



RESEARCH PAPER

Global Ecology
and BiogeographyA Journal of
Microecology

WILEY

Functional traits explain the Hutchinsonian niches of plant species

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Funding information

Claude Leon Foundation; National Research Foundation South Africa; Deutsche Forschungsgemeinschaft, Grant/Award Number: SCHU 2259/3-3 and SCHU 2259/5-1; German Research Foundation, Grant/Award Number: 5-1 and 3-3; Stellenbosch University

Editor: Benjamin Blonder

Abstract

Aim: The Hutchinsonian niche is a foundational concept in ecology and evolutionary biology that describes fundamental characteristics of any species: the global maximum population growth rate (r_{\max}); the niche optimum (the environment for which r_{\max} is reached); and the niche width (the environmental range for which intrinsic population growth rates are positive). We examine whether these characteristics are related to inter- and intraspecific variation in functional traits.

Location: Cape Floristic Region, South Africa.

Time period: Present day.

Major taxa studied: Twenty-six plant species (Proteaceae).

Methods: We measured leaf, plant-architectural and seed traits across species geographical ranges. We then examined how species-mean traits are related to demographically derived niche characteristics of r_{\max} , in addition to niche optima and widths in five environmental dimensions, and how intraspecific trait variation is related to niche widths.

Results: Interspecific trait variation generally exceeded range-wide intraspecific trait variation. Species-mean trait values were associated with variation in r_{\max} ($R^2 = 0.27$) but were more strongly related to niche optima (mean $R^2 = 0.56$). These relationships generally matched trait-environment associations described in the literature. Both species-mean traits and intraspecific trait variability were strongly related to niche widths ($R^2 = 0.66$ and 0.59 , respectively). Moreover, niche widths increased with intraspecific trait variability. Overall, the different niche characteristics were associated with few, largely non-overlapping sets of traits.

Main conclusions: Our study relating functional traits to Hutchinsonian niches demonstrates that key demographic properties of species relate to few traits with relatively strong effects. Our results further support the hypothesis that intraspecific trait variation increases species niche widths. Given that niche characteristics were related to distinct sets of traits, different aspects of environmental change might affect axes of trait variation independently. Trait-based studies of Hutchinsonian

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niches thus yield important insights into the mechanisms shaping functional biodiversity, which should reinforce the role of traits in functional biogeography.

KEYWORDS

demography, environmental niche, functional biogeography, Hutchinsonian niche, niche optimum, niche width, plant functional traits, plant performance, population growth rate

1 | INTRODUCTION

The Hutchinsonian niche is a cornerstone of ecology, evolution and biodiversity research (Holt, 2009; Hutchinson, 1957). This niche concept denotes the set of environmental conditions for which a species can persist because its intrinsic population growth rate (r_0) is positive (Holt, 2009; Hutchinson, 1978). The Hutchinsonian niche is thus determined by the response of population growth rate to environmental variation. Characteristics of the Hutchinsonian niche describe fundamental ecological properties of species (Figure 1): the global maximum population growth rate (r_{\max}) a species can achieve; the niche optimum (the environmental conditions for which r_{\max} is reached); and the niche width (the range of environmental conditions for which r_0 is positive).

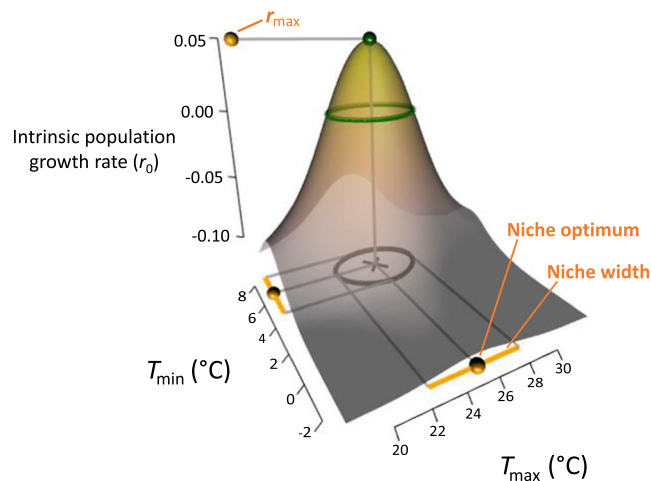


FIGURE 1 Characteristics of the Hutchinsonian niche of *Protea longifolia* (Proteaceae). The surface depicts the response of intrinsic population growth rate (r_0) to two environmental variables [minimum winter temperature (T_{\min}) and maximum summer temperature (T_{\max})]. Niche characteristics were derived from combining range-wide variation in key demographic rates and demographic niche models that estimated the responses of population growth rates to environmental variation in a Bayesian framework (see Materials and Methods section; Pagel et al., 2019). The orange point on the vertical axis is the global maximum population growth rate (r_{\max}). The niche optimum (indicated by the cross) is the combination of environmental conditions for which $r_0 = r_{\max}$. Orange points along the environmental axes depict the niche optimum in each environmental dimension. The green contour indicates the niche limit where $r_0 = 0$. Projecting this contour onto the environmental axes yields the niche width in each environmental dimension (orange lines) [Colour figure can be viewed at wileyonlinelibrary.com]

The Hutchinsonian niche is key to understanding how geographical ranges of species arise from environmental effects on demographic rates (Holt, 2009; Schurr, Pagel et al., 2012). The niche concept is also frequently invoked as the basis for species distribution modelling and to understand the shifts of species ranges under environmental change (Ehrlén & Morris, 2015; Guisan & Thuiller, 2005). Despite the central role of Hutchinson's niche framework for theoretical and applied ecology, our understanding of what determines interspecific variation in Hutchinsonian niches remains limited (Evans, Merow, Record, McMahon, & Enquist, 2016; Holt, 2009).

