

Looking back to the past to secure the future of *Rhododendron* in a changing world

A talk given by Dr. Juliana S. Medeiros, Holden Forests & Gardens

Niagara Chapter of the ARS, Spring Meeting March 21, 2021



Review and further insights by Dixie Szasz-Taylor.

Plant biologist and research scientist, Juliana Medeiros, from Medeiros Research Lab, Holden Forests and Gardens in Ohio, <http://medeiroslab.com/> gave another very engaging presentation to Niagara Chapter, March 21, 2021, on the role of climate change and geology in the evolution of *Rhododendron* over the last 65 million years of the Cenozoic - post-Chicxulub impact...not to mention the influence of plate tectonics on Cenozoic cooling that culminated in the Pleistocene Ice Ages. The Medeiros team focuses on *Rhododendron* as a model system that evolved initially in cool temperate montane regions, to understand how plants evolve and acclimate in response to the environment.

Juliana's unique perspective and 'boots on the ground tour' tells a fascinating story about the complex paleoecology and remarkable evolution and dispersal of *Rhododendron* from origins in NE Asia to subtropical and tropical regions by the late Eocene. As such *Rhododendron* has become one of the largest, most diverse flowering plant genera, and now one of the most threatened and endangered. Juliana's latest research on the physiology of climate tolerance and the legacy of ancient adaptations, however, provides a deeper insight into the future of *Rhododendron* in a rapidly changing world.

Climate change as old as life itself.

Today human activities are changing the climate at an unprecedented rate', Juliana says. Tropical and subtropical biodiversity hotspots like the southeastern Himalayas and the Malay Archipelago, including the islands of Java, Sumatra, Borneo, New Guinea and the Philippines, are especially sensitive to precipitation changes and global warming. 'This is supported by climate models and data from thousands of independent sources in an extensive effort to account for uncertainty,' Juliana says. An artistic visualization from 'The New Scientist', 2009, for example, depicts a consensus model climate prediction of a transformed future world at 4°C warmer. Juliana adds, 'No one knows exactly when this will happen, or what this warmer world will look like... models can only provide insights into the potential for forced human migrations to higher latitudes, or a greening Arctic, or future power generation with a mix of solar, geothermal and nuclear energy'. Under this scenario, models also predict that the Polar ice caps and alpine glaciers will melt with dramatic sea level rise, and tropical-subtropical rainforests from the Amazon, Central West Africa, SE Asia and Australia, could be replaced by desert, or savannah and grasslands.

A comprehensive study by Scotese et al (2021), on the Earth's climate volatility over the last 540 million years, in accordance with rising and falling atmospheric carbon dioxide levels, suggests: 'Although we are about halfway through a typical glacial/interglacial cycle, the Earth has now entered a super-interglacial...a consequence of burning fossil fuels that have warmed the Earth more than 1°C and will continue to warm the Earth for another 300 years.'

According to many climate scientists, most future warming is expected to take place during the mid-to-late twenty-first century. Rapid global warming is nearly unavoidable because of two key variables – global population and energy use per capita will naturally rise during the next several decades. To predict future climate scenarios, Scotese adds, 'we also need to know the future mix of renewable and non-renewable energy sources; the rate at which the ocean and the natural environment will absorb or sequester excess CO₂ emissions; and the warming effect of greenhouse gases, or the Earth's climate sensitivity to a doubling of atmospheric carbon dioxide'. According to conservative estimates for the year 2100, global climate will have warmed beyond the 2°C limit recommended by the Paris Accords. By 2200, the concentration of CO₂ could rise to 777 ppm, double the concentration of CO₂ in the year 2000 (369 ppm). As result, global average temperature (GAT) could rise about 5°C from today's 14.5°C to 19.5°C, or even 20.5°C, Scotese says.

According to Juliana, however, despite the models, extensive uncertainty is involved in trying to predict future changes in a highly complex system. 'Because we are so new on the planet and have such a limited perspective, uncertainty also dictates caution in making decisions that will affect the Earth's background or equilibrium climate state', she says. For example, in other studies, proxies for past CO₂ levels and oxygen isotope records from benthic foraminifera are used to estimate past temperatures and paleoclimate conditions. 'Looking at the past provides a better understanding of the Earth's climate sensitivity to a doubling of CO₂ levels', Tierney et al (2020) says, 'and enables finer tuning of sophisticated modern climate models to better predict future climate scenarios'. One of the main drawbacks, Tierney adds, is 'that climate models often disagree about basic predictions for future rainfall changes.'

Natural cycles, geologic processes and plate tectonics.

Natural climate forcing throughout geologic time has involved a wide range of processes that have been operating at widely different timescales from a few years to billions of years. A prime example of the longest-term natural forcing is the Sun, emitting 40% more energy now than it did at the beginning of geological time. Despite this, how has Earth's temperature remained at a reasonable and habitable level for most of the time? Studies show that Earth's relative climate stability is based primarily on changes in its atmosphere - from one initially dominated by CO₂, including significant levels of methane (CH₄), to one with only a few parts per million CO₂ and just under 1 part per million CH₄. Over geological time, life and its metabolic processes have evolved and changed the atmosphere to conditions that remained cool enough to be habitable (Earle, 2019). Notably in the Proterozoic, evolution of photosynthetic bacteria (cyanobacteria) that consume CO₂ from the atmosphere and release oxygen in the process...over eons contributed to rising oxygen levels in the ocean and the atmosphere (Earle, 2019).

As well, Juliana says, through photosynthesis plants affect climate by consuming atmospheric carbon dioxide to make their tissues and, when plants die and decay, almost all of this carbon is released back to the atmosphere over a period of years or decades. A small proportion of this biological carbon becomes buried in sedimentary rocks, however, and this becomes part of the geological carbon cycle which involves most of the Earth's carbon. Although the geological carbon cycle operates very slowly, it plays a fundamental role in weathering and climate change. The various steps in this process are described by Earle (2019) as follows:

1. Storage or sequestration of organic matter in lake sediments, peat, or permafrost for up to tens of thousands of years - and some may be buried deeper to form coal deposits that are stored for tens of millions of years. The evolution of trees in the Carboniferous, and subsequent burial as extensive coal deposits (350 Ma), for example, could have contributed to the Permo-Carboniferous Ice Ages (~335 to 260 Ma). Juliana also suggests that a massive *Azolla* bloom (fresh-water fern) in the restricted Arctic basin ~50 Ma, led to extensive carbon sequestration which contributed to Cenozoic cooling.
2. Mountain-building and associated mechanical and chemical weathering of silicate minerals, in particular the hydrolysis of feldspar, converts atmospheric carbon dioxide to dissolved bicarbonate, which is stored in the oceans for thousands to tens of thousands of years.
3. Dissolved carbon is subsequently converted by marine organisms to calcite (CaCO_3), which is stored in carbonate rocks for hundreds of million of years.
- 4.. Organic and inorganic carbon compounds are stored in sediments for tens to hundreds of millions of years, and may end up as petroleum deposits.
5. Carbon-bearing sediments are transferred to the mantle as subducted plates of ocean or continental lithosphere, where the carbon may be stored for tens of millions to billions of years.
6. During volcanic eruptions, carbon dioxide is released back to the atmosphere, where it is stored for years to decades.

