



# Before the ‘Big Chill’: Patterns of plant–insect associations from the Neogene of Iceland



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## ABSTRACT

Iceland is the only known terrestrial place in the subarctic North Atlantic providing a fairly continuous sedimentary and plant fossil record over the past 15 million years. While the basic palaeobotanical framework of this pattern has been well established during the last decade, less attention has been paid to the abundant insect traces on fossil leaves/leaflets. Here, we assess the diversity and frequency of insect herbivory on 4349 fossil angiosperm leaves/leaflets from six plant-bearing sedimentary formations exposed at 18 localities. By combining analyses of environmental factors, species interactions, ecology, biogeography, and the geological history, our results demonstrate how patterns of herbivory have changed over time in relation to temperature fluctuations that profoundly influenced levels of insect-mediated damage diversity and frequency. In addition, higher structural complexity, particularly the establishment of species-rich herb layer communities seems to have positively influenced the structure of insect communities in early late Miocene palaeoforests of Iceland.

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## 1. Introduction

Islands improve our understanding of the ecology and evolution of communities in general and have been model systems of choice for biologists ever since Wallace and Darwin (e.g. Warren et al., 2015). They normally provide excellent settings in which to make predictions about community assembly. Particularly, vegetation characteristics, such as the diversity and productivity of plants, which strongly influence the distribution and abundance of animals. Species-rich plant communities thriving in diverse habitats provide a heterogeneous resource base that allows a great number of herbivorous insect species to coexist, an effect that can cascade up to higher trophic levels (e.g. Brose, 2003; Haddad et al., 2009, 2011; Knops et al., 1999; Massad and Dyer, 2010; Siemann et al., 1998). As a result, today, food webs incorporating plants, phytophagous insects, and carnivorous insects account for up to 75% of non-microbial global terrestrial biodiversity (Price, 2002). Thus, ecosystem process rates such as herbivory may be altered significantly under climate change (e.g. Cornelissen, 2011). Subsequent studies have documented direct correlation between the quantity and diversity of interactions caused by insects and the temperature, also considering the effects

of pCO<sub>2</sub> concentration (e.g. Stiling and Cornelissen, 2007; Tuchman et al., 2002; Zavala et al., 2013). A recent study in Panama, comparing the past interactions with present herbivory pattern of multiple current sites, has confirmed that (specialized) interactions are robust indicators for changes in herbivory (Carvalho et al., 2014). Thus, the response of plants and insect herbivores to climate changes can be interpreted by analyzing insect herbivore damage preserved on fossil leaves, and used to provide feedbacks between assembly dynamics and community structures (e.g. Currano et al., 2008, 2010; Knor et al., 2012; Wappler and Denk, 2011; Wappler et al., 2009, 2012; Wilf and Labandeira, 1999; Wilf et al., 2001). Nevertheless, additional studies are required to provide a comprehensive overview of the evolution of different forms of interactions and their importance in various ecosystems around the globe and at different geological time frames.

As such, Iceland seems to be an “ideal island” as it is the only known terrestrial place in the subarctic North Atlantic providing a fairly continuous sedimentary record over the past 15 million years coupled with an extensive palaeobotanical record (summarized in Denk et al. (2011)), a moderate palaeoentomological record (Wappler et al., 2014), but also an until now unrecovered record of insect herbivore damage. Here, we assess the diversity and frequency of insect herbivory on 4349 fossil angiosperm leaves/leaflets from six plant-bearing sedimentary formations exposed at 18 localities (Table 1). The availability of such data from

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**Table 1**  
Fossil leaf sites from the Neogene of Iceland.

Age (Ma)	c. 15 <sup>a-e</sup>	c. 12 <sup>c,f,g</sup>	c. 10 <sup>c</sup>	9–8 <sup>c</sup>	7–6 <sup>h,i</sup>	4.4–3.8 <sup>j-l</sup>
Formation/beds/biozones	Selárdalur-Botn Fm.	Brjánslækur-Seljá Fm.	Tröllatunga-Gautshamar Fm.	Skarðsströnd-Mókollsdalur Fm.	Hreðavatn-Stafholt Fm.	Tjörnes beds (Mactra Zone)
Plant macrofossil localities	Þórisliðarfjall	Surtarbrandsgil, Seljá	Margrétarfell, Gautshamar, Húsavíkurkleif, Tröllatunga, Hólar	Hrútagil, Fell	Stafholt, Laxfoss, Veðilækur, Brekkuá, Hestabrekkur, Fifudalur, Þrimildalur	Skeifá
For geological and palaeontological background	Grímsson and Denk (2005), Grímsson et al. (2007), Denk et al. (2005, 2011)	Friedrich (1966), Denk et al. (2005, 2011), Grímsson (2007b)	Denk et al. (2005, 2011)	Friedrich et al. (1972), Denk et al. (2005, 2011)	Grímsson (1999, 2002, 2007a), Denk et al. (2005, 2011)	Bárðarson (1925), Strauch (1963), Símonarson and Eiríksson (2008), Denk et al. (2011)
Number of plant macro- and microfossil taxa <sup>m</sup>	21 woody- and 2 herbaceous angiosperms, 8 conifers, 1 liana, 2 ferns, and 1 incertae sedis	33 woody- and 4 herbaceous angiosperms, 1 liana, 1 <i>Ephedra</i> , 9 conifers, 8 spore plants, and 10 incertae sedis	34 woody- and 31 herbaceous angiosperms, 2 lianas, 1 <i>Ginkgo</i> , 7 conifers, 11 spore plants, and 13 incertae sedis	19 woody- and 5 herbaceous angiosperms, 9 conifers, 8 spore plants, 1 incertae sedis	13 woody- and 6 herbaceous angiosperms, 6 conifers, 4 spore plants, 1 incertae sedis	24 woody- and 43 herbaceous angiosperms, 6 conifers, 17 spore plants, 9 incertae sedis
Dominant macrofossils observed (leaves)	<i>Fagus</i> , <i>Tilia</i>	<i>Acer</i> , <i>Alnus</i> , <i>Betula</i> , <i>Magnolia</i> , Rosaceae, <i>Salix</i>	<i>Acer</i> , <i>Alnus</i> , Juglandaceae, <i>Rhododendron</i>	<i>Acer</i> , <i>Betula</i> , <i>Fagus</i> , <i>Pterocarya</i>	<i>Acer</i> , <i>Alnus</i> , <i>Betula</i> , <i>Salix</i>	<i>Alnus</i> , <i>Potamogeton</i> , <i>Rhododendron</i> , <i>Salix</i> , <i>Sorbus</i>
Vegetation types <sup>m</sup>	Backswamp-, levee-, foothill-, montane-, ravine-, and rocky outcrop forests	Backswamp forests and temporally flooded lake margins, levée forests and well-drained lake margins, well-drained lowland forests and lake margins, rocky outcrop-, foothill-, ravine-, and montane forests	Aquatic vegetation, backswamp forests and temporally flooded lake margins, levée forests and well-drained lake margins, well-drained lowland forests and lake margins, rocky outcrop-, foothill-, montane-, and ravine forests, and meadows and shrublands	Temporally flooded lake margins, well-drained lowland forests and lake margins, foothill-, montane-, and rocky outcrop forests, and meadows and shrublands	Aquatic- and swamp vegetation, backswamp forests and temporally flooded lake margins, levée forests and well-drained lake margins, well-drained lowland forests and lake margins, foothill-, montane-, ravine-, and rocky outcrop forests, and meadows and shrublands	Aquatic- and swamp vegetation, backswamp forests and temporally flooded lake margins, levée and well-drained lowland forests and lake margins, montane-, foothill-, and rocky outcrop forests
Climate signals of fossil floras <sup>m,n</sup>	Warm temperate, fully humid climate with hot or warm summers (Cfa, Cfb)	Warm temperate, fully humid climate with hot or warm summers (Cfa, Cfb)	Warm temperate, fully humid climate with warm summers (Cfb). Increase in Cfc- and Dfc-tolerant taxa.	Warm temperate, fully humid climate with warm summers (Cfb).	Warm temperate, fully humid climate with warm summers (Cfb). Increase in Dfc-tolerant taxa.	Warm temperate, fully humid climate with warm summers (Cfb cool variant). Increase in Cfc-, Dfc-, and ET-tolerant taxa.
MAT (°C) <sup>m</sup>	7–9.4	9.3–12.5	5.4–7.4	5.9–7.4	3.4–5.9	4.1–7.4
No. leaves in census	249	1612	1095	498	699	196

<sup>a</sup> See also Moorbath et al. (1968).

<sup>b</sup> See also Kristjansson et al. (1975).

<sup>c</sup> See also McDougall et al. (1984).

<sup>d</sup> See also Hardarson et al. (1997).

<sup>e</sup> See also Kristjansson et al. (2003).

<sup>f</sup> See also Friedrich (1966).

<sup>g</sup> See also Grímsson (2007b).

<sup>h</sup> See also Jóhannesson (1975).

<sup>i</sup> See also McDougall et al. (1977).

<sup>j</sup> See also Aronson and Saemundsson (1975).

<sup>k</sup> See also Albertsson (1976).

<sup>l</sup> See also Albertsson (1978).

<sup>m</sup> Data taken from Denk et al. (2011).

<sup>n</sup> Data taken from Denk et al. (2013).

Iceland now provides an excellent chance to explore whether coupling evolutionary and ecosystem dynamics can lead towards a better understanding of the processes shaping past and modern ecosystems and document shifts in trophic structures over geological time.

