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Plant–insect interactions from the Late Oligocene of Spain (La Val fossil site, Estadilla, Huesca) and their palaeoclimatological implications

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ABSTRACT

Trace fossils of insect herbivory are an important tool, which provide evidence for palaeoecological and palaeoclimatic interpretations, as well as being a unique and direct record of the plant–insect interactions in the geologic past. In the Iberian Peninsula, these types of surveys have been scarce and purely descriptive. The La Val fossil site is an interesting, new megaflora assemblage from the Late Oligocene of Spain, which encompasses numerous plant–insect interactions and their palaeoclimatic and palaeoecological implications. A total of 1337 fossil specimens from 13 stratigraphic levels were analyzed for this study. We identified 28 different types of plant–insect interactions belonging to seven Functional Feeding Groups (FFGs). Hole feeding was the most common category of external-feeding insect damage, followed by margin feeding, skeletonization, and surface feeding. Among the internal-feeding FFGs, galling was the richest and most abundant FFG. All other internal-feeding FFGs were relatively uncommon: piercing/sucking, and *incertae sedis* (DT114). Among stratigraphic levels, the mean herbivory frequency was significantly greater at lower levels compared to the upper levels. La Val presents a marked drop in the diversity of plant–insect interactions through time, possibly due to changes in temperature or humidity levels. A marked decrease in galling diversity and a generalized decrease in interactions are observed at the youngest levels. This could be related to an increase in humidity though time in the La Val palaeoforest, since modern xeric environments favour the proliferation of galls.

1. Introduction

Insect damage on fossil plant material provides important evidence for palaeoecological and palaeoclimatic interpretations, and can be used in conjunction with other fossil material to reconstruct entire landscapes (Wilf and Labandeira, 1999; Wilf et al., 2001; Currano et al., 2010, 2021; Wappler, 2010; Wappler et al., 2012; Labandeira and Currano, 2013; Pinheiro et al., 2016; Wappler and Grímsson, 2016). In particular, trace fossils of insect herbivory on plants provide a unique and direct record of plant–insect (and various other arthropod) ecological associations in the distant past (Labandeira, 2006; Wappler, 2010; Wappler et al., 2012; Peñalver et al., 2012, 2015; Pérez de la Fuente et al., 2012; Peris et al., 2017; Maccracken et al., 2021).

Recent studies of plant–insect interactions have covered the geologic ages starting from the Silurian Period, which coincides with the earliest primitive plants, to the Quaternary Period and nearly modern fossil floras (Labandeira, 2006; Labandeira and Currano, 2013); however, more work is needed to expand this record globally and fill previously under sampled time intervals and geographic localities (Labandeira, 2013a, 2013b). To date, the majority of plant–insect associational data comes from the northern hemisphere and the geologic ages of the floras examined are sporadic, rather than at consistent time intervals (Pinheiro et al., 2016). For instance, while literature covering the study of plant–insect interactions of the end-Cretaceous (Labandeira et al., 2002a, 2002b; Wilf et al., 2006; Donovan et al., 2014, 2016) and Paleocene–Eocene Thermal Maximum (PETM) (Currano et al., 2008; Azevedo-Schmidt et al., 2019) is extensive, relatively few studies have described such associations from the Oligocene period (e.g., Koch, 2010;

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Currano et al., 2011; Fodor, 2014; Gunkel and Wappler, 2015; Moreno-Domínguez, 2018) (see Table 1). Indeed, data on Oligocene plant–arthropod damage can help us bridge the interval between the late Mesozoic and early Cenozoic floras and modern floras, as the onset of Antarctic glaciation at the Eocene/Oligocene boundary represents the transition from the global hot house climate at the PETM to our current climate (e.g., Wappler, 2010).

In Spain a basic palaeobotanical framework of the Cenozoic vegetation has been established over the past few decades (Sanz de Siria, 1996; Barrón and Santos, 1998; Postigo-Mijarra et al., 2009; Barrón et al., 2010). However, very few quantitative analyses of insect damage on fossil plants have been conducted, and surveys of plant–insect interactions have primarily focused on Miocene and Quaternary floras (see Table 2). In Spain, the first publication documenting plant–insect interactions was by Villalta and Crusafont (1945), which described galls on *Fagus* leaves from the Late Miocene fossil site of La Cerdaña (Lérida,

Table 1
Arthropod damage on Oligocene plants. Modified from Labandeira (2006).

Age	Geographic area	Formation	Damage type	References
RUPELIAN (Early Oligocene)	Dynów, Skole Nappe (Poland)	Kliwa Sandstone	***Boring*** in Pinales wood.	Rajchel and Uchman (1998).
	Vargem, Grande do Sul, Sao Paulo (Brazil)	Tremembé Fm.	***External foliage feeding***: Malpighiaceae, Euphorbiaceae, Salicaceae, Fabaceae, Sapindaceae, Anacardiaceae, Rutaceae, Lamiales. ***Oviposition***: Lauraceae, Chloranthaceae, Fagaceae, Betulaceae, Juglandaceae, Myricaceae, Gentianiales.	Martins-Neto (1989, 1998).
	La Porte, Plumas County, California (USA)	Ione Fm.	***Leaf mining***: Ericaceae, Theaceae, Sapotaceae. ***Boring***: Sapindaceae, Anacardiaceae, Rutaceae. ***Galling***: Fagaceae, Betulaceae, Juglandaceae, Myricaceae. ***Seed predation***: Sapindaceae, Anacardiaceae, Rutaceae.	Potbury (1935).
	Kundratice, northern Bohemia (Czech Republic)	Diatomite	***External*** and ***internal foliage feeding***: Sapindaceae, Simoroubaceae, Betulaceae, Vitaceae, Juglandaceae, Celtidaceae, Cercidiphyllaceae, Lauraceae, Fabaceae, Magnoliaceae, Platanaceae, Salicaceae, Rosaceae, Ulmaceae and unidentified angiosperm morphotypes.	Koch (2010).
	Hammerunterwiesenthal, Saxony (Germany)	Laminated Tuffite	***Oviposition***: Lauraceae, Betulaceae and unidentified Angiosperms.	Hellmund and Hellmund (1998, 2002).
MIDDLE OLIGOCENE	Kis-Eged Hill, Eger (Hungary)	Kiscell Clay Fm.	***Hole*** and ***margin feeding***, ***skeletonization***, ***surface feeding***, ***piercing***, ***oviposition***, ***mining***, ***galling*** and ***incertae sedis*** in Rhamnaceae, Fagaceae and Crassulaceae.	Fodor (2014).
	Seifhennersdor, Sachsen (Germany)	"Kuclin" diatomite	***External foliage feeding***: Malpighiaceae, Euphorbiaceae, Salicaceae, Fabaceae, Sapindaceae, Anacardiaceae, Rutaceae, Lamiales. ***Oviposition***: Lauraceae, Chloranthaceae, Fagaceae, Betulaceae, Juglandaceae, Myricaceae, Gentianiales. ***Leaf mining***: Ericaceae, Theaceae, Sapotaceae. ***Boring***: Sapindaceae, Anacardiaceae, Rutaceae. ***Galling***: Fagaceae, Betulaceae, Juglandaceae, Myricaceae. ***Seed predation***: Sapindaceae, Anacardiaceae, Rutaceae.	Koch (2010). Hellmund and Hellmund (1996, 2002).
	Klepzig (Germany)	"lignite"	***Boring*** in Pinales wood. ***Oviposition*** on Filicales.	Linstow (1906).
	Chilga Basin (Ethiopia)	Laminated claystone to mudstone	***Galls***, ***External*** and ***internal foliage feeding***: Rubiaceae, Sapindaceae, Aristolochiaceae, Menispermeaceae, Euphorbiaceae, Salicaceae, Rutaceae, Arecaceae, Dioscoreaceae, Loganiaceae, Malvaceae s.l., Lauraceae, Myrtaceae, Fabaceae and Sapotaceae. ***Leaf mining***: Swartzieae, Fabaceae.	Currano et al. (2011).
	Windbrickyard, Baromállás (Hungary)	Formation not reported		Ambrus and Hably (1979).
	Ruby River, Madison County, Montana (USA)	Renova Fm.	***External foliage feeding***: Fagaceae, Betulaceae, Juglandaceae, Myricaceae, Rosaceae, Ulmaceae, Celtidaceae, Moraceae. ***Oviposition***: Fagaceae, Betulaceae, Juglandaceae, Myricaceae, Lauraceae, Chloranthaceae.	Lewis (1976). Becker (1965, 1969). Petrulevičius et al. (2011).
	Rött, Schwaben (Germany)	Köln Fm.	***Leaf mining***: Fagaceae, Betulaceae, Juglandaceae, Myricaceae, Malpighiaceae, Euphorbiaceae, Salicaceae. ***Galling***: Lauraceae, Chloranthaceae, Malpighiaceae, Euphorbiaceae, Salicaceae.	Wappler (2010). Hellmund and Hellmund (1991, 1993, 2002).
CHATTIAN (Late Oligocene)				Sittig (1927). von Heyden (1862).
		"porcellanite"	***Boring*** in Pinales wood. ***Oviposition*** on Filicales and Salviniaceae.	Hellmund and Hellmund (1991, 2002). Hellmund (1988).
	Enspel, Westerwald (Germany)	Enspel Fm.	***External*** and ***internal foliage feeding***: on Sapindaceae, Betulaceae, Juglandaceae, Lauraceae, Fagaceae, Fabaceae, Ulmacae and unidentified angiosperm morphotypes.	Gunkel and Wappler (2015).
	Freilendorf, Hessen (Germany)	"lignite"	***Boring*** in Pinales wood. ***Oviposition*** on Filicales.	Roselt and Feustel (1960).
	La Val, Estadilla (Spain)	Sariñena Fm.	***Hole feeding***, ***surface feeding***, ***margin feeding***, ***skelotinization***: Betulaceae. ***Galling***: Betulaceae, Lauraceae, Altingiaceae, Myricaceae and Rosaceae.	Moreno-Domínguez (2018).
	Patagonia (Argentina)	Rio Leona Fm.	***Hole feeding*** on Fabaceae. ***Piercing*** and ***sucking*** on Araucariales.	Césari et al. (2015).
	Southwestern Patagonia (Argentina)		***Boring*** in woods from Nothofagaceae.	Pujana (2009).

