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Pioneering polyploids: the impact of whole-genome duplication on biome shifting in New Zealand *Coprosma* (Rubiaceae) and *Veronica* (Plantaginaceae)

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The role of whole-genome duplication (WGD) in facilitating shifts into novel biomes remains unknown. Focusing on two diverse woody plant groups in New Zealand, *Coprosma* (Rubiaceae) and *Veronica* (Plantaginaceae), we investigate how biome occupancy varies with ploidy level, and test the hypothesis that WGD increases the rate of biome shifting. Ploidy levels and biome occupancy (forest, open and alpine) were determined for indigenous species in both clades. The distribution of low-ploidy (*Coprosma*: 2*x*, *Veronica*: 6*x*) versus high-ploidy (*Coprosma*: 4–10*x*, *Veronica*: 12–18*x*) species across biomes was tested statistically. Estimation of the phylogenetic history of biome occupancy and WGD was performed using time-calibrated phylogenies and the R package BioGeoBEARS. Trait-dependent dispersal models were implemented to determine support for an increased rate of biome shifting among high-ploidy lineages. We find support for a greater than random portion of high-ploidy species occupying multiple biomes. We also find strong support for high-ploidy lineages showing a three- to eightfold increase in the rate of biome shifts. These results suggest that WGD promotes ecological expansion into new biomes.

1. Introduction

Many genera in the New Zealand (NZ) flora (*ca* 55, 10% of all native genera) contain multiple discrete ploidy levels as a result of past whole-genome duplication (WGD) events [1,2], many of which have occurred in NZ [3]. These polyploids comprise diverse life forms and ecology, including 100% of indigenous *Veronica* (124/124 species; 6*x*, 12*x*, 18*x*) and 29% of indigenous *Coprosma* (16/55 species; 4*x*, 6*x*, 7*x*, 10*x*; the remaining 39 are 2*x*), among the largest genera in NZ [4]. Polyploidy in NZ is associated with all growth forms except large trees, being particularly common among shrubs and perennial herbs. Within the two indigenous NZ groups studied here, polyploids are all (*Coprosma*) or mainly (*Veronica*) woody shrubs/small trees, lifeforms equally common in forest, shrubland and grassland communities.

Globally, polyploids are more abundant at higher altitudes, higher latitudes and in post-glacial regions [5–9]. They have also been associated with arid/drought-prone conditions [10–12], greater soil productivity [13,14], younger/less stable environments [15–19] and isolated landmasses [1,2,20]. These patterns

may be caused by increased stress tolerance [18,21–23], reduced tolerance of nutrient limitation [14,24–26], ability to persist in small populations [5,27,28] and correlation with perennial/herbaceous lifeforms [9,17,29]. Whole-genome duplication may also be a key method of sympatric speciation, as it achieves immediate reproductive isolation [30–32]. Whole-genome duplication may create novel hybrids via allopolyploidy, with the potential to promote rapid adaptation [28,33–35]. However, despite being linked to important diversification processes, debate continues over how speciation and extinction rates change following WGD [18,36–40].

Although the role of WGD in biome occupancy remains little understood, several studies have indicated strong niche shifts in high-ploidy lineages [12,34,41]. Lineage biome occupancy has previously been thought to be generally conserved, with rare biome shifts, reflecting phylogenetic niche conservatism [42–44]. However, recent studies suggest that biomes are relatively permeable, with lineages crossing biome boundaries frequently and many species occupying multiple biomes [45–48]. When WGD promotes niche shifts, it may also foster lineage expansion into new biomes.

NZ contains three major biomes, based on vegetation structure and function [49]: forest, open and alpine [50,51]. Forest covered most of NZ throughout the Cenozoic before the uplift of the Southern Alps in the Pliocene–Pleistocene [52]. The two key NZ forest types are podocarp-broadleaf forest and southern beech forest [53]. The open biome occurs below the regional tree-line (*ca* 1050 m.a.s.l.) where local environmental conditions/disturbance limit tree growth. Examples of open habitat include shrubland, grassland, dunes and wetlands. Open habitats are diverse, often naturally uncommon with patchy distributions [54]. These habitats expanded *ca* 4 million years ago (Ma) with the emergence of the Southern Alps, increased seismic activity, river deposition, valley-floor temperature inversions and rain-shadow conditions [55]. Smaller areas of open habitat, e.g. those associated with wetlands and coastal conditions, would always have been present [50]. The alpine biome is the youngest, arising in the last 1.9Ma. It occurs above the tree-line (*ca* 1050 m.a.s.l.); its area has fluctuated through repeated glaciation in the Pleistocene [56]. Alpine habitats include shrubland, grassland, herbfield and fellfield as elevation increases [57]. Despite the young age and comparatively small size of the current alpine biome, it contains approximately half the vascular plant species native to NZ [58,59]. Throughout the mountainous regions of NZ, all three biomes can be found either adjoining or in close proximity.

Our focal genera *Coprosma* and *Veronica* are found across all three biomes, having speciated extensively within NZ [60–62]. *Coprosma* contains 55 species indigenous to NZ, representing five ploidy levels: 2*x*, 4*x*, 6*x*, 7*x* and 10*x* [63,64]. The genus likely originated in NZ before dispersing to other Pacific landmasses [61,65]. *Veronica* species in NZ belong to sect. *Hebe*, a diverse subclade comprising *ca* 124 indigenous species which are 6*x*, 12*x* or 18*x* [60,62]. Both groups are morphologically and ecologically diverse, encompassing a range of growth forms from low growing herbs to small trees [60,65,66]. In this paper, we test the hypothesis that WGD increases the rate of biome shifting in NZ *Coprosma* and *Veronica*.