According to Earle (2019), 'Throughout the Phanerozoic at least, the geological carbon cycle has remained mostly balanced with carbon being released by volcanism at approximately the same rate that it is stored or sequestered by organic or inorganic processes. During some periods of Earth's history, however, a carbon imbalance has been caused by prolonged periods of intense volcanism, e.g., Large Igneous Province (LIP) eruptions of < one million to a few million years, which can lead to dramatic climatic aberrations distinguished by radical changes in temperature, precipitation patterns, and ocean circulation. Not to mention significant mountain-building events associated with high rates of mechanical and chemical weathering, (the Himalayas and Tibetan Plateau 50 to 10 Ma, and the Alps and the Andes around the same time) that consumed atmospheric CO_2 and contributed to long-term global cooling (Hamon et al, 2013).

LIP eruptions can also trigger release of large amounts of CO_2 and CH_4 from melting permafrost, including methane hydrates from the sea floor (Scotese et al 2021). Conversely, temperatures can also fall rapidly leading to short-lived icehouse worlds due to massive asteroid impacts. Very large impact events (crater >150 km) such as Chicxulub (66 Ma), may also trigger large eruptions and

a period of global warming following impact-related cooling, e.g., the Chicxulub asteroid impact was preceded by massive LIP Deccan Trap eruptions in India a few million years before the impact and about one million years after - long before India collided with Asia.

A non-geological form of carbon-cycle imbalance is happening today on a very rapid time scale, however, as we extract vast volumes of fossil fuels, stored in rocks over the past several hundred million years. As such, Juliana says, ‘by changing the climate faster than has ever happened in the past, we are creating a climatic aberration - putting both the ecosystems and biological supports we depend on at considerable risk.’ Models predict that future warming will shift regional and seasonal patterns of rainfall and temperature. Regional changes in the land surface – reduced snow cover, melting permafrost, greening, desertification, could further trigger biogeochemical feedbacks that could dampen or amplify initial radiative forcing with further implications for climate sensitivity (Tierney et al, 2020).

Plate tectonics has also played a pivotal role in climate forcing throughout the Phanerozoic in several different ways, and on time scales ranging from tens of millions to hundreds of millions of years - particularly during the Cenozoic. Geographic configuration of the continents in high or low latitudes is one mechanism, which applies to the modern configuration of continents at high northern latitudes. Other climate-forcing mechanisms related to plate tectonics are continental collisions and the opening and closing of oceanic gateways. For example, the collision of India with south-central Asia (~50 Ma), was associated with not only uplift of the Himalayas and the Tibetan Plateau, but also closure of the equatorial eastern Tethys seaway. Around the same time, collision of the Afro-Arabian plate with Eurasia was associated with closure of the western Tethys seaway with the proto-Mediterranean Sea, and uplift of the Alps (Hamon et al, 2013). Collision of the Australian plate with the Pacific plate in SE Asia (23-24 Ma), contributed to the emergence of islands along Wallace’s Line in the eastern Malay Archipelago region, which restricted exchange between the equatorial Pacific and Indian Oceans. The net effect was a cooling of surface tropical waters, and this also contributed to expansion of the Antarctic icecap (~15 Ma) (Scotese, 2021). Along with regional cooling of the Southern Ocean during the Eocene-Oligocene transition, an earlier opening of the Drake Passage (~40 Ma) strengthened the Antarctic Circumpolar Current and isolated Antarctica, and by 35 Ma mountain glaciers had begun forming on Antarctica (Hamon et al, 2013).

Climate feedbacks also play a critical role in amplifying or suppressing weak climate forcings that have potential to develop into full-blown climate change. For example, the Pleistocene glaciations were driven primarily by subtle changes in the Earth’s orbital parameters, or Milankovitch cycles (1924). This forcing initiated a range of environmental feedback mechanisms that made the climate change.

However, because of the very large volumes of ice still in the continental ice sheets of Antarctica and Greenland, the large Himalayan cryosphere (Pant et al, 2021), and in permafrost – melting is another key feedback mechanism. Melting of ice and snow leads to important changes in the Earth’s albedo or reflectivity. In a rapidly warming Arctic, for example, as sea ice melts, albedo over large parts of the Arctic Ocean is significantly reduced - more heat is absorbed by the ocean – warming of the atmosphere is amplified - more sea ice melts, etc.

