

# Plant diversity in mediterranean-climate regions

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**T**he five mediterranean-climate regions of the world (Fig. 1, Box 1) occupy less than 5% of the Earth's surface yet harbour about 48 250 known vascular plant species (Table 1), almost 20% of the world total. These regions also have exceptionally high numbers of rare and locally endemic plants<sup>1-5</sup> and include two recognized species flocks, one in southwestern Australia and the other in the southwestern Cape, South Africa<sup>6</sup>. These patterns are of interest because they refute predictions on the relationships between diversity and area, productivity and latitude<sup>3,4,6</sup>.

There has been much interest recently in the patterns, determinants and function of biodiversity in mediterranean-climate ecosystems (e.g. Refs 6-8). Here, we review patterns and determinants of plant species diversity and rarity at various spatial scales. We also highlight aspects from research in mediterranean-climate regions that are salient to the evolution and conservation of plant biodiversity in general.

## Local diversity Patterns

At the local scale (0.1 ha or less), the vegetation of mediterranean-climate regions is moderately species-rich by global standards, on average less than half that recorded for tropical rainforests, but much richer than most other temperate communities<sup>3,9</sup>. Within each region, there is great variation in local diversity. Highest diversity occurs in frequently burnt open heath and scrub on nutrient-poor soils (Australian kwongan and South African fynbos), and the heavily grazed shrublands and woodlands of the eastern Mediterranean Basin (Table 2, see Box 1 for description of vegetation types). Denser shrublands (e.g. chaparral) and woodlands (e.g. eucalyptus forest) have lower diversity. However, diversity in the immediate post-fire year in chaparral, when a rich fire-ephemeral flora coexists with the resprouts and seedlings of long-lived shrubs, approximates that of mature fynbos and kwongan<sup>10</sup>.

Growth form diversity is low in fynbos and kwongan, which include many structurally and functionally similar species, often belonging to the same genus<sup>11-13</sup>, but it is high in vegetation that seldom burns, for example, South African scrub-forest<sup>13</sup> and Chilean matorral<sup>14</sup>. Annuals comprise 15% or more of the local floras in all the mediterranean-climate

**The high plant diversity of mediterranean-climate regions has attracted much attention over the past few years.**

**This review discusses patterns and determinants of local, differential and regional plant diversity in all five regions. Local diversity shows great variation within and between regions and explanations for these patterns invoke a wide range of hypotheses. Patterns of regional diversity are the result of differential speciation and extinction rates during the Quaternary. These rates have been influenced more by the incidence of fire and the severity of climate change than by environmental heterogeneity. All regions have a high number of rare and locally endemic taxa that survive as small populations, many of which are threatened by habitat transformation.**

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regions except those in Australia and South Africa, where only a few such species appear in the immediate post-fire period<sup>15-17</sup>. The average diversity of fynbos, kwongan and mallee communities in the western regions, which are more nutrient-impooverished and have high winter rainfall, is similar to that in the less-seasonal and more-fertile eastern regions of mediterranean South Africa and Australia<sup>3,18</sup>.

## Determinants

A wide range of equilibrium and non-equilibrium theories have been invoked to explain local diversity and species coexistence in mediterranean-climate shrublands. These include differentiation along structural or growth-form niche axes<sup>3,19</sup>, spatial variation in resource availability<sup>9,20</sup>, disturbances such as fire<sup>11,21</sup> and grazing<sup>22</sup>, neighbourhood effects<sup>19,23</sup>, lottery processes<sup>11,24</sup>, and the influence of regional processes<sup>3,25</sup>.

Huston<sup>7</sup> interprets the relative diversity of mediterranean plant communities in terms of a general model where low rates of competitive displacement result from low soil nutrients and summer drought, coupled with a moderately high frequency of disturbance in the form of fire and grazing. There is

good evidence from several mediterranean-climate regions that plant diversity is a unimodal function of productivity or other measures of nutrient supply<sup>9,21,26</sup>. Most studies on within-guild coexistence are for communities of proteoid (Proteaceae) shrubs in fynbos and kwongan. Cody<sup>19</sup> found clear patterns of segregation into leaf-dimension niches, and evidence for character displacement, for proteoid shrubs in fynbos (see also Ref. 11). Using a null model to generate a relationship between local and regional diversity among southwestern Australian *Banksia* (Proteaceae) species, Richardson *et al.*<sup>25</sup> recently showed that local diversity of real assemblages was rapidly saturated, suggesting that local-scale processes limit diversity. However, they could find no conclusive evidence that local assemblages are consistently structured by growth form or regeneration niche differentiation. Instead, they argued that habitat specialization of banksias<sup>23</sup> causes lower diversity than would be predicted from niche differentiation and from the size of the regional species pool.

