

Lupinus

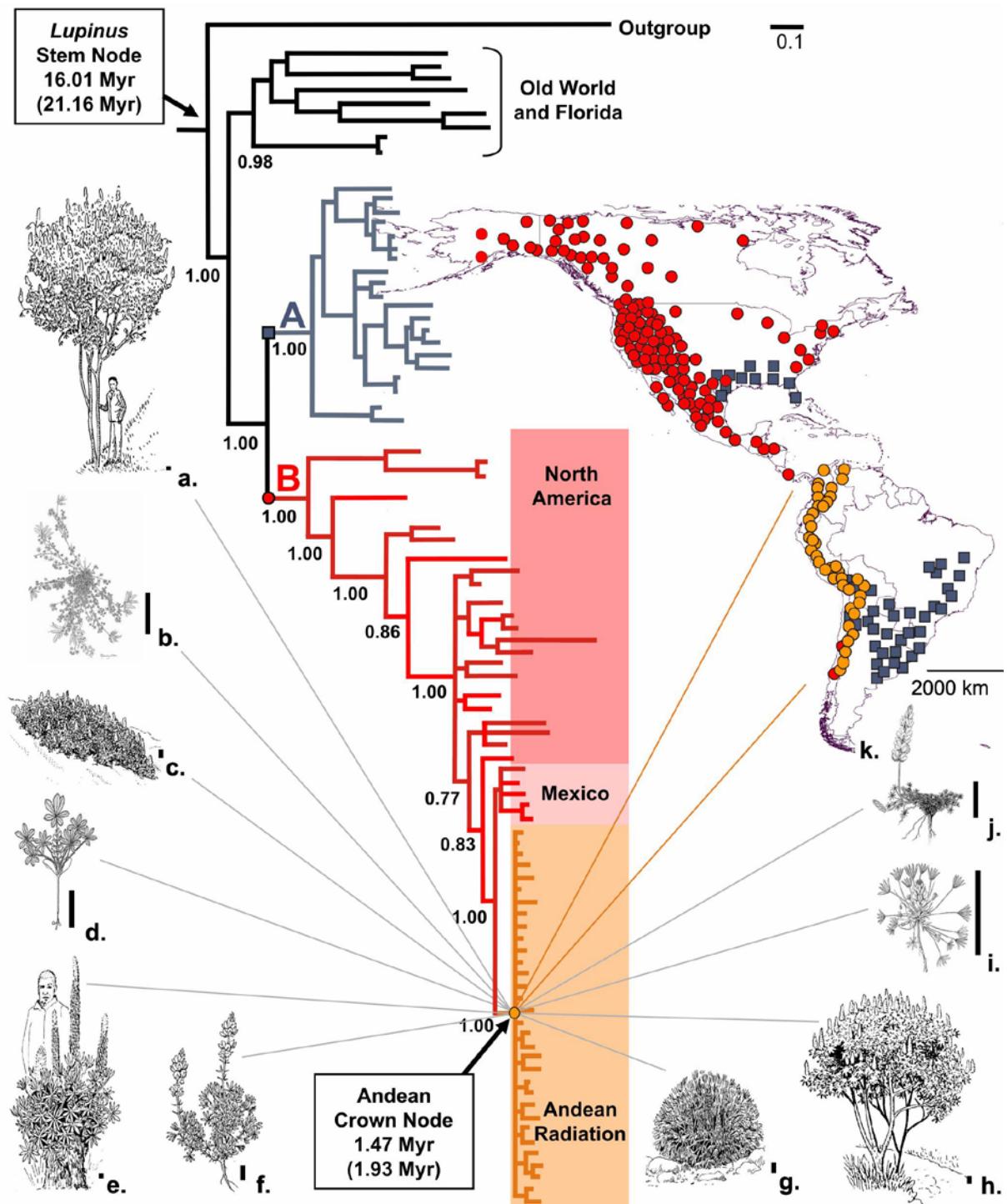
The ubiquitous familiarity of the common garden lupin provides little hint of the great diversity encompassed by the c. 280 of species in *Lupinus* as a whole. There are two main centres of species diversity in western North America and the Andes, as well as secondary clusters of species in eastern South America and around the Mediterranean. The taxonomy of *Lupinus* is notoriously problematic and overburdened by a surfeit of names (c. 1800), and while there are several authoritative regional floristic accounts, the last monographic account was that of Agardh in 1835, which recognised 83 species. The taxonomy of the Andean and Mexican species is particularly chaotic. Work on a new taxonomic account for the Andean species is in progress.



