976), Hably and Erdei (2013),
Ra	Rauscheröd	P	Germany	13.26	48.56	MN4	Seitner (1987)
En	Engelswies	B,F	Germany	9.13	48.03	MN5	Schweigert (1992)
Un	Unterneul 2	P	Germany	11.05	48.24	MN6	Fiest (1986); Seitner (1987)
So	Soblay	P	France	5.50	45.10	MN10	Ménouret and Mein (2008)
Te	Terrassa	B	Spain	2.00	41.57	MN10	Sanz de Siria (1997), Agustí et al. (2003)

Code	Name fauna	References fauna
Ka	Karaözü	Sümengen et al. (1990), Saraç (2003), Suata-Alpaslan (2004), Bosma et al. (2013), this paper
K2	Kargı 2	Theocharopoulos (2000); Van den Hoek Ostende (2001a,b), Ünay et al. (2003), De Bruijn et al. (2013), Bosma (pers. comm.)
Ke	Keseköy	De Bruijn and Saraç (1991, 1992), De Bruijn et al. (1993), Ünay, 1994; Van den Hoek Ostende (2001b), López-Antoñanzas et al. (2004)
Ak	Dinar Akçaköy	Sickenberg et al. (1975), Engesser (1980), Saraç (2003), Suata-Alpaslan (2010)
Ko	Koçgazi	Sickenberg et al. (1975)
Ye	Yeni Eskihisar	Sickenberg et al. (1975), Engesser (1980), Wessels et al. (1987), Saraç (2003)
Gd	Götzendorf 1&2	Bachmayer and Wilson (1985), Rögl et al. (1993), Daxner-Höck (2004), Ziegler (2006), Daxner-Höck and Höck (2009)
Ob	Oberdorf 3&4	Daxner-Höck et al. (1998a,b), Ziegler and Daxner-Höck (2005), Prieto and Van Dam (2013), Daxner-Höck and Höck (in press)
Ma	Massendorf	Schötz (1983, 1985, 1988, 1989, 1993, 2002)
Am/AS3	Ambérieu S3	Farjanel and Mein (1984)
Am/A1	Ambérieu 1	Mein (1999)
Am/A2C	Ambérieu 2C (corr to 119 m)	Mein (1999)
Ru	Rudabanya	Bernor et al. (2004), Daxner-Höck (2005), Kretzoi and Fejfar (2005), Ziegler (2005)
Ra	Rauscheröd 1b–c	Ziegler and Fahlbusch (1986), Ziegler (2006)
En	Engelswies 1	Ziegler (1995, 2006)
Un	Unterneul 1a	Heissig (1989)
So	Soblay	Ménouret and Mein (2008)
Te	Trinxera Sur Autopista 2	Agustí et al. (2003)

2.3.3. Keseköy

All small mammals from the Early Miocene Turkish site Keseköy are derived from one single thin green to black clay level (de Bruijn and Saraç, 1991; Saraç, 2003; Yavuz-Işik, 2008). The palynomorph record of this level consists of six samples (Yavuz-Işik, 2008).

High percentages of evergreen *Quercus* underline the thermophilous character of the vegetation, which consists of a zonal, mesophytic forest (mainly *Engelhardia, Quercus,* and *Capinus*). The pollen evidence a nearby alluvial wetland community (*Carya, Ulmus/Zelkova*), but also include bisaccate types that are probably allochthonous (*Pinus,* Pinaceae). The relative richness of the herbaceous components is 15%. The recorded proportion of Poaceae pollen (~5%) might point to the presence of open spaces. The small-mammal composition (de Bruijn and Saraç, 1991, 1992; de Bruijn et al., 1993; Ünay, 1994; van den Hoek Ostende, 2001b; López-Antoñanzas et al., 2004) is rather similar to that of Kargı 2, with *Glis* and *Glirulus* counting as arboreal components.

2.3.4. Afyon-Akçaköy/Dinar-Akçaköy

This Early Pliocene site is situated in the southern part of the Sandıklı Basin in western Anatolia According to the descriptions of the so-called 'Oberen Limnischen Schichten' (Sickenberg et al., 1975), the small-mammal fossils were found, in a ~10 m thick clayey interval, in which they were distributed homogeneously as well in small lenses. The small-mammal faunal list is based on the original publication (Sickenberg et al., 1975) and subsequent updates

(Engesser, 1980; Saraç, 2003; Suata-Alpaslan, 2010). Five palynomorph samples are described by Yavuz-Işik et al. (2011). It can be assumed that at least some of the stratigraphic levels with pollen correspond to micromammal-containing levels.

The palynomorph samples reveal significant herbaceous vegetation pointing to an open vegetation type. Raised percentages of Chenopodiaceae/Amaranthaceae in some of the sampled levels point to the temporary existence of salt steppe or salt marsh. The high proportion of elements probably brought in by transport (up to 60% *Pinus,* Pinaceae) either indicates nearby upland areas receiving more rainfall, or a comparatively low local pollen production. The small mammals indicate an environment that can be considered to have been relatively open, with only one supposedly tree-dwelling form present (*Keramidomys*).

2.3.5. Koçgazi

Like Akcaköy, Koçgazi is situated in the 'Oberen Limnischen Schichten' of the Sandıklı Basin in western Anatolia (Sickenberg et al., 1975). Details on the lithology of the site are not reported. The mentioned lacustrine unit is clearly time-transgressive given the Pliocene age of the Akcaköy site and late Middle Miocene age of Koçgazi. The single palynological sample is supposed to originate from the mammal locality (Yavuz-Işik et al., 2011).

The Koçgazi microflora contains a well-represented (72%) arboreal component, although the spectrum mainly comprises allochtonous conifers (*Pinus* sp., Pinaceae, undifferentiated) and riparian elements

Table 3

Micromammal absolute and relative richness values (Rodentia, Lipotyphla, Lagomorpha) of studied sites. N = number of species, (semi-)aquatic species excluded; NA = number of arboreal species; NI = number of non-(semi-)aquatic invertivorous species; NQ = number of (semi-)aquatic species; NQI = number of (semi-)aquatic, invertivorous species; PA = 100 × NA / N = percentage of arboreal species; PI = 100 × NI / N = percentage of invertivorous species, (semi-)aquatic species excluded.

Locality	N + NQ	NQ	NQI	NI	NI + NQI	NA	N	PI (%) (100 × NI / N)	PA (%) (100 × NA / N)
Karaözü	16	0	0	3	3	1	16	18.75	6.25
Kargı 2	19	0	0	8	8	1	19	42.11	5.26
Keseköy	24	0	0	9	9	2	24	37.50	8.33
Dinar-Akçaköy	14	3	3	2	5	1	11	18.18	9.09
Koçgazi	14	0	0	4	4	1	14	28.57	7.14
Yeni Eskihisar	19	1	0	6	6	0	18	33.33	0.00
Götzendorf 1&2	32	4	2	9	11	11	28	32.14	39.29
Oberdorf 3&4	42	0	0	18	18	13	42	42.86	30.95
Massendorf	36	2	1	10	11	14	34	29.41	41.18
Ambérieu 1	29	2	1	6	7	7	27	22.22	25.93
Ambérieu S3	15	1	0	4	4	1	14	28.57	7.14
Ambérieu 2C	27	1	1	8	9	5	26	30.77	19.23
Rudabánya 2	30	2	1	10	11	11	28	35.71	39.29
Rauscheröd	22	1	0	8	8	2	21	38.10	9.52
Engelswies 1	13	0	0	2	2	4	13	15.38	30.77
Unterneul 1a	14	0	0	3	3	4	14	21.43	28.57
Soblay	33	3	1	10	11	10	30	33.33	33.33
Trinxera Sur Autopista	11	0	0	3	3	0	11	27.27	0.00

(*Ulmus*, *Zelkova*, *Carya*, and *Parrotia*). Zonal components such as evergreen oak are represented by minor proportions only. Hence the spectrum represents local, riverine/wetland conditions. No mammal indicators such as beavers or water moles were found that could confirm the presence of deeper or permanent water bodies. The only forest indicator in the small mammal fauna is again *Keramidomys*.

2.3.6. Yeni Eskihisar

The mammal fossils from Yeni Eskihisar originate from three horizons within the lower half of a 6 m thick, dominantly grey to greygreen marl, containing sandy, clayey, browncoal (with plant remains) and tufftic intercalations. The sediments, which are Middle Miocene of age, belong to the so-called Sekköy beds (Becker-Platen, 1970; Sickenberg et al., 1975). The faunal list is based on the Sickenberg et al. publication and subsequent works (Engesser, 1980; Wessels et al., 1987; Saraç, 2003). The single pollen sample is derived from a lignitic lacustrine clay (Yavuz-Işık et al., 2011) and is assumed to correspond to one of the mammal-containing horizons.

