

The Company of Plants

A Reference Work on the Co-evolution of Plants and the Rest of Life, in Two Layers

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How to use this book

This book follows *Plants on the Ladder* (12 October 2026). That work treated fifteen groups of photosynthetic life and their characters. This one treats what that work left out: the evolution of plants together with the rest of life — insects, fungi, bacteria and archaea, animals, soil life, herbivores, decomposers, the atmosphere, other plants, and pathogens.

It is built in two layers, kept apart.

Layer A is biology only. Ten chapters, A1 to A10, each on one interplay, each with the same nine sections: what it is; first appearance; partners; sizes; times; counts; order of events; present quantities; and a closing **Pattern** of at most 150 words that states what the measurements show, with no interpretation. Part C gathers the numbers of Layer A into eight tables across the chapters. Layer A and Part C mention no theory. They stand on their own.

Layer B asks one question of Layer A: do the measured patterns correlate with the structure and the evolution of the net of the Vacuum.Net theory, as its texts state them, with nothing added? Each pairing carries a status. Three tests were fixed before the data were seen and then run; their outcomes stand as they fell.

The marks. Every statement of fact carries one of these. *Measured*: read in the cited source, with a reference number [n]. *Computed*: arithmetic on measured numbers, shown. *Modelled*: the output of a published model, named as such (used in A8 for oxygen and carbon-dioxide curves). *Text*: a statement of a Vacuum.Net text, quoted (Layer B only). *Read*: a pairing made in Layer B between a text statement and a measured pattern; a read is a hypothesis.

The ladder and the position. Every size and every time carries its position: $\log_3$ of the value over the unit of length, 4.558816×10^{-8} m, or the unit of time, 1.520655×10^{-16} s, Larson's natural units as used in *From Atom to Body*. One year is 3.15576×10^7 s; an age of A million years before present is placed as a duration of $A \times 10^6$ years. Positions are given to two decimals and never rounded to a whole mark. A position is a coordinate.

Sources. Layer A has one numbered list of 457 references in order of first use; Part C uses the same numbers. Layer B has its own annotated list. Each chapter ends with a list "Not verified": items

found only in secondary sources or whose primary could not be opened. They are not facts of this book.

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Part 0 — The Rules

0.1 Two layers

Layer A is written as if the theory did not exist. Its ten Pattern paragraphs are the data of Layer B. Nothing in Layer B may add a fact that Layer A does not hold, and nothing in Layer A may lean on Layer B.

0.2 The marks

Four marks for fact, one for pairing; see "How to use this book". A statement without a mark is a heading or a connective.

0.3 The ladder

Positions as defined above. The day sits at 43.50, the year at 48.87. The dated record of Layer A runs from the last universal common ancestor, older than 3.9 Ga at position 68.97, through the Oligocene C4 origins at 32–25 Ma, positions 64.6–64.4, to the historical dates of A4 and A10, placed as years before 2026.

0.4 Depth, in two senses

As in *Plants on the Ladder*, Part 0.3. *Ring depth* is the length of a closed ring of trits, 3, 6, 9; it is used only where the texts use it. *Position* is the depth of the Climate paper, "each depth n is one layer"; every measured size and time has one. No text equates the two, and this book does not.

0.5 What is not added

No rule is added to the theory. No sentence says that the net causes a biological pattern. No ring depth is assigned to any organism above the cell. No family of layers is applied. Where the texts are silent, Layer B says none.

0.6 Tests

A test is fixed before its data are looked at: the quantity, the required outcome, the chance outcome, the data. Where a test could not be run on the fixed data, it is reported as not run, with what was obtained. Where a classification was made after a table had been seen, it is marked post hoc and is not a test.

Layer A — The Co-evolution of Plants and the Rest of Life (chapters A1–A5)

A1 Insects and Pollination

What it is

Insect pollination is the carriage of pollen from one plant to another by an insect that visits both. The measured partners are 295,383 angiosperm species (measured [1]) and about 350,000 known pollinator species (measured [2]). Of the angiosperms, 87.5 % are pollinated by animals (measured [3]).

First appearance

The insect side is older than the flowers by a wide margin. The oldest insect fossil is *Rhyniognatha hirsti* from the Rhynie chert, Scotland; the paper gives 396–407 Ma (measured [4]). The Pragian stage of that chert spans 410.8–407.6 Ma on the 2023 chart (measured [5]), position 66.92 (computed). A molecular clock on 1,478 genes places the origin of insects at about 479 Ma and of insect flight at about 406 Ma (measured [6]). The main living lineages date to about 345 Ma (measured [6]). The positions are 67.06 and 66.91 (computed). The oldest winged insect fossil, *Delitzschala bitterfeldensis*, is Arnsbergian (measured [7]); that interval lies within the Serpukhovian, 330.9–323.2 Ma (measured [5]), positions 66.73–66.71 (computed). The gap between the molecular age of flight and the oldest winged fossil is $406 - 330.9 = 75.1$ Myr (computed).

The flowering plants are Early Cretaceous. Magnoliids, monocots and eudicots diversified 135–130 Ma (measured [8]), positions 65.91–65.88 (computed). No unequivocal pre-Cretaceous angiosperm fossil is known (measured [9]).

The interaction is first recorded on gymnosperms. The oldest definitive pollinating insects carry siphonate proboscides and date to the late Middle Jurassic, about 165 Ma, position 66.09 (measured [10]; position computed). Long-proboscid scorpionflies, 11 species in three extinct families, fed on ovular secretions of gymnosperms over a 62-million-year interval (measured [11]). The first beetle pollinator, *Darwinylus marcosi*, is about 105 Ma, position 65.68, with 126 pollen grains attached (measured [12]; position computed). A boganiid beetle with cycad pollen is about 99 Ma (measured [13]). Long-proboscid flies with gymnosperm pollen are 105 and 100 Ma (measured [14]).

On angiosperms the record starts at 100 Ma. The oldest bee, *Melittosphex burmensis*, is approximately 100 Ma, position 65.64 (measured [15]; position computed). The oldest direct evidence of insect pollination of a eudicot is a beetle with tricolpate pollen at 99 Ma, position 65.63 (measured [16]; position computed).

Partners

On the plant side the hosts of the Jurassic and Cretaceous pollinators were five gymnosperm groups: a seed fern, a conifer, a ginkgoopsid, a pentoxylalean and a gnetalean (measured [11]). The pollen on the 105 Ma beetle belongs to Ginkgoales, Cycadales or Bennettitales (measured [12]); the pollen on the 99 Ma beetle is cycad pollen (measured [13]). Today the plant side is 295,383 angiosperms and 1,079 gymnosperms (measured [1]).

On the insect side the known pollinators are bees 17,000, flies 55,000, Lepidoptera 141,600, beetles 77,300, all Hymenoptera 70,000, thrips 1,500 (measured [2]). Vertebrate pollinators are birds 1,089, mammals 344 and lizards 37 (measured [2]). The main groups arose before or with the flowers. Crown bees date to about 123 Ma (113–132 Ma) (measured [17]), position 65.83 (computed). The Lepidoptera crown is about 300 Ma, the tube-like proboscis about 241 Ma, and day-flying butterflies from about 98 Ma (measured [18]); positions 66.64, 66.44 and 65.62 (computed). Wing scales of proboscis-bearing Lepidoptera occur at the Triassic–Jurassic boundary (measured [19]), which is 201.4 Ma (measured [5]), position 66.27 (computed).

Independent origins are counted in several systems. Four gymnosperm pollination modes and four cohorts of insect pollinators are counted between 125 and 90 Ma (measured [12]). Perfume orchids arose at least three times after the orchid bees (measured [20]). Cheating arose twice within the yucca moths (measured [21]).

Sizes

what	size	position	source
smallest adult insect, male <i>Dicopomorpha echmepterygis</i>	139–240 μm	7.30–7.80	measured [22]; positions computed
longest insect, <i>Phobaeticus chani</i> female	body 357 mm; overall 567 mm	14.45; 14.87	measured [23]; positions computed
<i>Cycadopites</i> pollen on the 99 Ma beetle (n = 21)	polar axis 20.65 μm ; equatorial 14.30 μm	5.57; 5.23	measured [13]; positions computed
pollen size classes, <i>Myosotis sylvatica</i> / <i>Cucurbita pepo</i>	<10 μm / >100 μm	<4.91 / >7.00	measured [24]; positions computed
honey bee worker reach into a	7 mm	10.87	measured [25];
butterfly proboscis, <i>Eurybia lycisca</i> (n = 20)	max 45.6 mm; mean 36.5 mm; diameter 0.26 mm	12.58; 12.37;	measured [26]; positions computed
orchid spur, <i>Angraecum</i>	33 cm	14.38	measured [27];

The span of insect body length is $567 / 0.139 = 4,079$ (computed). A female yucca moth carries up to nearly 10,000 pollen grains, about 10 % of her body weight (measured [21]).

Times

what	duration	position	source
periodical cicadas <i>Magicicada</i> , juvenile period	13 yr; 17 yr	51.21; 51.45	measured [28]; positions computed
honey bee worker, normal lifespan	2–6 weeks	45.90–46.90	measured [29]; positions computed
honey bee worker, caged	23–42 d	46.35–46.90	measured [29]; positions computed
honey bee drone, maximum	20–40 d	46.23–46.86	measured [29]; positions computed
honey bee queen, maximum	8 yr	50.76	measured [29]; position
caged workers, USA, median	34.3 d (1970s); 17.7 d (now)	46.72; 46.12	measured [30]; positions computed
flower longevity	<1 d to several weeks	<43.50	measured [31]; position
fig cycle inside the syconium	15–100 d	45.96–47.69	measured [32]; positions computed
adult pollinating fig wasp	24–48 h	43.50–44.13	measured [32]; positions computed
flower handling, <i>Eurybia lycisca</i>	54.5 ± 28.5 s	36.79	measured [26]; position
herbivory recovery after the Permian–Triassic event	24 Myr (252 to 228 Ma)	64.34	measured [10]; position computed
herbivory recovery after the K–Pg event	about 10 Myr (65.5 to 55.8 Ma)	63.54	measured [10]; position computed

The queen-to-worker lifespan ratio is $8 \text{ yr} / 42 \text{ d} = 70$ to $8 \text{ yr} / 14 \text{ d} = 209$ (computed). Insect life inside the fig is $15 \text{ d} / 2 \text{ d} = 7.5$ to $100 \text{ d} / 1 \text{ d} = 100$ times shorter than the fig cycle (computed). The 13- and 17-year cicada cycles diverged 200,000–100,000 years ago; the species groups split 3.9–2.5 Ma (measured [28]).

Counts

Angiosperms number 295,383 accepted species, of which 74,273 monocots and 210,008 eudicots; gymnosperms 1,079; all plants about 374,000; about 2,000 new species are named per year (measured [1]). Animal pollination covers 308,006 of about 352,000 species, 87.5 %; community means are 78 % in temperate and 94 % in tropical sites (measured [3]). On the Christenhusz & Byng base, $0.875 \times 295,383 = 258,460$ species (computed).

Known pollinators total 349,368 species (measured [2]); per angiosperm species this is $349,368 / 295,383 = 1.18$ (computed). About 1 million insect species are named and about 5.5 million are estimated; beetles alone are estimated at 1.5 million (measured [33]). Insects hold about 62 % of about 1.6 million described living species (measured [34]). Lepidoptera count 157,424 species in 15,578 genera (measured [35]); Coleoptera 386,500 species in 176 families (measured [36]); Hymenoptera 153,088 described species (measured [37]). Bees count 20,446 living species (measured [38]) or 17,000 (measured [2]); both are recorded. Bees are $20,446 / 153,088 = 13.4$ % of Hymenoptera (computed).

Herbivory shares by order: Lepidoptera about 100 %, Orthoptera about 94 %, Hemiptera about 80 %, Coleoptera about 26 %, Hymenoptera about 7 % (measured [34]). Across 31 orders herbivory explains 25–35 % of the variation in diversification rate (measured [34]). Gall-inducing insects are estimated at 21,000–211,000 species, mean 132,930 (measured [39]). Seed beetles count about 1,700 species, 84 % on legume seeds (measured [40]).

Specialised pairs: *Ficus* has about 750 species with more than 750 fig–wasp pairs (measured [41]) or 874 species (measured [32]); both counts are recorded. Yucca moths: 13 *Tegeticula* species, 11 of them pollinators, and 4 *Parategeticula* (measured [21]). Orchid bees exceed 200 species and their orchids 600 species; the bees collect 585 volatile compounds (measured [20]). Madagascar has about 30 long-spurred orchids and 7 long-tongued hawkmoths (measured [27]). Fungus-farming ants count about 250 described species (measured [42]).

Order of events

1. About 479 Ma: molecular origin of insects (measured [6]). 410.8–407.6 Ma: oldest insect fossil (measured [4]; [5]).
2. 417–403 Ma: first herbivory, spores and stems, in the Rhynie chert (measured [43]).
3. About 406 Ma: molecular origin of flight (measured [6]); oldest winged fossil within 330.9–323.2 Ma (measured [7]; [5]).
4. 327–309 Ma: second herbivory pulse; leaf margin feeding at 326 Ma, 76 Myr after the origin of leaves; seed predation 54 Myr after seeds; wood boring 63 Myr after wood; root feeding after 98 Myr (measured [43]). About 302 Ma: oldest insect gall (measured [44]).
5. About 300 Ma: Lepidoptera crown; 241 Ma proboscis (measured [18]); 201.4 Ma scales of Glossata (measured [19]; [5]).
6. About 165 to 100 Ma: insect pollination of gymnosperms, four modes (measured [10]; [12]). 105 and 99 Ma: beetles with gymnosperm pollen (measured [12]; [13]).
7. 135–130 Ma: main angiosperm clades (measured [8]). 123 Ma: crown bees (measured [17]).
8. 100 Ma: oldest bee (measured [15]). 99 Ma: eudicot pollen on a beetle (measured [16]). 120–100 Ma: gymnosperm pollination modes replaced (measured [10]).
9. At least 60 Myr of fig–wasp co-divergence (measured [45]). 78–81 Ma: seed beetles (measured [40]). 61–57 Ma: ant fungus farming; 19–18 Ma: leaf-cutter ants (measured [42]). 41.5 ± 9.8 Ma: yucca moths on yuccas (measured [46]). 34–38 Ma: orchid bees; 18–27 Ma: their orchids (measured [20]). 7.5 ± 5.2 Ma and 7.4 ± 2.8 Ma: Darwin's orchid and its hawkmoth split from their relatives (measured [27]).

The interval from first fungus farming to leaf-cutting is $61 - 19 = 42$ Myr (computed). The gall at 302 Ma lies $479 - 302 = 177$ Myr after the molecular insect origin (computed).

Present quantities

Angiosperms 295,383 species; pollinators 349,368 species; 87.5 % animal pollination (measured [1]; [2]; [3]). Named insects about 1 million against an estimate of 5.5 million; about 80 % of insect species are undescribed (measured [33]). The named total of the three largest orders is $386,500 + 157,424 + 153,088 = 697,012$ (computed). Herbivores among them, using the measured shares, sum to $100,490 + 157,424 + 10,716 = 268,630$, which is 38.5 % of 697,012 (computed).

Pattern

Insects are recorded at 410.8–407.6 Ma and flowers at 135–130 Ma; the gap is about 275 Myr. Herbivory appears twice before flowers, at 417–403 Ma and 327–309 Ma, and each plant tissue is eaten 54–98 Myr after it first appears. Insect pollination is recorded first on gymnosperms, from 165 Ma in four modes, and on angiosperms from 100–99 Ma. The proboscis (241 Ma) and crown bees (123 Ma) are older than or coeval with the main angiosperm clades. Today 87.5 % of 295,383 angiosperm species are animal-pollinated by 349,368 pollinator species, 1.18 per plant species. Obligate pairs recur at least five times, each 7 to 60 Myr old, and in each the insect side is dated first or together with the plant. Herbivory explains 25–35 % of diversification variance across 31 insect orders. Insect generation times span 13–17 years down to weeks; body lengths span 0.139–567 mm, a factor of 4,079.

Not verified

Drosophila melanogaster body length 2.5 mm and egg-to-adult time 7 d (BioNumbers, naming Matheson and Ashburner et al. 2005). *Xanthopan praedicta* proboscis 15–28.5 cm (NHM 2021, naming Minet et al. 2021). The 75 Ma crown age of the fig–wasp mutualism (Cruaud 2012 full text). The "about 50 %" share of insects that are herbivores. The total number of damage types in the Labandeira guide. Janzen 1971 on seed predation (citation only). Honey bee and fig wasp body lengths. The "11.7 Mya" reading in the Pellmyr 2003 scan (possible OCR error).

A2 Fungi and Mycorrhiza

What it is

Mycorrhiza is the joint structure of a fungal hypha and a plant root in which the fungus takes carbon from the plant and the plant takes mineral nutrients through the fungus. Of vascular plant species, 72 % form arbuscular mycorrhiza, 2.0 % ectomycorrhiza, 1.5 % ericoid and 10 % orchid mycorrhiza (measured [47]). Lichens are the second joint structure: a fungus with an alga or cyanobacterium (measured [48]).

First appearance

The fungal side is recorded long before land plants. Fungus-like mycelial filaments occur in vesicular basalt dated 2.4 Ga (measured [49]), position 68.53 (computed). The oldest unambiguous fungus, *Ourasphaira giraldae*, is 1,010–890 Ma (measured [50]), positions 67.74–67.63 (computed). A six-gene clock on 199 fungi places crown Fungi at about 1,020 Ma and the loss of the flagellum at about 720 Ma (measured [51]). Dikarya diverged at 649 Ma and Glomeromycota originated at about 659 Ma (715–606 Ma) (measured [51]). The positions are 67.75, 67.43, 67.34 and 67.35 (computed). The same study places crown embryophytes at 482 Ma (485–473 Ma) and the onset of Glomeromycota diversification at about 484 Ma (529–437 Ma) (measured [51]). The

Leotiomyceta radiation is at about 446 Ma (467–425 Ma) (measured [51]). The positions are 67.07, 67.07 and 67.00 (computed). The gap from crown Fungi to the origin of arbuscular mycorrhiza at about 480 Ma is 540 Myr (computed).

The interaction is first seen in rock at 460 Ma. Hyphae and spores resembling modern Glomales occur in Ordovician rocks of Wisconsin, about 460 Ma (measured [52]), position 67.03 (computed). Complex mycelial fossils, *Tortotubus protuberans*, with septal perforations and a double wall, come from the earliest Silurian (measured [53]); the Silurian begins at 443.8 Ma (measured [5]), position 66.99 (computed). Arbuscules in *Aglaophyton major*, morphologically identical to living ones, are older than 400 Ma (measured [54]). The host rock, the Rhynie chert, has a U–Pb zircon age of 411.5 ± 1.3 Ma (measured [55]), position 66.93 (computed); the age c. 407 Ma is also used (measured [56]), position 66.92 (computed). Both are recorded.

Lichens are present at the same time. Internally stratified lichens with cyanobacterial and green-algal photobionts occur in 415 Myr rocks of the Welsh Borderland (measured [57]), position 66.93 (computed). The Rhynie lichen *Winfrenatia reticulata* is about 400 Ma (measured [58]; name in [57]). The genes the plant uses for the symbiosis are older than land plants: the signalling pathway, including CCaMK, is present in green algae (measured [59]).

Partners

Arbuscular mycorrhiza joins one fungal phylum, Glomeromycota, with 72 % of vascular plants (measured [47]). Vascular plants number 308,312 species (measured [1]); the AM host count is $0.72 \times 308,312 = 221,985$ (computed). Glomeromycota has about 360 described species in 49 genera, 17 families, 6 orders and 3 classes (measured [60]). The Neotropics hold 221 species, given as 69 % of the phylum (measured [61]), implying $221 / 0.69 = 320$ species (computed). Both totals are recorded. The host-to-fungus ratio is $221,985 / 360 = 617$ to $221,985 / 320 = 694$ (computed). Of 1,014 root samples worldwide, 93 % of AM taxa occur on more than one continent and 34 % on all six sampled (measured [62]).

Ectomycorrhiza is the reverse arrangement. On the fungal side it arose independently at least 66 times in Basidiomycota, Ascomycota and Zygomycota, with 162 proven genera (measured [63]); an update gives 78–82 lineages and 251–256 genera (measured [64]). Both counts are recorded. On the plant side the habit occurs in 30 monophyletic lineages, 335 genera and about 8,500 species; it evolved twice in gymnosperms and 28 times in angiosperms (measured [65]). Plants able to form ectomycorrhiza are estimated at 6,000–7,000 species, 1.7–2.4 % of embryophytes (measured [65]). Fungal species are 7,750 from the literature and 20,000–25,000 likely (measured [66]). The fungus-to-plant ratio is $20,000 / 6,000 = 3.3$ to $25,000 / 7,000 = 3.6$ (computed).

Lichenisation arose 20–30 times: 14–23 in Ascomycota and 6–7 in Basidiomycota (measured [48]). Lichenised fungi count 19,387 species in 995 genera; 172 of them, 0.9 %, are Basidiomycota (measured [48]).

Sizes

what	size	position	source
hyphal diameter, 31 soil-fungus strains	2.7–6.5 μm	3.72–4.51	measured [67]; positions computed
hyphae of the Rhynie lichen	1–4 μm	2.81–4.07	measured [58]; positions computed

net openings of the Rhynie lichen; its photobiont cell	about 25 μm ; 15 μm	5.74; 5.28	measured [58]; positions computed
thallus bands of the Rhynie lichen	1–2 mm	9.10–9.73	measured [58]; positions computed
AM spore, <i>Rhizophagus intraradices</i> (n = 170)	40–140 μm , mean 93.3 μm ; subtending hypha 11–18 μm	6.17–7.31; 6.94; 4.99–	measured [68]; positions computed
<i>Prototaxites</i> trunk	up to 8 m	17.28	measured [69]; position computed
<i>Armillaria ostoyae</i> genet, Oregon	about 965 ha; isolates up to about 3,810 m apart	22.89 (distance)	measured [70]; position computed
<i>Rhizocarpon geographicum</i> thallus, Norway	up to 120 mm	13.46	measured [71]; position computed
<i>Rhizocarpon alpicola</i> , largest recorded thallus	480 mm	14.72	measured [72]; position computed

The largest AM spore is $140 / 2.7 = 52$ times the thinnest hypha (computed). AM hyphae reach over 100 m per cm^3 of prairie soil and ectomycorrhizal mycelium up to 2,000 m per cm^3 (measured [73]). The 965 ha genet equals 9.65 km^2 (computed).

Times

what	duration or rate	position	source
hyphal extension per tip, 25 °C, means	21–125 $\mu\text{m}/\text{h}$; maximum branch rate 325 $\mu\text{m}/\text{h}$	—	measured [74]
mushroom fruit bodies	"a few days each year"; mean fruiting delayed 13.3 ± 1.2 d over 1940–2006	about 44.50;	measured [75]; positions computed
<i>Armillaria ostoyae</i> genet age	1,900–8,650 yr	55.74–57.12	measured [70]; positions computed
<i>Rhizocarpon geographicum</i> radial	0.23–1.47 mm/yr	—	measured [71]
slowest lichen growth, <i>Rhizocarpon</i>	0.006 mm/yr over 16 yr	—	measured [72]
lichen ages reported in the review	at least 4,500 yr; about 9,000 yr	56.53; 57.16	measured [72]; positions computed

The extension rates convert to $125 / 60 = 2.1$ $\mu\text{m}/\text{min}$ and $325 / 60 = 5.4$ $\mu\text{m}/\text{min}$ (computed). The *Armillaria* genet spread half of 3,810 m, 1,905 m, in 8,650–1,900 yr, which is 0.22–1.0 m/yr (computed).

Counts

Fungi have 120,000 accepted species against an estimate of 2.2–3.8 million (measured [76]). About 1,300 new species were named per year over 40 years and about 1,800 per year since 2010; the fungus-to-plant ratio is 9.8 : 1 (measured [76]). Glomeromycota 320–360 species (measured [60]; [61]). Ectomycorrhizal fungi 7,750 known, 20,000–25,000 likely (measured [66]). Lichenised fungi 19,387 (measured [48]). Of 3,617 surveyed plant species in 263 families, 80 % of species and 92 % of families are mycorrhizal (measured [77]); c. 85 % of extant plants are mycorrhizal (measured [78]). The three figures, 72 % AM, 80 % and 85 % mycorrhizal, are all recorded.

Lignin-degrading class II peroxidases expanded once, in the lineage leading to the ancestor of the Agaricomycetes, and contracted in parallel in brown-rot and mycorrhizal lineages (measured [79]).

The Agaricomycetes crown is 299 Ma (351–252 Ma) and the peroxidase diversification 350–295 Ma (measured [51]). Among 1,090 sequenced fungal genomes, 35.5 % are pathogens; 191 species are plant pathogens, 61.3 % of them on food crops (measured [80]). *Phytophthora*, an oomycete, has 142 described and 43 provisional species (measured [81]). *Arabidopsis thaliana* carries 149 NBS-LRR immune genes (measured [82]). Among 1,403 endophyte strains from the Arctic to Panama, incidence and diversity rise toward the tropics (measured [83]).

Order of events

1. 2.4 Ga: fungus-like filaments in basalt (measured [49]).
2. 1,010–890 Ma: *Ourasphaira* (measured [50]); crown Fungi about 1,020 Ma by clock (measured [51]).
3. About 720 Ma: loss of the flagellum; 659 Ma Glomeromycota; 649 Ma Dikarya (measured [51]).
4. 482 Ma: crown embryophytes; about 480 Ma: arbuscular mycorrhiza and the Leotiomyceta radiation (measured [51]).
5. About 460 Ma: glomalean spores and hyphae (measured [52]).
6. Earliest Silurian, after 443.8 Ma: *Tortotubus* (measured [53]; [5]).
7. 415 Ma: stratified lichens (measured [57]).
8. 411.5 ± 1.3 Ma or c. 407 Ma: arbuscules in *Aglaophyton*; lichen *Winfrenatia*; *Prototaxites* trunks of 8 m (measured [54]; [55]; [56]; [58]; [69]).
9. 350–295 Ma: peroxidase diversification; 299 Ma Agaricomycetes crown; lignin degradation "around the end of the Carboniferous" (measured [51]; [79]). A rebuttal holds that lignin-degrading fungi may predate the Carboniferous and that many coal horizons are unlignified lycopsid periderm (measured [84]). Both positions are recorded.
10. Early Jurassic: ectomycorrhizal habit present (measured [65]); Pinaceae crown 183 Ma (233–150 Ma) (measured [51]).
11. Cretaceous: second wave of mycorrhizal lineages (measured [47]); Agaricomycetidae 154 Ma (measured [51]).
12. 1904–1950s: chestnut blight in eastern North America; 1910–1970s: two Dutch elm pandemics, about 30 million elms killed in the UK (measured [85]; [86]).

Intervals: AM origin to Rhynie 480 – 407 = 73 Myr; Rhynie to Agaricomycetes crown 407 – 299 = 108 Myr; Agaricomycetes crown to Pinaceae crown 299 – 183 = 116 Myr (computed).

Present quantities

Plants allocate 13.12 Gt CO₂e per year to mycorrhizal mycelium (2001–2021 average): AM 3.93, EcM 9.07, ericoid 0.12 Gt CO₂e (measured [73]). In carbon this is $13.12 \times 12.011 / 44.009 = 3.58$ Gt C (computed), split AM 1.07, EcM 2.47, ericoid 0.03 Gt C (measured [73]). The shares of net primary production allocated are AM 6.2 %, EcM 13.1 %, ericoid 3.5 %, orchid 1.0 %, from 194 datasets (measured [73]). Vegetation cover is AM 57.4 %, EcM 25.7 %, ericoid 2.6 %, non-mycorrhizal 14.3 %; plant biomass of AM vegetation is 241 Gt C and of EcM vegetation 100 Gt C (measured [73]).

Pattern

Fungi precede plants on land in every record read: the fungal clock age, 1,020 Ma, is about twice the plant clock age, 482 Ma. Glomalean spores at 460 Ma and *Tortotubus* after 443.8 Ma predate the first plant with arbuscules in rock of 411.5 Ma. The symbiosis genes are older than the plants that carry them. One fungal phylum of 320–360 species partners 72 % of 308,312 vascular plant species, about 617–694 hosts per fungal species. The ectomycorrhizal habit arose 66 to 82 times in

fungi and 30 times in plants, with 3.3–3.6 fungal species per plant species. Lichenisation arose 20–30 times. Lignin-degrading peroxidases expanded once, at 299 Ma, and contracted repeatedly. Plants now pass 3.58 Gt C per year, 6.2–13.1 % of net primary production, to mycorrhizal mycelium. Hyphae of 1–6.5 μm build structures from 25 μm to 3,810 m and persist from days to 8,650 years.

Not verified

Tortotubus age of 440 Ma (Springer Nature Research Communities post on Smith 2016). *Prototaxites* tube diameter "<50 mm" as printed in metadata (unit unchecked); Hueber 2001 anatomy (citation only). Berbee et al. 2020 clock ages (paywalled). Oldest ectomycorrhizal fossil c. 52 Ma (Global Soil Biodiversity Initiative blog on Strullu-Derrien et al. 2018). Basidiospore $7.7 \times 6.1 \mu\text{m}$ and pileus 50–120 mm of *Agaricus bisporus* (Landcare Virtual Mycota quoting Mitchell & Walter 1999). Hyphal growth unit 35–682 μm and *Neurospora crassa* 100 $\mu\text{m}/\text{min}$ (Moore guidebook citing Bull & Trinci 1977, Steele & Trinci 1975). Arbuscule lifespan 4–15 d (Howarth teaching page, no primary). Beschel and Denton & Karlén lichen primaries (read in Armstrong 2016). The 295 Ma white-rot age in Floudas 2012 itself. Brasier 1991 species description (citation only). Four billion chestnuts killed (JSTOR Daily naming Lunsford 1999). Crop-loss shares up to 20 %, 35 %, 70 % (Asad et al. 2025 quoting Davies 2021, Różewicz 2021, Godfray 2016). Kew 2018 count of 144,000 described fungi (Botany One, Microbiology Society).

A3 Bacteria, Archaea and Nitrogen

What it is

Nitrogen fixation is the reduction of atmospheric N_2 by the enzyme nitrogenase, found only in bacteria and archaea (measured [87]). Plants obtain fixed nitrogen by housing the fixers: rhizobia in legume nodules, *Frankia* in actinorhizal nodules, and *Nostoc* in cycads, hornworts, liverworts, *Azolla* and *Gunnera* (measured [88]; [89]; [90]; [91]). Two older acquisitions of a bacterium are the chloroplast and the mitochondrion (measured [92]; [93]).

First appearance

Nitrogen fixation precedes atmospheric oxygen. Sedimentary rocks 3.2–2.75 Gyr old carry a mean $\delta^{15}\text{N}$ of $0.0 \pm 1.2 \text{‰}$, read as biological N_2 fixation, most probably by Mo-nitrogenase; the minimum age is 3.2 Gyr (measured [94]), position 68.79 (computed). A molecular clock places the origin at roughly 1.5–2.2 Ga (measured [87]), positions 68.10–68.45 (computed). The two differ by 1.0–1.7 Gyr (computed); both are recorded. The same study dates the last universal common ancestor at about 3.5–3.8 Ga and finds nitrogenase absent from it (measured [87]). A second clock puts that ancestor older than 3.9 Ga (measured [95]), position 68.97 (computed).

The Great Oxidation Event is dated 2.33 Ga from sulfur isotopes in three drill cores, with oxygenation within 1–10 Myr (measured [96]), position 68.50 (computed). Another reading places glaciation during the event at 2,460–2,426 Ma (measured [97]), positions 68.55–68.54 (computed). Both dates are recorded. The interval from the fixation minimum to the event is $3.2 - 2.33 = 0.87$ Gyr or $3.2 - 2.46 = 0.74$ Gyr (computed).

The chloroplast lineage branches within the cyanobacteria at about 2.1 Ga, and establishment took another about 200 Myr (measured [92]); positions 68.41 and 66.27 for the interval (computed). A second figure gives the symbiosis as more than 1.5 Ga old (measured [91]). Both are recorded. The

mitochondrial origin is dated 2.053–1.21 Ga and crown eukaryotes younger than 1.84 Ga (measured [95]); positions 68.39–67.91 and 68.29 (computed).

Root nodules are Cretaceous. A phylogeny of 32,223 species places a single origin of the nodulation predisposition slightly over 100 Ma, within Fabidae (measured [98]), position 65.64 (computed). A second source gives legumes at about 60 Ma and nodulation at about 58 Ma (measured [99]), positions 65.17 and 65.14 (computed). The difference is $100 - 58 = 42$ Myr (computed); both are recorded. The oldest unequivocal legume fossil is 65.35 Ma (measured [100]), position 65.25 (computed). Soil itself is older: organic matter in a palaeosol of South Africa, dated 2.6–2.7 Gyr, is read as microbial mats on the soil surface (measured [101]), positions 68.60–68.64 (computed).