Table 2
Previous studies of herbivory from Spain with plant–insect interactions identified on fossil leaves.

Age	Geographic area	Formation	Damage type	References
PLEISTOCENE	Beceite (Teruel)	Formation not reported	**Galling** (unidentified DTs): *Populus* sp.	Peñalver et al. (2002).
LATE MIOCENE (Vallesian)	La Cerdaña (Lérida)	Lower Neogene Unit B	**Galling** (unidentified DTs): *Fagus* sp., *Quercus* sp., Magnoliidae, *Persea* sp., *Zelkova* sp., *Acer* sp.	Diéguez et al. (1996). Villalta (1957). Villalta and Crusafont (1945).
EARLY MIOCENE (Early Aragonian-Ramblian)	Ribesalbes (Castellón)	Lacustrine Unit B	**Margin feeding** (unidentified DTs): Caesalpiniaceae. **Oviposition** (unidentified DTs): *Carya* sp., *Populus* sp., *Laurophyllum* sp., Caesalpiniaceae. **Mining** (unidentified DTs): *Celtis* sp., *Laurophyllum* sp.	Peñalver et al. (2016). Peñalver and Martínez-Delclòs (2004). Peñalver and Martínez-Delclòs (1997).
	Rubielos de Mora (Teruel)	depositional Unit C	**Margin feeding** (unidentified DTs): *Zelkova* sp., *Salix* sp., *Myrica* sp.	Peñalver and Martínez-Delclòs (1997). Peñalver (1997). Montoya et al. (1996).
LATE OLIGOCENE (Chattian)	La Val (Huesca)	Sariñena Fm.	**Hole feeding** (DT01, DT02, DT03, DT07): *Alnus* sp. **Margin feeding** (DT12, DT14, DT15): *Alnus* sp. **Surface feeding** (DT30): *Alnus* sp. **Skelotinization** (DT16): *Alnus* sp. **Galling** (DT32, DT33, T34, DT80, DT84): *Alnus* sp., *Daphnogene* sp., *Myrica* sp., Altingiaceae and Rosaceae.	Moreno-Domínguez (2018).
LOWER CRETACEOUS (Upper Albian)	Plou/Estercuel (Teruel)	Utrillas Fm.	**Hole feeding** (DT02): *Aquatifolia* cf. *fluitans*. **Hole feeding** (DT78): *Ploufolia cerciforme*. **Margin feeding** (DT12): *Ploufolia cerciforme*.	Estévez-Gallardo et al. (2018).
MIDDLE JURASSIC (Aalenian)	La Puebla de Valverde/ Camarena de la Sierra (Teruel)	El Pedregal Fm.	**Hole feeding** (DT01, DT02, DT03, DT04, DT64): Cycadophytes. **Margin feeding** (DT12, DT81): Cycadophytes. **Surface feeding** (DT29): Cycadophytes. **Piercing/Sucking** (DT46): Cycadophytes. **Oviposition** (DT76): Cycadophytes. **Mining** (unidentified DT): Cycadophytes.	Santos et al. (2021).
CARBONIFEROUS	La Magdalena coalfield (León)	Early Stephanian C	**Hole feeding** (unidentified DTs): *Spenopteris* sp., *Linopteris* sp., *Mixoneura* sp. **Margin feeding** (unidentified DTs): *Spenopteris* sp., *Linopteris* sp., *Mixoneura* sp. **Mining** (unidentified DTs): Pteridospermae. **Galling** (unidentified DTs): *Dicksonites* sp.	Castro (1997). Castro (1994). Van Amerom (1966). Van Amerom and Boersma (1971).

NE Spain). Later papers describe Miocene or Quaternary insect galls, such as Villalta (1957), Diéguez et al. (1996), Peñalver and Martínez-Delclòs (1997), and Peñalver et al. (2002), as well as other types of insect damage (e.g., leaf mines, leaf chew marks, oviposition), from the Miocene Rubielos de Mora and Ribesalbes localities (Montoya et al., 1996; Peñalver, 1997; Peñalver and Martínez-Delclòs, 1997, 2004; Peñalver et al., 2016). Apart from these Cenozoic fossil sites, there are some Cretaceous insect herbivore interactions on aquatic angiosperms from the Upper Albian (Early Cretaceous) of Teruel, SE Spain, (Estévez-Gallardo et al., 2018), plant–insect interactions from Middle Jurassic of Teruel (Santos et al., 2021), and from the Carboniferous of León, NW Spain, (Van Amerom, 1966; Van Amerom and Boersma, 1971; Castro, 1994, 1997) (see Table 2). Recently, a preliminary study by Moreno-Domínguez (2018) described numerous plant–insect interactions in the Late Oligocene, NE Spain, which is the cornerstone of the research documented herein.

Here, we present new evidence of plant–insect interactions from the Late Oligocene of the Iberian Peninsula. Our main goals are: (1) describe new plant–insect interactions on plant specimens from the macroflora fossil assemblage of La Val, (2) analyze all plant–insect interactions at La Val, including the dataset from Moreno-Domínguez (2018), (3) detect relationships between insect damage frequency, diversity of types of damage and palaeoclimatological variables within the La Val floral assemblage, and (4) compare these results with other European macrofloral assemblages dated to similar geologic ages.

2. Geological and biological setting

The plant fossils featured in this publication were excavated from the La Val fossil site (42°3′47.62″N, 0°15′3.34″E). This megaflora assemblage is situated in the northeast portion of the Huesca Province of Spain, along the border between the Ebro Basin and the Marginal Ranges (Moreno-Domínguez, 2019) (Fig. 1). This fossil site was deposited in the Sariñena Formation, which ranges from Late Oligocene to Early Miocene in age and is formed by a series of terrestrial facies; this formation is mainly comprised of alluvial deposits of conglomerates, sandstones and mudstones, which outcrop in the northern margin of the Ebro Basin (Fig. 1), as the result of the Alpine Orogeny (Pardo et al., 2004; Luzón, 2005).

La Val corresponds to a fluvial environment in which a riparian forest developed. The facies of La Val correspond to fluvial deposits of mudstones and sandstones (Luzón and González, 2003; Luzón, 2005) (Fig. 2), which were developed on the margin of a large alluvial fan (Moreno-Domínguez et al., 2015, 2016, 2021); the facies of levels LV0 to LV2 and LV4 to LV9 corresponded to floodplain deposits, meanwhile LV3 and LV10 corresponded to crevasse splay deposits. By contrast, the younger LVNH and LVNH2 levels were overbank deposits with ephemeral ponds (Moreno-Domínguez et al., 2016). These conditions represented fluvial environments with oxygenated and well-drained soils with fluctuating hydrological conditions (Moreno-Domínguez et al., 2015, 2016). According to Moreno-Domínguez et al. (2015, 2016), riparian vegetation developed along these fluvial environments, except in the upper levels (LVNH–LVNH2) in which the vegetation was mainly dominated by pioneer ferns, such as *Acrostichum*. This megaflora