The palynomorph sample mainly comprises deciduous, arboreal elements that are characteristic for alluvial wetland vegetation (*Ulmus, Zelkova, Carya, Alnus*). Consistently, the presence of castorid rodents points to the presence of a permanent water body. The herbaceous components represent around 30% of the palynomorph sum. At first sight, the flora looks surprisingly temperate, given the absence of *Engelhardia* and evergreen oaks, and the sparseness of mega-mesothermic elements. On the other hand, the fraction of less common forms includes a diverse record of warmth-loving plants such as Arecaceae, *Distylium* and *Castanopsis*. The herbaceous component is quite diverse and even comprises families with members that are indicative for steppe and salt steppe vegetation. On the other hand, Poaceae and *Artemisia* are not present, whereas most other herbaceous components belonging to Amaranthaceae, Apiaceae, Asteraceae, Chenopodiaceae, Chichorioideae and Mimosaceae may occur in both, mesic and dry environments. Micromammal indicators for full forest are lacking, which is in agreement with the wetland aspect as indicated by the tree pollen.

2.3.7. Götzendorf

The Late Miocene Austrian site Götzendorf is included in the upper, coal-rich unit (Zone F) of the fluviolacustrine Lower Neufeld beds in the southern Vienna Basin. The coal unit represents a transitional facies between the brackish Pannonian Lake facies and the freshwater (Zone G) facies. According to the descriptions (Rögl et al., 1993), the pollen collection is a combination of five samples, three of which correspond to the mammal horizon (a storm bed consisting of fine sand), one to a mudstone below it, and one to a lower level consisting of mudstone and lignite. Palynologically, the only difference between the plant samples is a lower abundance of *Pinus* in the lowest level. The small mammal assemblages (Rögl et al., 1993; Daxner-Höck, 2004; Ziegler, 2006; Daxner-Höck and Höck, 2009, in press) stem from a main excavation site (Gö1) and a second, lateral site (Gö2) (Daxner-Höck and Höck, 2009).

Apart from aquatic components (*Cladium, Potamogeton, Decodon*) and swamp forest trees (*Nyssa, Taxodium*), the spectrum evidences a thermophilous, mesophytic, broadleaved deciduous forest association with evergreen components (*Fagus, Quercus, Ulmus, Tilia, Reveesia, Oreomunnea/Alfaroa*), constituting a Cenozoic association often denoted as mixed mesophytic forest (Mai, 1995; Utescher et al., 2007). Also the micromammal composition (Bachmayer and Wilson, 1985; Rögl et al., 1993) is pointing to a forested environment as indicated by the presence of eleven micromammal species for which an arboreal life style can be assumed (five dormice, five flying squirrels, and one eomyid species). Also the presence of the fruit-eating (Bernor et al., 2004) primate *Anapithecus* is indicative for a closed environment. The additional presence of a permanent water body is evidenced by the presence of two beaver taxa (*Castor* and *Trogontherium*) and two water moles (*Archaeodesmana, Storchia*).

2.3.8. Oberdorf

The small-mammal collection from the Middle Miocene German site Oberdorf stems from the Oberdorf browncoal mine, 20 km west of Graz, SE Austria (Daxner-Höck et al., 1998a,b). The fossils originate from two levels with a very similar fauna: a thin brown clayey coal level (O3) and a 8–10 m higher level (O4) at the base of a double coal band (1–2 m thick). Dr. Daxner-Höck kindly supplied us with newest update of the Oberdorf fauna (levels 3 and 4 combined, Daxner-Höck and Höck, in press). The flora (leaves, fruits and seeds; Meller et al., 1999) was collected from various levels including O3 and O4, although most species originate from just above the double coal band.

The Oberdorf macroflora represents a mixed mesophytic forest association, which is characteristic for the mid-latitudes of Europe during the warmer climatic phases of the Neogene. The association is diverse containing a few herbs, around 20% deciduous and evergreen shrubs, and a comparatively high diversity proportion of mesophytic, evergreen arboreal components belonging to Mastixiaceae, Lauraceae, and Fagaceae. The presence of a large number of 13 (31%) of arboreal species (five dormice, five flying squirrels and one eomyid), confirms the presence of a forested environment (Daxner-Höck et al., 1998b; Daxner-Höck and Höck, in press). The presence of two small deer species points to the presence of forest conditions as well (Rössner, 1998). No (semi-) aquatic species were recorded.

2.3.9. Massendorf

Macrofloral and small mammal rests from this Middle Miocene German site are derived from a marl lens at the base of a fluviatile series in the Bavarian part of the North Alpine Foreland Basin (Schötz, 1983). The lens can be subdivided into a 0.2–0.5 m lower grey bed with poorly preserved leaves and gastropods, which is overlain by a 0.2–1.2 m thick upper bed of grey-green color, which is darkening downward, containing vertebrate fossils, gastropods and plant remains in the form of wood and seeds.

Apart from local, aquatic elements (*Nuphar, Potamogeton, Decodon*), the fruits, seeds, and leaves (Jung, 1963; Spitzlberger, 1986) comprise components that may thrive in both lakeshore communities and lowland broadleaved forest vegetation. As regards taxonomic composition, the vegetation represents a thermophilous, mesophytic forest with

diverse broadleaved evergreens such as Lauraceae, evergreen Fagaceae, and the liana *Toddalia*, which today is common in riparian habitats with higher rainfall (Gregor, 1979). Within the micromammals, Castoridae and Desmaninae point to the presence of a permanent water body. The presence of 14 arboreal species (nine dormice, 2 flying squirrels, 2 eomyids and *Neocometes*) (Schötz, 1983) representing 32 and 41% of the non-aquatic small mammal species, respectively, indicate a forested environment.

2.3.10. Ambérieu

A drilling across the Late Miocene "Marnes de Bresse" near Ambérieu in the Rhone basin (France) has revealed a detailed pollen record as well as a collection of small mammal remains (Farjanel and Mein, 1984). The lower levels of pollen unit S2 (143–147 m, five samples), with a lithology of grey or sometimes greenish carbonatic clays, stratigraphically correspond to the surface beds that have yielded the rich fauna Ambérieu 1 (Mein, 1984, 1999). Unit S3 (125–141, 15 pollen samples) is the most productive core unit in terms of micromammals (109 teeth). Its lithology consists of grey marl with abundant mollusc rests. This same lithology characterizes the next higher unit S4 (117 to 124 m, 5 pollen samples). Stratigraphically, the 119 m bed within S4 corresponds to the rich micromammal surface site Ambérieu 2C (Mein, 1984, 1999).

Apart from small-scale variability, the palynomorph diagram displays an upward decrease of the arboreal component (mainly Cupressaceae), while the herbaceous component (mainly Asteraceae and Polypodiaceae) shows a considerably increase. From the grey clays of S2 there is evidence for local swamp vegetation consisting of *Taxodium* and ferns (Osmundaceae, Polypodiaceae). Accessory riparian elements such as *Carya*, *Ulmus/Zelkova*, and *Salix* are also present. Elements of the zonal vegetation are rarely present (e.g., *Engelhardia*) and were probably transported over a longer distance. The spectra of intervals S3 and S4 display a significant decline of the Cupressaceae/Taxodioideae pollen (and thus of the swamp forest community) with respect to the spectrum of S2.

The micromammal fauna of Ambérieu 1 contains seven arboreal species (Gliridae, Petauristinae, Eomyidae), implying the presence of abundant trees. The fauna of Ambérieu 2C is very similar to that of Ambérieu 1, except for the presence of the rare *Glirulus diremptus* and *Blackia miocaenica* in the latter site. In the stratigraphically more or less equivalent assemblage S3 only one arboreal form (*Muscardinus*, Gliridae) was found. The presence of permanently open water is indicated by the beaver *Chalicomys* (Ambérieu 1), and the water mole *Archaeodesmana* (Ambérieu 1, 2C).