2. Methods

Biome occupancy (forest/open/alpine) for species in the study genera was determined through floras, ecological literature and expert opinion. Many species are present in two biomes (42% across both *Coprosma* and *Veronica*), though none are present in all three. Ploidy levels for species were compiled using the Chromosome Count Database [66]. Species with a ploidy level higher than the lowest in NZ were treated as 'high-ploidy', those at the lowest level were treated as 'low-ploidy'. Three species which lacked any chromosome count data were not included in this study (*Coprosma antipoda*, *C. polymorpha* and *Veronica spectabilis*). Eight *Veronica* species with multiple recorded cytotypes were treated as multiploids for the subsequent analyses [60,67]. A table showing data for every species can be found in the electronic supplementary material (electronic supplementary material, 1).

As an exploratory analysis to see if environment–polyploidy correlations reported for other clades hold in our genera, we conducted a non-phylogenetic test of association. We acknowledge that phylogenetic structure can mislead this test, so we conduct a fully phylogenetic test below. Contingency tables were constructed comparing presence/absence in each of the biomes against high/low-ploidy, while a fourth table compares ploidy against single versus multiple biome occupancy. The χ^2-test for independence was applied to these tables in R, with *p*-values corrected for multiple testing using the Holm method [68].

To test the impact of WGD on biome occupancy with an appropriate phylogenetic comparative method, we jointly estimated histories of biome occupancy and WGD using the R package BioGeoBEARS [69,70] and published dated phylogenies of the two genera [61,62]. Biome occupancy was modelled as a biogeography-like character using the six BioGeoBEARS base biogeography models [71]. For verification of the validity of these model comparisons, see Klaus & Matzke [71], Matzke [72]. A similar example of BioGeoBEARS being used to model biome occupancy can be seen in Cardillo *et al.* [45]. WGD was modelled in BioGeoBEARS as a binary trait, either low-ploidy or high-ploidy, with multiploid species coded as '?' to represent ambiguity.

Trait-dependent dispersal was implemented in BioGeoBEARS [71], allowing the rate of biome shifting to vary depending on the ploidy trait. This was done by adding a dispersal rate multiplier, *m*, which changes the rate of biome shifting for lineages with the high-ploidy trait character. Availability of the alpine biome was limited to less than 1.9 Ma, reflecting when this biome arose in NZ [55]. Results from the trait-dependent models were compared against models where ploidy and biome occupancy evolve independently. AICc was used to determine the relative level of support for each model, and to produce model-averaged parameter estimates [73].

In order to infer the types of biome shifts occurring, biogeographical stochastic mapping (BSM) was implemented [74,75]. This option cannot be run for trait-dependent dispersal models, so the best supported (AICc) non-trait model (BAYAREALIKE + J for both groups) was used. One thousand reconstructions were run for each genus, with the frequency of different biome shifts recorded.

Additional details on the data and methods used in this study can be found in electronic supplementary material, 2.

3. Results

A greater proportion of high-ploidy species are present in every biome (table 1). This difference is greatest in the open biome, where 85–88% of high-ploidy species are present versus 71–73% of low-ploidy species. The strongest difference between the high and low-ploidy species is the proportion occupying two biomes (58–63% versus 33–36%, respectively). This result is significant at $p = 0.05$, except with *p*-values corrected for multiple testing and multiploid species treated as low-ploidy. The greater proportion of high-ploidy species