## 2. Material and methods

### 2.1. Palaeobotanical data

In recent monographic works on the late Cenozoic plant fossils of Iceland, 68 taxa comprising dicot macrofossils were described, and their systematic affinities determined (e.g. Denk et al., 2005, 2011;

Grímsson and Denk, 2005; Grímsson et al., 2007). The age of the sedimentary formations, and hence of the fossil assemblages, is well constrained due to their position between basalts. Absolute K-Ar and Ar-Ar dates are available for most bracketing basalts. Remaining ages have been constrained by means of palaeomagnetostatigraphic correlation by Friedrich (1966), Moorbath et al. (1968), Aronson and Saemundsson (1975), Jóhannesson (1975), Kristjansson et al. (1975), Albertsson (1976), McDougall et al. (1977), Albertsson (1978), McDougall et al. (1984), Hardarson et al. (1997), Kristjansson et al. (2003), and Grímsson (2007b) (summarized in Denk et al. (2011)). MAT values from Denk et al. (2011) are based on lower limits of mean annual temperatures for potential modern analogues of fossil plant

species recorded from Iceland. The limit shown here indicates the four taxa defining the four warmest  $\text{MAT}_{\text{min}}$  values (i.e. the four most-cold sensitive taxa) in each formation. For a complete list of potential modern analogues see Appendix 13.1 in Denk et al. (2011). Also, palaeoclimate estimates by Denk et al. (2011, 2013) used modern distribution ranges of potential modern analogues of fossil taxa transferred into “Köppen signatures”. The material investigated originates from six plant-bearing sedimentary formations exposed at 18 localities (Fig. 1; Table 1) and combines material from historical collections stored in the Swedish Museum of Natural History, Stockholm (S), and the Icelandic Institute (Museum) of Natural History (IMNH), Reykjavík, with material collected during several new field campaigns (1998–2010). Unregistered specimens from the IMNH collections are marked with the collection letters (F, HB, HP, HU, TA) and numbers given by their respective collector. A single specimen is from the private collection of Dr. J. Vinther and marked as such.

## 2.2. Insect damage data

We analyzed 4349 fossil angiosperm leaves/leaflets from six well-dated stratigraphic levels. All these leaves were examined for damage caused by arthropods and the type of damage was categorized based on its position, size and morphology following the method of Labandeira et al. (2007). The different damage types (DTs) were then classified into one of eight functional feeding groups (FFGs): hole feeding (HF), margin feeding (MF), skeletonization (S), surface feeding (SF), galling (G), mining (M), piercing and sucking (PS) and oviposition (O) as described by Labandeira et al. (2002a, 2002b, 2007). To date, over 290 fossil DTs have been identified (C.C. Labandeira, pers. Comm., 2014). Each foliar element was photographed using a Canon EOS 350D camera with a Canon EF-S 60 mm f/2.8 macro lens or a Nikon Coolpix E4500. All photographs were optimized using Adobe Photoshop CS6 and Adobe Lightroom 5.

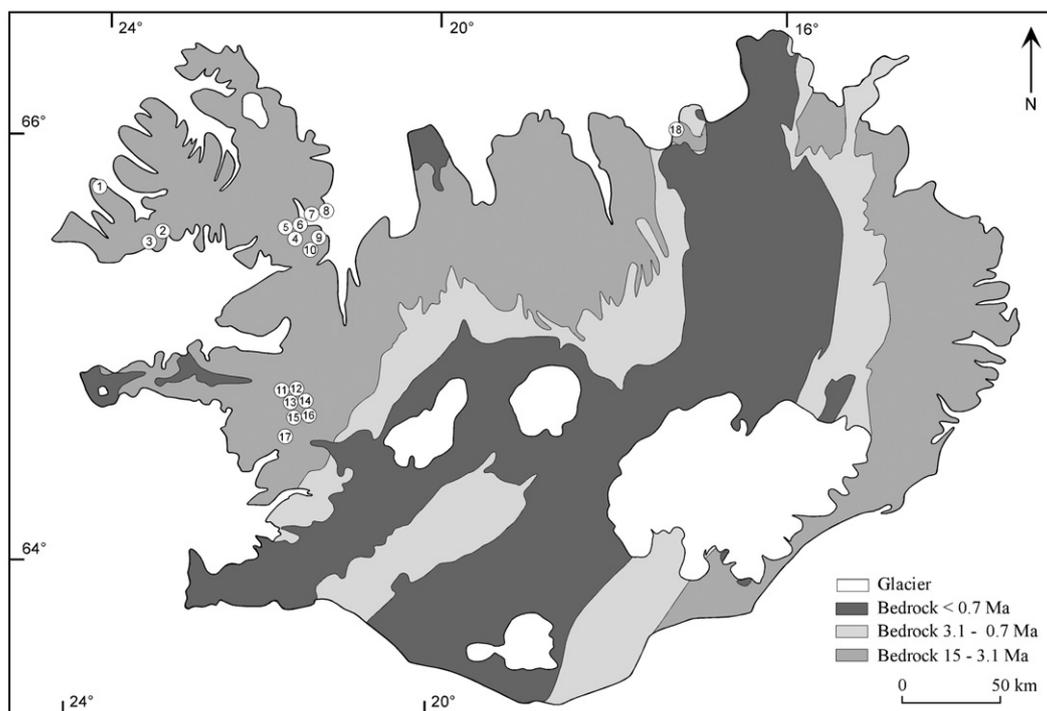
Quantitative analyses of insect damage were done using R version 3.1.0 ([www.r-project.org](http://www.r-project.org)) with the package ‘nlme’ (Pinheiro et al., 2014). For damage diversity analyses, sample size was standardized by selecting random subsets of foliar elements without replacement and calculating the damage diversity for the subsample. Subsets of the data were subjected to rarefaction using an analytic method detailed below, which extends the solution found by Wappler et al. (2012) to cases where individuals may belong to multiple classes and allows the explicit reconstruction of probability distributions for the rarefied sample (Gunkel and Wappler, 2015). This process was repeated 5000 times, and the results were averaged to obtain the standardized damage diversity for the six Neogene fossiliferous sedimentary formations.

Herbivore densities or damage metrics were the response variables used in the model, with percent abundance in the flora. The significance of the effect terms was tested using  $\text{Chi}^2$ -tests (command “anova” based on sequential models of “type I”). The data were transformed when necessary to comply with the assumptions of variance homogeneity (Bartlett test) and normal distribution (Shapiro-Wilk test) of the residuals, and quasi-Poisson distribution was assumed when transformation was unsuccessful. Tree diversity and herb diversity were expressed by the Shannon–Wiener diversity index ( $H'$ ).  $H'$  incorporates species richness as well as relative abundances of species (Maurer and McGill, 2011).

