

RELATING PLANT TRAITS AND SPECIES DISTRIBUTIONS ALONG BIOCLIMATIC GRADIENTS FOR 88 *LEUCADENDRON* TAXA

WILFRIED THUILLER,^{1,5} SANDRA LAVOREL,² GUY MIDGLEY,^{3,4} SÉBASTIEN LAVERGNE,¹ AND TONY REBELO³

¹Centre d'Ecologie Fonctionnelle et Evolutive, CNRS, 1919 route de Mende, 34293 Montpellier Cedex 5, France

²Laboratoire d'Ecologie Alpine, CNRS, Université J. Fournier, BP 53X, 38041 Grenoble Cedex 9, France

³Climate Change Research Group, Kirstenbosch Research Center, National Botanical Institute, P/Bag x7, Claremont 7735, Cape Town, South Africa

⁴Center for Applied Biodiversity Science, Conservation International, 1919 M Street, N.W., Washington, D.C. 20036 USA

Abstract. Convergence between species niches and biological traits was investigated for 88 *Leucadendron* taxa in the Cape Floristic region. First, niche separation analysis was performed to relate species' niche positions/breadths with bioclimatic gradients. These gradients of aridity, seasonality of water availability, heat, and cold stress explained almost all variation in niche distributions. Species present in zones of extreme aridity or temperature exhibited narrower niche breadths than species situated in moderate sites, suggesting that stress-tolerant species do not occupy broad environmental ranges. Second, species niche positions were related to selected biological traits. Species of arid sites had significantly lower blade areas than did species of moist sites, confirming a functional trade-off between stress tolerance and productivity for leaf design. Species dispersal mode was correlated to species niche positions on the aridity gradient, suggesting allometrically determined correlations between leaf design and the design of reproductive structures. Species niche positions were also correlated with flowering traits, with species that initiate flowering in winter found under Mediterranean climate influence and species that initiate flowering in spring in sites with greater summer rainfall input. By interrelating species niche positions on bioclimatic gradients with selected biological traits, we explored a novel biogeographical approach to understanding species distributions.

Key words: Cape Floristic region, South Africa; climatic niches; dispersal mode; flowering phenology; gradient analysis; *Leucadendron*; morphological traits; niche breadth; niche position; outlying mean index analysis (OMI).

INTRODUCTION

Hutchinson (1957), defining the concept of ecological niche, suggested that the niche could be modeled as an imaginary space with many dimensions, in which each dimension or axis represents the range of some environmental variable required by the species. Thus, the niche of a plant might include the range of temperatures that it can tolerate, the intensity of light required for photosynthesis, specific humidity regimes, or minimum quantities of essential soil nutrients for uptake (Huston 1994). A useful extension of the niche concept is the distinction between fundamental and realized niches (Hutchinson 1957). The fundamental niche of a species includes the total range of environmental conditions that are suitable for existence without the influence of interspecific competition, predation, dispersal limitation, and natural or human disturbances (Pulliam 2000). The realized niche describes that part of the fundamental niche actually occupied by the species under these constraints and defines the

spatial distribution of species in a community and in a study area (Austin and Smith 1989).

Correlative methods used to predict current or future spatial distributions of plant species are based on the concept of realized niche (Thuiller 2003, Thuiller et al. 2003). A range of methods has been used to describe and separate ecological species niches in an environmental space, including canonical correspondence analysis (ter Braak 1986) or redundancy analysis (ter Braak 1987). Several studies have related species niches to bioclimatic conditions and/or to geological and land use conditions to describe and predict environmental niche positions and tolerances, or to forecast the effects of climatic change on the dynamics and patterns of species distributions (Malanson et al. 1992).

However little concern has been applied to establish a link between physiological, morphological and reproductive attributes of species and their niche positions and/or tolerance (but see Niinemets [2001]). Thus, it remains a challenge to choose ecologically meaningful functional attributes to understand and predict species distribution (Grime 1974, 1979, Weiher et al. 1999). Several studies have attempted to select such traits (e.g., specific leaf area or plant height) a priori to define plant functional types (PFT) and forecast im-

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⁵ E-mail: wilfried.thuiller@cefe.cnrs-mop.fr

pacts of global climatic change (Díaz and Cabido 1997, Westoby 1998). Other researchers have identified biological traits directly influenced by climatic factors by measuring the degree of correlation between corresponding climatic gradients (e.g., temperature or precipitation) and biological traits of species distributed along them (Parkhurst and Loucks 1972, Fonseca et al. 2000). When few species are studied, "hard" plant physiological traits can be measured accurately and comprehensively (e.g., growth rate or individual biomass). But when large numbers of species are examined, more easily measured "soft" traits, often morphological and sometimes reproductive, must be used (Hodgson et al. 1999). Hypotheses must therefore be derived, based on these studies and the ecophysiological literature, to select such soft traits (Grime et al. 1997, Hodgson et al. 1999). Leaf parameters (e.g., leaf area, specific leaf area and leaf thickness) and plant height have appeared correlated with climatic conditions (Díaz et al. 1998). Other traits, such as dispersal modes (Díaz et al. 1998), seed reserve mass and specific root length (Wright and Westoby 1999), and flowering dates and duration (Hodgson et al. 1999), are thought to relate to species distributions by determining their colonization abilities. Analyses of this nature have been made possible by the recent availability of databases of morphological and reproductive traits to deal with significant numbers of species and large geographical scales (Grime et al. 1997, Reich et al. 1999).

The aim of the present research is to propose an original approach to examine relationships between species' biological traits and their distributions along bioclimatic gradients over large geographical scales. First, we identified the main climatic gradients separating species niches. A multivariate analysis is the best way to perform such an assignment, as it allows an overall view of the species assemblage. We used a recently described multivariate method, the outlying mean index analysis (OMI analysis), that allows us to separate species niches and to measure the distance between the mean habitat conditions used by each species and the mean habitat conditions of the study area (Doledec et al. 2000). The second step of our approach, which to our knowledge is entirely original, consisted of correlating species niche breadths (variability of used habitats) and mean positions along climatic gradients obtained with the OMI with their morphological (height and leaf area) and reproductive traits (dispersal mode and flowering phenology).