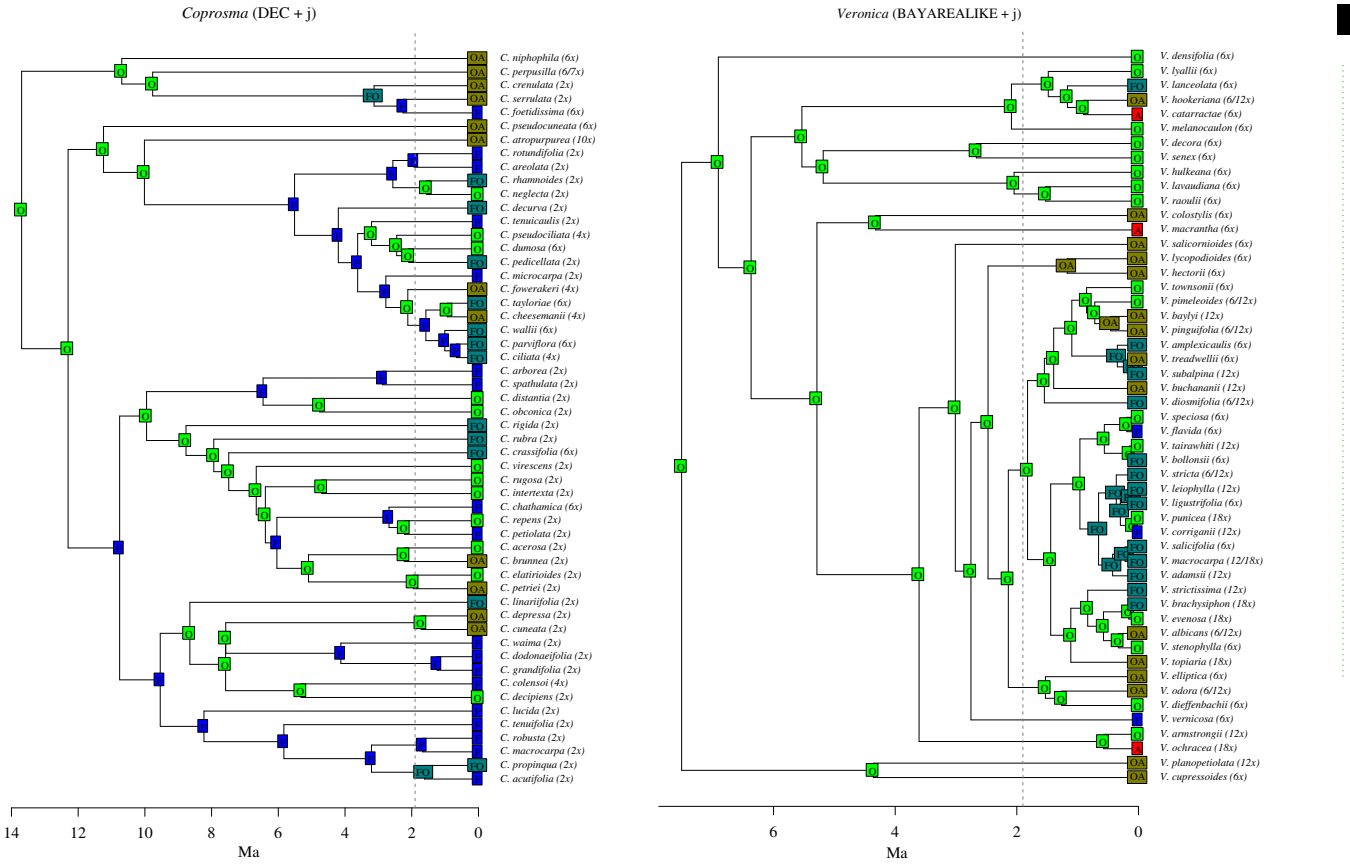

Figure 1. Ancestral range estimations of biome occupancy in *Coprosma* and *Veronica*. The dashed line shows when the alpine biome becomes available. Each node shows the single most probable range under the best-fit biogeographic model. F = forest (dark blue), O = open (light green), A = alpine (red). The breakdown of range probabilities at each node can be viewed in electronic supplementary material, 3c.

Table 1. The proportion of low- and high-ploidy species of *Coprosma* and *Veronica* present across three NZ biomes. Values on the left/right are obtained when multiploid species are treated as low or high-ploidy, respectively. *p*-Values were adjusted using the Holm–Bonferroni procedure. Results significant at $p = 0.05$ are shown in italics. Separate tables showing proportions for each genus are included in electronic supplementary material, 3a.

	proportion present in each biome		*p*-values	
	low-ploidy	high-ploidy	raw	adjusted
forest	0.29/0.29	0.33/0.34	0.5896/0.4719	1/1
open	0.72/0.71	0.85/0.88	0.0730/*0.0145*	0.5538/0.1452
alpine	0.34/0.33	0.40/0.41	0.4799/0.2843	1/1
two biomes	0.35/0.32	0.58/0.63	*0.0061/0.0001*	0.0713/*0.0020*

occupying multiple biomes accounts for why these species are more common across all three biomes relative to low-ploidy species. Every multi-biome species is present in the open biome (i.e. open + alpine or open + forest). No species have a forest + alpine biome pattern. When the tests above are repeated on a dataset with all multi-biome species removed (electronic supplementary material, 3b), there was no statistical support for a difference between high and low-ploidy groups in their presence in the open biome ($p = 0.464$ to 0.6175).

Based on the best fitting BioGeoBEARS models, the open biome is the most probable origin for both *Coprosma* and *Veronica* sect. *Hebe* in NZ (figure 1). Models where ploidy influences the rate of biome shifting receive 95.5% of the AICc model weight in *Coprosma* and 77.5% in *Veronica*. All analyses show an increase in the dispersal multiplier: 3.07–5.94*x* in *Coprosma* and 5.49–8.23*x* in *Veronica* (figure 2). The model-weighted increase is 4.74 for *Coprosma* and 4.73 for *Veronica* (electronic supplementary material, 3d). This indicates that biome shifts are more frequent among high-ploidy lineages.

The BSM analysis (electronic supplementary material, 3e–f) showed that the most common mode of biome shift in both genera is anagenetic expansion, where a lineage expands into a new biome without leaving its original biome. Jump dispersal, where one daughter lineage switches into a new biome at speciation, was also common in *Coprosma*. No instances of anagenetic biome contraction occurred, despite being allowed by the models used, perhaps because it is usually difficult to infer the rate of range contraction [76]. In both genera, the most frequent specific biome shift was expansion into the