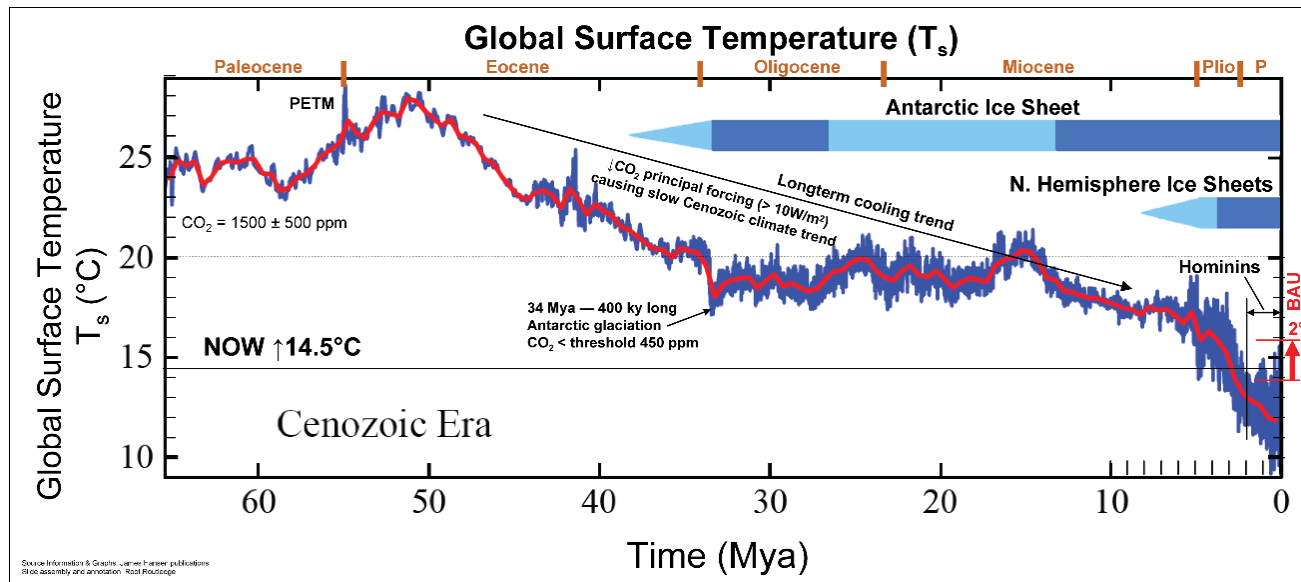


Figure 1: The global temperature trend over the past 65 Ma of the Cenozoic (*after* Earle, 2019).

From the end of the Paleocene to the height of the Pleistocene glaciation, global temperature dropped by about 14°C . There is evidence that the PETM, or Paleocene-Eocene Thermal Maximum (56 Ma), which may have been triggered by massive LIP eruptions in the North Atlantic, followed by at least two large releases of methane hydrates from the seafloor, may have been the warmest part of the Phanerozoic since the Cambrian (Earle, 2019).

Organisms can adapt and survive in the face of change.

In the face of considerable uncertainty regarding the Earth's climate sensitivity to atmospheric CO₂, Juliana asks, 'how can we learn to sail this ship called Earth?' Throughout Earth's history, mass extinction events due to asteroid impacts or other climatic aberrations were usually followed by rapid evolutionary innovation as climate change and geology created many new favorable habitat niches. The critical factor, Juliana says, is that 'temperature and water resources determine the Earth's habitable climate zones and the distribution of all living organisms on Earth'. 'Plant and animal life as we know it evolved in the Cenozoic (65 Ma to the present) during a global cooldown that lasted almost 50 million years, culminating in the last ice ages.'

How would subduction of the Tethys Ocean and the Indian tectonic plate beneath southern Asia that began in the late Cretaceous, have led to long-term global cooling in the Cenozoic (Hall, 2017)? Rapid ongoing uplift of the Himalayas and the Tibetan Plateau in the path of the Asian summer monsoons would have created the ideal warm, moist conditions that accelerated mechanical and chemical weathering of exposed silicate rocks. By consuming CO₂ from the atmosphere, chemical weathering slowly reduces the greenhouse effect. Chemical weathering also increases the flux of calcium and carbonate to the world's oceans, and when calcium cations combine with carbonate ions in the ocean, carbon is sequestered long term in the form of calcite or limestone, which also draws down levels of atmospheric carbon dioxide, and the Earth cools (Scotese et al, 2021).

Another example of a positive feedback loop, the expansion of the Antarctic icecap increased Earth's reflectivity or albedo, which led to further cooling, more reflective glacial ice, more cooling, more ice, etc. In addition, by the Pliocene, ~4-5 Ma, it got even colder with emergence of the Panama land bridge which blocked the flow of tropical Pacific and Atlantic waters to the Southern Ocean, and diverted warm Atlantic waters (the Gulf Stream) to higher northern latitudes and the Arctic. Along with global cooling, the increased moisture would have initiated the Greenland ice sheet and contributed to growth of ice sheets in northern Europe and the Arctic.

