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SPECIAL ISSUE—CELEBRATING WOMEN
IN PALEOBOTANY

SOUTHERN HIGH-LATITUDE PLANT-INSECT INTERACTIONS FROM THE MIOCENE OF TIERRA DEL FUEGO, ARGENTINA

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Premise of research. The Miocene Punta Basílica Beds (northeast of Tierra del Fuego, Patagonia, Argentina) preserved a flora rich in insect herbivory traces. Here we document its insect damage and compare it with three Miocene floras from northwestern Argentina (low-latitude San José and Palo Pintado) and New Zealand (high-latitude Hindon Maar). In addition, comparisons are established for insect damage observed on Miocene *Nothofagus* in the Punta Basílica flora and the New Zealand Hindon Maar, Double Hill, and Kaikorai floras.

Methodology. Plant-insect interactions were photographed and determined for 209 fossil leaves collected at the Punta Basílica locality. Leaves were censused for the presence/absence of functional feeding types.

Pivotal results. Six functional feeding groups and 26 damage types (DTs) were recognized: hole (seven DTs) and margin (five DTs) feeding, skeletonization (six DTs), piercing and sucking (two DTs), mining (three DTs), and galling (three DTs). *Nothofagus* spp. are the most affected members of the paleoflora. Both of the low-latitude paleofloras compared have lower percentages of damaged leaves than the high-latitude ones; hole and margin feeding, mining, and skeletonization are recognized at all floras. Hole and margin feeding and skeletonization are recognized on *Nothofagus* leaves and are the most common functional feeding groups; hole feeding on *Nothofagus* is more prominent at Hindon Maar and Kaikorai than at Double Hill and Punta Basilíca. Additionally, *Nothofagus* specimens from Hindon Maar and Punta Basílica have evidence of mining, whereas galling is observed only on the New Zealand leaves. The Punta Basílica *Nothofagus* specimens are the only ones with piercing and sucking.

Conclusions. Southernmost Miocene records of leaf herbivory worldwide and the first record from Argentine Patagonia are rich and comprise several functional feeding groups also observed in other Miocene paleofloras from the Southern Hemisphere. Clearly, multiple biotic and abiotic factors explain differences in the intensity of folivory. This report evidences the need for additional studies on herbivory at high-latitude floras.

Keywords: insect damage, leaves, Miocene, paleofloras, Southern Hemisphere.

Online enhancements: supplemental tables.

Introduction

One of the best-studied biological associations is plant-insect interactions (e.g., Bernays 1986; Herrera and Pellmyr 2002; Miller and Miller 2013), mainly because they have tremendous economic importance in agriculture (e.g., Voelckel and Jander 2014; Emani 2018). Remarkably, evidence of these interactions is recorded from soon after plants colonized the earth, and one indirect piece of evidence for the presence of herbivorous insects is the traces they left on fossils. The study of fossil traces (in general and on leaves in particular) is highly informative, as it increases knowledge on past insect diversity, interaction changes through time, past community dynamics, and even paleoclimate estimates and climate changes.

The first recorded evidence of plant-insect interactions is plant herbivory, which occurred in the middle Devonian (~400 mya; Labandeira et al. 2014; Pinheiro et al. 2016), and plant-insect interactions have been recorded worldwide, even from Antarctica in deep time (e.g., Scott and Taylor 1983; Chaloner et al. 1991; Scott 1991; Beck and Labandeira 1998; Labandeira 1998, 2002; Kellogg and Taylor 2004; Scott et al. 2004; McDonald et al. 2007; McDonald 2009; Labandeira et al. 2014; McLoughlin et al. 2015; Pinheiro et al. 2016). Furthermore, with the rise and diversification of the flowering plants during the Cretaceous and Tertiary, a sharp increase in insect herbivory can be observed (e.g., Labandeira et al. 2002; Currano et al. 2008; Labandeira and Currano 2013; Donovan et al. 2018). Occurrences in South America were briefly summarized by Robledo et al. (2018 and citations therein), and they revealed a rich fossil record of these associations in the region starting during the Paleozoic.

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In Argentina, plant-insect interactions are quite scarce. The oldest interactions correspond to coprolites and tunnels found in *Cuyoxylon* secondary xylem (Césari et al. 2012) collected at the Late Pennsylvanian–Early Permian San Ignacio Formation outcropping at San Juan Province, west-central Argentina. In Patagonia, the first margin feeding and oviposition scars were registered from the early Permian on *Glossopteris* leaves exhumed at the La Golondrina Formation (Santa Cruz Province; Cariglino and Gutiérrez 2011). Also in Patagonia, Gallego et al. (2014) recorded hole and margin feeding, surface abrasion, and oviposition on early Permian *Glossopteris*, *Cordaites*, and *Ginkgoites* leaves, while Aquino et al. (2015) mentioned the presence of nonmarginal feeding, skeletonization, oviposition, and bites on Permian sphenophyte and gymnosperm leaves.

Within the Triassic, Adami-Rodrigues et al. (2008) recognized 10 types of damage belonging to the functional feeding groups margin feeding, skeletonization, piercing and sucking, galling, and oviposition (sensu Labandeira et al. 2007) in the El Tranquilo Formation flora (Santa Cruz Province), whereas Lara et al. (2017) also registered margin, hole, and surface feeding; piercing and sucking; and oviposition damage in the typical *Dicroidium* flora of the Potrerillos Formation (Mendoza Province). There are no further records until the Maastrichtian-Paleocene (K-Pg) boundary.