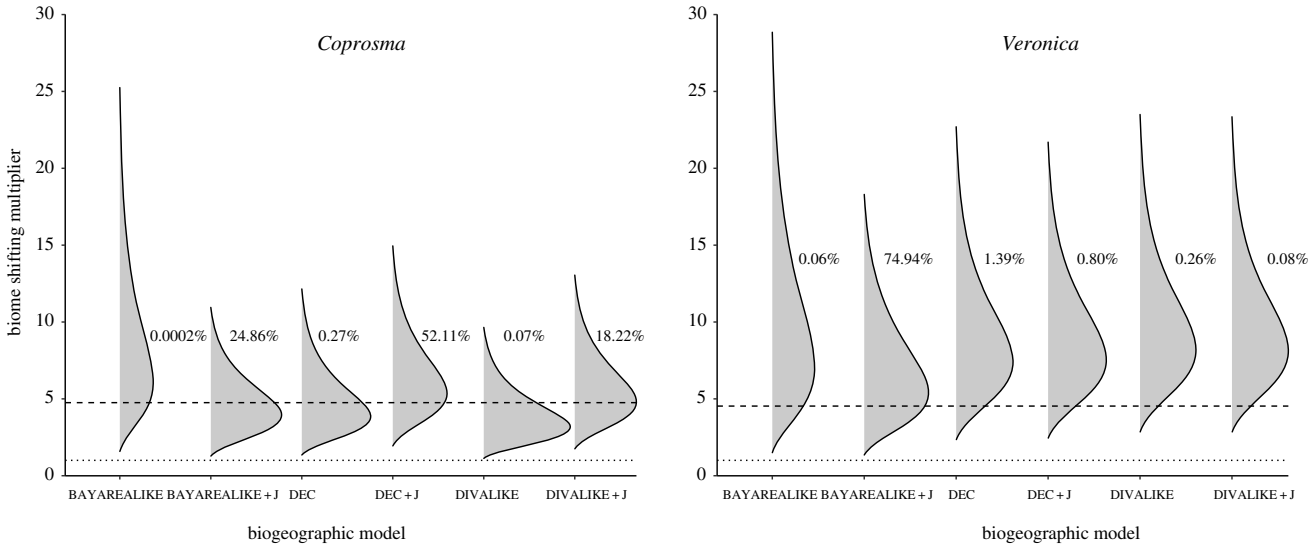

Figure 2. Likelihood profiles for the dispersal rate multiplier (*m*) in each trait-dependent model implemented. Per cent AICc support is shown for each model. Likelihood profiles are cut off at their upper and lower 95% confidence intervals. The dotted line at $m = 1$ represents the dispersal rate under trait-independent models. The dashed line shows the average *m* obtained per genus when averaging across all models based on % AICc support (in *Veronica* this line is below the peak of every likelihood profile as approx. 20% of model weight goes to trait-independent models). The maximum likelihood estimates for all parameters of each model can be found in electronic supplementary material, 3d.

alpine from the open. In *Coprosma*, the next four most frequent shifts all occurred between the forest and open biomes. In *Veronica*, the four most common biome shifts all came out of the open. Despite no extant species occupying forest + alpine, the forest → forest + alpine biome shift is occasionally inferred in *Veronica*.

Also included in the electronic supplementary material is

- A table comparing the ploidy and biome occupancies of *Veronica* species that are present versus absent on our phylogeny (electronic supplementary material, 3g).
- The BioGeoBEARS parameter estimates when presence in the open biome is limited to the last 4 Ma (electronic supplementary material, 3h).
- A table comparing how BayesTraits and BioGeoBEARS model biome occupancy (electronic supplementary material, 3i).
- Historic ploidy estimates and BioGeoBEARS parameters when high → low-ploidy transitions are allowed (electronic supplementary material, 3j–k).
- Historic estimates of dysploidy, and tables comparing dysploidy versus polyploidy and biome occupancy (electronic supplementary material, 3l–m).
- A list of all the unique combinations of extant homoploid hybrids found in *Coprosma* and *Veronica* (electronic supplementary material, 4).

4. Discussion

Our research suggests that high-ploidy species of NZ *Coprosma* and *Veronica* sect. *Hebe* are more likely to be found across multiple biomes and are inferred to have shifted into new biomes much more frequently than low-ploidy species (table 1 and figure 2). This supports our hypothesis that the rate of biome shifting increases among high-ploidy lineages in our genera, suggesting that WGD could be important in facilitating biome shifts. WGD may influence the ability of lineages to shift into new biomes, through mechanisms such as greater adaptive potential [12,33–35,41], improved ability to survive in small populations [27,28], increased stress tolerance [10,11,21–23] and broader environmental niche [18,77,78].

The open biome is a key origin for both genera in NZ. However, the preference of high-ploidy species for the open biome is a result of multi-biome occupancy—high-ploidy species occupying a single biome are not more common in the open than low-ploidy species (electronic supplementary material, 3b). Surprisingly, high-ploidy species in our study genera are not significantly more common in the alpine biome (table 1), despite the widespread positive relationship between polyploid distribution and cold climates [5,9]. Interestingly, no species have the forest + alpine biome occupancy despite this biome occupancy being observed in other genera [50]. This could be attributed to fact that this occupancy requires the most shifts from the ancestral open habitat. Additionally, shifts between forest and alpine biomes occur infrequently (electronic supplementary material, 3f), and these biomes differ in both temperature and light levels—the other two biome pairings differ by only one of these factors.

Another factor in *Veronica* is dysploidy: the genus is split between species with a base chromosome number of $x = 21$ versus $x = 20$, the latter being dysploids resulting primarily from a single $x = 21 \rightarrow 20$ chromosome transition (electronic supplementary material, 3l) [79]. A lower proportion of dysploid *Veronica* species occupy the alpine biome (0.28 versus 0.62; electronic supplementary material, 3m), while a higher proportion are present in the other two biomes (forest: 0.28 versus 0.04, open: 0.89 versus 0.66), across multiple biomes (0.46 versus 0.32) and in the high-ploidy group (0.36–0.45 versus 0.11–0.15). Based on this, dysploidy could also be an important factor in the evolution of biome occupancy in *Veronica*. However, because most dysploids result primarily from one event at the base of a diverse clade, it is difficult to establish whether dysploidy causes changes in biome occupancy or correlates with them. By contrast, WGD in *Veronica* occurs independently over a dozen times among the species present on our phylogeny.

The inferred relationship between WGD and biome shifting could occur if the sample of living high-ploidy species is

biased towards those which have successfully shifted biomes, e.g. if extinction rates were higher among high-ploidy species that remained in their ancestral biome due to competition with parent species. This is plausible given observations of increased extinction [36,37] and poor nutrient-competition [14,24] among polyploids. Lineage extinction is ignored in BioGeoBEARS, a key flaw in many phylogenetic models [80] that makes it difficult to test this proposition. However, such a situation is unlikely among our genera because of the higher proportion of multi-biome occupancy among high-ploidy species (table 1), high frequency of anagenetic biome expansions, and the absence of any inferred biome contraction events (electronic supplementary material, 3e). In NZ, it appears that high-ploidy lineages have shifted into novel biomes more often than their low-ploidy relatives, without losing their ancestral biome.