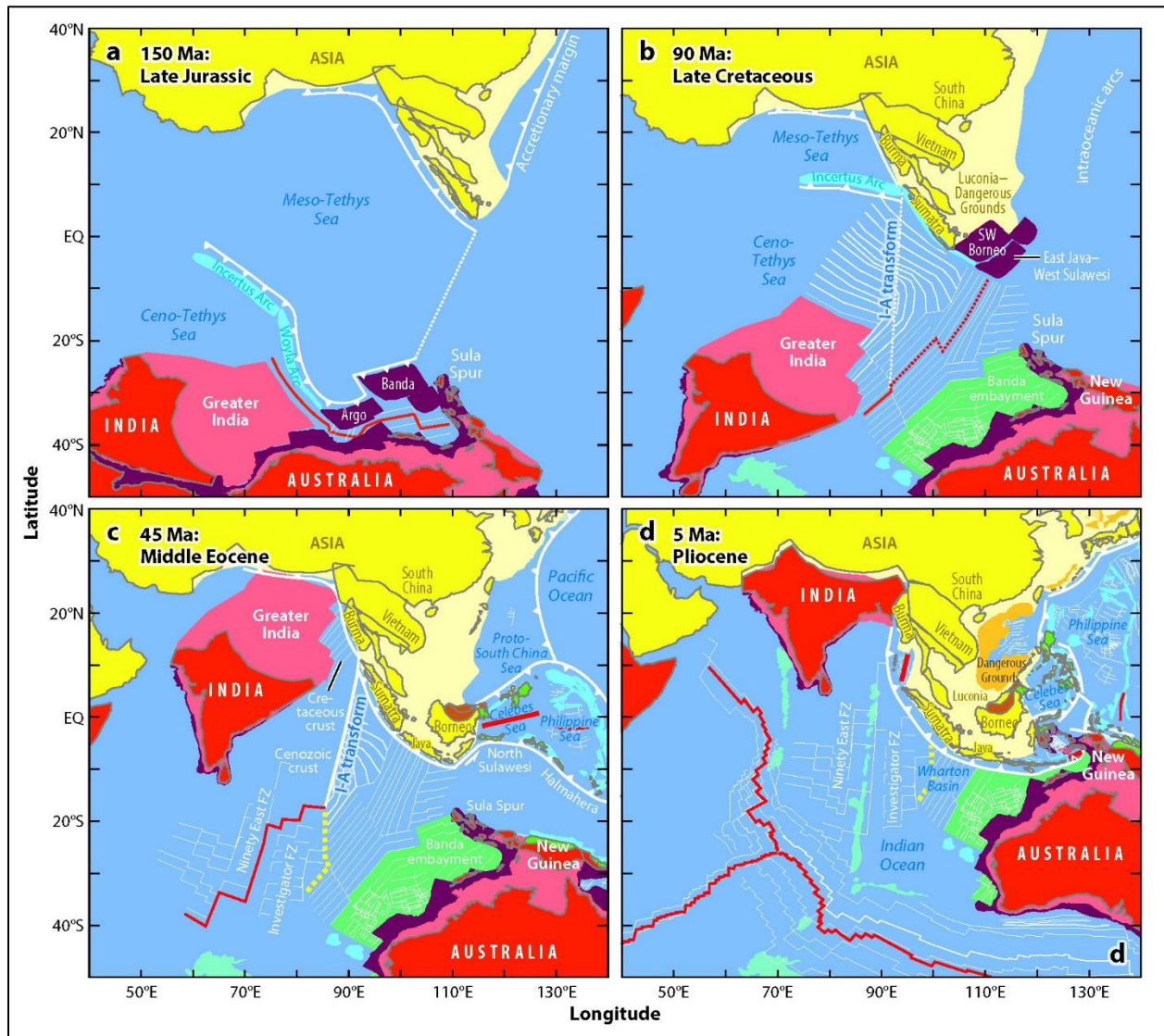


Figure 2. Reconstructions of Southeast Asia at (a) 150 Ma, (b) 90 Ma, (c) 45 Ma, and (d) 5 Ma. Modified from Hall (2012).

Uplift of the Himalayas, the Tibetan Plateau, and formation of SE Asia has profoundly affected global climate up to the present day. The 2400 km long arcuate Himalaya Mountain range bordering the Tibetan Plateau contains 18 peaks with altitudes >8000 m above sea level. The vast amount of snow and ice at relatively low latitudes (26-30° north) is due to the extreme elevation

of the Tibetan and Himalaya regions – the largest area of the cryosphere outside the Polar regions (Pant et al, 2021). According to Scotese, by 35 Ma, the Himalaya and Tibetan Plateau had achieved almost 90% of their modern height. Recent ice core records from the Tibetan Plateau also record that growth and decay of large ice fields at lower latitudes are often **asynchronous** with high-latitude polar glaciation and deglaciation that occur on Milankovitch time scales. Due to the lack of well-preserved glacial moraines, however, the history of late Quaternary glaciation in the monsoon-dominated Indian Himalayas remains poorly understood (Pant et al, 2021).

Nevertheless, according to Irving and Hebda (1993), an extremely heterogeneous landscape evolved in the southeastern Himalayas and the Malay Archipelago with a wide variety of diverse habitats - ideal for isolating populations of *Rhododendron* and increasing potential for allopatric speciation (Shrestha et al, 2018). As mountain glaciers grew or receded, ‘populations would have expanded or contracted in response, becoming isolated in warmer valleys or glacial refugia to the south and, as such, genetic differences would have accumulated over time’, Juliana says.

Genus *Rhododendron* – a model system to understand plant acclimation and adaption to climate.

Many organisms with unique genetic adaptations have managed to survive and evolve despite, or because of stressful environmental conditions such as the Pleistocene ice ages...with the caveat, Juliana says...’in a warmer world, ice age adaptations could be detrimental for both plants and animals. The effect of climate change on plant performance and survival is an important part of Juliana’s research. Juliana suggests that given favorable space and time, plants can track suitable habitat by moving either up or down the mountain, like *Rhododendron*, for example. But change may be happening at a significantly faster pace than plants can move ...and in the absence of suitable habitat, populations may go extinct; whereas some plants may be able to evolve climate tolerance over time, or even change climate tolerance in some cases, Juliana says.

Geology, paleoecology, and a strong montane association provide insight into the role of climate in the evolution of *Rhododendron* diversity and past and present distribution patterns – despite limited evidence of *Rhododendron* fossils in the geological record. Pollen of the *Ericaceae* family of flowering plants which includes *Rhododendron*, first appeared in the late Cretaceous about 68 Ma - before extinction of the dinosaurs. How quickly terrestrial ecosystems recovered after the Chicxulub asteroid impact 66 Ma, however, remains uncertain. The Cretaceous–Paleogene Extinction event, or KT Boundary, marks the Earth’s most recent mass extinction - 75% of species were wiped out, including the dinosaurs, and 50% of plant species. But as Juliana says, ‘extinction can be a beginning.’ Similar to the Permian-Triassic Extinction (252-250 Ma), the KT Boundary was followed by a burst of evolution of modern clades, including placental mammals, small reptiles, birds, and flowering plants or angiosperms, including *Ericaceae* (Lyson et al, 2019).

The earliest genus *Rhododendron* fossils identified have been seeds of *R. newburyanum* in England, dated to the late Paleocene, ~54.5 Ma, followed by leaf imprints in early Tertiary rocks about 50 million years old from Alaska, *R. crissum*, and other later fossils from Tertiary and Pleistocene deposits in North America. This establishes that genus *Rhododendron* has been in existence for at least 55 million years, and that the genus did not originate in the Himalayas, or in

the Malay Archipelago where *Vireya Rhododendron* is most abundant and diverse now – because these regions did not exist 55 Ma (Irving & Hebda, 1993).

Irving and Hebda also observed that *Rhododendron* today grows mainly in moist temperate montane regions. They are not common at low latitudes in hot equatorial forests, whereas they are abundant in the subtropical, glaciated mountains of the southeastern Himalayas and in the equatorial mountains of the Malay Archipelago. Absent in deserts and grasslands, they are usually rare, if sometimes abundant in boreal forests and Arctic tundra, albeit with a limited species, such as *R. lapponicum* or *R. groenlandicum*. Where favorable upland forests occurred in the past is a useful indicator of where *Rhododendron* may have thrived in the past 55 million years. Irving and Hebda suggested that scattered species of *Rhododendron* around the Northern Hemisphere were once part of much larger populations in North America and Europe that became isolated and fragmented over time due to climate change and loss of suitable habitats.