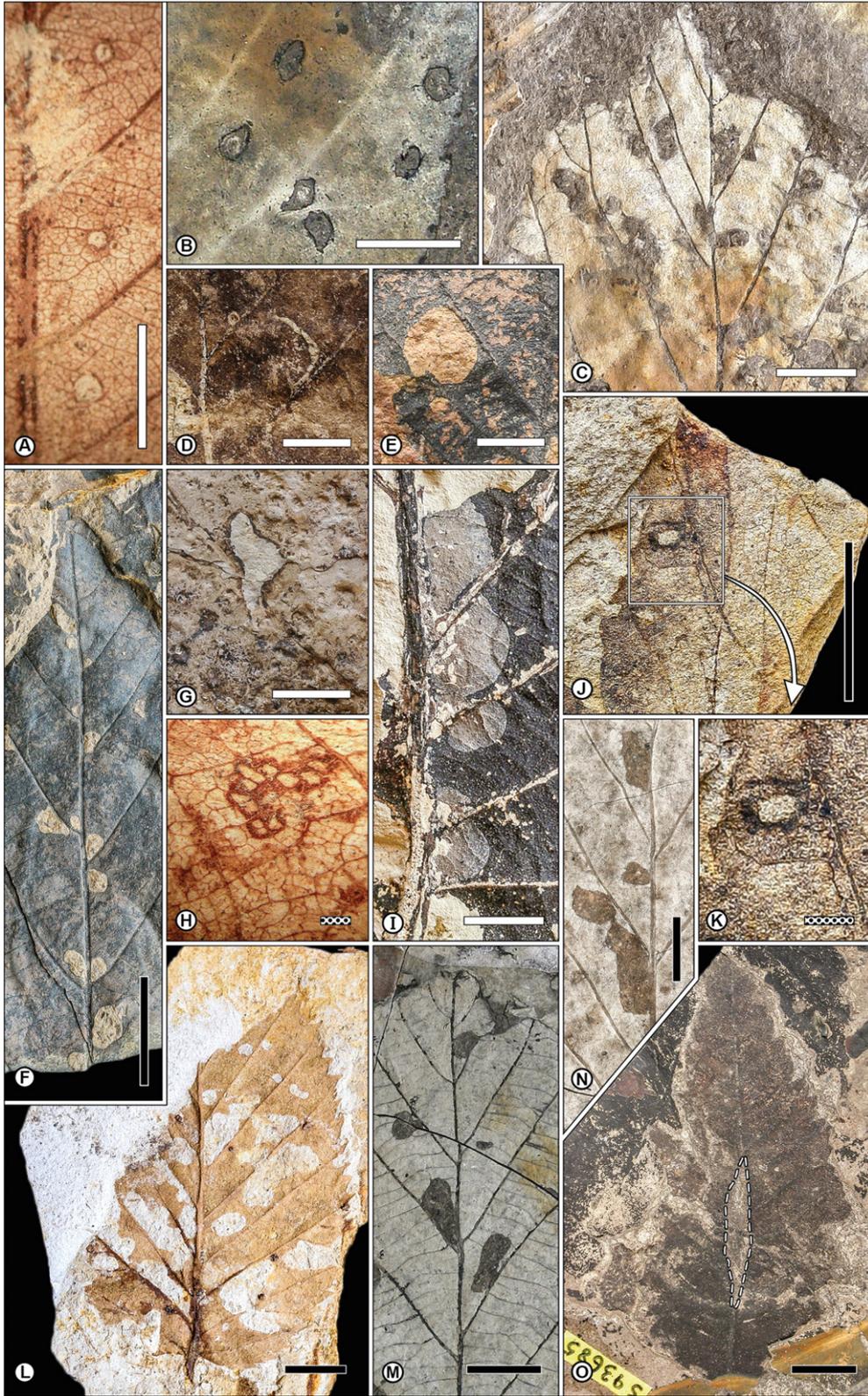
## 3. Results

### 3.1. Overall patterns of herbivory

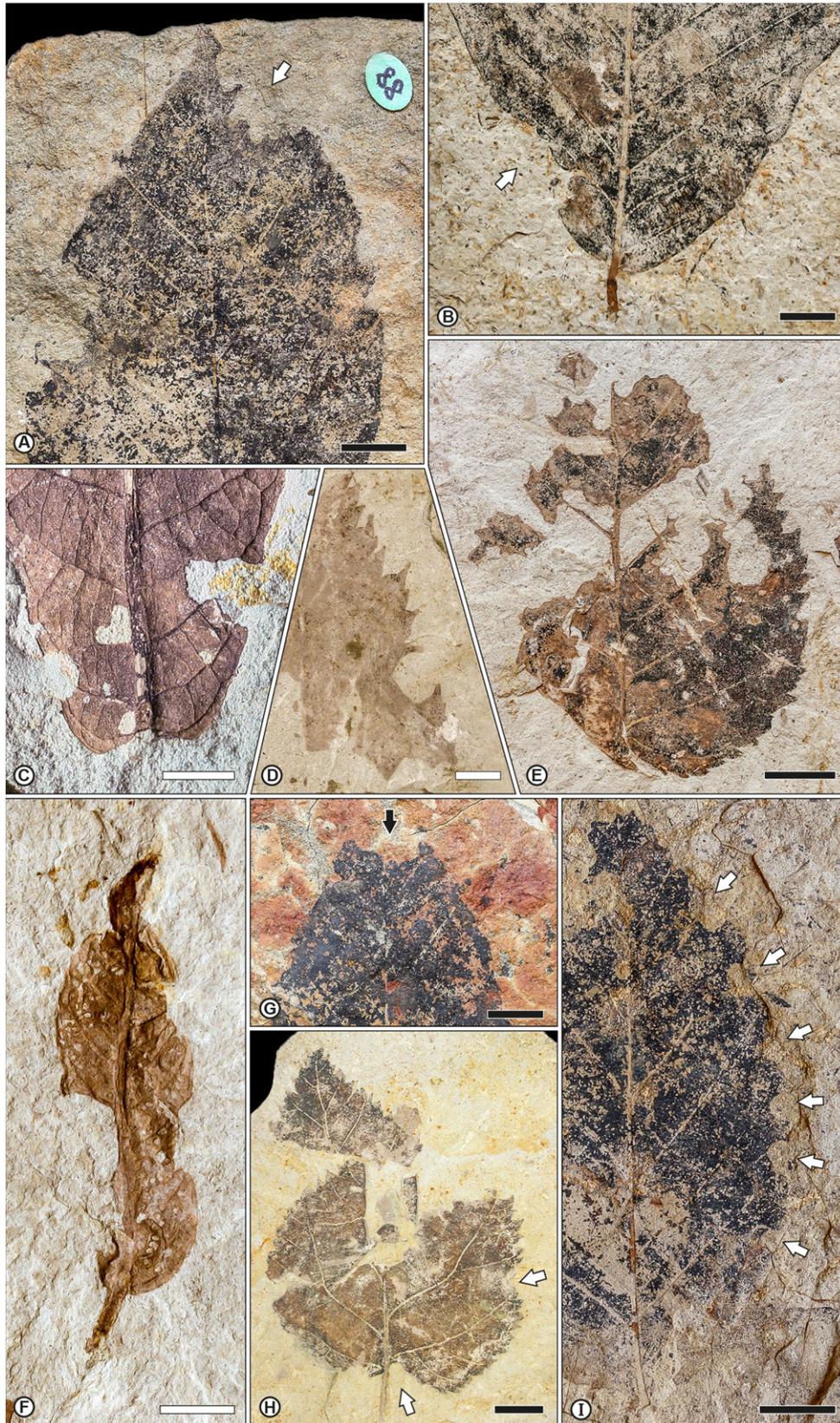
In total, we documented 47 DTs representing eight FFGs. The FFGs comprise external foliage feeding (hole, margin, skeletonization, and surface feeding), piercing-and-sucking, oviposition, galling, and mining on 42 plant hosts, occurring with a frequency of 5.3 to 24.1% of total herbivory (Table S1–S6). Of the 4349 leaves/leaflets, 680, or 15.63%,



**Fig. 1.** Schematic map showing bedrock geology of Iceland. Geological background modified after Jóhannesson and Sæmundsson (1989). Localities with leaf fossils investigated for this study are marked with numbers: (1) Þórisliðarfjall in Selárdalur (Selárdalur–Botn Formation, 15 Ma, early middle Miocene); (2) Surtarbrandsgil at Brjánslækur and (3) Seljá in Vaðalsdalur (Brjánslækur–Seljá Formation, 12 Ma, mid-middle Miocene); (4) Hólar in Miðdalur, (5) Grýlfoss at Tröllatunga, (6) Húsavíkurkleif in Steingrímsfjörður, (7) Kokkálsvík at Gautshamar, (8) Margrétarfell on Drangsnæs (Tröllatunga–Gautshamar Formation, 10 Ma, early late Miocene); (9) Fell in Kollafjörður and (10) Hrutagil in Mókollsdalur (Skarðsströnd–Mókollsdalur Formation, 9–8 Ma, early late Miocene); (11) Þrímilsdalur at Hreðavatn, (12) Fífudalur at Hreðavatn, (13) Hestabrekku at Hreðavatn, (14) Brekkú at Hreðavatn, (15) Laxfoss at Norðurá, (16) Veiðilækur at Norðurá, (17) Stafholt at Norðurá (Hreðavatn–Stafholt Formation, 7–6 Ma, mid Late Miocene); (18) Skeifá on Tjörnes (Mactra Zone, 4.0–3.6 Ma, early middle Pliocene). For more detailed locality maps see Denk et al. (2011).



**Fig. 2.** Hole feeding traces on leaves/leaflets from the Neogene of Iceland. (A) DT1 on *Alnus* sp. (HB\_120\_1). (B) DT2 on an unidentified Dicot. (S093488). (C) DT3 on *Alnus cecropiifolia* (IMNH 99). (D) Curvilinear to rectilinear elongate holes (DT7) on *Betula cristata* (IMNH 2019). (E) Large-sized, circular perforations (DT4) on *Salix gruberi* (HU\_42). (F) Three or more holes at the divergence point of secondary veins from the primary veins (DT57) on *Salix gruberi* (HU\_54). (G) Polylobate perforation (DT5) on *Betula cristata* (IMNH 8734). (H) Dense pattern of elliptical holes (DT9) on *Salix gruberi* (HP\_30). (I) Removed intercostal areas (DT78) on *Alnus cecropiifolia* (TA\_3\_1). (J) Central roundish hole, with a distinct edge, surrounded by a wide rim (DT113) on *Acer* sp. (F\_25) enlarged at (K). (L) DT78 on *Betula cristata* (IMNH 8833). (M) DT78 on *Alnus cecropiifolia* (IMNH 8). (N) DT4 on *Dicotylophyllum* sp. (IMNH 36). (O) Removal of primary vein tissue with adjacent reaction tissue, parallel to removed area (DT68) on Betulaceae indet. (S0936685–02). Scale bars: solid black, 10 mm; solid white, 5.0 mm; dotted, 1.0 mm.



**Fig. 3.** Margin feeding traces on leaves/leaflets from the Neogene of Iceland. (A) Isolated, circular, excision of a leaf margin (DT12) on *Fagus gussonii* (IMNH 6761\_1) close to the leaf apex (white arrow), and (B) close to the leaf blade base (white arrow) (IMNH 6760). (C) Deeply trenched excision (DT15) on *Salix gruberi* (IMNH 6747\_2). (D) Circular arc of leaf-margin excision (DT81) on *Betula cristata* (S094898). (E) Completely removed interveinal tissue surrounded by remaining veinal stringers (DT26) on *B. cristata* (HB\_71). (F) Excision of the leaf blade extending to the midvein (DT14) on *Salix* sp. (IMNH 8621). (G) Black arrow indicating apex feeding (DT13) on *F. gussonii* (IMNH 8864). (H) DT12 at different positions on the leaf blade (white arrows) on *B. cristata* (S094896). (I) Serial pattern of cusped margin excisions separated by a short segment of leaf margin (white arrows) on *F. gussonii* (IMNH 8940). Scale bars: solid black, 10 mm; solid white, 5.0 mm.

displayed one or more instances of herbivory. A total of 819 instances of herbivory were observed. Of the instances of herbivory recorded for the different Iceland localities, those allocated to the external foliage feeding FFGs, represented by the hole-feeding, margin-feeding, skeletonization, and surface-feeding subgroups, provided 87% of all DT occurrences, making external foliage feeding the dominant FFG within the Neogene Iceland biomes. Mining and galling FFGs are constituted for one-tenth of all DT occurrences. Minor levels of herbivory were present for the piercing-and-sucking and oviposition FFGs (<1%) (Table S7).