One factor complicating this study is the impact that allopolyploid reticulations have on the inference of biome shifts. It is possible that allopolyploidy involving parents in different biomes could produce high-ploidy lineages that occupy both biomes, making 'biome shifts' actually the result of combining the two parental biomes. Unfortunately, there are no estimates of allopolyploidy in *Coprosma* or *Veronica*, and phylogenetic methods cannot accurately model reticulations. It is plausible that many high-ploidy lineages could be allopolyploid—extant homoploid hybrids are common in both genera (electronic supplementary material, 4) and WGD in NZ may be biased towards allopolyploidy [1]. These points are discussed in more detail in electronic supplementary material, 2 (Point 14), however, even if the combination of parental biomes via allopolyploidy has occurred, it is still ultimately a case of WGD facilitating new lineages with novel biome occupancies.

This study is limited by the size of the phylogenies available. While previous work suggests that trait-dependent signal can be detected on smaller phylogenies [71,81], larger phylogenies allow the discovery of weaker trait-dependent effects and tighter confidence intervals. For *Veronica*, a full *ca* 124 species phylogeny of sect. *Hebe* would strengthen our findings. There are few NZ-centred groups large enough for the methods described here—further research could apply a similar approach to groups from other landmasses.

The positive relationships seen here between increased ploidy level and both multi-biome occupancy and the rate of biome shifting provide strong support for WGD being a factor that can facilitate shifts into novel biomes.

Data accessibility. Phylogenetic trees, R code and other raw data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.3bk3j9khj [82].

Authors' contributions. L.G.L., W.G.L. and N.J.M. designed the study. W.G.L. developed the biome classification scheme and determined biome occupancy, E.E.D. developed the method of applying BioGeoBEARS to biome occupancy. H.M.M. provided the *Veronica* phylogeny and contributed to all aspects of the study involving the genus. L.G.L. and N.J.M. ran the trait-dependent analysis and interpreted the results. All authors made substantial contributions to the conception/design, data collection or analysis of this study. All authors contributed to the drafting and revising of the article and agree to be accountable for all aspects of the work.

Competing interests. We declare we have no competing interests.

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References

1. Murray BG, De Lange PJ. 2011 Chromosomes and evolution in New Zealand endemic angiosperms and gymnosperms. In *The biology of island floras* (eds D Bramwell, J Caujapé-Castells), pp. 265–279. Cambridge, UK: Cambridge University Press.
2. Meudt HM, Albach DC, Tanentzap AJ, Igea J, Newmarch SC, Brandt AJ, Lee WG, Tate JA. 2021 Polyploidy on islands: its emergence and importance for diversification. *Front. Plant. Sci.* **12**, 637214. (doi:10.3389/fpls.2021.637214)
3. Hair JB. 1966 Biosystematics of the New Zealand flora, 1945–1964. *N. Z. J. Bot.* **4**, 559–595. (doi:10.1080/0028825X.1966.10430184)
4. Breitwieser I, Brownsey PJ, Nelson WA, Wilton AD. 2010 Flora of New Zealand Online. See http://www.nzflora.info/ (accessed 20 August 2020).
5. Brochmann C, Brysting AK, Alsos IG, Borgen L, Grundt HH, Scheen A-C, Elven R. 2004 Polyploidy in arctic plants. *Biol. J. Linn. Soc.* **82**, 521–536. (doi:10.1111/j.1095-8312.2004.00337.x)
6. Gustafsson Å. 1946 The plant species in relation to polyploidy and apomixis. *Hereditas* **32**, 444–448. (doi:10.1111/j.1601-5223.1946.tb02785.x)
7. Hagerup O. 1928 Morphological and cytological studies of Bicornes. *Dan. Bot. Ark.* **6**, 1–27.
8. Haskell G. 1952 Polyploidy, ecology and the British flora. *J. Ecol.* **40**, 265–282. (doi:10.2307/2256801)
9. Rice A, Šmarda P, Novosolov M, Drori M, Glick L, Sabath N, Meiri S, Belmaker J, Mayrose I. 2019 The global biogeography of polyploid plants. *Nat. Ecol. Evol.* **3**, 265–273. (doi:10.1038/s41559-018-0787-9)
10. Godfree RC, Marshall DJ, Young AG, Miller CH, Mathews S. 2017 Empirical evidence of fixed and homeostatic patterns of polyploid advantage in a keystone grass exposed to drought and heat stress. *R. Soc. Open Sci.* **4**, 170934. (doi:10.1098/rsos.170934)
11. Manzaneda AJ, Rey PJ, Bastida JM, Weiss-Lehman C, Raskin E, Mitchell-Olds T. 2012 Environmental aridity is associated with cytotype segregation and polyploidy occurrence in *Brachypodium distachyon* (Poaceae). *New Phytol.* **193**, 797–805. (doi:10.1111/j.1469-8137.2011.03988.x)
12. Gunn BF, Murphy DJ, Walsh NG, Conran JG, Pires JC, Macfarlane TD, Birch JL. 2020 Evolution of Lomandroideae: multiple origins of polyploidy and biome occupancy in Australia. *Mol. Phylogenet. Evol.* **149**, 106836. (doi:10.1016/j.ympev.2020.106836)
13. Raabová J, Fischer M, Münzbergová Z. 2008 Niche differentiation between diploid and hexaploid *Aster amellus*. *Oecologia* **158**, 463–472. (doi:10.1007/s00442-008-1156-1)
14. Šmarda P, Hejcman M, Březinová A, Horová L, Steigerová H, Zedek F, Bureš P, Hejcmanová P, Schellberg J. 2013 Effect of phosphorus availability on the selection of species with different ploidy levels and genome sizes in a long-term grassland fertilization experiment. *New Phytol.* **200**, 911–921. (doi:10.1111/nph.12399)
15. Fawcett JA, Maere S, Van de Peer Y. 2009 Plants with double genomes might have had a better chance to survive the Cretaceous–Tertiary extinction event. *Proc. Natl Acad. Sci. USA* **106**, 5737. (doi:10.1073/pnas.0900906106)
16. Oberlander KC, Dreyer LL, Goldblatt P, Suda J, Linder HP. 2016 Species-rich and polyploid-poor: insights into the evolutionary role of whole-genome duplication from the Cape flora biodiversity hotspot. *Am. J. Bot.* **103**, 1336–1347. (doi:10.3732/ajb.1500474)
17. Stebbins GL. 1971 *Chromosomal evolution in higher plants*. London, UK: Edward Arnold.
18. Van de Peer Y, Mizrachi E, Marchal K. 2017 The evolutionary significance of polyploidy. *Nat. Rev. Genet.* **18**, 411–424. (doi:10.1038/nrg.2017.26)
19. Vanneste K, Baele G, Maere S, van de Peer Y. 2014 Analysis of 41 plant genomes supports a wave of

