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Patterns of insect damage types reflect complex environmental signal in Miocene forest biomes of Central Europe and the Mediterranean

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ABSTRACT

Ecosystems are defined by the community of living organisms and how they interact together and with their environment. Insects and plants are key taxa in terrestrial ecosystems and their network determines the trophic structure of the environment. However, what drives the interactions between plants and insects in modern and fossil ecosystems is not well understood. In this study, we analyzed insect damage richness and frequency in 5000 fossil leaves deposited during the early Miocene at 20–17 Ma along a latitudinal gradient from Europe (two localities in Czech Republic) to Turkey (one locality) in a temperate climate setting. Damage frequency was mainly linked with abiotic factors (temperature, precipitation seasonality) whereas damage richness was mainly linked with biotic factors (plant richness, biome). Univariate analysis of insect damage types consistently suggested closer trophic similarity between the Mediterranean and either the one or the other Central European plant assemblage. In contrast, multivariate analysis of all insect damage types indicated closer similarity between the two Central European sites highlighting the importance of biogeographic legacy and geographic closeness to the plant-insect interaction patterns. Our results underscore the high complexity of the herbivory network and call for careful interpretations of plant-insect interaction patterns in palaeoecological studies. Finally, comparing the trophic similarity between different localities using total evidence plots as done in this work might be a promising complementary method in comparative studies of plant-insect interactions.

1. Introduction

Terrestrial ecosystems comprise complex networks of living organisms that share a set of common abiotic parameters through climate and soil characteristics, changing through geological time and across the globe. Documenting past environmental changes is of vital importance to understand future responses of our modern environment to global change (Meehl et al., 2007). In palaeontology, different proxies are used to quantify palaeoenvironmental change, one of which is based on the fossil leaf record and the insect feeding traces that can be measured on the leaf blades (Labandeira, 2002). In terrestrial ecosystems, plants and arthropods are among the most important components of the biodiversity (Yang and Gratton, 2014) and their interactions are fundamental for food webs (Forister et al., 2015). A wide range of palaeoecological studies described the dynamics of plant-insect interactions through time (Adroit et al., 2018a; Currano, 2009; Donovan et al., 2016; Labandeira et al., 2016; Wappler et al., 2009; Wappler and Denk, 2011; Wilf et al.,

2001). However, despite many theoretical assumptions, the sensitivity of plant insect-interactions to deep time environmental changes is still not well understood. This is mainly due to the great number of parameters involved in plant-insect interactions (Cornelissen, 2011; Felton and Tumlinson, 2008; Pérez-Harguindeguy et al., 2013).

Climate can act directly on an insect either as a mortality factor or by determining the rate of growth and development (Bale et al., 2002). Mostly attributed to temperature, because insects are poikilothermic (Meglitsch, 1972), climate variation directly affects herbivory rate in ecosystems (Bale et al., 2002; Currano et al., 2008). Contrary, bottom-up effects of particular plant types on insect herbivores involve, among other aspects, the richness of gall-inducing insects, which appears to be favored by sclerophyllous plants (Lara et al., 2002; Price, 2002; Price et al., 1998). Changes of plant communities can also alter insect herbivory through associational resistance (Hambäck et al., 2000). If insect herbivory is increasing along a latitudinal gradient, the same variables that determine plant richness along the same gradient should also

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govern insect herbivory richness (Dyer et al., 2007; Hawkins and Porter, 2003). Indeed, it was shown that relatively few variables, namely a combination of high annual energy input with constant water supply and extraordinarily high topographical and habitat heterogeneity, were able to accurately predict the location of global centers of plant richness (Hutchinson, 1959; Krefl and Jetz, 2007).

However, it is nearly impossible to record insect communities coexisting with fossil plant assemblages as insect body fossils are rare in outcrops with abundant plant remains, and there is no correlation between insect feeding richness and insect diversity. One insect can make different types of damage and identical damage can be done by several different insect species (Bernays and Minkenberg, 1997). Overall, high richness of insect feeding could imply large insect species diversity (Carvalho et al., 2014), but this relation has not yet been quantified in the fossil record. This lack of information can be overcome by using the guide to insect damage types in compressed plant fossils (Labandeira et al., 2007) that gathers known plant-insect interactions and offers a general method to identify them.

Using this method, we compared insect damage types (DT) from two regions in western Eurasia separated by 10° latitude and representing Central Europe (Czech Republic) and the eastern Mediterranean (Turkey) prior to the peak of Miocene warming at ca. 20–17 million years ago (Ma; Figs. 1, 2). The Miocene (23.3–5.333 Ma) was a showcase period including a major global warming, the Miocene Climate Optimum (MCO) at 17–14 Ma, followed by drying and cooling (Westerhold et al., 2020; Zachos et al., 2001, 2008), the global spread of grasslands (Cerling et al., 1997), and possibly the ephemeral occurrence of Mediterranean summer-dry climates (Tzedakis, 2007). Moreover, despite the profound impacts of the MCO and subsequent cooling on global sea currents, ice shield volume and climate (Flower and Kennett, 1994),

there was no global, uniform biotic response to such climate events. For example, in Antarctica, vegetation responded immediately to the Antarctic ice shield buildup after the MCO (Lewis et al., 2008), and this was also true for parts of Asia Minor (Bouchal et al., 2018); in contrast, vegetation did not respond immediately to the global cooling after the MCO in Iceland (Denk et al., 2013).

Here we investigated fossil plant assemblages and their DTs from Turkey and Czech Republic (Fig. 3) that were deposited prior and at the onset of the warmth peak of the MCO. We wanted to know whether insect damage types can be explained by a single, few or a set of abiotic and biotic factors, and whether particular types of DTs, functional feeding groups, are related to the same or several of these factors. Specifically, we demonstrate that insect damage traces in temperate forest ecosystems are the result of the complex interplay between plants, insects and environments.

2. Material and methods

2.1. Geological settings

2.1.1. Güvem Formation

The Beşkonak plant assemblages (40°37′30.17″N, 32°41′34.37″E; Fig. 1) belong to the Güvem Formation (GF), which is part of the Galatean Volcanic Province (Tankut et al., 1998; Toprak et al., 1996). The major phase of volcanic activity in this area was between 20 and 17 Ma based on K–Ar radiometric dating (Wilson et al., 1997). In the wider area, a succession from marine sedimentation to the north with submarine volcanism to continental deposition of diatomaceous rocks and subaerial volcanism to the south, can be observed (Paicheler et al., 1978). In the Güvem Basin, fluvio-lacustrine sediments alternate with