In the K-Pg boundary of Chubut Province, Donovan et al. (2018) reported the presence of seven functional feeding groups (hole, margin, and surface feeding; skeletonization; piercing and sucking; mining; and galling); 50 damage types (DTs) were observed at the Cretaceous (Maastrichtian) Lefipán Formation, while only 39–48 were found in the Paleocene (Danian) Salamanca and Peñas Coloradas Formations. Additionally, Donovan et al. (2017) detected that although the number of insect damages decreased from the Maastrichtian to the Paleocene, there was a rapid recovery of interactions in the Danian.

Plant-insect associations in the early Eocene caldera lake deposits of the Huitrera Formation (Chubut Province) were documented by Wilf et al. (2005), Sarzetti (2010), and Aquino et al. (2015). Wilf et al. (2005) noticed a high diversity of DTs and feedings, while Aquino et al. (2015) identified only marginal and nonmarginal feeding and skeletonization on some angiosperm leaves from the same locality; however, their sampling was extremely low compared with that of Wilf et al. (2005). Sarzetti (2010) described the plant-insect associations at the early middle Eocene Río Pichileufú locality (Río Negro Province). The only known records of plant-insect interactions from the Patagonian Oligocene come from the Río Leona Formation (Santa Cruz Province) and are a hole feeding on a *Leguminophyllum* leaf and possible piercing and sucking scars on *Elatocladus* leaves (Césari et al. 2015).

In Neogene sediments, plant-insect interactions are quite scarce in Argentina (Robledo et al. 2018), and surprisingly, all come from northwestern localities of the country. Evidence of margin, surface, and hole feedings; mining; galls; skeletonization; piercing and sucking; and oviposition on pteridophytes (including an aquatic fern) and leaf impressions of monocots and dicots from the middle Miocene San José Formation (Catamarca and Tucumán Provinces) and middle Miocene to early Pliocene Palo Pintado Formation (Salta Province), outcropping at the Valles Calchaquíes, were recorded by Horn et al. (2011) and Robledo et al. (2015, 2016, 2018). Additionally, Robledo et al. (2015, 2016) defined new DTs (window feeding, piercing and sucking with stretch marks, and blotch leaf mines). For the lacustrine Mio-Pliocene Quebrada del Toro locality (Salta Province) flora, Robledo et al. (2020) reported damages (marginal and nonmarginal excisions and piercing and sucking) on horsetail, fern, and monocot fossils.

The main goal of this contribution is to introduce the first Miocene records of herbivory from Argentine Patagonia, which are also the southernmost Miocene records worldwide. The insect-plant interactions are evidenced on fossil leaves collected at the Punta Basílica locality, in the southern margin of San Sebastián Bay on the east coast of Tierra del Fuego Island (fig. 1). The Punta Basílica insect damages are compared with those of other known Southern Hemisphere Miocene floras situated at different southern latitudes and with those of Miocene *Nothofagus* floras of New Zealand.

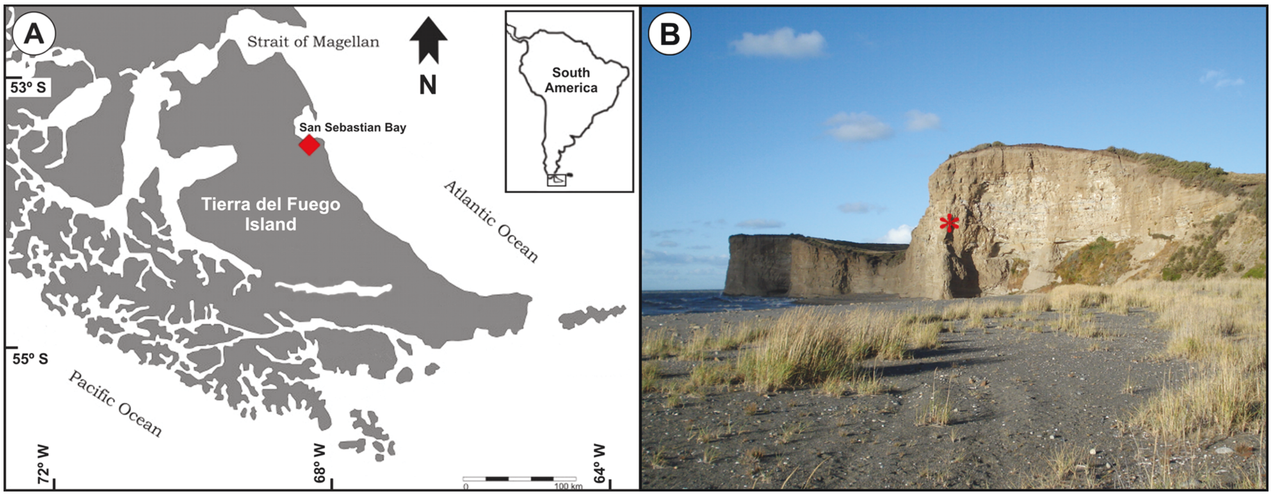

Fig. 1 *A*, Map showing the location, indicated by a diamond, of the studied paleoflora on the coast of San Sebastián Bay, Tierra del Fuego, Patagonia, Argentina. *B*, Landscape of the Punta Basílica Beds on coastal cliffs (ca. 150 m high). The asterisk indicates the main fossiliferous levels.

Material and Methods

Geological Setting and Age

The plant-insect interactions studied in this contribution come from the Punta Basílica Beds, currently considered part of the shallow marine delta-influenced Carmen Silva Formation (Olivero and López Cabrera 2020). These strata are exposed at the southern coast of San Sebastián Bay (lat. 53°17′S) on the east coast of Tierra del Fuego Island, Patagonia, Argentina (fig. 1*A*). These outcrops are also known as the "Barrancas de Carmen Sylva" (Dusén 1907), Arenisca Punta Basílica (Codignotto and Malumián 1981), and Cabo Viamonte Beds (Quattrocchio et al. 2018).