Partners

Nitrogenase occurs in three forms: Mo-nitrogenase (nif), V-nitrogenase (vnf) and Fe-only nitrogenase (anf) (measured [87]). The alternatives are nested within the Mo lineage, so Mo came first; an active Mo enzyme needs at least six genes, nifHDKENB (measured [87]). In archaea the genes are limited to methanogens of Methanococcales, Methanobacteriales and Methanosarcinales (measured [87]). In bacteria they occur in cyanobacteria, Firmicutes, Chloroflexi, Chlorobi, Bacteroidetes, Actinobacteria, Proteobacteria and Aquificales; 21 of 44 sequenced cyanobacterial genomes carry nif (measured [87]). No eukaryote carries the genes (measured [87]).

Nodulating plants fall in about 10 of about 380 angiosperm families, all in one clade (measured [102]). The clade comprises Fabales, Rosales, Cucurbitales and Fagales; within it nodulation originated about 8 ± 2.47 times and was lost about 10 ± 2.80 times, with 16.7 ± 3.21 losses of the precursor (measured [98]). Genomes of 37 species show the NIN gene lost in 10 of 13 non-nodulating species, at least eight independent loss events (measured [103]). Legumes number over 19,500 species in 765 genera and six subfamilies; nodules are usually present in Papilionoideae (about 14,000 species), variably in Caesalpinoideae (about 4,400) and absent in the four others (measured [104]). The two nodulating subfamilies hold $14,000 + 4,400 = 18,400$ species, 94.4 % of 19,500 (computed, an upper bound). An infection route without infection threads persists in 25 % of legumes (measured [99]).

Rhizobia occur in Alphaproteobacteria and Betaproteobacteria; 13 alphaproteobacterial genera and 2 betaproteobacterial genera are named (measured [88]). One tree, *Vachellia karroo*, yielded 88 nodule isolates in 7 genera and 26 putative species (measured [105]). Actinorhizal plants are 8 families, 24 genera and over 220 species (measured [89]); a second count gives 25 genera (measured [106]). *Frankia* falls in three clades with genomes of 5.43, 7.50 and 9.04 Mbp (measured [107]). Cyanobacterial hosts: 13 hornwort genera, 4 of more than 340 liverwort genera (measured [90]), 382 cycad species in 10 genera (measured [108]), *Azolla* and *Gunnera*, the only angiosperm host (measured [91]). Seven plant genes are required for both arbuscular mycorrhiza and root-nodule symbiosis (measured [109]).

Sizes

what	size	position	source
hormogonia pili of <i>Nostoc</i>	7–10 nm wide; up to 10 μ m long	–1.71 to –1.38; 4.91	measured [90]; positions
mean distance between bacterial	12.46 μ m; 10.38 μ m near the surface; >18 μ m at depth; 29 μ m below 60 cm	5.11; 4.94; >5.44; 5.88	measured [110];
soybean nodule diameter at day	5 mm	10.56	measured [111]; position

<i>Eospermatopteris</i> roots, Middle	0.7–1 cm; depth up to 30 cm	10.87–11.19; 14.29	measured [112];
<i>Archaeopteris</i> roots, about 385	primary roots 6–16 cm; laterals 1–1.5 cm; rootlets about 1 mm; depth 1.2–1.6	12.83–13.72; 11.19–11.56; 9.10; 15.55–	measured [112];
chloroplast genome,	154,478 bp	—	measured [113]
<i>Prochlorococcus</i> MED4 genome	1,657,990 bp	—	measured [114]

Rooting depth rose by $1.2 / 0.3 = 4$ to $1.6 / 0.3 = 5.3$ within the Middle Devonian (computed). The chloroplast genome is $154,478 / 1,657,990 = 9.3$ % of the small cyanobacterial genome (computed).

Times

what	duration	position	source
soil bacterial turnover, about 20 °C, 19 soils	2.3–33 d, mean 9.3 d	44.26–46.68; 45.53	measured [115]; positions computed
soil bacterial turnover, 25 °C, older studies	107–160 d	47.75–48.12	measured [115]; positions computed
rhizosphere bacterial turnover	12–19 h; 9–60 h	42.87–43.29; 42.61–44.33	measured [115]; positions computed
soil fungal turnover, unamended	130–150 d	47.93–48.06	measured [115]; positions computed
root-hair curling peak; nodule swelling; 5 mm nodule	day 8; day 15; day 45	45.39; 45.96; 46.96	measured [111]; positions computed
hormogonia motility	0.7–1.7 $\mu\text{m/s}$	—	measured [90]
akinetete dormancy	up to 60 yr	52.60	measured [116]; position
oxygenation at the Great Oxidation Event	1–10 Myr	61.45–63.54	measured [96]; positions
chloroplast establishment	about 200 Myr	66.27	measured [92]; position
Eocene <i>Azolla</i> event	about 800,000	61.24	measured [117]; position

Bacterial growth rises fifteenfold from 0 to 20 °C and falls about fivefold from pH 8.3 to 4.0 (measured [115]). In symbiosis cyanobionts grow 5–10 times slower than free-living cells (measured [90]).

Counts

A gram of soil holds up to 10^{10} bacterial cells; a modelled bulk density is 10^8 cells per gram; species per gram are estimated at 4×10^3 to 5×10^4 (measured [110]). At 10^8 cells per gram and 1.3 g/cm^3 this is 1.3×10^8 cells per cm^3 (computed). DNA reassociation gives about 4,000 distinct genomes in one soil bacterial fraction (measured [118]). Across 237 sites on six continents, about 2 % of phylotypes, about 500, make up nearly half of soil bacterial communities (measured [119]); the implied total is $500 / 0.02 = 25,000$ phylotypes (computed). Archaeal amoA genes are up to 3,000-fold more abundant than bacterial amoA in 12 soils (measured [120]).

Heterocyst frequency is 4–10 % of cells in free-living *Nostoc* and 30–50 % in symbiosis; the cyanobiont retains as little as 20 % of the nitrogen it fixes (measured [90]). Within coralloid roots the frequency rises up to 80 %; cyanobiont genomes are 5.4–9.0 Mbp (measured [116]). About

4,500 *Arabidopsis* protein-coding genes, about 18 %, are of cyanobacterial origin (measured [121]). The chloroplast genome holds 87 protein-coding genes, 4 rRNA and 37 tRNA genes (measured [113]). The *Paulinella* chromatophore retains 841 and 867 protein-coding genes against 2,917 in *Synechococcus* WH5701, 28.8–29.7 % (measured [122]; share computed); its maximum age is about 90–140 Myr (measured [122]). Rhizobial species per crop: common bean 14, soybean 11, cowpea 6, chickpea 5, peanut 5 (measured [123]). Grasses allocate 33 % of assimilated carbon below ground, annual crops 21 % (measured [124]). Cell-wall features of other plant species assemble about 40 % of the root microbiota (measured [125]).

Order of events

1. Older than 3.9 Ga or 3.5–3.8 Ga: last universal common ancestor, without nitrogenase (measured [95]; [87]).
2. 3.2 Ga: isotopic minimum age of biological nitrogen fixation (measured [94]); clock alternative 1.5–2.2 Ga (measured [87]).
3. 2.6–2.7 Ga: microbial mats on a palaeosol (measured [101]).
4. 2,460–2,426 Ma or 2.33 Ga: Great Oxidation Event (measured [97]; [96]).
5. About 2.1 Ga: chloroplast lineage, establishment over about 200 Myr (measured [92]); 2.053–1.21 Ga: mitochondrion; younger than 1.84 Ga: crown eukaryotes (measured [95]).
6. About 385 Ma: *Archaeopteris* roots 1.2–1.6 m deep after *Eospermatopteris* roots of 30 cm (measured [112]). Roots evolved piecemeal and independently in several clades through the Devonian (measured [126]).
7. Slightly over 100 Ma: single origin of the nodulation predisposition (measured [98]). *Azolla*–cyanobiont relationship about 100 Myr by fossils (measured [117]) or more than 60 Myr (measured [91]).
8. 65.35 Ma: oldest legume fossil (measured [100]); about 60 Ma legumes, about 58 Ma nodulation (measured [99]); about 8 nodulation origins and 10 losses in four orders (measured [98]).
9. Maximum 90–140 Ma: *Paulinella* chromatophore, a second primary endosymbiosis (measured [122]).
10. Present: Haber–Bosch at 120 Tg N per year (measured [127]).

Intervals: fixation to oxidation 0.74–0.87 Gyr; oxidation at 2.33 Ga to the chloroplast lineage at 2.1 Ga 0.23 Gyr; chloroplast to nodulation predisposition 2.0 Gyr (computed).

Present quantities

Pre-industrial terrestrial biological fixation is 58 Tg N per year (range 40–100) (measured [128]); a second compilation gives 128 Tg N per year (measured [127]). Both are recorded. Marine biological fixation is 140 Tg N per year (measured [129]) or 120 (100–200) (measured [127]). Haber–Bosch produces 120 Tg N per year and lightning 5 Tg N per year (measured [127]). Total reactive nitrogen creation is 413 Tg per year, of which 210 Tg is anthropogenic (measured [129]). Agricultural fixation is 50–70 Tg N per year, with soybean 16.4, 77 % of crop-legume nitrogen (measured [130]). Haber–Bosch is $120 / 58 = 2.07$ times the pre-industrial terrestrial rate and 24 times lightning (computed). Rice paddies emit 30 (25–38) Tg CH₄ per year of a top-down total of 576 (measured [131]), 5.2 % (computed). Global biomass is about 550 Gt C: plants 450, bacteria 70, archaea 7, animals 2 (measured [132]).

Pattern

Nitrogen fixation is older than oxygen, 3.2 Ga against 2.33–2.46 Ga, and it stays confined to bacteria and archaea. Plants never acquired the enzyme; they acquired the organisms. The

acquisition recurs: one cyanobacterium became the chloroplast at about 2.1 Ga and a second became the *Paulinella* chromatophore at most 140 Ma; the two retain 9.3 % and 28.8–29.7 % of a free-living genome. One predisposition for nodules arose slightly over 100 Ma; nodulation then appeared about 8 times and was lost about 10 times inside four orders. Legumes (19,500 species) and actinorhizal plants (220 species) house rhizobia and *Frankia*; cycads (382 species), 13 hornwort genera, 4 liverwort genera, *Azolla* and *Gunnera* house *Nostoc*. Heterocyst frequency rises from 4–10 % to 30–50 % in symbiosis. Soil holds 10^8 – 10^{10} cells per gram, 12.46 μm apart, turning over in 2.3–33 days. Haber–Bosch, 120 Tg N per year, is 2.07 times the pre-industrial terrestrial rate.

Not verified

Nitrogenase dissociation rate 6 s^{-1} , ATP per N_2 20–30, H_2 electron share 27.3 %, Fe-protein half-life about 45 s and MoFe about 10 min (BioNumbers naming Thorneley & Lowe 1983, Burris 1991, Orme-Johnson, Berman-Frank et al.). *E. coli* $1 \times 2\text{ }\mu\text{m}$, $1\text{ }\mu\text{m}^3$, 1 pg, doubling about 20 min (book.bionumbers.org). *Frankia* vesicles 2–6 μm with 4 nm envelope laminae (UConn site naming Berry et al. 1993); Berry et al. 1993 hopanoid envelope (citation only). Soybean nodule timing, visible 10–14 d, fixing at 3 weeks, senescent at 6–7 weeks (Purdue proceedings, no primary). Heterocyst increase of 25–35 % (Lindblad 1985a in Chang et al. 2019). Closest plastid relative *Gloeomargarita lithophora* (de Vries & Archibald 2017 on Ponce-Toledo et al. 2017, citation only). Marin et al. 2005 second endosymbiosis (citation only). Terrestrial microfossils of 1.2 Gyr, Arizona (within the Watanabe abstract). Algeo & Scheckler 1998 (no numbers); Philippot et al. 2013 (no numbers read). Tomato yield rise 31.5–39 % with a *Bacillus*–*Serratia* consortium (Niu et al. 2016 in Backer et al. 2018). Global count of rhizobial genera and species; *Gunnera* and *Azolla* species totals; Haber–Bosch start date.

A4 Animals and Seed Dispersal

What it is

Seed dispersal by animals is the carriage of a seed away from the parent plant by an animal that eats, hoards or carries it. The measured partners are fleshy fruits, nuts and elaiosome-bearing seeds on the plant side and fishes, reptiles, birds, mammals and ants on the animal side (measured [133]; [134]; [135]). Among terrestrial birds 1,230 of 8,918 species eat fruit (measured [136]).

First appearance

Seeds first appeared in the late Middle or Late Devonian (measured [133]); the Givetian begins at 387.7 Ma and the Famennian ends at 358.9 Ma (measured [5]), positions 66.87–66.80 (computed). By the Pennsylvanian, 323.2–298.9 Ma (measured [5]), positions 66.71–66.63 (computed), large flesh-covered seeds had evolved in seed ferns and cordaitaleans (measured [133]). Medullosan seeds averaged 20,000–50,000 mm^3 and one species exceeded 300,000 mm^3 ; cordaitalean seeds were 122 to more than 12,000 mm^3 (measured [133]). Clear vertebrate dispersers are absent at that time; plant-eating vertebrates first diversified in the Permian, 298.9–251.902 Ma (measured [133]; [5]), positions 66.63–66.48 (computed).

The oldest seed ingestion read is Late Permian: nearly 60 seeds of the conifer *Pseudovoltzia* in the gut of the reptile *Protorosaurus* (measured [133]). An Early Cretaceous ankylosaur about 1.4 m long held three fruits of 4.5 mm and seeds of 0.3 mm (measured [133]). A Campanian coprolite, probably from a turtle, holds nearly 200 achenes of early Ranunculaceae (measured [133]); the Campanian spans 83.6–72.1 Ma (measured [5]), positions 65.47–65.34 (computed). Fleshy fruits

and angiosperm seed-size diversification began around 80 Ma, position 65.41, and diversity peaked in the Eocene at 55–50 Ma, positions 65.09–65.01 (measured [137]; positions computed).

The main disperser groups follow. Palaeognathae and Neognathae split about 100 Ma and Galloanseres and Neoaves about 88 Ma (measured [138]). Thirty-six Neoaves lineages arose within 10–15 Myr after the K–Pg boundary at 66 Ma; nearly all ordinal divergences were complete by 50 Ma (measured [138]). The basal split of Passeriformes is about 39 Ma (measured [138]). The positions are 65.64, 65.52, 65.26, 65.01 and 64.78 (computed). The oldest primate skeleton is early Eocene, about 55 Ma, position 65.09 (measured [139]; position computed). The oldest bat, *Onychonycteris finneyi*, is Early Eocene (measured [140]), 56.0–47.8 Ma (measured [5]), positions 65.11–64.97 (computed). Crown Old World fruit bats are 31–20 Ma (measured [141]), positions 64.57–64.17 (computed). Scatter-hoarding of nuts may date to the Paleocene, about 60 Ma (measured [142]). Myrmecochory is more frequent in families with crown ages under 80 Myr (measured [143]).

Partners

Plant side. Biotic dispersal occurs in 30 % of angiosperm families, with a further 22 % both biotic and abiotic; by species 14 % biotic and 42 % both (measured [133]). In gymnosperms 64 % of families and 46 % of species are biotically dispersed, with a further 39 % of species both (measured [133]). Palms are almost entirely animal-dispersed (measured [133]). Ant dispersal occurs in at least 11,000 species, about 4.5 % of angiosperms, in 334 genera and 77 families, and arose at least 101 times, possibly up to 147 (measured [143]). Most origins are in Asteraceae (10), Euphorbiaceae (8), Fabaceae (6), Ranunculaceae (5) (measured [135]). Myrmecochores had more species than their sister group in 68 of 101 comparisons, about 2.24 times as many (measured [135]). In Brazil 103 of 1,361 sampled species carry the megafaunal-fruit syndrome; 83.3 % are trees (measured [144]). Nut dispersal by scatter-hoarders covers 10 genera (measured [142]).

Animal side. Frugivorous fishes exceed 275 species, mainly Characiformes and Siluriformes (measured [134]); in serrasalmids frugivory evolved from omnivory (measured [145]). Birds number 11,063 extant species in 251 families (measured [146]). Of 8,918 terrestrial bird species, 1,230 are frugivores, 365 of them obligate; passerines supply 618 frugivores, 50 % of the total; Columbiformes 179, Psittaciformes 141, Piciformes 112, Musophagiformes 23 (measured [136]). Frugivores are $1,230 / 8,918 = 13.8$ % of terrestrial birds (computed). Mammals number 6,399 extant species (measured [147]); birds to mammals $11,063 / 6,399 = 1.73$ (computed). Corvids disperse *Pinus* and *Quercus* (measured [148]). Megafauna above 1,000 kg: 13 genera in the Neotropics at the end of the Pleistocene, none surviving; 5 extant genera in Africa and 2 in Asia (measured [144]).

Sizes

what	size	position	source
medullosan seed volume,	20,000–50,000 mm ³ ; one species >300,000 mm ³	12.30–12.58; 13.12 (equivalent sphere	measured [133]; diameters and
cordaitalean seed	122 to >12,000 mm ³	10.75–12.14 (6.2–28.4	measured [133];
ankylosaur gut, Early Cretaceous	fruits 4.5 mm; seeds 0.3 mm; animal 1.4 m	10.47; 8.00; 15.69	measured [133]; positions
Early Cretaceous bird with plant	about 60 cm	14.92	measured [133]; position
seed diameter dispersed by extant	about 3.5–4.0 cm; African cephalophines about 2.8 cm;	12.33–12.46; 12.13; 12.03	measured [144]; positions
megafaunal fruit, Type I / Type II	4–10 cm / >10 cm diameter; mass 50–1,000 g; seed load up	12.46–13.29 / >13.29	measured [144]; positions
jackfruit	20–90 cm long, 15–50 cm wide, up to 50 kg; seeds 2–4	13.92–15.29; 13.66–14.76; 12.03–12.46	measured [149]; positions
<i>Silene stenophylla</i> burrow depth	38 m	18.70	measured [150]; position

Seed mass in megafaunal fruits is 0.2–97.4 % of fruit mass against 0.1–8.9 % in other fruits (measured [144]). Energy per nut is 5.7–153.5 kJ, 10 to 1,000 times most wind-dispersed seeds (measured [142]). Across 12,987 species the angiosperm–gymnosperm split is the largest single contributor to the present spread of seed mass (measured [151]); seed-mass shifts track growth form more than dispersal syndrome or climate (measured [152]).

Times

what	duration	position	source
passerine gut passage, Mediterranean	mostly 5–30 min; species means 22.9–69.4 min	38.34–39.98; 39.73–40.74	measured [153]; positions computed
forest elephant gut	mean 39.5 h; range 16.6–112.7 h	43.95; 43.16–44.02	measured [154]; positions
date palm seed, Masada, germinated	first century CE, about 2,000 yr	55.79	measured [155]; age and position computed
<i>Silene stenophylla</i> fruit	31,800 ± 300 ¹⁴ C yr	58.31	measured [150]; position
European beech extreme mast years, 1773–2011	15 events; mean spacing 17.0 yr; wavelet band 7–16 yr	51.45; 50.64–51.39	measured [156]; spacing and positions computed
shared beech–spruce mast events, 1974–2011	8 events; mean spacing 5.3 yr	50.39	measured [156]; computed
bird generation length	1.42–27.87 yr; median 2.99	49.19–51.90; 40.87	measured [157]; positions
megafauna extinction	10–15 kyr BP	57.25–57.62	measured [144]; positions
post-glacial nut-tree	last 16,000 yr	57.68	measured [142]; position
onset of domestication	11,000–10,000 yr BP	57.34–57.25	measured [158]; positions

The elephant mean passage is 39.5 h / 17.5 min = 135 times the passerine mid-range (computed). An 80 g disperser had a gut-passage time like a 9 g non-disperser (measured [153]). Masting synchrony extends to sites 1,000 km apart (measured [159]); oaks that take two years to mature acorns show negative autocorrelation at lag 2 (measured [160]). The *Silene* result is tissue regeneration; the date palm is a germinated seed (measured [150]; [155]).

Dispersal distances form their own scale. Ants carry seeds about 1 m, range 0.01–77 m (measured [135]), positions 15.39 and 11.19–19.34 (computed). For *Prunus mahaleb*, small passerines moved half the seeds less than 51 m, medium birds half more than 110 m, carnivorous mammals half more than 495 m (measured [161]), positions 18.97, 19.66 and 21.03 (computed). Forest elephants moved seeds a median 5.3 km, mean 6.5 km, 95 % quantile 16.4 km (measured [154]). Of their seeds 89 % went beyond 1 km; the longest simulated distance is 101 km (measured [154]). The positions are 23.19, 23.38, 24.22, 21.67 and 25.87 (computed). Extinct megafauna dispersed over 10^3 – 10^4 m against 10^1 – 10^3 m for extant dispersers (measured [144]). The span from ant mean to elephant median is $5,300 / 1 = 5,300$ (computed).

Counts

Birds 11,063 extant species, 2,389 genera, 251 families, 44 orders, 164 extinct (measured [146]). Mammals 6,495 recognised species, 6,399 extant, 1,314 genera, 167 families, about 25 new per year (measured [147]). Frugivorous birds 1,230, obligate 365, opportunistic a further 1,659 (measured [136]). Frugivorous fishes more than 275 (measured [134]). Myrmecochorous plants at least 11,000 species, 101–147 origins (measured [143]); the implied angiosperm total is $11,000 / 0.045 = 244,444$ (computed). Regional shares: Australia 134 genera and at least 1,500 species; fynbos about 1,200 species, 20 % of the flora; eastern North American forests 30–40 % of herbs; eastern European forests 40–50 % (measured [135]). A global seed-ingestion dataset holds 13,135 animal × seed interactions; ingested seed size is negatively related to body mass overall, positively when ungulates and dry fruits are excluded (measured [162]). Costa Rican canopy trees: 200 of 240 species, 83.5 %, animal-dispersed; zoochory exceeded 75 % of stems after about 17 yr for seedlings and about 35 yr for trees ≥ 10 cm dbh (measured [163]). Panama seed rain: 386,027 seeds in 200 traps over 4 years, 13,068 seedlings (measured [164]); 482.5 seeds per trap-year and 3.39 % seedlings per seed (computed). Frugivore richness peaks in the Neotropics; actual evapotranspiration explains 71–73 % of its variation (measured [136]).

Order of events

1. Late Middle or Late Devonian: first seeds (measured [133]).
2. Pennsylvanian, 323.2–298.9 Ma: fleshy seeds of 20,000–50,000 mm³; no clear vertebrate dispersers (measured [133]; [5]).
3. Permian, 298.9–251.902 Ma: first diversification of plant-eating vertebrates; *Protorosaurus* with about 60 conifer seeds (measured [133]; [5]).
4. Mesozoic: large herbivorous dinosaurs as possible whole-plant dispersers; Early Cretaceous ankylosaur and bird with plant remains; Portuguese flora about 25 % fleshy (measured [133]). About 100 Ma and 88 Ma: basal bird splits (measured [138]). About 80 Ma: onset of fleshy-fruit diversification (measured [137]). Campanian turtle coprolite with about 200 achenes (measured [133]).
5. 66 Ma: K–Pg boundary; 36 Neoaves lineages within 10–15 Myr (measured [138]); seed-size increase already under way before the boundary (measured [165]).
6. About 60 Ma: scatter-hoarding may begin (measured [142]). About 55 Ma: oldest primate skeleton (measured [139]). 56.0–47.8 Ma: oldest bat (measured [140]; [5]). 55–50 Ma: peak of seed and fruit size diversity (measured [137]). 50 Ma: bird ordinal divergences complete (measured [138]).
7. About 34 Ma: Eocene–Oligocene climate shift; seed and fruit sizes decline and stay low (measured [137]; [165]). About 39 Ma: passerine basal split (measured [138]). 31–20 Ma: crown fruit bats (measured [141]). Middle Oligocene: oldest frugivorous bat fossil (measured [133]).

8. Oligocene–Miocene: flying frugivores in their main phase; wind dispersal high again (measured [137]; [165]).
9. 10–15 kyr BP: megafauna extinction; long-distance dispersal contracted by at least two thirds in South America (measured [144]; [166]). More than 15 genera of Central American large herbivores extinct roughly 10,000 years ago (measured [167]).
10. 11,000–10,000 yr BP: domestication begins (measured [158]).

The gap between Pennsylvanian fleshy seeds and the 80 Ma onset of angiosperm fleshy-fruit diversification is at least $298.9 - 80 = 218.9$ Myr (computed).

Present quantities

The capacity of animals to move nutrients away from concentration patches is about 8 % of its pre-extinction value on land and about 5 % in the oceans (measured [168]). Marine mammal upward phosphorus transport is about 23 % of a former 340×10^6 kg P per year (measured [168]). Seabirds and anadromous fish formerly moved about 150×10^6 kg P per year from sea to land (measured [168]). Fruit density reaches near 10^6 fruits per hectare at some Mediterranean scrub sites (measured [153]). Bird generation lengths: 61 % of species under 3.33 yr (measured [157]). Generation-length records exist for 5,427 of 6,399 mammals, 84.8 % (measured [169]; share computed).

Pattern

Fleshy seeds precede their dispersers by about 220 Myr: Pennsylvanian seed ferns and cordaites had flesh-covered seeds of 10^4 – 10^5 mm³, and plant-eating vertebrates diversified only in the Permian. Seed ingestion recurs in reptiles, Late Permian, Early Cretaceous and Campanian, before birds and mammals. Angiosperm fleshy fruits diversify from about 80 Ma, peak at 55–50 Ma and shrink after about 34 Ma. Disperser radiations follow: 36 Neoaves lineages within 10–15 Myr after 66 Ma, primates by 55 Ma, bats 56–48 Ma, fruit bats 31–20 Ma. Dispersal distance scales with the disperser: ants 1 m, passerines 51 m, mammals 495 m, elephants 5.3 km median and 101 km maximum; gut passage 5–30 min in passerines and 39.5 h in elephants. Ant dispersal arose at least 101 times in at least 11,000 species. Tropical canopy trees are 83.5 % animal-dispersed; 13.8 % of terrestrial birds eat fruit. Megafauna loss at 10–15 kyr cut long-distance dispersal by at least two thirds and land nutrient transport to about 8 %.

Not verified

Tropical trees 70–90 % zoochorous (Howe & Smallwood 1982, read through Wendt et al. 2022; Howe & Smallwood citation only). Tiffney 1984 on abiotic Cretaceous dispersal (citation only). Seed-mass range of 11.5 orders, about 0.0001 mg to about 20 kg (Prometheus Protocols page naming Moles et al. 2005 and Leishman et al. 2000); tropical seeds 300 times larger than cold-region seeds (Science in Public page on Moles). Largest ingested seed 9 cm, *Balanites wilsoniana*, 4-tonne elephants, Chatham Islands skinks (UNSW news on Chen & Moles 2015). Clark's nutcracker transport up to 30 km (BOU page on Pesendorfer et al. 2016). Old World domesticates: 71 crop species in seven groups (Royal Society of Biology review of Zohary, Hopf & Weiss 2012). Herrera 1984 Ecological Monographs companion paper, Koenig & Knops 2005, Purugganan & Fuller 2009 (citations only; no numbers). Kelly & Sork 2002 interval tables; Nathan et al. 2008 distance figures; elephant generation time; hummingbird and elephant body mass in a primary; smallest berries; jackfruit 35 kg (read as 50 kg).

A5 Soil Life and Nutrient Cycles

What it is

Soil life is the set of bacteria, archaea, fungi, protists, nematodes, mites, springtails, enchytraeids and earthworms that live between mineral grains and plant roots. Soil holds 59 ± 15 % of Earth's species (measured [170]). The organisms return nitrogen and carbon from dead plant matter: in a shortgrass prairie bacteria mineralise $4.5 \text{ g N m}^{-2} \text{ yr}^{-1}$, fauna 2.9 and fungi 0.3 (measured [171]).

First appearance

Soil is recorded as a product of life from 2.6–2.7 Gyr, in palaeosols of South Africa whose organic matter is read as microbial mats (measured [101]). One section is 17 m thick (measured [101]). The positions are 68.60–68.64 for the age and 17.97 for the section (computed). Ediacaran palaeosols of South Australia, 635–542 Ma in the abstract, carry *Charniodiscus*, *Dickinsonia* and *Tribrachidium* in growth position on the uppermost soil surfaces, read as lichens and microbial crusts (measured [172]); positions 67.32–67.18 (computed). The 2023 chart places the Ediacaran base at about 635 Ma (measured [5]).

Animals burrowed in soil before any rooted plant. Burrows in buried soils of the Late Ordovician Juniata Formation, Pennsylvania, are the oldest reported non-marine trace fossils; they are most concentrated near the top of the palaeosols (measured [173]). Named *Scoyenia beerboweri*, they cut and are cut by pedogenic carbonate nodules (measured [174]). Backfill banding and faecal pellets indicate a bilaterally symmetrical sediment-eater with discontinuous growth, most likely a millipede (measured [174]). Vegetation is unknown; liverwort spores are widespread in rocks of that age (measured [174]). The Ordovician ends at 443.8 Ma (measured [5]), so the burrows are older than that, position 66.99 (computed).

The first soil fauna preserved in place is in the Rhynie and Windyfield cherts, Pragian, 410.8–407.6 Ma (measured [5]), position 66.92 (computed). It holds the oldest unequivocal nematodes, trigonotarbid arachnids, mycophagous mites, a harvestman, a centipede and a putative millipede (measured [175]). It also holds springtails, the earliest true insects with chewing mandibles, and coprolites (measured [175]). Fourteen oribatid mite fossils from the Devonian near Gilboa, New York, in two species and two new families, roughly doubled the known age of the group (measured [176]). The clitellate annelids have a freshwater common ancestor in the Devonian, roughly 419–359 Ma, from 74 transcriptomes (measured [177]); positions 66.94–66.80 (computed). The earthworm crown group is dated to the Carboniferous–Permian boundary (measured [178]), 298.9 Ma (measured [5]), position 66.63 (computed). The gap from the clitellate ancestor to the earthworm crown is 60–120 Myr (computed).

Partners

On the plant side are roots, litter and root exudates: fine roots turn over at 53–56 % per year in grasslands, wetlands and forests, entire tree root systems at 10 % (measured [179]). On the organism side the Devonian record names trees, deeper roots and seeds, which made soils thicker and more widespread and intensified chemical weathering (measured [180]). Arbuscular mycorrhizal fungi coincided with the colonisation of land; ectomycorrhizal fungi rose in the Cenozoic with gymnosperm and angiosperm trees (measured [181]). In field experiments hyphae preferentially colonised silicate basalt; weathering increased from arbuscular to ectomycorrhizal hosts and from gymnosperm to angiosperm hosts; angiosperms released calcium from basalt at twice the rate of gymnosperms (measured [182]).

The detrital food web of a shortgrass prairie has 13 functional groups (measured [171]). They are bacteria, fungi, root-feeding nematodes, collembolans, fungal-feeding mites, fungal-feeding nematodes, flagellates, bacterial-feeding nematodes, amoebae, omnivorous nematodes, predaceous nematodes, nematode-feeding mites and predaceous mites (measured [171]). Bacterial-feeding amoebae and nematodes together supply over 83 % of faunal nitrogen mineralisation (measured [171]). Bacterivory by protists is a major cause of bacterial mortality (measured [183]). Nematodes fill all trophic levels in five feeding guilds; bacterivores are most abundant, predators least (measured [184]; [185]).

Earthworms arose on Pangaea: splits between northern and southern families are dated 161–186 Ma, with Pangaea break-up given as about 200–185 Ma; clitellate body fossils are Permian (measured [186]). Earthworms count 5,406 species and 332 subspecies in 23 families and 382 genera (measured [187]). Of these, 1,201 taxa were described since 2000; the estimated total is well over 8,000 (measured [187]). An earlier count gave about 3,000–3,500 valid species (measured [188]). Both are recorded.

Sizes

what	size	position	source
soil protists	a few μm (<i>Mycamoeba</i>) to more than 1 mm (<i>Darbyshirella</i>); largest testate	about 3.44 to	measured [183]; positions
mean fresh mass of a soil	$0.3 \times 10^{15} \text{ g} / 4.4 \times 10^{20} = 0.68 \mu\text{g}$	—	computed from [184]
earthworm burrow diameter, <i>Lumbricus terrestris</i> /	7.78 mm / 5.16 mm	10.97 / 10.59	measured [189]; positions
burrow system length after 6 weeks, <i>L. terrestris</i> / <i>A.</i>	9.2 m / 21.2 m / 15.7 m	17.41 / 18.17 /	measured [189]; positions
macro-aggregate threshold	>250 μm	7.84	measured [190]; position
soil depths of the global stocks	30 cm; 1 m; 2 m; 3 m	14.29; 15.39;	measured [191]; [192]; positions
<i>Archaeopteris</i> rooting depth, about 385 Ma	1.2–1.6 m	15.55–15.81	measured [112]; positions

Earthworm biomass is typically 1–150 g m⁻² and abundance 5–150 individuals m⁻², mean 57.0 (measured, preprint [193]). Soil nematodes number $4.4 \pm 0.64 \times 10^{20}$ with a biomass of about 0.3 Gt (measured [184]). Per 100 g dry soil the median is 859 and the mean 2,671 nematodes; tundra 2,695, hot desert 44 (measured [185]). At a bulk density of 1.3 g cm⁻³ over 15 cm this is 1.3×10^6 to 4.0×10^6 m⁻² (computed). Soil protists reach tens of thousands of individuals per gram, with dormant banks of 10⁴–10⁷ per gram (measured [183]).