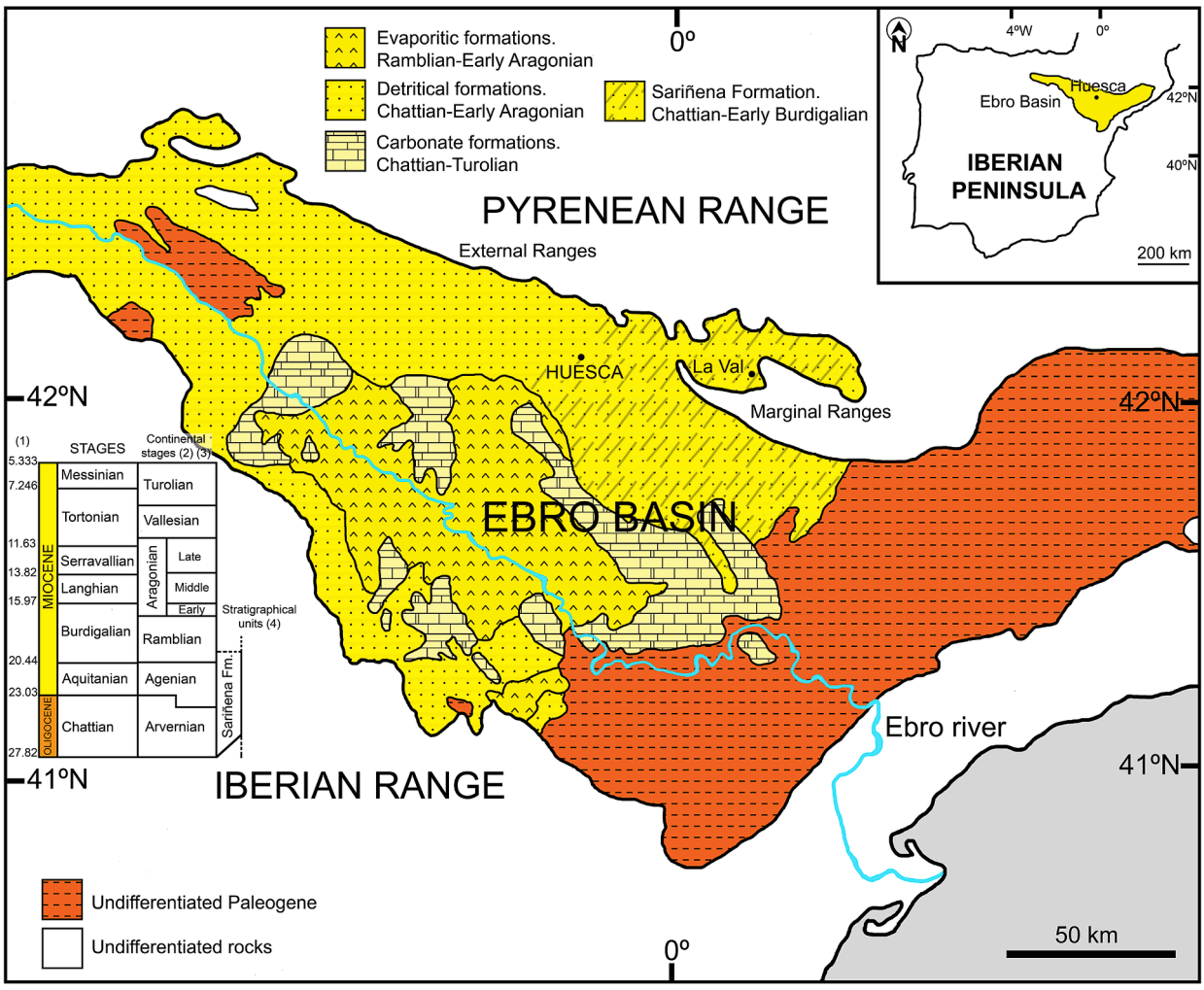

Fig. 1. Geography and geology of the La Val fossil site in the Ebro Basin (Iberian Peninsula) and geographical distribution of the Sariñena Formation. Modified from Arenas and Pardo (1999). Data from (1) Cohen et al. (2013; updates),(2) Sesé (2006), (3) Gradstein et al. (2005), and (4) Luzón (2005).

assemblage developed in a warm temperate climate with hot and dry summers (Moreno-Domínguez et al., 2021). The La Val fossil site is stratigraphically located in the lower part of this formation and is Late Oligocene in age (Moreno-Domínguez et al., 2016).

From taphonomic point of view, the ferns are autochthonous, while it is probable that the remains of various seed plants (angiosperms and gymnosperms) were allochthonous. In particular, Berberidaceae leaves are small and easily transported by the wind. In contrast, the riparian vegetation developed in LV3–LV4 and LV6, were mainly para-autochthonous and transported only a short distance by water (Moreno-Domínguez et al., 2015). These levels were totally fluvial with no temporal ponds (Moreno-Domínguez et al., 2016).

3. Materials and methods

We analyzed 1337 fossil leaves and leaflets from 13 well-constrained stratigraphic levels (Fig. 2, Appendices A1–A3) all of which represent floodplain, crevasse splay, overbank, and ephemeral pond depositional environments. Identification of plant–insect interactions was based on the *Guide to Insect (and Other) Damage Types on Compressed Plant Fossils* by Labandeira et al. (2007) and subsequent unpublished addenda. The damage types (DTs), or individual patterns of damage denoted numerically (e.g., DT001, DT219, DT330), are divided into six Functional Feeding Groups (FFG): hole feeding (HF), margin feeding (MF), skeletonization (S), surface feeding (SF), piercing and sucking (P/S), and galling (G), while the unknown plant–insect interactions were included in the *incertae sedis* (IS) group. The insect interactions on leaves were scored according to the richness, frequency and distribution for each plant species per level. These metrics were computed with the standard procedure from Gunkel and Wappler (2015). All analyses were performed in R i386 3.6.0 (R Development Core Team) and R Commander. For the full rarefaction results, the package *gmp* (Lucas et al., 2013) was used. We also calculated the diversity of different DTs and FFGs using analytical rarefaction and standard deviations were calculated using the method by Heck et al. (1975). In addition, the damage diversity was calculated for each general clade of plant (Angiospermae/angiosperms, Gymnospermae/gymnosperms, or Pteridophyta/ferns) with at least 10 specimens (Adroit et al., 2021; Knor et al., 2012; see also supplement data), and these different clades were compared using a Wilcoxon test with the plant species identity as explanatory variable and filter out the important variation due to it (Knor et al., 2012). Only those among-horizon differences significant in the analysis are due to actual shifts in arthropod species composition and their realized niches. The complete census data are shown in Appendices A1–A3.

Each foliar element was examined with a Nikon SMZ–2 stereo microscope and photographed using a Nikon–D 90 camera with an AF–S Micro Nikon 60 mm macro lens. All photographs were subsequently optimized using Adobe Photoshop version CS2. Specimens are reposited in the Museum of Natural Science of the University of Zaragoza (Zaragoza, Spain) (Canudo, 2018).

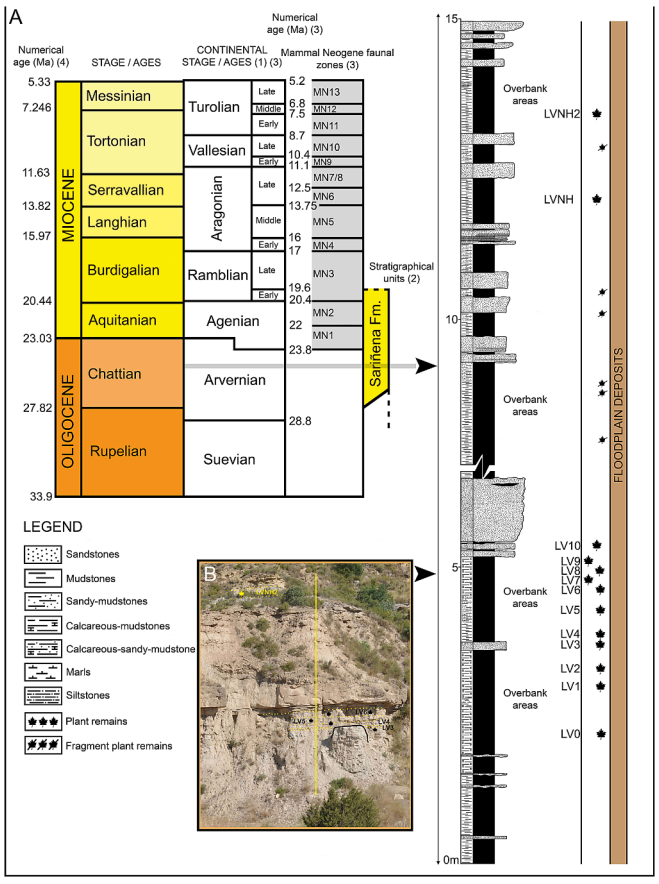

Fig. 2. A. Stratigraphic section of the La Val fossil site and chronostratigraphic chart for the study area. Figure shows all levels with fossil plants remains that occur in the La Val fossil assemblage. Modified from Moreno-Domínguez et al. (2016), data from (1) Gradstein et al. (2005), (2) Luzón (2005), (3) Sesé (2006), and (4) Cohen et al. (2013; updates). B. Photograph of the fossil outcrop showing several of the stratigraphic levels.

4. Results

4.1. Plant diversity

Fossil plant material analyzed in this study included angiosperm leaves, gymnosperm leaves, and fossil fern pinnae from Late Oligocene La Val fossil site (Sariñena Formation). To date, 18 plant families and 27 plant genera are known from this deposit (see Moreno-Domínguez et al., 2015, 2021; Moreno-Domínguez, 2019): Angiospermae: *Acer* (Sapindaceae), *Alnus* (Betulaceae), *Ampelopsis* (Vitaceae), *Berberis* (Berberidaceae), *Caesalpinites* (Leguminosae), cf. *Carpinus* (Betulaceae), *Celastrophyllum* (Celastraceae), *Daphnogene* (Lauraceae), *Dicotylophyllum* (Incertae sedis), *Engelhardia* (Juglandaceae), *Laurophyllum* (Lauraceae), *Leguminocarpon* (Leguminosae), *Leguminophyllum* (Leguminosae), cf. *Liquidambar* (Altingiaceae), *Liriodendron* (Magnoliaceae), cf. *Magnolia* (Magnoliaceae), *Myrica* (Myricaceae), cf. *Parrotia* (Hamamelidaceae), *Quercus* (Fagaceae), cf. *Rosa* (Rosaceae), cf. *Salix* (Salicaceae), cf. *Typha* (Typhaceae), Fabaceae, and Trapaceae; Gymnospermae: Cupressaceae, and *Pinus* (Pinaceae); Pteridophyta: *Acrostichum* (Pteridaceae), *Equisetum* (Equisetaceae), *Pronephrium* (Thelypteridaceae), and *Pteridium* (Dennstaedtiaceae).