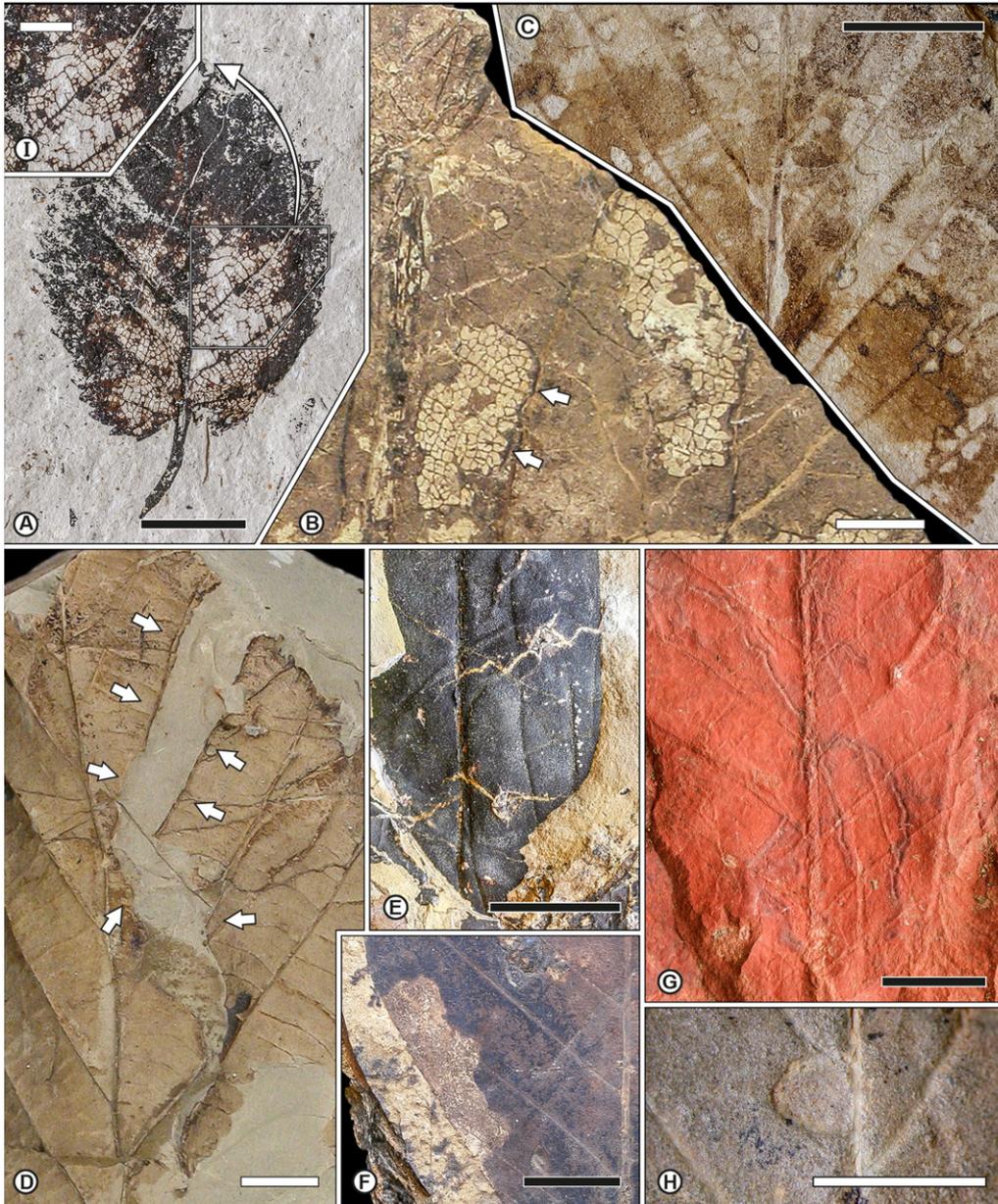
### 3.2. External foliage feeding

External foliage feeding is caused by larval and adult stages of mandibulate insects. The entire or partial thickness of the leaf tissue is

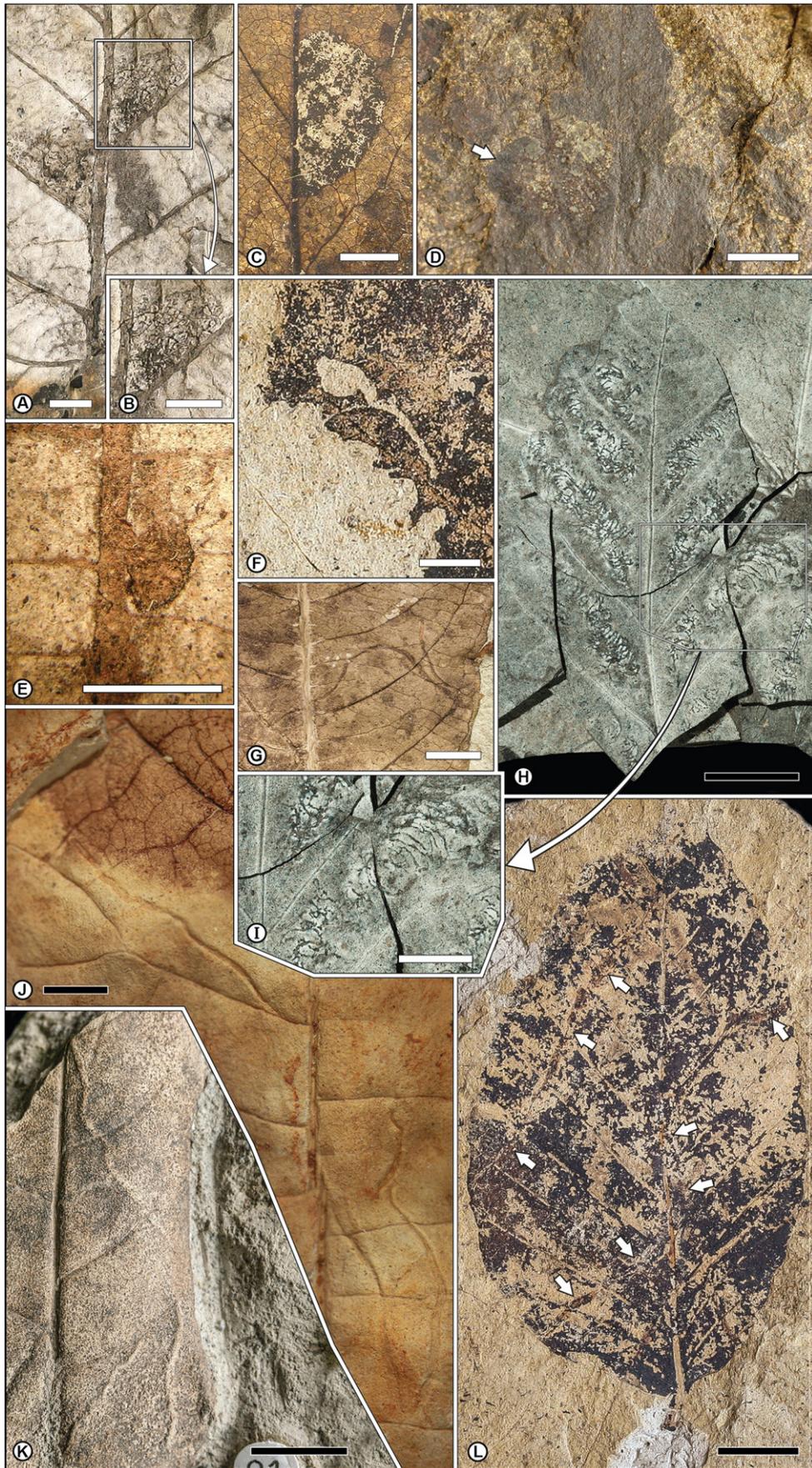
removed from the outside (Labandeira et al., 2002a). External foliage feeding consists of hole feeding, margin feeding, skeletonization, and surface feeding. However, unrelated insect lineages develop similar inventions of the same feeding strategy and therefore it is difficult to accurately identify the causal insect from such type of foliage feeding.

#### 3.2.1. Hole feeding

*Remarks.*—Hole feeding is more difficult for an insect than marginal chewing as it requires specialized mouthparts (Bernays, 1991), therefore, it is seen as an advanced feeding strategy and a derived character (Labandeira et al., 2007). This subgroup of external foliage feeding represents the most abundant and diverse type of damage in the Icelandic record (Fig. 2).



**Fig. 4.** Skeletonization (A–D) and surface feeding (E–H) traces on leaves/leaflets from the Neogene of Iceland. (A) Removal of interveinal tissue with a poorly developed reaction rim (DT16) on *Betula cristata* (IMNH 8743), enlarged at (I). (B) Removal of interveinal tissue with a thick (white arrows) developed reaction rim (DT17) on *Populus* sp. (S134362-02). (C) Patchy, unmined skeletonized zone that adjoins and follows one side of the primary and secondary venation (DT61) on *Alnus cecropiifolia* (IMNH 8543). (D) Highest orders of venation removed (white arrows) (DT21) on *A. cecropiifolia* (S106726). (E) Elongate, threadlike surface abrasion of constant width (DT25) on *Rhododendron ponticum* (TA\_42). (F) Polylobate shaped surface abrasion with a well developed reaction rim (DT30) on *Fagus gussonii* (UMNH 8998). (G) Linear swaths of removed surface tissues, criss-crossing branching, with well-developed reaction rims. (DT220) on *Fagus friedrichii* (IMNH 6705). (H) Surface abrasion with a poorly developed reaction rim (DT29) on *Aesculus* sp. (IMNH 289\_3). Scale bars: solid black, 10 mm; solid white, 5.0 mm.



