

## **Alpine insects – young mountains with old life**

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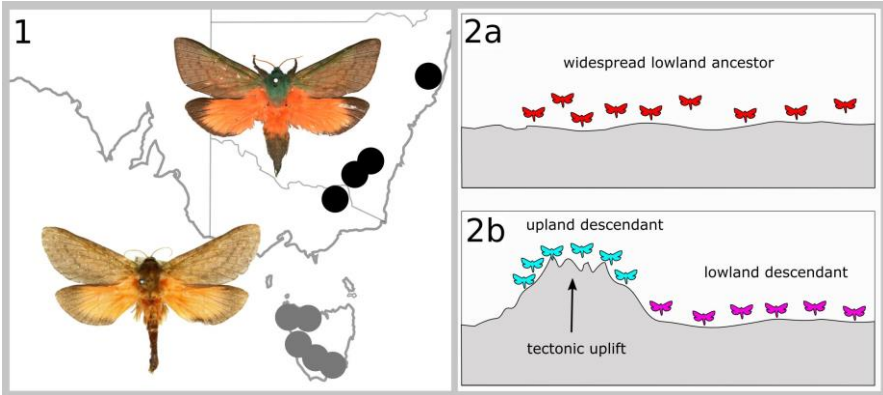
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New Zealand's alpine zone includes many animal and plant species absent from lower elevations. The evolutionary origins of such a distinct biota have long fascinated ecologists and biogeographers. How did these animals and plants establish and even flourish in what would seem to be a relatively recent and inhospitable environment? Biologists have long observed that endemic alpine taxa have lowland relatives. This has led to the conclusion that alpine endemics are descendants of species that have colonized the higher elevations when mountain building created new vacant habitats. But modern analogues of these 'vacant' mountain habitats, whether in New Zealand or in the world at large, do not exist. The only vacant environments are those at every high elevations, beyond the level inhabitable by plants and animals.

The idea of taxa colonizing empty, new environments is inherently tricky as it does not explain why the environments were empty to start with. An alternative possibility, investigated in New Zealand now for over three decades, is passive tectonic uplift (Heads 2019). In this model, the ancestors of alpine taxa were simply lifted up, in situ, with geological uplift. Whenever landscapes are geologically uplifted, which occurs at a rate of a few centimeters a year, so too are the animal and plant inhabitants that occupied the previous, lower-altitude habitats.

One example of this process is the common occurrence of seabird species nesting on upraised coastal benches. Their nests were originally at the water's edge, but as the nesting areas were lifted up, the birds (with natal philopatry) kept coming back to the same site which was rising imperceptibly. Ultimately, the nesting areas might become sub-alpine or

even alpine, while the sea birds continue to forage in coastal or marine environments (Heads 2019). A local example is Hutton's shearwater which breeds only at two subalpine and alpine sites (1200–1800 m) in the Kaikoura ranges of South Island (Heads 2017).



Figs. 1-2. Illustration of passive tectonic uplift. (1) for the sister species *Aenetus montanus* (black circles, upper elevation) and *A. ombraloma* (grey circles, lower elevation); (2) passive uplift model with distribution of lowland ancestor (2a), subsequently disrupted by uplift resulting in geographic and biological isolation and divergence (2b). From Grehan & Mielke (2018b).

Tectonic uplift has more than ecological impacts. It can promote differentiation and divergence of taxa. Uplifted populations may become increasingly isolated from other populations remaining at lower elevations. And if populations survive the uplift, they may become genetically as well as spatially isolated, and diverge. With enough time, this divergence can result in new species or higher taxa. An illustrative example is the allopatric and disjunct distribution of the Australian ghost moth species *Aenetus montanus* Tindale, 1953 at about 1500 m in eastern Australia, and its sister species *A. ombraloma* (Lower, 1902) at 300-1000 m in Tasmania (Fig. 1). This distribution can be derived simply from a widespread ancestral range across what is now Tasmania and southeastern Australia

followed by uplift and differentiation of northern populations during the Blue Mountains orogeny beginning ~ 90 million years ago (Fig. 2; Grehan & Mielke 2018a,b).

To summarise, there are two alternative evolutionary models for the origin of New Zealand alpine taxa – dispersal into empty habitat, and passive uplift. Debate about the models has significant implications for evolutionary studies in New Zealand, and if one or the other model is excluded from consideration, the resulting analysis becomes a distorted representation of the state of science. Unfortunately, this approach is seen in a recent paper by Buckley et al. (2022) that examines the evolution and biogeography of the alpine insect fauna. In this overview, only one evolutionary model is recognized – that of alpine colonisation in response to the opening of new habitats since Late Miocene time. One example of recent colonization cited by Buckley et al. (2022) is the alpine cicada *Maoricicada campbelli* (Fig. 3), in which evolution was attributed to a single colonization event about 2.3 million years ago. This age and origin were justified with reference to late Pliocene temperature fluctuations, accelerated uplift of the Southern Alps beginning about 5 Ma, and early glacial activity beginning 2.6–2.4 million years ago.