2.3.11. Localities with plants and mammals from closely spaced beds

In addition to the twelve sites above, we made precipitation estimates for six localities, for which plants and small mammals are derived from beds which are stratigraphically very close (within ~2 m), or for which a common origin of plant and mammal remains is possible but could not be established with certainty (Table 2; Fig. 1). The Hungarian Rudabánya flora (Kretzoi et al., 1976; Hably and Erdei, 2013; Boglárka Erdei, pers. comm.) has been collected from various levels within a short lateral distance from Rudabánya 2, the level of both small and large small mammals (Boglárka Erdei, Ray Bernor, pers. comm.). We note that precipitation estimates for Rudabánya using both of our methods were already included in Bernor et al. (2004), which includes the basic faunal list, which was slightly modified afterwards (Daxner-Höck, 2005; Kretzoi and Fejfar, 2005; Ziegler, 2005). Plants from the German site Rauscheröd (Seitner, 1987) are derived from a greenish-grey to yellow marl, which is positioned about 0.5 m higher than the micromammal-containing levels 1b-c (Ziegler and Fahlbusch, 1986; Ziegler, 2006) that consist of light- to dark-brown marls. The small mammals from Engelswies 1 (Germany, Ziegler, 1995) originate from marly levels 1 m (levels 2, 3) and 4 m (level 1) higher than a plant-containing limestone (Schweigert, 1992). The flora (Fiest, 1986;

Seitner, 1987) from the German site Unterneul 2 stems from clays, whereas the micromammals from Unterneul 1a (Heissig, 1989) originate from stratigraphically proximate silts and sands. The relative stratigraphy of plants and mammals in the French site of Soblay (Ménouret and Mein, 2008) is not known with certainty: the section contains four lignites (as described for two 10–13 m profiles), with the plants either originating from a lignite, or perhaps from a marl with wood remains (Gonzalo Jimenez-Moreno, pers. comm.). The majority of the micromammals stems from a lignite, and the remaining part from a grey marl, which was sampled later. Finally, the flora from Terrassa (Spain) is said to be "very close" to the small-mammal site Trinxera Sur Autopista 2 (Sanz de Siria, 1997; Agustí et al., 2003).

3. Results

All precipitation predictions shown in Tables 4–5 and Figs. 2–4. In 48 out of 54 cases (MAP, LMP, HMP for 18 sites), plant CA analysis provides a 100% overlapping of climatic requirements of the taxa included in the analysis, thus testifying highly significant results (Mosbrugger and Utescher, 1997). In the remaining cases, outliers are identified that have no overlap with the resulting CA intervals (see Appendix A). Among the outliers are *Myrica faya* from Massendorf (MAP, LMP and HMP), and *Lygodium* (LMP), *Craigia, Calamus* and *Heliconia* (HMP) from Engelswies (a total of 5 species for MAP, LMP and HMP). We refer to Utescher et al. (2014) for a detailed discussion on outliers in the CA.

Some of the calculated coexistence intervals are relatively broad, which is due to the lack of taxa with well-confined precipitation ranges (e.g. for MAP: Götzendorf, Ambérieu S2 and S3, Rudabánya and Unterneul 2). Some taxa are particularly important in setting the upper or lower limits of coexistence intervals. A good example is the upper MAP limit of *Ephedra* (932 mm/yr), which forms an important constraint for the upper limits for the Anatolian sites. Another case is *Engelhardia*, which constrains the lower MAP and HMP limits (740 mm; 150 mm) in several Anatolian sites and in the French sites of Ambérieu. As an example, Fig. 6 shows the plant ranges and coexistence intervals for the Central European sites Götzendorf, Oberdorf and Massendorf. The floras of latter two sites is based on macrofloral remains, allowing for higher taxonomic precision and hence producing more strictly confined climatic intervals, resulting in comparatively small coexistence intervals (Figs. 2–4, 6, Table 4).

Fig. 5 shows the combinations of micromammal PI and PA values. Whereas high values of 30–40% of both PI and PA characterize the central European sites Götzendorf, Oberdorf, Massendorf, Rudabánya and the French site Soblay, both indices are low (<20%) in the Anatolian sites Karaözü and Dinar-Akçaköy. The remaining Anatolian sites also have low proportions of tree-dwelling species, but invertivore proportions are variable and sometimes even rise to levels above those of the central European sites. By contrast, the German site Engelswies combines a low proportion of invertivores with relatively high proportions of arboreal forms.

Because the three variables MAP, LMP and HMP are estimated by different (sets of) independent variables, internal "inconsistencies" may arise when means and limits of the prediction intervals for wettest- or mean-month estimates (MAP/12) extend below those of driest-month estimates, or when means and limits of wettest-month estimates extend below mean-month estimates. Such inconsistencies indeed occur for some of the micromammal localities. Furthermore, because symmetric prediction intervals are used, lower limits may become negative. (One could either interpret negative values as shortage, or take 0 mm/yr as theoretical minimum.) Both the inconsistencies and the negative numbers are italicized in Tables 4 and 5.

Although the intervals of uncertainty for plants and mammals are not directly comparable (coexistence intervals vs. 95% prediction intervals), we regard a lack of overlap between these two types of intervals as an indication that both predictions are truly different. Here, we will

Table 4

Precipitation prediction results for plants (method: CA) and micromammals (method: CDA) originating (partly) from the same bed. Micromammal-based predictions based on linear Eq. (3) and non-linear Eq. (7). L and R in headers (plants): left and right limit of coexistence intervals; L95, R95 in headers (micromammals): limits of 95% prediction intervals. Values in italics do not satisfy one or more of the following relationships: values ≥ 0, and LMP means and limits lower than the corresponding mean monthly values, in turn lower than the corresponding HMP values.

Plants				Micromammals						
Locality name	MAP_L	MAP_R	MAP_midpoint	Locality name	MAP_mean (Eq. (3))	MAP_L95 (Eq. (3))	MAP_R95 (Eq. (3))	MAP_mean (Eq. (7))	MAP_L95 (Eq. (7))	MAP_R95 (Eq. (7))
Sivas Karaözü	473	932	702.5	Karaözü	378	*30*	726	430	*91*	769
Kargı 2	740	932	836	Kargı 2	746	373	1119	696	317	1074
Keseköy	740	932	836	Keseköy	681	313	1048	715	362	1068
Afyon Akçaköy	650	932	791	Dinar Akçaköy	421	*67*	776	490	*146*	835
Koçgazi	870	932	901	Koçgazi	533	185	881	576	238	913
Yeni Eskihisar	870	932	901	Yeni Eskihisar	471	90	853	427	59	796
Götzendorf	800	1724	1262	Götzendorf 1&2	*1164*	*643*	1686	1057	684	1430
Oberdorf mine (M)	1146	1258	1202	Oberdorf 3&4	1165	*735*	1596	1113	750	1476
Massendorf	979	1347	1163	Massendorf	*1160*	*609*	1711	1039	658	1420
Ambérieu S2 (=143–147 m)	740	1724	1232	Ambérieu 1	*783*	*344*	1221	801	430	1171
Ambérieu S3 (=125–141 m)	740	1551	1145.5	Ambérieu S3	533	185	881	576	238	913
Ambérieu S4 (=117–124 m)	740	932	836	Ambérieu 2C (~119 m)	782	*410*	1155	822	477	1167
	LMP_L	LMP_R	LMP_midpoint		LMP_mean (Eq. (4))	LMP_L95 (Eq. (4))	LMP_R95 (Eq. (4))	LMP_mean (Eq. (8))	LMP_L95 (Eq. (8))	LMP_R95 (Eq. (8))
Sivas Karaözü	8	45	26.5	Karaözü	15	−4	34	24	6	42
Kargı 2	9	38	23.5	Kargı 2	22	3	42	22	4	40
Keseköy	9	38	23.5	Keseköy	19	0	38	27	9	45
Afyon Akçaköy	5	41	23	Dinar Akçaköy	21	1	40	28	10	45
Koçgazi	9	36	22.5	Koçgazi	17	−3	36	25	7	43
Yeni Eskihisar	9	36	22.5	Yeni Eskihisar	3	−17	22	2	−17	20
Götzendorf 1&2	9	64	36.5	Götzendorf 1&2	80	53	108	43	24	62
Oberdorf mine (M)	30	43	36.5	Oberdorf 3&4	64	40	88	40	22	59
Massendorf	22	61	41.5	Massendorf	84	*56*	112	44	25	62
Ambérieu S2 (=143–147 m)	9	64	36.5	Ambérieu 1	54	*31*	76	39	20	57
Ambérieu S3 (=125–141 m)	9	41	25	Ambérieu S3	17	−3	36	25	7	43
Ambérieu S4 (=117–124 m)	9	45	27	Ambérieu 2C (~119 m)	41	20	61	35	17	54
	HMP_L	HMP_R	HMP_midpoint		HMP_mean (Eq. 5)	HMP_L95 (Eq. 5)	HMP_R95 (Eq. 5)	HMP_mean (Eq. 9)	HMP_L95 (Eq. 9)	HMP_R95 (Eq. 9)
Sivas Karaözü	71	191	131	Karaözü	52	−5	108	57	*1*	112
Kargı 2	150	191	170.5	Kargı 2	109	49	170	98	36	161
Keseköy	150	191	170.5	Keseköy	102	43	162	98	40	156
Afyon Akçaköy	108	200	154	Dinar Akçaköy	50	−7	107	63	*8*	119
Koçgazi	178	191	184.5	Koçgazi	78	21	135	78	22	133
Yeni Eskihisar	178	219	198.5	Yeni Eskihisar	91	33	149	71	12	130
Götzendorf 1&2	178	265	221.5	Götzendorf 1&2	*88*	*30*	146	154	90	217
Oberdorf mine (M)	182	195	188.5	Oberdorf 3&4	117	*55*	179	159	99	219
Massendorf	146	164	155	Massendorf	*80*	*23*	*138*	152	86	217
Ambérieu S2 (=143–147 m)	150	236	193	Ambérieu 1	*61*	*4*	117	110	49	171
Ambérieu S3 (=125–141 m)	150	225	187.5	Ambérieu S3	78	21	135	78	22	133
Ambérieu S4 (=117–124 m)	150	200	175	Ambérieu 2C (~119 m)	84	*27*	142	112	56	168