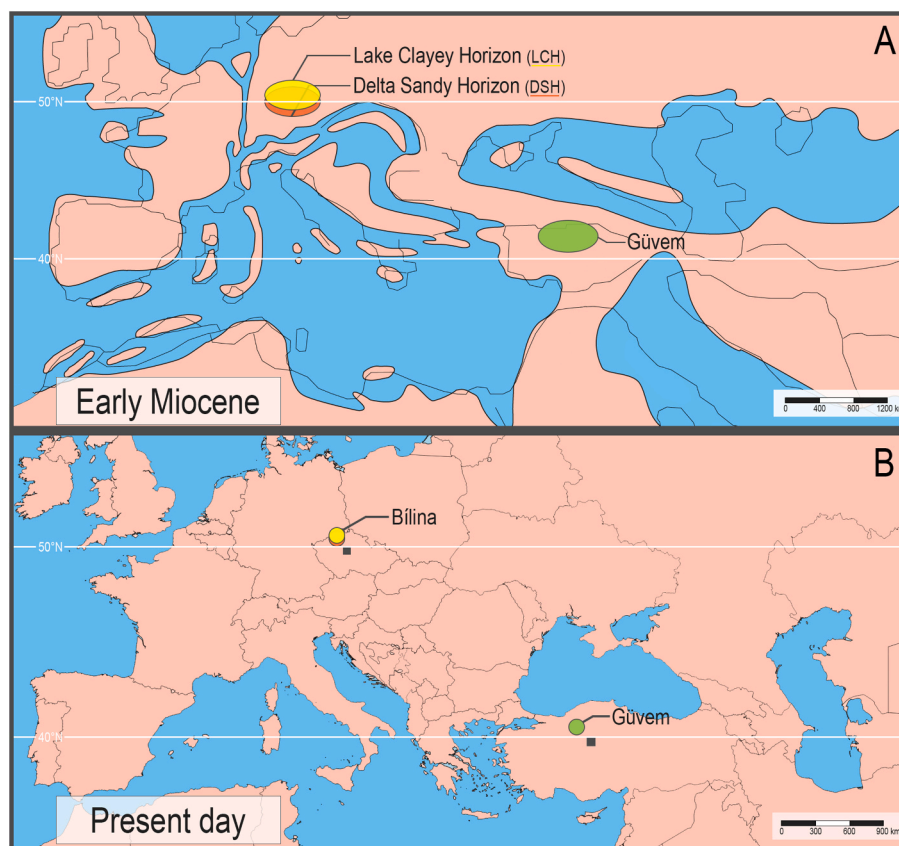


Fig. 1. The localities of Güvem (green), and Břilina Mine, DSH (orange) and Břest'any Clay, LCH (yellow) in Europe. (A) Early Miocene palaeogeography (Rögl, 1999). (B) Present-day Europe with study localities in Turkey and Czech Republic. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

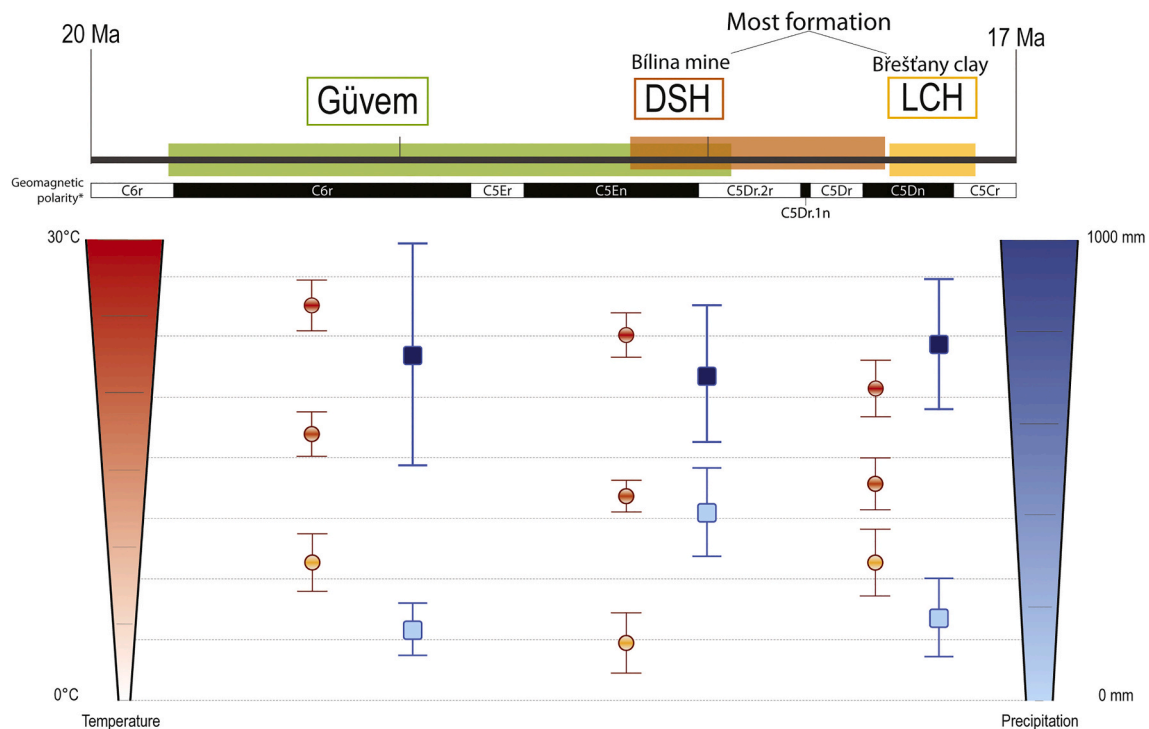


Fig. 2. Age of the three plant assemblages investigated in the present study, along with palaeotemperature and precipitation data (Denk et al., 2019; Teodoridis and Kvaček, 2015). Age shown by green, orange and yellow bars respectively for Güvem, DSH (Bilina Mine) and LCH (Breštany Clay). The length of each bar reflects the age resolution for the individual localities. Palaeotemperatures are represented by estimated values and STDEV in red. From top to bottom, temperature estimates show warmest month mean temperature, WMMT, mean annual temperature, MAT and coldest month mean temperature, CMMT in °C. Precipitation values are represented by estimated values and STDEV in blue. From top to bottom, precipitation estimates show precipitation of the consecutive three wettest (3-WET) and driest (3-DRY) months as mm/year. For both temperature and precipitation, the differences between top and bottom values allow estimating the seasonality of these climate parameters. Palaeomagnetic correlations based on Gradstein et al., 2004; Matys Grygar et al., 2017. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

pyroclastics. The GF overlies Çukurviran dacite dated at 19.7 ± 0.6 Ma (Wilson et al., 1997). The Beşkonak plant assemblages belong to the basal part of the Güvem Formation, the ca 300 m thick Dereköy pyroclastic deposits (Denk et al., 2017). Above the Dereköy pyroclastics, the 70 m thick Balta rhyolite is overlain by 200 m of Bakacak andesite with an absolute age of 17.9 ± 0.5 Ma (Tankut et al., 1998). The fossil locality Keseköy has yielded remains of small mammals that suggest a faunal age of MN3 (Wessels, 2009). Fission track analysis on zircons from volcanic tuff occurring in lignites ca 15 m below the mammal-bearing clay and the plant-bearing lacustrine diatomites suggested an age of ca 20 Ma (Wessels, 2009).

