

LETTERS

Phylogenetic biome conservatism on a global scale

Michael D. Crisp¹, Mary T. K. Arroyo², Lyn G. Cook³, Maria A. Gandolfo⁴, Gregory J. Jordan⁵, Matt S. McGlone⁶, Peter H. Weston⁷, Mark Westoby⁸, Peter Wilf⁹ & H. Peter Linder¹⁰

How and why organisms are distributed as they are has long intrigued evolutionary biologists^{1–4}. The tendency for species to retain their ancestral ecology has been demonstrated in distributions on local and regional scales^{5–7}, but the extent of ecological conservatism over tens of millions of years and across continents has not been assessed^{8–13}. Here we show that biome stasis at speciation has outweighed biome shifts by a ratio of more than 25:1, by inferring ancestral biomes for an ecologically diverse sample of more than 11,000 plant species from around the Southern Hemisphere. Stasis was also prevalent in transoceanic colonizations. Availability of a suitable biome could have substantially influenced which lineages establish on more than one landmass, in addition to the influence of the rarity of the dispersal events themselves. Conversely, the taxonomic composition of biomes has probably been strongly influenced by the rarity of species' transitions between biomes. This study has implications for the future because if clades have inherently limited capacity to shift biomes¹³, then their evolutionary potential could be strongly compromised by biome contraction as climate changes.

In recent years, the extent to which species retain ancestral ecological traits and environmental distributions ('niche conservatism') has been debated^{11,13–15}. Whether ecology is evolutionarily labile or conserved appears to be scale dependent, but most of the evidence for conservatism has come from studies at smaller (community-level) scales^{5–7,12}. Large-scale ecological conservatism is not well studied but there is evidence that ecological tolerances (for example as reflected in latitudinal range) are relatively conserved in lineages over long periods of macro-evolutionary time^{8–11}. This leads to the prediction that lineages might rarely colonize new biomes¹¹; however, the frequency of transitions has not been estimated¹³.

Biomes are broad vegetation types defined by climate, life-form and ecophysiology¹⁶ and, hence, are useful units for investigating the large-scale pattern of ecological conservatism. Biome conservatism might be a major determinant of the global distribution of biodiversity, such as the latitudinal gradient, which could have arisen because relatively few ancestrally tropical taxa were able to colonize temperate biomes¹⁷. Global comparisons across multiple lineages are needed to investigate the generality of conservatism and how much it has influenced the assembly of biomes¹⁸. Here we quantify the frequency of biome changes using a large sample of plant phylogenies distributed across multiple biomes and landmasses.

The widely separated landmasses in the Southern Hemisphere provide an outstanding opportunity to assess the relative frequency of phylogenetic biome conservatism on a broad scale and over long time periods (tens of millions of years). First, each southern continent contains a rich array of biomes among which taxa could have moved. Second, many taxa are spread across the southern landmasses and are

largely restricted to that region, defining a biogeographically meaningful study area^{2,4}. Although some of these transoceanic disjunctions are likely vicariant remnants of once-continuous distributions on Gondwana^{2,4,19}, many more are probably the result of long-distance colonization^{20,21}. Third, the oceanic gaps in the Southern Hemisphere are so wide that disjunct sister taxa are likely to have remained effectively separate in their new biomes, without ongoing gene flow confounding comparisons of their subsequent evolution. Last, the number of plant phylogenies that are dated and well sampled at species level for the Southern Hemisphere has grown to a statistically meaningful size.

We assembled a data set comprising 11,064 species of vascular plants in 45 taxa from extratropical Africa, Madagascar, Australia–New Guinea, New Caledonia, New Zealand and South America, equivalent to an estimated 15% of the total flora of these regions. We reconstructed ancestral distributions and, by dating divergences, inferred which disjunctions were likely to be the result of long-distance dispersal and establishment (colonization) across oceans. Each plant species was assigned to one or more of seven biomes (wet forest, sclerophyll, alpine, bog, temperate grassland, savannah and arid) and transitions among biomes were recorded.