The sedimentary deposits are exposed on 90° cliffs that reach highs of about 150–200 m and mainly consist of laminated and massive mudstones with intercalate gravelly and massive sandstones (Quattrocchio et al. 2018). There is no consensus on the age of the Punta Basílica strata. Codignotto and Malumián (1981) assigned a late Miocene–Pliocene age to the lower strata of the cliff on the basis of the presence of the fossil bivalve *Barnea* cf. *ornata*. Quattrocchio et al. (2018) analyzed the sporomorph and dinoflagellate cyst content and suggested a Miocene age (Late Aquitanian to Serravallian/Tortonian) for the time of the deposition of the sediments of the Punta Basílica section. Furthermore, they noted that the palynofacies content, consisting of abundant palynomorphs, phytoclasts, and amorphous organic matter, reflects a high continental input to the basin. Recently, Olivero and López Cabrera (2020) considered these beds part of the Carmen Silva Formation and assigned an early Miocene age on a stratigraphic basis.

Material

Although the presence of a paleoflora at the Punta Basílica locality has been known since the beginning of the twentieth century (Dusén 1907), it was not until recently that the flora was the subject of a comprehensive study (Caviglia 2017). This is probably because it is very difficult to work at these outcrops. Unfortunately, there are very few places along the coast with access to the beach where the outcrops are exposed in the fossiliferous 90° cliffs (fig. 1*B*); this is exacerbated by the constant winds and the daily tides during which the cold ocean water reaches the cliffs, making it almost impossible to work at the locality.

We collected the fossils during two field seasons in 1991 and 1992. The fossils come from the clay and silt mudstone facies exposed at the cliffs (see Quattrocchio et al. 2018, fig. 3, for a geologic profile and the levels with leaves). The specimens are housed in the Paleontological Collection of the Universidad de Buenos Aires, Buenos Aires, Argentina, under the acronym BAFC-Pb17210–17404 (even though some specimens have several preserved leaves, they are numbered only with a single collection number). Fossil leaves are abundant, diverse, and relatively well preserved, mostly as impressions. The flora is composed exclusively of dicot angiosperms, except for a single fern specimen; the leaves were classified into the morphological types entire margin (E) and nonentire margin (NE), and, when possible, they were identified to the family, genus, or species level. The complete list of the taxa of the specimens studied here, their abundance, and associated insect damages are provided in table S1 (tables S1, S2 are available online).

Methods

The traces were studied using a Wild M5A dissecting microscope and photographed with a Panasonic Lumix camera (model 20X, full HD), available at the Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires. The insect damages (trace fossils) were tabulated following the terminology of Labandeira et al. (2007).

Results and Discussion

Punta Basílica Paleoflora and Its Insect Damage

In this study, 209 specimens were examined (49 dicots and 1 fern). The paleoflora was dominated by Nothofagaceae; other components were *Atherospermophyllum* sp. (Atherospermataceae), Cunoniaceae, Proteaceae, Sterculiaceae, and 27 NE leaf morphotypes, in addition to six E morphotypes.

The paleoflora shows a highly diverse pattern of herbivory supported by the occurrence of 26 DTs, defined within the six functional feeding groups of Labandeira et al. (2007). Of the 209 leaves, 96 (45.9%) are damaged (sometimes the leaves have only one instance of damage, while others have more than one); 57 show margin feeding and 48 hole feeding, 16 present skeletonization, and only 4 specimens each demonstrate galling and piercing and sucking (fig. 2). Specimens that do not have evidence of insect damage constitute 54.1% of the paleoassamblage and include Proteaceae, Sterculiaceae, morphotypes E2, E5, NE1, NE4, NE5, NE6, NE10, NE12, NE16, NE17, NE20, NE21, NE22, and NE23, and three species of *Nothofagus* (*N. densinervosa*, *Nothofagus* sp. 1, and *Nothofagus* sp. 2).

Six functional feeding groups were identified (fig. 2). Hole feeding is the most diverse functional feeding group with seven recognized DTs, followed by skeletonization with six DTs and by margin feeding with five DTs. Piercing and sucking (two DTs), mining (three DTs), and galling (three DTs) were also recorded, but the percentage of leaves presenting these types of damage is overall very low compared with the rest of the DTs. Piercing and sucking was detected on two specimens of *N. elongata* and on one specimen each of *N. magelhaenica* and *N. simplicidens*; mining was found on one specimen each of *Atherospermophyllum* sp., morphotype E1, and *N. simplicidens*; and finally, two NE14 specimens and one specimen each of NE24 and NE25 preserved concrete evidence of galls. The fern fossil has only margin feeding (table S1).

Composition of Leaf Damage

Six functional feeding groups sensu Labandeira et al. (2007) were recorded in the Punta Basílica paleoflora: (1) hole feeding, (2) margin feeding, (3) skeletonization, (4) piercing and sucking, (5) mining, and (6) galling.