Few generalizations emerge from the many studies on local diversity in mediterranean vegetation. It appears,

however, that in frequently burnt shrublands on nutrient-poor soils (fynbos and kwongan), relatively low growth rates and the reshuffling of competitive hierarchies owing to differential post-fire regeneration, allows the coexistence of many seemingly equivalent shrubs and long-lived graminoids<sup>13,25</sup>. On more fertile soils, where fire-free intervals are longer (chaparral, garrigue, phrygana), shorter-lived species are rapidly excluded by the developing shrub canopy<sup>10,27</sup>. In Chilean matorral and grassy shrublands and woodlands in the eastern Mediterranean Basin, both of which seldom burn, grazing by livestock permits the coexistence of both short-lived and long-lived species<sup>14,17,22</sup>.

### Differentiation diversity

Differentiation diversity refers to compositional change along habitat gradients (beta diversity) and along geographical gradients (gamma diversity)<sup>2</sup>. High differentiation diversity is largely the product of the evolution of habitat specialists and geographical vicariants<sup>2,3</sup>.

Comparable and exceptionally high levels of differentiation diversity, amounting to almost complete turnover of fire-killed shrub species along edaphic and geographical gradients, have been recorded in the strongly winter rainfall zones of southwestern Australia and the southwestern Cape<sup>3,4,28</sup>. In the southeastern zones of these regions, which experience more summer rain, differentiation diversity is much lower<sup>3,18</sup>. In California, high turnover is associated mainly with predominantly fire-killed shrub lineages (*Arctostaphylos* and *Ceanothus*) and short-lived herbs or annuals<sup>2,21,29</sup>. A similar pattern occurs in the Mediterranean Basin where the shrub lineages include *Astragalus*, *Genista* and *Cistus*, and the herbs are mainly annual members of the Leguminosae, Compositae and Gramineae<sup>17,30</sup>. In Chile, high turnover is concentrated in suffrutescent shrubs and perennial herbs belonging to many genera including *Senecio*, *Adesmia*, *Oxalis* and *Calceolaria*<sup>14,15</sup>. The tall shrub and tree floras that have persisted since the Tertiary in all regions except Australia, and that regenerate mainly from vertebrate-dispersed propagules in the absence of fire, have wide geographical distributions and contribute little to turnover<sup>3,15,29</sup>.

### Regional diversity

Regional diversity (at a scale of 10–10<sup>6</sup> km<sup>2</sup>) in mediterranean-climate regions ranks among the highest in the world<sup>3,15</sup> (Fig. 2). The southwestern zone of the Cape has the highest diversity at this scale: for a given area, this region has, on average, 1.7 times the diversity of southwestern Australia, about 2.2 times the diversity of the southeastern Cape, California and the Mediterranean Basin, and 3.3 times the diversity of Chile<sup>3,15</sup>. Fox<sup>18</sup> suggests that regional diversity in the southeastern zone of mediterranean Australia is considerably lower than in the southwest although detailed data are lacking. Diversity in small areas (>30 km<sup>2</sup>) of southwestern Australia is not significantly different from similar areas of the southwestern Cape<sup>3</sup>.

In California and in the Cape, regional diversity peaks in topographically diverse areas that have high rainfall, providing support for the favourableness and environmental heterogeneity hypotheses, respectively<sup>31,32</sup>. The high topographical and climatic heterogeneity of Chile and the Mediterranean Basin (Table 3) might similarly explain their relatively high (at least at a global scale) regional diversity<sup>15,17</sup>. However, southwestern Australia, the second richest region, remains an exception since topographic heterogeneity is low and climatic heterogeneity is only moderate (Table 1). Edaphic complexity and associated specialization has been invoked as the principle determinant of the high diversity of south-