We found strong support for the hypothesis of phylogenetic biome conservatism because biome shifts were rare, being associated with only 396 (3.6%) of the approximately 11,000 evolutionary divergences. Of these shifts, 356 occurred within landmasses (Fig. 1) and 40 were linked to transoceanic colonizations (Fig. 2 and Table 1). Investigating taxa individually, we found a consistent pattern in which closely related species were more ecologically similar than would be expected by chance (Supplementary Results), irrespective of whether the taxa have been considered Gondwanan relics (for example *Araucariaceae*, *Casuarinaceae*, *Nothofagus*^{19,22}) or otherwise (for example eucalypts, grasses and some legume tribes^{23,24}).

Most transoceanic colonizations involved no change of biome (sign test: $n = 226$; biome shifts, 40; $P = 0.00001$). Moreover, a bias towards biome stasis in colonizations was consistent across all landmass pairs, in both directions (Fig. 2; Wilcoxon matched-pairs signed-rank test: $n = 30$, $z = -3.552$, $P = 0.00019$). Similarly, the bias towards stasis in colonizations was consistent among biomes (Table 1), whether comparing source biomes (Wilcoxon matched-pairs signed-rank test: $n = 7$, $z = -2.113$, $P = 0.017$) or destination biomes ($n = 7$, $z = -2.197$, $P = 0.014$). We suggest that constraint on biome shifts following colonization from one landmass to another is a consequence of the dynamics of colonization. The frequency at which propagules of a species have crossed the southern oceans is likely to be extremely small. For successful colonization, immigrant propagules must germinate and establish reproductively successful populations. Establishment should be easier in a biome to which the species is pre-adapted, that is, one approximately equivalent to its

¹School of Botany and Zoology, The Australian National University, Canberra, Australian Capital Territory 0200, Australia. ²Institute of Ecology and Biodiversity, University of Chile, Casilla 653, Santiago, Chile. ³School of Integrative Biology, The University of Queensland, Brisbane, Queensland 4072, Australia. ⁴L. H. Bailey Hortorium, Department of Plant Biology, Cornell University, Ithaca, New York 14853, USA. ⁵School of Plant Science, University of Tasmania, Private Bag 55, Hobart, Tasmania 7001, Australia. ⁶Landcare Research, PO Box 40, Lincoln 7640, New Zealand. ⁷National Herbarium of New South Wales, Mrs Macquaries Road, Sydney, New South Wales 2000, Australia. ⁸Department of Biological Sciences, Macquarie University, Sydney, New South Wales 2109, Australia. ⁹Department of Geosciences, Pennsylvania State University, University Park, Pennsylvania 16802, USA. ¹⁰Institute of Systematic Botany, University of Zurich, Zurich 8008, Switzerland.

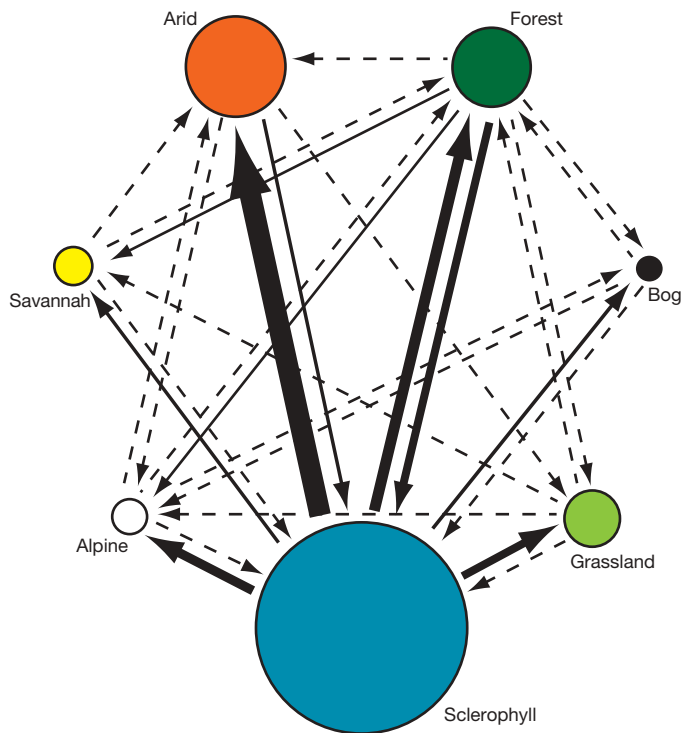


Figure 1 | Biome shifts within landmasses. Shifts occurred with only 356 of 10,800 speciation events within landmasses. Number of species sampled within each biome is proportional to the area of each circle: sclerophyll, 7,250; arid, 1,683; wet forest, 1,005; temperate grassland, 504; savannah, 242; montane, 186; bog, 84. Arrow thickness is proportional to the number of transitions in each direction, ranging from 6 to 95 events; dashed lines indicate 1–5 events and lack of an arrow indicates that there was no event.

source biome²⁵. An interesting parallel is the niche conservatism observed in many invasive species that are introduced by humans and usually establish in the same biomes as in their regions of origin^{26,27}.