successful genome duplications in association with the Cretaceous–Paleogene boundary. *Genome Res.* **24**, 1334–1347. (doi:10.1101/gr.168997.113)

20. Carr GD. 1998 Chromosome evolution and speciation in Hawaiian flowering plants. In *Evolution and speciation of island plants* (eds TF Stuessy, M Ono), pp. 5–42. Cambridge, UK: Cambridge University Press.
21. Deng B, Du W, Liu C, Sun W, Tian S, Dong H. 2012 Antioxidant response to drought, cold and nutrient stress in two ploidy levels of tobacco plants: low resource requirement confers polytolerance in polyploids? *Plant Growth Regul.* **66**, 37–47. (doi:10.1007/s10725-011-9626-6)
22. Madlung A. 2013 Polyploidy and its effect on evolutionary success: old questions revisited with new tools. *Heredity* **110**, 99–104. (doi:10.1038/hdy.2012.79)
23. Schoenfelder KP, Fox DT. 2015 The expanding implications of polyploidy. *J. Cell Biol.* **209**, 485–491. (doi:10.1083/jcb.201502016)
24. Guignard MS, Nichols RA, Knell RJ, Macdonald A, Romila C-A, Trimmer M, Leitch IJ, Leitch AR. 2016 Genome size and ploidy influence angiosperm species' biomass under nitrogen and phosphorus limitation. *New Phytol.* **210**, 1195–1206. (doi:10.1111/nph.13881)
25. Leitch AR, Leitch IJ. 2008 Genomic plasticity and the diversity of polyploid plants. *Science* **320**, 481–483. (doi:10.1126/science.1153585)
26. Neiman M, Kay AD, Krist AC. 2013 Can resource costs of polyploidy provide an advantage to sex? *Heredity* **110**, 152–159. (doi:10.1038/hdy.2012.78)
27. Comai L. 2005 The advantages and disadvantages of being polyploid. *Nat. Rev. Genet.* **6**, 836–846. (doi:10.1038/nrg1711)
28. Otto SP. 2007 The evolutionary consequences of polyploidy. *Cell* **131**, 452–462. (doi:10.1016/j.cell.2007.10.022)
29. Engemann K *et al.* 2016 Patterns and drivers of plant functional group dominance across the Western Hemisphere: a macroecological re-assessment based on a massive botanical dataset. *Bot. J. Linn. Soc.* **180**, 141–160. (doi:10.1111/boj.12362)
30. Ainouche ML, Wendel JF. 2014 Polyploid speciation and genome evolution: lessons from recent allopolyploids. In *Evolutionary biology: genome evolution, speciation, coevolution and origin of life* (ed. P Pontarotti), pp. 87–113. Cham, Switzerland: Springer International Publishing.
31. Otto SP, Whitton J. 2000 Polyploid incidence and evolution. *Annu. Rev. Genet.* **34**, 401–437. (doi.org/10.1146/annurev.genet.34.1.401)
32. Perrie LR, Shepherd LD, Lange PJD, Brownsey PJ. 2010 Parallel polyploid speciation: distinct sympatric gene-pools of recurrently derived allo-octoploid *Asplenium* ferns. *Mol. Ecol.* **19**, 2916–2932. (doi:10.1111/j.1365-294X.2010.04705.x)
33. Alix K, Gérard PR, Schwarzacher T, Heslop-Harrison J. 2017 Polyploidy and interspecific hybridization: partners for adaptation, speciation and evolution in plants. *Ann. Bot.* **120**, 183–194. (doi:10.1093/aob/mcx079)
34. Baniaga AE, Marx HE, Arrigo N, Barker MS. 2020 Polyploid plants have faster rates of multivariate niche differentiation than their diploid relatives. *Ecol. Lett.* **23**, 68–78. (doi:10.1111/ele.13402)
35. Ramsey J. 2011 Polyploidy and ecological adaptation in wild yarrow. *Proc. Natl Acad. Sci. USA* **108**, 7096. (doi:10.1073/pnas.1016631108)
36. Mayrose I, Zhan SH, Rothfels CJ, Magnuson-Ford K, Barker MS, Rieseberg LH, Otto SP. 2011 Recently formed polyploid plants diversify at lower rates. *Science* **333**, 1257. (doi:10.1126/science.1207205)
37. Mayrose I, Zhan SH, Rothfels CJ, Arrigo N, Barker MS, Rieseberg LH, Otto SP. 2015 Methods for studying polyploid diversification and the dead end hypothesis: a reply to Soltis *et al*. (2014). *New Phytol.* **206**, 27–35. (doi:10.1111/nph.13192)
38. Meyers LA, Levin DA. 2006 On the abundance of polyploids in flowering plants. *Evolution* **60**, 1198–1206. (doi:10.1111/j.0014-3820.2006.tb01198.x)
39. Soltis DE *et al.* 2014 Are polyploids really evolutionary dead-ends (again)? A critical reappraisal of Mayrose *et al*. (2011). *New Phytol.* **202**, 1105–1117. (doi:10.1111/nph.12756)
40. Wood TE, Takebayashi N, Barker MS, Mayrose I, Greenspoon PB, Rieseberg LH. 2009 The frequency of polyploid speciation in vascular plants. *Proc. Natl Acad. Sci. USA* **106**, 13 875–13 879. (doi:10.1073/pnas.0811575106)