*DT represented.*—DT1, DT2, DT3, DT4, DT5, DT7, DT9, DT57, DT68, DT78, DT113.

*Plant hosts.*—*Acer askelssonii*; *Acer islandicum*; *Aesculus* sp.; *Alnus cecropiifolia*; *Alnus gaudinii*; *Alnus kefersteinii*; *Arctostaphylos* sp.; *Betula cristata*; *Betula islandica*; *Carpinus* sp.; *Cercidiphyllum* sp.; *Comptonia hesperia*; *Cornus* sp.; *Corylus* sp.; *Crataegus* sp.; *Cyclocarya* sp.; *Dicotylophyllum* sp. 1–5; *Ericaceae* sp.; *Fagus friedrichii*; *Fagus gussonii*; *Juglans* sp.; *Laurophyllum* sp.; *Liriodendron proccacinii*; *Liriodendron* sp.; *Lonicera* sp.; *Magnolia* sp.; *Nuphar* sp.; *Nymphaeaceae* indet.; *Platanus leucophylla*; *Populus* sp.; *Pterocarya* sp.; *Ranunculaceae* indet.; *Rhododendron ponticum*; *Rosaceae* type A–C; *Salix gruberi*; *Salix* sp.; *Sassafras ferretianum*; *Sassafras* sp.; *Smilax* sp.; *Sorbus* sp.; *Tetracentron atlanticum*; *Tetracentron* sp.; *Tilia selardalense*.

*Distribution.*—15 Ma (2 DTs; 7 occurrences); 12 Ma (10 DTs; 300 occurrences); 10 Ma (7 DTs; 39 occurrences); 9–8 Ma (8 DTs; 60 occurrences); 7–6 Ma (8 DTs; 127 occurrences); 4–3 Ma (4 DTs; 15 occurrences).

### 3.2.2. Margin feeding

*Remarks.*—Larval and adult insects consume leaf tissue by making roughly semicircular to trench-shaped excisions from the leaf edge (Fig. 3). Many caterpillars and weevils, along with other insect groups, feed along the margin of leaves and are normally associated with reaction rims.

*DT represented.*—DT12, DT13, DT14, DT15, DT26, DT81, DT143.

*Plant hosts.*—*Acer askelssonii*; *Acer islandicum*; *Alnus cecropiifolia*; *Alnus gaudinii*; *Alnus* sp.; *Betula cristata*; *Betula islandica*; *Dicotylophyllum* sp. 1–2; *Fagus friedrichii*; *Fagus gussonii*; *Magnolia* sp.; *Pterocarya* sp.; *Rosaceae* type A, C; *Salix gruberi*; *Salix* sp.; *Sorbus* sp.

*Distribution.*—15 Ma (2 DTs; 4 occurrences); 12 Ma (3 DTs; 26 occurrences); 10 Ma (2 DTs; 3 occurrences); 9–8 Ma (4 DTs; 48 occurrences); 7–6 Ma (6 DTs; 58 occurrences); 4–3 Ma (2 DTs; 11 occurrences).

### 3.2.3. Skeletonization

*Remarks.*—Skeletonization is a type of external feeding wherein the softer parenchymatous interveinal tissue is completely removed without the lignified vascular or sclerenchymatous tissues (Fig. 4A–D).

*DT represented.*—DT16, DT17, DT21, DT61, DT79.

*Plant hosts.*—*Acer islandicum*; *Alnus cecropiifolia*; *Betula cristata*; *Corylus* sp.; *Fagus gussonii*; *Populus* sp.; *Pterocarya* sp.; *Ranunculaceae* indet.; *Rhododendron ponticum*; *Rosaceae* type C; *Salix gruberi*; *Salix* sp.; *Tetracentron atlanticum*.

*Distribution.*—12 Ma (3 DTs; 17 occurrences); 10 Ma (2 DTs; 2 occurrences); 9–8 Ma (2 DTs; 5 occurrences); 7–6 Ma (4 DTs; 12 occurrences); 4–3 Ma (1 DT; 1 occurrence).

### 3.2.4. Surface feeding

*Remarks.*—Larval and adult insects consume one or more layers of leaf blade from outside of the leaf, but do not consume the entire thickness of the blade and often show well-developed reaction rims (Fig. 4E–H). Some insect species in the Cecidomyiidae, Chrysomelidae, Curculionidae, and Thripidae, among others, surface feeders (Gullan and Cranston, 2010) produce similar DTs.

*DT represented.*—DT25, DT29, DT30, DT201, DT220.

*Plant hosts.*—*Acer askelssonii*; *Acer islandicum*; *Aesculus* sp.; *Corylus* sp.; *Fagus friedrichii*; *Fagus gussonii*; *Lonicera* sp.; *Rhododendron ponticum*; *Rosaceae* sp.; *Ulmus* sp.

*Distribution.*—15 Ma (2 DTs; 6 occurrences); 12 Ma (2 DTs; 3 occurrences); 10 Ma (1 DT; 3 occurrences); 9–8 Ma (1 DT; 1 occurrence); 7–6 Ma (1 DT; 1 occurrence).

### 3.3. Mining

*Remarks.*—Leaf mining is a highly specialized form of feeding behaviour that gives the insect protection from both predators and dehydration. Consisting of the tunnelling within plant tissues, especially foliage, by immature insect stages, especially larvae (Fig. 5).

*DT represented.*—DT35, DT36, DT38, DT41, DT66, DT90, DT93, DT94, DT104, DT105, DT176, DT208.

*Plant hosts.*—*Acer islandicum*; *Alnus cecropiifolia*; *Betula cristata*; *Betula islandica*; *Dicotylophyllum* sp. 2; *Fagus gussonii*; *Populus* sp.; *Rhododendron ponticum*; *Salix gruberi*; *Salix* sp.

*Distribution.*—15 Ma (1 DT; 1 occurrence); 12 Ma (7 DTs; 24 occurrences); 10 Ma (4 DTs; 6 occurrences); 9–8 Ma (2 DTs; 2 occurrences); 7–6 Ma (1 DT; 1 occurrence).

### 3.4. Galling

*Remarks.*—The most biologically complex of all major interactions, in which an immature insect or mite hormonally controls the host plant's developmental machinery by producing tissue that service the gall occupant (Fig. 6). Gallers are encapsulated by the hardened tissues of the host plant, which surrounds a layer of nutritive tissue that is consumed by an immature living in a chamber, all of which is nutritionally supplied by co-opted vascular tissue (Shorthouse and Rohfritsch, 1992).

*DT represented.*—DT11, DT32, DT33, DT34, DT62, DT80, DT107.

*Plant hosts.*—*Acer islandicum*; *Aesculus* sp.; *Alnus cecropiifolia*; *Betula cristata*; *Betula islandica*; *Dicotylophyllum* sp.; *Fagus friedrichii*; *Fagus gussonii*; *Rosaceae* type A; *Salix gruberi*; *Tetracentron atlanticum*; *Tilia selardalense*.

*Distribution.*—15 Ma (2 DTs; 7 occurrences); 12 Ma (4 DTs; 10 occurrences); 10 Ma (1 DT; 2 occurrences); 9–8 Ma (4 DTs; 5 occurrences); 7–6 Ma (2 DTs; 9 occurrences).

### 3.5. Piercing-and-sucking

*Remarks.*—Occurs when an herbivore targets and feeds on internal fluid tissues such as phloem, mesophyll or epidermis, but remains on the plant organ surface. The marks are dark and circular and normally are randomly distributed (Fig. 7A–B).

*DT represented.*—DT128.

*Plant host.*—*Betula cristata*.

*Distribution.*—7–6 Ma (1 DT; 1 occurrence).

### 3.6. Oviposition

*Remarks.*—Endophytic oviposition is common among Odonata, Orthoptera, Hemiptera, Coleoptera, Lepidoptera and Hymenoptera in modern insect groups. Female insect uses a piercing ovipositor, a sword-like device at the tip of the abdomen for inserting eggs into plant tissues (Fig. 7C). Although this interaction technically is not a mode of feeding since mouthparts are not used, oviposition has a well-established fossil record of plant damage (e.g. Laaß and Hoff, 2015).

*DT represented.*—DT101.

*Plant host.*—*Cercidiphyllum* sp.

**Fig. 5.** Leaf mining structures on leaves/leaflets from the Neogene of Iceland. (A) Blotch mine with small dispersed coprolites (DT35) on *Betula islandica* (IMNH 29), enlarged at (B). (C) Blotch mine lacking a central chamber (DT36) on *Lonicera* sp. (S093937-01). (D) Circular mined areas, appearing skeletonized (white arrow) (DT38) on *Salix gruberi* (S094631). (E) Mine in which the early to middle portion is coiled and contains an evenly-spaced (DT66) on *Acer islandicum* (IMNH 33\_1). (F) Small mine, thin linear-curved early phase of and a terminal ovoidal blotch (DT176) on *Fagus gussonii* (IMNH 8950\_1). (G) Linear mine of minimal width increase (DT90) on *S. gruberi* (S134358). (H) Serpentine, tightly folded mine; with a meniscate-sinusoidal frass trail (DT93) on *Acer islandicum* (Coll J. Vinther), frass pattern enlarged in (I). (J) Long, occasionally crisscrossing mine (DT104) on *Alnus cecropiifolia* (IMNH 6730\_2). (K) A full-depth, serpentine mine with rounded sides (DT94) on *Rhododendron ponticum* (IMNH 241). (L) Full-depth, serpentine mine with relatively smooth margins, that cross all, including major, veins (white arrows), lacking discrete size increases (DT41) on *F. gussonii* (IMNH 9410). Scale bars: solid black, 10 mm; solid white, 5.0 mm.