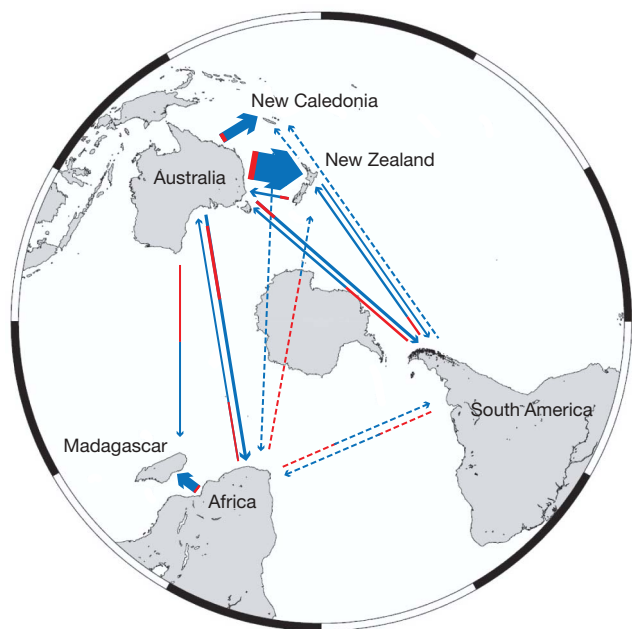


Figure 2 | Biome conservatism in transoceanic plant colonizations around the Southern Hemisphere. Proportion of colonizations into the same (blue) or a different (red) biome are shown along each arrow. Arrow thickness is proportional to the number of colonizations, ranging from 4 to 107 events; dashed lines indicate fewer than 4 events. Four ambiguous colonizations are not shown.

Table 1 | Biome transitions coincident with transoceanic colonizations

Destination	Source							Total
	Arid	Bog	Forest	Grassland	Sclerophyll	Alpine	Savannah	
Arid	2							
Bog		13.3			3.3			3.3
Forest			50.8		10			10
Grassland				21.7	5.3	1		6.3
Sclerophyll	1	0.3	3.5	2.7	87		1	8.5
Alpine			1	2	7	12		10
Savannah			1		0.5			1.5
Total	1	0.3	5.5	4.7	26.1	1	1	39.6

The number of biome transitions is shown for each biome in terms of source (columns) and sink (rows). Bold numbers along the diagonal show colonizations with no change of biome. Totals are for transitions only, that is, excluding values along the diagonal. Non-integer values result from fractional weighting of ambiguous reconstructions. For clarity, zeroes are left blank.

The frequency of transitions between biomes within continents varied markedly among biome pairs (Fig. 1). This variation is consistent with biome conservatism, given that biomes differ in their ecological similarity. For example, the sclerophyll and arid biomes in both Australia and Africa are characterized by extensive areas of oligotrophic soils and differ mainly in degree of moisture deficit²⁸. We recorded more transitions between sclerophyll and arid biomes than between any other pair, even after correcting for differential species richness of biomes (Supplementary Tables 1 and 2). Conversely, there were no transitions between strongly contrasting biome pairs, such as arid and bog, savannah and bog, and savannah and alpine (Fig. 2).

There has been directional bias in transitions among biomes, with the sclerophyll biome being a net source and the arid, alpine and grassland biomes being net sinks (Fig. 1 and Supplementary Tables 1 and 2). Consistent with this, the arid, alpine and grassland biomes expanded considerably during the last 25 Myr, whereas the forest and sclerophyll biomes were predominant in older fossil floras^{3,16,22,23}. The most frequent destination of transitions was the arid biome, which expanded mainly after 15 Myr ago^{3,16,22}. Nearly all of the dated shifts into the arid biome occurred after this time.