Most of fossil angiosperm leaves were found in the LV0 to the LV10 levels; in comparison, angiosperm leaves were relatively rarer in the LVNH and LVNH2 levels. By contrast, the fossil leaves of gymnosperms were poor in the angiosperm-rich levels and only abundant in LVNH. Similarly, fossil fern pinnae were also scarce in the La Val fossil site and only abundant in the LVNH and LVNH2 levels. The number of specimens excavated from each level was also not equal. The number of specimens from LV3–LV4, LV6 and LVNH were higher compared to LV0–LV2, LV5 and LV7–LV10; for instance, 455 leaves were collected from LV3 compared to 78 specimens from LV7, and only six specimens from LV9 (see Appendices A1–A3).

4.2. Plant–insect interactions

The proportion of fossil leaves with at least one type of insect damage at La Val was 34.6% and there were a total of 702 insect damage occurrences (see Appendices A1–A3). Although 74.3% of the La Val specimens are angiosperms, they make up 84% of the total plant–insect interactions. Gymnosperms (~3% of the total specimens) did not exhibit any insect damage (0%), while pteridophytes (equisetales and ferns) comprised 8.5% of the total plants and contained only 3.7% of the plant–insect interactions of La Val. Angiosperms also had the highest proportion of damaged leaves per clade, with 39.2% of all angiosperms showing insect damage. Within angiosperms, the different families present different incidences for plant–insect interactions (see Fig. 3); Betulaceae has the highest damage incidence rate (~41%), closely followed by the Myriaceae (~40%), while Berberidaceae and Lauraceae have somewhat lower incidences (~32% and ~ 29%, respectively). The high incidence rates of insect herbivory on angiosperms contrasts with the low incidence rates on gymnosperms, Equistaceae (~5%) and the rest of pteridophytes (~11%) (see Fig. 3).

Insect herbivory was also highly variable by stratigraphic position. Among stratigraphic levels, the mean herbivory frequency was significantly greater at lower levels compared to the upper levels ($F_{[1,\ 4]} = 2.73$, $p = 0.043$) (Fig. 4. A, B, C and D). For instance, the best-sampled levels, LV1, LV3, LV4, LV6, LV7 and LVNH, had damage frequencies of 55.6 ± 6.3%, 38.9 ± 3.9%, 36.0 ± 3.6%, 38.6 ± 3.3%, 10.3 ± 3.4% and 17.0 ± 2.9% respectively. Even in the poorly sampled levels, LV0, LV2, LV5, LV8, LV9, LV10 and LVNH2, we saw a general decrease in insect herbivory, with 58.8 ± 11.9%, 72.0 ± 8.9%, 37.9 ± 6.4%, 17.4 ± 7.9%, 16.7 ± 15.2%, 11.1 ± 10.5% and 20.0 ± 5.9% of leaves with insect damage, respectively. Using the classification of Labandeira et al. (2007), we identified 28 different types of plant–insect interactions (DTs) belonging to six Functional Feeding Groups (FFGs) (see Appendices A1–A3, Figs. 5, 6). In general, hole feeding was among the richest and most abundant forms of external-feeding insect damage (7 DTs; 344 total occurrences; and makes up 49% of all DT occurrences), followed by margin feeding (4 DTs; 71 occurrences, 10.1%); skeletonization (3 DTs; 7 occurrences, 1%); and surface feeding (3 DTs; 6 occurrences, 0.9%). Among the internal-feeding FFGs, galling was the richest and most abundant FFG (9 DTs; 253 occurrences, 36%); and all other internal-feeding FFGs were relatively uncommon: piercing/sucking (1 DT; 20 occurrences, 2.8%); and finally, *incertae sedis* (1 DT; 1 occurrence, 0.1%). Hole feeding is found in every level except for LV9, whereas galling is mainly restricted to the lower levels (LV0–LV7). Skeletonization is more dominant in the upper levels (LVNH and LVNH2), as is piercing/sucking (LVNH).

4.2.1. Damage types at La Val: Hole feeding (HF)

Seven DTs of hole feeding are present in La Val: DT001, DT002, DT003, DT004, DT005, DT007 and DT008 (Table 3) (Fig. 5A–E, see Appendices A1–A3). Among those, DT001, DT002 and DT003 are the most common of these damage types, are characterized by circular to polylobate, or sometimes curvilinear to rectilinear elongate, perforations (for more complete description see Labandeira et al., 2007), and are mainly found on members of the family Betulaceae. All hole feeding traces exhibit reaction rims and are not specialized on a particular portion of the leaf. The sizes of these holes range from one mm in diameter (e.g., Fig. 5A, DT001) to one cm in length (e.g., Fig. 5E, DT008).

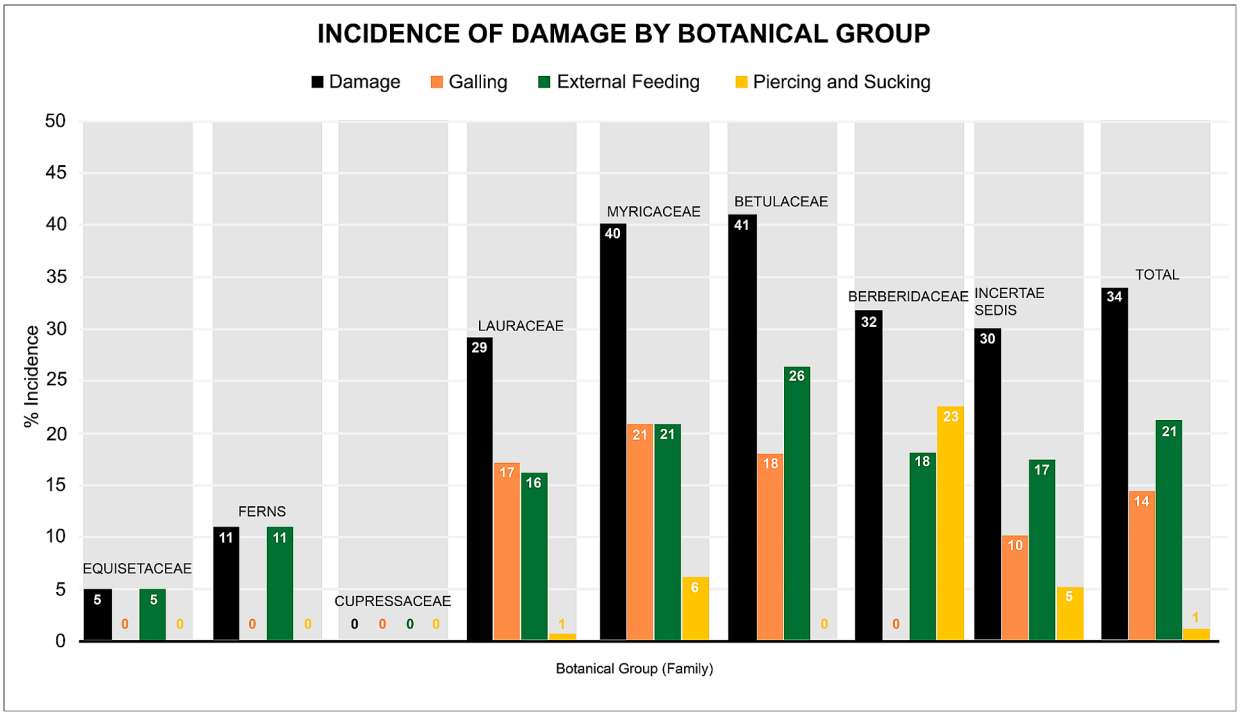

Fig. 3. Graphic showing the incidence of total damage, galling, external feeding and piercing and sucking in different botanical groups of La Val. All vegetal fragments that are not taxonomically recognized are included in the incertae sedis category.

