

# ECOGRAPHY

**Brevia**

## **Insect wing loss is tightly linked to the treeline: evidence from a diverse stonefly assemblage**

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**The secondary loss of flight in previously winged insect lineages has long fascinated biologists. Habitat stability and isolation are thought to play important roles in driving wing reduction (Roff 1990, 1994), with exposure to high winds suggested to accelerate this process (Darwin 1859), although the role exposure plays in insect wing loss has never been empirically demonstrated. Here we assess fine-scale distributional records from a diverse regional stonefly assemblage, to demonstrate a widespread association between wing loss and the treeline in New Zealand. The observed pattern suggests that exposure plays a crucial role driving wing loss in alpine insects.**

The astonishing diversity and evolutionary success of insects is often attributed to the evolution of flight ca 400 Ma (Wagner and Liebherr 1992, Misof et al. 2014). Flight confers insects a number of important advantages, including improved ability to locate resources, avoid predators, and find mates. Despite its clear benefits, this dispersal capacity has been lost repeatedly, across almost all winged orders (Wagner and Liebherr 1992, Roff 1994, Trautwein et al. 2012). Such secondary wing loss is often attributed to the high energetic costs of producing and maintaining wings at the expense of other life-history traits (Roff 1990, Wagner and Liebherr 1992). Additionally, environmental conditions appear to influence the frequency of wing loss, with flightless lineages disproportionately abundant in 1) stable habitats (where insects do not rely on flight for resource location and predator avoidance), and 2) isolated areas (where there is high mortality in dispersing individuals; Roff 1990, 1994).

Insect wing loss is particularly common at high altitudes (Hodkinson 2005), where habitats are typically more stable than in lowland areas, and where small habitat size apparently selects against flighted individuals (Harrison 1980). Darwin (1859) also suggested that exposure to high winds may play an important role in selecting against flighted individuals. Few studies, however, have directly assessed this hypothesis, although Darlington (1943) found no difference between the relative proportion of winged and wingless carabid beetles above and below the treeline. Importantly, the generality of Darlington's findings have yet to be assessed in other insect assemblages.



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Here we examine the relationship between the alpine treeline and wing loss in a species-rich, regional assemblage of stoneflies (New Zealand Plecoptera). Flight loss is widespread in this insect group, with at least 26 of New Zealand's 106 described species exhibiting wing reduction (McLellan 2006, McCulloch et al. 2017). The phylogenetic distribution of winged versus wingless (and wing dimorphic) lineages within the species-rich Gripopterygidae implies numerous independent losses of flight (Supplementary material Appendix 1), particularly associated with high altitude populations (McCulloch and Waters 2018; Fig. 1a). Despite this apparent trend, detailed

biogeographic analyses of these taxa are lacking, and thus the potential drivers of this wing reduction have remained unclear.

Our biogeographic analyses (Supplementary material Appendix 2) demonstrate a clear association between wing phenotype and altitude, tightly demarcated by the alpine treeline, with the 17 wingless gripopterygid species found almost exclusively above the treeline, and the 12 fully-winged species almost solely recorded below the treeline (Fig. 1b, c; Supplementary material Appendix 3). Crucially, this finding remains consistent regardless of the local altitude of the treeline (which ranges from ~200 m in southern Stewart