2.1.2. Most Formation

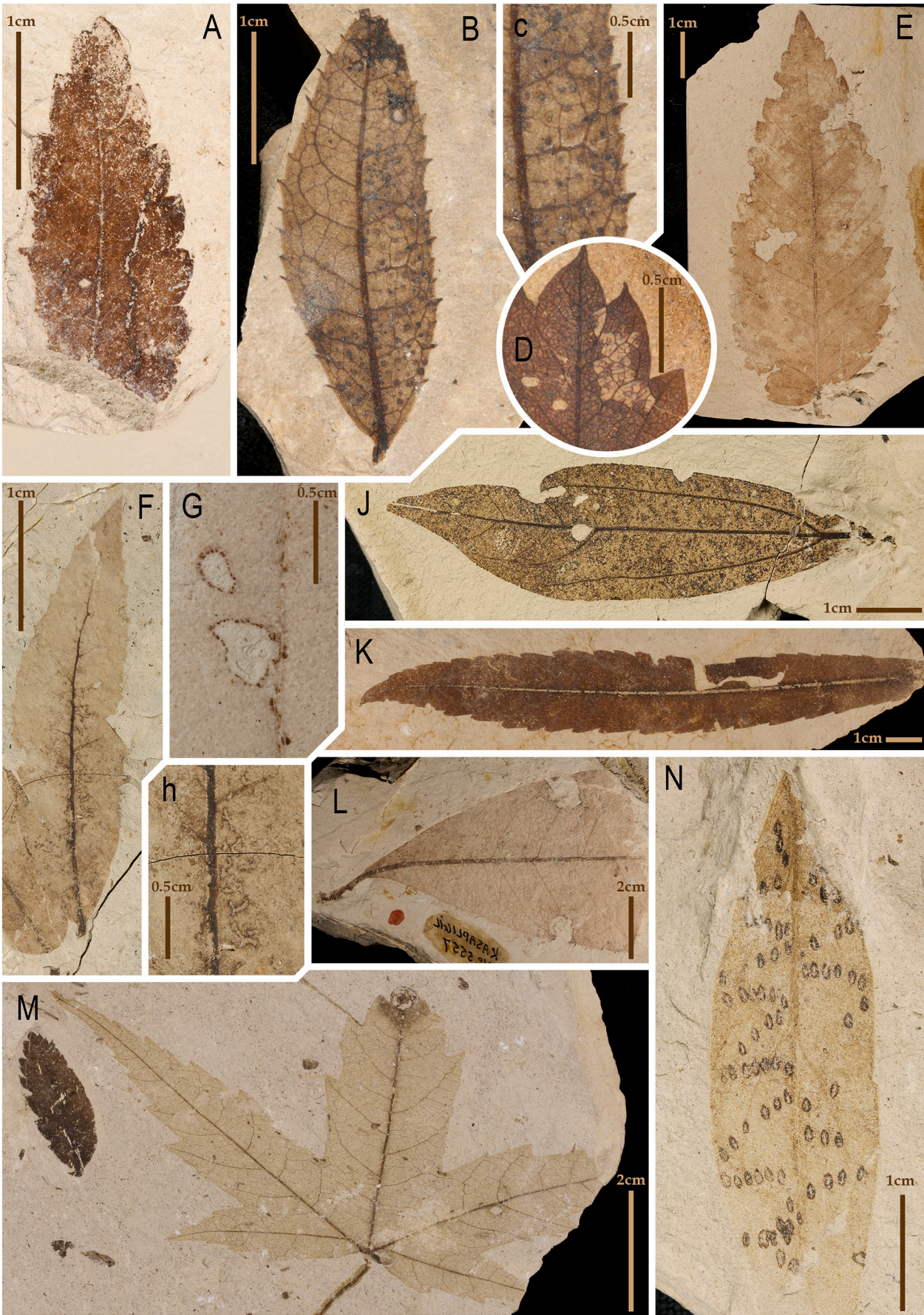
The Bílina Mine and Breštany Clay plant assemblages ($50^{\circ}34'28.08''\text{N}$, $13^{\circ}43'28.09''\text{E}$; Fig. 1) belong to the Most Formation (MF). Deposition of the MF started after a phase of volcanism. Its oldest member, the *Duchcov Member* (Mb.); corresponding to the Underlying Formation of Elznice (1973) is of latest Oligocene/earliest Miocene age and consists of claystone, proalluvial to alluvial deposits, and thin coal seams reflecting initial allochthonous sedimentation (Kvaček et al., 2004). During the early part of the early Miocene, subsidence caused flooding of the Most Basin by rivers; mires formed and peat accumulated up to 200 m thick (Mach et al., 2013). These mires were interrupted by interbeds of sand and clay. The resulting *Holešice Mb.* (~20–17.5 Ma) overlies the *Duchcov Mb.* It corresponds to the Main Seam or Coal Seam Formation of Elznice (1973; see also Konzalova, 1976) and consists of lignite deposits intercalated with the Žatec and Bílina delta facies of alluvial origin. The Merkur–North (Ahníkov) vertebrate fauna at its base suggests a faunal age of MN3a corresponding to an age of 19.5–17.2 Ma (NOW community, 2020). Other palaeobotanical localities of the same

age are the Bílina Mine and Želénky (Kvaček et al., 2004). Above the coal seam, the age of three lithological units is well constrained based on correlation with the geomagnetic time scale (Gradstein et al., 2004; Matys Grygar et al., 2017). The dark clays of the Clay Superseam Horizon correspond to chron C5En, ~18.6–18.25 Ma and are rich in complete specimens or disarticulated fragments of insects (Kvaček et al., 2004), suggesting autochthonous faunas. At some places, strongly disarticulated insect remains reflect occasional flooding events.

Subsequently, orogenic processes led to flooding, transforming the basin into a lake with deposition of thick beds of sand and clay (Bílina Delta, Hurník, 1959). During chron C5Dr, ~18.2–17.7 Ma, sandy/silty Bílina delta heteroliths were deposited in the Bílina Mine (Delta Sandy Horizon, DSH (Matys Grygar et al., 2017)). Insect fossils are less complete than those of the Clay Superseam Horizon and represent aquatic forms and terrestrial elements including termites.

The uppermost level of the *Holešice Mb.* comprises the Breštany Clay (Lake Clayey Horizon, LCH) that formed during a large (basin-wide) lake transgression (Matys Grygar et al., 2017). Deposition of the LCH coincided with a phase of global warming during chron C5Dn, ~17.6–17.5 Ma, and a substantial reduction of the Antarctic ice sheet prior to the onset of the Miocene climatic optimum (MCO; (Westerhold et al., 2020; Zachos et al., 2001)).

On top of the *Holešice Mb.*, the *Libkovice Mb.*, Overlying Formation of Elznice (1973), comprises lacustrine clay and delta facies deposits, which are overlain by the topmost members of the MF, the *Lom Mb.*, Lom Formation of Elznice (1973), and the *Osek Mb.* After deposition of the *Osek Mb.* deposition in the Most Basin was terminated in the earliest middle Miocene. The plant assemblages investigated for insect damage derive from the DSH and LCH.