According to Shrestha et al, 2018, however, *Rhododendron* likely originated in the high northern latitudes of NE Asia in the early Paleocene (65 Ma). Reconstructed ancestral mean annual and winter temperatures suggest it evolved in a cool climate, which corresponds to present day temperate broad-leaved forests in NE Asia. Paleontological evidence suggests temperate, broad-leaved forests occurred at much higher latitudes throughout the northern polar regions where *Rhododendron* may have originated. This is consistent with the age pattern of *Rhododendron* with fewer old species in SE Asia, and the ability of older species (subsection Ponticum) to tolerate extreme coldness. The fossil record also suggests that in its early history, *Rhododendron* was more or less continuously distributed across Eurasia and North America. After originating in NE Asia, *Rhododendron* likely dispersed on several occasions to other regions from the late Eocene through to the early Miocene. According to Shrestha, *Rhododendron* species colonized the subtropical and tropical mountains of the southeastern Himalayas and SE Asia relatively late in their history ~30-25 Ma, well after their origination. Recent studies found that the SE Asian clades, especially subgenus *Hymenanthus* have diversified more recently and are much younger than those occurring at higher latitudes...average age of species in the tropics and subtropics appear to be < 7 million years. *Rhododendron*, therefore exhibits a rare ‘into the tropics’ pattern of dispersal. Although genus *Rhododendron* may have originated in NE Asia, today the southeastern Himalayas and Malay Archipelago have the highest rates of diversification and species diversity with more than 80% of the known 900 extant *Rhododendron* species.

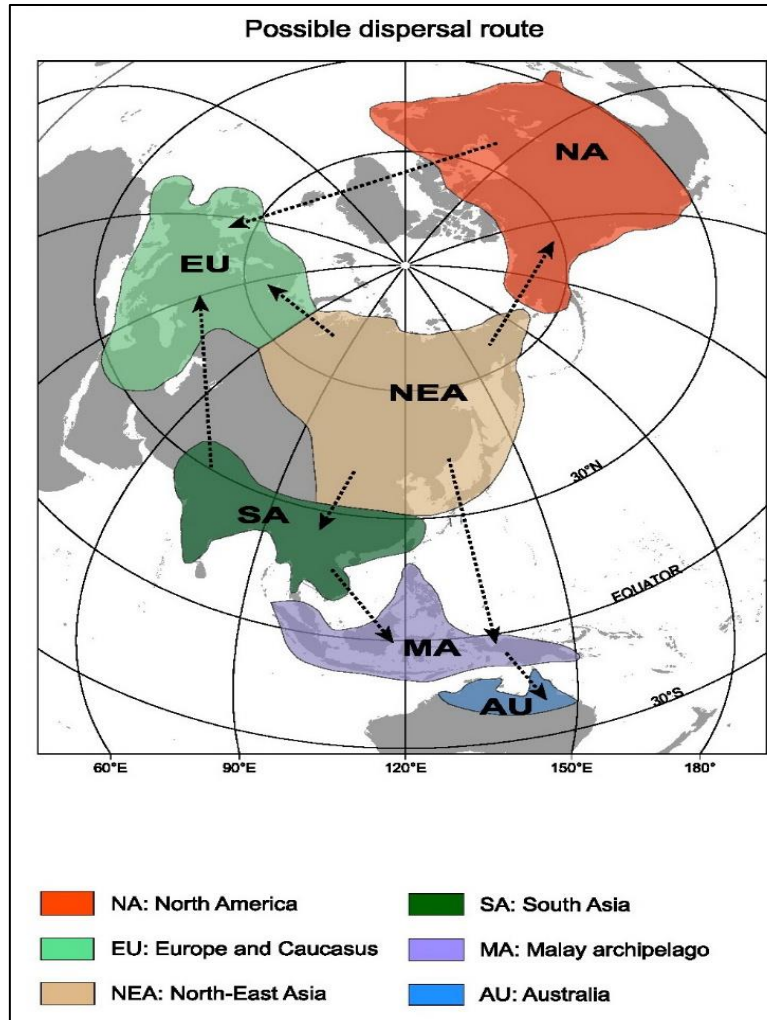


Figure 3. Possible dispersal routes of *Rhododendron*. (after Shrestha et al, 2018).

Why are diversification rates higher in the tropics?

Besides lower extinction rates in the tropics, recent studies suggest that of all the environmental variables, habitat heterogeneity may be the strongest predictor of *Rhododendron* diversity. In the southeastern Himalayas and SE Asia, for example, the development of complex topography due to ongoing uplift and accelerated weathering and erosion, could have led to a high rate of *Rhododendron* diversification through allopatric speciation and adaption to diverse environmental conditions (Shrestha et al, 2018; Ding et al, 2020).

Studies of the cold tolerance of *Rhododendron* suggest that most extant *Rhododendron* species grow well in cool climates and exhibit winter hardiness of -20 to -30°C . *Rhododendron* species likely acquired this cold adaption from their ancestors that originated in mid to high latitude montane regions. Overall, these results support a recent and rapid ‘into the tropics’ adaptive radiation of *Rhododendron*, and also highlights that tropical and subtropical mountains can be not only biodiversity hotspots, but also cradles for the diversification of *Rhododendron* and other alpine flora (Shrestha et al, 2018).