41. Han T-S, Zheng Q-J, Onstein RE, Rojas-Andrés BM, Hauenschild F, Muellner-Riehl AN, Xing YW. 2020 Polyploidy promotes species diversification of *Allium* through ecological shifts. *New Phytol.* **225**, 571–583. (doi:10.1111/nph.16098)
42. Donoghue MJ, Edwards EJ. 2014 Biome shifts and niche evolution in plants. *Annu. Rev. Ecol. Evol. Syst.* **45**, 547–572. (doi:10.1146/annurev-ecolsys-120213-091905)
43. Crisp MD *et al.* 2009 Phylogenetic biome conservatism on a global scale. *Nature* **458**, 754–756. (doi:10.1038/nature07764)
44. Cruz GAS, Zizka G, Silvestro D, Leme EMC, Schulte K, Benko-Iseppon AM. 2017 Molecular phylogeny, character evolution and historical biogeography of *Cryptanthus* Otto & A. Dietr. (Bromeliaceae). *Mol. Phylogenet. Evol.* **107**, 152–165. (doi:10.1016/j.ympev.2016.10.019)
45. Cardillo M, Weston PH, Reynolds ZKM, Olde PM, Mast AR, Lemmon EM, Lemmon AR, Bromham L. 2017 The phylogeny and biogeography of *Hakea* (Proteaceae) reveals the role of biome shifts in a continental plant radiation. *Evolution* **71**, 1928–1943. (doi:10.1111/evo.13276)
46. Dale EE, Larcombe MJ, Lee WG, Higgins SI. 2020 Diversification is decoupled from biome fidelity: *Acacia*—a case study. *J. Biogeogr.* **47**, 538–552. (doi:10.1111/jbi.13768)
47. Gamisch A, Fischer GA, Comes HP. 2016 Frequent but asymmetric niche shifts in *Bulbophyllum* orchids support environmental and climatic instability in Madagascar over Quaternary time scales. *BMC Evol. Biol.* **16**, 14. (doi:10.1186/s12862-016-0586-3)
48. Simon MF, Grether R, de Queiroz LP, Skema C, Pennington RT, Hughes CE. 2009 Recent assembly of the Cerrado, a neotropical plant diversity hotspot, by *in situ* evolution of adaptations to fire. *Proc. Natl Acad. Sci. USA* **106**, 20 359–20 364. (doi:10.1073/pnas.0903410106)
49. Higgins SI, Buitenwerf R, Moncrieff GR. 2016 Defining functional biomes and monitoring their change globally. *Glob. Change Biol.* **22**, 3583–3593. (doi:10.1111/gcb.13367)
50. Dale EE. 2019 The role of biome shifts in lineage diversification. PhD thesis. The University of Otago, Dunedin, Otago, New Zealand. See https://ourarchive.otago.ac.nz/handle/10523/9204.
51. Dale EE, Larcombe MJ, Lee WG. 2021 The effect of single biome occupancy on the estimation of biome shifts and the detection of biome conservatism. *PLoS ONE* **16**, e0248839. (doi:10.1371/journal.pone.0248839)
52. McGlone MS, Buitenwerf R, Richardson SJ. 2016 The formation of the oceanic temperate forests of New Zealand. *N. Z. J. Bot.* **54**, 128–155. (doi:10.1080/0028825X.2016.1158196)
53. Wardle P. 1991 *Vegetation of New Zealand*. Cambridge, UK: Cambridge University Press.
54. Holdaway RJ, Wiser SK, Williams PA. 2012 Status assessment of New Zealand's naturally uncommon ecosystems. *Conserv. Biol.* **26**, 619–629. (doi:10.1111/j.1523-1739.2012.01868.x)
55. Heenan PB, McGlone MS. 2013 Evolution of New Zealand alpine and open-habitat plant species during the late Cenozoic. *N. Z. J. Ecol.* **37**, 105–113.
56. McGlone MS, Duncan RP, Heenan PB. 2001 Endemism, species selection and the origin and distribution of the vascular plant flora of New Zealand. *J. Biogeogr.* **28**, 199–216. (doi:10.1046/j.1365-2699.2001.00525.x)
57. Mark A. 2012 *Above the treeline: a nature guide to alpine New Zealand*. Nelson, NZ: Craig Potton Publishing.
58. Heenan PB, McGlone MS. 2019 Cenozoic formation and colonisation history of the New Zealand vascular flora based on molecular clock dating of the plastid *rbcL* gene. *N. Z. J. Bot.* **57**, 204–226. (doi:10.1080/0028825X.2019.1632356)
59. Winkworth RC, Wagstaff SJ, Glenny D, Lockhart PJ. 2005 Evolution of the New Zealand mountain flora: origins, diversification and dispersal. *Org. Divers. Evol.* **5**, 237–247. (doi:10.1016/j.ode.2004.12.001)
60. Bayly M, Kellow A. 2006 *An illustrated guide to New Zealand hebes*. Wellington, New Zealand: Te Papa Press.
61. Cantley JT, Markey AS, Swenson NG, Keeley SC. 2016 Biogeography and evolutionary diversification in one of the most widely distributed and species rich genera of the Pacific. *AoB PLANTS* **8**, plw043. (doi:10.1093/aobpla/plw043)
62. Meudt HM, Rojas-Andrés BM, Prebble JM, Low E, Garnock-Jones PJ, Albach DC. 2015 Is genome downsizing associated with diversification in

polyploid lineages of *Veronica*? *Bot. J. Linn. Soc.* **178**, 243–266. (doi:10.1111/boj.12276)