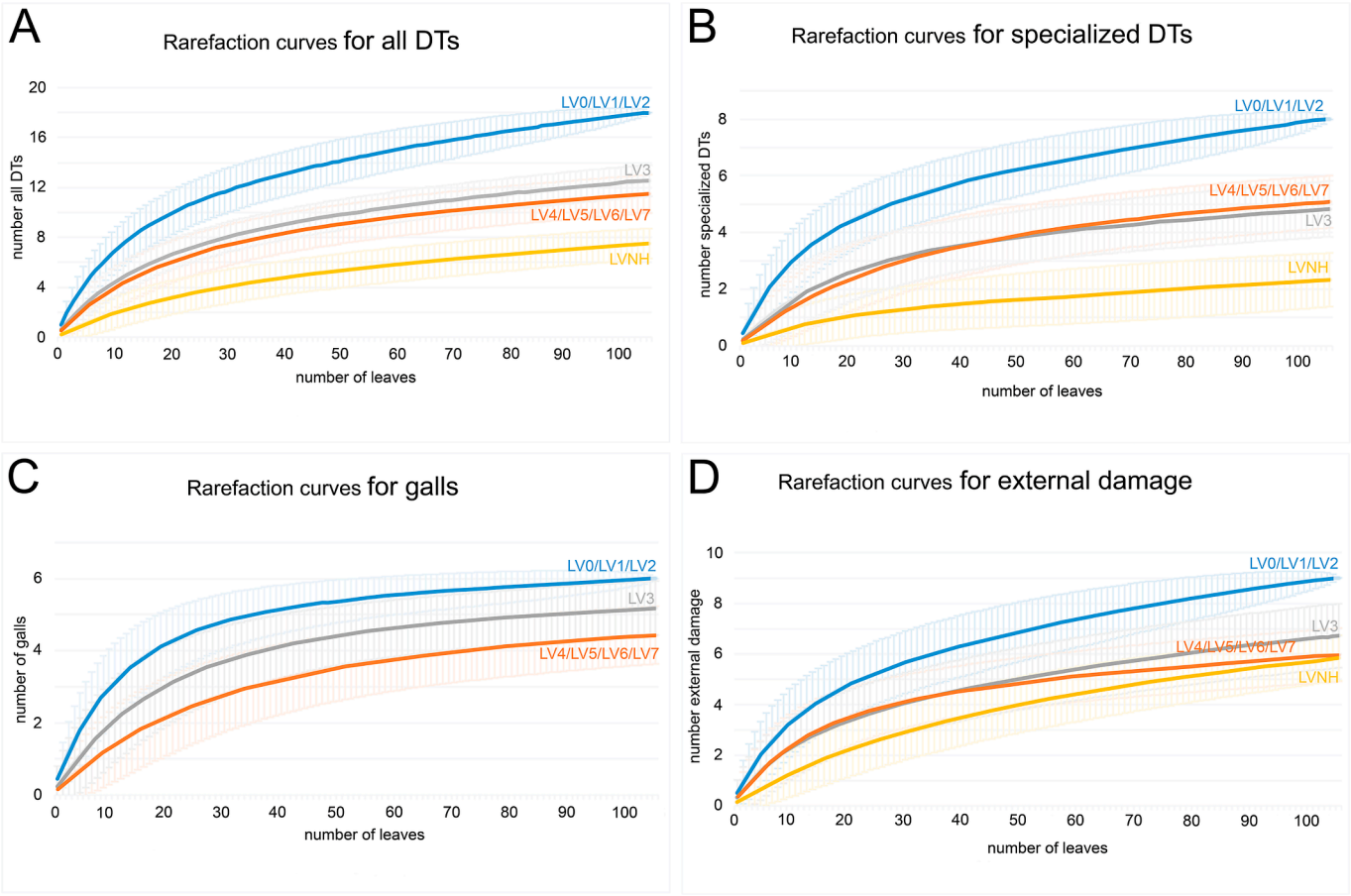

Fig. 4. Rarefaction curves for LV0 to LV7 and LVNH levels. (A) For all DTs, (B) specialized damage, (C) galling, and (D) external damage. LVNH is not represented in (C) because there were no galls recorded. The levels are grouped by sedimentary environment. LV0–LV2, LV4–LV7 represent overbank areas, LV3 represent crevasse deposits, while LVNH corresponds to ponds developed on the overbank areas. LV8-LV10, and LVNH2 levels have been excluded by low sample sizes.

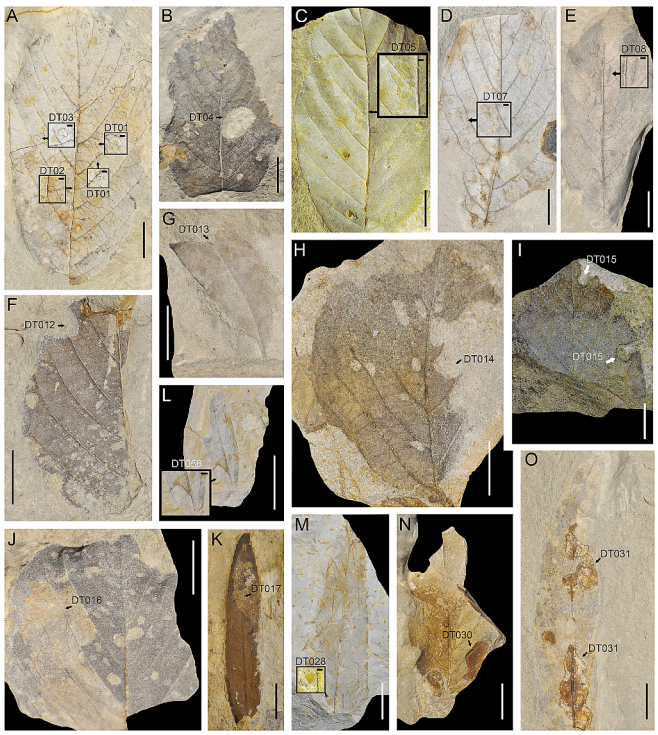

Fig. 5. Plant–insect interactions documented at La Val fossil site. Hole feeding: (A) DT001, DT002, DT003 on Betulaceae (EMPZ2018/17–2021/115 – LV4–8 – 1B); (B) DT004 on Betulaceae (EMPZ2018/17–2021/118–LV4–112–1); (C) DT005 on Betulaceae (EMPZ2018/17–2019/1557–LV6–115–1A); (D) DT007 on *Alnus* cf. *gaudinii* (EMPZ2018/17–2021/106–LV2–22–1); (E) DT008 on *Alnus* sp.(EMPZ2018/17–2021/110–LV3–194–1). Margin feeding: (F) DT012 on Betulaceae (EMPZ2018/17–2021/104–LV2–14–1A); (G) DT013 on *Laurophyllum* sp. (EMPZ2018/17–2021/117–LV4–27–1); (H) DT014 on Betulaceae (EMPZ2018/17–2018/80–LV3–222–1 specimen from Moreno-Domínguez, 2018); (I) DT015 on *Alnus* sp.(EMPZ2018/17–2018/251–LVR–60–1B). Skeletonization: (J) DT016 on *Alnus* sp. (EMPZ2018/17–2019/1556–LV6–114–1); (K) DT017 on unidentified leaf (EMPZ2018/17–2021/95–LV0–12–1); (L) DT056 on cf. *Berberis* sp. (EMPZ2018/17–2021/138–LVNH–75–2D). Surface feeding: (M) DT028 on *Acrostichum lanzeanum* (EMPZ2016/11–2017/288–LVNH2–9–1 specimen from Moreno-Domínguez et al., 2016); (N) DT030 on Betulaceae (EMPZ2018/17–2018/57–LV3–8–1 specimen from Moreno-Domínguez, 2018); (O) DT031 on *Laurophyllum* sp. (EMPZ2018/17–2021/102–LV2–8–1A). Big scale bar is one cm. Small scale bar is one mm.

4.2.2. Damage types at La Val: Margin feeding (MF)

The margin feeding types that appear in La Val are DT012, DT013, DT014, and DT015 (Table 3) (Fig. 5F–I, see Appendices A1–A3). DT012 occurs in almost all levels, while DT013, DT014, and DT015 are confined to a smaller number of levels. These excisions range from a few millimeters to several centimeters (Fig. 5F–I), and are sometimes situated at the leaf apex (Fig. 5I). These DTs are delimited by smooth reaction rims and are also found primarily on Betulaceae leaves.

4.2.3. Damage types at La Val: Skeletonization (S)

Skeletonization is extremely uncommon in La Val; the DTs represented are DT016 with five occurrences, and DT017 and DT056 with one occurrence each (Fig. 5J–L, see Appendices A1–A3) (Table 3). At La Val, these types of external foliage feeding damage are situated at the leaf base (Fig. 5L) or in distinct sections of the leaf lamina (Fig. 5J, K), and all have interveinal tissue removed and poorly developed reaction rims. Their size ranges from several millimeters up to three centimeters, depending on the size of the foliar lamina. Betulaceae and Berberidaceae are the taxa affected by skeletonization.

4.2.4. Damage types at La Val: Surface feeding (SF)

Surface feeding DTs at La Val included DT028, DT030, and DT031, with 1, 3, and 2 occurrences, respectively (Fig. 5 M–O, see Appendices A1–A3) (Table 3). Surface feeding DTs are the least common external foliage feeding damage at La Val. Alongside the abrasion or removal of surface tissues are often distinct polylobate or circular to ellipsoidal reaction rims (Fig. 5N–O), while abrasion between parallel veins results in a rectangular reaction rim (Fig. 5M). These damage types range between 2 and 30 mm in length, and are not specialized to a particular plant taxon or clade.

4.2.5. Damage types at La Val: Galling (G)

Galling is the most abundant FFG at La Val. There are a total of 9 DTs that vary in diameter and shape from millimeter to centimeter in size: DT011, DT032, DT033, DT034, DT049, DT055, DT084, DT116, and DT127 (Table 3) (Fig. 6A–D, F–H, J, see Appendices A1–A3), of which DT032, DT033, and DT034 are the most abundant. At La Val, galls are found within the foliar lamina (Fig. 6B, C), petiole (Fig. 6J) or at the leaf margin (Fig. 6G). Galling is mostly found on specimens of Betulaceae and are much less common in other taxa.