Multispecies comparative studies such as this can be accused of phylogenetic mismatching, i.e., comparing species traits among species with very different evolutionary histories. One way to control for phylogenetic history is to apply this analysis to related species, preferably within a single genus, comprising species with a wide range of traits and occupying a broad geographical area. The genus *Leucadendron* provides just such an opportunity, as it is speciose, endemic to a con-

strained geographic region in the Cape Floristic region in South Africa, and has known monophyletic origin. The genus *Leucadendron* comprises short to tall evergreen shrubs with a variety of ecological requirements and contains both widespread and rare species.

Our analysis addressed the following questions: (1) What are the climatic gradients separating niches among *Leucadendron* species of the Cape Region? (2) What are the distributional amplitudes of different species on these main gradients? (3) Can species responses to these climatic gradients be related to biological traits, allowing for a first identification of climatic response groups?

DATA AND METHODS

Data set

Location.—The study area is situated in the Cape Floristic region (CFR, hereafter), in the southwestern corner of southern Africa. This region is made up of lowland coastal sandy plains and adjacent inland mountains of the Cape Fold Belt, with a sandstone-dominated geology. The region is a known biodiversity hotspot, and is covered by Fynbos vegetation, which can be described as a sclerophyll scrubland dominated by small-leaved shrubs (Ericaceae), aphyllous grass-like forms (Restionaceae), and broad-leaved shrubs (Proteaceae; Goldblatt and Manning 2000). Fynbos is fire prone vegetation, and burns with a frequency of 5–25 yr, but generally within 10–20 yr.

The genus *Leucadendron* (Proteaceae) is endemic to the CFR, and comprises 88 taxa (species and distinct subspecies) found throughout the region (Williams 1972). Species in this genus are evergreen, low to medium-high shrubs (0.5–3 m tall), and are dioecious, with females in half the species retaining seeds in serotinous cones until they are released after occasional fires, and the remainder cached by ants and rodents (Rebello 2001). The genus has many species that are killed by fire and dependent on seed regeneration (seeders), as well as a few species that are able to resprout after fire and thus not obligatorily dependent on seed regeneration (sprouters). Seed dispersal in most species in this genus is predominantly by wind dispersal, and this mode is common in several Proteaceae (Bond 1988), but in some species either ants or rodents disperse seeds.

The spatial distribution of species was recorded in a massive effort to atlas the family Proteaceae in southern Africa (Rebello 1992). Species presences were noted at more than 30 000 sites throughout the southern Cape region, and are available in GIS format (Rebello 2001). Species morphological traits were extracted from a related database (Rebello 2001).

Climatic variables.—The climatic data set used for this study contained 10 climatically derived variables considered critical to plant physiological function and survival. Variables used (see also Midgley et al. 2003)

TABLE 1. Percentages of explained inertia and cumulated explained inertia by axes following the multivariate analysis.

Axis	Explained inertia (%)			Cumulated explained inertia (%)		
	OMI	CCA	RDA	OMI	CCA	RDA
1	46	26	34	46	34	26
2	27	24	28	73	62	51
3	21	15	15	94	77	66

Note: Outlying mean index analysis (OMI) yields explanatory performance superior to both canonical correspondence analysis (CCA) and redundancy analysis (RDA).

were mean annual temperature (MAT), mean minimum temperature of the coldest month (MMTC), mean maximum temperature of the warmest month (MMTW), heat units (annual sum of daily temperatures exceeding 18°C, reported in degrees Celsius; Htunt), mean annual precipitation (MAP), summer (Sumprec) and winter precipitation (Winprec), annual potential evaporation (Apann), winter soil moisture days (Smdwin), and summer soil moisture days (Smdsum). The latter parameters refer to the number of days for which soil moisture was sufficient and air temperature appropriate for plant growth.

Niche separation

A number of multivariate methods are available to determine and separate species niches (Green 1971, Austin et al. 1984). The best-known technique is correspondence analysis (CA; Hill 1974), which is particularly well adapted for investigating habitat amplitudes of species (Chessel et al. 1982). Correspondence analysis has served as a basis for more complex approaches to relate the distribution of species in a study area to environmental factors. Canonical correspondence analysis (CCA) was originally developed to separate species niches along environmental gradients (ter Braak 1986) under the assumption of unimodal response curves. Similarly, redundancy analysis (RDA; ter

Braak 1987) has been used for analyzing linear relationships between species and gradient, and is particularly well adapted to situations with one strong limiting factor (Doledec et al. 2000).

Recently, Doledec et al. (2000) proposed a new multivariate analysis (implemented in ADE4 software; Thioulouse et al. 1997) that makes no assumption about the shape of species response curves to the environment and, unlike CCA and RDA, gives equal weight to species-rich and species-poor sites. This technique appeared as particularly suitable for our purpose. The result of this analysis describes the mean position of the species in the environmental space, which represents a measure of the distance between the mean habitat conditions used by the species and the mean habitat conditions of the study area. It measures the propensity of the species to select a specialized environment. Therefore, following the main gradients (or axes), we could analyze the variability of habitats used by each species ("niche breadth").

Niche separation and biological traits

We analyzed the relationship between species niche position on the main gradients and the biological traits selected as relevant to response to climate. These traits included quantitative (height and leaf area) and categorical traits (dispersal modes, season of beginning and end of flowering).

To analyze relationships between quantitative traits and the mean position of species on gradients, we used least-trimmed-squares (LTS) robust regressions, which are useful for fitting linear relationships when the data are not Gaussian and contain significant outliers (Rousseeuw and Leroy 1987). Like a usual linear regression, LTS provides an R -squared test value (called robust- R^2) that evaluates variance explained by the independent variables. We performed LTS regressions with the software S-Plus 2000 (Anonymous 1999).

Nonparametrical tests (Kruskal-Wallis and Wilcoxon tests) were used to analyze the relationships between

TABLE 2. Canonical correlation between bio-climatic variables and the first three axes for each multivariate analysis.