From our broad sample of taxa across continents and biomes of the temperate Southern Hemisphere, we can confidently conclude that phylogenetic biome conservatism has been prevalent during the radiation of plant lineages, both within continents and in transoceanic colonizations. The great majority of pairs of sister species (>96%) occurred in the same biome as their most recent shared ancestor. Such conservatism is probably accepted in the popular imagination for iconic Gondwanan plants such as Araucariaceae, Casuarinaceae and *Nothofagus*, but we have found it also characterized clades within the eucalypts, grasses and legumes that have diversified greatly during the last 20 Myr. Their evolutionary success might have resulted not from adaptation to new biomes but from expansion of their biome as climate changed. Thus, our results have implications for the better understanding of biological invasions and the survival of species under global climate change.

METHODS SUMMARY

A large data set was assembled comprising 45 molecular phylogenies of vascular plants occurring in seven biomes across all major Southern Hemisphere landmasses except Antarctica.

Ancestral landmasses and biomes were reconstructed at nodes, and transitions inferred, using parsimony optimization. By dating transoceanic divergences using fossils and relaxed molecular clocks, transoceanic colonizations were distinguished from vicariance events.

The extent of biome conservatism was assessed for 226 transoceanic colonizations using a sign test with the null expectation that biomes within each landmass were colonized in proportion to their areas. Whether clades tend to remain in their ancestral biomes was tested in 13 individual phylogenies using Monte Carlo randomizations of the tips. Whether biome conservatism was consistent between all 30 pairwise combinations of landmasses was tested using a Wilcoxon matched-pairs signed-rank test.

Within landmasses, directional bias in transitions among biomes was assessed using a binomial test, with a correction for species richness effects.

Full Methods and any associated references are available in the online version of the paper at www.nature.com/nature.

Received 19 August 2008; accepted 12 January 2009.

Published online 15 February 2009.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

Acknowledgements We thank the Australian Research Council–New Zealand Research Network for Vegetation Function for facilitating this collaboration. Participation by M.A.G. and P.W. was supported in part by a grant from the US National Science Foundation.

Author Contributions All authors participated in two workshops where the phylogenetic and biome data were initially compiled. All authors participated in analysis and interpretation at the workshops and subsequently by email. M.W. designed and facilitated the study. M.A.G., G.J.J. and P.W. provided palaeobotanical dates. M.D.C. drafted the paper in collaboration with H.P.L., and provided supplementary statistical analyses during review.

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METHODS

Data and sampling. Molecular phylogenies of vascular plants were sampled representing 11,064 species in 45 taxa from extratropical Africa, Madagascar, Australia–New Guinea, New Caledonia, New Zealand and South America, equivalent to an estimated 15% of the total flora of these regions. Seven biomes (wet forest, sclerophyll, alpine, bog, temperate grassland, savannah and arid) were recognized. Landmasses and biomes are defined below.

We aimed to include all monophyletic vascular plant taxa (Supplementary Table 4) satisfying the following conditions: (1) they have adequately sampled molecular phylogenies; (2) there is a plausible source for dating of significant nodes; (3) they are centred in the Southern Hemisphere temperate and subtropical regions (more or less south of latitude 23° S). We excluded taxa occurring mainly in the tropics but included some primarily temperate taxa with northern outliers, usually in higher elevation habitats, such as the central African mountains and New Guinea highlands.

We considered the following areas.

(1) South America: excludes the equatorial areas and the northern and north-central Andes.

(2) New Zealand: includes Chatham and associated islands.

(3) Australia: includes Tasmania and New Guinea but not Timor.

(4) Southern Africa: includes the areas in the Cape Provinces (Northern, Western and Eastern) south of the Orange River.

(5) New Caledonia and (6) Madagascar: both of these islands extend into the tropics but have a small upland temperate flora element.

(7) Rest of the world: several of the sampled taxa included clades occurring north of the limit of 23° S set above. Inferred transitions in both directions between these and the defined southern temperate areas were noted but excluded from our analysis (but see notes above on montane outliers).

We considered the following biomes.

(1) Wet forest: closed canopy of trees, typically in high-precipitation climate.