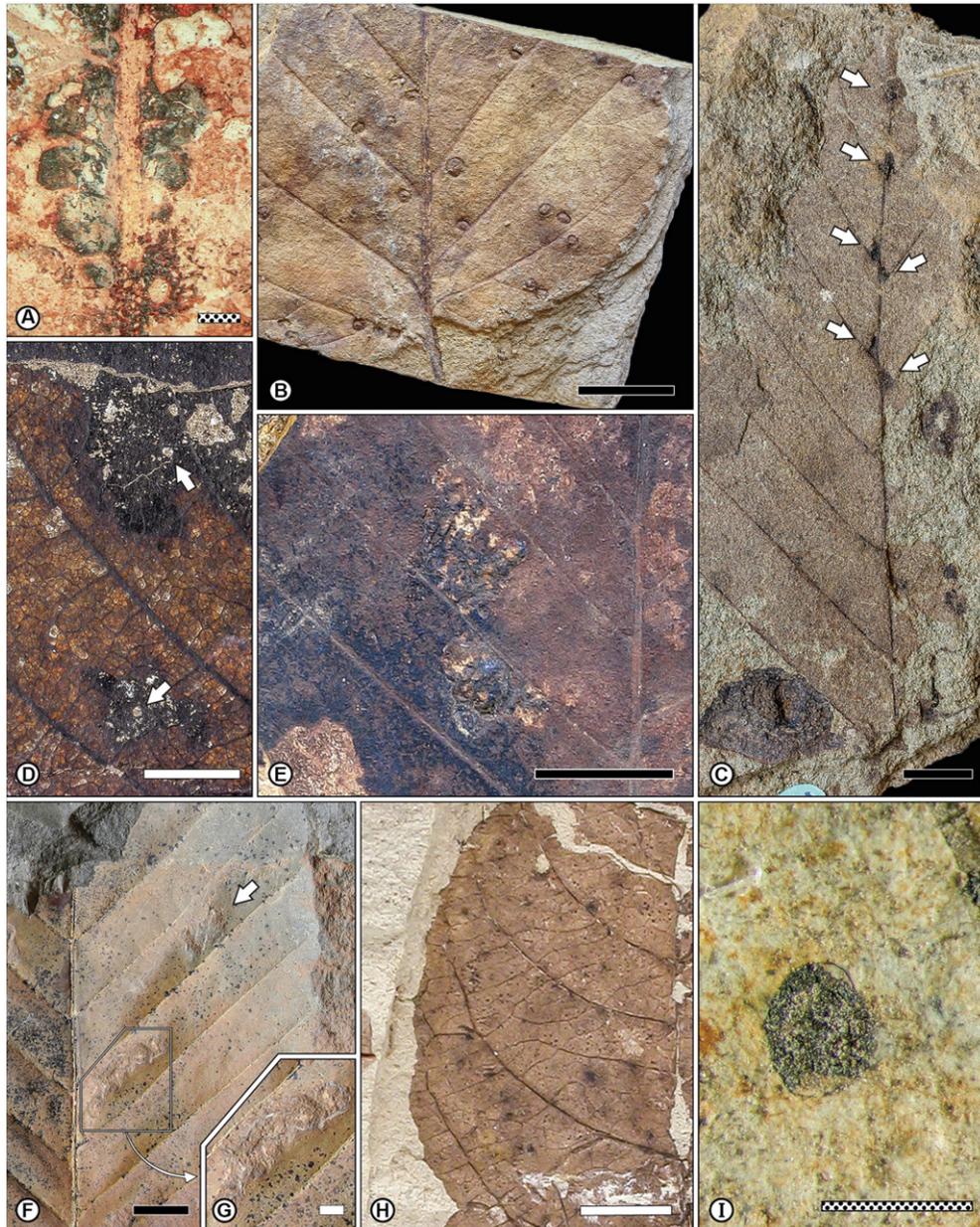
*Distribution.*—15 Ma (1 DT; 1 occurrence).

### 3.7. Insect damage on Iceland throughout the Neogene

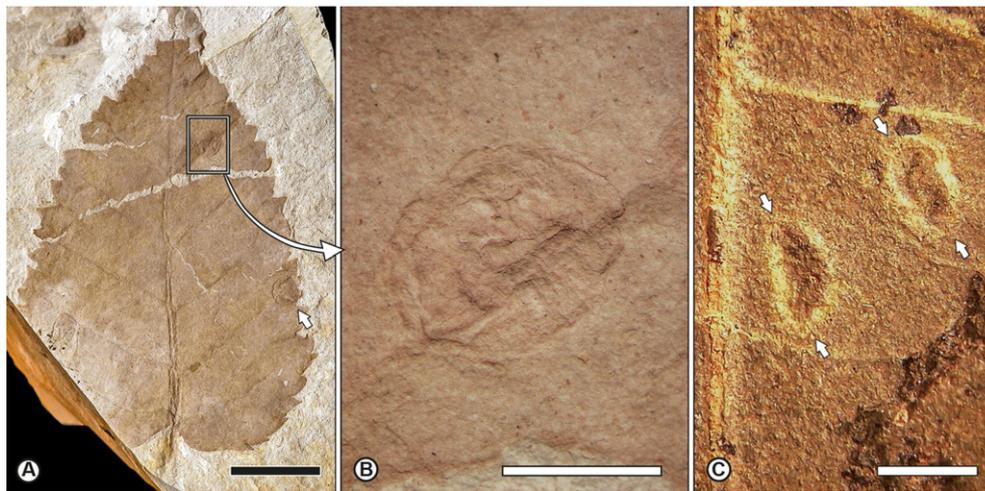
In general, the linear regression showed a significant and positive relationship between the number of leaves/leaflets analyzed and the number of leaves/leaflets with traces of herbivory ( $R^2 = 0.642$ ,  $F = 8.276$ ,  $df = 29$ ,  $p = 0.045$ ; Table 2). Thus, variations in composition through time are two-fold and reveal the particular relationships between host plants and insect herbivores and illustrate changes in the importance of different DTs or FFGs, but also reflects the response of plant-insect feeding associations to major environmental stresses and climate change. We found clear indications for such climate relations and DT diversity when data from the early middle to early late Miocene

(Langhian to Tortonian; 15–10 Ma) floras insect damage censuses are compiled ( $p = 0.005$ ); however the correlation for the period from the middle late Miocene to the Pliocene (9–3.8 Ma) showed no significant differences ( $p = 0.98$ ) (Fig. 8). Although the two Miocene formations yielding the “warmest” floras also have the highest species diversity (e.g. Denk et al., 2011, 2013), the data show only a weak, positive correlation between floral richness (rarefied to 195 leaves; Tables 1 and 3) and MAT index when all sites are included (Spearman:  $r = 0.27$ ;  $p = 0.2899$ ).

During the 15 Ma interval damage diversity (9 DTs) and damage intensity was low (~8%) and very generalized (~96%), except an imbalance in specialized associational diversity, overwhelmingly on *Fagus* as illustrated by an elevated galling frequency up to 2% (Fig. 9C). Upon plant diversification during the 12 Ma interval, plant-insect associations became significantly more diverse in the total number of DTs (28) and



**Fig. 6.** Galling structures on leaves/leaflets from the Neogene of Iceland. (A) Galls with a thin, unhardened central area and surrounded by a thick ring of dense tissue (DT11) on *Salix gruberi* (HB\_55). (B) Circular galls occurring on the interveinal regions of the leaf lamina (DT32) on *Betula cristata* (IMNH 8850). (C) Circular galls occurring on the primary veins (white arrows) of the leaf (DT33) on *Fagus gussonii* (IMNH 9026). (D) Circular galls occurring on the secondary veins of the leaf (DT34), with centrally positioned “exit holes” (white arrows) (or possibly larval chambers) on *Acer islandicum* (S093783-01). (E) Modestly thickened galls, presenting a pockmarked surface (DT62) on *F. gussonii* (IMNH 8998). (F) Compound, surface-pockmarked gall (DT107) on *Fagus friedrichii* (IMNH 4844\_1), enlarged at (G). (H) Small, hemispherical, characterized by dark, thickened carbonized material (DT80) on *S. gruberi* (S134390). (I) DT80 on Rosaceae Type A (IMNH 42\_3). Scale bars: solid black, 10 mm; solid white, 5.0 mm; dotted, 1.0 mm.



**Fig. 7.** Piercing-and-sucking (A–B) and oviposition (C) traces on leaves/leaflets from the Neogene of Iceland. (A) Distinctive ellipsoidal to spheroidal scale-insect impression marks (white arrows) on epidermal tissues causing a roughened surface (DT128) on *Betula cristata* (IMNH 8614), enlarged at (B). (C) Lenticular to ovoidal scars with a prominent reaction rim (white arrows) (DT101) on *Cercidiphyllum* sp. (IMNH 311\_2). Scale bars: solid black, 10 mm; solid white, 2.0 mm.

greater host specialization occurred, as evidenced by the highest levels of total and leaf-mine DT diversity (Fig. 9B). Particularly, *Salix gruberi* exhibits a preponderance of mining (11.2%) and secondarily external foliage feeding (5%).

