

SPECIATION

How predictable is genome evolution?

Similar patterns of genomic divergence have been observed in the evolution of plant species separated by oceans.

MATTHEW J COATHUP, OWEN G OSBORNE AND VINCENT SAVOLAINEN

Related research article Dong Y, Chen S, Cheng S, Zhou W, Ma Q, Chen Z, Fu CX, Liu X, Zhao YP, Soltis PS, Wong GKS, Soltis DE, Xiang J. 2019. Natural selection and repeated patterns of molecular evolution following allopatric divergence. *eLife* 8: e45199. DOI: [10.7554/eLife.45199](https://doi.org/10.7554/eLife.45199)

Understanding the formation of new species – a process called speciation – is a central challenge in evolutionary biology and genomics, but many questions remain (*Arnegard et al., 2014; Riesch et al., 2017*). In particular, are there certain patterns of genome evolution that are repeated? And, if there are, can we predict how genomes will change as new species emerge and diverge?

To date, most studies have focused on the genomes of pairs of closely related species living in close proximity (such as two species of whitefish living in the same set of lakes; *Gagnaire et al., 2013*), or on the genomes of different lineages within a single species (such as one species of stick insect living on two different host plants; *Soria-Carrasco et al., 2014*), and have predominantly investigated scenarios where there is some degree of gene flow between the different species or lineages (*Wolf and Ellegren, 2017*). However, it is thought that most new species emerge in geographically isolated populations and in the absence of gene flow. Now, in eLife, a team of

researchers from the United States, China and Canada – including Yibo Dong (North Carolina State University) and Shichao Chen (University of Florida and Tongji University) as joint first authors – report how pairs of closely related flowering plants which live thousands of miles apart genetically diverged during evolution (*Dong et al., 2019*).

Dong et al. systematically collected and sequenced 20 pairs of closely related species, including 16 pairs that diverged between 2 and 10 million years ago as a result of the Eastern Asian–Eastern North American floristic disjunction (*Figure 1*). These pairs of species are the ideal system in which to study allopatric speciation (that is, speciation in geographically isolated populations).

Dong et al. examined divergence in thousands of genes by measuring the rate at which nucleotide substitutions resulted in a change in the amino acid coded for (Ka), and the rate of nucleotide substitutions that did not result in such a change (Ks). The ratio Ka/Ks is a common index for identifying the selective pressure on a gene: values significantly above one indicate positive selection (i.e. an increase in the frequency of beneficial mutations), and values significantly below one indicate purifying selection (i.e. the removal of deleterious mutations). Despite investigating a diverse range of taxa, Dong et al. found that all species pairs experienced similar patterns of genomic divergence and selection, regardless of their ecologies and morphologies.

In fact, most of the genes measured showed little divergence and, intriguingly, the peak