1. Hole feeding (fig. 3A, 3C, 3E, 3G, 3J–3O*).* Seven hole-feeding DTs were identified: DT1, DT2, DT3, DT57, DT63, DT78, and DT148. DT1 and DT2 are circular perforations ranging from 0.5 to 4 mm, while DT3 is represented by polylobate perforations measuring between 2 and 5 mm. DT57 elliptical and triangular holes are found at the secondary vein divergence angles and the midvein and vary in size from 0.3 to 1.5 mm long and 0.2 to 0.8 mm wide. DT63, DT78, and

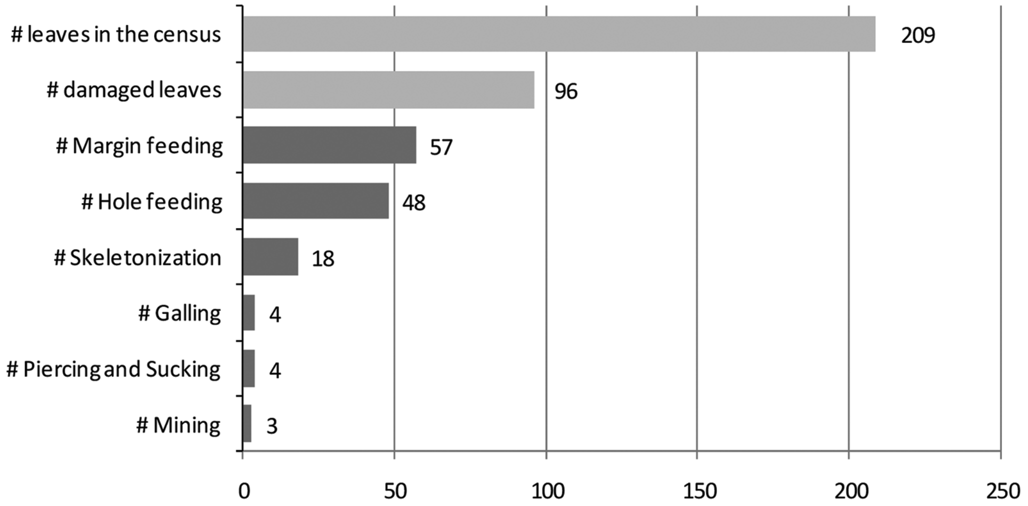

Fig. 2 Number of functional feeding groups for all leaves examined from the Miocene Punta Basílica flora, Tierra del Fuego, Patagonia, Argentina.

DT148 were each recorded only once. BAFC-Pb17373 shows damage consistent with DT63, as the feeding holes were observed at both sides of the middle vein. DT78 was observed on BAFC-Pb17322, in which the entire tissue of three intercostal areas was partially removed. Finally, DT148, consisting of round holes with a broad flange, was recorded on BAFC-Pb17227.

2. *Margin feeding (fig. 3*A–*3*D, *3*H–*3*J, *3*L, *3*M, *3*O*).* Of the six margin-feeding DTs, five were recognized in the paleoflora: DT12, DT13, DT14, DT15, and DT81. DT12, characterized by its circular shallow incisions on the margins, was the most common of all the margin-feeding damages, and it was quite variable in size (1–0.8 mm wide and 0.4–5.2 mm deep). DT12 was the only damage identified on BAFC-Pb17372 (fig. 3*I*), the only fern fossil specimen found in the flora. DT13 excision of the leaf apex was detected on several specimens. Leaf margin excisions that expand toward the primary veins are DT15; this DT was recorded as well. DT14 and DT81 are quite similar. DT14, indicated by an excision in the leaf reaching the primary vein(s), was found on BAFC-Pb17227 alone, while the excision of DT81 is considered to be almost circular (>180° arc).

3. *Skeletonization (fig. 3*B, *3*D, *3*F, *3*G, *3*J, *3*N*).* This is represented within the paleoflora by DT16, DT17, DT19, DT21, DT24, and DT61. DT16 and DT17 involve patches of interveinal tissue; in DT16, the edges of the patches are poorly defined, while in DT17, they are thick and well developed. DT24 features two ovoidal skeletonized areas close to the secondary veins. DT19, DT21, and DT61 were each recorded on single specimens. DT19 was observed on BAFC-Pb17391 and comprises several broad and elongated rectangular patches. Specimen BAFC-Pb17232 is an E morphotype, and it is the only specimen on which DT21 was detected. DT61 involves skeletonization at both sides of the midvein forming elongated zones; this DT was detected only on BAFC-Pb17279.

4. *Piercing and sucking.* This is represented by DT46 and DT47; these two DTs are quite similar, as both are represented by clusters of small punctures that are less than 2 mm in diameter. They differ in the presence of a depression (DT46) or of a dome (DT47) in the center. DT46 was noticed only on specimen BAFC-Pb17283.

5. *Mining (fig. 3*H*).* This functional feeding group has the most diverse insect damages, with 35 DTs; of those, merely three of them were distinguished in the paleoflora: DT90, DT99, and DT131. Interestingly, specimen BAFC-Pb17385, an E leaf morphotype, preserved DT90 and DT99. DT90 is represented by two mines; one mine originated on the leaf margin, curving toward the primary vein, and is approximately 2 cm long, and the other is slightly undulated and measures 1 cm. DT99 is a thick linear mine running parallel to the margin, and it is 1.5 cm long. DT131 is observed on a *Nothofagus* specimen (BAFC-Pb17331) and has the typical cigar shape.

6. *Galling (fig. 3*G*).* This functional feeding group was recognized by the presence of DT11, DT80, and DT49. DT11 was observed on two specimens that have small circular galls that measure between 1 and 1.5 mm; the center of the gall is dark and is surrounded by a well-defined rim. DT49, the only damage scored for BAFC-Pb17308, comprises a circular fusanized center encircled by a distinctive rim. BAFC-Pb17291 has only DT80, which is represented by small hemispherical galls that are less than 0.5 mm wide.