Lupinus species from the Andes

New phylogenies

Insights into the diversity and evolutionary and biogeographical history of lupins have been limited by confusion about species delimitation, conflicting nomenclature, and sparse sampling and lack of resolution in previous phylogenetic studies. Over the last few years we have generated a series of more densely sampled (including c. 40% of species), well-resolved, and robustly supported time-calibrated phylogenies, based on DNA sequences from multiple nuclear and plastid genes (Hughes and Eastwood, 2006; Eastwood et al., 2008). While some uncertainty remains as to the precise sister group relationships of the 13 Old World species, current data suggest that the ancestral range for the genus is in the Old World, with at least two independent dispersal events to the New World within the last 5-10 million years. The New World species (excluding the unifoliolate species from Florida) are placed in two robustly supported clades: (i) an eastern, largely lowland $2n = 36$ clade comprising c. 35 species and (ii) a western, largely montane $2n = 48$ clade comprising c. 225 species. These two clades are distributed largely allopatrically with only limited overlap in Texas and the south-central

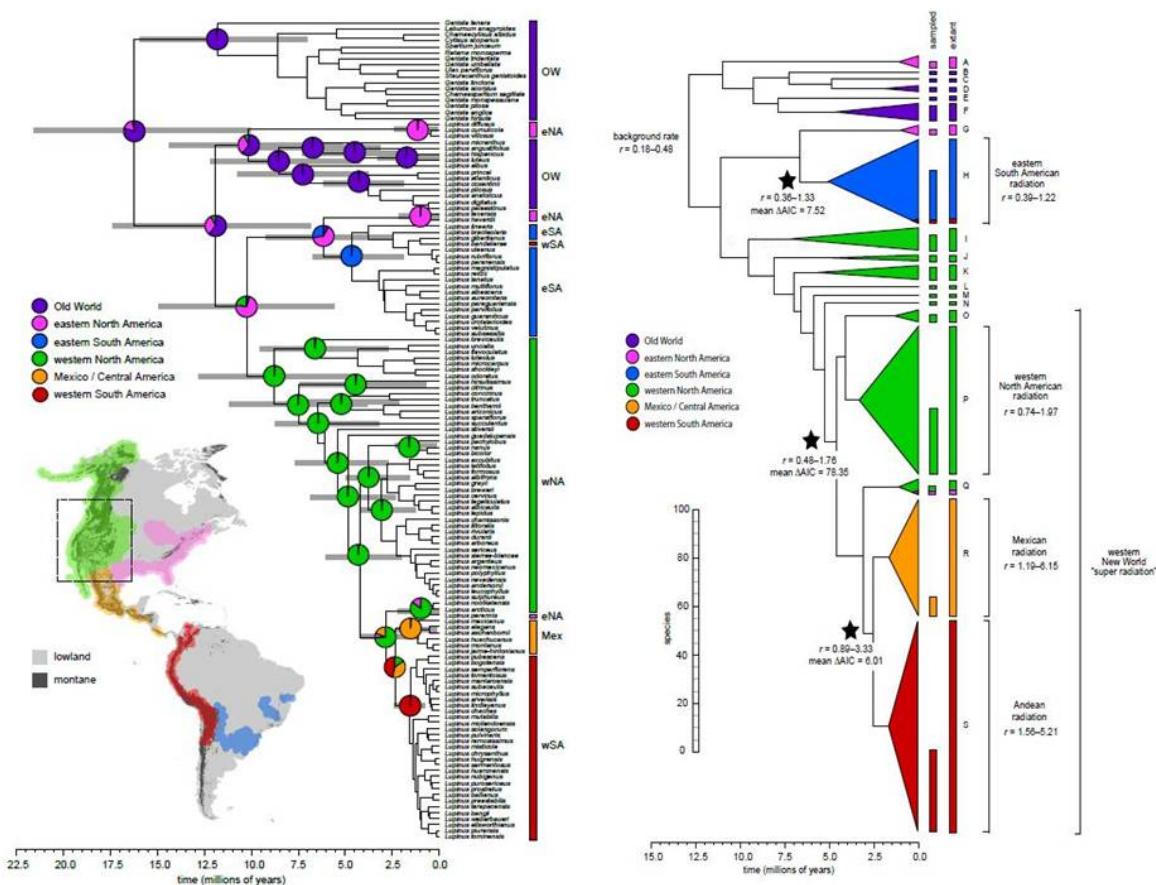


Phylogeny of *Lupinus* showing the distributions of the two major New World clades and the diversity life history characteristics of the Andean species. Reproduced from Hughes & Eastwood (2006).