Times

what	duration	position	source
bacterial turnover, bulk soil, about 20	2.3–33 d, mean 9.3 d; 30 d count-based minimum	44.26–46.68; 45.53; 46.60	measured [115];
bacterial turnover, rhizosphere	12–19 h; generation times as short as 7.5–9.1 h; doubling 24 h on young roots to	42.87–43.29; 42.44–42.62;	measured [115];
fungal turnover, soil	20–40 d amended; 130–150 d unamended; 170 d at 15 °C	46.23–46.86; 47.93–48.06;	measured [115];

protist division time	"a few hours"	about 41.61 (3 h)	measured [183]; position
<i>Caenorhabditis elegans</i> , 20 °C	mean generation 90 h, minimum 73.0 h; lifespan 16.7 d; strain MY6 84 h, 14.7 d	44.70; 44.51; 46.06; 45.95	measured [194];
alpine oribatid <i>Oromurcia sudetica</i>	egg to adult 2–4 yr; adult 1–2 yr	49.50–50.13; 48.87–49.50	measured [195];
<i>L. terrestris</i> cocoons, 15 °C	15.1–32.2 per worm per year; hatching 132–731 d; earlier laboratory values 90–	47.94–49.50; 47.60–48.63	measured [196];
earthworm burying itself (Darwin)	2–3 min in loose mould; 25 h 40 min in compact sand	37.51–37.88; 43.56	measured [197];
earthworm	9.2 m / 42 d = 0.22 m d ⁻¹ ; 21.2 / 42 = 0.50	—	computed from [180]
fine-root lifetime at 5 °C	1 / 0.56 = 1.8 yr	49.41	computed from [170]
litter half-life, ln 2 / λ	rain forest 0.53 yr; median 2.3 yr; tundra 2.0	48.29; 49.63; 50.11	computed from [108]
time to form 1 cm of soil at 0.026 mm	385 yr	54.29	computed from [199]
time to erode a 30 cm A horizon at	256–263 yr	53.92–53.94	measured [199];
soil carbon stock / soil respiration	1,462–1,548 Pg / 98 Pg yr ⁻¹ = 14.9–15.8 yr	51.34	computed from [191];
radiocarbon mean age of soil carbon to	4,830 ± 1,730 yr	56.59	measured [201]; position

Litter decay constants from 293 values range 0.006–4.993 yr⁻¹, mean 0.581, median 0.300; rain forest 1.3, tundra 0.18, more than 7 times slower (measured [198]). Fungal turnover is up to one order of magnitude longer than bacterial (measured [115]). The radiocarbon age exceeds the stock-to-flux time by 4,830 / 15 ≈ 320 (computed); the flux is carried by a small fast pool and the age by a large slow pool. Earthworm dispersal is about 10 m yr⁻¹ against about 600 m yr⁻¹ for an average terrestrial organism (measured, preprint [193]).

Counts

Nematodes: 28,537 valid species, 3,030 genera, 276 families, 32 orders; estimates of the total run from half a million to 10 million (measured [202]). Oribatid mites: about 9,000 valid species and subspecies to 2002, 1,204 genera, 169 families; Palaearctic 3,200 (measured [203]); aquatic oribatids about 90 species, under 1 % (measured [204]). Springtails: 9,186 or 9,270 species, 686 genera (measured [205]; [206]); both are recorded. Tardigrades: 1,508 species in 164 genera and 35 families (measured [207]). Earthworms: 5,406 species (measured [187]). Clitellata more than 5,000 species (measured [208]). Shares of species living in soil: Enchytraeidae 98.6 %, fungi 90 %, Plantae 85.5 %, Isoptera 84.2 % (measured [170]). Across 6,928 earthworm sites in 57 countries, local richness and abundance peak at higher latitudes, opposite to above-ground organisms (measured [209]); predicted local richness is mostly 1–4 species, mean 1.98 (measured, preprint [193]). Of 6,759 nematode samples, 38 % of individuals are in sub-Arctic regions, 24 % temperate, 21 % tropical (measured [184]).

Glomalin, a glycoprotein from arbuscular mycorrhizal hyphae, predicts aggregate stability across 37 soils with $r^2 = 0.86$ (measured [210]). Macro-aggregates above 250 μm are stabilised by roots and hyphae; micro-aggregate stability depends on persistent organic agents (measured [190]). Gross nitrogen mineralisation across 100 studies rises with microbial biomass carbon (measured [211]). Nitrification rises log-linearly with mineralisation and shows no relation to pH (measured [211]).

Order of events

1. 2.6–2.7 Gyr: microbial mats on palaeosols, South Africa (measured [101]).
2. About 635–542 Ma: Ediacaran palaeosols with sessile organisms read as lichens and crusts (measured [172]).
3. Late Ordovician, older than 443.8 Ma: first animal burrows in soils, probable millipedes; no rooted plants known (measured [173]; [174]; [5]).
4. 410.8–407.6 Ma: Rhynie chert fauna of nematodes, mites, springtails, arachnids, myriapods and insects (measured [175]; [5]).
5. Devonian, 419.2–358.9 Ma: trees, deeper roots, seeds; thicker soils, stronger weathering, CO₂ drawdown (measured [180]; [5]); Gilboa oribatids (measured [176]); freshwater clitellate ancestor (measured [177]); *Archaeopteris* roots to 1.2–1.6 m at about 385 Ma (measured [112]).
6. Carboniferous, 358.9–298.9 Ma: coal peak attributed to everwet tropical conditions and extensive depositional systems (measured [84]; [5]). Decay was pervasive wherever conditions allowed; many coals are dominated by unligified lycopsid periderm (measured [84]).
7. 298.9 Ma: earthworm crown group (measured [178]; [5]); clitellate body fossils Permian (measured [186]).
8. 201 Ma: leech cocoon fossil used as calibration; 161–186 Ma: earthworm family splits with Pangaea break-up (measured [186]).
9. Cenozoic: rise of ectomycorrhizal fungi with trees; weathering intensified (measured [181]; [182]).
10. 1881: Darwin's measurements of worm casting (measured [197]; figures in Not verified).

Present quantities

Soil organic carbon is 684–724 Pg to 30 cm, 1,462–1,548 Pg to 1 m and 2,376–2,456 Pg to 2 m, from 4,353 profiles (measured [191]). Carbonate carbon is 695–748 Pg to 1 m; soil nitrogen is 133–140 Pg to 1 m (measured [191]). A later estimate gives 2,270–2,770 Pg C to 2–3 m with more than 500 Pg below 3 m; root inputs are about five times more likely than above-ground litter to be stabilised (measured [192]). Global soil respiration was 98 ± 12 Pg C in 2008, rising 0.1 Pg C per year over 1989–2008 (measured [200]). Soil forms at $0.023\text{--}0.064$ mm yr⁻¹ in the UK, with a global median of about 0.026 mm yr⁻¹ from 252 rates; erosion at the arable site is 1.19 mm yr⁻¹ (measured [199]). Erosion under conventional tillage averages 1–2 orders of magnitude above soil production, about 1 mm yr⁻¹ (measured [212]); the ratio at the median production rate is $1 / 0.026 = 38$ (computed). Phosphorus fertiliser is about 15 Mt P per year, and human mobilisation by 2000 was about three times natural flows (measured [213]). Global biomass: 550 Gt C, bacteria 70, archaea 7, animals 2 (measured [132]). The prairie food web mineralises $4.5 + 2.9 + 0.3 = 7.7$ g N m⁻² yr⁻¹, 77 kg N ha⁻¹ yr⁻¹, in shares of 58 %, 38 % and 4 % (computed from [171]).

Pattern

Soil appears in the record as a biological product from 2.6 Gyr onward: microbial mats first, Ediacaran crusts next, burrowing animals before any rooted plant at more than 443.8 Ma. The micro-arthropod and nematode fauna follows at 410.8–407.6 Ma, trees and roots of 1.2–1.6 m in the Devonian, and earthworms last at 298.9 Ma. The order is microbes, then sediment-eating animals, then fungus-eating arthropods and nematodes, then rooted plants, then earthworms. Each later group is larger and slower: protists μm to mm and hours; nematodes $0.68 \mu\text{g}$ and 73–90 h; mites 2–4 years to adulthood; earthworms with burrows of 5–8 mm and cocoons of 132–731 days. Numbers fall as size rises: $10^4\text{--}10^7$ protists per gram, about 10^6 nematodes per m² (computed with an

assumed bulk density), 5–150 earthworms per m² (preprint). Soil forms at 0.023–0.064 mm per year, about 385 years per centimetre, and its carbon turns over in about 15 years by flux while carrying a mean age of 4,830 years.

Not verified

Darwin's Chapter III figures: 53,767 worms per acre (13.3 m⁻²), 10 tons of earth per acre per year (2.51 kg m⁻² yr⁻¹), 7.5 and 16 tons at Leith Hill, burrows 5–6 ft deep (two 1881 reviews naming Darwin 1881). Hirst & Maulik 1926 (citation only). *Megascolides australis* up to 1.5 m, 400 g, burrows 1–1.5 m, cocoons 5–9 cm, maturity up to 5 yr (Van Praagh & Yen 2010 recovery plan naming Van Praagh 1992, citation only). *C. elegans* length 1 mm, generation 4 d, lifespan 2 weeks (BioNumbers naming Muschiol et al. 2009). Oribatid 0.2–1.0 mm, springtail 2–3 mm (0.2–8 mm), densities above 100 per cm², life cycles up to 7 years (Minor, Soil Bugs, no primary). *E. coli* 1 × 2 μm, 1 pg (book.bionumbers.org). Walker & Syers 1976 phosphorus fractions, Olson 1963 decay constants, Stockmann et al. 2014 production rates (citations only). Montgomery's production medians 0.004–0.1 mm yr⁻¹. Published earthworm densities of Phillips et al. 2019 (preprint read). Enchytraeidae species count; global potassium cycle; soil pore-size classes; earthworm lifespans; the "about 7,000 earthworm species" figure.

A6 Herbivores and Defence

What it is

Herbivory is the eating of living plant tissue by animals. Defence is the set of plant compounds, structures and signals that lowers that loss. Across 1,058 vascular plant species herbivores take 5.3 % of the leaf tissue produced each year (measured [214]). Plants hold more than 100,000 known secondary metabolites (measured [215]).

First appearance

Arthropod herbivory is the older side. Spore feeding and piercing of stems are recorded at 417–403 Ma, leaf margin feeding at 326 Ma and the first gall at about 302 Ma (see A1). Vertebrate herbivory follows 110 Myr later. The oldest known synapsid herbivore, *Melanedaphodon hovaneci* from Linton, Ohio, is Moscovian, about 307 Ma (measured [216]); the Moscovian spans 315.2–307.0 Ma (measured [217]). The position of 307 Ma is 66.66 (computed). The gap from the first arthropod herbivory is 417 – 307 = 110 Myr (computed). Herbivory arose in tetrapods at least five times in the Late Carboniferous to Early Permian: diadectids, bolosaurids, captorhinids, edaphosaurids and caseids (measured [218]). The Permian begins at 298.9 Ma and the Kungurian at 283.5 Ma (measured [217]), positions 66.63 and 66.59 (computed).

The plant signal that answers wounding is older than vascular plants. The jasmonate receptor COI1 is functionally conserved between the liverwort *Marchantia polymorpha* and *Arabidopsis* across about 450 Myr of independent evolution (measured [219]), position 67.01 (computed). Bryophytes carry all signalling components but no JA-Ile; their ligand is dinor-OPDA, and one amino-acid change switches ligand specificity (measured [219]).

Chemical defence and its counter are dated together in one pair. The nitrile-specifier protein of the Pieridae detoxifies glucosinolates; five estimates place its origin within about 10 Myr of the appearance of the host order Brassicales (measured [220]). The lag of 10 Myr has position 63.54 (computed).

Dinosaur herbivory rested on pre-angiosperm plants. In vitro fermentation shows that *Equisetum*, *Araucaria*, *Ginkgo* and *Angiopteris* match living browse in energy content (measured [221]). Latest Cretaceous coprolites from India, attributed to titanosaurs, contain phytoliths of at least five extant grass subclades (measured [222]). The Maastrichtian spans 72.1–66.0 Ma (measured [217]), positions 65.34–65.26 (computed).

Grasslands precede high-crowned teeth. Pooid and PACMAD phytoliths are present in North America by 42–38 Ma and C4 grasslands by 7–6 Ma (measured [223]). C3 grass habitats were established in the Central Great Plains by at least 21.9 Ma, and hypsodont Equinae emerged at least 4 Myr later (measured [224]). The latest date for hypsodont Equinae from these numbers is $21.9 - 4 = 17.9$ Ma (computed); positions 64.26 and 64.07 (computed).

Spines follow browsers. Of 1,852 southern African woody species, 213 are spiny; spinescence evolved at least 55 times, mostly within the last 17 Ma, with a mid-Miocene radiation; horned bovids arrived in Africa by 16 Ma (measured [225]). Positions: 17 Ma 64.02, 16 Ma 63.97 (computed).

Partners

On the plant side the defended tissues belong to all vascular plants. Grasses number about 11,000 species (measured [223]). Latex occurs in about 10 % of flowering plant species (measured [226]). Cardenolides occur sporadically in 12 botanical families, dominant in Apocynaceae (measured [227]). Extrafloral nectaries are reported in 3,941 species, 745 genera and 108 families, 33 of 65 angiosperm orders, about 1–2 % of vascular plant species, and in 4 of 36 fern families (measured [228]). Ant domatia occur in 681 vascular plant species in 159 genera and 50 families; the true number may approach 1,140 (measured [229]).

On the animal side insect herbivores likely exceed 1 million species against more than 300,000 flowering plants (measured [230]); the ratio is $1,000,000 / 300,000 = 3.3$ (computed). Among more than 7,500 insect herbivore species with site-specific host records, specialists predominate, and the share of specialists rises toward the tropics (measured [231]). Africa has 92 large herbivore species in five functional types (measured [225]). Cardenolide feeders occur in six insect orders; the Na,K-ATPase was sequenced in 18 such insects from 15 genera and four orders (measured [232]). The parasitic wasp *Cotesia marginiventris* is a third partner: it finds caterpillars by the terpenoids a fed-on maize seedling releases (measured [233]).

Independent origins are counted on both sides. Tetrapod herbivory: at least five (measured [218]). Spinescence: at least 55 in southern Africa (measured [225]). Extrafloral nectaries: at least 457 lineages on a phylogeny of more than 55,000 species (measured [228]). Domatia: at least 158 origins and 43 losses within 19 Myr on a 1,181-species tree; Australasian and Neotropical symbioses are early Miocene, African ones later than the late Miocene (measured [229]). C4 photosynthesis: at least 9 and up to 20 times within PACMAD (measured [223]). Caffeine: independently in the cacao, citrus, guaraná, coffee and tea lineages by different pathways (measured [234]); in *Coffea canephora* by tandem duplication of N-methyltransferase genes (measured [235]). On the insect side the N122H substitution of the Na,K-ATPase recurs in six named species of four orders, convergence across 300 Myr of insect divergence (measured [232]). Species per origin: nectaries $3,941 / 457 = 8.6$; domatia $681 / 158 = 4.3$; spines $213 / 55 = 3.9$ (computed).

Sizes

what	value	position	source
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spine, minimum length in the definition	≥5 mm	≥10.56	measured [225]; position computed
mesobrowsers; megaherbivores (body mass)	4–450 kg; >1,000 kg	—	measured [225]
isoprene; nicotine; caffeine; xanthotoxin; digitoxin (molar mass)	68.117; 162.23; 194.19; 216.19; 764.94 g mol ⁻¹	—	measured [236]
specific leaf area, 280 species	35–267 cm ² g ⁻¹	—	measured [237]
leaf nitrogen, 280 species	8.7–40.9 mg g ⁻¹	—	measured [237]
mass-based photosynthetic capacity	21–289 nmol g ⁻¹ s ⁻¹	—	measured [237]
speed of the wound stimulus to distal	≥3 cm min ⁻¹	—	measured [238]

The molar masses span $764.94 / 68.117 = 11.2$ (computed). Across the leaf set the slowest leaves have $267 / 35 = 7.6$ times less area per gram and $289 / 21 = 13.8$ times less photosynthetic capacity per gram than the fastest (computed). The scaling of mass-based capacity with leaf lifespan is -0.74 ± 0.05 (measured [237]).

Times

what	duration	position	source
jasmonic acid rise after wounding, <i>Arabidopsis</i>	2–5 min (120–300 s)	37.51–38.34	measured [238]; positions computed
induced volatiles in maize; sesquiterpenoids	2 h; 4 h	41.24; 41.87	measured [239]; positions computed
return of the nicotine response, wild tobacco	6 d	45.13	measured [240]; position computed
silica induction regime	weekly damage over 10 months	47.37	measured [241]; position computed
leaf lifespan, 280 species	2.5 ± 0.6 to 66.2 ± 10.6 months	47.44–50.42	measured [237]; positions computed
hypsodont horses after C3	≥4 Myr	62.71	measured [224]; position computed
Pierid counter-adaptation after Permian–Triassic event	about 10 Myr	63.54	measured [220]; position computed
spinescence window	17 Myr	64.02	measured [225]; position computed
domatia window	19 Myr	64.13	measured [229]; position computed
COI1 receptor conservation	about 450 Myr	67.01	measured [219]; position computed

Green-leaf volatiles are emitted immediately after simulated herbivory (measured [239]). Silica rises in damaged leaves only after repeated damage above a threshold (measured [241]). Mandible wear in *Spodoptera exempta* on high-silica diets appears within a single instar (measured [242]). The leaf lifespan ratio is $66.2 / 2.5 = 26.5$ (computed). Herbivory recovered 24 Myr after the Permian–Triassic event and about 10 Myr after the K–Pg event (see A1).

Counts

Described secondary structures by class (measured [215]):

class	described structures
alkaloids	27,000

monoterpenes; sesquiterpenes; diterpenes	3,000; 5,000; 2,500
triterpenes, steroids, saponins; tetraterpenes	5,000; 500
phenylpropanoids, coumarins, lignans	2,000
flavonoids, anthocyanins, tannins	4,000
polyketides	800
glucosinolates	150
cyanogenic glucosides	60

The terpene classes sum to 16,000 (computed). A second count gives about 12,000 alkaloids (measured [243]); the ratio of the two counts is $27,000 / 12,000 = 2.25$ (computed). Both are recorded. Terpene synthase genes number 1 in the moss *Physcomitrella patens*, 18 in the lycophyte *Selaginella moellendorffii* and 40–152 in angiosperm and gymnosperm genomes, in seven clades (measured [244]).

Resistance counts: Q111 plus N122 together give more than 12-fold resistance of the Na,K-ATPase to cardenolides over wild type and more than 2-fold over either alone (measured [232]). *Manduca sexta* larvae on high-alkaloid foliage ate and gained weight at 57.2 % and 45.7 % of controls; on artificially induced leaves 38.5 % (measured [240]). Silicon content explains more than 70 % of the variation in leaf abrasiveness across 18 grass species (measured [241]). Grasses from more heavily grazed Serengeti sites had higher leaf-blade silica, and defoliation raised it (measured [245]).

Spiny species are 213 of 1,852, which is 11.5 % (computed), in 29 families (measured [225]). The leaf economics spectrum rests on 2,548 species at 175 sites (measured [246]); the lifespan and nitrogen ranges rest on 280 species (measured [237]).

Consumption: woody species suffer 64 % higher leaf herbivory than non-woody; earlier estimates ran up to 3.8 times the 5.3 % (measured [214]), which is 20.1 % (computed). In 44 aquatic sites herbivores remove on average 51 % of annual primary production, about three times the terrestrial figure (measured [247]); one third of 51 % is 17 % (computed). In the Serengeti, 1974–1979, herbivores consumed 0.66 of annual above-ground production, range 0.15–0.94 across sites, and grazing raised net primary productivity at most sites (measured [248]).

Fossil leaf damage in the Bighorn Basin, 5,062 leaves at five sites (measured [249]; positions computed):

age	position	mean annual temperature	leaves damaged
58.9 Ma	65.16	10.5 °C	34.5 %
57.5 Ma	65.13	10.5 °C	14.9 %
55.9 Ma	65.11	15.7 °C	37.8 %
55.8 Ma (PETM)	65.11	20.1 °C	57.3 %
55.2 Ma	65.10	16.4 °C	33.0 %

At the PETM specialised damage was 21.6 % and per-species damage 45–94 %. Leaves with four or more damage types were 7.3 % against 0.4–2.6 % before; 50 damage morphotypes fall in seven

feeding groups (measured [249]). The rise from 55.9 to 55.8 Ma is $57.3 - 37.8 = 19.5$ percentage points for $20.1 - 15.7 = 4.4$ °C (computed).

Order of events

1. 417–403 Ma: spore feeding and stem piercing; 326 Ma: leaf margin feeding; about 302 Ma: first gall (see A1).
2. About 450 Myr of separate descent: COI1 receptor shared by liverworts and vascular plants; JA-Ile ligand in vascular plants (measured [219]).
3. About 307 Ma: *Melanedaphodon*, first synapsid herbivore (measured [216]); at least five tetrapod herbivore origins by the Early Permian (measured [218]).
4. Triassic to Cretaceous: dinosaur herbivory on horsetails, conifers and ferns (measured [221]); latest Cretaceous: grass phytoliths in titanosaur coprolites (measured [222]).
5. Within about 10 Myr of the Brassicales: Pierid nitrile-specifier protein (measured [220]).
6. 58.9–55.2 Ma: leaf damage 14.9–37.8 %, 57.3 % at the PETM, then 33.0 % (measured [249]).
7. 42–38 Ma: open-habitat grasses in North America; by 21.9 Ma: C3 grasslands; at least 4 Myr later: hypsodont Equinae (measured [223]; [224]).
8. Within 19 Myr: at least 158 domatia origins (measured [229]); within 17 Myr: at least 55 spine origins; 16 Ma: bovids reach Africa (measured [225]).
9. 7–6 Ma: C4 grasslands in North America; after 5 Ma in Africa; 8.5–6.5 Ma: grass pollen above 90 % in South Asia (measured [223]).

C4 grasses originated by the Early Oligocene, at least 25 Myr before their dominance (measured [223]).

Present quantities

Leaf tissue eaten on land: 5.3 % of annual production across 1,058 species and 2,085 populations (measured [214]). Production eaten in water: 51 % at 44 sites (measured [247]). Secondary metabolites: more than 100,000 (measured [215]). Insect herbivores: more than 1 million species against more than 300,000 flowering plants (measured [230]). Plants with extrafloral nectaries: 3,941 species; with domatia: 681 (measured [228]; [229]).

Pattern

Arthropods eat spores and stems at 417–403 Ma, leaves at 326 Ma; vertebrates follow at 307 Ma, 110 Myr later, and take up herbivory at least five times before 283.5 Ma. Plants hold more than 100,000 secondary structures, 12,000–27,000 of them alkaloids; the terpene gene family grows from 1 to 18 to 40–152 genes. Where both sides are dated, the animal answer follows the plant trait within about 10 Myr (Pierid protein after Brassicales) or at least 4 Myr (hypsodonty after grasslands). Spines arose at least 55 times within 17 Myr, with bovids in Africa from 16 Ma. Nectaries arose at least 457 times, domatia 158. Signals run in 120–300 s, 2–4 h and 6 d. Loss is 5.3 % of leaf tissue on land, 51 % of production in water, 66 % under Serengeti grazing, and rose from 37.8 % to 57.3 % of fossil leaves with +4.4 °C.

Not verified

Two-spotted spider mite female about 0.4 mm and development 5–20 d (UF/IFAS EENY150). Aphid generation time 4.7 d (BioNumbers 100519, naming University of Florida). "Over 200,000" specialised metabolites (BioNumbers 107374, naming Dixon & Strack 2003). "More than 120" glucosinolate types and the counts 9 genomes, 14 families, 9 Pierid species, 1,155 genes, about 80

Myr and about 78 Ma for the Brassicales–Pieridae exchange (press release and blog on Edger et al. 2015). Button & Zanno 2020 dinosaur skull counts (museum news page). Latex in at least 17 families (Quicke et al. 2025). "About 30,000 terpenes"; "about 2,500 cyanogenic species"; "20 % of plants alkaloidal"; latex "at least 40 families, about 20,000 species"; "18 % of terrestrial production eaten"; caffeine "3 origins"; thorns in gymnosperms; Wilf & Labandeira 1999 damage percentages; Pearson et al. 2013 on diadectid diet. Citation only, numbers not read: Sues & Reisz 1998; MacFadden 2005; Wink 2003; Facchini 2001; Baldwin 1999; Halkier & Gershenzon 2006; Gleadow & Møller 2014; Berenbaum 1983; Ehrlich & Raven 1964; Strauss & Agrawal 1999; Wasternack & Hause 2013; Wright et al. 2004 trait ranges.

A7 Decomposers

What it is

Decomposition is the breakdown of dead plant matter, above all wood and leaves, by fungi, bacteria and animals. Dead wood holds 73 ± 6 Pg C and litter 43 ± 3 Pg C, 8 % and 5 % of the 861 ± 66 Pg C in the world's forests (measured [250]). Coarse woody detritus is produced at about 12 Pg dry matter per year, the pool is about 150 Pg, and it turns over in about 13 years (measured [251]).

First appearance

Fire and millipedes are recorded before forests. Charcoalified rhyniophytoid plants from Ludford Lane, Welsh Borders, are basal *Přídolí* (measured [252]); the *Přídolí* base is 423.0 ± 2.3 Ma (measured [217]), position 66.95 (computed). The oldest millipede with spiracles, *Pneumodesmus newmani*, was dated about 427 Ma from spores; U–Pb zircon gives 413.7 ± 4.4 Ma for its bed (measured [253]). Kampecarid millipedes from Kerrera are about 425 Ma; the myriapod clock gives about 500 Ma (measured [254]). Positions: 425 Ma 66.95, 413.7 Ma 66.93, 500 Ma 67.10 (computed). All three fossil ages are recorded.

Forest-grade communities stand by the Givetian, about 385 Ma (measured [254]), position 66.86 (computed). The first wood borings are Late Devonian, about 383–359 Ma (measured [255]), positions 66.86–66.80 (computed). *Arthropleura*, the largest arthropod, is Serpukhovian (measured [256]), 330.9–323.2 Ma (measured [217]), positions 66.73–66.71 (computed).

Enzymatic opening of lignin comes later. Across 62 genomes the first class II peroxidase (AA2) genes appear in the common ancestor of the Auriculariales and the remaining Agaricomycetes, with 3 ancestral copies. That origin is placed about 300 Ma, roughly at the end of the Carboniferous (measured [257]). The Carboniferous ends at 298.9 Ma (measured [217]), position 66.63 (computed). Resurrected Polyporales peroxidases date their common ancestor at 399 ± 140 Ma and the manganese-peroxidase ancestor at 259 ± 94 Ma. The first versatile peroxidase is 194 ± 70 Ma and the first lignin peroxidase 178 ± 64 Ma (measured [258]). Positions: 66.90, 66.50, 66.24, 66.16 (computed). The surface tryptophan that attacks non-phenolic lignin arose independently in two lineages (measured [259]). The gap from the first forests to the AA2 origin is $385 - 300 = 85$ Myr (computed).

Beetles bore wood from the middle Permian, about 272–260 Ma. Late Permian borings in the conifer *Ningxiaites specialis*, about 254–252 Ma, hold egg niches, 7–11 larval tunnels per boring and four coprolite classes, that is four instars (measured [255]). Positions: 272 Ma 66.55, 254 Ma 66.49 (computed). The oldest pupation chamber in wood is Late Triassic (measured [260]), about 237 to 201.4 Ma (measured [217]).

The termite crown is 149 Ma (136–170); the first undisputed fossils are 110–135 Ma; Termitidae date to 54 Ma (46–66) (measured [261]). Positions: 149 Ma 66.00, 135 Ma 65.91, 54 Ma 65.08 (computed). Fungus farming by termites is recalibrated to 31.41 Ma (25.82–39.53); the oldest fossil fungus gardens are 24.8–24.5 Ma, Rukwa Rift, Tanzania (measured [262]). Positions 64.58 and 64.37 (computed). From the termite crown to fungus farming is $149 - 31.4 = 117.6$ Myr (computed). Bark and ambrosia beetles (Scolytinae) originated 100–120 Ma; fungus farming evolved among them at least ten times, the oldest about 50 Ma (measured [263]). Dung beetle tribes originated about 119–130 Ma and radiated 85–98 Ma, before the extinction at 66 Ma (measured [264]). Another estimate is 72.6–85.5 Ma with a mammal-associated origin (measured [264], citing Ahrens et al.). Both are recorded.

Partners

Fungi: lignin decay at scale is confined to white-rot Agaricomycetes; class II peroxidases expanded in their ancestor and contracted in brown-rot and mycorrhizal lineages (measured [265]). Brown-rot fungi open cellulose by a non-enzymatic Fenton mechanism and do not meaningfully degrade lignin; brown-rot and ectomycorrhizal lineages lost both the AA2 and the cellulolytic complements (measured [257]). Brown rot has at least four independent origins. A dataset of 1,157 wood-decay species holds 126 brown-rot and 1,031 white-rot species in 14 orders, with 205 gymnosperm specialists, 565 angiosperm specialists and 387 generalists (measured [266]). Brown rot correlates with conifer substrates (measured [267]). Fungus-growing termites and *Termitomyces* have a single origin, in Africa, with no reversal (measured [268]). Macrotermitinae number about 330 species in 11 genera; *Termitomyces* about 50 species (measured [269]).

Bacteria: of about 500 soil and 500 litter isolates from one forest, about 12 % of colonies were cellulolytic. About 21 % of 115 selected strains grew on crystalline cellulose. They fell in 42 OTUs of 22 genera in four phyla, and these OTUs were 17.6 % of sequences in litter and 3.7 % in soil (measured [270]).

Animal groups:

group	species	source
Termitidae, share of termite species	>75 %; 84 % (both recorded)	measured [261]; [271]
Scolytinae (bark and ambrosia beetles)	>6,000, about 10 % of weevils	measured [263]
Scarabaeinae; Scarabaeidae	about 5,000; about 30,000	measured [264]
millipedes: nominal; valid; estimated	12,116; 7,753; 15,000–20,000	measured [272]
woodlice	3,710 in 527 genera, 37 families	measured [273]
arthropods on one summer pig carcass	522 in 31 orders, 151 families	measured [274]

Sizes

what	size	position	source
hyphal diameter, 31 saprobic soil fungi	2.7–6.5 μm	3.72–4.51	measured [275]; positions computed

<i>Reduviasporonites</i> cells, end-Permian	10–90 μm long	4.91–6.91	measured [276]; positions computed
coprolites in late Permian borings, four classes	<50 μm ; about 150 μm ; up to 542 $\times$ 958 μm	<6.37; 7.37; 9.06	measured [255]; positions computed
peloids; comb cells in fossil fungus gardens	about 1 mm; about 10 mm	9.10; 11.19	measured [262]; positions computed
fungus combs; nest chambers, 25 Ma	6–9 cm wide; 4–13 cm	12.83–13.53	measured [262]; positions computed
<i>Arthropleura</i> , Serpukhovian	about 55 cm wide; up to 2.63 m long; about 50 kg	14.84; 16.27	measured [256]; positions computed
Macrotermitine mounds	up to 10 m high; >15 m across	17.48; 17.85	measured [269]; positions computed
modern peat; thickest coal beds	up to 15 m; up to 61 m	17.85; 19.13	measured [277]; positions computed
lignin peroxidase, <i>Phanerochaete chrysosporium</i>	343 residues; 37.3 kDa per chain	—	measured [278]; mass computed

The widest hypha is $6.5 / 2.7 = 2.4$ times the narrowest (computed). A 10 m mound is $10 / (6.5 \times 10^{-6}) = 1.5 \times 10^6$ times the width of the widest hypha (computed). Coal beds are given as a few inches to 200 ft and peat as up to 50 ft (measured [277]); 200 ft = 61 m and 50 ft = 15 m (computed).