refer to both types of intervals as "uncertainty intervals". For MAP, all estimates in Table 4 and Fig. 2, except those for Yeni-Eskihisar show overlap of their uncertainty intervals. This result may be interpreted as an indication that both methods broadly predict comparable amounts of precipitation. Nevertheless, some systematic differences appear to be present. MAP estimates for the three (wet) central European sites Götzendorf, Oberdorf and Massendorf appear to match well: plant-based estimates of range midpoints are 1262, 1202 and 1163 mm/yr (but note the large uncertainty interval for Götzendorf), whereas the three micromammal-based predictions reach (extremely similar) values of 1160, 1164 and 1165 mm/yr. On the other hand, the micromammal-based mean values for the (drier) Anatolian sites (400–700 mm/yr) generally correspond to the lower parts of the coexistence interval for plants. Plant- and mammal-based estimates for Ambérieu 2C fit well, whereas the former are higher for the two other Ambérieu sites, although uncertainty intervals do overlap.

Driest-month (LMP) plant-based and mammal-based estimates for the Anatolian sites match better than their corresponding MAP estimates, although ranges are relatively broad (Fig. 3). On the other hand, the micromammal-based estimates for the Austrian/German

sites are significantly higher than the corresponding plant-based estimates, although there is still overlap of the uncertainty ranges (Fig. 3). Wettest-month (HMP) predictions (Fig. 4) differ most between the two methods, with plant-based estimates being much higher, and with only three out of twelve localities showing overlap.

Table 5 shows the predictions for the six localities for which plants and micromammals originate from different, but closely spaced levels. Clearly, any comparison should be made with care, as in this case differences between precipitation values may simply reflect age differences. Nonetheless, MAP intervals show overlap except for one site (Rauscheröd), although overlap is small for Engelswies and Trinxera Sur Autopista. As in Table 4, LMP micromammal-based estimates are higher than the corresponding plant-based estimates in the more northern sites, although there is overlap for each site. The reversed situation applies to the Spanish site Terrassa/Trinxera Autopista Sur 2, for which the micromammal-based estimate is lower. Wettest-month (HMP) intervals only show a slight overlap for Unterneul. As in Table 4, plant-based HMP estimates for the other five sites (Table 5) are much higher than the micromammal-based estimates.

Table 5

Precipitation prediction results for fossil sites with plants (method: CA) and small mammals (method: CDA) from stratigraphically closely spaced beds (within few meters of sediment). Abbreviations and italics: see caption Table 4.

Plants				Micromammals						
Locality name	MAP_L	MAP_R	MAP_midpoint	Locality name	MAP_mean	MAP_L95	MAP_R95	MAP_mean	MAP_L95	MAP_R95
					(Eq. (3))	(Eq. (3))	(Eq. (3))	(Eq. (7))	(Eq. (7))	(Eq. (7))
Rudabánya	578	1944	1261	Rudabánya 2	*1215*	*705*	1724	1102	733	1470
Rauscheröd	1096	1547	1321.5	Rauscheröd 1b-c	711	343	1078	748	395	1102
Engelswies	1194	1356	1275	Engelswies	*774*	*259*	*1288*	767	360	1175
Unterneul 2	619	1724	1171.5	Unterneul 1a	*819*	*355*	1283	820	441	1199
Soblay	740	932	836	Soblay	1074	*610*	1536	1017	655	1380
Terrassa	641	1230	935.5	Trinxera Sur Autopista 2	386	24	747	352	1	703
	LMP_L	LMP_R	LMP_midpoint		LMP_mean	LMP_L95	LMP_R95	LMP_mean	LMP_L95	LMP_R95
					(Eq. (4))	(Eq. (4))	(Eq. (4))	(Eq. (8))	(Eq. (8))	(Eq. (8))
Rudabánya	24	55	39.5	Rudabánya 2	80	53	108	43	24	62
Rauscheröd	8	41	24.5	Rauscheröd 1b-c	21	2	41	28	10	46
Engelswies	29	51	40	Engelswies	63	*39*	88	40	22	59
Unterneul 2	8	56	32	Unterneul 1a	59	*36*	82	40	21	58
Soblay	17	45	31	Soblay	69	44	93	41	23	60
Terrassa	12	38	25	Trinxera Sur Autopista 2	3	*−17*	22	2	*−17*	20
	HMP_L	HMP_R	HMP_midpoint		HMP_mean	HMP_L95	HMP_R95	HMP_mean	HMP_L95	HMP_R95
					(Eq. (5))	(Eq. (5))	(Eq. (5))	(Eq. (9))	(Eq. (9))	(Eq. (9))
Rudabánya	175	210	192.5	Rudabánya 2	*98*	*40*	156	160	97	223
Rauscheröd	204	245	224.5	Rauscheröd 1b-c	104	46	162	102	44	160
Engelswies	164	170	167	Engelswies	*42*	*−16*	*100*	107	39	174
Unterneul 2	109	265	187	Unterneul 1a	*59*	*1*	117	114	51	176
Soblay	150	159	154.5	Soblay	91	*33*	149	145	85	206
Terrassa	135	159	147	Trinxera Sur Autopista 2	75	17	133	60	3	117

4. Discussion

4.1. Comparing precipitation estimates from plant-based CA and micromammal-based CDA

Our results show that precipitation estimates based on plant coexistence and linear regression on micromammal relative diversity indices reasonably agree for mean annual precipitation (MAP), partially agree for driest-month precipitation (LMP), and generally do not agree for wettest-month (HMP) precipitation (Tables 4,5; Figs. 2–4). Looking into more detail, it appears that the micromammal-based MAP mean values for the Central European (drier) sites are positioned in the lower parts of the plant-based coexistence intervals. The reversed situation is true for LMP, but more dramatically, with micromammal-based values for LMP of the Central European sites ranging to much higher values than the corresponding plant-based estimates. On the other hand, micromammal-based HMP values are structurally lower than plant-based estimates. Differences between the two types of estimates will partly represent random noise, but other factors play a role as well. Below we will discuss these potential factors, which relate to sampling, taxonomic resolution, taphonomy, and method assumptions and limitations.
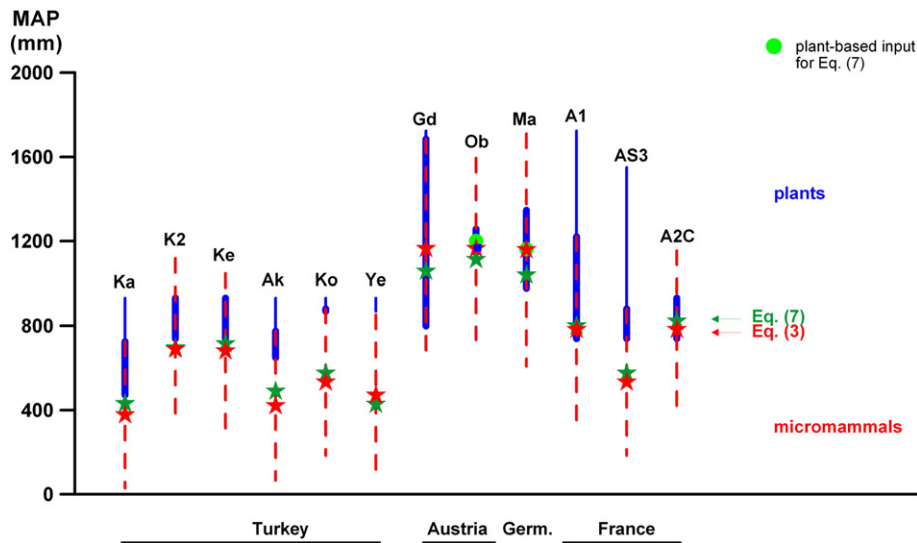