A major floristic and climatic change is encountered in the 10 Ma formation, with a sudden appearance of many herbaceous plants that significantly re-structured the organisation of the plant community in distinct layers (comp. Denk et al., 2011: Figs. 5.6, 6.5). Both affect the structure of insect communities coupled with a significant climate cooling in the early late Miocene, and the lowest values of herbivory during the studied interval (5.3%; Figs. 8, 9). Nevertheless, several warmth-loving elements persisted, including *Platanus*, *Pterocarya*, and *Tilia*. The two overwhelmingly herbivorized taxa, in rank order, were *Pterocarya* and *Alnus cecropiifolia*. *Pterocarya* consists of only 3.3% of the specimens but accounted for 14.2% of all instances of herbivory. Analogous values for *Alnus cecropiifolia* are 10% of specimens, 12.1% of all instances of herbivory. All other plant hosts exhibited approximately an order-of-magnitude less herbivory or absence of herbivory, when compared to that of *Pterocarya* and *Alnus*.

Even though compositional changes within species in the sedimentary formations reflect a shift from warm temperate to cool temperate conditions from the late middle Miocene to the Pliocene with a further stepwise cooling (Fig. 8), floras preserved in strata between 9 and 6 Ma show an opposing trend assuming that herbivore communities were largely driven by canopy and herb layer characteristics. Damage metrics within the Skarðsströnd-Mókollsdalur Formation (9–8 Ma) and Hreðavatn-Stafholt Formation (7–6 Ma) indicate a significant spatial

trend, with plant (herb) diversity ( $H'$ ) increasing alongside damage type occurrence (DTO) abundance, affecting both general as well as specialized damage types (Fig. 10). Particularly, galling damage occurring on multiple hosts and in many cases at high densities on the foliar surface (Fig. 6B), whereas leaf-mine DT diversity shows an overall decreasing trend since 10 Ma (Fig. 9B). A second significant drop in diversity and abundance of plant-insect interactions characterizes the transition between the latest Miocene (7–6 Ma) and Pliocene (4.0–3.6 Ma), recorded in the Tjörnes beds (Figs. 8, 9A), with the lowest levels of specialized foliage feeding (0.5%) and the total disappearance of gall-inducing taxa and leaf-mining larvae.

#### 4. Discussion

In our study we focus on understanding the dynamic of an island ecosystem with regards to plant-insect relationships. As Iceland is the only place in the subarctic North Atlantic providing a fairly continuous terrestrial sedimentary and plant fossil record over the past 15 million years, we are able to show the dynamics of an ecosystem during different geological time frames of the Neogene in this part of the globe. Most significantly, the relationship between folivores and plants are two-fold in the present study and provide (1) insight into the biotic respond to climate change, and (2) changes of community structures.

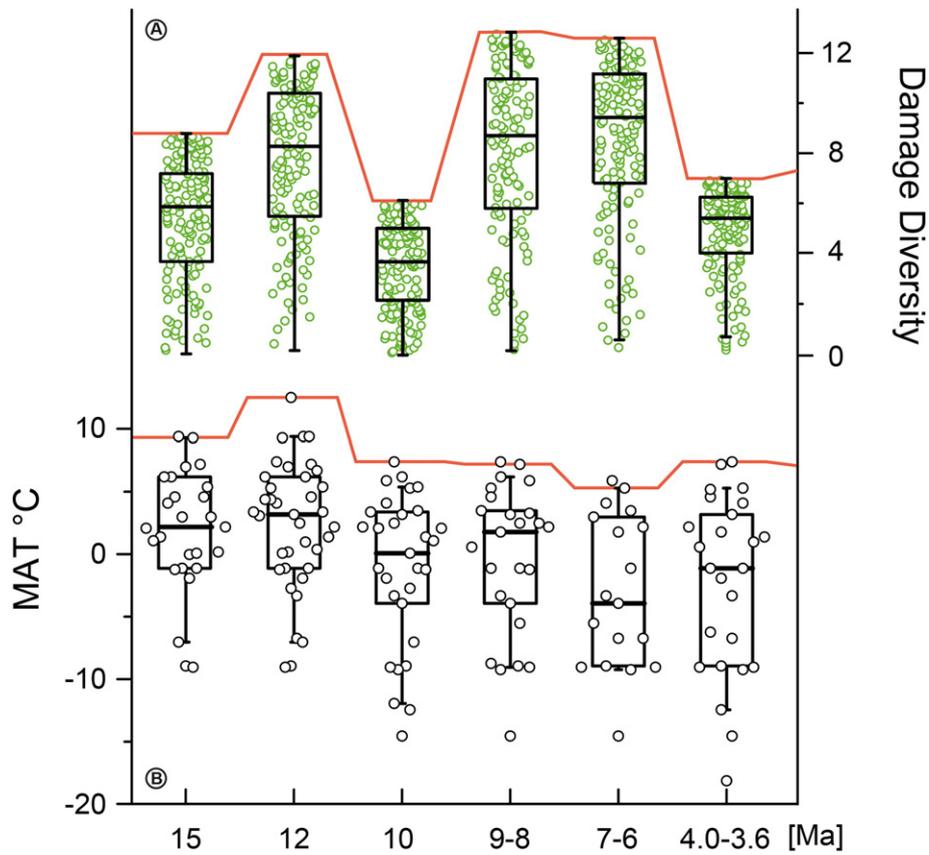
Generally, the Miocene floras of Iceland belonged to a widespread, Neogene, northern hemispheric forest vegetation whose representatives are restricted to East Asia, North America and western Eurasia at the present time, and represents broad-leaved (deciduous) to

**Table 2**  
Correlations between plant host's relative abundance and insect damage.

% abundance in flora vs.	Residual SE	R <sup>2</sup>	F statistic	P value	df
Damage frequency	22.63	0.642	8.276	<b>0.045</b>	29
Mine frequency	16.23	0.1206	1.235	<b>0.02953</b>	9
Gall frequency	10.56	0.7388	36.76	<b>4.012e-05</b>	13
Total DTL	22.4	0.3153	0.944	<b>0.03393</b>	29
Specialized DTL	17.9	0.7344	1.427	<b>0.02478</b>	18
Mine DTL	14.9	0.2594	3.153	<b>0.01095</b>	9
Gall DTL	20.59	0.00592	0.07742	0.07852	13
Total DTO	22.75	0.000631	0.01831	0.08933	29
Specialized DTO	16.43	0.1915	4.5	<b>0.04727</b>	19

Results from R's linear model function with percent abundance in the flora as the independent variable and damage metrics as the dependent variable. Total, specialized, mine, and gall DTL are at 25 leaves. Total and specialized DTO are at 5 DT occurrences. DTL, number of damage types standardized by leaves; DTO, number of damage types standardized by damage occurrences.

Values shown in bold indicate significance for  $\alpha \leq 0.05$ .



**Fig. 8.** Box-plots based comparison of mean annual temperature (MAT) estimates and the number of damage types (DTs) standardized. (A) Total DT diversity within each fossiliferous sedimentary formations on Iceland (standardized to 195 leaves/leaflets, represented by open green circles). (B) Lower limits of MATs for potential modern analogues of fossil species recorded from Iceland (represented by open circles, modified from Denk et al., 2011).

coniferous mixed forest (e.g. Denk et al., 2011), at respectively 15, 12, 10, 9–8 and 7–6 Ma. Furthermore, these floras suggest a humid warm temperate climate probably attributable to an increase in northward energy transport in the North Atlantic realm that was likely related to an already effective Gulf Stream, causing a delayed climatic decline following the Mid-Miocene Climatic Optimum (MMCT) in the subarctic North Atlantic region (Denk et al., 2013). The results presented here favour the hypothesis that such climatic conditions positively affect ecosystem process rates such as herbivory as shown by a diversity peak of recovered plant fossil taxa increasing markedly from 35 to 65 taxa in the middle Miocene (mainly occurring within the Brjánslækur-Seljá Formation, c. 12 Ma) (Denk et al., 2005, 2011). Together with plant diversity, overall insect herbivory in leaves is known to be greatest in tropical lowland rainforests (e.g. Coley and Barone, 1996; Hunter and Price, 1998). Insect herbivory has been widely discussed as an explanation for the maintenance of high tree species diversity (Leigh et al., 2004), in the so-called Janzen-Connell hypothesis (Connell, 1971; Janzen, 1970) and many recent experiments have proven this

mechanism (Comita et al., 2010; Johnson et al., 2012; Mangan et al., 2010). In the early and middle Eocene, leaf floras from North America, Patagonia, and Europe show a marked increase in the amount and diversity of insect damage and specialized associations (Wilf et al., 2005; Curran et al., 2008, 2010; Wappler et al., 2012). This increase in diversity appears to be highly correlated with rising temperature, CO<sub>2</sub> levels, as well as plant diversity and plant selection by insects is influenced by pCO<sub>2</sub> concentrations due to its indirect effect on plant quality for herbivores and natural enemies (e.g. Lindroth, 2010). So, indirectly it is possible to relate changes in herbivory that are altered significantly under climate change (e.g. Cornelissen, 2011; Lau and Tiffin, 2009), but also allow assessing changes in insect diversity when body fossils on Iceland are rare, during a period that witnessed the most significant Cenozoic climate changes (e.g. Su et al., 2015; Wappler et al., 2009; Wappler and Denk, 2011; Wappler et al., 2014; Wilf, 2008).