Functional traits are measurable features of an organism that affect fundamental processes of growth, reproduction and survival (*sensu* Violle et al., 2007) and play a central role in ecology (Díaz et al., 2016; McGill, Enquist, Weiher, & Westoby, 2006; Violle, Reich, Pacala, Enquist, & Kattge, 2014). Ecological theory has long postulated that traits such as rapid development and small body size should increase population growth in optimal environments (r_{\max} ; Pianka, 1970). Nowadays, the emerging research agendas of “functional population ecology” (Adler, Salguero-Gómez, Compagnoni, Hsu, & Ray-Mukherjee, 2014; Salguero-Gómez, Violle, Gimenez, & Childs, 2018) and “functional biogeography” (Violle et al., 2014; Yang, Cao, & Swenson, 2018) aim to link functional traits, fitness proxies and environmental gradients for multiple species. Studies generally address this challenging task by relating traits to niche estimates derived from species distribution models (SDMs) based on presence and abundance data (e.g., Chacón-Madrigal, Wanek, Hietz, & Dullinger, 2018; Costa et al., 2018). However, these approaches generally estimate occurrence probabilities of species and cannot necessarily resolve responses of population growth rates to environmental gradients across species geographical ranges (Ehrlén & Morris, 2015; Schurr, Pagel et al., 2012; but see Merow et al., 2014). Although trait-based studies of species' ecological niches have fundamental and applied importance in ecology, it remains largely unknown how functional traits relate to variation in demography and population growth rates, and thus to the Hutchinsonian niches of species.

In plant ecology, the task of linking traits, demographic performance and environmental variation is hampered by a lack of trait- and demographic data across the geographical ranges of multiple species (McGill et al., 2006; Salguero-Gómez et al., 2018; Violle et al., 2014; but see Treurnicht et al., 2016). Most trait-based studies thus examined trait-performance relationships from single, life stage-specific proxies of performance, often measured at single or few localities. For example, trait-based studies on tropical forest

trees have identified relationships between traits and demographic parameters such as individual growth and mortality (Poorter et al., 2008, 2010). However, recent studies show that functional traits have rather weak relationships to demography (Paine et al., 2015; Yang et al., 2018) and vital rate elasticities (Adler et al., 2014). Notably, these proxies may not fully reflect performance across an organism's life cycle and are not necessarily under strong selection (Reich, 2014; Violle et al., 2007). More integrative approaches that examine the associations between traits and multiple demographic rates across the life cycles of species (e.g., Visser et al., 2016), and how traits relate to variation in population growth rates may yield a better understanding of trait–performance relationships (Yang et al., 2018). Such integrative analyses are largely lacking in plant ecology, and it is thus not clear how functional traits relate to demographic niches and whether such trait–niche relationships match trait–environment associations reported in the literature (Table 1).

Trait–performance relationships may be further obscured by focusing on mean trait values at the species level alone while neglecting intraspecific trait variation across species' geographical ranges (Albert et al., 2010; Sides et al., 2014; Violle et al., 2012). Notably, intraspecific trait variation is important for determining the range limits of species (Estrada, Morales-Castilla, Caplat, & Early, 2016). Although species-mean trait values (which reflect the general phenotype across a species' geographical range) should relate to species niches, greater intraspecific trait variation also allows populations to grow in a broader range of environments, thereby extending niche widths (Fajardo & Siefert, 2019; Violle et al., 2012; Violle & Jiang,

2009). Positive relationships between intraspecific trait variation and niche widths result from phenotypic plasticity or adaptive trait differentiation between populations, both of which can increase the range of environmental conditions where population growth is positive (see Violle et al., 2012 and references therein). Despite these conceptual expectations regarding the underlying role of trait variation for niche optima and widths (e.g., Violle et al., 2012; Violle & Jiang, 2009), the real-world relevance of trait variation for species' Hutchinsonian niches has not been quantified for multiple species.