Bio-climatic variable	OMI			CCA			RDA		
	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3	Axis 1	Axis 2	Axis 3
Potential evapotranspiration	-0.946	-0.051	-0.088	-0.722	0.251	0.469	0.770	0.253	0.379
Soil moisture in summer	0.244	0.501	-0.244	0.848	0.320	-0.151	-0.823	0.330	-0.349
Soil moisture in winter	0.393	-0.834	0.321	-0.180	-0.678	-0.506	0.055	-0.865	-0.243
Mean annual precipitation	0.905	-0.132	0.201	0.393	-0.098	-0.568	-0.484	-0.268	-0.596
Summer precipitation	0.728	0.490	-0.278	0.757	0.396	-0.092	-0.741	0.410	-0.317
Winter precipitation	0.694	-0.565	0.341	0.048	-0.450	-0.598	-0.171	-0.651	-0.466
Mean annual temperature	-0.452	-0.233	-0.915	0.090	-0.285	0.828	-0.149	0.119	0.838
Maximum temperature of the warmest month	-0.759	0.133	-0.153	-0.481	0.368	0.426	0.498	0.381	0.271
Maximum temperature of the coldest month	0.077	-0.538	-0.761	0.294	-0.711	0.524	-0.420	-0.345	0.741
Heat units	-0.636	-0.205	-0.695	-0.228	-0.084	0.738	0.182	0.178	0.668

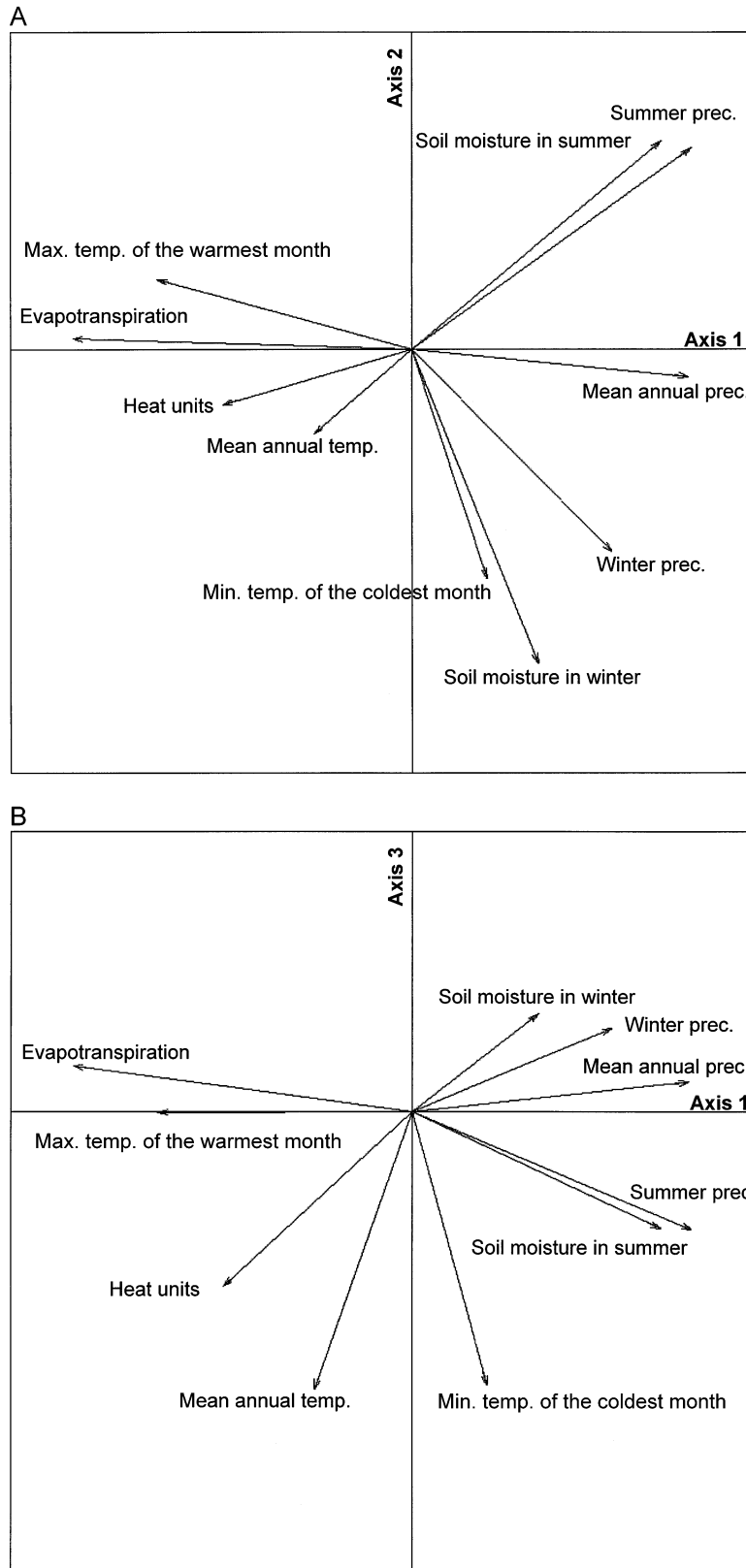


FIG. 1. Ordination diagrams on the first two axes of outlying mean index analysis (OMI): (A) representation of the explicative variables in OMI for axes 1 and 2; (B) representation of the explicative variables in OMI for axes 1 and 3.