4.2.6. Damage types at La Val: Piercing/Sucking (P/S)

Piercing and sucking is only represented by DT046, with 20 occurrences (Fig. 6E, Appendices A1–A3) (Table 3). DT046 is found almost exclusively in the stratigraphic level LVNH, and on Berberidaceae leaves. These punctures are characterized as circular marks with a central depression that are less than two millimeter in diameter. They are found anywhere on the leaf lamina, and occasionally alongside the primary vein.

4.2.7. Damage types at La Val: Incertae sedis (IS)

Here, we have included one possible occurrence of DT114 (Fig. 6I) (Table 3). These marks consists of a strip of necrotic tissue occurring along the left margin of a Betulaceae. Distinct reaction tissue abuts unaffected foliar tissue. The size of this *incertae sedis* is 2–4 mm in width and is present on one leaf from stratigraphic level LV3 (Appendices A1–A3).

5. Discussion

The La Val site captures landscape changes through time in a constrained geographic area, which is a rare occurrence in the fossil record. In general, the insect herbivory at La Val is highly variable between levels, both in terms of richness, percentage and/or frequency of damage types. The insect herbivory of LV0–LV2, LV5, LV7, LV8–LV10 and LVNH2 levels are highly heterogeneous; in contrast, the insect damage within levels LV3–LV4, LV6 and LVNH are relatively similar to one another (see Appendices A1–A3). This variability depends on several factors: (1) the depositional environments, which have an effect on the type of flora and its diversity, (2) the taphonomic conditions; and (3) the sampling quality (Wappler, 2010), as we will discuss.

5.1. Plant–insect associations and palaeoclimatic implications at La Val

The La Val palaeoforest presents a marked drop in the diversity of plant–insect interactions throughout the levels. For example, the well-sampled lower levels (LV3, LV4 and LV6) present similar percentages of specimens with DTs: 38.9%, 36.9% and 38.6% respectively, while the equally well-sampled upper level (LVNH) shows a considerably lower percentage of DTs (17%) (Appendices A1–A3). Possible causes of this decrease in the abundance and diversity of interactions in the different levels of La Val could be due to changes in temperature or humidity levels.

According to Moreno-Domínguez et al., (2021), the disparity in the temperature values between levels at La Val is quite high, because of the limited number of specimens used to calculate the LMA at some levels is

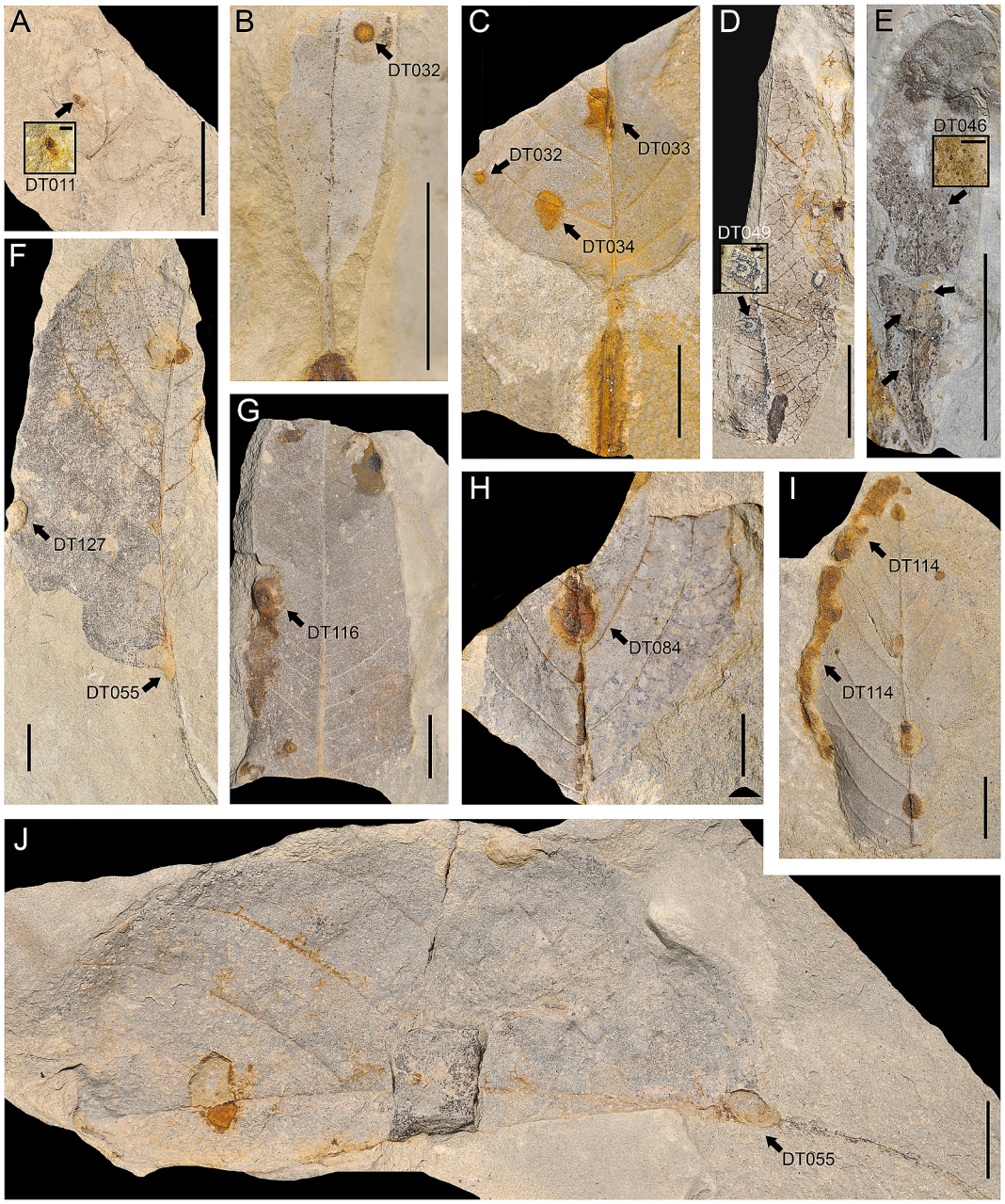

Fig. 6. Plant–insect interactions from La Val fossil site. Galling: (A) DT011 on *Dicotylophyllum* sp. (EMPZ2018/17–MPZ 2021/116–LV4–23–1); (B) DT032 on cf. *Salix varians* (EMPZ2018/17–2021/100–LV2–3–2B); (C) DT033, DT034 on *Alnus* sp. (EMPZ2018/17–2018/64–LV3–14–1B); (D) DT049 on cf. *Magnolia* sp. (EMPZ2018/17–2021/119–LV8–2–1); Piercing/Sucking: (E) DT046 on cf. *Berberis* sp. (EMPZ2018/17–2021/120–LVNH–4–1); Galling: (F) DT127 on Betulaceae (EMPZ2018/17–2021/107–LV3–25–1A); (G) DT116 on *Myrica* sp. (EMPZ2018/17–2021/101–LV2–7–1); (H) DT084 on *Alnus* sp. (EMPZ2018/17–2018/78–LV3–158–1 specimen from Moreno-Domínguez, 2018); Incertae sedis: (I) DT114 on Betulaceae (EMPZ2018/17–2018/60–LV3–12–1). Galling: (J) on Betulaceae (EMPZ2018/17–2021/108–LV3–25–1B). Big scale bar is one cm. Small scale bar is one mm.

low and should be treated with caution. Although temperature could be a factor that affects the diversity and intensity of interactions at each level (e.g., Wilf and Labandeira, 1999; Labandeira et al., 2002a), we cannot reliably verify the temperature changes between each level in La Val site.

However, there is a generalized decrease in interactions and a marked decrease in galling diversity at the youngest levels. This could be related to an increase in humidity though time in the La Val palaeoforest, since modern xeric environments favour the proliferation of galls (Fernandes and Price, 1992). During the Late Oligocene a warm interval takes place, with subhumid to semi-arid conditions in the northern hemisphere (Wolfe, 1992; Gastaldo et al., 1998). A fluctuation in humidity at La Val could have occurred between the upper and lower levels, possibly explaining the proportion in galling between levels. However, Moreno-Domínguez et al. (2021) interpret La Val specifically and the NE of the Iberian Peninsula in general as having a warm temperate climate with hot and dry summers during this period. Therefore, in the case of La Val, variations in temperature and humidity could be due not only to seasonal changes, but also to local changes over time and local habitat heterogeneity. Furthermore, the flora in levels from LV0 to LV10 are dominated by angiosperm leaf remains, which are by far the most herbivorized clade of plant hosts at La Val; the prevalence of galling at the upper levels could be due to tracking of particular, angiosperm host plants by galling insects. In contrast, ferns,

Table 3
Distribution of observed plant–insect interactions per sampled level of the Sariñena Formation from La Val fossil site. Interpretation of damage types based on Labandeira et al. (2007).