(2) Sclerophyll woodland or heathland: most species are sclerophyll shrubs; either on low-nutrient soils or in Mediterranean climate or both. Local types include fynbos (Africa); eucalypt-dominated woodland and open forest, kwongan, wallum and *Triodia*-dominated 'hummock-grasslands' (Australia); chaparral (America); and maquis (New Caledonia). However, this biome excludes true grasslands and rainforests with scattered emergent eucalypts.

(3) Savannah: most species are graminoids or forbs, with variable presence of trees and shrubs; dominant grasses always C4; climate monsoonal (summer rain, dry winter).

(4) Temperate grassland: most species are grasses or forbs, with variable presence of trees and shrubs; grasses can be either C3 or C4; climate has cold winters, otherwise various but not arid. Can include ruderal and grassy riparian patches.

(5) Arid: mean annual rainfall <300 mm, to <400 mm in subtropics; includes semi-arid under European definitions; graminoid cover sparse in comparison with grasslands, if present at all; variable mixture of forbs, shrubs and trees.

(6) Alpine or tundra: above treeline, cover comprises graminoids, forbs and shrubs.

(7) Bog: permanently saturated peaty soil normally lacking surface water; not including seasonally flooded ground (swamps, floodplains) or riparian habitat, which we include in the wider biome within which they are embedded, such as sclerophyll or forest.

Species of other azonal habitats (cliffs, riverbeds, coastal strands, aquatics) were few in our data set and were included in the biome in which they are embedded.

We are aware that, as climate changed through the Cenozoic era, biomes fluctuated in size and changed in taxonomic composition, and that some were more stable than others^{22,29,30}. Despite these changes, the defining characteristics of the biomes, which are reflected in the physiological and morphological adaptations of species to the biome, have been maintained from the late Eocene epoch to the present^{22,29,30}.

Scoring and optimization. Terminal taxa (species) in the phylogenies were scored for occurrence in the biomes and landmasses. The few widely distributed species, that is, those occurring in more than one landmass or biome, were scored as polymorphic. Parsimony optimization was used to infer both ancestral biome and area of occurrence at internal nodes of the phylogenies, either by hand or using MESQUITE³¹.

In cases of ambiguous reconstructions at a node, all equally parsimonious alternatives were scored as fractions of a single state transition at that node. For example, if a shift from bog to alpine, or the reverse, were equally parsimonious at a node, each was scored with a weight of 0.5. Each polymorphism was counted as a single transition within the terminal species. For 'soft' polytomies in the phylogenies (reflecting uncertain or conflicting resolution³¹), all alternative resolutions

of the tree were treated as equally likely. This created ambiguity where a transition was inferred at a polytomy and the alternative transitions were weighted as above.

Apart from parsimony, maximum-likelihood and Bayesian methods are available for inferring ancestral traits³², but these do not necessarily perform better with biogeographical data³³ and their use was not practicable given the size of our meta-data set. Moreover, these methods require branch length estimates and monomorphic terminals, requirements that were not satisfied for several data sets. Comparative maximum-likelihood and parsimony optimizations were made in MESQUITE for four suitable phylogenies: Mirbeliaceae-Bossiaeeae (Fabaceae), Casuarinaceae, *Scaevola* (Goodeniaceae) and *Eucalyptus*. For maximum-likelihood optimization we used the MK1 model, shown to be suitable for discrete-state data such as biome occurrences³⁴. Parsimony inferred the same number of biome transitions (eucalypts) or a few more (remaining taxa) in comparison with the maximum-likelihood model (Supplementary Table 5). Therefore, our use of parsimony for the main analyses, rather than maximum likelihood, might have slightly underestimated the extent of biome conservatism. In other words, the degree of phylogenetic biome conservatism could be even more impressive than estimated here, given that parsimony might overestimate transitions.

Interpretation of transoceanic disjunctions. All landmasses in this study are now separated by oceanic gaps. Therefore, disjunct occurrences of sister taxa (inferred by optimization to occur in different landmasses) could have resulted from either vicariance or transoceanic colonization²⁰. By definition, the process of vicariance does not involve a biome transition⁴; therefore, it was necessary to detect likely vicariant disjunctions and eliminate them from the analysis. Colonization and vicariance were distinguished by the estimated age of the disjunct pairs of lineages: those disjunctions that predate the severance of the last connections between the lands were classed as vicariants; those younger could have been established only by transoceanic colonization. Timing of divergences at nodes was taken from molecular dating studies where available. Alternatively, we used fossil evidence directly mapped onto trees following the approach of ref. 35, for example for the Cupressaceae, which have an excellent Southern Hemisphere macrofossil record.