Fig. 3. *Maoricicada campbelli*. Photo by William Harland (with permission) <https://www.inaturalist.org/observations/115485091>

Attributing the origin of alpine *Maoricicada campbelli* to colonization is not based on analytical evidence, but on the assumption that the species cannot be older than the current alpine environment. One problem with this view is that the 'alpine' cicada is not entirely alpine, but has an elevation range of 300-1580 m. Most of the other 'alpine' *Maoricicada* species are also known from some localities below the alpine zone. The lower elevation records show that at least some of the habitat diversity of *Maoricicada* species could have existed before the present alpine environment (Heads 2017). This pre-alpine existence is supported by Buckley and Simon (2007) who calculated a mid-Miocene age for *Maoricicada* which predates the Alpine uplift. But even this timeline may underestimate the divergence age of *Maoricicada*. This is because Buckley and Simon (2007) calibrated their divergence estimates using the age the modern Norfolk and Kermadec islands to date endemic cicadas there. This overlooks the possibility that these species may be older than the current islands if they are derived from ancestors inhabiting former islands in the region (Heads 2017).

The biogeographic-tectonic correlation approach that is missing from Buckley et al. (2022) provides an alternative method for evaluating the origin of *Maoricicada campbelli* and its presence in the alpine zone. Biogeographic-tectonic correlation closely examines the spatial relationships between biological distributions and tectonic structures (such as faults, suture zones, spreading ridges, metamorphic belts etc.), and the evolutionary significance of these relationships. Distributions matching particular tectonic structures provide a way of estimating the age of taxa, as the age of geological activity on the tectonic structure is often well known (Heads 2017).

The distribution of *Maoricicada campbelli* includes both North and South Islands, with five allopatric clades (Buckley et al. 2001). Allopatry is consistent with an evolutionary model of local differentiation of each clade from a widespread ancestor. In other words, the *M. campbelli* subgroups did not each migrate to their respective locations, but evolved locally as fragments of the ancestral range. In the southern part of the range there is a phylogenetic split separating a "Central Otago clade" from the other four allopatric subgroups. The geographic location of the phylogenetic break separating the Central Otago clade occurs along two break zones, one

corresponding spatially with the Moonlight tectonic zone, the other with the Waihemo fault zone (Fig. 4).

The Moonlight tectonic zone represents a failed geological rift that was active in the Cretaceous. At that time it formed an arm of sea that was part of the 1200 km long Challenger Rift System. This zone was also active in western New Zealand during Eocene and Oligocene time. Similarly, the Waihemo fault zone developed in the Cretaceous about 112–113 Ma, following collision and suturing of the Torlesse and Caples terranes (Heads 2017).

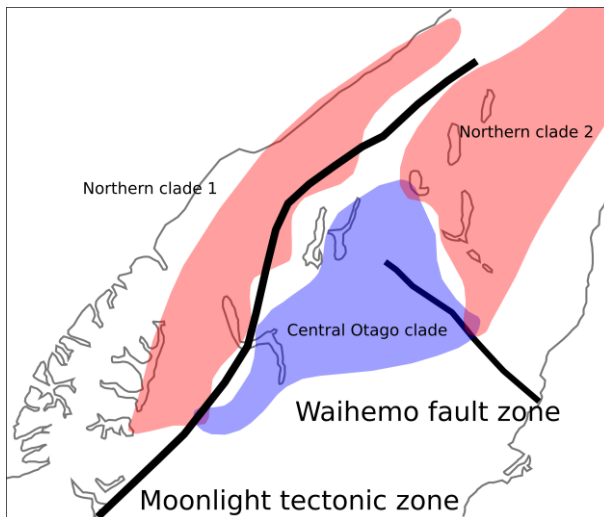


Fig. 4. Distribution of *Maoricicada campbelli* subclades in the southern South Island. Modified from Heads (2017: fig. 7.12).

The example of *Maoricicada campbelli* presents two very different possibilities for the origin of alpine taxa. The ‘colonization’ model for *Maoricicada* relies on an assumption of recent origin, whereas the tectonic correlation provides evidence of evolutionary divergence within *M. campbelli* that long predates the Kaikoura orogeny and the alpine habitats of the present day. This tectonic age is consistent with an “ancient

cladogenetic event” proposed by Buckley et al. (2001) rather than the recent alpine colonization model of Buckley et al. (2022).

Whatever position one may choose to take on such matters, overviews should at least acknowledge the existing alternatives. As illustrated by the case of *Maoricicada campbelli*, the two different explanations for New Zealand's alpine biodiversity imply profoundly different evolutionary origins. Central to this critical question is to recognize that biological distributions are just as much records of life as are morphology or DNA sequences. The next time you see an alpine cicada in the wild, keep in mind that just as its structure is telling you something about its evolutionary past, so too is its location.

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