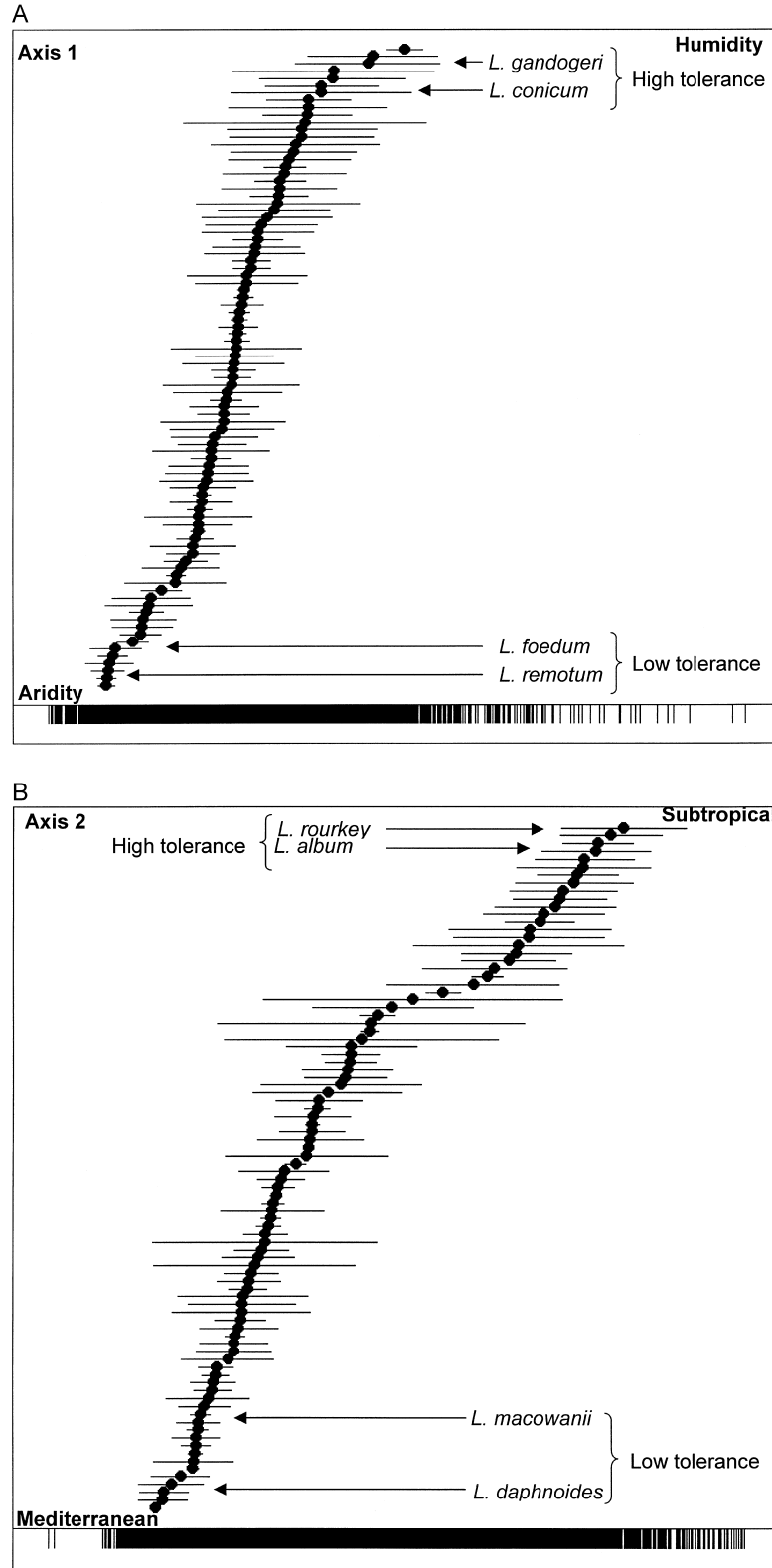


FIG. 2. Species niche position and niche breadth on the OMI axes for *Leucadendron* in the Cape Floristic region: (A) axis 1, aridity gradient; (B) axis 2, seasonality of precipitation; and (C) axis 3, temperature. The horizontal bars correspond to ± 1 SD and are interpreted as niche breadths. Small vertical bars at the bottom of each panel correspond to the position of sites along the axes.

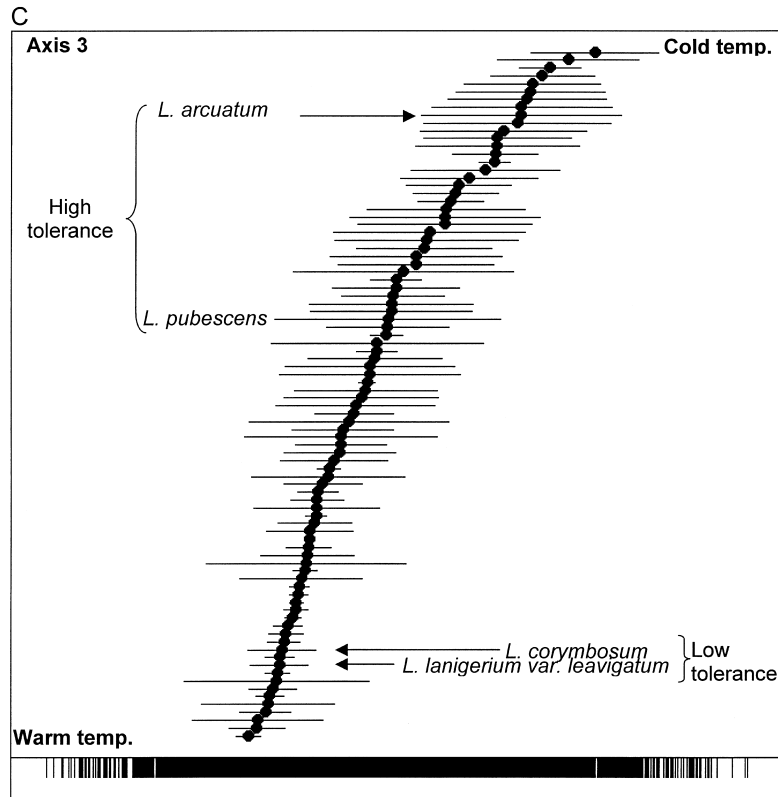


FIG. 2. Continued.

species niche position on bioclimatic gradients and categorical traits, for which the homoscedasticity (Levene test: $P > 0.05$) and Gaussian conditions were violated so that ANOVA could not be used. Kruskal-Wallis tests were performed to detect significant differences among traits attributes according to species niche positions. Wilcoxon tests were used to make pair-wise comparisons across attributes.