We used the geological estimates of the times of separation of the landmasses by continental drift^{36–38} (Supplementary Table 6). Our approach was conservative, erring on the side of a vicariance interpretation. If the confidence interval of a disjunction age estimate overlapped with that for the corresponding geological separation in Supplementary Table 6, we inferred vicariance and excluded the disjunction from further analysis.

For some taxa, the root (basal) node was dated to a time younger than the geological isolation of the landmass that was inferred as ancestral for the taxon. The relevant geological dates are in Supplementary Table 6. For example, *Chaetanthera* is endemic in South America, which was isolated from 30 Myr ago, but the root node of *Chaetanthera* was dated to 11 Myr ago. In other cases, a taxon was present in a landmass before its isolation but the area of occurrence of its sister taxon could not be determined. For example, the mirbelioid legumes were present in Australia 50 Myr ago. This occurrence is old enough to be vicariant with South America, but its sister group is uncertain and, thus, reconstruction of the ancestral area is not possible. In such cases, the origin of the taxon, whether 'in situ' by vicariance, or by colonization from elsewhere, was undetermined and the basal node was not scored for analysis, although all its descendent nodes were scored.

Tests of biome conservatism. To test whether biome stasis associated with transoceanic colonization was more prevalent than might be expected by chance, we used a null hypothesis that the probability of colonization of a destination in any of the seven biomes (including that of the source) depended on the available area of that biome. For a given biome in a given destination landmass, we assumed that if there were no biome stasis, then all colonizations originating from that biome overseas would be distributed among destination biomes in proportion to their areas. Thus, the expected frequency of stasis was calculated as the proportional area of that biome in the destination landmass (Supplementary Table 3). This calculation was repeated across all 226 observed colonizations, grouped by destination biomes ($n = 28$) and evaluated statistically using the sign test implemented at Simple Interactive Statistical Analysis (SISA, <http://www.quantitativeskills.com/sisa/index.htm>).

Although the test reported above indicated greater-than-expected biome conservatism in the data as a whole, there could have been significant departures from this pattern in colonizations between individual pairs of landmasses. We tested whether biome stasis was consistent across all 30 pairwise combinations of landmasses, in both directions (Fig. 2 and Table 1) using the Wilcoxon matched-pairs signed-rank test, implemented at SISA. The rationale was that each pairwise combination provided an independent test of departure from the null expectation of equal probabilities of biome shift/non-shift during transoceanic colonizations. We used the same rationale and test to ask whether biome stasis in transoceanic colonizations was consistent among biomes.

For 13 individual phylogenies, we tested the hypothesis of phylogenetic biome conservatism using a Monte Carlo approach implemented in MESQUITE. The terminals of each original phylogeny were randomized 100 times and the number of biome transitions estimated by parsimony optimization in each randomized tree. If the number of transitions in the original data fell below the tail of the distribution of values from the randomized trees, then transitions were inferred to be significantly fewer than expected by chance ($P = 0.01$). This test perturbed the clustering of biomes in clades while preserving the tree topology and the number of species in each biome. Thus, rejection of the null hypothesis indicates that closely related species are more likely to occupy the same biome than would be expected on the basis of their phylogenetic relationships.

Tests of bias in biome shifts. Within landmasses, where the great majority of biome shifts were observed (356 of 396), directional bias in biome shifts was evident; for example, it appears that there were many more shifts from sclerophyll into other biomes than vice versa (Fig. 1 and Supplementary Table 1). For each biome, we asked whether there was a significant bias, that is, whether the biome was a net source or sink for transitions. The null expectation is that shifts were equally probable in either direction and the binomial test was used at SISA. We repeated this test, correcting for a correlation between the number of transitions and the species richness of the source biome (Supplementary Fig. 1). Values in Supplementary Table 1 were multiplied by one minus the fractional contribution of source biome to total richness and rescaled to the original total number of transitions (Supplementary Table 2).

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