Andes, but both contain ancestral North American and derived South American elements, suggesting at least two independent dispersal events between North America and South America. These new phylogenies also provide clear evidence for two independent evolutionary origins of unifoliate leaves in Florida and Brazil (congruent with chromosome data), resolving longstanding debate about the relationships of these two groups. Of particular note is the exceptionally high rate of diversification in the western New World $2n = 48$ clade. In this group a rapid rate of speciation coincides with the transition from annual to perennial life history and colonization of montane

habitats, permitting the exploitation of novel ecological opportunities following recent uplift of the northern Andes.

In 2012, we published a new time-calibrated phylogeny for the genus (Drummond et al., 2012) and used this to further investigate the evolutionary dynamics of species diversification in *Lupinus*. In this analysis three species diversification rate shifts were discovered and used as the basis for defining a set of four continental-scale species radiations, three of them nested within a large montane western New World ‘super-radiation’ spanning Alaska to the Andes. The primary diversification rate shift defining this super-radiation is strongly associated with a shift from annual to perennial habit, and a shift from lowland to montane habitats, suggesting that this combination of evolutionary innovation (perennial life history) coincided with ecological opportunities for expansion across upland habitats in western North America, Mexico and the Andes, could account for the accelerated rate of species diversification in this clade, a rate that matches the most rapid plant diversifications documented to date.



Time-calibrated phylogeny of *Lupinus* showing geotemporal patterns of species diversification and the occurrence of three species diversification rate shifts defining a set of multiple parallel and nested species radiations from Drummond et al. (2012).

Origin of domesticated *L. mutabilis*

Lupinus mutabilis Sweet is apparently unknown in the wild but is cultivated as an important food crop throughout the Andes and is also the focus of crop breeding and development elsewhere in Australia and Europe. The species exhibits typical legume domestication syndrome traits including indehiscent pods, large seeds, water permeable seed coats, reduced seed pigmentation, rapid and uniform germination and growth, and a nearly annual life history, but retains higher seed alkaloid levels than other lupin domesticates.



Despite this importance as a crop, the origins of domestication of *L. mutabilis* in terms of where, when, how many times and from what wild progenitors it was domesticated remain unknown. Our phylogenetic studies place *L. mutabilis* in a well-supported Andean clade, ruling out earlier speculations that the crop might have originated from wild North American species (Eastwood and Hughes, 2008). However, within the Andes, research to identify the progenitors of *L. mutabilis* is hampered by chaotic taxonomy, the very low levels of DNA sequence divergence amongst the Andean species, and limited lupin seed remains retrieved from archaeological sites. Despite these challenges, recent field, herbarium and laboratory investigation of *L. mutabilis* provide new evidence from morphology (leaves, indumentum, habit, flower size, flower colour variation, pod and seed size) and DNA sequence data that suggest *L. piurensis* as the most likely wild progenitor of domesticated *L. mutabilis* (Eastwood and Hughes, 2008). This species has not previously been proposed as a putative progenitor of *L. mutabilis* despite its clear morphological similarities and large seeds. *Lupinus piurensis* is restricted to the western slopes of the Andes between 1650 and 3300m altitude in northern Peru and southern Ecuador, suggesting that domestication of *L. mutabilis* may have occurred in that area. A limited number of flower and seed colour variants are documented within *L. mutabilis*, but in many respects the species is rather uniform.

Publications on *Lupinus*

- Drummond, C.S., Eastwood, R.J., Miotto, S.T.S. & **Hughes, C.E.** 2012. Multiple continental radiations and correlates of diversification in *Lupinus* (Leguminosae): testing for key innovations with incomplete taxon sampling. *Systematic Biology*. doi: [10.1093/sysbio/syr126](https://doi.org/10.1093/sysbio/syr126)
- Eastwood, R.J. & **Hughes, C.E.** 2008. Origins of domestication of *Lupinus mutabilis* in the Andes. Pp. 373-379, in: Palta, J.A. & Burger, J.B. (Eds.) Lupins for Health & Wealth, Proceedings 12th

International Lupin Conference, Fremantle, Australia, International Lupin Association, Canterbury, New Zealand.

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Stepkowski, T., **Hughes, C.E.**, Law, I.J., Markiewicz, L., Gurda, D., Chlebicka, A. & Moulin, L. 2007. Diversification of lupin *Bradyrhizobium* strains: evidence from nodulation gene trees. *Applied & Environmental Microbiology* 73: 3254-3264. [doi:10.1128/AEM.02125-06](https://doi.org/10.1128/AEM.02125-06)

Hughes, C.E. & Eastwood, R.J. 2006. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proceedings National Academy of Sciences* 103: 10334-10339. [doi:10.1073/pnas.0601928103](https://doi.org/10.1073/pnas.0601928103)