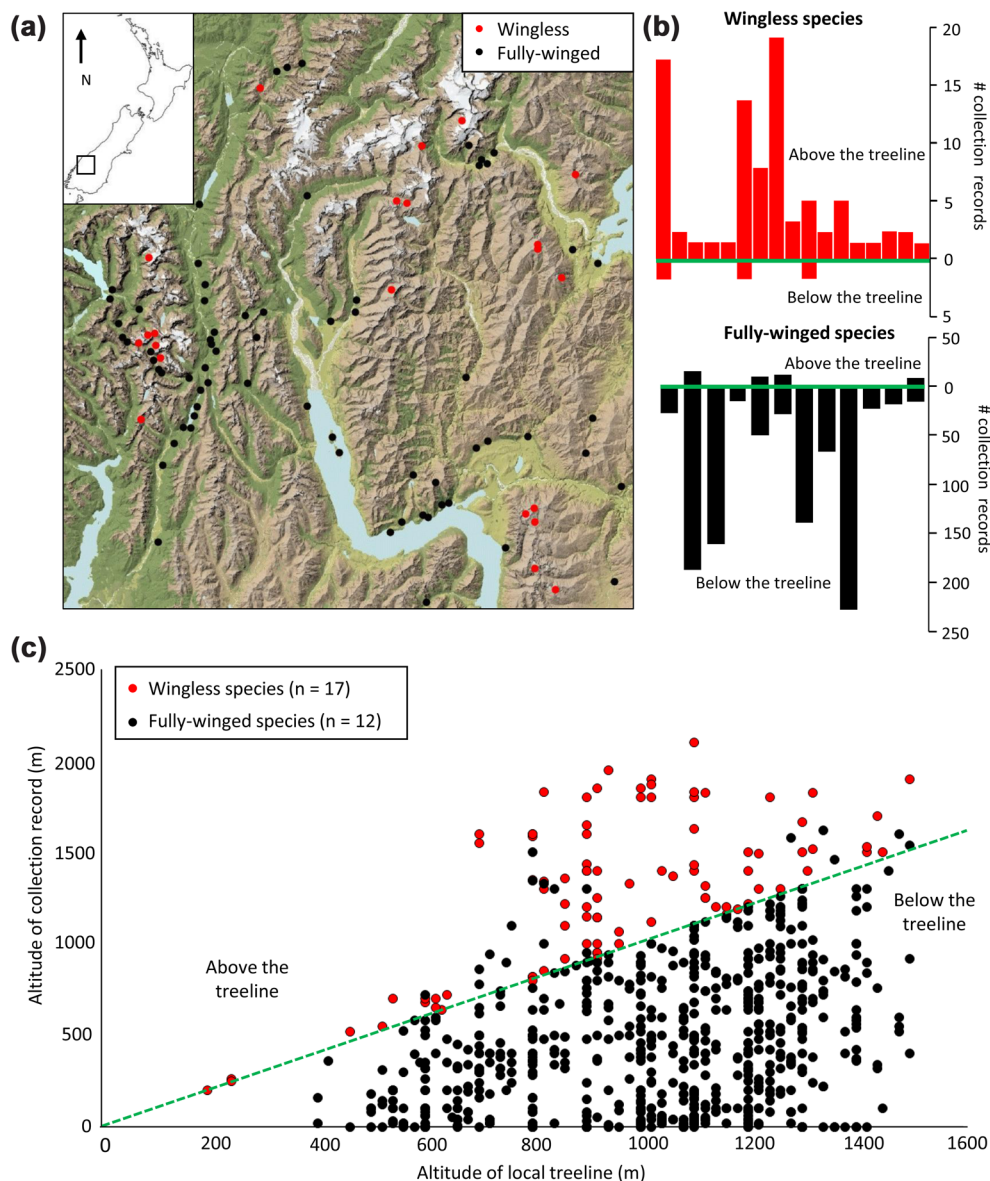


Figure 1. (a) Collection locality data for three wingless (red circles) versus nine fully-winged (black circles) stonefly taxa from southwest New Zealand, indicating representative distributions of fully-winged (forest; green) and wingless taxa (alpine; brown), delineated by the treeline. (b) Number of collection records above or below the treeline for 17 wingless (red bars; top) and 12 fully-winged (black bars; bottom) New Zealand gripopterygid stonefly species. (c) Distributional data showing stonefly collection altitude relative to the altitude of the local treeline, for 17 wingless (red circles) versus 12 fully-winged (black circles) New Zealand gripopterygid stonefly species. The dashed line delineates specimens collected above versus below the local treeline.

Island, to ~1500 m in the North Island; Fig. 1c), suggesting that the observed pattern is driven by exposure associated with the position of the treeline, rather than by altitude per se. We used phylogenetic multiple logistic regression (Ives and Garland 2010, Ho and Ané 2014) to confirm that the wingless phenotype is better-predicted by the proportion of a species' occurrence records above the treeline ( $p=0.016$ ) than by mean altitude ( $p=0.57$ ). The finding that wingless stonefly taxa are seldom found below the treeline, and likewise fully-winged gripterygids scarcely penetrate into alpine habitats (Fig. 1b, c), implies strong selective pressure gradients associated with this environmental variation.

We suggest that exposure (e.g. strong winds) immediately above the alpine treeline presents a strong selective force favouring wingless individuals in these severe conditions. In addition, the increased energetic requirements of flight above the treeline (due to decreased temperatures) may also select against fully-winged individuals. As many stonefly taxa are not strong fliers, even in optimal conditions (McCulloch et al. 2009), these lineages may be particularly prone to the effects of high winds. Conversely, taxa with stronger flight ability may be less impacted by such exposure gradients, which may explain why such patterns apparently vary across taxonomic groups (e.g. carabid beetles; Darlington 1943).

In summary, we present the first quantitative evidence for the role of the treeline, and associated gradients in exposure, in driving the evolution of wing loss in a diverse insect assemblage. These intriguing findings highlight the crucial need for more detailed altitudinal biogeographic analyses of insect assemblages – taxa that are highly diverse yet severely understudied. Future spatial analyses of wing dimorphic taxa should provide additional fine-scale tests for this potentially globally important biogeographic phenomenon.

## Data deposition

Data available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.j64s5rn>> (McCulloch et al. 2018).

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Supplementary material (Appendix ECOG-04140 at <[www.ecography.org/appendix/ecog-04140](http://www.ecography.org/appendix/ecog-04140)>). Appendix 1–3.

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