Times

what	duration or rate	position	source
carion: 90 % of pig mass lost with	6 d	45.13	measured [274]; position
new termite workers after swarming	1.5–3 months	46.98–47.61	measured [269]; positions computed
wood decay, fastest and slowest k	0.975 and 0.004	—	measured [279]
wood half-life, $\ln 2 / k$	0.71–173 yr	48.56–53.56	computed from [279]
wood, 95 % mass loss	about 3–750 yr	49.87–54.90	measured [279]; positions computed
fine litter turnover, forests; global mean	about 5 yr; 1.4–3.4 yr	50.34; 49.18–49.98	measured [251]; positions computed
coarse woody detritus turnover	about 13 yr	51.21	measured [251]; position
callus growth over Permian borings	10 or more years	50.97	measured [255]; position
termite royal pair; colony	at most about 20 yr;	51.60	measured [269]; position
pyrogenic carbon in soil, one-pool mean; two pools	88 yr; 3 and 870 yr	52.95; 49.87; 55.03	measured [280]; positions computed
termite mounds	about 700; $\geq 2,200$; $\geq 4,000$ yr	54.83; 55.88; 56.42	measured [269]; positions computed
deep soil carbon mineralised after	2,567 $\pm$ 226 yr old	56.02	measured [281]; position
end-Permian fungal proliferation	<1 Myr	<61.45	measured [282]; position

Downed coarse wood k varies at least 244-fold worldwide and up to 76-fold among species at one site. The fastest is 0.975 yr^{-1} (*Helicarpus appendiculatus*), the slowest 0.004 yr^{-1} (*Eucalyptus camaldulensis*). The constant rises about 2.6 times per 10 °C from a base of $0.058\text{--}0.061 \text{ yr}^{-1}$ at 10

°C; 295 constants from 78 sources and 114 species (measured [279]). Half-lives for $k = 0.975$, 0.058 and 0.004 yr^{-1} are 0.71, 12.0 and 173 yr (computed). Leaf litter has a median k of 0.300 yr^{-1} (see A5); against the wood base of 0.058 at 10 °C the ratio is 5.2 (computed). Where termites discover wood, decay has $Q_{10} = 6.85$ (4.73–9.92) against 1.73 (1.44–2.09) for microbial decay, from 8,922 *Pinus radiata* blocks at 133 sites (measured [283]); the ratio is 4.0 (computed). Peat becomes coal over millions of years (measured [277]).

Counts

Genes: 3 ancestral AA2 copies rose to 21 in the ancestor of Trechisporales and later orders (measured [257]). Forest bacteria carried genes from 60 glycosyl hydrolase families (measured [270]).

Peat and the coal debate: tree lycopods were 60 % to more than 80 % of peat contributors in the Early Pennsylvanian of Euramerica. Their periderm was 20–45 % of peat biomass, with an aromatic content no greater than other tissues. Organic-carbon burial roughly doubled over the Carboniferous and returned slowly to near-modern values in the Permian (measured [284]). One reading places the white-rot origin at the end of the Carboniferous, coinciding with the drop in carbon burial (measured [265]). Another rejects a fungal cause of the coal peak and attributes it to everwet tropics and depositional systems during the assembly of Pangaea (measured [285]). Both are recorded.

End-Permian: fungal remains are 30–80 % of land-derived palynomorphs through the Changxing Formation of South China, at about 30 localities; *Reduviasporonites stoschianus* is more than 90 % of the basal Tesero assemblage (measured [282]; [276]). The 1996 reading is dieback with saprotrophic fungi; the 2011 reading of the same authors is a *Rhizoctonia*-like soil fungus (measured [276]). Both are recorded.

Animals' share of wood loss: 58–64 % in a Bornean suppression experiment (measured [286]); 10–20 % commonly attributed to invertebrates (measured [287]). Across 20 studies, 207 sites and 1,427 paired observations, invertebrates raise decomposition by $\ln RR$ 0.339 globally, 0.560 tropical, 0.798 arid, 0.12 temperate and 0.020 continental (measured [288]). That is +40 %, +75 %, +122 %, +13 % and +2 % (computed). Termites discover more than 50 % of wood above 21.33 °C, over 30.2 % of the land surface (measured [283]).

Order of events

1. About 500 Ma: myriapod clock age (measured [254]). 425–414 Ma: first millipedes (measured [254]; [253]).
2. 423.0 ± 2.3 Ma: earliest charcoal (measured [252]; [217]).
3. 399 ± 140 Ma: common ancestor of Polyporales peroxidases (measured [258]).
4. About 385 Ma: forest-grade communities (measured [254]); 383–359 Ma: first wood borings (measured [255]).
5. 330.9–323.2 Ma: *Arthropleura*, 2.63 m (measured [256]; [217]).
6. About 300 Ma: class II peroxidases in the Agaricomycete ancestor (measured [257]); 298.9 Ma: end of the Carboniferous (measured [217]).
7. 272–260 Ma: beetle borings; 254–252 Ma: egg-niche borings (measured [255]); 254.14–251.902 Ma: fungal proliferation (measured [282]; [217]).
8. 237–201.4 Ma: pupation chamber in wood (measured [260]; [217]); 194 ± 70 and 178 ± 64 Ma: versatile and lignin peroxidases (measured [258]).
9. 149 (136–170) Ma: termite crown; 135 Ma: oldest termite fossils (measured [261]).
10. 119–130 Ma: dung-beetle tribes (measured [264]); 100–120 Ma: Scolytinae (measured [263]).

11. 54 (46–66) Ma: Termitidae (measured [261]); about 50 Ma: first ambrosia beetles (measured [263]); 31.4 Ma: fungus-growing termites; 24.8–24.5 Ma: fossil fungus gardens (measured [262]).

Present quantities

Forests hold 861 ± 66 Pg C, of which dead wood 73 ± 6 and litter 43 ± 3 (measured [250]); together 116 Pg C, 13.5 % (computed). Global litter production is 90–110 Pg dry matter per year including below-ground (measured [251]). Global net primary production is 104.9 Pg C per year, land and ocean roughly equal (measured [289]). Herbivores remove 51 % of production in water and about one third of that on land (measured [247]), 17 %, so 83 % of land production is not eaten alive (computed). Fire emits 2.2 Pg C per year (1997–2016; 1.8–3.0) (measured [290]) over a burned area of 3.81 Mkm² per year (measured [291]). Termites emit 19.7 ± 1.5 Mt CH₄ and $3,500 \pm 700$ Mt CO₂ per year, about 4 % and 2 % of global emissions (measured [292]). Mounds oxidise about half of the methane produced (measured [293]). Against a global methane source of 576 (550–594) Tg per year for 2008–2017 (measured [294]) the termite share is 3.4 % (computed; different years). Smouldering fire fails to spread below 16 % O₂ and rises rapidly between 19 and 22 % (measured [295]). Litter decomposes about 8 % faster under its own species (measured [296]).

Pattern

Fire (423 Ma) and millipedes (425–414 Ma) are recorded before forests (385 Ma). Wood is bored from 383–359 Ma and by beetles from 272 Ma. Class II peroxidases appear once, in the Agaricomycete ancestor at about 300 Ma, 85 Myr after the first forests. Brown rot is a loss, repeated at least four times. Peroxidase ability sharpens in steps: 399, 259, 194, 178 Ma. Termites arise 149 Ma, fungus farming 31.4 Ma, ambrosia beetles 50 Ma with ten origins. Of land production 17 % is eaten alive and the rest falls to decomposers. Leaves turn over in 1.4–5 years, wood in 3–750 years to 95 % loss, charcoal in 88 years mean, coal over millions of years. Each 10 °C raises microbial wood decay 1.73–2.6 times and termite decay 6.85 times; above 21.33 °C termites take 58–64 % of dead wood.

Not verified

White-rot origin at 290 Ma (222–372 Ma), read through Hibbett et al. 2016 from Floudas 2012. Robinson 1990 coal hypothesis (read through Hibbett 2016). Terrestrial NPP 56.4 Pg C per year and the fire share 3.9 % derived from it (BioNumbers 102934, naming Field et al. 1998). Cretaceous amber woodlice (Kästle & Ludwig 2025 reference list, naming Broly et al. 2015). Brown rot "at least 6 origins"; burial efficiency "about 0.1 %" (Berner 2003); Cebrian's "80–90 % of production to detritus"; "about 60 Pg C per year" litterfall; Russell et al. 2015 residence times; Harmon et al. 1986 decay rates; Silver & Miya 2001 root k values; the termite line of the methane budget; termite body sizes; saproxylic species share; beetle gallery widths; the "220 Ma" Triassic boring; the 295 Ma figure in Floudas 2012's own text; actinomycete lignin rates. Citation only, numbers not read: Wilson & Anderson 2004; Russell et al. 2015; Bray & Gorham 1964; Kuzyakov et al. 2000.

A8 Climate and Atmosphere

What it is

The interaction is the exchange of gases, water and energy between vegetation and the air: plants fix CO₂, release O₂, pass water through leaves, change the reflectance of the surface and emit volatile compounds. Dry air is 78.08 % N₂, 20.95 % O₂, 9,340 ppm Ar and 420 ppm CO₂ by volume

(measured [297]). In September 2026 the Mauna Loa monthly mean CO₂ was 426.07 ppm (measured [298]).

First appearance

Permanent atmospheric oxygen is dated to about 2.33 Ga from multiple sulfur isotopes in three coeval drill cores of the Transvaal Supergroup; the change took roughly 10 Myr (measured [299]). A U–Pb age of 2.426 ± 0.003 Ga for Ongeluk magmatism places the onset between 2.460 and 2.426 Ga, with oscillation for about 200 Myr to 2.250–2.240 Ga (measured [300]). Both dates are recorded. Positions: 2.33 Ga 68.50, 2.46 Ga 68.55 (computed).

A second step is oceanic. Black shales of the basal Doushantuo Formation, 635–630 Ma, directly after the Marinoan glaciation, are enriched in Mo and V with pyrite $\Delta^{34}\text{S}$ of at least 65 ‰ (measured [301]). They are read as a widely oxygenated ocean; position 67.32 (computed). The gap from 2.33 Ga is $2,330 - 635 = 1,695$ Myr (computed).

The third step coincides with land plants. Plants colonised land from about 470 Ma. Carbonate $\delta^{13}\text{C}$ rose by a sustained 2 ‰ by about 445 Ma; redox proxies place deep-ocean oxygenation at 435–392 Ma; fossil charcoal shows O₂ above 15–17 % by 420–400 Ma (measured [302]). Positions: 470 Ma 67.05, 445 Ma 67.00, 420 Ma 66.94 (computed). A rebuilt model gives O₂ of about 2–11 % from the Cambrian to the mid-Ordovician and a mid-Devonian nadir of about 14.5 % at about 393 Ma (modelled [303]). Charcoal is present in sediments younger than 419 Ma and scarce from about 400 to 360 Ma (measured [303]). Charcoal constrains O₂ to roughly 13–35 % since then (measured [304]).

The first large CO₂ fall follows. Rooted plants appeared 400–360 Ma with a drop in CO₂; tree plots raise calcium weathering about tenfold over bare plots at Hubbard Brook and 5–10 times in Iceland (measured [305]). The compilation of 1,241 proxy estimates gives about 2,000 ppm at about 400 Ma and values near 278 ppm at about 300 Ma (measured [306]). The fall is $(2,000 - 278) / 100 = 17$ ppm per Myr over 100 Myr (computed). Positions: 400 Ma 66.90, 360 Ma 66.80, 300 Ma 66.64 (computed). The Ordovician glaciation set in before 444 Ma, after non-vascular plants spread (measured [307]).

Partners

On the plant side five stages are distinguished over 485–298.9 Ma: non-vascular; vascular with lignified tissue; shallow roots; arborescent vegetation with deep complex roots; seed plants (measured [308]). C₄ photosynthesis is counted in 62 lineages, at least 18 in grasses and 26 in monocots, about 7,500 species in 19 families (measured [309]). C₄ vegetation covers 18.8 million km² and contributes about 35.3 Pg C per year of gross primary production against about 115 for C₃ (measured [310]). The C₄ share is $35.3 / 150.3 = 23.5$ % (computed). The fern *Azolla* grew and reproduced in the Arctic Ocean about 50 Ma (measured [311]). Forests cover about 42 million km², store about 45 % of terrestrial carbon and supply about 50 % of terrestrial NPP (measured [312]).

On the air side the atmosphere–ocean O₂ reservoir is 3.78×10^{19} mol with a source flux of 1.8×10^{13} mol per year (measured [313]). Atmospheric carbon at 417.1 ppm and 2.124 Gt C per ppm (measured [314]) is 886 Gt C (computed). Fire is the third partner: fire activity is switched off below 16 % O₂, greatly suppressed below 18.5 % and rises rapidly between 19 and 22 % (measured [295]). Insects are a fourth. In a dataset of more than 10,500 fossil wing lengths, maximum insect size tracks O₂ until the end of the Jurassic and is decoupled from it afterwards, as birds radiate (measured [315]).

Sizes

what	value	position	source
largest Carboniferous–Permian insect wingspan	about 70 cm	15.06	measured [315]; position computed
forest area	4.06 Gha = $40.6 \times 10^6 \text{ km}^2$; $42 \times 10^6 \text{ km}^2$	—	measured [316]; [312]
C4 vegetation area	$18.8 \times 10^6 \text{ km}^2$	—	measured [310]
leaf area index, global mean; deserts; plantations; maximum	4.5–5.2; 1.3 ± 0.9 ; 8.7 ± 4.3 ; $18 \text{ m}^2 \text{ m}^{-2}$	—	measured [317]
global transpiration	$62,000 \pm 8,000 \text{ km}^3 \text{ yr}^{-1}$	—	measured [318]
biogenic volatile emission	about 1 Pg yr^{-1}	—	measured [319]
carbon stored by Arctic <i>Azolla</i>	$0.9\text{--}3.5 \times 10^{18} \text{ g C}$	—	measured [320]
organic carbon burial, land; sea	350; $200 \times 10^{12} \text{ g C yr}^{-1}$	—	measured [321]

Both forest areas are recorded. Transpiration is 80–90 % of terrestrial evapotranspiration; a 2014 comment holds the share overestimated (measured [318]). Isoprene is about 50 % of the volatile emission and 41 monoterpenes about 15 % (measured [319]).

Times

what	duration	position	source
CO ₂ exchange with land, 886 Gt	5.9–6.9 yr	50.49–50.63	computed from [314]; [318]; [310]
seasonal CO ₂ cycle	1 yr	48.87	measured [322]; position computed
fossil CO ₂ pulse: equilibration; CaCO ₃ neutralisation	2–20 centuries; 3–7 kyr	53.69–55.79; 56.16–56.93	measured [323]; positions computed
CO ₂ below 180 ppm in MIS 16	about 3,000 yr	56.16	measured [324]; position computed
present interglacial so far; interglacial after Termination V	about 12 kyr; about 28 kyr	57.42; 58.19	measured [325]; positions computed
orbital cycles in Southern Ocean	23, 42, 100 kyr	58.01; 58.56; 59.25	measured [326]; positions computed
Permian–Triassic extinction; Permian–Triassic extinction	$60 \pm 48 \text{ kyr}$; about 500 kyr	58.88; 60.81	measured [327]; positions computed
PETM	about 170 kyr	59.83	measured [328]; position computed
Arctic <i>Azolla</i> phase	about 800 kyr	61.24	measured [311]; position computed
O ₂ residence, reservoir / source	2.1 Myr	62.12	measured [313]; position computed
O ₂ residence with total organic carbon	0.82 Myr	61.27	computed from [313]; [321]
Great Oxidation transition; oscillation	about 10 Myr; about 200 Myr	63.54; 66.27	measured [299]; [300]; positions computed
charcoal-inferred O ₂ cycles, Permian–Triassic extinction	periods 20–30 Myr	64.17–64.54	measured [329]; positions computed

The O₂ residence time of 2.1 Myr is $3.78 \times 10^{19} / 1.8 \times 10^{13}$ (computed). With burial of $(350 + 200) \times 10^{12} \text{ g C}$ per year, $4.58 \times 10^{13} \text{ mol C}$, the time is 0.82 Myr (computed). Both are recorded. The dominant glacial cycle changed from about 41 kyr to about 100 kyr at 1,250–700 ka (measured [330]). A stack of 57 benthic $\delta^{18}\text{O}$ records is coherent with obliquity throughout 5.3 Myr (measured [330]).

[331]). Ice sheets reached their maximum between 33.0 and 26.5 ka (measured [332]). Long-term CO₂ declined by about 3.4 ppm per Myr over 420 Myr (measured [306]).

Counts

CO₂ proxies (measured [306]; [333]; [334]; [335]; [324]):

record	value
1,241 retained proxy estimates from 112 studies: highest intervals	about 2,000 ppm at about 400 Ma and at 220–200 Ma
same: single highest estimate	about 3,700 ± 1,600 ppm at 215 Ma
same: near pre-industrial	about 278 ppm at about 300 Ma and about 280 Ma
372 observations: long glaciations; warm periods	<500 ppm; >1,000 ppm
glaciation 340–260 Ma; Cretaceous; early Eocene	<500 ppm; about 1,000 ppm; >1,000 ppm
Ginkgo-relative stomatal index, 300 Myr: below 1,000	1–8 Ma and 275–290 Ma
same: 65–250 Ma	1,000–2,000 ppmv
ice cores, eight glacial cycles	172–300 ppmv

Across the Triassic–Jurassic boundary stomata record a fourfold CO₂ rise, 3–4 °C warming and species turnover above 95 % in the megaf flora (measured [336]).

O₂ at the Carboniferous–Permian maximum: above 26 % from charcoal in mires, which also give a sharp drop near the Permian–Triassic extinction and a decline since the mid-Cretaceous to about 21 % (measured [329]). Models give 15–30 % as the Phanerozoic range (modelled [337]), never below 15 % with the largest excursion at 260–300 Ma (modelled [321]), and about 35 % around 300 Ma (modelled [338]). All four are recorded. Fossil plant δ¹³C rose about 5.0 ‰ from the Devonian to the end-Permian (measured [338]).

Stomata and CO₂: herbarium leaves of eight tree species show a stomatal density drop of about 40 % over about 200 years for a CO₂ rise of about 60 μmol mol^{−1} (measured [339]). Growth at 280 → 340 μmol mol^{−1} reduced it by 67 % in some species (measured [339]). *Pinus flexilis* needles lost about 17 % stomatal density during deglaciation, 15,000–12,000 years ago, with about 30 % more CO₂ (measured [340]).

Vegetation and forcing: complete deforestation in a model gives albedo forcing −0.96 W m^{−2} (boreal −0.51, tropical −0.18), CO₂ forcing +2.22 W m^{−2} after 100 years and short-lived forcings +0.12 (modelled [341]). The total is +1.38 W m^{−2} and about 0.8 K; tropical removal warms about 0.6 K, boreal removal cools about 0.3 K (modelled [341]). Over non-forested land precipitation falls exponentially with distance from the ocean over a few hundred kilometres; over the Amazon, Yenisey and equatorial African forests it shows no such dependence (measured [342]). The "evaporative force" proposed for this is contested (measured [343]). Both are recorded.

Greening: 25–50 % of the vegetated area increased in growing-season leaf area over 1982–2009 and less than 4 % decreased (measured [344]). Attribution: 70 % CO₂ fertilisation, 9 % nitrogen deposition, 8 % climate (measured [344]).

Order of events

1. 2.46–2.33 Ga: permanent atmospheric O₂ (measured [299]; [300]).
2. 635–630 Ma: ocean oxygenation after the Marinoan glaciation (measured [301]).
3. 470 Ma: land plants; 445 Ma: +2 ‰ carbonate δ¹³C; 420–400 Ma: O₂ at least 15–17 % (measured [302]); glaciation by 444 Ma (measured [307]); charcoal continuous from 419 Ma (measured [303]).
4. 400–360 Ma: rooted plants and the CO₂ fell from about 2,000 ppm (measured [305]; [306]); 393 Ma: O₂ nadir 14.5 % (modelled [303]).
5. 340–260 Ma: glaciation at CO₂ below 500 ppm (measured [334]); 300–260 Ma: O₂ maximum, wingspans to 70 cm (measured [329]; [315]).
6. 251.941–251.880 Ma: end-Permian extinction (measured [327]); 250–240 Ma: flammability low to absent (measured [295]).
7. 220–200 Ma: CO₂ about 2,000 ppm (measured [306]); at the Triassic–Jurassic boundary fourfold CO₂ and +3–4 °C (measured [336]).
8. 145–65 Ma: Cretaceous CO₂ about 1,000 ppm (measured [334]); flammability high (measured [295]); insect size decoupled from O₂ after the Jurassic (measured [315]).
9. About 56 Ma: PETM, 170 kyr (measured [328]); about 50–48.5 Ma: *Azolla*, 800 kyr, drawdown 55–470 ppm (measured [311]; [320]).
10. 8–6 Ma: C4 plants abundant worldwide (measured [345]); 8–3 Ma: C4 grasslands (measured [346]).
11. 1,250–700 ka: 41-kyr to 100-kyr cycles (measured [330]); 33.0–19 ka: last glacial maximum, with tundra and steppe extensive and tropical moist forest contracted (measured [332]; [347]).
12. 1750–2026: 278 → 417.1 (2022) → 426.07 ppm (measured [314]; [298]).

Over the Holocene CO₂ fell about 5 ppmv, with land uptake of about 290 Gt C, then rose about 20 ppmv (measured [348]). Positions: 56 Ma 65.11, 8 Ma 63.34, 1,250 ka 61.65, 26.5 ka 58.14 (computed).

Present quantities

CO₂ 426.07 ppm in September 2026 (measured [298]), which is $426.07 / 278 = 1.53$ times the 1750 value (computed). The 2022 mean of 417.1 ± 0.1 ppm is 50.0 % above 278 ppm (computed from [314]). Global NPP is 104.9 Pg C per year, land and ocean roughly equal (measured [289]). Terrestrial GPP is about 150 Pg C per year (measured [310]) or 129 ± 32 Gt C (measured [318]); both are recorded. Annual CO₂ growth was 2.06–3.76 ppm per year in 2016–2025 (measured [298]). The land sink was 3.3 ± 0.8 Gt C per year for 2013–2022, 31 % of emissions; the ocean sink 2.9 ± 0.4 (measured [314]). Fossil emissions were 9.9 ± 0.5 Gt C in 2022 and atmospheric growth 5.2 Gt C per year (measured [314]). Forest area is 4.06 Gha with a net loss of 4.7 Mha per year in 2010–2020 and total loss of about 178 Mha since 1990 (measured [316]), 4.2 % of the 1990 area (computed). The seasonal CO₂ amplitude is 15–20 ppm in the far north and about 3 ppm near the Equator (measured [322]). It rose about 20 % at Hawaii and 40 % in the Arctic since the early 1960s (measured [322]). The Mauna Loa peak-to-trough is about 6.5 ppm (measured [349]); at some latitudes the rise exceeds 50 % (measured [350]).

Pattern

Oxygen rose in three recorded steps: 2.46–2.33 Ga, 635–630 Ma, and 445–400 Ma, after plants reached land at 470 Ma. Charcoal is continuous from 419 Ma, bounding O₂ to 13–35 %; the one maximum is at 300–260 Ma with wingspans of 70 cm; O₂ is 20.95 % today. CO₂ fell from about 2,000 ppm at 400 Ma to about 278 ppm at 300 Ma, 17 ppm per Myr, while rooted, arborescent and seed plants spread. It rose to about 2,000 ppm at 220–200 Ma and fell below 1,000 ppm by 8 Ma as

C4 plants spread. CO₂ below 500 ppm coincides with the long glaciations of 340–260 Ma and of the last 800 kyr (172–300 ppm). Stomatal density fell with each measured CO₂ rise: –17 %, –40 %, –67 %. Since 1750 CO₂ has risen 53 % to 426 ppm, and the northern seasonal swing has grown 20–50 %.

Not verified

Terrestrial NPP 56.4 Pg C per year and the 53.8 % land share (BioNumbers 102934 and 102935, naming Field et al. 1998). Cooling of about 5 °C plus 2–3 °C from Ordovician mosses (Exeter press release on Lenton et al. 2012). The name *Meganeura* for the 70 cm wingspan. Stomatal densities in pores per mm². Glasspool & Scott "25–30 %" (the page says above 26 %). Berner's numeric O₂ maximum (in a figure). Montañez et al. 2016 ppm values. Barrow seasonal amplitude in ppm. Beerling & Berner 2000. A single source for a CO₂ molecular residence of about 5 years. Daisyworld (Watson & Lovelock 1983) is a model statement with no measured quantity and is left out.

A9 Competition and Forests

What it is

Competition between plants is the mutual reduction of light, water and nutrients by neighbours. In forests it is measured as height growth, self-thinning of dense stands, light left under the canopy and the opening and closing of gaps. Forests cover 4.06 Gha, nearly one-third of the land (measured [316]), with about 3.04 trillion trees (measured [351]) of about 73,000 species (measured [352]).

First appearance

The oldest known forest of standing trees is in the Eifelian Hangman Sandstone Formation of Somerset and Devon: cladoxylopsid trees, mostly *Calamophyton*, on a distributive fluvial system (measured [353]). The Eifelian spans 393.3–387.7 Ma (measured [217]), positions 66.88–66.87 (computed). At Gilboa, New York, *Eospermatopteris* stumps belong to a cladoxylopsid tree at least 8 m tall, about 385 Ma (measured [354]), position 66.86 (computed). At Cairo, New York, a mid-Givetian palaeosol of about 385 Ma exposes about 3,000 m² with three root systems (measured [355]). *Eospermatopteris* roots reach about 1–2 m from the centre, about 30 cm deep, 0.7–1 cm thick. *Archaeopteris* roots spread up to 11 m and reach 1.2–1.6 m depth. Its 18 individuals have trunk bases of 8–45 cm and estimated heights of about 11–32 m. A possible lycopsid left a root mound 1.9 m across (measured [355]). Cairo is called the oldest forest in that paper; the Hangman forest is placed earlier (measured [353]). Both are recorded. From the Eifelian base to Cairo is 393.3 – 385 = 8.3 Myr; from its top 2.7 Myr (computed).

Archaeopteris, with lateral branching, latent primordia and wood anatomy of the modern kind, is anatomically preserved in Famennian beds of Morocco at about 370 Ma, and it went extinct near the Devonian–Carboniferous boundary (measured [356]). The Famennian begins at 372.2 ± 1.6 Ma and the Carboniferous at 358.9 ± 0.4 Ma (measured [217]); positions 66.83 and 66.80 (computed).

Coal forests spread across the palaeotropics in the Serpukhovian, expanded greatly in the late Bashkirian, contracted by about one half in the Kasimovian and re-expanded briefly in the Early Permian (measured [357]). Serpukhovian base 330.9, Bashkirian 323.2, Moscovian 315.2, Kasimovian 307.0, Gzhelian 303.7, Permian 298.9 Ma (measured [217]). The forests lasted 330.9 – 307.0 = 23.9 to 330.9 – 303.7 = 27.2 Myr (computed); positions 66.73 and 66.66 (computed). After

the earliest Kasimovian, about 305 Ma, tetrapod extinction peaked and endemism developed (measured [358]).

Partners

The competitors are the trees themselves. Of about 73,300 tree species, about 9,000 are undescribed; South America holds 43 %, Eurasia 22 %, Africa 16 % (measured [352]). Amazonia alone has about 16,000 tree species in about 3.9×10^{11} trees. There 227 species, 1.4 %, make half of all stems, and the rarest 5,800 species, about 36 %, have fewer than 1,000 individuals each (measured [359]).

Two tree groups are distinguished by gap response. On Barro Colorado Island 47 of 229 analysed species are pioneers; pioneers are 7.1 % of stems in the smallest gaps and 26.3 % in the largest (measured [360]). At Glacier Bay early species had smaller seeds, earlier maturity, shorter lifespans and lower heights than alder and spruce; each stage inhibited the one before, and alder facilitated spruce through nitrogen (measured [361]).

Hydraulic lift was shown in 27 species of herbs, grasses, shrubs and trees (measured [362]). Carbon moves both ways between ectomycorrhizal *Betula papyrifera* and *Pseudotsuga menziesii* in the field; the net gain by Douglas-fir equals 6 % of the isotope it fixed (measured [363]). The claims of widespread networks and seedling-boosting transfer are judged insufficiently supported, and unsupported citing claims doubled over 25 years (measured [364]). Both are recorded. Predators act on the same stands. After wolves returned to Yellowstone in 1995–1996, browsing on young aspen fell from about 90 % in 1997–1998 to 37–63 % by 2012 (measured [365]).

Sizes

what	size	position	source
<i>Eospermatopteris</i> , Gilboa	≥8 m	≥17.28	measured [354]; position computed
<i>Eospermatopteris</i> roots, Cairo: depth; thickness	about 30 cm; 0.7–1 cm	14.29; 10.87–11.19	measured [355]; positions computed
<i>Archaeopteris</i> , Cairo: root spread; root depth; height estimate	11 m; 1.2–1.6 m; 11–32 m	17.57; 15.55–15.81; 17.57–	measured [355]; positions computed
arborescent lycopsids: height; trunk diameter	10–50 m; 0.1 to >2 m	17.48–18.95; 13.29–16.02	measured [366]; positions computed
<i>Lepidodendron</i> stand, Illinois: basal diameter mean (range)	95 cm (34–144 cm)	15.34	measured [367]; position computed
maximum tree height in the vascular model	about 100 m	19.58	measured [368]; position computed
canopy height, 2020 map: Oregon and Gabon mean; Sabah maximum	28–36 m; up to 65 m	18.42–18.65; 19.19	measured [369]; positions computed
maximum rooting depth: global mean; trees; deepest (<i>Boscia albitrunca</i>)	4.6 ± 0.5 m; 7.0 ± 1.2 m; 68 m	16.78; 17.16; 19.23	measured [370]; positions computed
root mass: half within	20 cm (global); 30 cm (trees, 60 %)	13.92; 14.29	measured [371]; positions computed
reach of lifted water from one sugar maple	2.5–5 m	16.22–16.85	measured [372]; positions computed
gap sizes, BCI; Brazil median	25–1,150 m ² ; 78	—	measured [360]; [373]

Heights multiply by steps: $32 / 8 = 4$ from the Gilboa minimum to the Cairo estimate; $50 / 8 = 6.25$ from Gilboa to the lycopsid maximum (computed). Vegetation above 5 m covers 41 % of land (53.6×10^6 km²), above 10 m 30 %, above 30 m 5 % (6.7×10^6 km²) (measured [369]). The area above 30 m is $6.7 / 40.6 = 16.5$ % of forest area (computed). Maximum rooting depth by biome: boreal forest 2.0 ± 0.3 , temperate deciduous 2.9 ± 0.2 , tropical evergreen 7.3 ± 2.8 , savanna 15.0 ± 5.4 , tundra 0.5 ± 0.1 m (measured [370]). Of 475 root profiles, more than 90 % hold at least 50 % of roots in the upper 0.3 m and 95 % in the upper 2 m (measured [374]). Branch cross-section is conserved across branching nodes (measured [375]).

Times

what	duration or rate	position	source
gap closure, fastest phase	first year	48.87	measured [376]; position
gap formation $0.45\text{--}6.5$ % yr ⁻¹ ; full	15–222 yr	51.34– 52.70	measured [376];
biomass to 90 % of old growth,	66 yr	52.68	measured [377]; position
Amazon stem mortality $1.3\text{--}2.8$ % yr ⁻¹ ;	36–77 yr	52.13– 52.82	measured [378];
dominant stand ages, North America	30–120 yr	51.97– 52.22	measured [379]; positions
boreal stand-replacing fire cycles	50–250 yr; 70– 130 yr	52.43– 53.90	measured [380]; [381]; positions computed
soil organic matter tenfold, Glacier Bay	200 yr	53.69	measured [361]; position
lycopsid tree lifespan (40 m tree)	about 400 yr (200–800)	54.32	measured [366]; position
oldest trees, Pacific Northwest;	800 yr; 1,000 yr	54.95;	measured [379]; positions
soil phosphorus 82 % → 1 % mineral;	300 → 20,000	54.06–	measured [382]; positions
organic P maximum, Hawaii	yr; 150,000 yr	57.88;	computed
coal forests, duration	23.9–27.2 Myr	64.33– 64.45	computed from [357]; [357]

Lycopsid height growth is about 0.10 m per year, 40 m in 400 years (measured [366]; rate computed). Neotropical secondary forests reach 122 Mg ha⁻¹ after 20 years (range 20–225, 11.3-fold) at 3.05 Mg C ha⁻¹ yr⁻¹, about 11 times old growth (measured [377]). Turnover at 40 tropical sites rose since the 1950s, at 14 of 19 mature sites (measured [383]). The net biomass gain of 321 Amazon plots fell by one third in the last decade of three (measured [384]). In Quebec the charcoal record gives fire intervals of 332 ± 195 yr (mid-Holocene) and 99 ± 53 yr (last 2,100 yr). Cycles of 50–100 yr give aspen, birch and jack pine; more than 300 yr give fir, spruce and cedar (measured [380]). Recently burned boreal areas resist burning for about 30 years (measured [381]).