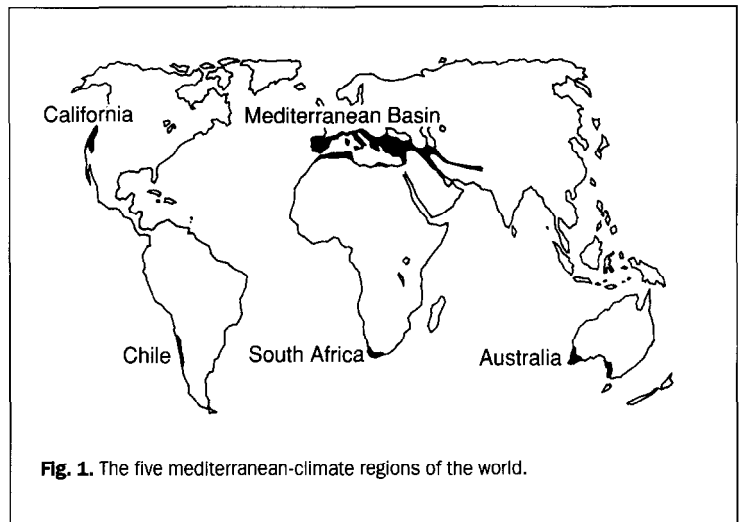


Fig. 1. The five mediterranean-climate regions of the world.

western Australia<sup>4</sup>. A similar explanation has been invoked for the species-rich but topographically and climatically uniform lowlands of the southwestern Cape<sup>3</sup>.

Cowling *et al.*<sup>3</sup> have suggested that regional diversity in mediterranean-climate regions is the product of local diversity and differentiation diversity in relation to environmental heterogeneity. Thus, regions with high local diversity and high turnover associated with long habitat and geographical gradients will support species-rich landscapes (Table 3). The driving force is rapid speciation and/or low extinction rates of habitat specialists and geographical vicariants<sup>6,33</sup>. This would explain why regional diversity converges in small areas of the southwestern Cape and southwestern Australia, which have similar heterogeneity and

### Box 1. Plant life in mediterranean-climate regions

Five geographically remote regions (Fig. 1, Table 1) have mediterranean-type climates with warm, dry summers and cool, wet winters. By agricultural standards, all these regions have infertile soils, especially in southwestern Australia and the southwestern Cape of South Africa (Table 3). These two areas also differ from the others in that they are ancient and relatively subdued landscapes on sheared continental margins; the landscapes of the Mediterranean Basin, California and Chile are in subduction zones and are consequently much younger and topographically complex – here, mountain building has occurred as recently as the late Tertiary and Quaternary<sup>8</sup>.

Before the onset of global cooling and aridification in the Pliocene, all five regions were clothed in subtropical forest<sup>15,36,37</sup>. These forests were subsequently replaced by sclerophyllous vegetation and dry woodlands, especially during the Quaternary when seasonal mediterranean-type climates developed. At the same time, fire became a significant factor in all regions except Chile, although contemporary natural fire regimes vary regionally (Table 3). Although the frequency of Quaternary climatic cycles was probably similar for all regions, glacial conditions were more severe in the northern than southern hemisphere areas<sup>36</sup>.

The contemporary vegetation of mediterranean-climate regions comprises an admixture of floras derived from relic subtropical forest and recent drought- and fire-adapted lineages, with the latter predominating in all regions, especially in Australia and the Cape<sup>4,15,17,33,35,37</sup>. The typical vegetation type is evergreen, sclerophyllous shrubland or heathland, namely chaparral in California; matorral in Chile; matorral, maquis and garrigue in the Mediterranean Basin; kwongan and mallee in Australia; and fynbos and renosterveld in South Africa<sup>8</sup>. However, most regions also support extensive areas of forest, woodland and xeric, drought-deciduous and semi-succulent shrubland.

The sclerophyllous shrublands of mediterranean-climate regions show varying degrees of ecological convergence<sup>8</sup>. The most striking is between kwongan and fynbos. They are distinguished from other shrublands by their relatively open shrub cover, high shrub species diversity, and the highest incidence in the world of obligate post-fire re-seeders, canopy seed storage (serotiny), and ant seed dispersal (myrmecochory)<sup>10,16</sup>. The remaining shrublands have denser shrub canopies; burn at much longer intervals; and have their diversity concentrated in short-lived herbs and subshrubs<sup>15,17,21</sup>.