(caption on next page)

Fig. 3. Examples of plant-insect interactions on leaf blades from the Gvem Formation. (A) *Zelkova zelkovifolia* with mining DT90, (B) *Ilex mioidipyrena* with piercing and sucking DT46, (C) enlargement of *I. mioidipyrena* leaf (see B), (D) *Sorbus aucuparia* with skeletonization DT61, (E) *Zelkova zelkovifolia* with both hole and margin feeding (respectively DT03 and DT12), (F) *Quercus drymeja* with surface feeding DT207, (G) *Fagus castaneifolia* with hole feeding DT05, (H) enlargement of DT207 on *Q. drymeja* (see F), (J) *Daphnogene polymorpha* with both hole and margin feeding (respectively DT68 and DT12), (K) *Myrica* sp. with margin feeding DT198, (L) *Magnolia sturii* with margin feeding DT12, (M) *Acer angustilobum* with galling DT62, (N) *Salix* sp. with exceptional preservation of insect oviposition DT102.

2.2. Fossil plant assemblages

The material from the GF is stored at University of California Museum of Paleontology (UCMP), Berkeley, and Musum National d'Histoire Naturelle (MNHN), Paris. It contains 1199 specimens of which 157 belong to gymnosperms (Denk et al., 2017). Of the remaining ca 1000 specimens, 624 are dicot leaves that were screened for insect damage. The two collections show high taxonomic coherence and similar frequencies for main taxa (Denk et al., 2017); this pattern was confirmed to be a real pattern not biased by selective collecting in a subsequent field trip by TD. The material from the MF (DSH and LCH horizons) is stored mainly at the National Museum in Prague. More than 4000 specimens comprise 2235 dicot leaf specimens for DSH and 1260 dicot leaves for LCH (Knor et al., 2013; Prokop et al., 2010).

2.3. Analysis of plant-insect interactions, damage type identification

Patterns of insect feeding, damage types were determined using the "Guide to insect damage types on compressed plant fossils" (Labandeira et al., 2007). A dark reaction mark surrounding the damage is characteristic of insect herbivory (Labandeira, 2002) and allows distinguishing it from detritivory. In this study, plant-insect interactions are classified into seven functional feeding groups (FFG): Hole feeding, margin feeding, skeletonization, surface feeding, piercing and sucking, galling and mining. Within each group, several DTs are distinguished, and each of them can be described as generalist or specialist. In the fossil record, the degree of specialization is defined by the number of hosts (distinct leaf morphotypes) and the number of outcrops, from where the DT was recorded (Labandeira et al., 2007). Overall, external damage (hole, margin, surface feeding, skeletonization) is commonly generalist, although some types of skeletonization have been highly host specific over millions of years (Adroit et al., 2020). Conversely, plant-insect interactions, which are not necessarily reflecting direct herbivore behavior (such as galling or mining), but depend on more complex processes in the insect life cycle, are very often specialized damage types.

2.4. Comparing damage type richness and frequency between localities

Because the number of leaf specimens differs among the outcrops used in this study, we performed sample-based rarefaction (Gotelli and Colwell, 2001) to compare insect damage richness and plant species richness, i.e. the number of different damage types represented in each collection. Each dataset was randomly resampled 1000 times using R version 4.0 (R Development Core Team, 2014) with a specific code (Gunkel and Wappler, 2015), and comparisons between localities were based on 600 leaf specimens. Rarefaction curves were generated to compare datasets (cf. Schachat et al., 2018). Damage frequency, i.e. the relative abundance of DTs in each locality, is presented as box-plots with the number of DTs standardized.

In addition, we assessed the relative richness of each FFG in the fossil leaf assemblages in order to estimate trophic similarity between the palaeoforests. We used the rarefied data of each DT linked to their functional feeding group within each locality. We produced spider-charts (Kiviat diagram (Kolence, 1973)) using R with the package "fmsb" (Nakazawa, 2007) to display those multivariate data.

Lastly, in order to check for possible taphonomic and/or sampling biases, all statistical analyses were done on the entire leaf assemblages and on subsets of them with only species represented by at least 10

specimens included (Knor et al., 2012).

2.5. Inferring palaeoclimate parameters using Climate Leaf Association Multivariate Program (CLAMP)

We used CLAMP to compare the climatic signal encoded in the dicot leaf assemblages of the GF, DSH, and LCH. CLAMP is based on the observation that leaf physiognomy is a function of its environment (Yang et al., 2011) <http://clamp.ibcas.ac.cn>. Using canonical correspondence analysis, leaf physiognomic data from a fossil assemblage are compared to modern calibration datasets comprising several hundreds of modern vegetation sites. Since climate parameters for the modern sites are known, climate parameters can be inferred for the fossil assemblage based on its position in "physiognomic space".

3. Results

3.1. Taxon richness comparison

Species richness differs among the three plant assemblages. In the Gvem Formation, 120 plant taxa, excluding spores and pollen (Denk et al., 2019; Denk et al., 2017), comprise 12 gymnosperms and 88 dicot leaf taxa. DSH comprises >99 plant taxa, of which some Fabaceae leaflets of different species were not treated separately in the dataset (Prokop et al., 2010). DSH comprises 6 conifers and ca. 64 dicot leaf taxa. In the LCH dataset, 6 species are conifers and ca. 48 are dicot leaf taxa (supplement 1). Sample based rarefaction curves for the three localities (Fig. 3A) showed markedly higher species richness for G than for the DSH and LCH localities.

3.2. Palaeoenvironment and palaeoclimate characteristics comparison

The more southerly Gvem plant assemblage is characterized by a higher proportion of evergreen broadleaf taxa (28.4% of woody angiosperm taxa) than the Czech assemblages (10.9% and 16.7% for DSH and LCH, respectively; Supplement 1). The higher proportion of evergreen taxa in the GF corresponds to a change from Mixed Mesophytic Forest biomes to the north to Laurel Forest biome to the south (Denk et al., 2019; Mai, 1995; Supplement 2).

Palaeoclimate parameters were inferred for the LCH facies (Supplement 2 with Supplement 3a and 3b). For GF and LCH, previously published CLAMP data were used (Denk et al., 2019; Teodoridis and Kvaek, 2015; Fig. 1). Inferred temperature parameters suggested a significantly warmer mean annual temperature for GF, whereas both GF and LCH had significantly warmer temperatures of the coldest month than DSH. Rainfall characteristics suggest higher precipitation seasonality for GF and LCH than for DSH expressed in reduced rainfall during the consecutive three driest months for the GF and LCH (Fig. 1; Supplement 2).