Fig. 2. Annual precipitation estimates (MAP) based on flora and micromammal fauna. Red dashed lines: micromammal 95% prediction intervals; blue solid lines: plant coexistence intervals, thick parts indicate overlap with micromammal prediction intervals; red stars: estimates for mean MAP based on micromammal Eq. (3); dark green stars: estimates for mean MAP based on micromammal Eq. (7); light green circles: plant-based estimates used for Eq. (7); locality symbols: see Table 2.
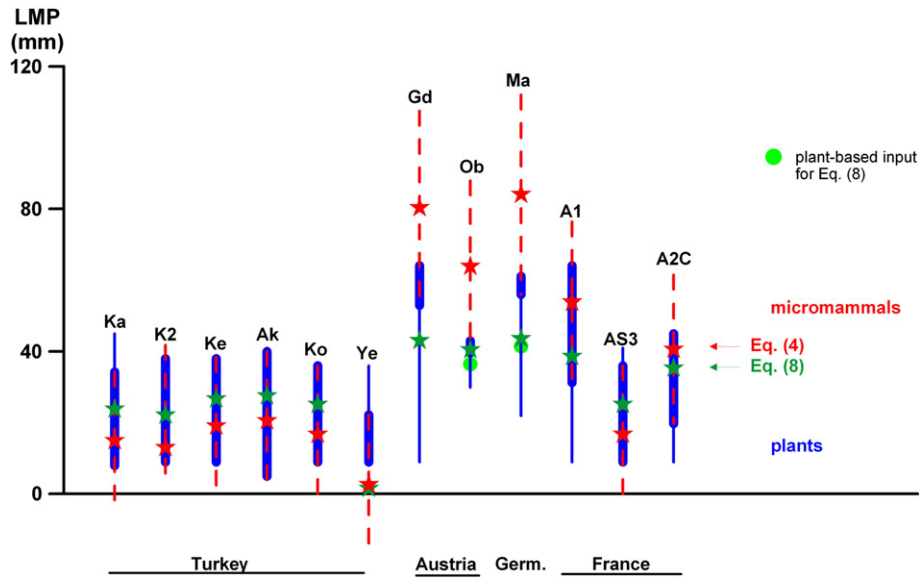
Fig. 3. Driest month precipitation estimates (LMP). Lines and symbols: see caption Fig. 2.

4.1.1. Sampling

Although we have attempted to focus on sites where plant and mammal fossils originate from the same bed, this condition is only realized fully at Karaözü, Kargı 2, Keseköy and probably Koçgazi. At the other sites, only part of the material is derived from the same level(s). But even when the fossils originate from the same bed, predictions may differ when mammal and plant materials originate from different parts or horizons within that bed. In addition, fossil samples are time-averaged units, implying (assuming complete preservation) that the total number of recovered species will be equal or more than the number at any specific moment. Consequently, if the durations of deposition of the two types of fossils do not correspond, discrepancies may arise. It is difficult to know the impact of these stratigraphic effects. It could be that the better fit of MAP at Karaözü, Kargı 2, Keseköy with regard to the other three Anatolian sites (Fig. 2) reflects the common origin of both types of fossils in these sites.

Rare species represent another potential source for discrepancies between the two types of estimates. For instance, the standard CA approach requires the exclusion of rare microfloral species as represented by single grain records (Utescher et al., 2000). In the present study this step was not followed because for various sites only information on presence or absence was available in the literature. By including rare elements the amount of climatic information increases, but, on the other hand, these elements may be allochthonous and dispersed over considerable distances. For instance, rare components may originate from more humid, productive stands, e.g. elevated areas with orographic precipitation, and bias the results towards wetter conditions. In the studied floral record a clear identification of altitudinal elements (e.g. at the species level) was not possible and hence, altitudinal signals in the precipitation reconstruction are not clearly identified. For example, *Engelhardia* pollen, causing a wetter plant-based precipitation reconstruction in five of the studied floras when compared to mammal data (Kargı 2, Keseköy, the 3 Ambérieu levels; MAP > 740 mm, HMP > 150 mm), might originate from more humid, elevated areas. Generally, non-riparian trees with a high pollen production and dispersal (Barrón et al., 2006) were common in thermophilous, diverse broadleaved mesophytic forests of the Neogene of Western Eurasia (Ivanov et al., 2011) including mid-altitudes (up to 700 m,
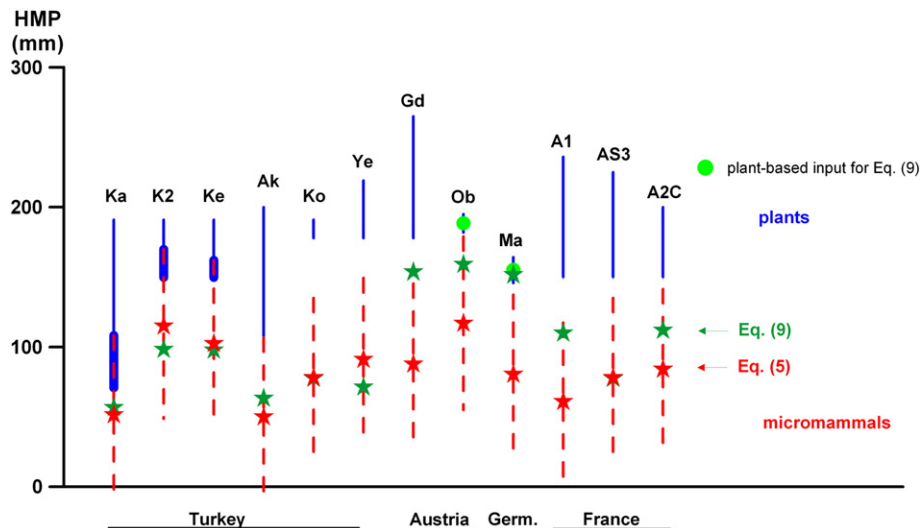

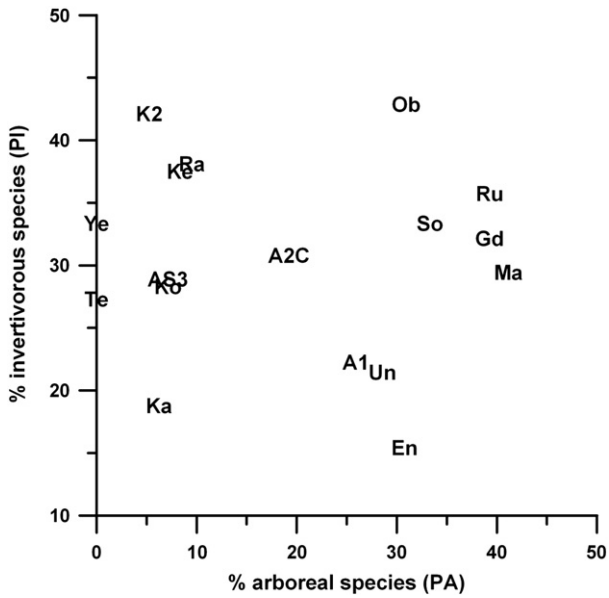**Fig. 4.** Wettest month precipitation estimates (HMP). Lines and symbols: see caption Fig. 2.

Fig. 5. Plot of % invertivorous species (PI) against % of arboreal species (PA) for all studied sites. For codes and full names: see Table 2.

Jiménez-Moreno et al., 2008), depending on the latitudinal position of a given flora.

Although the problem of incomplete sampling of micromammal species is in principle circumvented in the CDA by using relative numbers of species, there would still be bias if ecological preferences would systematically differ between common and rare (i.e., partly not sampled) species. This possibility is best illustrated by looking at the three assemblages from Ambérieu (Appendix B; Figs. 2, 3): whereas the rich surface sites Ambérieu 1 and 2C contain a series of arboreal forms (Gliridae, Sciuridae and Eomyidae), only one of such forms (the glirid *Muscardinus*) is present in the poorer core assemblage S3. Because the relative abundance of these forms in the levels 1 and 2C is very low, the absence in S3 might well be explained as a sampling effect. If

this example represents a general pattern, the lower values for micromammal-based MAP values with regard to plant-based estimates we inferred for the drier sites (Fig. 2), could be due to non-recovered wet-adapted small mammals. On the other hand, LMP predictions for the drier sites, which are entirely based on the arboreality index PA, do not show such a systematic offset.