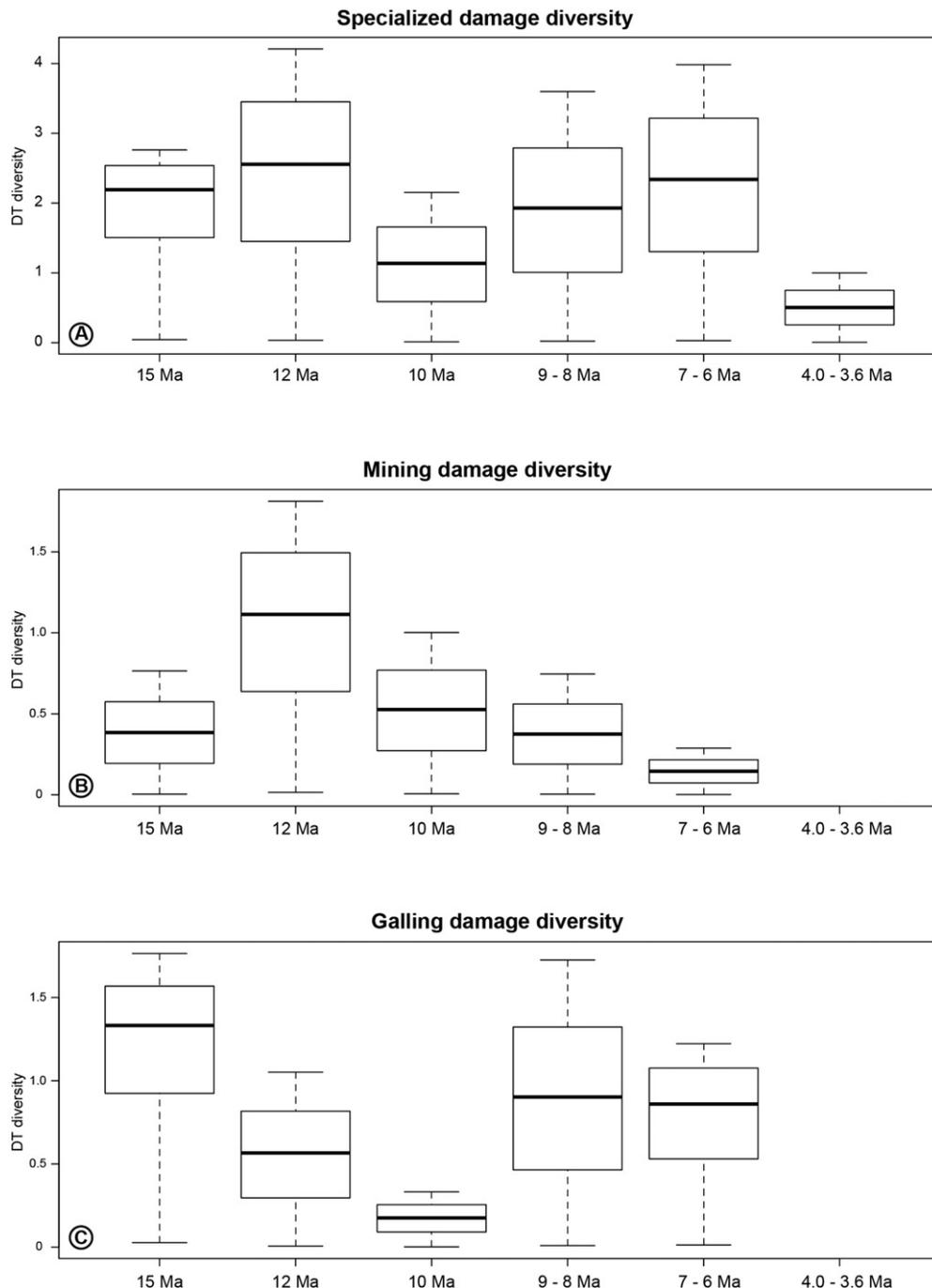
According to the global deep-sea δ<sup>18</sup>O record, the late middle Miocene climatic optimum was followed by a gradual cooling and re-

**Table 3**  
Floral diversity and evenness for the single time horizons.

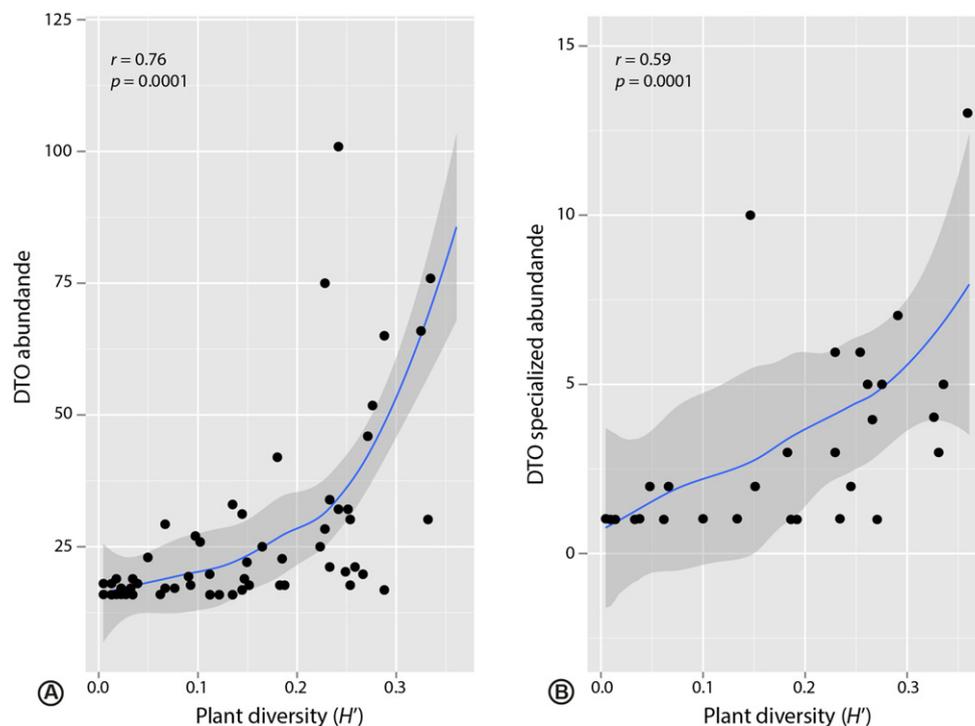
Age (Ma)	S	Diversity at 195 leaves	Diversity error	Pielou's J evenness	Shannon index (H')	Fisher's alpha (α)
15	12	11.4	1.1	0.43	1.09	2.91
12	35	23.0	2.2	0.71	2.55	6.53
10	28	20.8	1.9	0.71	2.39	5.47
9–8	23	17.9	1.6	0.58	1.85	5.26
7–6	20	14.1	1.6	0.63	1.91	4.07
4.0–3.6	10	11.0	0.1	0.49	1.17	2.52

establishment of a major ice-sheet on Antarctica by 10 Ma (e.g. Zachos et al., 2001, 2008). Mean  $\delta^{18}\text{O}$  values then continued to rise gently through the late Miocene until the early Pliocene, indicating additional cooling and small-scale ice-sheet expansion in the Arctic. Besides these climate cycles and long-term oceanic conditions the signal within the Tröllatunga-Gautshamar Formation (~10 Ma) encountered a major floristic change that demonstrated shifts in the trophic structures over time, with a sudden appearance of many herbaceous plants, particular an increase in Cfc- and Dfc-tolerant taxa. This trend is also coupled with a proportional increase of specialized DTOs during food-web assembly relative to generalized DTOs. Across broader scales tree and herb layer diversity often show linkages (e.g. Barbier et al., 2008;

Scherber et al., 2014; Vockenhuber et al., 2011), as herb layer contains most of a forest's plant diversity (Gilliam, 2007), and consequently more-intense biotic interactions in forest ecosystems could be observed (Basset et al., 2012; Coley and Barone, 1996; Dyer et al., 2007; Pennings and Silliman, 2005). Thus, the plant-insect associational record between 9 and 6 Ma shows an opposing trend, as documented in the peak of gall occurrences during that period, probably related to an increased moisture transport from low to high northern latitudes by the Loop Current–Gulf Stream causing water stress, which may be a disadvantage to the palaeoflora, while giving support for galling insects, as described for the modern insects by Blanche and Westoby (1995).



**Fig. 9.** Box plots of DT diversity within each fossiliferous sedimentary formations on Iceland. (A) Specialized types of damage. (B) Mining. (C) Galling; standardized to 195 leaves/leaflets.



**Fig. 10.** Effects of plant diversity ( $H'$ ) (based on the fossil pollen and macrobotanical record) on the number of damage types standardized by damage occurrence (DTO). (A) Bulk DTO data. (B) Specialized DTO data. Blue lines show model predictions, grey fields show  $\pm 1$  SE of the predictions.

Whereas the overall trend, preserved in strata between <10 and 3 Ma generally reflect a further stepwise cooling followed by a significant drop in diversity and abundance of plant–insect interactions in the Pliocene and the complete loss of the overwhelmingly host specialized damage types, as a consequence of a lack of suitable hosts, like *Fagus* sp. and *Quercus* sp., that cause extinction of these types of functional feeding groups on Iceland during the latest Miocene and Plio-/Pleistocene transition.

## 5. Conclusions

Palaeoecological studies that combine analyses of environmental factors, species interactions, ecology, biogeography, and geological history may better estimate the feedbacks between assembly dynamics and community structures and provided new insights into the formation of ecological communities. This study presents an extensive dataset of palaeo-herbivory combining for the first time quantitative studies of middle Miocene to Pliocene fossil plant–animal interactions on Iceland. Our results demonstrate how patterns of herbivory have changed over time in direct relation to climate change that profoundly influenced levels of insect-mediated damage diversity and frequency. In addition, higher structural complexity, particularly the establishment of species-rich herb layer communities seem to have positively influence the structures of insect communities in Icelandic palaeoforests.

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.gloplacha.2016.05.003>.

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