**Table 1. Plant species diversity and conservation status of mediterranean-climate regions**

Region	Area (10 <sup>6</sup> km <sup>2</sup> )	Native flora <sup>a</sup>	Threatened taxa <sup>b</sup>	Major threats <sup>a</sup>
California	0.32	4300 (35)	718	urbanization, agriculture
Central Chile	0.14	2400 (23)	?	deforestation, grazing, agriculture
Mediterranean Basin	2.30	25 000 (50)	4251	deforestation, agriculture, grazing, urbanization
Cape	0.09	8550 (68)	1300	invasive alien plants, agriculture, urbanization
SW Australia <sup>c</sup>	0.31	8000 (75)	1451	agriculture, deforestation, introduced pathogens

<sup>a</sup>Data from Refs 3–5, 17 and 21. Percentage endemic is shown in brackets.

<sup>b</sup>Data from Ref. 1.

<sup>c</sup>Data for SE Australia are unavailable.

speciation histories<sup>28</sup>. But why does Chile, which has high topographical and climatic heterogeneity, and California, where these forms of heterogeneity combine with edaphic complexity to produce an enormous diversity of habitats<sup>21,29</sup>, have lower regional diversity than featureless landscapes of southwestern Australia and the ancient, worn-down 'hills' of the southwestern Cape? Why does the southwestern Cape have more than twice the species of similar-sized and equally heterogeneous landscapes of the southeast? We return to these questions in the section on speciation.

**Rarity**

Mediterranean-climate regions generally include very high numbers of rare taxa most of which are locally endemic habitat (principally edaphic) specialists associated with a limited number of lineages<sup>1–4,33</sup>. Levels of endemism and rarity are most pronounced in the southwestern Cape and southwestern Australia, where many hundreds of species occur naturally in limited numbers of populations (each <100 individuals)<sup>2–4</sup>. In these regions, range-restricted, rare taxa are overrepresented among fire-killed shrubs with short dispersal distances<sup>3,28,34</sup>. A possible (and testable) generalization regarding local endemics from all mediterranean-climate regions is that they are invariably poorly dispersed,

short-lived herbs or fire-sensitive shrubs with high numbers of sexually produced generations – attributes that would invariably lead to high rates of genetic recombinations and rapid speciation<sup>3,21,29</sup>.

**Speciation**

Speciation models in mediterranean-climate regions usually invoke climate change as the driving force for geographic speciation in topographically heterogeneous environments<sup>4,33</sup>. Cowling *et al.*<sup>3</sup> suggest that sympatric speciation could occur when disruptive selection operates on populations that have been isolated by fire or climate change, in habitats (usually soil types) that differ from those of the larger populations of the parent species. There are numerous examples of edaphically differentiated sister taxa in the Cape<sup>3</sup>, southwestern Australia<sup>4</sup> and California<sup>33</sup>. Since many of these neoendemics are short-lived and have discrete generations, speciation rates may have been very rapid<sup>3,4</sup>.

What do these models tell us about the evolution of regional diversity in the different mediterranean-climate regions? These patterns can be interpreted in terms of differential speciation and extinction rates<sup>6</sup>. In Chile, for example, the absence of fire as a natural factor and the relative mildness of Quaternary climates, owing to low continentality, resulted in the persistence of many long-lived and slow-evolving Tertiary forest lineages<sup>15</sup>. Although there has been considerable diversification of herbaceous lineages in response to aridification since the late Tertiary, limited speciation within woody genera has occurred<sup>15</sup>. Environmental conditions in California and the Mediterranean Basin are intermediate between those in Chile and those in South Africa/Australia (Table 3). During the Quaternary, a reasonably large flora of persistent Tertiary forest species would have been supplemented by moderate diversification of annuals and fire-adapted shrubs<sup>33,35</sup>. However, relatively extreme glacial conditions<sup>36</sup> would have resulted in high extinction rates, thereby depressing regional diversity.