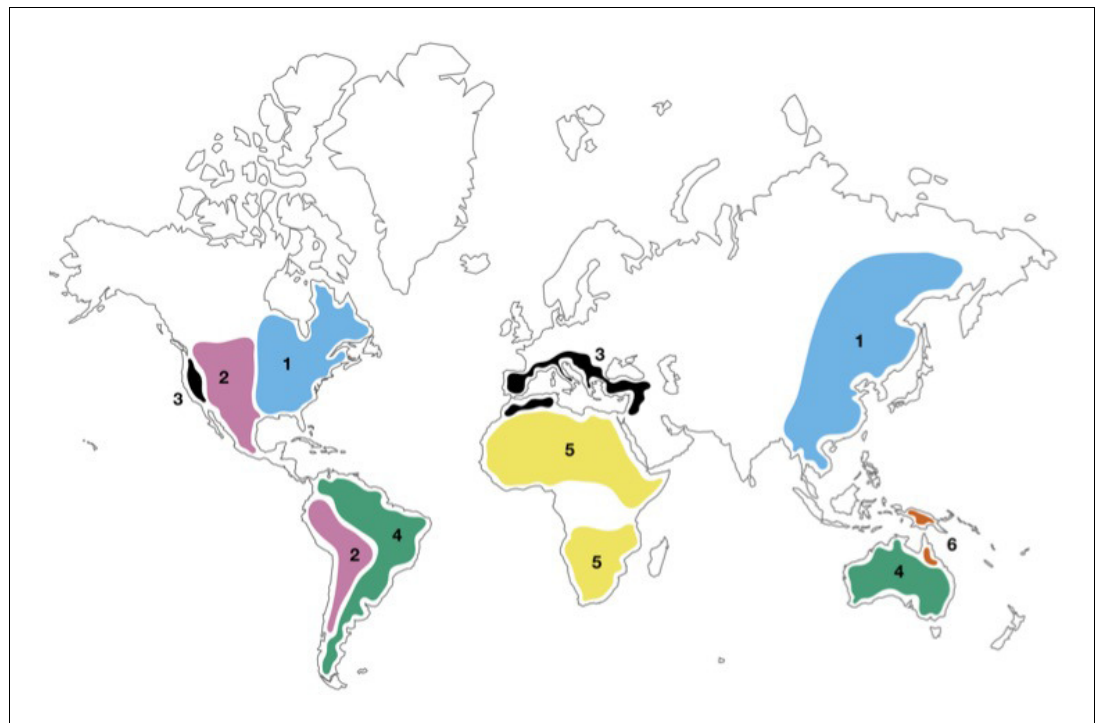


Figure 1. Geographical distribution of closely related plant species. Map showing floristic disjunctions – geographically separated regions that contain closely related plant species: 1) the Eastern Asian–Eastern North American floristic disjunction (blue; [Dong et al., 2019](#)); 2) the American Amphitropical floristic disjunction (pink; [Raven, 1963](#)); 3) the Madrean–Tethyan floristic disjunction (black; [Wen and Ickert-Bond, 2009](#)); 4) the Australia–South America floristic disjunction (green; [van den Ende et al., 2017](#)); 5) the Northern–Southern Africa floristic disjunction (yellow; [Jürgens, 1997](#)); 6) the disjunction between *Linospadix minor* in North-East Queensland and *L. albertisianus* in New Guinea (brown; [Osborne et al., 2019](#)).

Image credit: Matthew Coathup.

frequencies of K_s , K_a and K_a/K_s for each pair clustered within narrow ranges of small values. This is indicative of a common pattern in the relative numbers of genes at different levels of divergence during allopatric speciation, with only a small number of loci in the genome displaying high levels of divergence. Furthermore, by categorising the K_a/K_s ratios into six groups, Dong et al. found that in all pairs of species the relative number of genes under different selection pressures followed the same order. Moderate purifying selection was most common, followed by strong purifying selection, relaxed purifying selection, weak/moderate positive selection, putatively neutral selection and, finally, strong positive selection. Overall the patterns observed by Dong et al. suggest that it might be possible to make predictions about genome evolution.

While the study focused on the Eastern Asian–Eastern North American floristic disjunction, it is likely that these patterns of genome evolution are a common feature of allopatric

speciation. Many other disjunctions exist around the world ([Figure 1](#)), and similar analyses of these would determine whether the findings of Dong et al. represent a common rule of genomic divergence. Indeed, recent work by some of the present authors and colleagues has shown that two pairs of palm species – one widely separated, the other not – have values of K_a , K_s and K_a/K_s similar to those reported by Dong et al. ([Osborne et al., 2019](#)). This supports the idea that these patterns may be common to genomic divergence in general, regardless of geography.

Matthew J Coathup is in the Department of Life Sciences, Silwood Park Campus, Imperial College London, London, United Kingdom

[id https://orcid.org/0000-0002-4152-3049](https://orcid.org/0000-0002-4152-3049)

Owen G Osborne is in the School of Natural Sciences, Bangor University, Bangor, United Kingdom

[id https://orcid.org/0000-0002-1213-1169](https://orcid.org/0000-0002-1213-1169)

Vincent Savolainen is in the Department of Life Sciences, Silwood Park Campus, Imperial College London, London, United Kingdom

v.savolainen@imperial.ac.uk

 <https://orcid.org/0000-0001-5350-9984>

Competing interests: The authors declare that no competing interests exist.