3.3. Damage type richness and abundance comparison

All functional feeding groups are represented in the leaf assemblages from Gvem (Fig. 2; Supplement 4), DSH and LCH (Supplement 5). Of 624 leaves from the GF, 36% showed some form of damage and a total of 45 damage types was observed (Supplement 6). For the DSH facies of the MF, Prokop et al. (2010) reported 25.6% of 2233 leaves damaged, and a total of 54 damage types. For the LCH, they reported 18.1% of 1261 leaves damaged, and a total of 28 damage types. To account for

differences in sampling effort, sample-based rarefaction was used to compare the three localities. Based on the rarefied data, richness of all damage types is highest in the GF (Fig. 3B). This was also true when distinguishing between external and specialized damage (Supplement 7). In contrast, galling richness did not show differences between the three assemblages (Fig. 3C). Total damage frequency is significantly higher in the GF than in DSH and LCH (not shown), whereas external damage frequency is significantly higher in GÜvem and DSH than in LCH. For specialized damage frequency, the result is reversed with GÜvem being slightly higher than LCH, and both localities being higher than DSH (Fig. 4). Galling frequency is higher in GÜvem and LCH (being slightly more abundant in LCH; p -value of t -test 0.2417 for GF and LCH) than in DSH (p -value 0.003349 for LCH-DSH) (Fig. 4). Multivariate Kiviat diagrams show the relative contributions of each of the eight damage types to the entire damage spectrum. Here, LCH and DSH differ markedly from GÜvem by the weak contributions of piercing and sucking, and surface feeding and the more pronounced contributions of margin feeding and partly of hole feeding (DSH) and galling (LCH; Fig. 5).

4. Discussion

4.1. Palaeoenvironmental and palaeoclimatic setting of the GÜvem and the Most Formations

Dicot taxa of the GÜvem Formation (GF) showed higher richness and frequency of evergreen foliage than those from the Most Formation (Supplements 2, 5). The main vegetation types represented by plant fossils from both formations correspond to the terrestrial ecoregion (biome) ‘temperate broadleaf and mixed forests’ of Olson et al. (2001). This broad ecoregion can be characterized as follows: “In regions where rainfall is broadly distributed throughout the year, deciduous trees mix with species of evergreens. Species such as oak (*Quercus* spp.), beech (*Fagus* spp.), birch (*Betula* spp.), and maple (*Acer* spp.) typify the composition of the temperate broadleaf and mixed forests (TBMF)” (<https://www.worldwildlife.org/biomes/temperate-broadleaf-and-mixed-forests>). During large parts of the Cenozoic, two forest types conforming to the TBMF biome occurred, laurel forest and mixed mesophytic forest. Laurel forests were much more widespread during the Cenozoic than they are today (Axelrod, 1975; Walter, 1985; Körner, 2013). They are characterized by the dominance of broadleaf evergreen taxa with laurophyllous leaves. For a detailed definition of the laurel forest biome, see Schroeder (1998) and Denk et al. (2019). Mixed mesophytic forests are the most diverse forests in extratropical regions. They are multilayered, polydominant forests, rich in lianas and characterized by a very large number of canopy species, most of which are deciduous, and diverse evergreen species in the subcanopy layer (see, for example, Hinkle et al., 1993; Mai, 1995, p. 525).

The principal forest type on well-drained soils during deposition of the GF was laurel forest dominated by evergreen elements of the oak family (Fagaceae; Denk et al., 2019, Denk et al., 2017) with a few Arcto-Tertiary elements such as *Acer* spp. and Betulaceae. Other forest types were swamp forest dominated by *Glyptostrobus* and mixed conifer forest with a high diversity of conifers (Denk et al., 2017). Palaeoclimate as inferred from leaf physiognomic data was warm temperate, frost-free with some seasonality in rainfall (Fig. 2).

In contrast, main vegetation during deposition of the DSH of the Most Formation (MF), comprised riparian broadleaf deciduous forest over the delta plain and river banks with drier sites on adjacent slopes covered by mixed mesophytic forest or basin swamp forest. Mixed assemblages of laurophyllous and Arcto-Tertiary (deciduous) taxa included several elements that were widespread across northern parts of western Eurasia but have not been recorded for the eastern Mediterranean early Miocene (e.g. *Platanus neptunii*, *Parrotia*, *Koeleruteria*, *Podocarpium*). Conifers were diverse both in the macrofossil and pollen records (Kvaček et al., 2004). Other elements typical of Central Europe (*Pungiphyllum*,

Nelumbium) are not known from GÜvem, but occur in coeval strata of Turkey (*Pungiphyllum*, *Nyssa* from Soma; *Nelumbium* from Balya; unpublished data). The inferred palaeoclimate suggests a temperate climate with marked temperature but weak rainfall seasonality (Fig. 2). The LCH of the Brešt'any Clay (Holešice Member of the MF) represents a return to swamp conditions as a consequence of a large lake transgression connected to riparian broadleaf deciduous and mixed-mesophytic forests on slopes or uplands including evergreen elements represented by Lauraceae, Engelhardioidae, Symplocaceae, Ericaceae and Theaceae (Kvaček et al., 2004) mixed with Arcto-Tertiary elements (Teodoridis and Kvaček, 2015). Rare extinct plants such as *Chaneya* are also known from GÜvem (Denk et al., 2017). The inferred palaeoclimate suggests a temperate, frost-free climate with some seasonality in rainfall (Fig. 2).

4.2. Environmental information from plant-insect interactions

We investigated plant-insect interactions with three complementary approaches, which focussed on (i) richness, (ii) frequency, and, (iii) the relative contributions of different functional feeding groups to each locality. The latter approach has not been used in previous studies on plant-insect interactions.

4.3. Damage richness related to environmental complexity

Greater plant species and damage richness in GÜvem may imply a higher insect species richness causing an increase of damage richness (Knops et al., 1999; Liebhold et al., 2018; Mulder et al., 1999; Siemann et al., 1996; Wright and Samways, 1998). However, comparison of the fossil excavations in the GÜvem area and the Bílina mine (DSH) and Brešt'any Clay (LCH) is not straightforward. Whereas plant fossils from the GF were mainly collected by two people during the second half of the last century and were shipped to the US and France (Denk et al., 2017), sampling from the MF commenced in the early 19th century (Kvaček and Teodoridis, 2007; Pešek et al., 2010) and has continued until the present (Knor et al., 2015; Knor et al., 2013, 2012). Thus, there may be a bias for well-preserved and complete specimens from the GF and this may explain the great plant richness documented for the GF along with the larger number of taxa that are only represented by two or three specimens and the overall smaller plant collection. Consequently, to exclude potential sampling bias, we separately computed taxon richness by considering only plant species represented by at least 10 specimens, still based on the rarefied data. By doing so, the remaining plant species richness of GÜvem was lower than those of the DSH and LCH (GÜvem: 14 species; LCH: 19 species; DSH: 53.2 species), but damage richness remained significantly higher for GÜvem (GÜvem: 34 DTs; LCH: 18.4 DTs; DSH: 26.3 DTs, Supplement 5). Consequently, our data support the notion that differences in damage richness between the GF and MF are controlled by additional parameters than plant species richness alone as also suggested in previous studies (Adams et al., 2010; Antoniazzi et al., 2019; Blanche and Ludwig et al., 2001; Fernandes and Price, 1992; Fernandes and Price, 1988, p. 199; Hawkins and Porter, 2003; Kozlov et al., 2013; Liebhold et al., 2018). Specifically, the greater richness of damage types in GÜvem may also be the result of its more southerly position as insect herbivore diversity is known to increase closer to the tropics (Coley and Aide, 1991; Coley and Barone, 1996). Moreover, the environmental complexity (i.e. the heterogeneity of the landscape where the palaeoforests developed) was higher during deposition of the GF (Denk et al., 2019) and these complex environments could have hosted highly speciose insect diversity (Hawkins and Porter, 2003; Hutchinson, 1959; Kreft and Jetz, 2007) that caused greater damage richness.