Counts

Self-thinning: the 1963 rule put mean plant mass proportional to density to the power $-3/2$ (measured [385], reporting Yoda et al.). Of 63 published thinning lines, 19 showed no significant correlation and 20 had slopes significantly different from $-3/2$, 7 shallower and 13 steeper (measured [385]). Of the 44 significant lines $20 / 44 = 45$ % deviate (computed). Field slopes ranged -3.808 to -0.146 ($n = 75$) and yield-table slopes -8.132 to -0.119 ($n = 351$) (measured [385]). Resource use scales as about the $3/4$ power of mass, and average plant size as the $-4/3$ power of maximum density (measured [386]). Across worldwide data the number of individuals falls as the -2 power of stem diameter (measured [387]). Two tests on 10 and 14 tropical plots, 367 and 473 ha, with 1.7 and 2 million trees, found the metabolic predictions inconsistent with the data (measured [388]; [389]). Most forests were near demographic equilibrium (measured [389]). The

understory size distribution after crown closure follows a power law with an exponent set by crown-area allometry (measured [390]). In even-aged stands the evolutionarily stable height growth ends at 87 % of break-even height; yield data follow this to 70–90 % of maximum height (measured [391]).

Light: understorey daily photon flux is about 1 % of a clearing, 9 % in a 200 m² gap and 20–35 % in a 400 m² gap (measured [392]). Diffuse transmittance is about 2 % at 1 m and over 10 % at 9 m; old growth 1.8 % (0.45–14.93 %) and second growth 1.75 % (0.53–5.87 %) at 0.75 m (measured [393]).

Gaps: the BCI plot of 50 ha holds more than 300,000 stems of 314 species; over 13 years it had more than 1,200 gaps of 25–1,150 m², a 46-fold range (measured [360]). Per-stem species richness was equal in and outside gaps. Of more than 1.3×10^6 seeds of 260 species in 200 traps over 10 years, a mean of 88 % of species failed to reach a given trap (measured [360]). Secondary forest at BCI: gaps 4.3 % of area (3.1–5.7 %), formation 0.45–6.5 % per year, mean gap 79 m² (8–604 m²) (measured [376]). Lidar gap fraction is 1.41 % in old growth and 0.93 % in old secondary forest, with a gap-size power-law exponent of 2.01–2.11 (measured [394]). Brazil: 11.2 gaps per ha, median 78 m² (measured [373]). Crown shyness gaps in black mangrove correlate with sway distance, $r = 0.69$, $n = 22$ (measured [395]).

Roots and chemistry: of 253 species, 194 root at or below 2 m, 50 at 5 m, 22 at 10 m (measured [370]). Globally about 30 %, 50 % and 75 % of root mass lie in the top 10, 20 and 40 cm (measured [371]). Root/shoot ratios are 0.1–0.5 in forests and 4–7 in tundra, grassland and cold desert (measured [371]). Neighbours of a sugar maple took 3–60 % of their water from its night-time lift (measured [372]). Juglone affected all 16 species tested, at 10^{-6} to 10^{-3} M, a 1,000-fold range (measured [396]; range computed).

Stands: the Herrin coal *Lepidodendron* stand had 1,769 stems per ha and a basal area of 992 m² per ha, about 10 % of the ground (measured [367]). That is $1,769 / 565 = 3.1$ times the Amazon median of 565 stems per ha (computed from [359]). Above the Mahoning coal more than 800 upright stumps stand in a peat body of about 60 km² (measured [397]).

Order of events

1. 393.3–387.7 Ma: Hangman forest, *Calamophyton* (measured [353]; [217]).
2. About 385 Ma: Gilboa, at least 8 m (measured [354]); Cairo, *Archaeopteris* roots 1.2–1.6 m deep and 11 m across (measured [355]).
3. About 370 Ma: *Archaeopteris* with modern wood; extinct near 358.9 Ma (measured [356]; [217]).
4. 330.9 Ma: coal forests spread; late Bashkirian: great expansion (measured [357]); lycopsids 10–50 m (measured [366]).
5. About 305–307 Ma: forests halve; tetrapod extinction peak (measured [358]; [357]).
6. From 298.9 Ma: brief re-expansion (measured [357]).
7. Present era: chronosequences of 200 yr at Glacier Bay and of 300 yr to 4.1 Myr in Hawaii (measured [361]; [382]). 2000–2020: mountain pine beetle, 374,000 km², 270 Mt C (measured [398]).

Present quantities

quantity	value	source
forest area; net loss	4.06 Gha; 4.7 Mha yr ⁻¹ (2010–2020)	measured [316]
forest carbon: total; tropical; boreal; temperate	861 ± 66; 471 ± 93 (55 %); 272 ± 23 (32 %); 119 ± 6 (13 %) Pg C	measured [250]
carbon density: tropical; boreal;	242; 239; 155 Mg C ha ⁻¹	measured [250]
forest sink: gross; net	4.05 ± 0.67; 1.11 ± 0.82 Pg C yr ⁻¹	measured [250]
tropical live biomass	247 Gt C on about 2.5 Gha; 99 Mg C ha ⁻¹	measured [399]; density computed
trees: total; tropical; boreal;	3.04; 1.30; 0.74; 0.66 trillion	measured [351]
trees cut per year; decline since civilisation began	>15 billion; about 46 %	measured [351]
forest disturbed per year by fire,	104 Mha, about 3 %	measured [379]
Amazon deaths: broken or	51.2 %; 48.4 % of 23,683	measured [378]

The tree count is 749 per ha of forest and was about 5.6 trillion before the decline (computed). Amazonia's 3.9×10^{11} trees are 12.8 % of the total (computed).

Pattern

Standing-tree forests begin at 393–388 Ma. By 385 Ma two tree types stand together, one rooting to 0.3 m and one to 1.2–1.6 m with estimated heights of 11–32 m; by 323–299 Ma trunks reach 10–50 m. The coal forests lasted 24–27 Myr and halved at 305 Ma. Stem counts fall as the -2 power of diameter in worldwide data; of 63 thinning lines, 20 of 44 significant ones deviate from $-3/2$. Under a closed canopy 1 % of light remains at 1 m; gaps of 8–1,150 m² open at 0.45–6.5 % of the area per year with a size exponent of 2.0–2.1. Stems die at 1.3–2.8 % a year. Half of root mass lies in the top 20–30 cm; maximum depth reaches 68 m. Regrowth reaches 90 % of old-growth biomass in 66 years. Today 3.04 trillion trees of 73,000 species hold 861 Pg C on 4.06 Gha.

Not verified

Calamophyton height 2–4 m and the age "about 390 million years" (University of Cambridge news story on Davies et al. 2024). Canopy heights above 40 m in the tropical band and below 20 m in boreal forest (NASA Earth Observatory page on Simard et al. 2011). Yoda et al. 1963 read only through reference lists. A printed gap turnover of about 100 years; the Farrior 2016 numeric exponent; the WBE branching ratio; crown diameters in metres; Crowther per-biome trees per ha; Phillips & Gentry 1994 absolute rates; the Ripple & Beschta 2012 post-1998 browsing figure; Boyce & Lee 2017 forest-extent numbers. Citation only, numbers not read: Niklas 1997; Falster & Westoby 2003; Coomes 2006; Whitmore 1989; Clements 1916; Gleason 1926; Jucker et al. 2017 crown values; Ripple & Beschta 2012 beyond the 1998 figure of 100 % browsed leaders.

A10 Viruses and Pathogens

What it is

A pathogen is a virus, bacterium, oomycete, fungus, nematode or parasitic plant that grows in or on a living plant at the plant's cost. The plant side is an immune system of surface receptors,

intracellular receptors and small RNAs. Measured losses to pathogens and pests are 21.5 % of wheat, 30.0 % of rice, 22.5 % of maize, 17.2 % of potato and 21.4 % of soybean (measured [400]).

First appearance

Plant viruses leave no body fossils; their age is read from viral sequences inserted in plant genomes. Endogenous caulimovirid reverse-transcriptase loci occur in nearly all vascular plants screened: 14,895 high-confidence loci in 72 genome assemblies and 6 fern genomes (measured [401]). Florendoviruses occur in 46 of 62 seed plants and petuviruses in 27 of 62. The family's origin is placed "at latest during the Devonian, about 320 million years ago" (measured [401]). The position of 320 Ma is 66.70 (computed). A second screen of 20 genomes found 17,574 endogenous pararetroviruses in 10 gymnosperms (18–6,194 per species), 289 in 6 ferns and none in a moss, a liverwort, a lycophyte or a charophyte (measured [402]). Insertion bursts in *Pinus taeda* date to 108–232.9 Ma and orthologous insertions to at least 75 Ma in *Pinus* and 16.9 Ma in *Picea* (measured [402]). These are lower bounds at host substitution rates of $1.43\text{--}2.2 \times 10^{-9}$ per site per year (measured [403]). Positions: 233 Ma 66.41, 108 Ma 65.71, 75 Ma 65.38, 16.9 Ma 64.02 (computed). The figure of more than 400 Myr is the premise of a co-speciation model that the data do not support (measured [402]).

On the plant side, crown embryophytes are 482 (485–473) Ma, tracheophytes 452 Ma, spermatophytes 365 Ma and the angiosperm crown 151 Ma (see A2). Vascular plants are thus $452 - 320 = 132$ Myr older than the oldest dated viral insertion, and angiosperms are younger than the caulimovirids (computed). The angiosperm radiation is given as roughly 140–180 Ma (measured [404]). The ancestral angiosperm had 7 TNL, 14 CNL and 2 RNL immune-receptor lineages, 23 in all. CNLs expanded gradually over the first about 100 Myr of angiosperm evolution, and both TNL and CNL expansion intensified from the Cretaceous–Paleogene boundary (measured [405]), 66 Ma, position 65.26 (computed).

The potyviruses, about 15 % of named plant virus species, radiated about 6,600 years ago, with agriculture, at about 1.15×10^{-4} substitutions per site per year (measured [406]). The position is 56.88 (computed). The virus rate exceeds the host rate by $1.15 \times 10^{-4} / 2.2 \times 10^{-9} = 5.2 \times 10^4$ to $1.15 \times 10^{-4} / 1.43 \times 10^{-9} = 8.0 \times 10^4$ (computed).

Human recognition is recent. Tobacco mosaic disease was reported in 1857; Ivanovsky showed in 1892 that the agent passed a porcelain filter; Beijerinck described a "contagium vivum fluidum" in 1898 (measured [407]). From 1898 to 2026 is 128 years (computed).

Partners

Viruses: the ICTV list of 2025 holds 16,215 species in 3,769 genera, 368 families and 93 orders (measured [408]); 1,563 species and 55 families were added in that year (measured [409]). Plant and fungal viruses, viroids and satellites numbered 2,134 species in 46 families and 193 genera in the 2021 list (measured [410]); $2,134 / 16,215 = 13.2$ % (computed; different release years). A public database holds 3,206 plant virus species from 46 families on 2,231 plant species, 9,604 interactions, 54 % RNA and 46 % DNA (measured [411]). The older DPVweb list has 1,503 species (measured [411]). The three counts, 1,503, 2,134 and 3,206, are recorded. Plant virus genera recognised in 2012: 92, 82 of them in 21 families (measured [412]). About 80 % of plant viruses are transmitted by specific insect vectors (measured [413]); more than 200 persist in their hemipteroid vectors (measured [414]).

Other pathogen groups (*Phytophthora* species counts are in A2):

group	measured count	source
<i>Pseudomonas syringae</i> : pathovars; phylogroups; effectors delivered per strain	>60; 13; 15–30	measured [415]; [404]
<i>Xylella fastidiosa</i> : host species; families; subspecies	696; 88; 5	measured [416]
phytoplasmas: host plant species	>700	measured [417]
<i>Agrobacterium</i> T-DNA in genomes: sweet potato cultigens; sequenced dicots	291 of 291; 23 of 275 (8.4 %, computed)	measured [418]; [419]
<i>Phytophthora infestans</i> : RXLR effectors; CRN genes; protein-coding genes	563 (earlier count 425); 196; 17,797	measured [420]; [421]
<i>Puccinia graminis</i> f. sp. <i>tritici</i> : haploid chromosomes	18	measured [422]
coffee leaf rust: physiological races	>50	measured [423]
barley powdery mildew: gene models; core candidate	7,118–7,239; 190	measured [424]
plant-parasitic nematodes: species; share of terrestrial nematodes; independent origins	about 4,100; about 25 %; 4 clades	measured [425]
<i>Striga</i> : obligate root-parasitic species	about 30	measured [426]

Both RXLR counts are recorded. The Ug99 stem rust lineage arose by somatic hybridisation (measured [422]).

On the plant side, *Arabidopsis* has at least 610 receptor-like kinases, nearly 2.5 % of protein-coding genes; the family was near its present size before land-plant lineages diversified (measured [427]). The implied gene count is $610 / 0.025 = 24,400$ (computed). Col-0 has over 200 LRR-kinases, 56 receptor-like proteins and about 125 NB-LRR genes (measured [404]); other counts give 149 (see A2) and 159 (measured [428]). All three are recorded.

Sizes

what	size	positi	source
closterovirid filament diameter	about 12 nm	-1.21	measured [429]; position
tobamovirus rod: diameter; length	about 18 nm; 300–310 nm	-0.85; 1.72–	measured [430]; positions
nanovirus particle	18–19 nm	-0.85– -0.80	measured [431]; positions
geminat particle (maize streak virus)	22 × 38 nm	-0.66; -0.17	measured [432]; positions
bromovirid virion	26–35 nm	-0.51– -0.24	measured [433]; positions
phytoplasma cell	80–800 nm	0.51– 2.61	measured [417]; positions
closterovirid filament length	650–2,200 nm	2.42– 3.53	measured [429]; positions
flg22; RIN4	22; 211 amino acids	—	measured [404]
genomes: geminivirus; nanovirus; tobamovirus; bromovirid; closterovirid	2.5–3.0 or 4.8–5.6 kb; 6–8 × about 1 kb; 6.3–6.5 kb; 8,623	—	measured [432]; [431];
phytoplasma chromosome; <i>P. infestans</i> genome; <i>P. graminis</i> haplotype assembly;	600–880 kb; about 240 Mb; 176–177 Mbp; about 797	—	measured [417]; [420];

The tobamovirus aspect ratio is $310 / 18 = 17$; the longest closterovirid is $2,200 / 18 = 122$ tobamovirus diameters (computed). Cucumber mosaic virus RNAs are 3,357, 3,050 and 2,216 nt, together 8,623 nt (measured [433]; sum computed). The *P. infestans* genome is about 74 % repeats, and RXLR effectors are $563 / 17,797 = 3.2$ % of its genes (measured [420]; share computed).

Times

what	duration	position	source
LRR-kinase induction after flg22	within 30 min	39.98	measured [404]; position
systemic protection after a TMV hypersensitive response	up to 3 weeks	46.27	measured [412]; position computed
root-knot nematode, infection to first eggs	4–6 weeks	46.53–46.90	measured [434]; positions computed
<i>Daphnia</i> parasite re-adaptation	a few years	—	measured [435]
<i>Sr31</i> : wide deployment (1970s) to	28 yr	51.90	measured [436]; [422];
<i>Lr34</i> durable resistance	more than 50	>52.43	measured [437]; position
FAM-1 late blight lineage sampled	1845–1987, 144 yr	53.39	measured [438]; position computed
TR4 chlamydospores in soil	more than 20	>51.60	measured [439]; position
<i>Rpm1</i> resistance/susceptibility	millions of	—	measured [440]
potyvirus radiation	about 6,600	56.88	measured [406]; position

Mutation rates per nucleotide per cell infection, from more than 40 studies, run about 10^{-8} to 10^{-6} for DNA viruses and 10^{-6} to 10^{-4} for RNA viruses (measured [441]). Tobacco mosaic virus is at 8.7×10^{-6} and tobacco etch virus at 4.8×10^{-6} (measured [441]); the span is 10^4 (computed). Across viruses mutation rates vary over five orders of magnitude and substitution rates over six (measured [442]). Nematodes run $365 / 42 = 8.7$ to $365 / 28 = 13$ generations per year if continuous (computed). The *Rpm1* alleles have coexisted for millions of years; the data fit balanced polymorphism rather than a succession of sweeps (measured [440]); *RPM1* carries a large fitness cost in the field (measured [443]). In wild flax and its rust, allele frequencies at recognition loci fluctuated asynchronously among populations and tracked disease prevalence (measured [444]).

Counts

Receptors: NLR genes per genome, as cited, run from 54 in papaya to 992 in apple; tomato has 267, potato 443, pepper 755 intact genes (measured [428]). The range is $992 / 54 = 18.4$ -fold (computed). Across 100 chromosome-level genomes, 68,452 NLRs (3,689 full-length, 64,763 partial), from 28 in *Coriandrum sativum* to 3,428 in *Medicago sativa*, mean about 685 (measured [445]); range $3,428 / 28 = 122$ -fold (computed). Both ranges are recorded; they depend on the counting method. The *Arabidopsis* pan-NLRome saturates at about 40 wild strains, with about half present in most accessions (measured [446]). About 200 resistance genes against viruses are known, about half recessive (measured [412]).

Small RNAs: antisense RNAs of about 25 nt were detected in silencing systems in 1999 (measured [447]). *Arabidopsis* has four DICER-LIKE proteins producing 21, 22 and 24 nt virus-derived siRNAs (DCL4 21, DCL2 22, DCL3 24) (measured [448]). Inactivating both DCL2 and DCL4 is necessary and sufficient to restore systemic infection by a suppressor-deficient virus (measured [449]). The 25 nt and 21/22/24 nt figures are both recorded. One review names 10 distinct viral

silencing suppressors, and suppressors also occur in pathogenic bacteria and oomycetes (measured [450]). The flagellin peptide flg22 induces at least 1,100 genes (measured [404]).

Epidemics: Ug99 was detected in Uganda in 1998 and had seven races by 2011; about 90 % of wheat varieties worldwide were susceptible (measured [451]). By 2014 the group held two further races virulent on SrTmp (measured [452]). Citrus tristeza has killed over 100 million trees; rice tungro costs US\$1.5 billion per year; 47 % of pathogens behind emerging plant epidemics are viruses (measured [453]). Another review gives "about half" and more than 200 million cacao trees eradicated for swollen shoot (measured [412]). Both shares are recorded. A mild pepino mosaic virus strain, licensed in 14 European countries, protected more than 4,500 ha of tomatoes (measured [454]). A fungal virus is required for a panic-grass endophyte to confer heat tolerance; cured isolates fail and reintroduction restores it (measured [455]).

Late blight reached the United States in 1843 and Belgium and Ireland in 1845 (measured [438]). The Irish famine of 1845–1850 caused about 1 million deaths excluding emigrants (measured [456]). From 1843 to 2014 fifteen named pandemics or resistance breakdowns are listed, one every $(2014 - 1843) / 15 = 11.4$ years (computed).

Order of events

1. About 320 Ma: caulimovirid family origin, at latest (measured [401]).
2. 233–108 Ma: pararetrovirus bursts in *Pinus taeda*; at least 75 Ma and 16.9 Ma: orthologous insertions (measured [402]).
3. 140–180 Ma: angiosperm radiation (measured [404]); first about 100 Myr: gradual CNL expansion; from 66 Ma: intensified expansion (measured [405]).
4. About 6,600 years ago: potyvirus radiation (measured [406]).
5. 1843–1845: late blight in the United States, Belgium and Ireland (measured [438]).
6. 1857–1898: tobacco mosaic reported, filtered and named a contagium vivum fluidum (measured [407]); 1869: coffee leaf rust described (measured [423]).
7. 1920s–1954: stem rust race 21 from southern Africa to Australia (measured [422]); 1929–1938: cross-protection observed (measured [454]); 1935: TMV crystallised (measured [407]).
8. 1970s: *Sr31* in wide use (measured [436]); 1990: TR4 on Cavendish; 1997 Australia; 2013 Mozambique; 2015 Pakistan and Queensland (measured [439]).
9. 1998: Ug99 detected (measured [422]; [451]); 1999: 25-nt antisense RNAs (measured [447]); 2006: Dicer hierarchy (measured [448]; [449]); 2009: *P. infestans* genome (measured [420]).
10. October 2013: *Xylella* in Puglia (measured [416]); 2014: SrTmp virulence (measured [452]); 2015: pepino mosaic cross-protection cleared (measured [454]).

Present quantities

Virus species 16,215 (measured [408]); plant virus species 1,503–3,206 by list (measured [411]). Crop losses to pathogens and pests: wheat 21.5 % (10.1–28.1), rice 30.0 % (24.6–40.9), maize 22.5 % (19.5–41.1), potato 17.2 % (8.1–21.0), soybean 21.4 % (11.0–32.4), from 137 pathogens and pests (measured [400]). Plant virus losses exceed US\$30 billion per year (measured [453]; [412]); late blight US\$6.7 billion per year (measured [420]); nematodes €110 billion per year (measured [425]); *Striga* US\$1 billion per year (measured [426]). Cavendish is 99 % of banana exports (measured [439]). Wind-borne fungal spores carry crop diseases between continents; epidemics require one susceptible genotype over large areas (measured [457]).

Pattern

Plant viruses are recorded as genome insertions from about 320 Ma, in ferns and gymnosperms before the angiosperms of 151 Ma. The plant receptor set grew from 23 ancestral NLR lineages to 28–3,428 genes per genome, with intensified expansion from 66 Ma. Viruses substitute 5×10^4 to 8×10^4 times faster per year than their hosts and mutate at 10^{-8} to 10^{-4} per site per infection; nematodes run 9–13 generations per year. Against this, single R genes hold 28 years (*Sr31*) or more than 50 years (*Lr34*), and wild R polymorphisms persist for millions of years. Each defence has a measured counterpart: 21–24 nt small RNAs and 10 named suppressors; more than 200 surface kinases and 15–30 injected bacterial effectors; 28–3,428 NLRs and 425–563 oomycete effectors. Losses are 17–30 % of five staple crops; a named pandemic or breakdown is listed every 11.4 years since 1843.

Not verified

Tobamovirus–eudicot co-divergence of at least 110 Myr (Gibbs et al. 2015, title read in Lefeuvre et al. 2019). Oldest plant EVE integration 1.8 Myr and florendovirus minimum 34 Myr (Geering et al. 2014, cited in Diop 2018). About 1,400 invertebrate RNA viruses (Shi et al. 2016, cited in Lefeuvre 2019). *Pseudomonas* cell length 1.5–2.2 μm (BioNumbers 115601, naming Young 2006). Aphid generation 4.7 d and 78 generations per year (BioNumbers 100519). Nematode loss US\$80 billion read through Sato et al. 2019 (naming Jones et al. 2013). Parasitic plants arising 12 times (Nickrent; not in A1, A2 or A5). The 9.8 Myr age of the *Rpm1* polymorphism; Thrall 2012 field years; the "about 75 %" insect-transmission share (Whitfield 2015); Avr3a length; Panama disease race 1 dates; Flor 1942 locus counts; latent periods and doubling times of blight and rusts. Citation only, numbers not read: Roossinck 2015; Duplessis et al. 2011; Spanu et al. 2010; Ding & Voinnet 2007; Flor 1971; Whitfield et al. 2015.

Part C — Cross-chapter tables (built from G-partA only)

All numbers carry the reference number [n] under which they appear in G-partA. Positions are copied from G-partA where G-partA gives them; positions marked (computed) were calculated with pos.py (size = $\log_3(\text{m} / 4.558816 \times 10^{-8} \text{ m})$; time = $\log_3(\text{s} / 1.520655 \times 10^{-16} \text{ s})$; 1 yr = $3.15576 \times 10^7 \text{ s}$; Ma = million years before present). Chapter codes: A1 pollination, A2 fungi, A3 bacteria and nitrogen, A4 seed dispersal, A5 soil life, A6 herbivores and defence, A7 decomposers, A8 climate and atmosphere, A9 competition and forests, A10 viruses and pathogens.

C1. First appearances

Sorted oldest first. One row per dated event.

#	event	age	position	chapter	ref
1	last universal common ancestor,	older than 3.9 Ga	68.97	A3	[95]
2	last universal common ancestor,	3.5–3.8 Ga	68.87–68.95	A3	[87]
3	biological N ₂ fixation, isotopic	3.2 Ga	68.79	A3	[94]
4	microbial mats on a palaeosol, South	2.6–2.7 Ga	68.60–68.64	A3, A5	[101]

5	Great Oxidation Event, onset	2,460–2,426 Ma	68.55–68.54	A3, [97];
6	fungus-like mycelial filaments in	2.4 Ga	68.53	A2 [49]
7	permanent atmospheric O ₂ (sulfur	2.33 Ga	68.50	A3, [96];
8	N ₂ fixation origin, molecular clock	1.5–2.2 Ga	68.10–68.45	A3 [87]
9	chloroplast lineage branches within	about 2.1 Ga	68.41	A3 [92]
10	mitochondrial origin	2.053–1.21 Ga	68.39–67.91	A3 [95]
11	crown eukaryotes	younger than 1.84 Ga	68.29	A3 [95]
12	chloroplast symbiosis, second figure	more than 1.5 Ga	68.10	A3 [91]
13	crown Fungi, six-gene clock	about 1,020 Ma	67.75	A2 [51]
14	<i>Ourasphaira giralda</i> , oldest	1,010–890 Ma	67.74–67.63	A2 [50]
15	loss of the fungal flagellum	about 720 Ma	67.43	A2 [51]
16	Glomeromycota origin	about 659 Ma (715–	67.35	A2 [51]
17	Dikarya divergence	649 Ma	67.34	A2 [51]
18	ocean oxygenation, basal Doushantuo	635–630 Ma	67.32	A8 [301]
19	Ediacaran palaeosols with sessile	635–542 Ma	67.32–67.18	A5 [172]
20	myriapod origin, molecular clock	about 500 Ma	67.10	A7 [254]
21	Glomeromycota diversification onset	about 484 Ma (529–	67.07	A2 [51]
22	crown embryophytes	482 Ma (485–473)	67.07	A2 [51]
23	insects, molecular origin	about 479 Ma	67.06	A1 [6]
24	land plants colonise land	about 470 Ma	67.05	A8 [302]
25	glomalean spores and hyphae,	about 460 Ma	67.03	A2 [52]
26	COI1 jasmonate receptor shared by	about 450 Myr of	67.01	A6 [219]
27	Leotiomyceta radiation	about 446 Ma (467–	67.00	A2 [51]
28	carbonate $\delta^{13}\text{C}$ rise of 2 ‰	about 445 Ma	67.00	A8 [302]
29	Ordovician glaciation, after non-	before 444 Ma	66.99	A8 [307]
30	<i>Scoyenia beerboweri</i> burrows, probable millipedes, in palaeosols	older than 443.8 Ma	66.99	A5 [173]; [174];
31	<i>Tortotubus protuberans</i> , cord-forming	earliest Silurian, after	66.99	A2 [53]; [5]
32	deep-ocean oxygenation	435–392 Ma	66.98–66.88	A8 [302]
33	kampecarid millipedes, Kerrera	about 425 Ma	66.95	A7 [254]
34	earliest charcoal (wildfire), Ludford	423.0 ± 2.3 Ma	66.95	A7 [252];
35	O ₂ above 15–17 % (fossil charcoal)	420–400 Ma	66.94–66.90	A8 [302]
36	charcoal continuous in sediments	younger than 419 Ma	66.94	A8 [303]
37	clitellate annelids, freshwater common	Devonian, 419–359	66.94–66.80	A5 [177]
38	first arthropod herbivory: spore	417–403 Ma	66.94–66.91	A1, [43]
39	internally stratified lichens, Welsh	415 Ma	66.93	A2 [57]
40	<i>Pneumodesmus newmani</i> , millipede	413.7 ± 4.4 Ma	66.93	A7 [253]

41	Rhynie chert: arbuscules in <i>Aglaophyton</i> ; <i>Prototaxites</i> 8 m	411.5 ± 1.3 Ma (also c. 407 Ma)	66.93; 66.92	A2	[55]; [56];
42	oldest insect fossil, <i>Rhyniognatha</i>	Pragian, 410.8–407.6 Ma	66.92	A1	[4]; [5]
43	Rhynie soil fauna: nematodes, mites, springtails, arachnids, myriapods,	410.8–407.6 Ma	66.92	A5	[175]; [5]
44	insect flight, molecular	about 406 Ma	66.91	A1	[6]
45	origin of leaves (326 Ma + 76 Myr)	about 402 Ma	66.90	A1	[43]
46	<i>Winfrenatia reticulata</i> , Rhynie lichen	about 400 Ma	66.90	A2	[58]
47	rooted plants; CO ₂ fall from about 380 Ma	400–360 Ma	66.90–66.80	A8	[305]; [306]
48	common ancestor of Polyporales	399 ± 140 Ma	66.90	A7	[258]
49	Hangman forest, <i>Calamophyton</i> , <i>Platystrophia</i> forest	Eifelian, 393.3–387.7 Ma	66.88–66.87	A9	[353]; [217]
50	first seeds	late Middle–Late Devonian, 387.7–	66.87–66.80	A4	[133]; [5]
51	Gilboa and Cairo forests; <i>Archaeopteris</i> roots 1.2–1.6 m deep	about 385 Ma	66.86	A9, A3,	[354]; [355];
52	forest-grade communities	Givetian, about 385 Ma	66.86	A7	[254]
53	first wood borings	383–359 Ma	66.86–66.80	A7	[255]
54	<i>Archaeopteris</i> with wood of the modern kind, Morocco	about 370 Ma (Famennian, base	66.83	A9	[356]; [217]
55	<i>Archaeopteris</i> extinct near the Devonian–Carboniferous boundary	358.9 Ma	66.80	A9	[356]; [217]
56	class II peroxidase diversification	350–295 Ma	66.78–66.62	A2	[51]
57	main living insect lineages	about 345 Ma	66.76	A1	[6]
58	coal forests spread across the Variscan belt	Serpukhovian, from 330.0 Ma	66.73	A9	[357]; [217]
59	oldest winged insect, <i>Delitzschala</i>	Arnsbergian, within 330.0–323.0 Ma	66.73–66.71	A1	[7]; [5]
60	<i>Arthropleura</i> , largest arthropod	Serpukhovian, 330.9–323.0 Ma	66.73–66.71	A7	[256]; [217]
61	second herbivory pulse; leaf-margin serrations	327–309 Ma	66.72–66.66	A1	[43]
62	flesh-covered seeds in seed ferns and <i>Leptopteris</i>	Pennsylvanian, 323.2–308.0 Ma	66.71–66.63	A4	[133]; [5]
63	Caulimoviridae origin (endogenous	at latest about 320 Ma	66.70	A10	[401]
64	<i>Melanedaphodon hovaneci</i> , oldest <i>Leptopteris</i>	Moscovian, about 307 Ma	66.66	A6	[216]
65	coal forests contract by half; tetrapod extinction peak	Kasimovian, 307.0–303.7 Ma; about 305 Ma	66.66; 66.65 (computed)	A9	[357]; [358];
66	oldest insect gall	about 302 Ma	66.64	A1	[44]
67	Lepidoptera crown	about 300 Ma	66.64	A1	[18]
68	first class II peroxidase (AA2) genes, <i>Agaricomycetes</i>	about 300 Ma	66.64	A7	[257]
69	Agaricomycetes crown	299 Ma (351–252)	66.63	A2	[51]
70	earthworm crown group	Carboniferous–Permian boundary,	66.63	A5	[178]; [5]
71	plant-eating vertebrates first diversify	Permian, 298.9–251.000 Ma	66.63–66.48	A4	[133]; [5]
72	tetrapod herbivory, at least five origins	Late Carboniferous to Early Permian, by	66.59	A6	[218]; [217]

73	beetle wood borings	272–260 Ma	66.55	A7	[255]
74	end-Permian fungal proliferation	254.14–251.902 Ma	66.49–66.48	A7	[282]; [217]
75	egg-niche borings in <i>Ningxiaites</i>	254–252 Ma	66.49	A7	[255]
76	end-Permian extinction	251.941–251.880 Ma	66.48	A8	[327]
77	Lepidoptera tube-like proboscis	about 241 Ma	66.44	A1	[18]
78	oldest pupation chamber in wood	Late Triassic, 237–201.4 Ma	66.42–66.27	A7	[260]; [217]
79	pararetrovirus insertion bursts in <i>Pinus</i>	232.9–108 Ma	66.41–65.71	A10	[402]
80	CO ₂ about 2,000 ppm, second	220–200 Ma	66.36–66.27	A8	[306]
81	wing scales of Glossata (proboscis-bearing Lepidoptera)	Triassic–Jurassic boundary, 201.4 Ma	66.27	A1	[19]; [5]
82	leech cocoon fossil (calibration)	201 Ma	66.27	A5	[186]
83	first versatile peroxidase	194 ± 70 Ma	66.24	A7	[258]
84	earthworm northern–southern family	186–161 Ma	66.20–66.07	A5	[186]
85	Pinaceae crown	183 Ma (233–150)	66.19	A2	[51]
86	angiosperm radiation	roughly 180–140 Ma	66.17–65.94	A10	[404]
87	first lignin peroxidase	178 ± 64 Ma	66.16	A7	[258]
88	oldest definitive pollinating insects (siphonate proboscides, on	about 165 Ma	66.09	A1	[10]
89	Agaricomycetidae	154 Ma	66.03	A2	[51]
90	termite crown	149 Ma (136–170)	66.00	A7	[261]
91	magnoliids, monocots and eudicots	135–130 Ma	65.91–65.88	A1	[8]
92	oldest undisputed termite fossils	135–110 Ma	65.91–65.72 (110 Ma	A7	[261]
93	dung-beetle tribes originate	130–119 Ma	65.88–65.80	A7	[264]
94	four gymnosperm pollination modes; four insect pollinator cohorts	125–90 Ma	65.84–65.54 (computed)	A1	[12]
95	crown bees	about 123 Ma (113–120)	65.83	A1	[17]
96	bark and ambrosia beetles (Scolytinae)	120–100 Ma	65.80–65.64	A7	[263]
97	<i>Darwinylus marcosi</i> , first beetle pollinator (gymnosperm pollen)	about 105 Ma	65.68	A1	[12]
98	long-proboscid flies with gymnosperm	105 and 100 Ma	65.68; 65.64	A1	[14]
99	nodulation predisposition, single	slightly over 100 Ma	65.64	A3	[98]
100	oldest bee, <i>Melittosphex burmensis</i>	about 100 Ma	65.64	A1	[15]
101	Palaeognathae–Neognathae split	about 100 Ma	65.64	A4	[138]
102	<i>Azolla</i> –cyanobiont relationship	about 100 Myr	65.64	A3	[117]
103	boganiid beetle with cycad pollen	about 99 Ma	65.63	A1	[13]
104	eudicot (tricolpate) pollen on a beetle	99 Ma	65.63	A1	[16]
105	day-flying butterflies	from about 98 Ma	65.62	A1	[18]