Plant–arthropod interactions			
Functional feeding group (FFG)	Damage-type (DT) (Labandeira et al., 2007)		SAMPLED LEVELS FROM LA VAL FOSSIL SITE (SARIÑENA FM.)
	Description	Code	
Hole feeding (HF)	*Circular perforations, < 1 mm in diameter.*	DT001	LV0-LV7, LVNH, LVNH2
	Circular perforations, 1 to 5 mm in diameter.	DT002	LV0-LV8, LV10, LVNH, LVNH2
	Polylobate perforations, 1 to 5 mm in diameter	DT003	LV0-LV7, LVNH
	Circular perforations, > 5 mm in diameter.	DT004	LV4
	Polylobate perforations, > 5 mm in diameter.	DT005	LV3, LV6
Margin feeding (MF)	*Curvilinear to rectilinear elongate perforations.*	DT007	LV2, LV3, LV5, LV6
	Parallel sided, rectilinear or curvilinear; length / width ratio > 2.5.	DT008	LV3, LV4
	Circular, shallow to deep excision of leaf margin, < 180 degrees of arc.	DT012	LV0-LV6,LV9, LVNH, LVNH2
	Excision of leaf apex, including primary vein.	DT013	LV0, LV4, LV6, LV8, LVNH
	Excision of leaf to a primary vein.	DT014	LV3, LV4, LV5, LV6, LVNH
	An excision that is deeply incised or expands toward a primary vein.	DT015	LV1, LV3, LV4, LV6
Skeletonization (S)	*Interveinal tissue removed; reaction rim poorly developed.*	DT016	LV3, LV6, LV8, LVNH
	Interveinal tissue removed; reaction rim well developed and/or thickened.	DT017	LV0
	At leaf base, between two or more basal veins.	DT056	LVNH
	Abrasion between parallel veins with ragged margin and reaction rim.	DT028	LVNH2
Surface feeding (SF)	*Removal or abrasion of surface tissues with a distinct polylobate reaction rim.*	DT030	LV2, LV3
	Removal or abrasion of surface tissues with a distinct circular to ellipsoidal reaction rim.	DT031	LV2
Piercing and sucking (P/S)	*Circular punctures < 2 mm diameter; central depression.*	DT046	LV2, LV4, LV6, LVNH
Galling (G)	*Circular or poly-lobate; minimal central tissue, surrounded by a wide rim of thick tissue.*	DT011	LV1, LV2, LV3, LV4, LV6
	Circular to ellipsoidal; avoiding major veins.	DT032	LV0, LV1, LV2, LV3, LV4, LV5, LV6, LV7
	Circular to ellipsoidal; on 1° veins.	DT033	LV0, LV1, LV3, LV4, LV5, LV6
	Circular to ellipsoidal; on 2° veins. Middle 70% of 0.5–1.1 mm wide mine.	DT034	LV0, LV1, LV2, LV3, LV4, LV6
	Circular, large fusanized core separated from distinct outer rim by 1 to 3 mm.	DT049	LV6, LV8
	On petiole.	DT055	LV1, LV2, LV3, LV5, LV6
	Elliptical, on 1° vein; x2 long as wide; elongate fusain core thinner than margin; small peripheral holes.	DT084	LV1, LV3
	Circular, columnar, deeply attached; thin outer wall; contents a chamber enveloped by amber or sediment.	DT116	LV2
	Ellipsoidal-spheroidal galls extending beyond leaf margin; with a botryoidal to roughened surface.	DT127	LV1, LV2, LV3, LV4
Incertae sedis (IS)	*Necrotic tissue occurring along the leaf-margin, usually ranging from 1 to 5 mm in thickness, but with a distinct reaction front abutting unaffected foliar tissue; sometimes showing signs of tearing or other abrasion.*	DT114	LV3

sphenophytes, and gymnosperms secondarily are much more abundant in the higher levels (LVNH and LVNH2) and, in general, insect herbivory is either wholly absent or very infrequent at these levels and on these plant hosts. This compositional change in the flora may also indicate an increase in humidity. Nevertheless, these changes in DTs may ultimately reflect the low sample sizes for LV7, LV8, LV9 and LV10 rather than environmental and climatic conditions changes in La Val.

The differences in the incidences of plant–insect interactions for each group of plants are also potentially due to the palatability of each type of leaf. While the leaves of angiosperms tend to be relatively soft and fleshy, the leaves of most gymnosperms and pteridophytes tend to be harder and more coriaceous. Toughness in extant plants has been associated with lower rates of insect herbivory (Clissold et al., 2009; Fuentealba et al., 2020), so given the abundance and diversity of the flora of La Val, it is likely that the insects more frequently selected the softer and easier to digest angiosperm leaves. However, the sample size of gymnosperms and ferns are smaller compared to that of angiosperms.

Betulaceae are the most abundant plant hosts at La Val (Moreno-Domínguez et al., 2015) and abundance of Betulaceae leaves can reach up to 70% of the total plant specimens within a level. Betulaceae leaves are mainly affected by hole feeding and galling in the lower levels (LV3–LV4, LV6), while in the uppermost level (LVNH), Betulaceae specimens do not exhibit many types of insect herbivory. This may be because Betulaceae leaves are scarce in LVNH and appear to be ecologically replaced by small leaves of the family Berberidaceae. Therefore, in LVNH, the change of DTs is likely caused by the turn over in floral composition of the angiosperm taxa. Unlike Betulaceae, Berberidaceae are generally afflicted by margin feeding, skeletonization and, particularly, by piercing and sucking herbivory (see Appendices A1–A3). According to Moreno-Domínguez et al. (2016), the plants found in LVNH were pioneer vegetation, which was dominated by ferns, such as *Acrostichum*, and sphenophytes. The floristic compositional change was likely the result of a change in depositional environment from crevasse splay to overbank deposits. These depositional environment changes also meant a potential change in the humidity.

5.2. Comparison with other Oligocene sites

According to Gunkel and Wappler (2015), studies of plant–insect associations from Oligocene deposits are rare (see Table 1), which makes

comparisons with coeval deposits limited. However, the Oligocene is an important time interval in Earth's history as it is characterized by sweeping climate change, with cooling and ultimately glaciation in the polar regions during Rupelian (Early Oligocene), followed by a warming event in the Chattian (Late Oligocene) (Zachos et al., 2001; Wappler, 2010). This climate change sets the stage to study plant–insect interactions during a period of rapid climate change and to compare La Val to other, spatiotemporally similar floras (Gunkel and Wappler, 2015).

We compare the set of ecological interactions of the La Val palaeoforest with the interactions of the Late Oligocene floras of Rott and Enspel (Germany). Both Rott (e.g, Wappler, 2010) and Enspel (e.g.,