4.1.2. Taxonomic resolution

Potential indicators for dry climate conditions recorded in the floras such as Compositae, Asteroideae, Caryophyllaceae, Cichorioideae and Poaceae are only identified at the family or subfamily level, resulting in very wide ecological and climatological tolerance ranges because of their cosmopolitan distribution (Appendix A). These dominantly herbaceous floral components, which are mainly traceable in microfloras, could bias CA-based precipitation values in the higher range. On the other hand, they will hardly contribute with climate data in the CA analysis. Currently, work is in progress to improve taxonomic resolution in fossil herbaceous pollen.

Although micromammal specialists may disagree on the species-level taxonomy of certain taxa, they usually fairly well agree on the number of micromammal species in a sample. Thus, a lack of species-specific taxonomic precision does not need to be problematic as such when using the CDA as presented here, as most assignments to invertivory, arboreality or aquatic habitat are applied to the genus level, or sometimes even at the level of complete subfamilies or, in the case of the invertivorous Lipotyphla, orders (Table 1).

4.1.3. Taphonomy and zonal vs. local signals

Fossil plant and mammal samples may differ in what they represent spatially, i.e. the degree to which they reflect a local or regional signal. As discussed in Section 2, there are arguments to assume that most micromammal assemblages represent the regional ("zonal") climate relatively well (even more when (semi-)aquatic species are not considered). For plant-based reconstructions, the distinction between local/extrazonal or regional/zonal taxa will be more relevant (see Section 2.1). Because such a distinction is not made in the CA calculations, the presence of local wetland elements within drier zones may bias reconstructions towards wetter conditions, especially when many
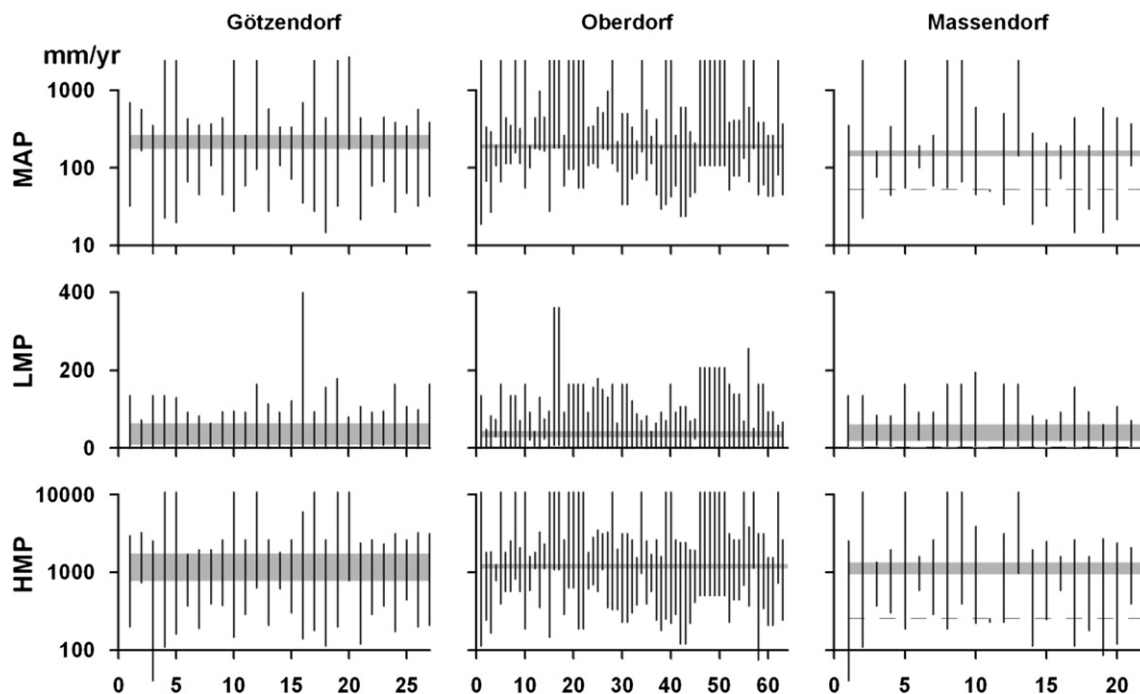

Fig. 6. Application of Coexistence Approach to the floras of Götzendorf, Oberdorf and Massendorf. Numbers on X-axis correspond to list sequence in Appendix A. Vertical lines: precipitation ranges of reference taxa; horizontal grey bars/solid lines: coexistence interval; horizontal dashed lines: precipitation limits as excluded by method (outliers).

such elements are present. Our MAP results may reflect this bias, as presumed alluvial wetland-type of environments (Karaözü, Afyon Akçaköy, Koçgazi, Yeni-Eskihisar, and partly Ambérieu) show the largest differences between (higher) plant-based and (lower) micromammal-based predictions (Fig. 2). Consistently, differences for forest sites (Götzendorf, Oberdorf, Massendorf and to a lesser degree Kargı 2 and Keseköy) are small, which could be explained by assuming that plant taphocoenoses from forests represent larger (zonal/regional) and more homogeneous areas compared to those from wetlands.

In the Koçgazi and Yeni-Eskihisar microfloras, *Distylium, Loropetalum, and Alchornea* (MAP > 870 mm; > 693 mm; > 629 mm) indicate higher MAP compared to the mammal-based results. Today, *Alchornea* may be part of the pioneer vegetation in riparian wetlands (Cohen et al., 2008), in which case they do not directly depend on precipitation. The same is true for the Cyrillaceae (MAP > 650 mm) in the Afyon Akçaköy flora. This taxon includes various typical wetland species, while *Distylium* and *Loropetalum*, both belonging to the Hamamelidaceae family and being part of the upland forest in Southern China, most probably were part of the zonal vegetation and therefore should depend more on regional precipitation. In the Ambérieu 2 levels, some taxa indicating higher MAP (>600 mm; *Ilex* and *Liquidambar*) may have belonged to the alluvial wetland vegetation (e.g., Carolina, USA: Brownwater River Forest, *Ilex decidua, Ilex opaca, Liquidambar styraciflua*; Schafale and Weakley, 1990).

Perhaps surprisingly, LMP predictions for the wetland-type of sites mentioned above (Karaözü, Koçgazi, Yeni-Eskihisar, Ambérieu) agree very well between the two methods (Table 4, Fig. 3). Although driest-month tolerance limits may theoretically be confounded by the presence of local groundwater, our results do not indicate that this effect played an important role. It should be noted, however, that the micromammal-based predictions for Anatolia partly depend on the assumption of the eomyid *Keramidomys* having an arboreal lifestyle (see also below).

4.1.4. Application of the actualistic principle

The occurrence of outliers during the construction of coexistence intervals proves that errors may occur by extrapolating modern tolerance ranges. Modern taxa may constitute relics, or nearest living relatives may have been identified incorrectly. Alternatively, the cited ranges may be incomplete due to vague chorological information (Utescher et al., 2014). This latter problem applies particularly the wet side of the ranges, because unlike water shortage, excess water is usually not acting as a limiting factor. The lack of correspondence between plant- and micromammal HMP predictions may therefore partially be related the absence of limiting effects and/or imprecise knowledge of limits.

The actualistic approach may also lead to errors when using the micromammal CDA. While invertivory can directly be checked or deduced by inspecting tooth morphology, arboreality is mostly inferred indirectly (using nearest-relative extrapolations and correlations to molar morphology). For example, the persistent occurrence of the eomyid *Keramidomys* as the sole, presumably arboreal taxon in various drier Anatolian sites is slightly suspect. On the other hand, *Keramidomys* could have adapted itself to a riparian-type of forest (as reconstructed by plants for some of these sites). In addition, there is a good fit between plant- and micromammal-based estimates for LMP in the Anatolian sites. Assuming an open-country feeding habitat for *Keramidomys* would lower mammal-based LMP predictions to a value close to zero (as in Yeni-Eskihisar, where this form is absent; see Fig. 3).

The principle of actualism applies also to richness patterns as a whole. If the richness of a certain subgroup or a certain area would increase without any change in climate (evolutionary time hypothesis, see Section 2), prediction bias may be introduced. For instance, problems could arise when regions differ in their (long-term) ecosystem stability. Central European forest environments may have been more stable (at a million-year scale) than time-equivalent drier Mediterranean environments (Van Dam, 2004, 2006). This could have led to a stronger evolutionary accumulation of (wet-adapted) species in the

former region. In this context, it is relevant to mention the high diversity of Central European Miocene–Pliocene micromammal species (species richness may be 50 in a single site) when compared to modern numbers (maximally 30). Similarly, the high proportions of arboreal micromammals in the Mio-Pliocene of Central Europe (up to 40%) is not paralleled in the modern forests of western Eurasia. Obviously, subsequent Plio-Pleistocene cooling and drying have resulted in the cumulative disappearance of huge, forested areas together with many of their long-lasting micromammal species. On the other hand, the good correspondence between CDA and CA predictions of MAP in our Neogene Central European sites suggests that the impact of this evolutionary time effect may not have been so profound, and that high numbers of arboreal species may truly reflected high precipitation levels that are not attained today.