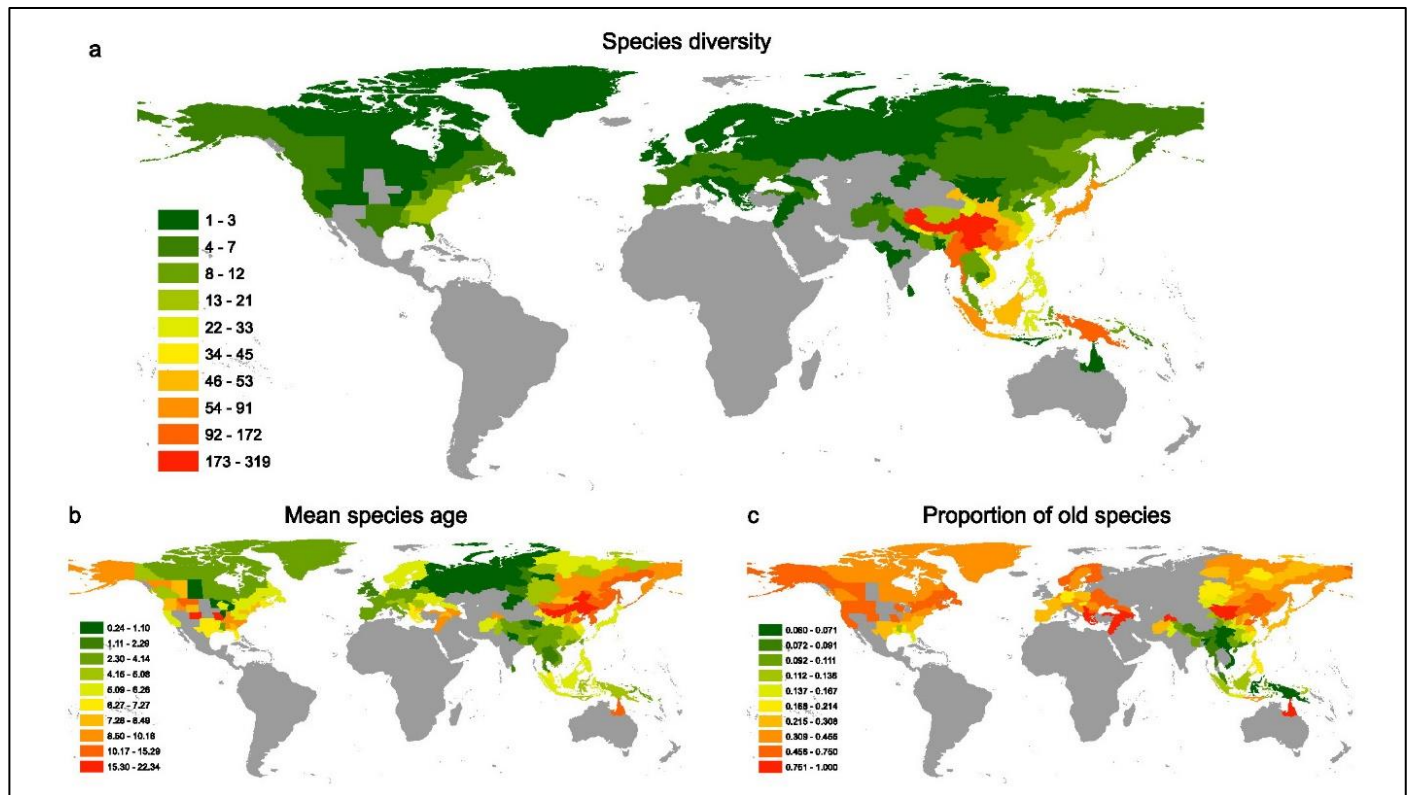


Figure 4. Spatial patterns of *Rhododendron* species diversity (a), mean species age (b), and the proportions of the species from the oldest quartile in the total species diversity (c) (after Shrestha et al, 2018).

Where are *Rhododendrons* located today?

Consensus is that the modern distribution of *Rhododendron* has been shaped by evolution in cold to temperate montane regions in the Northern Hemisphere. Juliana examines the distribution of five *Rhododendron* clades, namely: Lepidotes - generally found in tundra and sunny montane slopes in Alaska and northern Canada, northwestern Europe, and in the central and southeastern Himalayas; deciduous azaleas - sunnier slopes in coastal southwest and southeast of North America and in Japan; evergreen azaleas - sun-drenched volcanic slopes in Japan; Elepidotes - temperate montane forests in coastal southwest and southeast North America, south central Europe and in the southern Himalayas; and Vireyas - tropical epiphytic habitats mainly in the volcanic islands of the Malay Archipelago.

Ancient climate adaptations could affect response to future climate change.

When it comes to *Rhododendron* and their early evolution in cold, frost-prone montane regions in NE Asia, North America and Eurasia, ancestral adaptations to frost would have been an important adaptation. Plant vascular systems in the form of xylem vessels transport water to leaves, and xylem are vulnerable to air bubbles or embolisms caused by frost. Small xylem vessels, however, are less prone to frost damage, and apparently all *Rhododendron* xylem vessels are tiny, suggesting that survival in the ancestral habitat depended on frost resistance. However, small xylem vessels can be a liability under warmer conditions, in contrast to larger xylem vessels which are able to

transport more water, stomata can stay open longer, more photosynthesis takes place, and larger vessels provide better evaporative cooling when it's hot - therefore larger vessels are better competitors in the absence of frost. Juliana examines whether the exceptional leaf diversity observed between *Rhododendron* species, i.e., size, shape, abundance, evergreen or deciduous, leaf hairs or other epidermal traits could have evolved to compensate for the problem of water per unit leaf area under stressful environmental conditions, including warmer climates? In her research paper, *Medeiros et al, 2020, International Journal of Plant Sciences*, Juliana compares leaf and xylem traits for three clades: Pentanthera, Tsutsusi, and Ponticum with different leaf types at two gardens, namely the Rhododendron Species Foundation with a coastal oceanic climate in Washington State, and the Holden Arboretum in Ohio with a more extreme continental climate.

Juliana discovered that Pentanthera (deciduous azaleas) have smaller 'branch leaf area', or fewer leaves per branch, and therefore higher water supply to each stem. Fewer leaves and larger xylem vessels provide higher stem transport which enables Pentanthera to grow fast, and escape seasonal or environmental stress by dropping leaves. In contrast, Ponticum (evergreen Elepidotes) leaf canopy is undersupplied with water because of low stem transport capacity due to large leaf area, leaky leaves (through the stomata), and notably, much smaller xylem vessels. As such, Ponticum sun and shade leaves end up competing for water, and unless in the shade, the sun leaves win. 'Sun leaves are essential for photosynthesis', Juliana says, 'but need more water due to higher evaporation'. ...'and as humidity drops...the water demand of sun leaves may exceed water supply'...'ultimately Ponticum grows a bit faster in the shade'. Tsutsusi (evergreen azaleas) leaves, however, are over-supplied with water due to small leaf area, water-tight leaves, and xylem vessels that are intermediate between Pentanthera and Ponticum, which equals high stem transport capacity, and fast growth under good conditions. 'Tsutsusi are unique for always being prepared', Juliana says...'they acclimate by changing leaf properties and leaf area'.