4.4. Damage frequency and abiotic environmental factors

Frequency of insect damage is higher in GÜvem than in the two

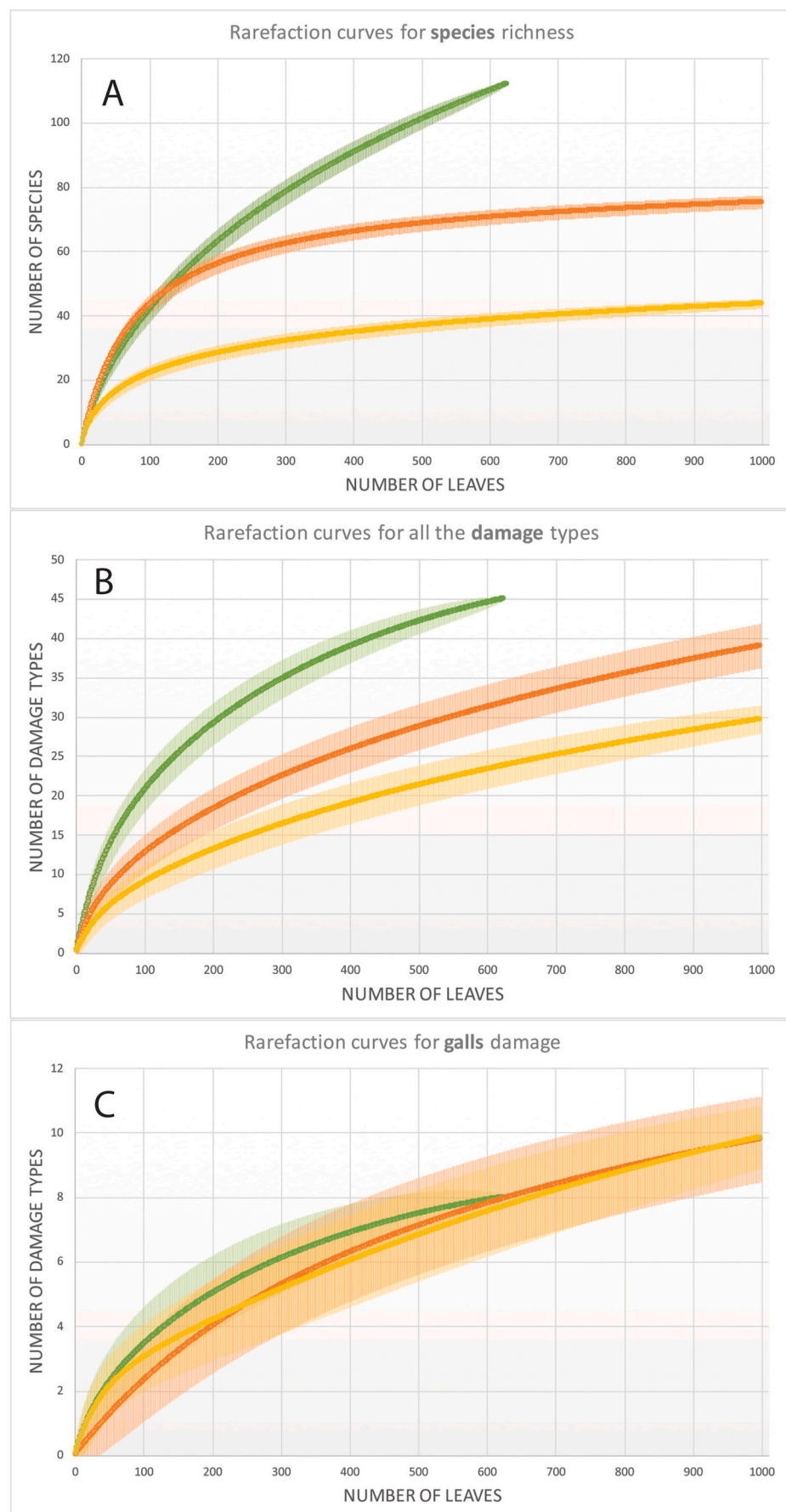


Fig. 4. Rarefaction curves comparing plant species richness (A), damage type richness (B) and gall richness (C) among the Güvem Formation, Břlina Mine (DSH) and Breštany Clay (LCH) plant assemblages.

When damage type richness was divided into external and specialized damage richness (Supplement 7) a rarefaction curve very similar to the present one (B) was generated. The shaded area represents the standard error of the rarefaction calculated after (Heck et al., 1975). The abscissa is reduced to 1000 for detail.