RESULTS

Niche separation

Although not presented in detail, canonical correspondence analysis (CCA) and redundancy analysis (RDA) were also performed at the same time as the outlying mean index analysis (OMI). There was evidence that OMI was more suitable than CCA or RDA to separate climatic species niches, and it successfully explained 94% of the total variability (Table 1). Ordination diagrams on the first two axes of the OMI analysis separated species niches according to two main gradients. Aridity, represented by a precipitation–evapotranspiration gradient, was the strongest gradient to affect species distributions (Table 2 and Fig. 1A). This factor did not have the same impact on all *Leucadendron* species (Fig. 2A). Species occurring in arid sites (*L. foedum* and *L. remotum*) had narrower niches (specialist species) than species present in more zones

of higher humidity (generalist species), such as *L. conicum* and *L. gandogeri*. However, some species found at sites in the middle of the gradient also had narrow niches. Hence, the aridity gradient separated out species tolerant to water stress, with a narrow climatic niche from generalist species occurring in more mesic sites. The second climatic gradient (Fig. 1B) appeared to represent seasonality of water availability (Table 2). This gradient was interpreted as a gradient from Mediterranean (high water availability in winter) to subtropical (low water availability in winter, but high in summer) influence. As occurred in the case of the aridity gradient, there were differences in terms of niche breadth across the gradient (Fig. 2B). Species situated in sites with Mediterranean climates (e.g., *L. daphnoides* and *L. macowanii*) seemed to be more specialized than species found in more subtropical areas (e.g., *L. rourkei* and *L. album*). The ordination diagram therefore separated species climatic niches into four zones: Mediterranean humid, Mediterranean dry, subtropical humid, and subtropical dry (Fig. 3), corresponding respectively to the southwestern Cape mountains, western Cape Mountains and coastal lowlands, southern Cape coastal lowlands, and eastern Cape interior.

The ordination diagram with the first and third axes displayed a third gradient driven by temperature (minimum temperature of the coldest month and mean an-

nual temperature variables) (Fig. 1B), separating species according to their tolerance of warm temperatures. As observed for the first two axes, this gradient also separated specialist and generalist species, and species tolerant vs. intolerant to high temperatures (Fig. 2C). Species present in sites with high mean temperature had narrower niches (e.g., *L. corymbosum* and *L. lanigerium* var. *leavigatum*) than species occurring elsewhere (*L. arcuatum* and *L. pubescens*).

Niche positions and biological traits

Relation between niche positions and dispersal modes.—Significant differences between positions on axis 2 indicated that species dispersed by ants were preferentially found in subtropical sites (low soil moisture in winter; Fig. 4B), compared to wind-dispersed species, which were present on the entire gradient, but preferentially in zones with Mediterranean climates (Wilcoxon test, $P = 0.008$). The other significant difference was between species dispersed by rodents and wind (Wilcoxon test, $P = 0.031$). Species dispersed by rodents were present primarily in the middle of the gradient, in climates typical of the mountains, and lowlands of the southern Cape (Fig. 4B). Relationships between dispersal modes and the mean position of species on of first and third axes, representing aridity and temperature, respectively, were not significant (Wilcoxon tests, $P > 0.05$; Fig. 4A, C).

Relation between niche positions and morphological traits.—There was no relationship between the mean position of species on gradients and plant height. Leaf area was correlated with the mean position of species on the aridity gradient (Fig. 5). Species present in arid sites had smaller individual leaf blade areas than species present in more humid habitats. Likewise, species occurring at sites with high potential evapotranspiration had small leaves, while species occurring in sites with high annual precipitation had larger leaves.

There was no relationship between leaf area and the mean position of species on both OMI axis 2 (seasonality of water availability) and OMI axis 3 (temperature); robust- $R^2 = 0.8\%$ and 1.6% , respectively.

Relationships between dispersal modes and morphological traits.—To further clarify the relationships between dispersal mode and species mean position on the three main gradients, we analyzed relationships between morphological traits (leaf area and height) and dispersal mode (Fig. 6). Species dispersed by ants or rodents were significantly shorter than wind-dispersed species (Wilcoxon test, $P = 0.007$ and 0.02 , respectively; Fig. 6A). The apparent difference between species dispersed by ants and rodents was not significant (Wilcoxon test, $P > 0.05$).

Species dispersed by ants had smaller leaf area than species dispersed by rodents and wind (Wilcoxon test, $P < 0.001$ in both comparisons). Species dispersed by rodents had greater leaf area than species dispersed by wind (Wilcoxon test, $P < 0.001$; Fig. 6B).

Relationships between niche positions and flowering phenology.—Dates of onset of flowering differed significantly according to the positions of species on the gradient of seasonality of water availability gradient (Kruskall-Wallis test, $P < 0.001$; Fig. 7). Species occurring in Mediterranean-climate sites tended to flower more frequently in winter; whereas, in subtropical sites, species flowered preferentially in spring (Wilcoxon test, $P = 0.000$). Similarly, the date of the onset of flowering changed significantly along the aridity gradient (Wilcoxon test, $P = 0.023$; Fig. 7A). Thus the beginning of flowering appeared highly dependent on the type of eco-region in which a species is present. Species found under a Mediterranean climate initiated flowering mainly in winter, whereas species found in the humid subtropical zone flowered in spring, and species occurring under dry subtropical climate flowered mainly in autumn.

Dates of end of flowering differed significantly according to the positions of species on the gradient of aridity (Kruskall-Wallis test, $P = 0.0276$; Fig. 7D). Similarly, the date of the end of flowering changed significantly along the seasonality of water availability gradient (Wilcoxon test, $P = 0.0259$; Fig. 7E). Species occurring in humid subtropical regions ended their flowering in spring rather than in winter and therefore had a shorter flowering period than species from other climatic areas.