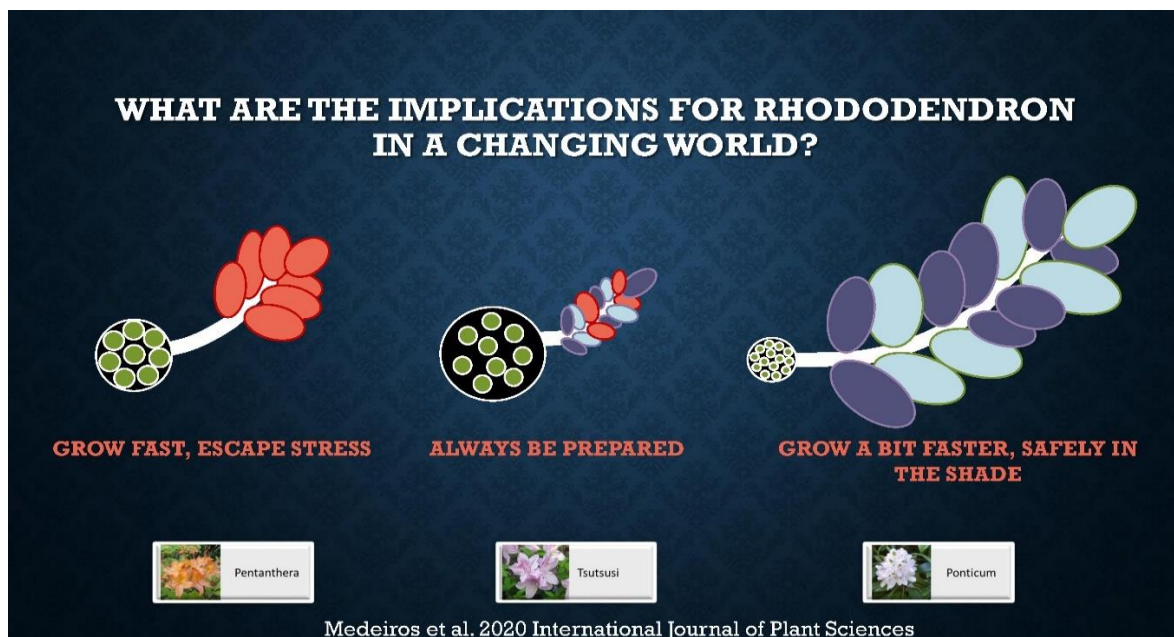


Figure 5. What are the implications for *Rhododendron* in a changing world? Medeiros et al, 2020. "Looking back to the past to secure the future of *Rhododendron* in a changing world".

Implications for *Rhododendron* in a changing world.

Global warming and altered precipitation patterns are likely to increase atmospheric and soil drought which are predicted to have an adverse affect on *Rhododendrons* and the habitats they are adapted to. In *Pentanthera*, leaves may die of dehydration, but leaf loss protects the plant; in *Tsutsusi* leaf area and type vary to match supply and demand for water; but in *Ponticum* sun-lit leaves are more prone to over-spend water supply. Providing extra water in times of drought will definitely help deciduous *Pentanthera* azaleas and evergreen *Tsutsusi* azaleas survive...but as Juliana says, ‘*Ponticum* is water-limited and remains vulnerable to low humidity - extra watering may be insufficient.’

Acclimation and frost tolerance in *R. minus*.

Are *Rhododendron* species from different locations adapted to current climate, and can they acclimate to a change in climate? In two unpublished papers: *Medeiros, Hewins, Arora and Krebs*, manuscript in preparation; and *Medeiros, Hewins, Krebs and Wei*, in progress, the researchers compare and contrast frost tolerance and acclimation of *R. minus* populations from five different locations in the southeastern U.S from North Carolina down to Alabama. Seeds of *R. minus* were collected from these locations by Steve Krebs, and then grown at Holden Arboretum in Ohio over fall and winter. The results indicated that *R. minus* populations from warmer climates in Alabama and Georgia have a faster growth rate, show reduced leaf curling and drooping, don’t have photoprotective leaf pigments like northern *R. minus* which change color in fall, waited until a light frost to acclimate (whereas northern populations acclimate to shorter days), and southern populations of *R. minus* could continue growing on warm fall or spring days. Notably all populations survived a day of minus 24°C, colder than any native habitats in the southeastern U.S - confirming the legacy of frost tolerance. The other implication is that *R. minus* populations in Alabama and Georgia have acclimated to a warmer climate, and in the process may have separated into a North and South species. To confirm this, *Medeiros et al* are looking for the genetic changes that account for these physiological differences.

The tropics puzzle can be solved!

Most spectacularly, *Vireya Rhododendrons* made it to the tropics by the late Cenozoic and adopted a primarily epiphytic or semi-terrestrial lifestyle, possibly as a low competition niche, according to Juliana. Now there are over 300 *Vireya* species within *Rhododendron* sect. *Schistanthe*, a taxon with four major clades: *Euvireya*, *Malayovireya*, *Pseudovireya* and *Discovireya* - unique for distinctive leaf scales, winged seeds, and tropical island habitat in SE Asia. *Vireya Rhododendrons* experienced rapid speciation and diversification when populating the islands of the Malay Archipelago, occurring mainly on the Malay Peninsula, New Guinea and the islands between – in many unique ecological niches from sea level to 4000 m elevation. Phylogenetic studies support a stepwise progression of *Schistanthe* beginning in South Asia, proceeding eastward and reaching New Guinea within the last 15 Ma, when movement of the Australian tectonic plate brought New Guinea into the Malesian domain (Goetsch et al, 2011). Seed dispersal by wind is apparently common in *Rhododendron*, and given that seeds of *Vireya* are winged and tiny, wind dispersal could have contributed to their wide geographic range. Another contributing factor to their success

in the tropics would have been the proliferation of leaf idioblasts, or giant water storage cells - an important innovation for diversification into tropical epiphytic habitats characterized by frequent mild droughts. According to Tulyananda & Nilsen (2017), ‘all *Vireya* possess idioblasts, but idioblasts have not been found in other subgenera of *Rhododendron*.’