In the Cape and Australia, two factors would have combined to elevate speciation rates and to depress extinction rates of their mediterranean floras: (1) high fire frequencies, which are a consequence of low soil fertility and associated high flammability<sup>16</sup>, and (2) relatively mild Quaternary climates – a result of strong maritime influences<sup>35</sup>. Although the incidence of frequent, high-intensity fires resulted in the large-scale extinction of many Tertiary forest lineages<sup>36,37</sup>, this loss was offset by the massive diversification within a limited number of predominantly fire-sensitive shrub lineages<sup>3,28</sup>. This, coupled with the persistence of many species (often in very small populations), has produced the remarkable species-flocks of the fynbos and kwongan floras.

Why then is regional diversity in the southwestern Cape higher than that in the southeastern Cape and southwestern Australia? The existence of greater topography in the Cape may have promoted greater geographical speciation than in topographically uniform Australia<sup>3,28</sup>. There is good evidence that glacial climates in the southeastern Cape were harsher than those in the southwest, and that this resulted in the widespread disappearance of fynbos (and consequently in

**Table 2. Patterns of local plant diversity in mediterranean-climate regions<sup>a</sup>**

	Shrublands			Woodlands and forest		
	n <sup>b</sup>	1 m <sup>2</sup>	1000 m <sup>2</sup>	n <sup>b</sup>	1 m <sup>2</sup>	1000 m <sup>2</sup>
California	13	7±6	31±10	18	14±3	56±9
Central Chile	3	8±2	100±15	1	7	25
Mediterranean Basin	29	14±10	70±54	8	11±7	64±50
Cape	54	16±6	70±21	11	10±4	56±21
SW Australia	33	13±10	68±20	10	7±3	33±13

<sup>a</sup>Data from Refs 3,38 and 39.

<sup>b</sup>n is the number of plots sampled.

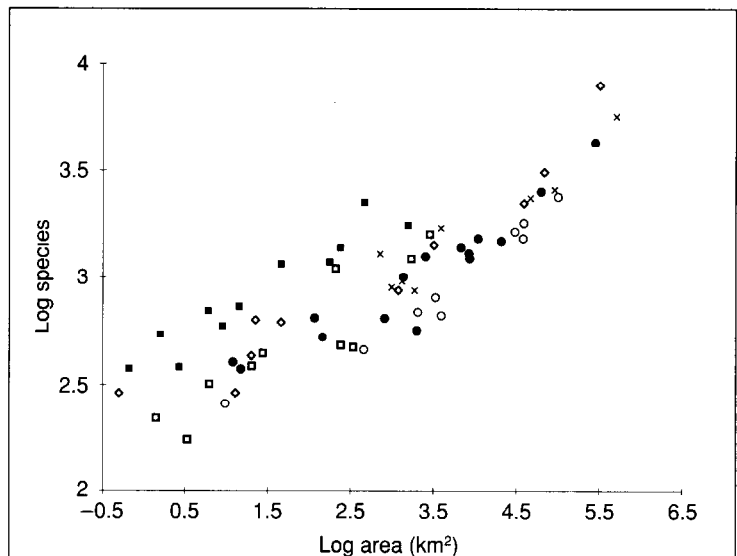
high extinction rates) during much of the Quaternary<sup>3</sup>. A similar scenario may apply to the southeastern zone of mediterranean Australia<sup>18</sup>. An important point is that the differences and similarities in patterns in regional diversity among mediterranean-climate regions are not the product of chance (cf. Ref. 38), but the deterministic outcome of the effects of slightly different selective forces on speciation and extinction rates of phylogenetically disparate floras<sup>15,28</sup>.

The interesting implication of these comparisons is that environmental heterogeneity *per se* is an unsatisfactory predictor of regional diversity patterns<sup>6,29</sup>. Given certain conditions (stable climates, predictably frequent fires and periodic drought, which promote generation turnover and diversification-prone lineages), natural selection will result in a very fine-scale discrimination of habitats<sup>6</sup>. This is precisely what has happened in the southwestern Cape and southwestern Australia: rapid speciation, coupled with low extinction rates, has produced extremely species-rich landscapes in otherwise relatively homogeneous areas. Here, botanists have identified a multitude of edaphic habitats<sup>3,4</sup> that may well be the product of rapid speciation leading to high diversity: in Rosenzweig's<sup>6</sup> words, 'Species diversity is the horse; habitat diversity is the cart' (p. 176).