Whereas the calibration set of micromammals is deliberately restricted to the western part of the Old World (because of the unique diversity histories of large regions, see above), ranges inferred for plant reference taxa are identified at the global scale (cf. Section 2.1), i.e. they are allowed to be extrapolated from one continent to another unless they represent a clear relic (Mosbrugger and Utescher, 1997). At this point, the possibility should be considered that Nearest Living Relatives of Cenozoic taxa presently restricted to Southeast Asia might introduce a monsoonal signature (high HMP and high seasonality of precipitation) into CA-based precipitation reconstruction when using climate data from that region. In the present study, this holds for *Engelhardia, Distylium*, and *Reevesia* represented in the pollen record, as well as *Distylium, Mastixia, Gironniera* and *Turpinia* present in the megafloras. This effect, which possibly contributes to the discrepancy of both approaches when reconstructing HMP, can only be overcome if these taxa are excluded from the analysis. However, exclusion at the same time would cause signal loss because all these taxa can be regarded as indicative for the presence of mesic habitats.

LMP predictions for the forested central European sites Götzendorf, Oberdorf, Massendorf differ strongly, with micromammal-based values being much higher (80, 64 and 84 mm, respectively) than the corresponding plant-based values (37, 25 and 23 mm). It could be argued that the micromammal-based estimates are too high, simply because they approach the estimated mean/midpoint amounts per month (MAP/12, 97 mm based on micromammals and 87–98 mm based on plants). Even if the micromammal-based LMP estimates would be correct, rainfall regimes at these sites would be extremely homogeneous across the year. While this possibility cannot be excluded, we believe it is improbable that such a low degree of seasonality existed in this region during the Middle–Late Miocene. Moreover, micromammal LMP predictions are based on a calibration equation with PA recorded across modern sites across the Western Old World (Eq. (4)), which generally do not exceed 20%. LMP estimates based on PA values up to 40%, as recorded for the fossil Central European sites, require significant extrapolation outside the calibration domain. In fact, there are reasons to believe that the relation between precipitation and PA is non-linear, implying a leveling-off of LMP at higher values of PA (see 4.2).

The micromammal-based prediction of a homogeneous within-year rainfall regime is also caused by low wettest month (HMP) estimates, which are lower than the corresponding plant-based values (Fig. 4). For some Central European sites this even leads to internal inconsistencies, with HMP estimates being lower than mean monthly estimates (Table 4). While some of the plant-values may be too high ("monsoonal bias", see above), micromammal based HMP values could be too low, with extrapolation beyond the calibration domain (PA) being the most likely cause.

4.2. Alternative CDA equations: an attempt at proxy inter-calibration

In the preceding sections we have tried to identify the conditions and regions for which plant CA and micromammal CDA precipitation predictions agree or disagree. In this section we attempt to go one

step further and increase the accuracy and predictive power of the micromammal-equations in two ways: 1) extending the modern calibration set for the Western Old World, characterized by low too moderately high PA and MAP values (maxima of ~20% and 900 mm/yr), with several higher-range values (up to ~40% and 1200 mm/yr) as inferred from fossil sites without modern analogues, using precipitation estimates derived from plant CA (thereby partly inter-calibrating both methods); 2) introducing non-linear terms that better describe the relationship between PA and precipitation.

In the modern micromammal calibration dataset for western Eurasia and northern Africa (see Van Dam, 2006), PA values > 0 are exclusively associated with MAP values that exceed levels of ~500 mm/yr (Fig. 7). In other words, the relationship between PA and MAP is basically non-linear, involving a precipitation threshold below which arboreal species do not thrive. (The reversed relationship is not always true: if no arboreal species are present, levels higher than 500 mm/yr do occur. For instance, rainfall in modern Mediterranean woodland sites such as Doñana (Spain) and Algiers amounts to 531 and 691 mm per year.) In both cases, the yearly precipitation regime is highly seasonal. The threshold behavior of MAP with regard to PA implies that a non-linear equation may better describe the relationship between MAP and PA than a linear one.

In order to address both non-linearity and the problem of no-analogue, "high-PA" faunas we performed curvilinear fitting of MAP on an extended data set including the PA values and flora-based MAP estimates (midpoints of coexistence intervals) from the two fossil Central European sites Oberdorf and Massendorf,. These floras were selected because they are of the macro type with a high-resolution taxonomy resulting in relative narrow coexistence intervals.

We used Datafit to find the type of regression equation that could best explain MAP as a function of PA (as measured by the highest R^2). Of all monotonically increasing functions, the best fit was attained by a 3rd-order polynome of logarithmically transformed values ($R^2 = 0.76$, Fig. 7). This function not only mimics well the ~500 mm/year threshold behavior, but also shows the subsequent more gradual rise of MAP values towards higher values:

$$MAP = 233.3952 + 578.7961\ ln(PA1) - 331.6126\ ln(PA1))^2 + 66.6752(ln(PA1))^3 \tag{6}$$

with

$$PA1 = PA + 1$$

(1 was added to all independent values to allow the use of zero percentages.)

In order to arrive at a more convenient equation including also PI, we performed a stepwise regression of MAP on PI, PA, ln(PA1), ln^2(PA1) and ln^3(PA1). This resulted in a simpler model containing only the terms ln^2(PA+1) (highest correlation with MAP) and PI:

$$MAP = 11.080 + 47.178\ ln^2(PA + 1) + 12.492\ PI, \tag{7}$$

$$\left(R^2 = 0.82\right).$$

Because of the logarithmic transformation, rainfall below ~500 mm/yr is largely controlled by PI, whereas above this level it is controlled by both PI and PA. R^2 is high (0.82), i.e. the model fits the data very well. The average interval for individual prediction is smaller than for Eq. (3) (360 compared to 406 mm to either side of the mean as inferred from Table 4). Although somewhat higher than in Eq. (1), the theoretical minimum is still close to zero (11.1 mm/yr, when both PA and PI are zero).

As discussed above, linear driest-month (LMP) estimates (Eq. (4); Table 4) for Central European do not agree very well, with micromammal-based estimates being much higher, approaching mean monthly values. For this reason, we also explore alternative calibration equations for LMP, by adding PA and plant-based LMP values for the same two sites (Oberdorf and Massendorf). If these latter values would be correct, the relation between LMP and PA would be strongly non-linear (Fig. 8). A stepwise regression of LMP on PI, PA and the logarithmic powers of PA+1 (up to and including the third power) on the extended calibration set results in a best-fitting equation that only includes only the logarithmic transformation of PA:

$$LMP = 1.525 + 11.250\ ln(PA + 1), \tag{8}$$
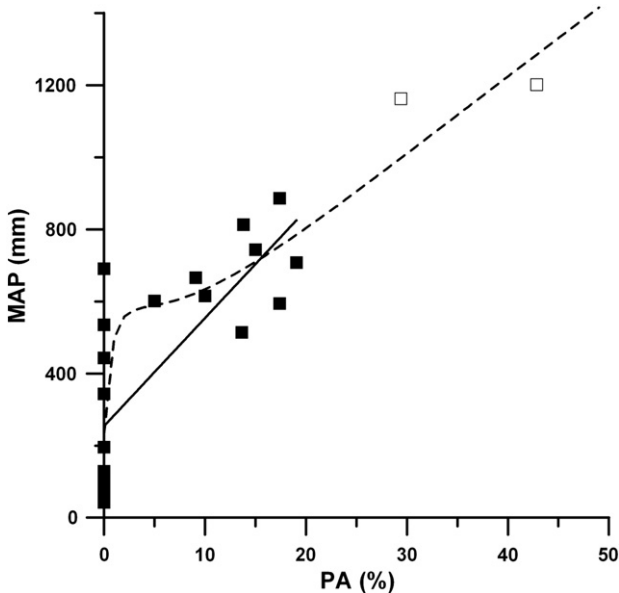
$$\left(R^2 = 0.80\right).$$