DISCUSSION

Niche separation

The OMI analysis provided a powerful framework to separate niches of 88 *Leucadendron* species in the Cape Floristic region. We identified three main gradients governing the distributions of *Leucadendron* species. The gradients of aridity and precipitation seasonality defined four eco-regions: arid and humid Mediterranean, and arid and humid subtropical zones (roughly coincident with Köppen and Holdridge classifications for this region as mapped by Schulze [1973]). A third temperature gradient separated species tolerant to heat from those tolerant to cooler conditions. On each of these gradients, the *Leucadendron* genus included both generalists, with a wide distribution along a given gradient, and specialists of specific habitat positions, usually towards the more “stressful” part of the gradient (dry and hot, or with a winter rainfall regime). Specialists may be constrained to these conditions by competition or represent true stress-tolerant species.

Relationships among niches and soft plant traits

Based on the theory of natural selection, we would expect species with similar niches to share similar biological characteristics. Species in more arid sites were indeed found to have smaller leaves than species occurring in more humid sites, a pattern commonly ob-

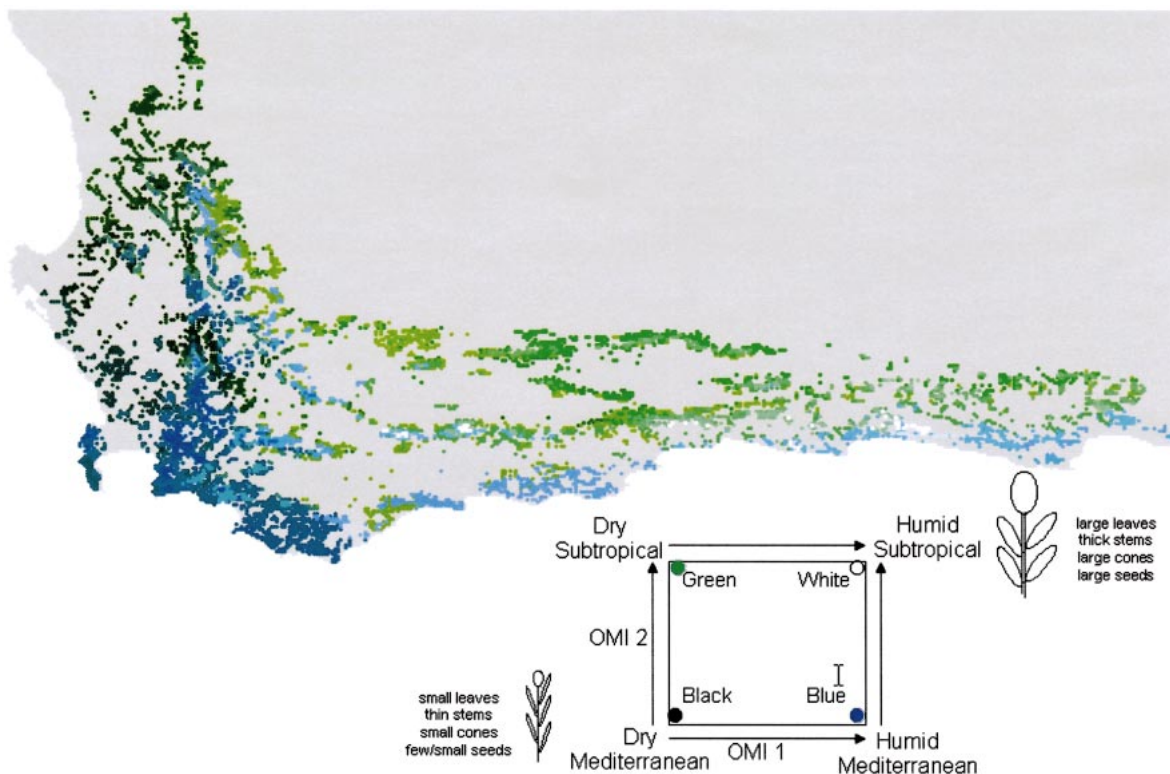


FIG. 3. Geographical variation in the first two OMI axes scores (axis 1, aridity gradient; axis 2, seasonality of precipitation) among the samples in the Cape Floristic region. Both OMI axes were overlaid, showing regional differences in the overall variation between the OMI axes. Black grid cells show low scores for both axes; white cells show high scores for both. Increasing blue color represents increasing scores along the aridity gradient; increasing intensities of green represent decreasing scores of seasonality of precipitation. Shoot designs and allometrically related aspects associated with moisture availability are indicated alongside these axes, with larger coned, larger leaved species associated with more humid climates.

served in a range of floras (Parkhurst and Loucks 1972, Givnish 1987, Fonseca et al. 2000). Physiologically, species occurring in arid environments developed strategies to limit the loss of water by reducing the exchange area with air. In terms of ecological strategies, species tolerant of water stress were mainly found in specialized habitats of arid zones, which possibly reflected a poorer competitive ability than generalists in more humid habitats. Inversely, species with larger leaves had a more generalist behavior, with widespread distributions and high habitat occupancy. This type of distribution may reflect a high competitiveness across a range of habitats, in accordance with previous research (Grime et al. 1997, Westoby et al. 2002), based on which individual leaf area may be interpreted as a trait associated with high competitiveness.

On the other hand, contrary to what might have been expected from plant strategy schemes (Grime 1979, Westoby 1998) and previous regional studies (Díaz and Cabido 1997), plant response to climate was independent of plant height. Considering that the analysis was conducted within a single genus representing a single life form, it may be worth considering a more detailed measure of plant aboveground biomass than plant

height (e.g., canopy volume, if not biomass itself). We can also not exclude confounding phylogenetic effects that might hide a general relationship between plant height and climatic distribution (Ackerly et al. 2000), although the likelihood is low due to the group's monophyly. Finally, our analysis did not consider a complicating factor, disturbance, and in particular fire, which represents a major disturbance in the study region, but for which no regional data set was available. Should plant height be related to response to disturbance (Grime 1979), the expected response (smaller plants in more disturbed habitats) would run counter to that expected for climate (taller plants in more mesic habitats). Over the climatic range of interest, the importance of fire is related to fuel load, which increases with decreasing aridity. Taken together, this combination of factors and expected responses would yield a globally neutral response.