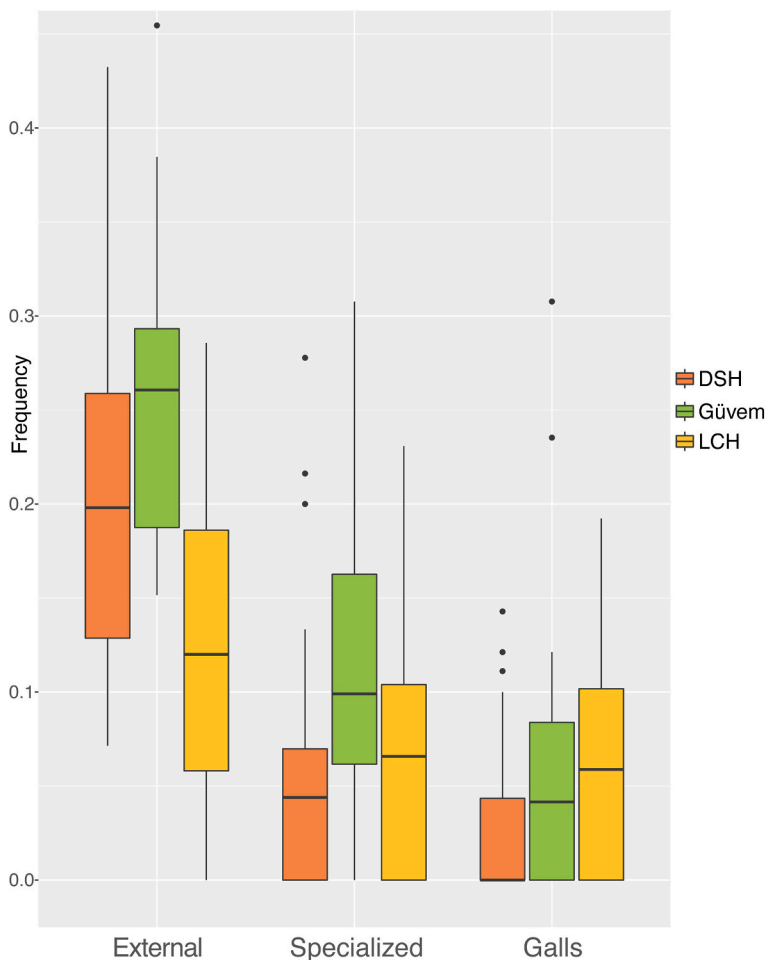


Fig. 5. Box-plots of the frequency of damages in Güvem Formation (green), Břilina Mine - DSH (orange) and Břestany Clay - LCH (yellow). 'External' refers to damage where a part of the leaf blade is removed, such as hole feeding, margin feeding, surface feeding, and skeletonization, of which almost all is generalist damage. 'Specialized' refers to plant-insect interactions that not necessarily reflect a direct herbivory behavior as they result from more complex processes in the insect's life-cycle (such as galling, mining, piercing and sucking, and oviposition). 'Galls' refers to galling damage frequency. Box-plots are based on the plant fossil-species represented by more than 10 specimens. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

localities of the MF (DSH, LCH). Nevertheless, it is important to make the distinction between the abundance of external damage (mostly related to direct feeding behavior) and specialized damage (typically involved in the reproduction cycle of the insects) such as galling, which is the most abundant specialist damage in the present study. Indeed, gall-inducing insects are herbivores that modify the metabolism of the host plant leading to abnormal outgrowths of nutritious tissue in which the insect larvae can feed (Espirito-Santo and Fernandes, 2007; Redfern, 2011).

The frequency of external damage in Güvem is similar to the DSH ($\alpha = 0.1$), and both have a significantly higher damage frequency than the LCH (Fig. 5). The frequency of insect herbivory is linked to two main parameters: (i), the metabolism of the insect itself, which usually is directly dependent on climate conditions (Archibald et al., 2010; Melanby and Gardiner, 1939; Woods and Hill, 2004); and (ii), the metabolism of the plant, its quality and quantity of nutrients, conditioned by both climate (Ahmad and Prasad, 2011; Dusinge et al., 2019) and soil (Drew, 1992; Helal and Sauerbeck, 1984). Indeed, a soil rich in nutrients results in greater levels of plants in sequestering additional nutrients (Augustine et al., 2003; Melo Júnior et al., 2019; Olf et al., 2002; Olf and Ritchie, 1998), and consequently can decrease insect herbivore activity. Previous studies in the Güvem and Most formations suggested forest development on fertile soils during deposition of the GF and the DSH (Kvaček et al., 2004; Paicheler et al., 1978), whereas the episodic return of swamp conditions during deposition of the LCH suggested lower nutrient availability (Kvaček et al., 2004). Changes in soil fertility can partly explain the differences of external damage frequency measured in our study. Likewise, external damage frequency appears to be coupled with taxonomic richness (Fig. 5, Supplement 1). External

damage frequency for Güvem is slightly but significantly more impacted by herbivore activity ($\alpha = 0.01$) than DSH (Fig. 5). Despite a similar soil richness and relative closer age of the plant assemblages recorded from Güvem and the DSH, the difference in temperature resulting from a latitudinal gradient can explain the larger herbivory abundance in Güvem. Estimated temperature in Güvem is significantly higher than in DSH (Fig. 2). In particular, temperature seasonality is markedly lower in Güvem than DSH (Fig. 2). These estimates are not unexpected (Saikonen et al., 2012) due to a 10° latitudinal difference (Fig. 1), and suggest greater herbivory activity for Güvem, because of a shortened diapause time for insects (Archibald et al., 2010; Bale and Hayward, 2010) and a mild winter (Fig. 2). Such observations support previous findings for other outcrops in Europe (Adroit et al., 2018a) and Asia (Ma et al., 2020). In general, differences of temperature are always partly contributory to the different herbivory abundances across outcrops (Bale et al., 2002; Cornelissen, 2011; Jamieson et al., 2012; O'Connor et al., 2011).

In contrast to external damage, the frequency of specialized plant-insect interactions is similar between Güvem and LCH and for both localities is significantly higher than in the DSH. Thus, the trophic structures of the palaeoforests from Güvem and the LCH differ from the one of the DSH. In general, specialist damage reflects a more intimate and much more complex relation between host plant and insect that may involve several parameters including the evolution of strong host-fidelity over long periods (Leckey and Smith, 2015). Because several specialist damage types most likely evolved differently, we cannot offer a universal explanation for all of them (Jousselin and Elias, 2019). Thus, among different kinds of specialist damage, we considered galling separately. Galling is the most important specialized FFG in our study

and its function in terrestrial ecosystems has been intensively studied (Abrahamson and Weis, 1987; Blanche and Ludwig, 2001; Cuevas-Reyes et al., 2003; Fernandes et al., 2010; Fernandes and Price, 1992; Julião et al., 2014; Knor et al., 2013; Knuff et al., 2019; Lara et al., 2002; Melo Júnior et al., 2019; Price et al., 1998; Wright and Samways, 1998). Gall richness was similar between Güvem and the localities of the MF (Fig. 4). About half of the recorded galls are shared between GF and MF (the most common ones) and half are exclusive to either one or the other (Supplement 6). This difference is likely due to the geographic distance and the different taxonomic compositions of the Turkish and Czech localities that reflect distinct biogeographic patterns. In contrast, gall frequency is distinct for Güvem and LCH, both of which had high numbers of galls, and DSH, with a significantly lower abundance (Fig. 5). Gallings is commonly viewed as an adaptation to stressful environments whereby water stress would have a positive effect on galling quantity (Fernandes and Martins, 1985; Fernandes and Price, 1992; Fernandes and Price, 1988; Lara et al., 2002; Price et al., 1998). Alternatively, wet habitats are disadvantageous for galls because of increasing development of fungi, which are the main parasites of gall-making insects (Carroll, 1988; Fernandes and Price, 1992; Fernandes and Price, 1988; Lara et al., 2002). The marked differences of precipitation between the three consecutive wettest and driest months in Güvem and LCH indicate moderate seasonality of precipitation and may have contributed to increased gall frequency. This has previously been suggested in modern and palaeoecological studies (Adroit et al., 2018a, 2018b; Gratton and Denno, 2003; Hare, 1983).

4.5. Total evidence plot of plant-insect interactions

Counterintuitive to the relation between the localities from the GF and the MF, as outlined above, which stresses particular similarities between Güvem and LCH, a reversed trend appears in the plant insect-interaction spider-charts (Fig. 6).