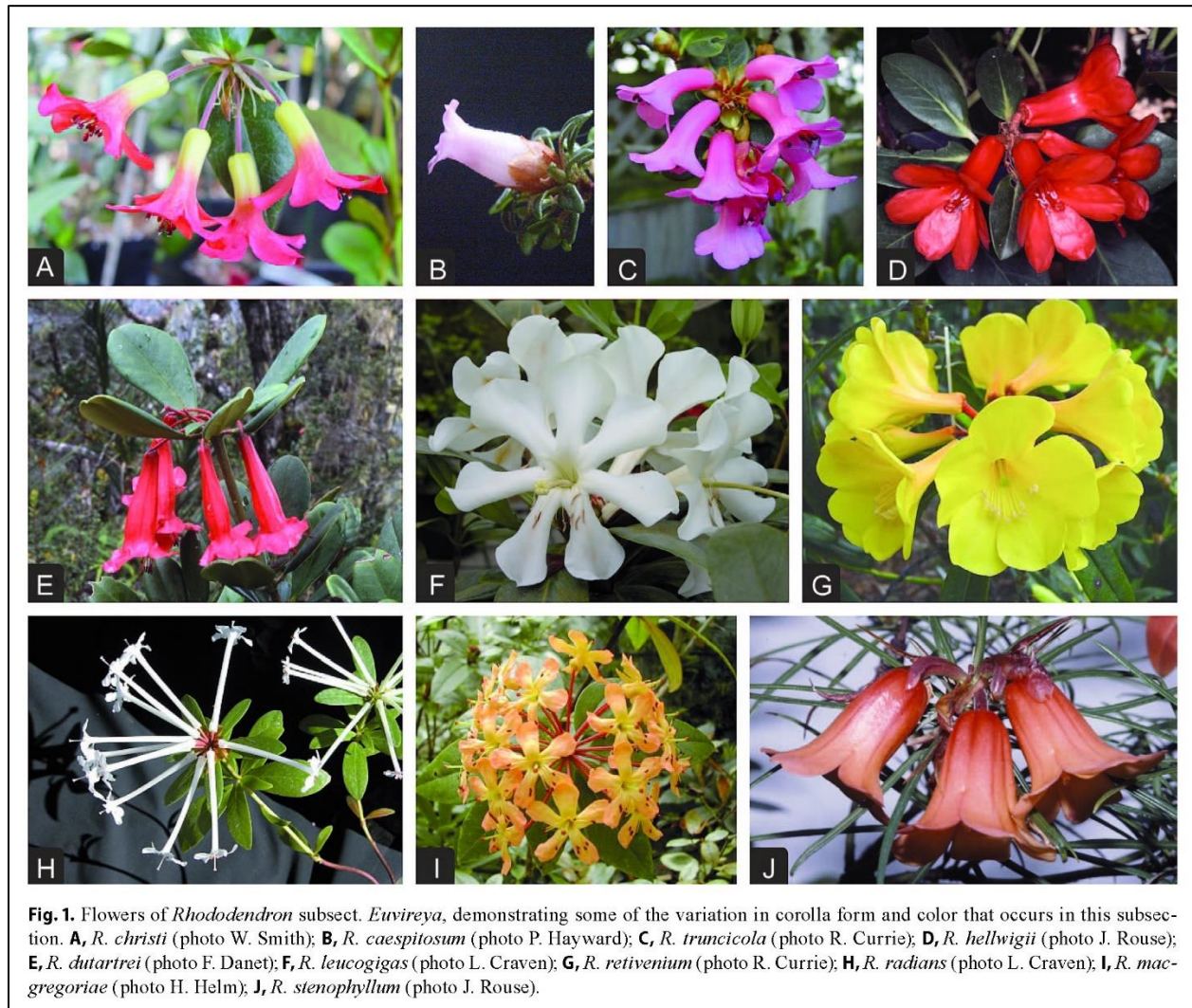


Figure 6. The variety of *Euvireya* flower morphology in New Guinea, from Goetsch et al, 2011.

According to Goetsch, ‘the many distinctive flower types found only in *Euvireya* species endemic to New Guinea, are possibly adaptations to specific pollinators, e.g., birds, ants, nocturnal moths, diurnal butterflies, bees, etc.’ As mentioned, the remarkable radiation and diversification of *Vireya* *Rhododendron* in the eastern Malay Archipelago, is attributed to the relatively recent juxtaposition of New Guinea with SE Asia, following collision of the Australian plate with the Pacific plate in the early Miocene. Subsequently many new diverse habitats were formed by the accretion of multiple volcanic terrains and mountain building that continues today. Phylogenetic analyses indicate that all *Euvireya* species native to New Guinea, Australia and the Solomon Islands share a common ancestor (Goetsch et al, 2011).

What can the past tell us about the future of *Rhododendron* in a changing world?

Paleoclimate perspective and experimental data show that *Rhododendron* can adapt to climate change...and evolution is happening now in natural populations, Juliana says, as she concludes her ‘boots on the ground tour’. She reminds us, ‘So much remains unknown, and uncertainty dictates caution...let’s learn how to sail our ship;’ adding, ‘habitat conservation is one of the best things we can do ... plants need space and time to respond and adapt to stressful environmental conditions. Ex-situ conservation also provides a lifeline...and ultimately your garden can be a climate change refugia!’

References

- Ding, W-N. et al, 2020. Ancient orogenic and monsoon-driven assembly of the world’s richest temperate alpine flora. *Science* 369 578-581.
- Earle, S., 2019. *Physical Geology* - 2nd Edition. BCcampus OpenEd.
- Goetsch, L.A. et al 2011. Major speciation accompanied the dispersal of *Vireya* *Rhododendrons* through the Malay Archipelago: evidence from nuclear gene sequences. *Taxon* v. 60, no. 4, pp. 1015-1028.
- Hall, R., 2017. Southeast Asia: New Views of the Geology of the Malay Archipelago. *Annu. Rev. Earth Planet. Sci.* 45:331-358.
- Hamon, N. et al, 2013. The role of eastern Tethys seaway closure in the Middle Miocene Climatic Transition (ca 14 Ma.). *Clim. Past*, 9, 2687-2702.
- Irving, E, and Hebda, R., 1993. Concerning the Origin and Distribution of *Rhododendrons*. *JARS* v47n3.
- Lyson, T.R, et al, 2019. Exceptional continental record of biotic recovery after the Cretaceous-Paleogene mass extinction. *Science* 366, 977-983.
- Pant, N.C., et al, 2021. The Himalayan cryosphere: past and present variability of the ‘third pole’. *Geol. Soc. London Spec. Pubs.* 462.
- Scotese, C.R., et al, 2021. Phanerozoic paleotemperatures: The earth’s changing climate during the last 540 million years. *Earth-Science Reviews*.
- Shrestha, N. et al, 2018. Global Patterns of *Rhododendron* diversity: The role of evolutionary time and diversification rates. *Global Ecol. Biogeog.* 2018 27 913-924.
- Tierney, J.E., et al, 2020. Past climates inform our future. *Science* 370.
- Tulyananda, T. and Nilsen, E.T., 2017. The role of idioblasts in leaf water relations of tropical *Rhododendrons*. *American Journal of Botany* 104(6) 1-12.
- Tyrell, T., 2020. Chance played a role in determining whether Earth stayed habitable. *Commun. Earth Environ.* 1, 61.