Changes in leaf area along the aridity gradient might be the main cause of the relationship observed between dispersal mode and climate. Indeed, leaf area increased from species dispersed by ants to species dispersed by wind and species dispersed by rodents. Cornelissen (1999) demonstrated for 58 British semiwoody species

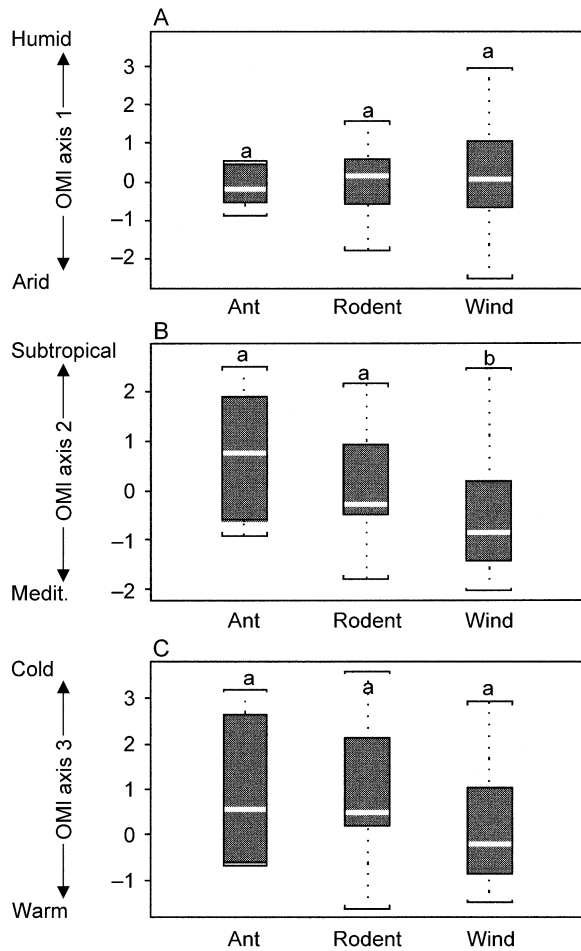


FIG. 4. Difference between *Leucadendron* species following the dispersion mode on the three OMI axes: (A) axis 1, aridity gradient; (B) axis 2, seasonality of precipitation; (C) axis 3, temperature. The only significant differences are for seasonality of precipitation between species dispersed by wind and ants ($P = 0.008$). Lowercase letters are placed above the bars that were compared using Wilcoxon tests. Bars with the same letters are not significantly different ($P > 0.05$).

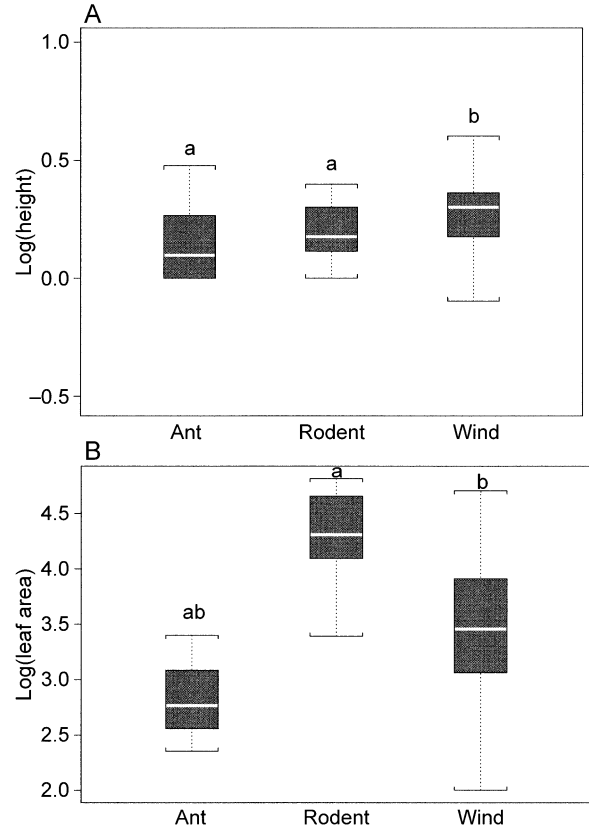


FIG. 6. Relation between (A) plant height or (B) leaf area and plant dispersion mode for *Leucadendron* in the Cape Floristic region.

that small seed mass and leaf area were found among species from stress-prone and early-successional habitats, whereas large seeds and leaves were found among competitive plants of later successional stages. In our study, this pattern may be explained by climatic and developmental constraints. Water stress decreases leaf size, thereby narrowing cone size and total seed mass

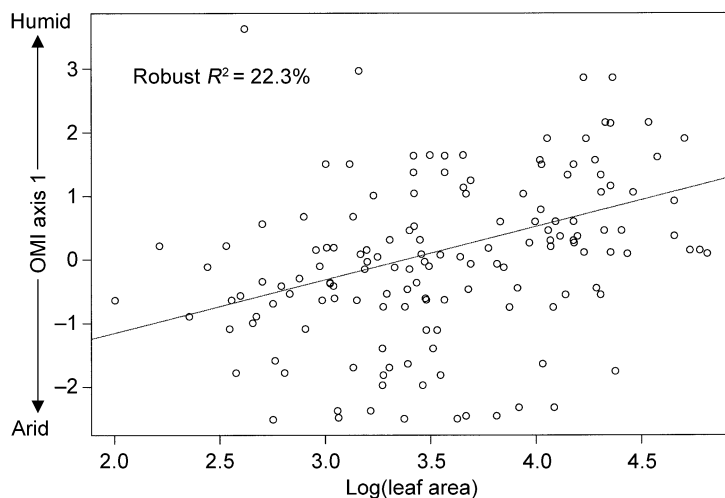


FIG. 5. Linear relation between the plant leaf area and the first OMI axis (aridity gradient) for *Leucadendron* in the Cape Floristic region.