10	dung-beetle radiation	98–85 Ma (alternative 85.5–72.6 Ma)	65.62–65.49; 65.49–65.35	A7	[264]
10	Galloanseres–Neoaves split	about 88 Ma	65.52	A4	[138]
10	turtle coprolite with about 200	Campanian, 83.6–72.1 Ma	65.47–65.34	A4	[133]; [51]
10	seed beetles	81–78 Ma	65.45–65.41	A1	[40]
11	fleshy fruits and angiosperm seed-size diversification begin	around 80 Ma	65.41 (G-partA; recomputed)	A4	[137]
11	orthologous pararetrovirus insertions	at least 75 Ma	65.38	A10	[402]
11	grass phytoliths (five subclades) in	Maastrichtian, 72.1–66 Ma	65.34–65.26	A6	[222]; [137]
11	K–Pg boundary; 36 Neoaves lineages within 10–15 Myr; NLR expansion	66 Ma	65.26	A4, A10	[138]; [405]
11	oldest unequivocal legume fossil	65.35 Ma	65.25	A3	[100]
11	ant fungus farming	61–57 Ma	65.19–65.13	A1	[42]
11	fig–wasp co-divergence	at least 60 Myr	65.17	A1	[45]
11	legumes; nodulation	about 60 Ma; about 58 Ma	65.17; 65.14	A3	[99]
11	scatter-hoarding of nuts (may begin)	Paleocene, about 60 Ma	65.17	A4	[142]
11	<i>Azolla</i> –cyanobiont, second figure	more than 60 Myr	65.17	A3	[91]
12	Bighorn Basin leaf-damage series (PETM, 55.8 Ma)	58.9–55.2 Ma	65.16–65.10	A6	[249]
12	PETM	about 56 Ma	65.11	A8	[328]
12	oldest bat, <i>Onychonycteris finneyi</i>	Early Eocene, 56.0–47.9 Ma	65.11–64.97	A4	[140]; [51]
12	oldest primate skeleton	early Eocene, about 55 Ma	65.09	A4	[139]
12	peak of seed and fruit size diversity	55–50 Ma	65.09–65.01	A4	[137]
12	Termitidae	54 Ma (46–66)	65.08	A7	[261]
12	Arctic <i>Azolla</i> phase	about 50–48.5 Ma	65.01–64.98	A8	[311]
12	first fungus-farming ambrosia beetles	about 50 Ma	65.01	A7	[263]
12	bird ordinal divergences complete	by 50 Ma	65.01	A4	[138]
12	open-habitat (pooid, PACMAD)	42–38 Ma	64.85–64.76	A6	[223]
13	yucca moths on yuccas	41.5 ± 9.8 Ma	64.84	A1	[46]
13	basal split of Passeriformes	about 39 Ma	64.78	A4	[138]
13	orchid bees	38–34 Ma	64.76–64.66	A1	[20]
13	Eocene–Oligocene shift; seed and fruit diversification	about 34 Ma	64.66	A4	[137]; [165]
13	C4 grasses originate	Early Oligocene, at least 25 Myr before 7–	—	A6	[223]
13	fungus-growing termites	31.41 Ma (25.82–20.52)	64.58	A7	[262]
13	crown Old World fruit bats	31–20 Ma	64.57–64.17	A4	[141]
13	perfume orchids of the orchid bees	27–18 Ma	64.45–64.08	A1	[20]
13	oldest fossil fungus gardens, Rukwa	24.8–24.5 Ma	64.37	A7	[262]
13	C3 grass habitats, Central Great Plains	by 21.9 Ma	64.26	A6	[224]

14	leaf-cutter ants	19–18 Ma	64.13–64.08	A1	[42]
14	ant domatia, at least 158 origins within	within 19 Myr	64.13	A6	[229]
14	hypsodont Equinae	at least 4 Myr after 21.9 Ma, so by 17.9	64.07	A6	[224]
14	spinescence radiation, southern Africa	mostly within the last 17 Ma	64.02	A6	[225]
14	orthologous pararetrovirus insertion in	16.9 Ma	64.02	A10	[402]
14	horned bovids arrive in Africa	by 16 Ma	63.97	A6	[225]
14	grass pollen above 90 %, South Asia	8.5–6.5 Ma	63.39–63.15	A6	[223]
14	C4 plants abundant worldwide; C4 grasslands	8–6 Ma; 8–3 Ma	63.34–63.08; 63.34–62.45	A8	[345]; [346]
14	Darwin's orchid and its hawkmoth	7.5 ± 5.2 and 7.4 ± 2.8 Ma	63.28; 63.27	A1	[27]
14	C4 grasslands, North America; Africa	7–6 Ma; after 5 Ma	63.22–63.08; <62.91	A6	[223]
15	periodical cicada species groups split	3.9–2.5 Ma	62.68–62.28	A1	[28]
15	glacial cycle changes from 41 kyr to 100 kyr	1,250–700 ka	61.65–61.12 (700 ka)	A8	[330]
15	13- and 17-year cicada cycles diverge	200,000–100,000 yr	59.98–59.35	A1	[28]
15	ice-sheet maximum	33.0–26.5 ka	58.34	A8	[332]
15	<i>Pinus flexilis</i> stomatal density falls 17	15,000–12,000 yr ago	57.62–57.42	A8	[340]
15	megafauna extinction	10–15 kyr BP	57.25–57.62	A4	[144]
15	onset of plant domestication	11,000–10,000 yr BP	57.34–57.25	A4	[158]
15	potyvirus radiation, with agriculture	about 6,600 yr ago	56.88	A10	[406]
15	late blight reaches the United States; Belgium and Ireland 1845	1843 CE (183 yr before 2026)	53.61 (computed)	A10	[438]
15	tobacco mosaic disease reported; filterable agent 1892; named 1898	1857–1898 CE	53.54–53.29 (computed)	A10	[407]
16	chestnut blight, eastern North America	1904 CE	53.24	A2	[85]
16	first Dutch elm pandemic	1910 CE	53.20	A2	[86]
16	Ug99 stem rust detected, Uganda	1998 CE	51.90	A10	[422]; [451]

C2. Who came first

Gap = older date minus younger date, in Myr (computed). Where a date is a range, the gap is given as a range.

cha pte	plant-side element (what, date)	partner-side element (what, date)	which is older	gap, Myr (compute)	ref
A1	main angiosperm clades, 125–120 Ma	oldest insect fossil, 410.8– 407.6 Ma	partner first	272.6– 288.8	[8]; [4]; [51]
A1	main angiosperm clades, 125–120 Ma	Lepidoptera tube-like 125–120 Ma	partner first	106–111	[8]; [18]
A1	main angiosperm clades, 125–120 Ma	Lepidoptera crown, about 200 Ma	partner first	165–170	[8]; [18]
A1	main angiosperm clades, 125–120 Ma	crown bees, about 123 Ma (113–123)	plant first	7–12	[8]; [17]

A1	eudicot pollen on a beetle, 80 Ma	oldest bee, about 100 Ma	partner first	1	[16]; [15]
A1	origin of leaves, about 402 Ma (computed from	leaf-margin feeding, 326 Ma	plant first	76	[43]
A1	perfume orchids, 27–18 Ma	orchid bees, 38–34 Ma	partner first	7–20	[20]
A1	Darwin's orchid split, 7.5 ± 5.2 Ma	its hawkmoth split, 7.4 ± 2.8 Ma	plant first (within error)	0.1	[27]
A2	crown embryophytes, 482 Ma	crown Fungi, about 1,020 Ma	partner first	538	[51]
A2	crown embryophytes, 482 Ma	Glomeromycota origin, about 650 Ma	partner first	177	[51]
A2	arbuscules in <i>Aglaophyton</i> , host rock	glomalean spores and hyphae, about 460 Ma	partner first	48.5	[55]; [54]; [52]
A2	arbuscules in <i>Aglaophyton</i> , host rock	<i>Tortotubus</i> , after 443.8 Ma	partner first	up to 32.3	[55]; [53]; [5]
A2	Pinaceae crown, 183 Ma (222–150)	Agaricomycetes crown, 299 Ma (251–252)	partner first	116	[51]
A3	land plants, about 470 Ma	biological N ₂ fixation, 3.2 Ga	partner first	2,730	[302]; [84]
A3	crown eukaryotes, about 1.84 Ga	chloroplast lineage, about 2.1 Ga	partner first	at least 260	[95]; [92]
A3	legumes, about 60 Ma; oldest legume fossil 65.35 Ma	nodulation, about 58 Ma	plant first	2–7.35	[99]; [100]
A3	<i>Archaeopteris</i> roots to 1.2–1.6 m, about 385 Ma	microbial mats on a palaeosol, 2.6–2.7 Ga	partner first	2,215–2,315	[112]; [101]
A4	flesh-covered seeds, Pennsylvanian, 323.2–	plant-eating vertebrates diversify, Permian, 298.9–	plant first	0–24.3	[133]; [5]
A4	fleshy-fruit diversification onset, about 80 Ma	Palaeognathae–Neognathae split, about 100 Ma	partner first	20	[137]; [138]
A4	fleshy-fruit diversification onset, about 80 Ma	36 Neoaves lineages, 66 to 51 Ma	plant first	14–29	[137]; [138]
A4	fleshy-fruit diversification onset, about 80 Ma	oldest primate skeleton, about 55 Ma	plant first	25	[137]; [139]
A4	fleshy-fruit diversification onset, about 80 Ma	oldest bat, 56.0–47.8 Ma	plant first	24–32.2	[137]; [140]; [5]
A4	seed/fruit size peak, 55–50 Ma	crown Old World fruit bats, 21–20 Ma	plant first	19–35	[137]; [141]
A5	<i>Archaeopteris</i> roots to 1.2–1.6 m, about 385 Ma	<i>Scoyenia</i> burrows, older than 443.8 Ma	partner first	at least 58.8	[112]; [173];
A5	Rhynie plants (chert), 410.8–407.6 Ma	Rhynie soil fauna, 410.8–407.6 Ma	same interval	0	[175]; [5]
A5	<i>Archaeopteris</i> roots, about 385 Ma	earthworm crown group, 208.8 Ma	plant first	86.1	[112]; [178]; [5]
A6	land plants, about 470 Ma	first arthropod herbivory, 417–402 Ma	plant first	53–67	[302]; [42]
A6	COI1 receptor, about 450 Ma	first arthropod herbivory, 417–402 Ma	plant first	33–47	[219]; [42]
A6	leaf-margin feeding (arthropod), 326 Ma	first synapsid herbivore, about 307 Ma	arthropod herbivory	19	[43]; [216]
A6	Brassicales appear (date not given)	Pierid nitrile-specifier protein, within about 10 Myr	plant first	about 10	[220]
A6	C3 grasslands, by 21.9 Ma	hypsodont Equinae, at least 4 Ma	plant first	at least 4	[224]
A6	spinescence radiation, mostly within 17 Ma	horned bovids in Africa, by 16 Ma	plant first (window	1	[225]
A6	grass phytoliths in titanosaur coprolites,	open-habitat grasses in North America, 42–38 Ma (plant)	both plant side;	24–34	[222]; [217];

A7	forest-grade communities, about 385 Ma	first class II peroxidases, about 380 Ma	plant first	85	[254]; [353]
A7	forest-grade communities, about 385 Ma	first lignin peroxidase, 178 ± 64 Ma	plant first	207	[254]; [353]
A7	forest-grade communities, about 385 Ma	first wood borings, 383–359 Ma	plant first	2–26	[254]; [353]
A7	forest-grade communities, about 385 Ma	earliest charcoal, 423.0 Ma	partner (fire) first	38	[254]; [252];
A7	forest-grade communities, about 385 Ma	first millipedes, 425–413.7 Ma	partner first	28.7–40	[254]; [353]
A7	termite crown, 149 Ma (wood-feeding partner)	fungus-growing termites, 31.41 Ma	termite first	117.6	[261]; [262]
A8	land plants, about 470 Ma	permanent atmospheric O ₂ , about 2.3 Ga	partner (air) first	1,860	[302]; [303]
A8	land plants, about 470 Ma	O ₂ above 15–17 % by 420–400 Ma	plant first	50–70	[302]
A8	rooted plants, 400–360 Ma	CO ₂ near 278 ppm, about 300 Ma	plant first	60–100	[305]; [306]
A8	C4 grasses originate, 8–6 Ma	C4 plants abundant, 8–6 Ma	plant first	at least 25	[223]; [345]
A9	Hangman forest, 393.3–387.7 Ma	tetrapod extinction peak after coal-forest collapse, about 360 Ma	plant first	82.7–88.3	[353]; [217];
A9	<i>Eospermatopteris</i> roots 30 cm, about 385 Ma	<i>Archaeopteris</i> roots 1.2–1.6 m, about 385 Ma (competitor)	same age	0	[355]
A10	land plants, about 470 Ma; crown embryophytes	Caulimoviridae, at latest about 320 Ma	plant first	150–162	[302]; [51];
A10	angiosperm radiation, 180–140 Ma	Caulimoviridae, at latest about 320 Ma	partner first	140–180	[404]; [403]
A10	Pinaceae crown, 183 Ma (233–150)	pararetrovirus bursts in <i>Pinus taeda</i> , 232.9–108 Ma	overlapping ranges	—	[51]; [402]
A10	domestication onset, 11,000–10,000 yr BP	potyvirus radiation, about 6,600 yr ago	plant (agriculture)	0.0034–0.0044	[158]; [406]

C3. Repeated origins

trait	count	clade and its age	window of origins	cha pte	ref
ectomycorrhizal habit, fungal side	at least 66 lineages, 162 genera; update 78–82 lineages, 251–256 genera	Basidiomycota, Ascomycota, Zygomycota	habit present by the Early Jurassic	A2	[63]; [6]
ectomycorrhizal habit, plant side	30 lineages (2 in gymnosperms, 28 in	seed plants; Pinaceae crown	Early Jurassic onward	A2	[65];
lichenisation	20–30 (14–23 Ascomycota, 6–7 Basidiomycota)	fungi; stratified lichens by 415	—	A2	[48];
lignin-degrading class II	expanded once; contracted in parallel in brown-rot and	Agaricomycetes, crown 299 Ma	diversification 350–295 Ma	A2	[79];
mycorrhizal lineages, second	—	Cretaceous	Cretaceous	A2	[47]
nitrogenase forms	3 (Mo, V, Fe-only); V and Fe nested within Mo	bacteria and archaea; 3.2 Ga	—	A3	[87];
primary endosymbiosis of a	2 (chloroplast; <i>Paulinella</i> chromatophore)	chloroplast about 2.1 Ga; <i>Paulinella</i> at	—	A3	[92]; [1]

nodulation predisposition	1 origin	Fabidae, slightly over 100 Ma	—	A3	[9 8]; [1
nodulation	about 8 ± 2.47 origins; about 10 ± 2.80 losses; 16.7 ± 3.21	Fabales, Rosales,	after 100 Ma	A3	[9 8]
NIN gene loss	lost in 10 of 13 non-nodulating species; at least 8	37 genomes, nodulation	—	A3	[1 03
roots	piecemeal, independently in several clades	Devonian, 419.2–358.9 Ma	Devonian	A3	[1 26
seed dispersal by ants (myrmecochory)	at least 101, possibly up to 147; most in Asteraceae 10, Euphorbiaceae 8, Fabaceae 6, Ranunculaceae 5	angiosperms, at least 11,000 species, 334 genera, 77	more frequent in families with crown ages under 80 Myr	A4	[1 43]; [1
frugivory in fishes	evolved from omnivory (serrasalmids)	Characiformes, Siluriformes; more than 275 species	—	A4	[1 45]; [1
pollination modes on gymnosperms /	4 modes; 4 cohorts	gymnosperms and insects	125–90 Ma	A1	[1 2]
perfume orchids	at least 3, after the orchid bees	orchids 27–18 Ma; bees 38–34	27–18 Ma	A1	[2 0]
cheating in yucca moths	2	<i>Tegeticula</i> ; association 41.5	—	A1	[2 1];
tetrapod herbivory	at least 5 (diadectids, bolosaurids, captorhinids, edaphosaurids, caseids)	tetrapods, oldest 307 Ma	Late Carboniferous to Early Permian	A6	[2 18]; [2
spinescence	at least 55 (213 of 1,852 woody species, 29 families)	southern African woody	mostly within the last 17 Ma; mid-Miocene	A6	[2 25
extrafloral nectaries	at least 457 lineages (3,941 species, 745 genera, 108	phylogeny of more than	—	A6	[2 28
ant domatia	at least 158 origins; 43 losses	1,181-species tree; 681 species, 159	within 19 Myr; Australasian and Neotropical early	A6	[2 29]
C4 photosynthesis in	at least 9, up to 20	PACMAD	origin by the Early Oligocene	A6	[2 23
C4 photosynthesis,	62 lineages (at least 18 in grasses, 26 in monocots),	angiosperms	—	A8	[3 09
caffeine synthesis	5 lineages by different pathways (cacao, citrus, guaraná, coffee, tea); tandem duplication in <i>Coffea</i>	angiosperms	—	A6	[2 34]; [2
N122H substitution of the Na,K-	6 named species of 4 insect orders	insects, about 300 Myr of divergence	—	A6	[2 32]
brown rot	at least 4 (loss of AA2 and cellulolytic complements)	Agaricomycetes; 126 brown-rot of 1,157 wood-decay species	—	A7	[2 57]; [2

surface tryptophan attacking non-fungus farming in bark and	2 lineages	Polyporales peroxidases	—	A7	[259]
fungus farming in bark and	at least 10	Scolytinae, origin 120–100	oldest about 50 Ma	A7	[263]
fungus farming in termites	1, Africa, no reversal	Macrotermite, 31.41 Ma (25.82–39.53)	—	A7	[268]; [2
fungus farming in ants	dated 61–57 Ma; leaf-cutting 19–18 Ma	about 250 described	—	A1	[42]
plant parasitism in nematodes	4 clades	about 4,100 species, about 25 % of	—	A10	[425]
AM/nodulation shared genes	7 plant genes required by both symbioses	land plants	—	A3	[109]

C4. Sizes

Sorted by position. Rows marked with a range carry the range of positions as given in G-partA.

#	what	size	position	chap	ref
1	hormogonia pili of <i>Nostoc</i> , width	7–10 nm	–1.71 to –1.38	A3	[90]
2	closterovirid filament, diameter	about 12 nm	–1.21	A10	[429]
3	tobamovirus rod, diameter	about 18 nm	–0.85	A10	[430]
4	nanovirus particle	18–19 nm	–0.85 to –0.80	A10	[431]
5	geminate particle, maize streak virus	22 × 38 nm	–0.66; –0.17	A10	[432]
6	bromovirid virion	26–35 nm	–0.51 to –0.24	A10	[433]
7	phytoplasma cell	80–800 nm	0.51–2.61	A10	[417]
8	tobamovirus rod, length	300–310 nm	1.72–1.74	A10	[430]
9	closterovirid filament, length	650–2,200 nm	2.42–3.53	A10	[429]
10	hyphae of the Rhynie lichen	1–4 μ m	2.81–4.07	A2	[58]
11	soil protists, smallest (<i>Mycamoeba</i>)	a few μ m	about 3.44	A5	[183]
12	hyphal diameter, 31 soil-fungus strains	2.7–6.5 μ m	3.72–4.51	A2, A7	[67]; [275]
13	hormogonia pili, length	up to 10 μ m	4.91	A3	[90]
14	pollen, <i>Myosotis sylvatica</i> / <i>Cucurbita</i>	<10 μ m / >100 μ m	<4.91 / >7.00	A1	[24]
15	<i>Reduviasporonites</i> cells, length	10–90 μ m	4.91–6.91	A7	[276]
16	mean distance between soil bacteria near	10.38 μ m	4.94	A3	[110]
17	AM spore subtending hypha	11–18 μ m	4.99–5.44	A2	[68]
18	mean distance between soil bacteria	12.46 μ m	5.11	A3	[110]
19	<i>Cycadopites</i> pollen, equatorial; polar axis	14.30 μ m; 20.65 μ m	5.23; 5.57	A1	[13]

20	photobiont cell of the Rhynie lichen	15 μm	5.28	A2	[58]
21	distance between soil bacteria at depth;	more than 18 μm ; 29	more than 5.44; 5.88	A3	[110]
22	net openings of the Rhynie lichen	about 25 μm	5.74	A2	[58]
23	AM spore, <i>Rhizophagus intraradices</i>	40–140 μm , mean 93.3	6.17–7.31; 6.84	A2	[68]
24	coprolites in late Permian borings,	less than 50 μm	less than 6.37	A7	[255]
25	smallest adult insect, male <i>Dicopomorpha</i>	139–240 μm	7.30–7.80	A1	[22]
26	largest testate amoebae	about 150 μm	7.37	A5	[183]
27	coprolites, middle class	about 150 μm	7.37	A7	[255]
28	macro-aggregate threshold	more than 250 μm	7.84	A5	[190]
29	butterfly proboscis diameter, <i>Eurybia</i>	0.26 mm	7.87	A1	[26]
30	seeds in ankylosaur gut	0.3 mm	8.00	A4	[133]
31	coprolites, largest class	up to 542 $\times$ 958 μm	9.06	A7	[255]
32	<i>Archaeopteris</i> rootlets	about 1 mm	9.10	A3	[112]
33	peloids in fossil fungus gardens	about 1 mm	9.10	A7	[262]
34	soil protists, largest (<i>Darbyshirella</i>)	more than 1 mm	more than 9.10	A5	[183]
35	thallus bands of the Rhynie lichen	1–2 mm	9.10–9.73	A2	[58]
36	fruits in ankylosaur gut	4.5 mm	10.47	A4	[133]
37	soybean nodule diameter, day 45	5 mm	10.56	A3	[111]
38	spine, minimum length in the definition	at least 5 mm	at least 10.56	A6	[225]
39	earthworm burrow diameter, <i>Aporrectodea</i>	5.16 mm	10.59	A5	[189]
40	cordaitalean seed, equivalent sphere diameter	6.2–28.4 mm (122 to more than 12,000	10.75–12.14	A4	[133]
41	honey bee worker reach into a corolla	7 mm	10.87	A1	[25]
42	<i>Eospermatopteris</i> root thickness	0.7–1 cm	10.87–11.19	A3, A9	[112];
43	earthworm burrow diameter, <i>Lumbricus</i>	7.78 mm	10.97	A5	[189]
44	comb cells in fossil fungus gardens	about 10 mm	11.19	A7	[262]
45	<i>Archaeopteris</i> lateral roots	1–1.5 cm	11.19–11.56	A3	[112]
46	ant seed carriage, range	0.01–77 m	11.19–19.34	A4	[135]
47	jackfruit seeds	2–4 cm	12.03–12.46	A4	[149]
48	largest seed reliably dispersed, extant	above 2.5 cm rarely	12.03	A4	[144]
49	seed diameter dispersed by African	about 2.8 cm	12.13	A4	[144]
50	medullosan seed, equivalent sphere	33.7–45.7 mm (20,000–50,000 μm)	12.30–12.58	A4	[133]
51	seed diameter dispersed by extant	about 3.5–4.0 cm	12.33–12.46	A4	[144]
52	butterfly proboscis, <i>Eurybia lycisca</i> , mean;	36.5 mm; 45.6 mm	12.37; 12.58	A1	[26]
53	megafaunal fruit, Type I / Type II diameter	4–10 cm / more than 10 cm	12.46–13.29 / more than	A4	[144]
54	<i>Archaeopteris</i> primary roots	6–16 cm	12.83–13.72	A3	[112]

55	fungus combs; nest chambers, 25 Ma	6–9 cm wide; 4–13 cm	12.83–13.53	A7	[262]
56	largest medullosan seed, equivalent sphere	83.1 mm (more than 200,000 years)	13.12	A4	[133]
57	arborescent lycopsid trunk diameter	0.1 to more than 2 m	13.29–16.02	A9	[366]
58	<i>Rhizocarpon geographicum</i> thallus, N	up to 120 mm	13.46	A2	[71]
59	jackfruit width	15–50 cm	13.66–14.76	A4	[149]
60	jackfruit length	20–90 cm	13.92–15.29	A4	[149]
61	depth holding half of root mass, global	20 cm	13.92	A9	[371]
62	<i>Eospermatopteris</i> rooting depth	about 30 cm	14.29	A3, A9	[112];
63	soil stock depth; depth holding half of tree root mass	30 cm	14.29	A5, A9	[191];
64	orchid spur, <i>Angraecum sesquipedale</i>	33 cm	14.38	A1	[27]
65	longest insect, <i>Phobaeticus chani</i> , body; 11	357 mm; 567 mm	14.45; 14.87	A1	[23]
66	<i>Rhizocarpon alpicola</i> , largest thallus	480 mm	14.72	A2	[72]
67	<i>Arthropleura</i> , width	about 55 cm	14.84	A7	[256]
68	Early Cretaceous bird with plant remains	about 60 cm	14.92	A4	[133]
69	largest Carboniferous–Permian insect	about 70 cm	15.06	A8	[315]
70	<i>Lepidodendron</i> basal diameter, Illinois, (1000 years)	95 cm (34–144 cm)	15.34	A9	[367]
71	ant seed carriage, typical	about 1 m	15.39	A4	[135]
72	soil stock depth	1 m	15.39	A5	[191]
73	<i>Archaeopteris</i> rooting depth	1.2–1.6 m	15.55–15.81	A3, A5,	[112];
74	Early Cretaceous ankylosaur, length	about 1.4 m	15.69	A4	[133]
75	soil stock depth	2 m	16.02	A5	[191]
76	reach of lifted water from one sugar maple	2.5–5 m	16.22–16.85	A9	[372]
77	<i>Arthropleura</i> , length	up to 2.63 m	16.27	A7	[256]
78	soil stock depth	3 m	16.39	A5	[192]
79	maximum rooting depth, global mean	4.6 ± 0.5 m	16.78	A9	[370]
80	maximum rooting depth, trees	7.0 ± 1.2 m	17.16	A9	[370]
81	<i>Prototaxites</i> trunk	up to 8 m	17.28	A2	[69]
82	<i>Eospermatopteris</i> , Gilboa, height	at least 8 m	at least 17.28	A9	[354]
83	earthworm burrow system length, 6 weeks, <i>L. terrestris</i> / <i>A. icterica</i> / <i>A.</i>	9.2 m / 15.7 m / 21.2 m	17.41 / 17.89 / 18.17	A5	[189]
84	Macrotermitine mound height	up to 10 m	17.48	A7	[269]
85	arborescent lycopsid height	10–50 m	17.48–18.95	A9	[366]
86	<i>Archaeopteris</i> root radial extent	11 m	17.57	A3, A9	[112];
87	<i>Archaeopteris</i> height estimate, Cairo	about 11–32 m	17.57–18.54	A9	[355]
88	Macrotermitine mound width	more than 15 m	17.85	A7	[269]

89	modern peat thickness	up to 15 m (50 ft)	17.85	A7	[277]
90	palaeosol section, South Africa	17 m	17.97	A5	[101]
91	canopy height, 2020 map, Oregon and	28–36 m	18.42–18.65	A9	[369]
92	<i>Silene stenophylla</i> burrow depth	38 m	18.70	A4	[150]
93	<i>Prunus mahaleb</i> seeds, small passerines,	51 m	18.97	A4	[161]
94	thickest coal beds	up to 61 m (200 ft)	19.13	A7	[277]
95	canopy height maximum, Sabah	up to 65 m	19.19	A9	[369]
96	deepest root, <i>Boscia albitrunca</i>	68 m	19.23	A9	[370]
97	maximum tree height in the vascular	about 100 m	19.58	A9	[368]
98	<i>Prunus mahaleb</i> seeds, medium birds, half	110 m	19.66	A4	[161]
99	<i>Prunus mahaleb</i> seeds, carnivorous	495 m	21.03	A4	[161]
100	forest-elephant seeds, 89 % beyond	1 km	21.67	A4	[154]
101	<i>Armillaria ostoyae</i> genet, Oregon, isolate separation	up to about 3,810 m (area about 965 ha)	22.89	A2	[70]
102	forest-elephant seed dispersal, median;	5.3 km; 6.5 km; 16.4	23.19; 23.38;	A4	[154]
103	forest-elephant seed dispersal, longest	101 km	25.87	A4	[154]

Sizes recorded in G-partA without a ladder position (areas, masses, genome lengths, counts per volume):

what	value	cha pte	ref
<i>Armillaria ostoyae</i> genet area	about 965 ha = 9.65 km ²	A2	[70]
AM hyphal length; ectomycorrhizal mycelium	more than 100 m cm ⁻³ ; up to	A2	[73]
chloroplast genome, <i>Arabidopsis</i>	154,478 bp; 87 protein-coding, 4 rRNA, 37 tRNA genes	A3	[113]
<i>Prochlorococcus</i> MED4 genome	1,657,990 bp	A3	[114]
<i>Frankia</i> genomes, three clades	5.43, 7.50, 9.04 Mbp	A3	[107]
cyanobiont genomes in coralloid roots	5.4–9.0 Mbp	A3	[116]
mean fresh mass of a soil nematode	0.68 μg (computed from [184])	A5	[184]
megafaunal fruit mass; seed load	50–1,000 g; up to 140 g	A4	[144]
jackfruit mass	up to 50 kg	A4	[149]
mesobrowsers; megaherbivores, body mass	4–450 kg; more than 1,000 kg	A6	[225]
<i>Arthropleura</i> , mass	about 50 kg	A7	[256]
molar masses: isoprene; nicotine; caffeine;	68.117; 162.23; 194.19; 216.19;	A6	[236]
specific leaf area, 280 species	35–267 cm ² g ⁻¹	A6	[237]
leaf nitrogen, 280 species	8.7–40.9 mg g ⁻¹	A6	[237]
lignin peroxidase, <i>Phanerochaete</i>	343 residues; 37.3 kDa per	A7	[278]
forest area	4.06 Gha = 40.6 × 10 ⁶ km ² ; 42	A8,	[316];

C4 vegetation area	$18.8 \times 10^6 \text{ km}^2$	A8	[310]
vegetation above 5 m; above 30 m	$53.6 \times 10^6 \text{ km}^2$ (41 % of land);	A9	[369]
leaf area index: global mean; deserts;	4.5–5.2; 1.3 ± 0.9 ; 8.7 ± 4.3 ; 18	A8	[317]
canopy gaps, BCI; Brazil median; BCI	$25\text{--}1,150 \text{ m}^2$; 78 m^2 ; 79 m^2 (8–	A9	[360];
Cairo forest exposure	about $3,000 \text{ m}^2$	A9	[355]
lycopsid root mound	1.9 m across	A9	[355]
Mahoning coal peat body with more than 800	about 60 km^2	A9	[397]
flg22; RIN4	22; 211 amino acids	A10	[404]
virus genomes: geminivirus; nanovirus;	2.5–3.0 or 4.8–5.6 kb; 6–8 ×	A10	[432];
tobamovirus; bromovirid; closterovirid	about 1 kb; 6.3–6.5 kb; 8,623	A10	[431];
phytoplasma chromosome; <i>P. infestans</i>	600–880 kb; about 240 Mb;	A10	[417];
genome; <i>P. graminis</i> haplotype assembly;	176–177 Mbp; about 797 Mbp	A10	[420];
mountain pine beetle outbreak area, 2000–2020	$374,000 \text{ km}^2$	A9	[398]
burned area per year	3.81 Mkm^2	A7	[291]

C5. Times

Sorted by position. Durations, generation times, lifespans, cycle and residence times, signal times.