Published 13 September 2019

References

- Arnegard ME**, McGee MD, Matthews B, Marchinko KB, Conte GL, Kabir S, Bedford N, Bergek S, Chan YF, Jones FC, Kingsley DM, Peichel CL, Schluter D. 2014. Genetics of ecological divergence during speciation. *Nature* **511**:307–311. DOI: <https://doi.org/10.1038/nature13301>, PMID: 24909991
- Dong Y**, Chen S, Cheng S, Zhou W, Ma Q, Chen Z, Fu CX, Liu X, Zhao YP, Soltis PS, Wong GKS, Soltis DE, Xiang J. 2019. Natural selection and repeated patterns of molecular evolution following allopatric divergence. *eLife* **8**:e45199. DOI: <https://doi.org/10.7554/eLife.45199>, PMID: 31373555
- Gagnaire PA**, Pavey SA, Normandeau E, Bernatchez L. 2013. The genetic architecture of reproductive isolation during speciation-with-gene-flow in lake whitefish species pairs assessed by RAD sequencing. *Evolution* **67**:2483–2497. DOI: <https://doi.org/10.1111/evo.12075>, PMID: 24033162
- Jürgens N**. 1997. Floristic biodiversity and history of African arid regions. *Biodiversity and Conservation* **6**: 495–514. DOI: <https://doi.org/10.1023/a:1018325026863>
- Osborne OG**, Ciezarek A, Wilson T, Crayn D, Hutton I, Baker WJ, Turnbull CGN, Savolainen V. 2019. Speciation in *Howea* palms occurred in sympatry, was preceded by ancestral admixture, and was associated with edaphic and phenological adaptation. *Molecular Biology and Evolution*:msz166. DOI: <https://doi.org/10.1093/molbev/msz166>, PMID: 31318434
- Raven PH**. 1963. Amphitropical relationships in the floras of North and South America. *The Quarterly Review of Biology* **38**:151–177. DOI: <https://doi.org/10.1086/403797>
- Riesch R**, Muschick M, Lindtke D, Villoutreix R, Comeault AA, Farkas TE, Lucek K, Hellen E, Soria-Carrasco V, Dennis SR, de Carvalho CF, Safran RJ, Sandoval CP, Feder J, Gries R, Crespi BJ, Gries G, Gompert Z, Nosil P. 2017. Transitions between phases of genomic differentiation during stick-insect speciation. *Nature Ecology & Evolution* **1**:0082. DOI: <https://doi.org/10.1038/s41559-017-0082>
- Soria-Carrasco V**, Gompert Z, Comeault AA, Farkas TE, Parchman TL, Johnston JS, Buerkle CA, Feder JL, Bast J, Schwander T, Egan SP, Crespi BJ, Nosil P. 2014. Stick insect genomes reveal natural selection's role in parallel speciation. *Science* **344**:738–742. DOI: <https://doi.org/10.1126/science.1252136>, PMID: 24833390
- van den Ende C**, White LT, van Welzen PC. 2017. The existence and break-up of the Antarctic land bridge as indicated by both amphi-Pacific distributions and tectonics. *Gondwana Research* **44**:219–227. DOI: <https://doi.org/10.1016/j.gr.2016.12.006>
- Wen J**, Ickert-Bond SM. 2009. Evolution of the Madrean-Tethyan disjunctions and the North and South American amphitropical disjunctions in plants. *Journal of Systematics and Evolution* **47**:331–348. DOI: <https://doi.org/10.1111/j.1759-6831.2009.00054.x>
- Wolf JB**, Ellegren H. 2017. Making sense of genomic islands of differentiation in light of speciation. *Nature Reviews Genetics* **18**:87–100. DOI: <https://doi.org/10.1038/nrg.2016.133>, PMID: 27840429