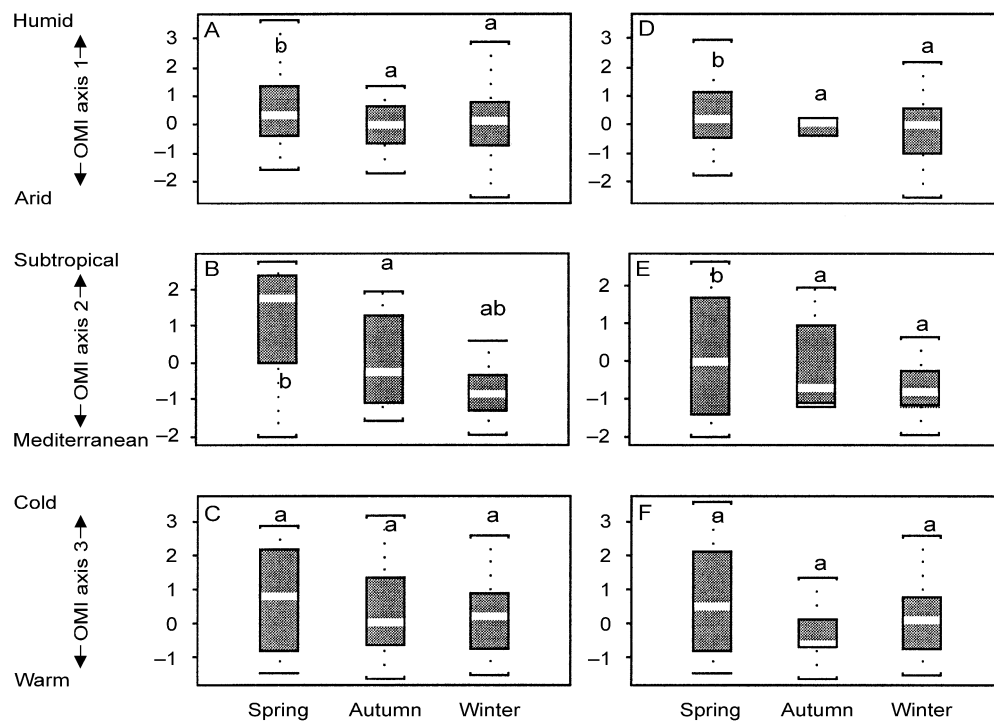


FIG. 7. Difference between (A–C) the onsets of flowering and (D–F) ends of flowering for *Leucadendron* species in the Cape Floristic region on the first three OMI axes: (A, D) OMI axis 1, aridity gradient; (B, E) OMI axis 2, seasonality of precipitation gradient; (C, F) OMI axis 3, temperature gradient. Upper extreme, upper quartile, median, lower quartile, and lower extreme are represented by each box. Lowercase letters are placed above or below the boxes that were compared using Wilcoxon tests. Boxes with the same letters are not significantly different ($P > 0.05$).

by an allometric effect (Bond and Midgley 1988). This relation implies strong environmental selection on dispersal adaptations in this genus that has evolved a remarkable range of dispersal mechanisms. In particular, dispersal by rodents (which is possibly unique to this genus in the Fynbos Biome) requires plants with large biomass that can afford a high absolute energy allocation to develop large seeds. Such interpretations would need to be tested by measurements of plant and seed biomass across habitat types. Finally, our results seem to support the hypothesis that species growing at the edge of environmental gradients (“stress-tolerators”) are slow growing, assuming that small leaves and associated low dispersal ability (by ants) implies slow growth (Grime et al. 1997).

Flowering phenology of *Leucadendron* species also varied with species niche positions along climatic gradients of the Cape region. We showed that species growing in similar eco-regions (humid and arid mediterranean and humid and arid subtropical eco-region) have developed similar phenologies. Consistent with Europe, species beginning to flower in winter are mainly found in the Mediterranean-climate zone. Our analysis indicated that in South Africa coexisting *Leucadendron* species, share attributes that give similar flowering phenology.

This study shows that to define reliable functional groups sharing similar traits and response to environment, a preliminary biogeographical study is needed to separate ecological niches, followed by the correlation of these to functional attributes. The biological traits used for this study were dependent on data availability, but additional analyses using traits with better established functional significance could further the study of patterns of adaptive evolution under climatic constraints. Westoby (1998) proposed the use of leaf mass per area (LMA), seed mass, and specific root length (SRL). In addition, other traits relevant to climate response could be used, such as leaf dry matter content (LDMC; Niinemets 2001), or seedling relative growth rate (RGR) and seed reserve mass (Wright and Westoby 1999). For instance, average LMA is well known to be higher at low rainfall, owing to thicker leaves, denser tissue, or both (Westoby et al. 2002). Further useful insights into leaf design in this group would derive from study of the geographic variation in LMA.

Relevance for global change studies

Rapid changes of climate and land use could have unexpected consequences for biodiversity (Chapin et al. 2000). Because of the enormous complexity of in-

dividual species and populations, an alternative to assess the effect of global change on diversity is to summarize species information into a relatively small number of general recurrent patterns: functional groups (Woodward and Cramer 1996, Smith et al. 1997). However, to date few studies have directly analyzed the response of functional groups, determined from direct distribution analyses and not a priori defined, to global change. Instead, global biome models to assess impacts of future climate changes on potential natural vegetation patterns have used plant functional types based on plant life forms and phenology (e.g., Prentice et al. 1992, Bachelet et al. 2001).

A more comprehensive framework would involve defining climate response groups based on responses of species distributions to climatic variables and on their functional attributes. As such, this paper presents one possible approach that simultaneously links distribution data, environmental variables and functional traits (Doledec et al. 1996, Legendre et al. 1997). Niche-based models could then be used to assess the impact of climate change on these groups by predicting their current climatic distributions and projecting future climatic envelopes under scenarios of climate change, as is commonly done for species distributions (e.g., Iverson and Prasad 1998, Thuiller 2003).

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