**Threats**

The mediterranean-climate regions of the world comprise a substantial portion of the world's vascular plant flora (Table 1), including many ancient and taxonomically distinctive taxa; thousands of recently evolved species; 26 200 endemic species; many hundreds of endemic genera; several endemic families; and the Cape Floristic Region (the world's smallest floral kingdom)<sup>1-4</sup>. The conservation status of these regions is, however, very poor, and biodiversity is under severe and rapidly escalating threats<sup>8</sup>.

Agriculture and animal husbandry have been practised in the Mediterranean Basin for 10 000 years, and most ecosystems are now 'human-modified'<sup>17</sup>. Extensive transformations of the other regions began only after colonization by Europeans, about 500 years ago in Chile (earliest), and only 170 years ago in southwestern Australia (latest)<sup>8</sup>. All of the regions have very high concentrations of rare plant taxa, whose survival is threatened mainly by clearing for agriculture and urbanization, but also by alien plants and pathogens (Table 1). With the exception of the montane areas of the Cape, the current reserve networks in mediterranean-climate regions are inadequate<sup>4,8</sup>. Currently, some 142 vascular plant taxa from these regions are presumed extinct, 55 of these from southwestern Australia<sup>1</sup>. Although extinction rates may have peaked in some regions (e.g. California,



**Fig. 2.** Species-area curves and regressions from mediterranean-climate regions. Diamonds, SW Australia; filled squares, Cape (SW); unfilled squares, Cape (SE); crosses, Mediterranean Basin; unfilled circles, Chile; filled circles, California. Mediterranean Basin data are from the Iberian Peninsula. All slopes are homogeneous but intercepts (*k*-values) vary. Relative diversities of the different regions (see text) are ratios of their respective *k*-values. Data from Refs 3, 15 and 41.

Australia), they are probably accelerating in the Cape, Chile and the African zone of the Mediterranean Basin<sup>1</sup>.

**Conclusions**

Mediterranean ecosystems provide many opportunities for the comparative study of the determinants of plant diversity at local and regional scales. In particular, they offer unique potential for evaluating the effects of mediterranean-type climates and recurrent fire (both relatively recent selective forces) on coexistence and diversification in phylogenetically unrelated floras (true replicates). Moreover, the existence of richly diversified genera in each of the regions [e.g. *Carex* (126 spp.) and *Erigeron* (82 spp.) in California; *Senecio* (109 spp.), *Adesmia* (82 spp.) in central Chile; *Astragalus* (450 spp.), *Silene* (365 spp.) in the Mediterranean Basin; *Erica* (526 spp.), *Aspalathus* (245 spp.) in the Cape; *Acacia* (>400 spp.), *Eucalyptus* (>300 spp.) in southwestern Australia]<sup>3,4,15,17,33</sup> provide excellent material for the comparative study of ecological variation within monophyletic lineages. The large numbers of naturally rare species that have persisted for tens to hundreds of thousands of years

**Table 3. Relative environmental characteristics and plant diversity components in mediterranean-climate regions**

	Soil fertility <sup>a</sup>	Topographic heterogeneity <sup>b</sup>	Climatic heterogeneity <sup>b</sup>	Modal natural fire frequency (yr) <sup>c</sup>	Local diversity <sup>d</sup>	Differentiation diversity <sup>e</sup>	Regional diversity <sup>f</sup>
California	moderate	high	very high	40-60	low-moderate	moderate	moderate
Central Chile	high	very high	high	fire-free	low-?high	low-moderate?	low
Mediterranean Basin	high-moderate	high	very high	25-50	low-very high	moderate?	moderate
Cape (SW)	very low-moderate	moderate-high	high	10-20	moderate-high	high	high
Cape (SE)	low-moderate	moderate	high	10-20	moderate-high	moderate	moderate
SW Australia	very low-low	low	moderate	10-15	low-high	high	high

<sup>a</sup>Data from Ref. 8; <sup>b</sup>data from Refs 8 and 15; <sup>c</sup>data from Refs 8, 18 and 40; <sup>d</sup>see Table 2; <sup>e</sup>data from Refs 2-4; <sup>f</sup>see Fig. 2.

in small, fluctuating and poorly dispersed populations represent a challenge to population geneticists and conservation biologists<sup>4</sup>. However, without significant progress in halting the transformation and degradation of natural habitats in mediterranean-climate regions, many of these populations will soon disappear.

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