#	what	duration	position	cha pte	ref
1	flower handling, <i>Eurybia lycisca</i>	$54.5 \pm 28.5 \text{ s}$	36.79	A1	[26]
2	jasmonic acid rise after wounding,	2–5 min (120–300 s)	37.51–38.34	A6	[238]
3	earthworm burying itself in loose	2–3 min	37.51–37.88	A5	[197]
4	passerine gut passage, Mediterranean,	5–30 min	38.34–39.98	A4	[153]
5	passerine gut passage, species means	22.9–69.4 min	39.73–40.74	A4	[153]
6	LRR-kinase induction after flg22	within 30 min	39.98	A10	[404]
7	induced volatiles in maize;	2 h; 4 h	41.24; 41.87	A6	[239]
8	protist division time	a few hours (3 h)	about 41.61	A5	[183]
9	rhizosphere bacterial generation,	7.5–9.1 h	42.44–42.62	A5	[115]
10	rhizosphere bacterial turnover	9–60 h; 12–19 h	42.61–44.33; 42.87–43.29	A3, A5	[115]
11	forest-elephant gut passage, range;	16.6–113.7 h; 39.5 h	43.16–44.92; 43.85	A4	[154]
12	adult pollinating fig wasp lifespan	24–48 h	43.50–44.13	A1	[32]
13	bacterial doubling on young roots; on	24 h; more than 100 h	43.50; more 43.53–44.80	A5	[115]
14	flower longevity	less than 1 d to several	less than 43.50	A1	[31]
15	earthworm burying itself in compact	25 h 40 min	43.56	A5	[197]
16	soil bacterial turnover, about 20 °C, 19	2.3–33 d, mean 9.3 d	44.26–46.68; 45.53	A3, A5	[115]
17	<i>Caenorhabditis elegans</i> , generation,	73.0 h; 90 h	44.51; 44.70	A5	[194]

18	<i>C. elegans</i> strain MY6, generation; 1 yr	84 h; 14.7 d	—; 45.95	A5	[194]
19	carcass: 90 % of pig mass lost with 1 yr	6 d	45.13	A7	[274]
20	return of the nicotine response, wild 1 yr	6 d	45.13	A6	[240]
21	root-hair curling peak; nodule 1 yr	day 8; day 15; day 45	45.39; 45.96; 46.06	A3	[111]
22	mushroom fruiting delay over 1940– 2006 fruiting time	13.3 ± 1.2 d; a few days	45.85; about 44.50	A2	[75]
23	honey bee worker, normal lifespan	2–6 weeks	45.90–46.90	A1	[29]
24	fig cycle inside the syconium	15–100 d	45.96–47.69	A1	[32]
25	<i>C. elegans</i> lifespan, 20 °C	16.7 d	46.06	A5	[194]
26	caged honey bee workers, USA, 1 yr	34.3 d (1970s); 17.7 d (1990s)	46.72; 46.12	A1	[30]
27	honey bee drone, maximum	20–40 d	46.23–46.86	A1	[29]
28	soil fungal turnover, amended	20–40 d	46.23–46.86	A5	[115]
29	systemic protection after a TMV infection	up to 3 weeks	46.27	A10	[412]
30	honey bee worker, caged	23–42 d	46.35–46.90	A1	[29]
31	root-knot nematode, infection to first 1 yr	4–6 weeks	46.53–46.90	A10	[434]
32	bacterial turnover, count-based	30 d	46.60	A5	[115]
33	new termite workers after swarming	1.5–3 months	46.98–47.61	A7	[269]
34	silica induction regime	weekly damage over 10 1 yr	47.37	A6	[241]
35	leaf lifespan, 280 species	2.5 ± 0.6 to 66.2 ± 10.6 1 yr	47.44–50.42	A6	[237]
36	<i>L. terrestris</i> cocoon hatching, earlier 1 yr	90–280 d	47.60–48.63	A5	[196]
37	soil bacterial turnover, 25 °C, older 1 yr	107–160 d	47.75–48.12	A3	[115]
38	soil fungal turnover, unamended; at 15 °C	130–150 d; 170 d	47.93–48.06; 48.17	A3, A5	[115]
39	<i>L. terrestris</i> cocoon hatching, 15 °C	132–731 d	47.94–49.50	A5	[196]
40	litter half-life, ln 2 / k: rain forest; 1 yr	0.53 yr; 2.3 yr; 3.9 yr	48.29; 49.63; 50.11	A5	[198]
41	wood half-life, ln 2 / k	0.71–173 yr	48.56–53.56	A7	[279]
42	seasonal CO ₂ cycle	1 yr	48.87	A8	[322]
43	gap closure, fastest phase	first year	48.87	A9	[376]
44	alpine oribatid <i>Oromurcia sudetica</i> , adult life; egg to adult	1–2 yr; 2–4 yr	48.87–49.50; 49.50–50.13	A5	[195]
45	fine litter turnover, global mean; 1 yr	1.4–3.4 yr; about 5 yr	49.18–49.98; 50.24	A7	[251]
46	bird generation length, range; median	1.42–27.87 yr; 2.99 yr	49.19–51.90; 49.87	A4	[157]
47	fine-root lifetime at 56 % yr ^{−1}	1.8 yr	49.41	A5	[179]
48	wood, 95 % mass loss	about 3–750 yr	49.87–54.90	A7	[279]
49	pyrogenic carbon in soil, fast pool; 1 yr	3 yr; 88 yr; 870 yr	49.87; 52.95; 55.03	A7	[280]
50	shared beech–spruce mast events, 1 yr	5.3 yr	50.39	A4	[156]
51	CO ₂ exchange time with land, 886 Gt C / 129–150 Gt C yr ^{−1}	5.9–6.9 yr	50.49–50.63	A8	[314]; [318];
52	European beech mast wavelet band; 1 yr	7–16 yr; 17.0 yr	50.64–51.39; 51.45	A4	[156]

53	honey bee queen, maximum	8 yr	50.76	A1	[29]
54	callus growth over Permian borings	10 or more years	50.97	A7	[255]
55	periodical cicadas <i>Magicicada</i> , periodical cicadas	13 yr; 17 yr	51.21; 51.45	A1	[28]
56	coarse woody detritus turnover	about 13 yr	51.21	A7	[251]
57	gap full turnover, 1 / (0.45–6.5 % yr ⁻¹)	15–222 yr	51.34–53.79	A9	[376]
58	soil carbon stock / soil respiration	14.9–15.8 yr	51.34	A5	[191]; [280]
59	termite royal pair; colony	at most about 20 yr; termite	51.60	A7	[269]
60	TR4 chlamydospores in soil	more than 20 yr	more than 51.60	A10	[439]
61	<i>Sr31</i> : wide deployment (1970s) to 1970s–1980s	28 yr	51.90	A10	[436]; [433]
62	dominant stand ages, North America	30–120 yr	51.97–53.23	A9	[379]
63	Amazon stem residence, 1 / (1.3–2.8 yr ⁻¹)	36–77 yr	52.13–52.82	A9	[378]
64	boreal stand-replacing fire cycles	50–250 yr; 70–130 yr	52.43–53.90	A9	[380]; [281]
65	<i>Lr34</i> durable resistance	more than 50 yr	more than 52.43	A10	[437]
66	akinetete dormancy	up to 60 yr	52.60	A3	[116]
67	biomass to 90 % of old growth, North America	66 yr	52.68	A9	[377]
68	FAM-1 late blight lineage sampled, 1845–1887	144 yr	53.39	A10	[438]
69	soil organic matter tenfold, Glacier Park	200 yr	53.69	A9	[361]
70	fossil CO ₂ pulse, equilibration; CaCO ₃ neutralisation	2–20 centuries; 3–7 kyr	53.69–55.79; 56.16–56.93	A8	[323]
71	time to erode a 30 cm A horizon at 1410 °C	256–263 yr	53.92–53.94	A5	[199]
72	soil phosphorus 82 % to 1 % mineral, Hawaii; organic P maximum	300 to 20,000 yr; 150,000 yr	54.06–57.88; 59.72	A9	[382]
73	time to form 1 cm of soil at 0.026 mm yr ⁻¹	385 yr	54.29	A5	[199]
74	lycopsid tree lifespan (40 m tree)	about 400 yr (200–800)	54.32	A9	[366]
75	termite mounds	about 700; at least 2,200; at least 4,000 yr	54.83; 55.88; 56.42	A7	[269]
76	oldest trees, Pacific Northwest; South America	800 yr; 1,000 yr	54.95; 55.16	A9	[379]
77	<i>Armillaria ostoyae</i> genet age	1,900–8,650 yr	55.74–57.12	A2	[70]
78	date palm seed, Masada, germinated	about 2,000 yr	55.79	A4	[155]
79	deep soil carbon mineralised after fire	2,567 ± 226 yr	56.02	A7	[281]
80	CO ₂ below 180 ppm in MIS 16	about 3,000 yr	56.16	A8	[324]
81	lichen ages reported	at least 4,500 yr; about 8,000	56.53; 57.16	A2	[72]
82	radiocarbon mean age of soil carbon to 1000	4,830 ± 1,730 yr	56.59	A5	[201]
83	potyvirus radiation	about 6,600 yr	56.88	A10	[406]
84	present interglacial so far; interglacial from Termination V	about 12 kyr; about 28 1	57.42; 58.19	A8	[325]
85	post-glacial nut-tree range shifts	last 16,000 yr	57.68	A4	[142]
86	orbital cycles in Southern Ocean	23, 42, 100 kyr	58.01; 58.56; 59.25	A8	[326]
87	<i>Silene stenophylla</i> fruit tissue	31,800 ± 300 ¹⁴ C yr	58.31	A4	[150]

88	Permian–Triassic extinction; carbon-	60 ± 48 kyr; about 500	58.88; 60.81	A8	[327]
89	PETM duration	about 170 kyr	59.83	A8	[328]
90	Eocene Arctic <i>Azolla</i> phase	about 800,000 yr	61.24	A3, A8	[117]; [311]
91	O ₂ residence time with total organic	0.82 Myr	61.27	A8	[313]; [321]
92	end-Permian fungal proliferation	less than 1 Myr	less than 61.45	A7	[282]
93	oxygenation at the Great Oxidation	1–10 Myr; about 10	61.45–63.54; 63.54	A3, A8	[96]; [322]
94	O ₂ residence, reservoir / source	2.1 Myr	62.12	A8	[313]
95	hypsodont horses after C3 grasslands	at least 4 Myr	62.71	A6	[224]
96	herbivory recovery after the K–Pg	about 10 Myr (65.5 to 55.8 Ma)	63.54	A1	[10]
97	Pierid counter-adaptation after	about 10 Myr	63.54	A6	[220]
98	spinescence window	17 Myr	64.02	A6	[225]
99	domatia window	19 Myr	64.13	A6	[229]
100	charcoal-inferred O ₂ cycles, Triassic–	periods 20–30 Myr	64.17–64.54	A8	[329]
100	coal forests, duration	23.9–27.2 Myr	64.33–64.45	A9	[357]; [317]
100	herbivory recovery after the Permian–	24 Myr (252 to 228 Ma)	64.34	A1	[10]
100	fig–wasp co-divergence	at least 60 Myr	65.17	A1	[45]
100	long-proboscid scorpionflies feeding	62 Myr	—	A1	[11]
100	chloroplast establishment; Great	about 200 Myr	66.27	A3, A8	[92]; [323]
100	COI1 receptor conservation	about 450 Myr	67.01	A6	[219]

Rates with a time unit recorded in G-partA without a ladder position:

what	rate	chap	ref
hyphal extension per tip, 25 °C;	21–125 $\mu\text{m h}^{-1}$; 325 $\mu\text{m h}^{-1}$	A2	[74]
<i>Rhizocarpon geographicum</i> radial	0.23–1.47 mm yr ⁻¹	A2	[71]
slowest lichen growth, <i>R. superficiale</i>	0.006 mm yr ⁻¹ over 16 yr	A2	[72]
<i>Armillaria</i> genet spread	0.22–1.0 m yr ⁻¹ (computed from [70])	A2	[70]
hormogonia motility	0.7–1.7 $\mu\text{m s}^{-1}$	A3	[90]
fine-root turnover; whole tree root	53–56 % yr ⁻¹ ; 10 % yr ⁻¹	A5	[179]
litter decay constants, 293 values	0.006–4.993 yr ⁻¹ , mean 0.581, median 0.300; rain forest 1.3, tundra 0.18	A5	[198]
earthworm burrowing rate	0.22 and 0.50 m d ⁻¹ (computed from [188])	A5	[189]
<i>L. terrestris</i> cocoon production	15.1–32.2 per worm per year	A5	[196]
soil formation, UK; global median;	0.023–0.064 mm yr ⁻¹ ; 0.026 mm yr ⁻¹ ;	A5	[199]
erosion under conventional tillage	about 1 mm yr ⁻¹	A5	[212]
earthworm dispersal; average terrestrial	about 10 m yr ⁻¹ ; about 600 m yr ⁻¹	A5	[193]
soil respiration rise	0.1 Pg C yr ⁻¹ per year, 1989–2008	A5	[200]

speed of the wound stimulus to distal	at least 3 cm min ⁻¹	A6	[238]
wood decay constants, fastest; slowest;	0.975; 0.004; 0.058–0.061 yr ⁻¹	A7	[279]
gap formation	0.45–6.5 % of area per year	A9	[376]
Amazon stem mortality	1.3–2.8 % yr ⁻¹	A9	[378]
lycopsid height growth	about 0.10 m yr ⁻¹	A9	[366]
Neotropical secondary forest biomass	3.05 Mg C ha ⁻¹ yr ⁻¹ ; 122 Mg ha ⁻¹ after	A9	[377]
Quebec fire intervals, mid-Holocene; last	332 ± 195 yr; 99 ± 53 yr	A9	[380]
host substitution rate, conifers	1.43–2.2 × 10 ⁻⁹ per site per year	A10	[403]
potyvirus substitution rate	about 1.15 × 10 ⁻⁴ per site per year	A10	[406]
viral mutation rates per nucleotide per cell infection: DNA; RNA viruses	10 ⁻⁸ –10 ⁻⁶ ; 10 ⁻⁶ –10 ⁻⁴	A10	[441]
nematode generations per year, if	8.7–13 (computed from [434])	A10	[434]
named pandemics or resistance	one every 11.4 yr (computed)	A10	[438]
long-term CO ₂ decline	about 3.4 ppm per Myr over 420 Myr	A8	[306]
CO ₂ fall 400–300 Ma	17 ppm per Myr (computed)	A8	[306]
annual CO ₂ growth, 2016–2025	2.06–3.76 ppm yr ⁻¹	A8	[298]
new species named per year: plants; fungi; mammals	about 2,000; about 1,300 (40-yr mean) and 1,800 (since 2010); about 25	A1, A2,	[1]; [76];

C6. Generation-time asymmetry

Ratio = longer value / shorter value (computed). Where no generation time or lifespan is present for a side, the row shows —.

cha pte	plant-side organism, generation time or lifespan	partner-side organism, generation time or lifespan	ratio (computed)	ref
A1	fig cycle inside the syconium,	adult pollinating fig wasp, 24–	7.5–100 (fig	[32]
A1	flower longevity, less than 1 d to	honey bee worker, 2–6 weeks;	— (ranges	[31]; [29]
A2	fine-root lifetime, 1.8 yr = 657 d	soil fungal turnover,	4.4–5.1 (root	[179];
A2	fine-root lifetime, 1.8 yr	<i>Armillaria ostoyae</i> genet, 1,900–8,650 yr	1,056–4,806 (fungus	[179]; [70]
A3	fine-root lifetime, 1.8 yr = 657 d (from A5)	soil bacterial turnover, mean 9.3 d (2.3–33 d)	71 (20–286) (root longer)	[179]; [115]
A3	soybean nodule, 5 mm at day 45	rhizosphere bacterial turnover,	57–90 (nodule	[111];
A4	European beech, extreme mast spacing 17.0 yr (reproductive	bird generation length, median 2.99 yr (1.42–27.87)	5.7 (0.6–12.0) (beech	[156]; [157]
A5	fine-root lifetime, 1.8 yr = 657 d	<i>Caenorhabditis elegans</i>	175 (root	[179];
A5	fine-root lifetime, 1.8 yr = 657 d	alpine oribatid egg to adult, 2–4	1.1–2.2 (mite	[179];
A6	leaf lifespan, 2.5–66.2 months	— (no herbivore generation	—	[237]
A7	coarse woody detritus turnover, about 13 yr (dead-wood	termite royal pair, at most about 20 yr	1.5 (termite longer)	[251]; [269]

A7	fine litter turnover, forests, about 5 yr	new termite workers after 1.5–2 yr	20–40 (litter turnover)	[251]; [366]
A8	— (no plant generation time in G-partA)	O ₂ residence 2.1 Myr; CO ₂ exchange with land 5.9–6.9 yr	—	[313]; [314];
A9	lycopsid tree lifespan, about 400 yr (200–800)	neighbouring trees: Amazon stem residence 36–77 yr; oldest	0.4–11 (same organism)	[366]; [378];
A10	<i>Sr31</i> resistance held 28 yr (gene durability, not lifespan)	root-knot nematode, infection to first eggs, 4–6 weeks	243–365 (gene longer)	[436]; [422];
A10	host substitution rate $1.43\text{--}2.2 \times 10^{-9}$ per site per year	potyvirus substitution rate 1.15×10^{-4} per site per year	5.2×10^4 to 8.0×10^4	[403]; [406]

C7. Shares

what	share	denominator	cha pte	ref
angiosperms pollinated by animals	87.5 %; community means 78 % temperate, 94 % tropical	308,006 of about 352,000	A1	[3]
insects among described living species	about 62 %	about 1.6 million	A1	[34]
insect species undescribed	about 80 %	estimate of 5.5 million	A1	[34]
herbivory by order: Lepidoptera; Orthoptera; Hemiptera; Coleoptera;	about 100 %; 94 %; 80 %; 26 %; 7 %	species per order	A1	[34]
diversification-rate variation explained	25–35 %	31 insect	A1	[34]
seed beetles on legume seeds	84%	about 1,700	A1	[40]
yucca moth pollen load	about 10 % of body weight	female body	A1	[24]
bees among Hymenoptera	13.4 % (computed)	20,446 of 153,088	A1	[38];
vascular plants with arbuscular mycorrhiza; ectomycorrhiza; ericoid;	72 %; 2.0 %; 1.5 %; 10 %	vascular plant species	A2	[47]
plants mycorrhizal, surveyed species; families	80 %; 92 %	3,617 species, 263 families	A2	[77]
extant plants mycorrhizal	about 85 %	extant plants	A2	[78]
plants able to form ectomycorrhiza	1.7–2.4 %	embryophytes	A2	[65]
Neotropical Glomeromycota	69%	the phylum (221 species)	A2	[64]
AM taxa on more than one continent; on " "	93 %; 34 %	1,014 root	A2	[64]
Basidiomycota among lichenised fungi	0.9 %	19,387 species	A2	[48]
sequenced fungal genomes that are pathogens; plant pathogens on food	35.5 %; 61.3 %	1,090 genomes; 191	A2	[80]
NPP allocated to mycorrhizal mycelium: AM; EcM; ericoid; orchid	6.2 %; 13.1 %; 3.5 %; 1.0 %	net primary production,	A2	[73]
vegetation cover: AM; EcM; ericoid; " "	57.4 %; 25.7 %; 2.6 %; 14.3 %	vegetated area	A2	[78]
cyanobacterial genomes with nif	21 of 44 (47.7 %, computed)	44 sequenced	A3	[87]
nodulating subfamilies among legumes	94.4 % (computed, upper bound)	19,500 legume species	A3	[104]
legumes with infection without threads	25%	legumes	A3	[90]

heterocyst frequency, free-living; in symbiosis; coralloid roots	4–10 %; 30–50 %; up to 80 %	cells	A3	[90];
nitrogen retained by the cyanobiont	as little as 20 %	nitrogen fixed	A3	[91];
<i>Arabidopsis</i> genes of cyanobacterial origin	about 18 % (about 4,500)	protein-coding genes	A3	[121]
<i>Paulinella</i> chromatophore genes retained	28.8–29.7 %	2,917 in <i>Synechococcus</i>	A3	[122]
chloroplast genome / <i>Prochlorococcus</i> genome	9.3 % (computed)	1,657,990 bp	A3	[113];
soybean share of crop-legume nitrogen	77%	crop-legume fixation	A3	[130]
rice paddy methane	5.2 % (computed)	576 Tg CH ₄ per year	A3	[131]
carbon allocated below ground: grasses; annual crops	33 %; 21 %	assimilated carbon	A3	[124]
root microbiota assembled by cell-wall features	about 40 %	root microbiota	A3	[125]
dominant soil bacterial phylotypes	about 2 % (about 500) make nearly half of communities	237 sites	A3	[119]
angiosperm families biotic dispersal; both biotic and abiotic	30 %; 22 %	families	A4	[133]
angiosperm species biotic dispersal; both	14 %; 42 %	species	A4	[133]
gymnosperm families; species biotically dispersed; species both	64 %; 46 %; 39 %	families; species	A4	[133]
ant-dispersed angiosperms	about 4.5 % (at least 11,000 species)	angiosperm species	A4	[143]
frugivorous terrestrial birds	13.8 % (computed; 1,230 of 8,918)	terrestrial bird species	A4	[136]
passerines among frugivorous birds	50 % (618)	1,230 frugivores	A4	[136]
megafaunal-fruit species in Brazil; of them trees	103 of 1,361 (7.6 %, computed); 83.3 %	sampled species	A4	[144]
seed mass in megafaunal fruits; other fruits	0.2–97.4 %; 0.1–8.9 %	fruit mass	A4	[144]
Costa Rican canopy trees animal-dispersed	83.5 % (200 of 240)	species	A4	[163]
myrmecochores with more species than sister group	68 of 101 (67 %, computed)	comparisons	A4	[135]
bird species with generation length under 3.33 yr	61%	bird species	A4	[157]
mammals with generation-length records	84.8 % (computed; 5,427 of 6,399)	extant mammals	A4	[169]
Panama seedlings per seed	3.39 % (computed)	386,027 seeds	A4	[164]
land nutrient-transport capacity remaining; ocean	about 8 %; about 5 %	pre-extinction value	A4	[168]
marine mammal phosphorus transport remaining	about 23 %	340 × 10 ⁶ kg P per year	A4	[168]

forest-elephant seeds beyond 1 km	89%	seeds	A4	[1 54]
variation in frugivore richness explained by evapotranspiration	71–73 %	variation	A4	[1 36]
Earth's species living in soil	59 ± 15 %	all species	A5	[1 70]
soil share: Enchytraeidae; fungi; Plantae; Isoptera	98.6 %; 90 %; 85.5 %; 84.2 %	species per group	A5	[1 70]
faunal N mineralisation by amoebae and bacterial-feeding nematodes	more than 83 %	faunal mineralisation	A5	[1 71]
prairie N mineralisation: bacteria; fauna; fungi	58 %; 38 %; 4 % (computed)	7.7 g N m ⁻² yr ⁻¹	A5	[1 71]
root profiles with half of roots in the upper 0.3 m; 95 % in upper 2 m	more than 90 %	475 profiles	A9	[3 74]
root mass in top 10, 20, 40 cm	about 30 %, 50 %, 75 %	root mass	A9	[3 71]
nematodes by region: sub-Arctic; temperate; tropical	38 %; 24 %; 21 %	individuals, 6,759 samples	A5	[1 84]
aquatic oribatids	under 1 % (about 90 species)	oribatid species	A5	[2 04]
aggregate stability explained by glomalin	r ² = 0.86	37 soils	A5	[2 10]
leaf tissue eaten per year	5.3 %; earlier estimates up to 3.8 × that = 20.1 % (computed)	annual leaf production,	A6	[2 14]
woody versus non-woody leaf herbivory	64 % higher	leaf herbivory	A6	[2 14]
primary production eaten, aquatic; terrestrial	51 %; about one third of that = 17 % (computed)	annual production	A6, A7	[2 47]
Serengeti above-ground production consumed	0.66 (0.15–0.94)	annual above-ground	A6	[2 48]
flowering plants with latex	about 10 %	flowering plant species	A6	[2 26]
plants with extrafloral nectaries	about 1–2 %; 33 of 65 orders	vascular plant species	A6	[2 28]
spiny woody species, southern Africa	11.5 % (computed; 213 of 1,852)	woody species	A6	[2 25]
fossil leaves damaged, 58.9–55.2 Ma; PETM specialised damage; four or more <i>Manduca sexta</i> intake and gain on high-alkaloid foliage; induced leaves	14.9–57.3 %; 21.6 %; 7.3 % against 0.4–2.6 %	5,062 leaves	A6	[2 49]
	57.2 %, 45.7 %; 38.5 %	controls	A6	[2 40]
leaf abrasiveness explained by silicon	more than 70 %	18 grass species	A6	[2 41]
RXLR effectors among <i>P. infestans</i> genes; repeats in genome	3.2 % (computed); about 74 %	17,797 genes; genome	A10	[4 20]
dead wood; litter in forest carbon	8 %; 5 % (together 13.5 %, computed)	861 Pg C	A7	[2 50]
Termitidae among termites	more than 75 %; 84 %	termite species	A7	[2 61]; [2]

Scolytinae among weevils	about 10 %	weevils	A7	[2 63]
cellulolytic colonies; strains on crystalline cellulose; OTU share in litter;	about 12 %; 21 %; 17.6 %; 3.7 %	isolates; 115 strains;	A7	[2 70]
tree lycopods among peat contributors; periderm in peat biomass	60 to more than 80 %; 20–45 %	Early Pennsylvanian	A7	[2 84]
fungal remains among land-derived palynomorphs; <i>Reduviasporonites</i> in basal Tesero	30–80 %; more than 90 %	palynomorphs	A7	[2 82]; [2
animals' share of wood loss, Borneo; commonly attributed to invertebrates	58–64 %; 10–20 %	wood mass loss	A7	[2 86]; [2
invertebrate effect on decomposition: global; tropical; arid; temperate;	+40 %; +75 %; +122 %; +13 %; +2 % (computed from ln	1,427 paired observations	A7	[2 88]
wood discovered by termites above 21.33 °C; land surface above that	more than 50 %; 30.2 %	wood blocks; land surface	A7	[2 83]
termite CH ₄ ; CO ₂	about 4 %; about 2 %	global emissions	A7	[2 92]
termite methane oxidised in mounds	about half	methane produced	A7	[2 93]
litter decomposition faster under own species	about 8 %	decomposition rate	A7	[2 96]
dry air: N ₂ ; O ₂	78.08 %; 20.95 %	volume	A8	[2 97]
C4 share of terrestrial GPP	23.5 % (computed; 35.3 of 150.3 Pg C)	GPP	A8	[3 10]
forests: terrestrial carbon; terrestrial NPP	about 45 %; about 50 %	terrestrial totals	A8	[3 12]
transpiration in terrestrial evapotranspiration	80–90 %	evapotranspiration	A8	[3 18]
isoprene; monoterpenes in biogenic volatile emission	about 50 %; about 15 %	about 1 Pg per year	A8	[3 19]
stomatal density change: herbarium 200 yr; 280 to 340 $\mu\text{mol mol}^{-1}$; <i>Pinus flexilis</i> deglaciation	–40 %; –67 %; –17 %	stomatal density	A8	[3 39]; [3
vegetated area with increased leaf area; decreased, 1982–2009	25–50 %; less than 4 %	vegetated area	A8	[3 44]
greening attribution: CO ₂ ; N deposition; climate	70 %; 9 %; 8 %	greening trend	A8	[3 44]
land sink share of emissions, 2013–2022	31%	emissions	A8	[3 14]
CO ₂ rise since 1750	53 % (426.07/278, computed); 50.0 % in 2022	278 ppm	A8	[2 98]; [3

seasonal CO ₂ amplitude rise since the 1960s, Hawaii; Arctic	about 20 %; 40 %; more than 50 % at some latitudes	amplitude	A8	[3 22]; [3
forest loss since 1990	4.2 % (computed; 178 Mha)	1990 forest area	A8	[3 16
megaflora species turnover at the Triassic–Jurassic boundary	above 95 %	megaflora	A8	[3 36
Amazon tree species: hyperdominants making half of stems; rare species	1.4 % (227 species); about 36 % (5,800 species)	about 16,000 species	A9	[3 59
tree species undescribed; by continent S America; Eurasia; Africa	about 9,000 of 73,300; 43 %; 22 %; 16 %	tree species	A9	[3 52
pioneers at BCI: of species; of stems in smallest gaps; largest gaps	47 of 229; 7.1 %; 26.3 %	species; stems	A9	[3 60
Douglas-fir net carbon gain from birch	6 % of carbon fixed	isotope fixed	A9	[3 63
aspen browsing, Yellowstone, 1997–1998; by 2012	about 90 %; 37–63 %	young aspen	A9	[3 65
vegetation above 5 m; 10 m; 30 m	41 %; 30 %; 5 % of land; above 30 m = 16.5 % of forest	land area	A9	[3 69
understorey light: closed canopy at 1 m; 200 m ² gap; 400 m ² gap	about 1 %; 9 %; 20–35 %	clearing	A9	[3 92
diffuse transmittance, old growth; second growth	1.8 % (0.45–14.93); 1.75 % (0.53–5.87)	above-canopy light	A9	[3 93
gap area at BCI secondary forest; lidar gap fraction old growth; old secondary	4.3 % (3.1–5.7); 1.41 %; 0.93 %	forest area	A9	[3 76]; [3
seed species failing to reach a given trap	88%	260 species	A9	[3 60
thinning lines deviating from $-3/2$	20 of 44 significant lines (45 %, computed); 19 of 63 not	63 lines	A9	[3 85
height growth ends at	87 % of break-even height; yield data 70–90 %	maximum height	A9	[3 91
Amazon deaths broken or uprooted; standing	51.2 %; 48.4 %	23,683 deaths	A9	[3 78
forest disturbed per year	about 3 % (104 Mha)	forest area	A9	[3 79
tree decline since civilisation began	about 46 %	former total	A9	[3 51
Amazonia's trees	12.8 % (computed)	3.04 trillion	A9	[3 59]; [3
Lepidodendron stand ground cover	about 10 %	ground	A9	[3 67
crop losses to pathogens and pests: wheat; rice; maize; potato; soybean	21.5 %; 30.0 %; 22.5 %; 17.2 %; 21.4 %	crop yield	A10	[4 00
plant viruses transmitted by insect vectors	about 80 %	plant viruses	A10	[4 13

plant and fungal viruses among all virus species	13.2 % (computed; 2,134 of 16,215; different years)	ICTV list	A10	[4 10]; [4
plant virus database: RNA; DNA	54 %; 46 %	3,206 species	A10	[4 11
potyviruses among named plant viruses	about 15 %	plant virus species	A10	[4 06
receptor-like kinases among <i>Arabidopsis</i> genes	nearly 2.5 % (at least 610)	protein-coding genes	A10	[4 27
sequenced dicots with <i>Agrobacterium</i> T-DNA; sweet potato cultigens	8.4 % (computed; 23 of 275); 291 of 291	genomes	A10	[4 19]; [4
emerging plant epidemics caused by viruses	47 %; about half	emerging epidemics	A10	[4 53]; [4
wheat varieties susceptible to Ug99	about 90 %	wheat varieties worldwide	A10	[4 51
virus resistance genes that are recessive	about half of about 200	resistance genes	A10	[4 12
Cavendish in banana exports	99%	banana exports	A10	[4 39
NLR genes in most accessions, <i>Arabidopsis</i>	about half	pan-NLRome	A10	[4 46
plant-parasitic among terrestrial nematodes	about 25 % (about 4,100 species)	terrestrial nematodes	A10	[4 25
legume-nodulating plant families	about 10 of about 380	angiosperm families	A3	[1 02
coal forests lost in the Kasimovian	about one half	forest extent	A9	[3 57
long-distance dispersal lost after megafauna extinction, South America	at least two thirds	pre-extinction	A4	[1 44]; [1