Comparisons among Southern Hemisphere Miocene Floras with Recorded Insect Damage

To fully understand Punta Basílica plant herbivory, we compare its raw herbivory data with that of the only three known Miocene Southern Hemisphere paleofloras showing plant-insect interactions, the Argentinean San José and Palo Pintado Formations and the New Zealand Hindon Maar (fig. 4). When comparing herbivorized paleofloras, there are multiple caveats. Some of them are related to sampling efforts, for example, disparate paleobotanical collections and sampling methods in the field and the dissimilarities between data obtained when working with

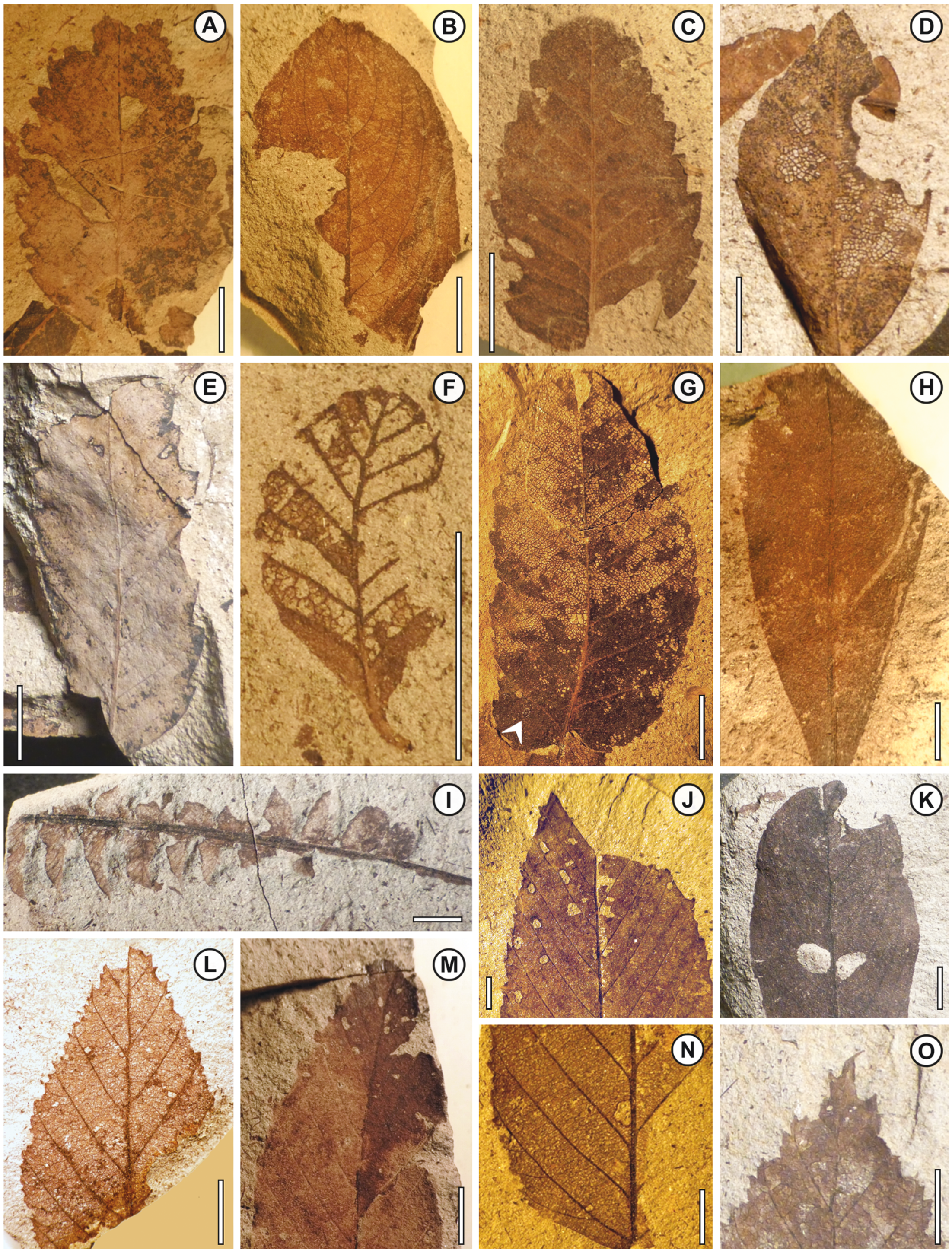

Fig. 3 Examples of different feeding damage types (DTs) at the Miocene Punta Basílica flora. *A*, BAFC-Pb17322: DT12 (margin feeding) and DT57 and DT78 (hole feeding). *B*, BAFC-Pb17223: DT14 (margin feeding) and DT17 (skeletonization). *C*, BAFC-Pb17319: DT2 and DT3 (hole feeding) and DT12 (margin feeding). *D*, BAFC-Pb17233: DT12 (margin feeding) and DT17 (skeletonization). *E*, BAFC-Pb17219: DT1, DT2, and DT3 (hole feeding) and DT12 (margin feeding). *F*, BAFC-Pb17232: DT17 and DT21 (skeletonization). *G*, BAFC-Pb17308: DT2 (hole feeding), DT17 (skeletonization), and DT80 (galling; arrowhead indicates a gall). *H*, BAFC-Pb17385: DT12 (margin feeding) and DT90 and DT99 (mining). *I*, BAFC-Pb17372: DT12 (margin feeding). *J*, BAFC-Pb17279: DT2 and DT3 (hole feeding), DT12 and DT13 (margin feeding), and DT61 (skeletonization). *K*, BAFC-Pb17222: DT57 (hole feeding). *L*, BAFC-Pb17296: DT1 and DT2 (hole feeding) and DT12 (margin feeding). *M*, BAFC-Pb17307: DT1, DT2, and DT3 (hole feeding) and DT12 (margin feeding). *N*, BAFC-Pb17296: DT3 (hole feeding) and DT16 (skeletonization). *O*, BAFC-Pb17317: DT1 and DT2 (hole feeding) and DT12 (margin feeding). Scale bars = 1 cm.