63. Beuzenberg EJ. 1983 Contributions to a chromosome atlas of the New Zealand flora—24 *Coprosma* (Rubiaceae). *N. Z. J. Bot.* **21**, 9–12.
64. Dawson MI. 2000 Index of chromosome numbers of indigenous New Zealand spermatophytes. *N. Z. J. Bot.* **38**, 47–150. (doi:10.1080/0028825X.2000.9512673)
65. Cantley JT, Swenson NG, Markey A, Keeley SC. 2014 Biogeographic insights on Pacific *Coprosma* (Rubiaceae) indicate two colonizations to the Hawaiian Islands. *Bot. J. Linn. Soc.* **174**, 412–424. (doi:10.1111/boj.12130)
66. Rice A, Glick L, Abadi S, Einhorn M, Kopelman NM, Salman-Minkov A, Mayzel J, Chay O, Mayrose I. 2015 The chromosome counts database (CCDB)—a community resource of plant chromosome numbers. *New Phytol.* **206**, 19–26. (doi:10.1111/nph.13191)
67. Garnock-Jones PJ, Lloyd DG. 2004 A taxonomic revision of *Parahebe* (Plantaginaceae) in New Zealand. *N. Z. J. Bot.* **42**, 181–232. (doi:10.1080/0028825X.2004.9512899)
68. Holm S. 1979 A simple sequentially rejective multiple test procedure. *Scand. J. Stat.* **6**, 65–70.
69. Matzke NJ. 2013 Probabilistic historical biogeography: new models for founder-event speciation, imperfect detection, and fossils allow improved accuracy and model-testing. *Front. Biogeogr.* **5**, 243–248. (doi:10.21425/f5fbg19694)
70. Matzke NJ. 2014 Model selection in historical biogeography reveals that founder-event speciation is a crucial process in island clades. *Syst. Biol.* **63**, 951–970. (doi:10.1093/sysbio/syu056)
71. Klaus KV, Matzke NJ. 2020 Statistical comparison of trait-dependent biogeographical models indicates that Podocarpaceae dispersal is influenced by both seed cone traits and geographical distance. *Syst. Biol.* **69**, 61–75. (doi:10.1093/sysbio/syz034)
72. Matzke N. 2021 Statistical comparison of DEC and DEC + J is identical to comparison of two ClaSSE submodels, and is therefore valid. OSF Preprints. (doi:10.31219/osf.io/vqm7r)
73. Burnham KP, Anderson DR. 2002 *Model selection and multimodel inference*, 2nd edn. New York, NY: Springer-Verlag.
74. Dupin J, Matzke NJ, Särkinen T, Knapp S, Olmstead RG, Bohs L, Smith SD. 2017 Bayesian estimation of the global biogeographical history of the Solanaceae. *J. Biogeogr.* **44**, 887–899. (doi:10.1111/jbi.12898)
75. Matzke NJ. 2016 Stochastic mapping under biogeographical models. PhyloWiki BioGeoBEARS website. See http://phylo.wikicom/biogeobears#stochastic_mapping.
76. Ree RH, Smith SA. 2008 Maximum likelihood inference of geographic range evolution by dispersal, local extinction, and cladogenesis. *Syst. Biol.* **57**, 4–14. (doi:10.1080/10635150701883881)
77. McIntyre PJ. 2012 Polyploidy associated with altered and broader ecological niches in the *Claytonia perfoliata* (Portulacaceae) species complex. *Am. J. Bot.* **99**, 655–662. (doi:10.3732/ajb.1100466)
78. te Beest M, Le Roux JJ, Richardson DM, Brysting AK, Suda J, Kubesová M, Pyšek P. 2012 The more the better? The role of polyploidy in facilitating plant invasions. *Ann. Bot.* **109**, 19–45. (doi:10.1093/aob/mcr277)
79. Albach DC, Martínez-Ortega MM, Delgado L, Weiss-Schneeweiss H, Özgökce F, Fischer MA. 2008 Chromosome numbers in Veroniceae (Plantaginaceae): review and several new counts. *Annals of the Missouri Botanical Garden* **95**, 543–566. (doi.org/10.3417/2006094)
80. Marshall CR. 2017 Five palaeobiological laws needed to understand the evolution of the living biota. *Nat. Ecol. Evol.* **1**, 1–6. (doi:10.1038/s41559-017-0165)
81. Matos-Maraví P, Matzke N, Larabee FJ, Clouse RM, Wheeler WC, Sorger DM, Suarez AV, Janda M. 2019 Trait-dependent biogeography: model-based inference of dispersal and distribution patterns of Indo-Pacific trap-jaw ants (Hymenoptera: Formicidae: *Odontomachus*). See https://researchspace.auckland.ac.nz/handle/2292/48034 (accessed 19 August 2020)
82. Liddell L, Lee W, Dale E, Meudt H, Matzke N. 2021 Data from: Pioneering polyploids: the impact of whole-genome duplication on biome shifting in New Zealand *Coprosma* (Rubiaceae) and *Veronica* (Plantaginaceae). Dryad Digital Repository. (doi:10.5061/dryad.3bk3j9khj)