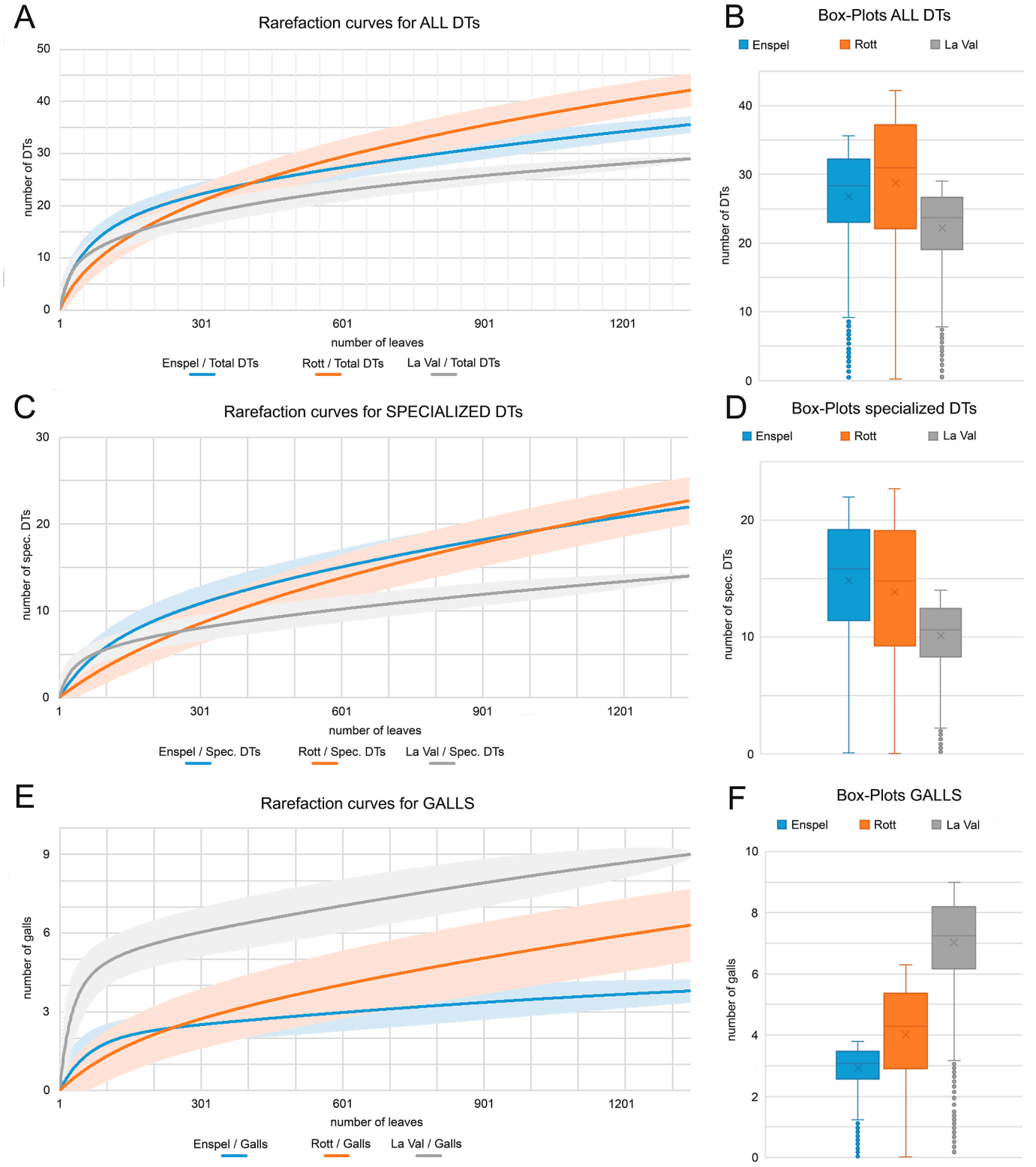

Fig. 7. Rarefaction curves and box-plots. A–B. For all DTs. C–D. For specialized damage. E–F. For galling. Data from Oligocene European palaeoforest of La Val, Enspel and Rott.

Gunkel and Wappler, 2015) are Chattian (Late Oligocene) sites situated in Central Europe (Germany) that have detailed surveys of plant–insect interactions. Enspel is an ancient volcanic lake from Late Oligocene, which is considered as a fossil-Lagerstätte. The vegetation was dominated by zonal assemblages of a mesophytic forest, although, a riparian forest was also present. The Enspel flora preserved the vegetation bordering the lake, as well as transported material from streams or small rivers that fed into the lake (Köhler and Uhl, 2014). According to Gunkel and Wappler (2015), 40.8% of the leaves at Enspel had at least one type of insect damage, and a total of 39 DTs, belonging to seven functional feeding groups. Hole feeding (55.7%), margin feeding (20.0%), skeletonization (15.7%) and galling (7.2%) dominated in this flora, while piercing and sucking (0.4%), mining and surface feeding (0.2% respectively) were scarce. The Rott fossil site also represents lacustrine deposits, which are interpreted as volcanic crater fillings (Wappler, 2010). The bordering mixed mesophytic forest was well-represented in this floral assemblage, as well as specimens from the belt of riparian forest surrounding the deposit (Kvacek and Walther, 2001). This post-volcanic–lacustrine floral assemblage developed when the volcanic activity ended in the region. Wappler (2010) found that 19.7% ±0.8 of the leaves at Rott included insect damage, with a total of 55 DTs for the deposit, belonging to six functional feeding groups. The plant–insect associations of the Rott flora were dominated by margin feeding (10%), hole feeding (6.5%) and galling (1.9%), followed by skeletonization (1.7%), surface feeding (1.5%) and, rarely, mining (1.2%). In general, there is some overlap when comparing the proportions of herbivorized leaves and richness of DTs at Rott and Enspel to La Val (see Appendices A1–A3).

There appears to be varying degrees of homogeneity among the plant–insect interactions of the European Late Oligocene floras. The diversity of all DTs and specialized damage (specialized DTs) are similar between the three European floras ($p = 0.108$),. La Val appears to have lower instances of DTs and specialized DTs compared to Enspel and Rott, although the richness of gall DTs at La Val is high (Fig. 7). La Val and Enspel also show similar proportions of insect herbivory within the floras (38.9% and 40.8%, respectively), whereas Rott (19.7%) is much lower. This variability may be caused by differences in the depositional environments, that would affect both the floral diversity and taphonomic conditions (Wappler, 2010), as is the case for the LVNH level in La Val, where in there was an ecological turnover of plant taxa due to differences in the depositional environments. Interestingly, we would expect that Rott (16.5–20.8 °C MAT; see Moreno-Domínguez et al., 2021) would have a greater proportion of insect-damaged leaves than Enspel (15.9–16-6 °C MAT; see Moreno-Domínguez et al., 2021) and La Val (15.5–18.9 °C MAT; see Moreno-Domínguez et al., 2021), as Rott was deposited under a warmer climate than the other two floras. It is well known that in modern and fossil studies, the increase of pCO_2, which is closely tied to an increase in temperature, generally leads to an increase in the amount of insect herbivory (Currano, 2013). This is due to the decreased foliar carbon:nitrogen ratio, forcing insects to eat more plant material to consume the necessary amount of nitrogen (e.g., Wappler, 2010). While these studies did not measure surface area removed by insect herbivores, it appears that Rott had much lower levels of insect herbivory than expected and this may reflect the unique composition of this flora.

Regarding the richness of DTs, La Val and Enspel have relatively lower values (28 and 39 DTs, respectively) than Rott (55 DTs). According to Wappler (2010), these results are expected because the Rott flora grew in a warmer climate, which is known to elevate the diversity of damage types compared to colder climates (i.e., Currano et al., 2010). In terms of galling occurrences, Rott has a greater richness of galls (8 DTs) than Enspel (3 DTs), but both floras are overall relatively unaffected by galling (Wappler, 2010; Gunkel and Wappler, 2015). La Val presents the highest abundance of galling and a modestly higher richness of galling (9 DTs) compared to Enspel and Rott (see Fig. 7 E and F). For example, while Myricaceae leaves at La Val present a 21% incidence of galling, this trend is not observed in the Rott flora (Wappler, 2010), wherein Myricaceae has only a 2% incidence of galling. Wappler (2010) found that increased galling is associated with subtropical aridity and a greater gall diversity has also been found in drier habitats (Fernandes and Price, 1992; Cuevas-Reyes et al., 2004, 2006; Moreno-Domínguez, 2018). This latter fact may imply drier climatic conditions for particular levels at La Val fossil site compared to Rott and Enspel; Moreno-Domínguez et al. (2021) hypothesize that the climatic conditions during the Late Oligocene of La Val would be similar to those of Rott, so that the differences in galling between these two palaeoforest do not seem to be linked to overall climatic differences, but perhaps to localized differences in humidity.

In addition, piercing and sucking appears to be more specialized at La Val compared to Rott or Enspel. Berberidaceae at La Val are modestly affected by piercing and sucking (23%) compared to all other groups of plants, where piercing and sucking does not exceed 6% per group. Berberidaceae is a group of bushy plants which are not present in Enspel or Rott (e.g., Wappler, 2010; Gunkel and Wappler, 2015). Only the megaflora of Enspel shows piercing and sucking damage, but in a very low percentage and on leaves of an unknown taxon (see Wappler, 2010). The high incidence of piercing and sucking in Berberidaceae in La Val suggests some degree of specialization by the insects of this FFG and their preference for this group of plants. Piercing-and-sucking damage likely corresponds to hemipteran feeding, as they have perforating and sucking mouthparts.

Finally, leaf mining is rare in Enspel (2 DTs) and absent in La Val, but very rich at Rott (12 DTs) (Wappler, 2010). Gunkel and Wappler (2015) stated that the mine diversity appears to be correlated with the leaf species diversity at Rott. However, these authors also note that abiotic environmental factors, changing climatic and atmospheric conditions, such as repeated local volcanic eruptions (e.g., Enspel), may have affected the diversities of plants, insects, and their ecological relationships. This may account for the differences in mining damage abundance between the three deposits, as changes in pCO_2 concentrations are known to decrease the abundance of leaf-mining herbivores and increase leaf-miner mortality (Stiling et al., 1999). Volcanic eruptions associated with Enspel could have increased global and local pCO_2 concentrations over short- and long-term episodes (e.g., Werner and Brantley, 2003; Burton et al., 2019; Fischer et al., 2019), which could have contributed to lower leaf-miner activity. More work is needed, however, to understand the low abundance of leaf mining at La Val, although it is likely that a combination of environment (see e.g., Faeth et al., 1981; Godfray, 1985; Hespenheide, 1991), taphonomy, and host plant diversity and taxonomy are responsible (see e.g., Knor et al., 2012).

6. Conclusions

The plant–insect associations at the Oligocene La Val site are abundant and diverse, and most interestingly, heterogeneous through time and among levels. In this survey of Oligocene plant–insect interactions, 30 types of insect herbivory were recorded, belonging to seven Functional Feeding Groups: hole feeding, margin feeding, skeletonization, surface feeding, galling, piercing and sucking, and incertae sedis. Galls are the richest and most abundant type of insect damage, followed by hole feeding. Importantly, galling, hole feeding and margin feeding mainly dominate in the lower levels (LV0–LV7), while hole and margin feeding and skeletonization dominate in the upper levels (LVNH and LVNH2). By contrast, piercing and sucking is relatively scarce throughout La Val, except in the LVNH level. These results can indicate an ecological turnover of the flora, likely due to changing depositional environments and/or changing climate. Finally, when compared to other Oligocene sites from Europe, Rott and Enspel, La Val had a relatively lower richness of damage types, except for galling DTs.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.palaeo.2021.110782.

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