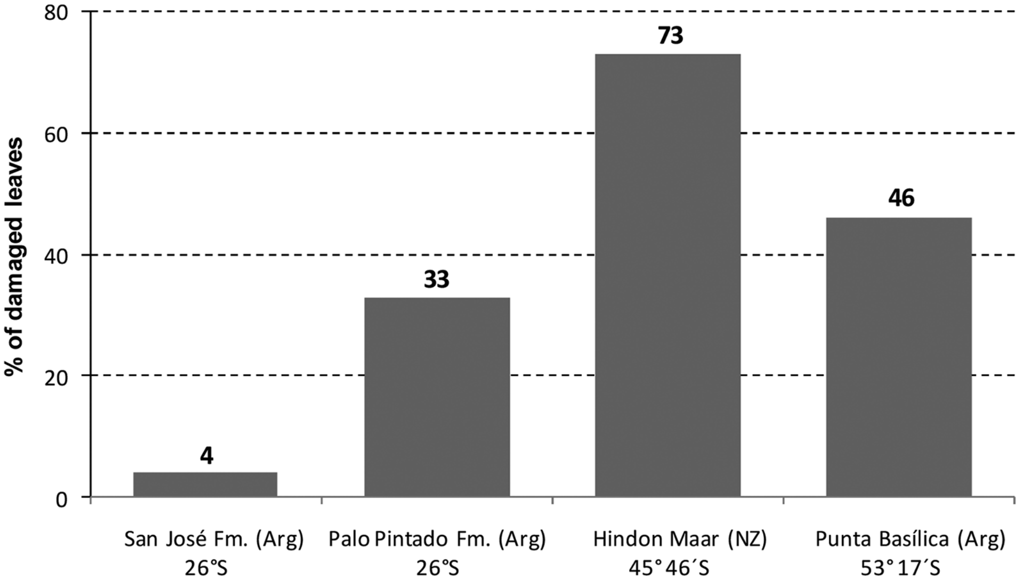

Fig. 4 Comparison of the percentages of damaged leaves from New Zealand (NZ) and Argentine (Arg) Miocene floras. Comparative data are from Möller et al. (2017) and Robledo et al. (2018). Fm. = Formation.

preexisting collections and data from field-censused collections. Others are related to the biology of the plant and insect communities, such as differences in the defenses of the plants, the abundance of insect herbivores, the location of the plants in the community, the diversity of feeding behaviors, and the specificity of herbivory, among others (Schachat et al. 2018). Finally, and most importantly, the paleofloras compared here exhibit differences in depositional environments and climate growing conditions mainly linked to the latitudinal position of the landmasses and the climate variations during the Miocene.

Considering the position of the landmasses, it is important to take into account that South America moved approximately 10° toward the equator and New Zealand moved more than 20° northward during the Cretaceous-Tertiary. Conversely, the position of the continents did not change dramatically during the Miocene, as the landmasses moved only 1° north; therefore, their positions were very similar to their current positions. Therefore, even if these floras are all from the Southern Hemisphere, their latitudinal positions are different (figs. 4, 5). Indisputably, major changes occurred in the climate at a global scale in the Miocene in general (Zachos et al. 2001) but particularly around ~14 Ma because of the expansion of the Antarctic ice sheet (Zachos et al. 2008). During a prolonged interval in the Miocene, New Zealand was a small oceanic landmass under a benign warm-temperate climate (Pole 2014), while southern South America (Tierra del Fuego Island was still part of the continent) was under the first incursion of temperate-cold to cold Antarctic waters (Shevenell et al. 2004) because of the Falkland (Malvinas) Current, initiated during the middle Miocene, the opening of the Drake Passage, and the establishment of the Antarctic Circumpolar Current. Consequently, depending specifically on when these floras grew during the Miocene (during brief periods of glaciations or in warm phases), they could represent very different local conditions. Wilf (2008) mentioned that it is critical to have exact chronological and stratigraphic information when studying insect damage in a paleoflora.

The Punta Basílica locality outcrops at San Sebastián Bay (lat. 53°17′S) on the east coast of Tierra del Fuego Island, Patagonia, Argentina, and preserves a subantarctic flora dominated by *Nothofagus* growing in cool and biseasonal weather with moderate rains all year long (Caviglia 2017). Herbivory was recorded in 45.9% (96) of the fossil leaves; 26 DTs within six functional feeding groups were recognized (fig. 2). The middle Miocene San José and the late Miocene–early Pliocene Palo Pintado floras outcrop at lat. 26°S in the Valles Calchaquíes, northwestern Argentina. Both floras are composed of fern and angiosperm leaf impressions; the first comprises 348 leaves, and 4% show insect damages represented by 9 DTs, whereas the second encompasses 856 impressions, and 33% have insect damage within 35 DTs (Robledo et al. 2018). The paleofloristic components of the San José flora indicate that the area was covered by wooded savannas under dry conditions. The paleoenvironment of the Palo Pintado flora was quite different, as it was mostly composed of hydrophilous communities growing under a warm and humid climate.