C8. Present-day global quantities

what	value	cha pte	ref
global net primary production	104.9 Pg C per year, land and	A7, A8	[289]
terrestrial gross primary production	about 150 Pg C per year; 129 ± 32 Gt C per year (both recorded)	A8	[310]; [318]
C4 gross primary production; C3	about 35.3 Pg C per year; about 11.5	A8	[310]
plant carbon to mycorrhizal mycelium	13.12 Gt CO ₂ e per year = 3.58 Gt C (computed); AM 1.07, EcM	A2	[73]
plant biomass of AM vegetation; EcM	241 Gt C; 100 Gt C	A2	[73]
global biomass: total; plants; bacteria; archaea; fungi	about 550 Gt C; 450; 70; 7; 2	A3, A5	[132]

pre-industrial terrestrial biological N fixation	58 Tg N per year (40–100); 128 Tg N per year (both recorded)	A3	[128]; [127]
marine biological N fixation	140 Tg N per year; 120 (100–200)	A3	[129]; [127]
Haber–Bosch; lightning	120 Tg N per year; 5 Tg N per year	A3	[127]
total reactive nitrogen creation;	413 Tg per year; 210 Tg per year	A3	[129]
agricultural biological N fixation;	50–70 Tg N per year; 16.4 Tg N	A3	[130]
rice paddy methane; global methane	30 (25–38) Tg CH ₄ per year; 576 (550–590) Tg CH ₄ per year	A3, A7	[131]; [294]
termite CH ₄ ; CO ₂	19.7 ± 1.5 Mt CH ₄ per year; 3,500 ± 700 Mt CO ₂ per year	A7	[292]
phosphorus fertiliser	about 15 Mt P per year; human mobilisation about three times	A5	[213]
former seabird and anadromous fish P	about 150 × 10 ⁶ kg P per year	A4	[168]
former marine mammal upward P	340 × 10 ⁶ kg P per year	A4	[168]
soil organic carbon to 30 cm; 1 m; 2 m	684–724 Pg; 1,462–1,548 Pg; 2,376–2,456 Pg (4,353 profiles)	A5	[191]
soil carbon to 2–3 m; below 3 m	2,270–2,770 Pg C; more than 500 Pg	A5	[192]
soil carbonate carbon; soil nitrogen, to 1 m	695–748 Pg; 133–140 Pg	A5	[191]
global soil respiration, 2008	98 ± 12 Pg C per year	A5	[200]
soil bacteria per gram; species per gram	up to 10 ¹⁰ cells; 4 × 10 ³ to 5 × 10 ⁴	A3	[110]
soil nematodes: number; biomass	4.4 ± 0.64 × 10 ²⁰ ; about 0.3 Gt	A5	[184]
forest carbon: total; dead wood; litter	861 ± 66 Pg C; 73 ± 6; 43 ± 3	A7, A9	[250]
forest carbon by biome: tropical; boreal; temperate	471 ± 93; 272 ± 23; 119 ± 6 Pg C	A9	[250]
forest sink: gross; net	4.05 ± 0.67; 1.11 ± 0.82 Pg C per year	A9	[250]
tropical live biomass	247 Gt C on about 2.5 Gha	A9	[399]
coarse woody detritus: production; pool	about 12 Pg dry matter per year; about 150 Pg	A7	[251]
global litter production	90–110 Pg dry matter per year	A7	[251]
fire carbon emissions, 1997–2016	2.2 Pg C per year (1.8–3.0)	A7	[290]
burned area	3.81 Mkm ² per year	A7	[291]
forest area; net loss; loss since 1990	4.06 Gha; 4.7 Mha per year (2010–2020); about 178 Mha	A8, A9	[316]
forest area, second figure	about 42 million km ²	A8	[312]
trees: total; tropical; boreal; temperate; tree species	3.04; 1.30; 0.74; 0.66 trillion; more than 15 million	A9	[351]
tree species	about 73,000 (73,300)	A9	[352]
Amazonian trees; tree species	about 3.9 × 10 ¹¹ ; about 16,000	A9	[359]
forest disturbed by fire, pests, weather	104 Mha per year	A9	[379]
mountain pine beetle, 2000–2020	374,000 km ² ; 270 Mt C	A9	[398]
global transpiration	62,000 ± 8,000 km ³ per year	A8	[318]
biogenic volatile emission	about 1 Pg per year	A8	[319]
organic carbon burial, land; sea	350; 200 × 10 ¹² g C per year	A8	[321]

atmosphere–ocean O ₂ reservoir; source	3.78×10^{19} mol; 1.8×10^{13} mol per	A8	[313]
dry air composition	N ₂ 78.08 %; O ₂ 20.95 %; Ar 9,340	A8	[297]
CO ₂ , Mauna Loa, September 2026	426.07 ppm	A8	[298]
CO ₂ , 2022 global mean; carbon per ppm; atmospheric carbon	417.1 ± 0.1 ppm; 2.124 Gt C per ppm; 886 Gt C (computed)	A8	[314]
fossil emissions 2022; atmospheric growth; land sink; ocean sink	9.9 ± 0.5 Gt C; 5.2 Gt C per year; 3.3 ± 0.8; 2.9 ± 0.4 Gt C per year	A8	[314]
seasonal CO ₂ amplitude: far north; Tropics	15–20 ppm; about 3 ppm; about 6.5 ppm	A8	[322]; [349]
Holocene CO ₂ change; land uptake	–5 ppmv then +20 ppmv; about 200 Gt C	A8	[348]
deforestation forcing (modelled):	–0.96; +2.22; +0.12; +1.38 W m ^{–2} , 1.5–2.0 W m ^{–2}	A8	[341]
angiosperm species; monocots; eudicots; gymnosperms; all plants	295,383; 74,273; 210,008; 1,079; about 374,000	A1	[1]
vascular plant species	308,312	A2	[1]
pollinator species	349,368 (about 350,000)	A1	[2]
pollinators by group: bees; flies; Lepidoptera; beetles; Hymenoptera;	17,000; 55,000; 141,600; 77,300; 70,000; 1,500; 1,089; 344; 37	A1	[2]
insects named; estimated; beetles	about 1 million; about 5.5 million; 1.5 million	A1	[33]
Lepidoptera; Coleoptera; Hymenoptera; Hymenoptera	157,424; 386,500; 153,088; 20,446 (about 17,000)	A1	[35]; [36]; [37]; [38]; [39]
gall-inducing insects	21,000–211,000, mean 132,930	A1	[39]
<i>Ficus</i> species; fig–wasp pairs	about 750 (or 874); more than 750	A1	[41]; [32]
fungi accepted; estimated	120,000; 2.2–3.8 million	A2	[76]
Glomeromycota species	about 360 (or 320)	A2	[60]; [61]
ectomycorrhizal fungi known; likely; plant hosts	7,750; 20,000–25,000; 6,000–7,000 (8,500 in 335 genera)	A2	[66]; [65]
lichenised fungi	19,387 species, 995 genera	A2	[48]
<i>Phytophthora</i> species	142 described, 43 provisional	A2	[81]
legume species; actinorhizal species; actinorhizal species	more than 19,500; more than 220; 282	A3	[104]; [89]; [100]
birds; mammals	11,063 extant (251 families); 6,399 extant (6,495 recognised)	A4	[146]; [147]
frugivorous birds; frugivorous fishes	1,230 (365 obligate); more than 275	A4	[136]; [134]
myrmecochorous plants	at least 11,000 species, 334 genera, 776 families	A4	[143]
nematodes; oribatid mites; springtails; tardigrades; earthworms	28,537; about 9,000; 9,186–9,270; 1,508; 5,406 (3,000–3,500 earlier)	A5	[202]; [203]; [205]; [206];
secondary metabolites known; alkaloids	more than 100,000; 27,000 (or 12,000)	A6	[215]; [243]
insect herbivore species; flowering plants	more than 1 million; more than 200,000	A6	[230]
grass species	about 11,000	A6	[223]
plants with extrafloral nectaries; with domatia	3,941 (745 genera, 108 families); 681 (159 genera, 50 families)	A6	[228]; [229]
African large herbivore species	92 in five functional types	A6	[225]
termites: Macrotermitinae; Termitinae	about 330 species; about 50	A7	[269]

Scolytinae; Scarabaeinae; millipedes valid; woodlice	more than 6,000; about 5,000; 7,753 (12,116 nominal); 3,710	A7	[263]; [264]; [272]; [273]
wood-decay fungi dataset	1,157 species: 126 brown rot, 1,031 white rot	A7	[266]
virus species (ICTV 2025); plant virus	16,215; 1,503–3,206 by list	A10	[408]; [411]
plant virus losses; late blight; nematodes; <i>Striga</i>	more than US\$30 billion; US\$6.7 billion; €110 billion; US\$1 billion	A10	[453]; [412]; [420]; [425];
citrus tristeza trees killed; cacao trees	more than 100 million; more than 200 million	A10	[453]; [412]
elms killed in the UK, 1910–1970s	about 30 million	A2	[86]
Irish famine deaths, 1845–1850	about 1 million	A10	[456]

Checks

Rows per table: C1 162; C2 49; C3 31; C4 103 with positions + 28 without = 131; C5 106 with positions + 29 rates = 135; C6 16; C7 126; C8 79.

Values not placed:

- A10 dates given only as "(see A2)" — tracheophytes 452 Ma, spermatophytes 365 Ma, angiosperm crown 151 Ma — carry no (measured [n]) mark in G-partA and are left out of C1 and C2.
- *Protorosaurus* seed ingestion (Late Permian, no number), Gilboa oribatids (Devonian, no number), Early Jurassic ectomycorrhizal habit (no number), Middle Oligocene frugivorous bat (no number), C4 origin "Early Oligocene" (no number; C1 row without position).
- Modelled values (O₂ nadir 14.5 % at 393 Ma [303]; O₂ ranges [337]; [321]; [338]; deforestation forcing [341]) are not in C1; the forcing row in C8 is marked modelled.
- Positions for the two historical series in A10 (1843–2015) are given as years before 2026.

Recomputed positions differing by more than 0.01 from G-partA:

- A4, fleshy-fruit diversification onset, 80 Ma: G-partA gives 65.41; pos.py gives 65.43 (also the 80 Ma CO₂ point in A8 would be 65.43). All other checked positions (about 270 time values and 120 size values) agree within 0.01.

Layer B — The Patterns Set Beside the Net

B1 Method

The data of this layer are the ten Pattern paragraphs of Layer A and the eight tables of Part C. The other side is the set of statements the Vacuum.Net texts make about the structure and the evolution of the net, quoted in B2. A pairing is a statement from each side with the same form. A pairing is a read, and a read is a hypothesis until a test decides it. No statement about the net is added. Where nothing pairs, the entry says none.

Three tests were fixed before their data were looked at (B10). One tabulation, in B3, was classified after Table C2 had been seen; it is marked post hoc and is not a test.

B2 What the texts say that can be set beside Layer A

From the texts fetched for *Plants on the Ladder* and refetched for this book (the *Balanced Tree* PDF, §2, §5 and §11, on 11 October 2026), these statements have a form that Layer A can meet (text):

1. **Two classes.** "The closed class persists and holds form." "The unclosed class decays, and while it lasts it carries tension from one closure to the next." (*Where Illness Comes From; From Atom to Body*, Part 0.5.)
2. **Residue and alphabet.** "The residue of depth n is the alphabet of depth $n+1$." "No closure is ever exact: each depth leaves a remainder." (*Where Illness Comes From*.)
3. **Filling.** "A species is a subtree; an organism is a closure at a depth." "Evolution is not selection on frequency — frequency does not place — but the filling of depths until the next is forced." (*Balanced Tree*, §11.)
4. **Scale.** "N5, Scale. The same winding appears at every depth." (*The Vacuum.Net Theory*; Climate paper §2.)
5. **Memory.** "N3, Memory. The net keeps the orientation of what was first laid down." (*The Vacuum.Net Theory*; Climate paper §2.) "Heredity is memory in form with reach two." (*Balanced Tree*, §11.)
6. **Community and conflict.** "Community is topological, not chosen: shared prefix. Conflict is phase interference between closures without shared form." (*Balanced Tree*, §11.)
7. **Loading, holding, discharge.** "Earthquakes, eruptions, storms: loading, holding, discharge." (*Balanced Tree*, §11.)

Statements the texts do not make: nothing on proportions of species in a mode of life; nothing on the order in which partners appear; nothing on rates of mutation or generation; nothing on oxygen, carbon dioxide or climate as such; nothing on forests. These absences are recorded so that they are not filled.

B3 The order of arrival

Measured (Layer A, Table C2). Forty-nine dated pairs across the ten chapters, each with a plant-side element and a partner-side element. In 19 the partner is older, in 24 the plant-side element is older; 3 coincide or overlap, and 3 compare two elements on the same side.

Post hoc classification. Read after the table was built, not before. The partner is older when the partner supplies something the plant takes in or stands on: the fungal lineages before the first land plant (538 and 177 Myr), the glomalean spores before the first arbuscules (48.5 Myr), nitrogen fixation before land plants (2.73 Gyr), the chloroplast lineage before crown eukaryotes (≥ 260 Myr), microbial mats and burrowing animals before rooted soils (≥ 2.2 Gyr; ≥ 59 Myr), insects, the proboscis and the Lepidoptera before flowers (273–281, 106–111, 165–170 Myr), orchid bees before perfume orchids (7–20 Myr), fire and millipedes before forests (38; 29–40 Myr), caulimoviruses before angiosperms (140–180 Myr), free oxygen before land plants (1.86 Gyr). The plant-side element is older when the partner answers a plant trait: nodulation after legumes (2–7 Myr), the disperser radiations after fleshy fruit (14–35 Myr), arthropod herbivory after land plants (53–67 Myr), the Pierid protein after Brassicales (about 10 Myr), hypsodonty after grassland (≥ 4 Myr), bovids and spines together (1 Myr), peroxidases and wood borings after forests (85; 2–26 Myr), oxygen above 15–17 per cent and carbon dioxide near 278 ppm after rooted plants (50–70; 60–100 Myr). The rule does not sort every row. Of the 19 partner-first pairs, 13 are suppliers in this sense; the others are an unrelated bee and beetle one million years apart, orchid bees before the orchids that answer them, a bird split before fleshy fruit, fire and millipedes before forests, and a virus before angiosperms. Of the 24 plant-first pairs, 19 or 20 are responders; the others set a plant trait against its own spread (C4 origin and abundance), against the air (oxygen, carbon dioxide), or against a plant organ (nodulation after legumes). Counts from Table C2; classification post hoc. The air appears on both sides of the rule, as supplier in one row and responder in two.

Text. Statement 2: the residue of one depth is the alphabet of the next. Statement 1: carriers run between closures.

Read. The plant is assembled from closures older than itself — the cyanobacterium that became its plastid, the fungus that became its root partner, the fixer that became its nodule, the insect that became its pollinator — and these are the alphabet of the plant as a word. What answers the plant — the browser, the disperser, the rot, the pathogen's counter-move — is written after the word. The order in Table C2 is, in 32 or 33 of 43 ordered rows, the order the two statements give. The pairing is read; the classification that makes it visible was made after the fact, sorts three quarters of the rows, and is therefore not a test. A test would fix the classification rule first and apply it to pairs not yet dated here.

Status. Read; post hoc; three quarters of the rows; untested.

B4 The two classes and the asymmetry of time

Measured (Table C6; Layer A). Where both sides carry a time, the partner that moves between plants is faster than the plant it moves between, by 4.4 to 8×10^4 . Soil bacteria turn over in 2.3–33 days against fine roots of 1.8 years and trees of centuries (ratio 20–286). Rhizosphere bacteria turn over in 12–19 hours against a nodule of 45 days (57–90). Fig wasps live 24–48 hours against a fig cycle of 15–100 days (7.5–100). Viruses substitute 5.2×10^4 to 8.0×10^4 times faster per site per year than their hosts. Nematodes run 9–13 generations a year; a resistance gene holds 28 years against them. Two chapters, A6 and A8, carry no pair; in A1 the ranges of flower and bee overlap, in A4 the longest-lived birds outlast the beech mast interval, in A9 the two sides are both trees. The exceptions are the closed forms on the partner's side: the *Armillaria* genet of 1,900–8,650 years outlives any root (1,056–4,806 times); the termite royal pair of 20 years outlasts coarse litter (1.5); alpine oribatid mites take 2–4 years to adulthood, longer than a fine root (1.1–2.2).

Text. Statement 1: the unclosed class decays while it carries; the closed class persists.

Read. The carriers of Layer A — spores, hyphal tips, bacteria, pollen, pollinators, viral particles, effectors, small RNAs, volatiles — are the fast class; the plant body, the fungal genet, the termite mound, the soil carbon pool of 4,830 years are the slow class. The exceptions are not exceptions to the statement: a fungal genet and a mound are closed forms, and they are slow. The division runs through each partner, not between plant and partner. That is the form of the text statement, and it is what Table C6 shows where it shows anything. Read.

Tested. Test B2 fixed four obligate pollination pairs and required the insect's generation to be shorter in all four. Three were obtained and all three are consistent (fig wasp 15–100 days against figs from the second year; yucca moth 1–4 years against yucca flowering at 5–6 years; orchid bee 29–32 days against *Coryanthes* flowering at 2–3 years). The fourth pair, *Angraecum* and *Xanthopan*, has no sourced value on either side. **Not run** by the rule; no counter-example found.

Status. Read; consistent in every obtained case; the test awaits one pair.

B5 Repeated origins and filling

Measured (Table C3; A1). Table C3 holds 31 rows, of which at least 25 are traits that arose more than once; the rest are single origins or shared gene sets listed for comparison. Among the repeated: ectomycorrhiza 66–82 times in fungi and 30 in plants; lichenisation 20–30; nodulation about 8 times with about 10 losses; ant dispersal at least 101 times; spines at least 55; extrafloral nectaries at

least 457; domatia 158; brown rot at least 4 losses; ambrosia beetles 10; C4 photosynthesis 62; tetrapod herbivory at least 5; parasitic nematodes 4; and, from A1, obligate pollination pairs at least 5.

Text. Statement 3: filling of depths until the next is forced; a species is a subtree.

Read. As in *Plants on the Ladder*, Part 4.6: if the same depth is reached by many subtrees once the one below is full, the same form appears many times without a single inventor. The inference from "closure at a depth" to "form" is made here, not in the texts.

Tested. Test B3 required that for at least half of the runnable traits half of the dated origins fall within a window no longer than one fifth of the clade's crown age, with at least four traits runnable. Three were runnable and all three are clustered: C4, half of 53 origins within 7.75 Myr (0.05–0.15 of the crown age); spinescence, half of 36 dated clades within 8.57 Myr (0.07 of the eudicot crown age); domatia, all 158 origins within 19 Myr (≤ 0.14). Five traits have no per-origin dates in the sources reachable. **Not run** by the rule. And the three that ran are all Miocene windows in clades older than 120 Myr; a Miocene trigger — falling CO₂, aridity, the arrival of bovids — gives the same clustering. The traits whose origins are spread across the Mesozoic, which would separate the two readings, are the ones without dates.

Status. Read; descriptive; the clustering is real in three traits and does not discriminate.

B6 The alphabet and gene retention

Text. Statement 2, read as a corollary in *Plants on the Ladder*: a partner that becomes a letter of a later closure is reduced to what the closure needs.

Tested. Test B1 required that the fraction of the free-living gene number retained by a resident partner fall monotonically with the age of the association, over at least five points. Obtained: the chloroplast keeps 87 of 3,168 protein genes, 2.75 per cent, after about 2.1 Ga; the *Paulinella* chromatophore keeps 854 of 2,917, 29.3 per cent, after at most 90–140 Ma; the *Azolla* cyanobiont keeps 3,668 intact genes against 5,368 in its free-living relative, 68.3 per cent, after about 100 Myr; the *Nostoc* of *Gunnera* and the hornworts keeps or expands its genome, 7.1–10.4 Mb, after a comparable age; rhizobia keep everything after 58 Myr. Spearman $\rho = -0.71$, $p = 0.18$.

Monotonicity breaks at the facultative *Nostoc*. The mitochondrion, outside the plant line, keeps 13 of about 834 genes, 1.6 per cent, after 2.05–1.21 Ga, less than the older chloroplast: a second break.

Fail on the rule.

Read after the test. Retention is not a function of age. It falls in the obligate residents — mitochondrion, chloroplast, chromatophore, the *Azolla* cyanobiont, in that order of loss — and it does not fall in the facultative ones, whatever their age. Two regimes, not one slope. In the words of statement 1: a letter that has closed into the word loses what the word supplies; a carrier that still runs between closures keeps its own. The corollary as fixed was wrong; the two-class form survives it. That survival is itself a read, made after the data; it is not a pass.

Status. Failed as fixed; reformulated as two regimes; untested in that form.

B7 Scale in the forest

Measured (A9). In worldwide plot data the number of stems falls as the -2 power of trunk diameter. Gap sizes in a tropical forest follow a size exponent of 2.0–2.1. Of 63 self-thinning lines,

20 of 44 significant ones deviate from $-3/2$. Under a closed canopy 1 per cent of light remains at 1 m. Branch cross-section is conserved at forks.

Text. Statement 4: the same winding appears at every depth.

Read. A stem distribution that falls as a power of diameter is a straight line on log–log axes: the same rule at every size, with no characteristic scale. Exponent -2 gives equal basal area per unit of diameter, not per logarithmic class. That form is what N5 names. The gap exponent of 2 has the same form. Against it: of 44 significant self-thinning lines 20 deviate from the predicted slope, and two tests on 10 and 14 tropical plots, 1.7 and 2 million trees, found the -2 prediction inconsistent with the data (A9). The pairing rests on two exponents and is contradicted by two sets. Read; weak; untested.

B8 Where nothing pairs

- **Shares.** 87.5 per cent of angiosperms animal-pollinated; 72 per cent of vascular plants arbuscular-mycorrhizal; 83.5 per cent of canopy trees animal-dispersed; 17 per cent of production eaten alive; 5.3 per cent of leaf tissue; 6.2–13.1 per cent of production to fungi; 59 per cent of species in soil (Table C7). The texts make no statement about proportions. None.
- **Oxygen and carbon dioxide.** Three recorded oxygen steps; carbon dioxide falling 17 ppm per Myr with rooted plants; stomatal density falling with each rise (A8). Statement 7 names loading, holding and discharge for storms and earthquakes, not for the air. The Devonian drawdown has that form in words only. None.
- **Closure depths.** Depth 12 at 24.23 mm and 80.8 ps, 41 at 92.4 min, 53 at 93.4 years. Tables C4 and C5 hold no characteristic size or time of the plant's company at these. None.
- **The ladder.** Tables C1, C4 and C5 give 162 dated events, 103 sizes and 106 durations their positions. These are coordinates. No clustering test was run; the lists are drawn from ten topics, not from one population. No claim.
- **Memory with reach two.** Statement 5 names a reach of two rings for direct inheritance. Layer A holds no measurement of inheritance across a fixed number of generations in a plant–partner pair. None.

B9 Summary

B2 statement	Measured pattern (Layer A)	Status
2 Residue of depth n is the alphabet of depth n+1; 1	13 of 19 partner-first pairs are suppliers; 19–20 of 24 plant-first pairs are responders	Read; post hoc; three quarters; untested
1 Two classes: closed forms persist, carriers decay	Partners 4.4 to 8×10^4 times faster where both sides are dated; exceptions are closed	Read; consistent in 3 of 3 obtained pairs; test
3 Filling of depths until the next is forced	≥ 25 traits with repeated origins; three dated traits cluster in Miocene windows	Read; not discriminating
2, corollary: retention falls	Fails; two regimes, obligate residents lose,	Failed as fixed;
4 N5, the same winding at every depth	Stem exponent -2 , gap exponent 2.0–2.1; self-thinning and two plot tests deviate	Read; weak
—	Shares, oxygen and carbon dioxide, closure depths, memory with reach two	None

What Layer B yields is one firm description and no passed test. The description: the company of plants divides into what the plant is made of, which is older than the plant, and what answers the

plant, which is younger; and where both sides are dated the partner that moves is faster than the form it moves between, except where the partner is itself a form. Both halves are in the texts. Neither has yet been put to a test that it could fail and did not.

B10 The tests, fixed first and then run

Fixed on 13 October 2026 before the data were looked at; run by Claude Code the same day on the data named. The attestation is the author's. Protocol, rows and computation are in the file TB-tests.md that accompanies this book.

B1, gene retention against age. Required: Spearman negative, $p < 0.05$, $n \geq 5$, and no older point above a younger one. Found: $\rho = -0.71$, $p = 0.18$, $n = 5$; two breaks of monotonicity (facultative *Nostoc*; mitochondrion against chloroplast). **Fail.**

B2, generation time in obligate pollination pairs. Required: insect shorter in 4 of 4 fixed pairs. Found: 3 of 3 obtainable pairs consistent; the fourth pair unsourced on both sides; the ant–fungus pair has no independent fungal generation time. **Not run.**

B3, windows of repeated origins. Required: at least 4 runnable traits, clustered in at least half. Found: 3 runnable, all clustered, all Miocene; 5 traits without dated origins. **Not run.**

Together with the three tests of *Plants on the Ladder*, the theory has now been set against plant data six times with the outcome fixed first. None passed. Two failed outright: the count list on a text chosen in advance, and the retention corollary. One failed on its own rule, which was ill-posed, while confirming its measured half. Three could not be completed on the data reachable here, and in those three the obtained part was consistent with the reading. That is the state.

Part D — Not Verified, and Left Out

D.1 Not verified

Each chapter of Layer A ends with its own list. Gathered, the items that bear on Layer B:

- The dates that would complete B3: per-origin ages for extrafloral nectaries (Weber & Keeler 2013), ectomycorrhizal lineages (Tedersoo & Smith 2013), nodulation (Werner 2014 supplement), myrmecochory (Lengyel 2010), lichenisation (Lücking 2017).
- The pair that would complete B2: *Angraecum sesquipedale* years to first flowering and *Xanthopan* generation time.
- Martin 2002's 5–10 per cent plastid retention range (PNAS, blocked); Stahl 1999's 9.8 Myr for *RPM1* (only "millions of years" read).
- Howe & Smallwood 1982's own figures; the "~75 per cent insect-transmitted" of Whitfield 2015 (80 per cent used, from Huang 2022).
- Latent periods and epidemic doubling times of late blight and rusts: every page on the topic was refused by the fetch tool; no latency numbers stand in A10.
- Berner's own numeric oxygen maximum; absolute stomatal densities per mm²; the Barrow seasonal amplitude in ppm.
- Falster & Westoby 2003 and Farrior 2016 numeric content; the WBE branching ratio; crown diameters in metres.

- Erséus et al. 2020 is in *Zoologica Scripta*, not *Proceedings B*; Warshan et al. 2018 is in *Molecular Biology and Evolution*, not *ISME Journal*; Belcher 2010 is in *PNAS*; Glasspool 2004 is in *Geology*; Delaye 2016 is in *PLoS Currents*. The corrected venues stand in the reference lists.

D.2 Left out, by rule

- Any sentence in which the net causes a biological pattern; any ring depth above the cell; any family of layers; any rounding of a position.
- Lichens as plants (they are fungi with partners; they appear in A2 as fungi); corals and animal photosymbioses; rhodopsin phototrophs.
- Human agriculture beyond its dated onset (A4) and its crop losses (A10).
- Secondary sources as facts.

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Annotated references for Layer B

The texts

Konstapel, J. (2026). *The Vacuum.Net Theory: Complete Derivation*. Constable Research, Leiden, 28 September 2026. Why read? The five axioms, among them N3 memory and N5 scale, quoted in B2.

Konstapel, J. (2026). *The Balanced Three, the Balanced Tree and the Vacuum.Net Theory*. Constable Research, Leiden, 29 August 2026; PDF *Balanced Ternary and the Balanced Tree: One Balance and What Follows From It*. Why read? §11, "The other sciences": the sentences on biology, sociology and earth science that B2 quotes — species as subtree, filling until forced, community as shared prefix, loading–holding–discharge.

Konstapel, J. (2026). *The Climate on the Ladder of Three*. Constable Research, Leiden, 3 October 2026. Why read? Depth as layer, $3^n \cdot S_0$, the definition behind every position in this book.

Konstapel, J. (2026). *Where Illness Comes From*. Constable Research, Leiden, ninth edition. Why read? The two classes, closed forms and carriers, and "the residue of depth n is the alphabet of depth $n+1$ ": the two statements that B3, B4 and B6 rest on. *Reading advice*: Chapter 2 for the transitions and the remainder.

Konstapel, J. (2026). *From Atom to Body*. Constable Research, Leiden, first edition. And *Plants on the Ladder*. Constable Research, Leiden, 12 October 2026, version 1.1. Why read? The marks, the ladder, the test that showed the ladder orders but does not select, and the three earlier tests whose outcomes B10 counts with these.

Sources of the tests (beyond the Layer A list)

Kaneko, T., et al. (1996). "Sequence analysis of the genome of the unicellular cyanobacterium *Synechocystis* sp. strain PCC6803. II." *DNA Research* 3, 109–136. DOI 10.1093/dnares/3.3.109. — 3,168 potential protein genes; the denominator of the chloroplast's retention.

Kaneko, T., et al. (2001). "Complete genomic sequence of the filamentous nitrogen-fixing cyanobacterium *Anabaena* sp. strain PCC 7120." *DNA Research* 8, 205–213. DOI 10.1093/dnares/8.5.205. — 5,368 protein-encoding genes; the denominator for the *Azolla* cyanobiont.

Ran, L., et al. (2010). "Genome erosion in a nitrogen-fixing vertically transmitted endosymbiotic multicellular cyanobacterium." *PLoS ONE* 5, e11486. DOI 10.1371/journal.pone.0011486. — 5,357 coding sequences, 31.2 per cent pseudogenes, 3,668 intact; the one streamlined plant cyanobiont.

Warshan, D., et al. (2018). "Genomic changes associated with the evolutionary transitions of *Nostoc* to a plant symbiont." *Molecular Biology and Evolution* 35, 1160–1175. DOI 10.1093/molbev/msy029. — facultative symbiont genomes of 7.1–10.4 Mb, expansion rather than loss; the point that broke test B1's monotonicity.

Anderson, S., et al. (1981). "Sequence and organization of the human mitochondrial genome." *Nature* 290, 457–465. DOI 10.1038/290457a0. Unseld, M., et al. (1997). "The mitochondrial genome of *Arabidopsis thaliana* contains 57 genes in 366,924 nucleotides." *Nature Genetics* 15, 57–61. DOI 10.1038/ng0197-57. Andersson, S. G. E., et al. (1998). "The genome sequence of *Rickettsia prowazekii* and the origin of mitochondria." *Nature* 396, 133–140. DOI 10.1038/24094. — 13 and 57 genes against 834: the mitochondrial comparison.

Borges, R. M. (2021). "Interactions between figs and gall-inducing fig wasps." *Frontiers in Ecology and Evolution*. (Layer A [32].) Orwa, C., et al. (2009). *Agroforestry Database 4.0*, *Ficus carica*. World Agroforestry Centre. — fig wasp development 15–100 days plus 24–48 hours adult life; figs fruiting from the second year.

Alexander, R. R., Pond, F. W., and Rodgers, J. E. *Yucca*. In: USDA Forest Service, *The Woody Plant Seed Manual*, pp. 1175–1177. COSEWIC (2013). *Assessment and status report on the Yucca Moth Tegeticula yuccasella in Canada*. — yucca flowering at 5–6 years; moth generation 1–4 years with diapause.

Gerlach, G. (2011). "The genus *Coryanthes*: a paradigm in ecology." *Lankesteriana* 11(3), 253–264. Peruquetti, R. C. (1998). "Notas sobre a biologia de *Euglossa townsendi*." *Anais da Sociedade Entomológica do Brasil* 27(2), 309–311. DOI 10.1590/S0301-80591998000200021. — orchid flowering at 2–3 years from seed; bee development 29–32 days.

Charles-Dominique, T., et al. (2016). "Spiny plants, mammal browsers, and the origin of African savannas." *PNAS* 113, E5572–E5579. (Layer A [225]; postprint and Table S5 read at the University of Pretoria repository.) — 36 dated spiny clades, median 13.65 Ma, half within 8.57 Myr.

Chomicki, G., and Renner, S. S. (2015). "Phylogenetics and molecular clocks reveal the repeated evolution of ant-plants after the late Miocene in Africa and the early Miocene in Australasia and the Neotropics." *New Phytologist* 207, 411–424. (Layer A [229].) — 158 domatium origins and 43 losses within 19 Myr.

Christin, P.-A., et al. (2008). *Current Biology* 18, 37 ff.; Christin, P.-A., et al. (2011). *Journal of Experimental Botany* 62, 3171 ff. — the 53 dated C4 origins, as extracted for *Plants on the Ladder*, test 3; half within 7.75 Myr.

Weber, M. G., and Keeler, K. H. (2013), "The phylogenetic distribution of extrafloral nectaries in plants," *Annals of Botany* 111(6), 1251–1261, DOI 10.1093/aob/mcs225 (Layer A [228]); Tedersoo, L., May, T. W., and Smith, M. E. (2010), *Mycorrhiza* 20, 217–263, DOI 10.1007/s00572-009-0274-x (Layer A [63]) and Tedersoo, L., and Smith, M. E. (2013), *Fungal Biology Reviews* 27, 83–99, DOI 10.1016/j.fbr.2013.09.001 (Layer A [64]); Werner, G. D. A., et al. (2014), *Nature Communications* 5, 4087, DOI 10.1038/ncomms5087 (Layer A [98]); Lengyel, S., et al. (2009), *PLoS ONE* 4, e5480, DOI 10.1371/journal.pone.0005480 (Layer A [135]) and Lengyel, S., et al. (2010), *Perspectives in Plant Ecology, Evolution and Systematics* 12, 43–55, DOI 10.1016/j.ppees.2009.08.001 (Layer A [143]); Lücking, R., Hodkinson, B. P., and Leavitt, S. D. (2017), *The Bryologist* 119(4), 361 ff., DOI 10.1639/0007-2745-119.4.361 (Layer A [48]). — the five repeated-origin traits whose origins are counted but not dated in the reachable text; the reason test B3 could not reach four runnable traits.