Fig. 7. Linear and curvilinear regressions of MAP on PA. Solid line: linear fit to modern data only (Eq. (3)); dashed line: curvilinear (3rd-order logarithmic) fit (Eq. (6)), based on modern localities (closed squares) and plant-based estimates for the fossil localities Massendorf and Oberdorf (open squares).
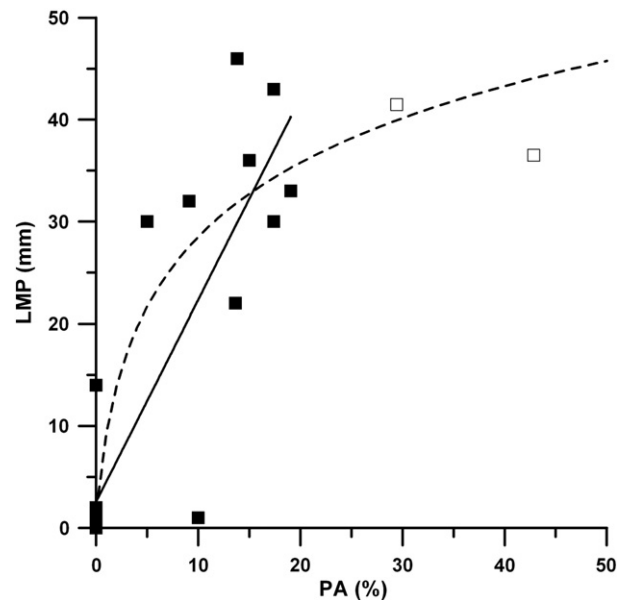

Fig. 8. Linear and curvilinear regressions of LMP on PA. Solid line: linear fit to modern data only (Eq. (4)); b) curvilinear (logarithmic) fit (Eq. (8)), based on modern localities (closed squares) and plant-based estimates of the fossil localities Massendorf and Oberdorf (open squares).
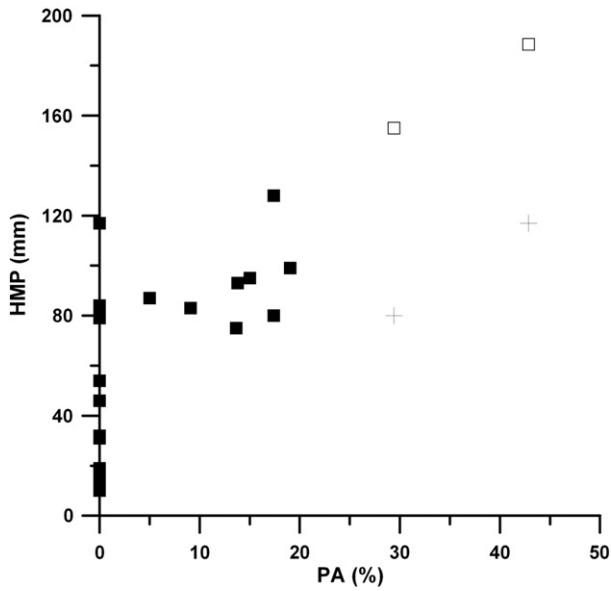
Fig. 9. Plot of HMP against PA. Filled squares: modern data (van Dam, 2006); open squares: fossil localities Massendorf and Oberdorf.

Also the relationship between HMP and PA has a non-linear (threshold) component: no arboreal species occur below 80 mm rainfall in the wettest month (Fig. 9). Although plant-based predictions might be biased to the wet side themselves (see above), we follow the same procedure and add the two fossil sites with their plant-based estimates to the calibration set, and perform a stepwise regression on PI, PA and the logarithmic powers of PA+1. (As in Van Dam (2006), we exclude the modern site Lebanon, because of its exceptionally high rainfall in the wettest month.) The resulting model includes PI and the third logarithmic power of PA1, and has an R^2 of 0.74.

$$HMP = 8.108 + 1.674\,ln^3(PA + 1) + 1.896\,PI \qquad (9)$$

$$\left(R^2 = 0.74\right)$$

An issue not addressed earlier concerns the normality of the data as formally required for regression analysis. Although with small sample sizes (<100) the issue is difficult to assess in the first place, we did perform univariate Kolmogorov–Smirnov tests on dependent and independent variables as used in Eqs. (3)–(5) and (7)–(9) (Table 6). The tests show that the hypothesis that PI, MAP, and HMP are normally distributed cannot be rejected at the 5% level. Both LMP and PA differ from the normal distribution at the 5% level, which is due to the relatively large number of zero values. Also the logarithmic transformations of PA are not normally distributed. We nevertheless consider PA and its

logarithmic terms as crucial variables for predicting rainfall and retain them in our equations.

The linear and non-linear equations produce partly different results because of 1) the inclusion of additional (fossil) sites, and 2) the addition of logarithmic terms (compare red and green stars in Figs. 2–4). MAP predictions only slightly differ (Tables 4–5, Fig. 2): in the non-linear results, smaller MAP values result when PA = 0 (Yeni Eskihisar), and larger MAP are predicted for small and intermediate PA values (up to 30%, compare Figs. 3, 7). LMP predictions for sites with large PA values are now much lower than when using Eq. (4), approaching the level of the two fossil calibration sites, whereas sites with small PA values get a somewhat higher LMP. Values for sites with PA = 0 (Yeni Eskihisar) remain virtually unchanged. As expected, Eq. (9) produces higher micromammal-based HMP estimates for wetter sites than Eq. (5).

The application of the non-linear Eqs. (7)–(9) to the six localities of Table 5 yields a similar pattern: MAP values are similar, and wet sites such as Rudabánya 2, Engelswies, Unterneul 1A and Soblay show lower estimates for LMP and higher estimates for HMP. A positive byproduct of using the non-linear equations is the reduction of the number of "internal inconsistencies" (italicized values in Tables 4 and 5), caused by the net lowering of LMP values and net increase of HMP values. For instance, the number decreases from ten down to three, and from eight down to zero, in the upper (MAP) parts of Tables 4 and 5, respectively.

5. Conclusions

1) With the aim of evaluating precipitation proxies for the Western Old World, we compared predictions from the Coexistence Approach (CA) using fossil plants and the Climate-Diversity Approach (CDA) using fossil micromammals. In order to optimally compare the estimates, we focused on sites where at least a part of the plants and the mammals originated from the same stratigraphic bed, or from beds that were stratigraphically very close. Despite a large number of sources that potentially could lead to discrepancies, both approaches separate wetter Central-European from drier, Anatolian sites, with almost all mean annual precipitation (MAP) predictions showing overlap of uncertainty intervals.

2) Despite prediction overlap, MAP estimates for the drier sites appear to be structurally higher when estimated by CA than when estimated by CDA. Differences may be due to the inclusion of local (e.g., wetland, or rare allochtonous) plant species or lack of taxonomic resolution in pollen samples, and/or to non-recovery of rare wet-adapted micromammal species. Driest-month (LMP) predictions for the two methods do agree rather well for the drier Anatolian sites, but micromammal-based LMP predictions are considerably higher for the wetter, Central-European sites. Micromammal-based estimates may over-estimate true rainfall, as the high LMP values imply an extremely homogeneous rainfall regime across the year when combined with MAP estimates. Predictions of wettest-month (HMP) precipitation between the two methods strongly differ as well, with the micromammal CDA

Table 6
Kolmogorov–Smirnov test for normality of independent and dependent variables for calibration sets underlying linear Eqs. (3)–(5) and non-linear Eqs. (7)–(9). Significance based on Kolomogorov–Smirnov Z statistic, with Lillefors correction; 0.200 values are lower bounds of true significance (SPSS Statistics, Version 22).

Variable	Linear models (3)–(5)			Non-linear models (7)–(9)		
	Z	Significance	Normal (5%)	Z	Significance	Normal (5%)
PI	0.151	0.200	Yes	0.137	0.200	Yes
PA	0.353	0.000	No	0.292	0.000	No
ln(PA + 1)				0.340	0.000	No
(ln(PA + 1))2				0.321	0.000	No
(ln(PA + 1))3				0.297	0.000	No
MAP	0.181	0.070	Yes	0.153	0.172	Yes
LMP	0.329	0.000	No	0.306	0.000	No
HMP (excl. Lebanon)	0.178	0.099	Yes	0.120	0.200	Yes

method yielding lower values than the plant CA method. The main reasons for this difference may be that no sites with extremely high PA are part of the micromammal calibration set, that a monsoonal signature is introduced for plants currently restricted to Southeast Asia, or that high rainfall is not very well constraining the occurrence of both plants and mammals.

3) An attempt to increase the accuracy and predictive power of the micromammal-based proxies is made by extending the modern calibration set for the Western Old World with plant-based predictions for fossil sites that have a micromammal community structure without a modern analogue (one characterized by very high values of the arboreality index PA). The modified equations include logarithmic terms mimicking minimum precipitation thresholds for arboreal micromammals. By adding this explicit inter-calibration step, we feel that MAP and LMP predictions by the two methods can now be used interchangeably, whereas HMP predictions are still waiting to be satisfactory reconciled.

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Acknowledgments

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