The early Miocene Hindon Maar Lagerstätte is located at lat. 45°46′S (paleolatitude 45°–50°S) near Dunedin, Otago, southern South Island, New Zealand (Möller et al. 2017). This paleoassemblage was rich in angiosperms (both monocots and dicots) and cycads and conifers; Nothofagaceae was the dominant group of the flora. The composition of the flora suggests that subtropical to warm-temperate conditions prevailed at the time of deposition. Data used for comparison comprise 24 morphotypes based on 584 fossil angiosperm leaves; of those, 73% show insect damages representing 87 DTs of all the functional feeding groups (Möller et al. 2017)

This comparison (fig. 4) shows that the San José and Palo Pintado (low latitude) floras have lower percentages of damaged

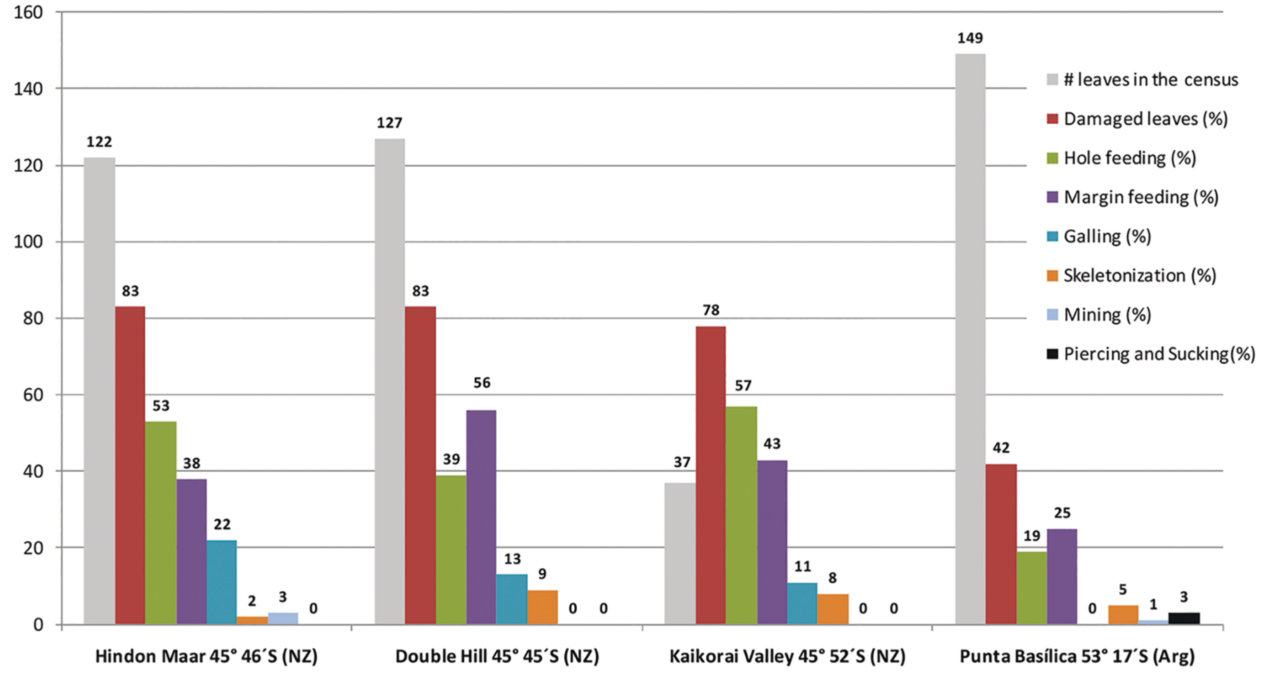

Fig. 5 Comparison of the *Nothofagus* censused leaves and the percentages of damaged leaves and functional feeding groups from New Zealand (NZ) and Argentine (Arg) Miocene floras. Comparative data are from Reichgelt et al. (2016) and Möller et al. (2017).

leaves than the Hindon Maar and Punta Basílica (high latitude) floras. These four floras show the presence of plant-insect interactions, and all have evidence of hole and margin feeding, mining, and skeletonization. In addition, for the Palo Pintado, Hindon Maar, and Punta Basílica floras, piercing and sucking and galling are recorded as well. Surface feeding is observed at Palo Pintado and Hindon Maar, while oviposition is documented only at Hindon Maar (Möller et al. 2017; Robledo et al. 2018); these functional feeding types are not recognized among the fossils of the Punta Basílica flora.

The differences in the frequency of herbivory among the paleofloras may be explained by the convergence of multiple factors, such as the very distinctive floristic components and their interaction with herbivorous insects, the environmental conditions in which the floras grew, and the climate conditions at the time of the deposition of the floras. The low-latitude San José flora was a xerophilous savanna growing in dry conditions, whereas the Palo Pintado flora was mostly a hydrophilous riverside and marsh forest plant community that developed under a warmer humid climate. These two floras are characterized by taxa such as Meliaceae, Fabaceae, Euphorbiaceae, and Anacardiaceae (Robledo et al. 2018). Both high-latitude floras treated here were dominated by *Nothofagus*; the Hindon Maar was a mixed broad-leaved rain forest including podocarps and cycads, monocots (*Ripogonum* and palms), and dicots such as Araliaceae, Myrtaceae, and Lauraceae (Möller et al. 2017) that developed in humid and moist conditions. The Punta Basílica flora was a typical subantarctic flora dominated by taxa with NEs such as *Nothofagus*, Proteaceae, and Cunoniaceae (although it lacked gymnosperms) growing in cool and biseasonal weather with moderate rains all year long (Caviglia 2017). Climate and latitude can easily explain the differences among the components of the floras and therefore the disparities in the frequency of insect damages recorded.

Insect Herbivory on Miocene Nothofagaceae

Nothofagus was dominant in the Punta Basílica paleoflora; 149 (~71%) of the 209 censused leaves corresponded to *Nothofagus* (table S2). Following Romero and Dibbern (1985) and Caviglia (2017), we identified *N. australis*, *N. densinervosa*, *N. elongata*, *N.* “*dicksoni*,” *N. magelhaenica*, *N. serrulata*, *N. simplicidens*, *N. variabilis*, *N. integrifolia*, and three *Nothofagus* spp. *Nothofagus elongata*, *N. simplicidens*, *N. variabilis*, and *N. integrifolia* are the most abundant species within the paleoassamblage. Surely, *Nothofagus* species were the most affected by insect damage of all the components of the Punta Basílica flora, as five functional feeding groups were observed (hole and margin feeding, skeletonization, mining, and piercing and sucking). Interestingly, there are significant differences among the *Nothofagus* species in the intensity of the damage and the presence/absence of DTs.