The total evidence reveals structural similarities between the DSH and LCH that are independent of the evidence discussed in the previous sections. The similarities in the relative contributions of different DTs to overall DT richness of the DSH and LCH reflect the high taxonomic similarity but not relative abundance of fossil-species between these two localities. Several genera existed both at the Czech and Turkish localities, but at the species level only very few taxa are shared (Supplement 1). For example, both DSH and LCH record locally abundant swamp oaks (*Quercus rhenana*) of the modern section *Lobatae*, which are absent from Güvem. In contrast, diverse evergreen oaks of well-drained soils characteristic of Güvem and belonging to the only distantly related sections *Ilex* are entirely absent from DSH and LCH. Similarly, among species shared between DSH, LCH, and Güvem, *Zelkova* leaves have substantial

amounts of galling in Güvem, while none in Bílina Mine (DSH) and Brešt'any Clay (LCH). This might be related to specific site conditions (more xeric in Güvem, more mesic in the DSH and LCH (Denk et al., 2017; Teodoridis and Kvaček, 2015) and perhaps to the general warmer temperature in Güvem.

Based on our independent palaeoclimate data and biotic properties such as galling frequency, Güvem and the LCH are very similar. Despite the same frequency of galling between Güvem and the LCH, and 50% of shared galling damage types, the total evidence plots show that relative diversification of galls is an important component in the LCH and DSH palaeoforests while it is relatively less so for the Güvem locality (Figs. 6, 7). Overall, the shape of the spider chart appears to reflect trophic similarity between localities (DSH + LCH) that cannot solely be explained by climate. As stated above, biogeographic legacy may contribute to this pattern. Both studied plant assemblages from the Czech Republic belong to a different forest biome (mixed mesophytic forest) than the Turkish assemblage, which represents laurel forest. Significant differences seen in the frequency of all DT between DSH and LCH (DSH > LCH), appear to reflect reorganization of plant communities (swamp, riparian, well-drained hinterland forest) and species abundances, whereas the reverse pattern seen in galling frequency (LCH > DSH) reflects a climate driven signal (warming in LCH). Although, we are unable to link the total evidence pattern – linking the Czech plant assemblages together and highlighting their difference with the Turkish assemblage – to a particular set of biotic and abiotic factors, biogeographic legacy is a chief suspect for this pattern. In the future, comparison of trophic similarity between different localities using total evidence plots, as done in this work, might be a promising complementary method in comparative studies of plant-insect interactions.

5. Summary and conclusions

We compared two regions in western Eurasia, Central Europe (Czech Republic, two plant assemblages) and the eastern Mediterranean (Turkey, one assemblage), during the early Miocene at ca. 20–17 Ma. We inferred several climatic and environmental parameters using information from leaf physiognomy (CLAMP, <http://clamp.ibcas.ac.cn/>), taxon richness, and occupation of a major biome. We then analyzed more than 5000 fossil leaves and established insect DT richness and frequency. We found that subsets of DTs correspond to different abiotic and biotic patterns. Specifically, external damage frequency is partly related to temperature (MAT and mean of the coolest month) and partly to soil richness, and to taxon richness. Among specialized damage, galling frequency seems to be related to the seasonality of precipitation while galling richness did not show a clear response to any of the measured biotic and abiotic parameters. The latter might reflect the overall

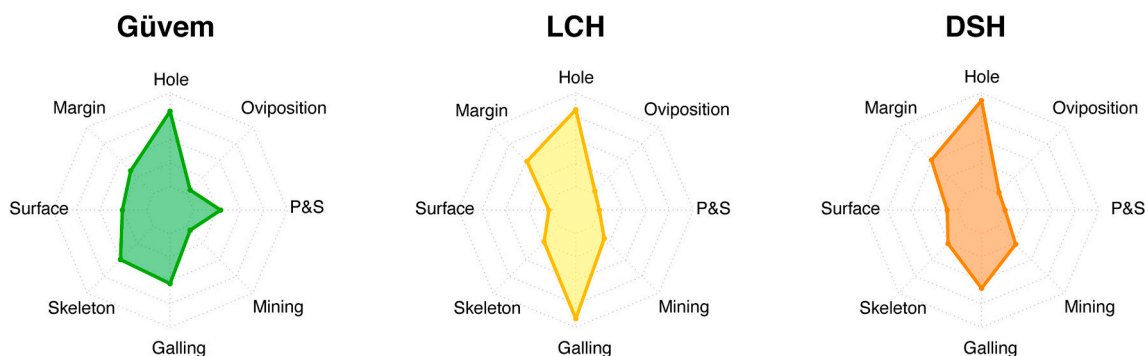


Fig. 6. Spider-charts of the relative contributions of different functional feeding group richness to the overall DT richness from Güvem Formation (green), Brešt'any Clay - LCH (yellow) and Bílina Mine - DSH (orange). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Rarefaction data to produce the spider-charts are based on the plant fossil-taxa represented by more than 10 specimens. The spider-chart was calculated using the package “fmsb” on R version 4.0.0. Abbreviations: P&S, piercing and sucking; Skeleton, skeletonization

Plant-insect interactions	Observed patterns & explanations
External damage Frequency Fig. 4	
Specialized damage Frequency Fig. 4	
Damage type (DT) Richness Fig. 3	
Galling Frequency Fig. 4	
Galling Richness Fig. 3	
Totale Evidence Fig. 5	

Fig. 7. Observed insect feeding patterns for the three plant assemblages and their possible explanations. All explanations are based on modern studies that established a clear relationship between insect damage patterns and environmental parameters. The patterns shown in the right column are summaries of Figs. 4, 5, 6. “>”, “≥” and “=”: greater than, greater than or equal to, and equal. Colored connecting lines indicate which part of the pattern is explained by the respective environmental factors; dashed connecting lines indicate that there is no clear explanation for a particular pattern.

temperate setting of the compared localities in Central Europe and Asia Minor (Fig. 7). DT richness corresponds with species richness and soil richness. The markedly higher species richness in Güvem may also be linked to the latitudinal gradient and higher environmental complexity, which in turn could explain the greater DT richness. The richness and frequency of specialist damage can be partly linked to the lower latitudinal position of Güvem, but apart from that it is difficult to treat specialist damage in a general way as it involves different insect behavior such as herbivory and reproduction. Despite various closer links between the Turkish and one or the other Czech localities, the multivariate spider-chart plots of all damage types richness suggested closer similarity between the two Czech sites (Fig. 7). We interpret the multivariate plots of DT richness as used here to reflect major differences between Central European and East Mediterranean forest biomes and biogeographic legacy. These two components would need more attention in deep time plant-insect interactions studies.

The results of our study underscore the high complexity of the

herbivory network and reiterate findings from modern ecological studies. This calls for careful interpretations of plant-insect interaction patterns in palaeoecological studies in order to avoid generalizations that can potentially be misleading.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gloplacha.2021.103451>.

Data availability

The data supporting our results are provided as Supplementary data to this article.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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