Nothofagus elongata, comprising 36 fossils, is the dominant species, and 40% of the leaves show damages that include several DTs of the hole, margin, and surface feeding and piercing and sucking functional feeding types. *Nothofagus integrifolia* is represented by 21 specimens, and 90% of them have signs of insect damage; the functional feeding groups hole and margin feeding are highly diverse in this species, and only three specimens also have skeletonization. *Nothofagus magelhaenica* comprises 16 specimens, and 70% have significant, variable damage. *Nothofagus variabilis* and *N. simplicidens* are represented by

27 and 26 specimens, respectively, and are the most abundant in the paleoflora after *N. elongata*; remarkably, only 20% of the leaves of these species have insect traces. Both species mainly present margin feedings (DT12). But on one specimen of *N. simplicidens*, hole feeding (DT2 and DT3) and mining (DT131) were recorded; the last DT was observed only on this species in the whole paleoflora. For *N. variabilis*, hole feeding (DT2) and skeletonization (DT16) were counted as well. Only seven specimens correspond to *N. australis*, and 40% of them have insect damage, including hole (DT1) and margin (DT12) feeding and skeletonization (DT19). *Nothofagus* "*dicksoni*" and *N. serrulata* are singletons; the first has only hole feeding (DT2), while in the second, margin feeding (DT12 and DT15) was detected. Curiously, *N. densinervosa* (eight specimens total), *Nothofagus* sp. 1, and *Nothofagus* sp. 3 do not show any type of insect damage, while other species such as *N. elongata*, *N. magelhaenica*, and *N. integrifolia* were greatly affected (fig. 5).

In addition to the Hindon Maar plant-insect interactions studied by Möller et al. (2017), Reichgelt et al. (2016) investigated insect herbivory on Miocene Nothofagaceae leaf impressions at two other New Zealand localities. Both localities, Double Hill and Kaikorai, belong to the Dunedin Volcano Group, Otago, South Island, and are considered to be mid–upper Miocene in age. These paleofloras were dominated by Nothofagaceae; in Double Hill, 127 leaves were identified as *Nothofagus* (representing 70%–80% of the flora), whereas only 35 were recognized in the Kaikorai flora. Reichgelt et al. (2016) found 37 DTs, including 21 hole and margin feeding types, 3 types of skeletonization, 4 types of surface feeding, 8 types of galling, and 1 unknown. Because the Punta Basílica flora was also dominated by *Nothofagus*, comparisons were established to evaluate herbivory of the same taxon from two distanced regions. When comparing the herbivory of *Nothofagus* (fig. 5), it is clear that hole and margin feeding and skeletonization are the most common functional feeding groups for *Nothofagus* leaves. Hole feeding is more prominent in Hindon Maar and Kaikorai than in Double Hill and Punta Basílica. Hindon Maar and Punta Basílica have evidence of mining. Galling is present only in the New Zealand floras, whereas Punta Basílica is the only one with piercing and sucking (fig. 5). Disparities among the functional feeding groups observed on Miocene *Nothofagus* can be due to several causes, including abiotic (such as geographical position—New Zealand is almost 9° north of Tierra del Fuego—the timing of deposition, when during the Miocene these floras grew, and biases during sampling and in preservation during the fossilization process) and biotic (such as different folivory resistance between the New Zealand and South American *Nothofagus* species and variations in the complex plant-insect interactions among forests of different species of *Nothofagus*) factors.

Conclusions

On the basis of the discussion presented above, we are aware that the results of this contribution are preliminary and that there are several factors that can be misleading (e.g., lack of exact sediment dating, differences in sample sizes, differences in environmental, geographical, and ecological conditions, etc.). Nevertheless, we present for the first time the southernmost Miocene records of herbivory worldwide and the first record from the Miocene of Argentine Patagonia. The Punta Basílica leaf paleoassamblage is diverse in foliar morphotypes (209), ~46% of which exhibit evidence of folivory. Insect damage includes several functional feeding groups also observed in other Miocene paleofloras from the Southern Hemisphere. Six functional feeding groups and 26 DTs were recognized: hole (seven DTs) and margin (five DTs) feeding, skeletonization (six DTs), piercing and sucking (two DTs), mining (three DTs), and galling (three DTs). *Nothofagus* spp. are the most affected members of the paleoflora.

The San José and Palo Pintado low-latitude paleofloras have lower percentages of damaged leaves than the Hindon Maar and Punta Basílica high-latitude ones; hole and margin feeding, mining, and skeletonization are recognized at all floras. Hole and margin feeding and skeletonization are recognized on *Nothofagus* leaves and are the most common functional feeding groups; hole feeding on *Nothofagus* is more prominent at Hindon Maar and Kaikorai than at Double Hill and Punta Basílica. Additionally, *Nothofagus* specimens from Hindon Maar and Punta Basílica have evidence of mining, whereas galling is observed only on the New Zealand leaves. The Punta Basílica *Nothofagus* specimens are the only ones with piercing and sucking. There is no doubt that southern forest angiosperms hosted a diverse group of herbivores during the Miocene; however, we need additional studies on folivory at high-latitude floras (past and present), together with precise ages, to further understand herbivory during such a critical time in the history of earth and its role in paleoecosystems.

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