A trait-based understanding of species niches requires the identification of functional traits that relate to variation in demographic performance across environmental gradients. Although Westoby's (1998) leaf–height–seed (LHS) scheme provides a preliminary short-list of trait spectra [specific leaf area (SLA), plant height and seed mass], other traits may also describe plant responses to competition, environmental stress and disturbance (reviewed by Westoby & Wright, 2006). For example, responses to variation in climate and soil conditions depend jointly on leaf and wood traits (leaf economics spectrum: Wright et al., 2004; and wood economics spectrum: Chave et al., 2009; Reich, 2014) and seed traits (Lamont & Groom, 2013). In contrast, responses to disturbance, such as fire, depend on architectural traits and resprouting ability (Clarke et al., 2013), as well as seed traits (Lamont & Groom, 2013). Recent studies show that a suite of functional traits interact to define plant form and function (e.g., Díaz et al., 2016; Messier, Lechowicz, McGill, Violle, & Enquist, 2017). Traits can thus be used to position species along

TABLE 1 Functional traits measured for the 26 Proteaceae study species, with inter- and intraspecific trait variation [expressed as proportion of variance (%); see Figure 2b], major expected species-mean trait–environment associations and direction of the effect (+/–) from major literature sources and whether the pattern was found in our study (Figure 5a)

Functional trait	Interspecific variation (%)	Intraspecific variation (%)	Expected species-mean trait–environment associations (direction of effect; +/-)	Literature citations (see Appendix S1)	Supported in this study (Figure 5a)
SLA (m ² /kg)	89	11	Aridity (–), T_{\min} (–), soil fertility (+)	[1–6]	T_{\min}
Leaf width (mm ²)	98	2	Aridity (–), T_{\min} (–), T_{\max} (+), soil fertility (+)	[4–8]	–
Leaf longevity (years)	53	47	Aridity (+), T_{\min} (+); soil fertility (–)	[2, 3, 8–11]	–
Leaf N (mass %)	43	57	Aridity (+), T_{\min} (+); fire interval (+)	[4, 8–10, 12, 13]	–
Plant height (cm)	77	23	Aridity (–); T_{\min} (–); soil fertility (+)	[6, 14–16]	T_{\min}
Wood density (g/cm ³)	77	23	Aridity (+); T_{\max} (+); soil fertility (–)	[2, 3, 9, 12, 17, 18]	–
Ramification	88	12	Aridity (+); fire interval (+)	[9, 10, 19]	–
Sprouting	100	0	Fire interval (–); T_{\min} (+)	[10, 20, 21]	Fire interval
Seed mass (g)	97	3	Aridity (+); T_{\min} (+); soil fertility (–)	[12, 20, 22, 26]	Aridity, T_{\min}
Seed N (mass %)	51	49	Aridity (+); soil fertility (–)	[28]	–
Seed N:P ratio	54	46	Aridity (–); T_{\min} (–); soil fertility (+)	[10, 22, 27]	Aridity, T_{\min}

Note: The Supporting Information (Appendix S1) provides a description of the field methods for measuring traits and full citations for major literature sources. The Supporting Information (Table S3) provides details on the environmental variables. Literature sources: [1] McDonald et al. (2003); [2] Reich et al. (2003); [3] Carlson et al. (2011); [4] Cunningham et al. (1999); [5] Yates et al. (2010); [6] Fonseca et al. (2000); [7] Thuiller et al. (2004); [8] Wright et al. (2004); [9] Ackerly (2004); [10] Lavorel and Garnier (2002); [11] Reich et al. (1992); [12] Díaz et al. (2016); [13] Reich and Oleksyn (2004); [14] Moles et al. (2009); [15] Westoby and Wright (2006); [16] Weiher et al. (1999); [17] Chave et al. (2009); [18] Reich (2014); [19] Harris and Pannell (2010); [20] Bond and Midgley (2001); [21] Clarke et al. (2013); [22] Lamont and Groom (2013); [23] Stock et al. (1990); [24] Westoby (1998); [25] Salisbury (1974); [26] Baker (1972); [27] Lamont et al. (1985); [28] Milberg et al. (1998).

the slow–fast continuum of plant life histories (Adler et al., 2014; Salguero-Gómez et al., 2016). For example, long-lived perennial plants with slow growth and delayed reproduction are characterized by ‘slow’ traits (low SLA; long leaf longevity, high wood density and large seeds; Díaz et al., 2016; Reich, 2014; Salguero-Gómez et al., 2016). Furthermore, population persistence should increase with the ability to store reproductive potential during periods of adverse environmental conditions; for example, by longevity of stress-tolerant adults or seed banks, or resprouting from storage organs after disturbance (Bond & Midgley, 2001; Tonnabel et al., 2018).

Here, we relate inter- and intraspecific variation in 11 functional traits to the Hutchinsonian niches of 26 Proteaceae species in the Cape Floristic Region (CFR; South Africa). We measure major leaf, plant-architectural and seed traits across species’ geographical ranges and relate these to key characteristics of species’ Hutchinsonian niches (the global maximum population growth rate, r_{\max} , as well as niche optima and widths along individual environmental dimensions; Figure 1) that were derived from demographic responses to major environmental gradients (aridity, maximum summer and minimum winter temperature, soil fertility and fire disturbance; Pagel et al., 2019). Our main objective is to examine how species-mean trait values and intraspecific trait variation relate to these characteristics of species’ niches. In light of this, we hypothesize that: (a) traits vary more between species than within species’ geographical ranges; (b) species-mean traits relate to niche characteristics, notably to the r_{\max} and niche optima along environmental gradients; (c) relationships between species-mean traits and niche optima generally match individual trait–environment associations reported in the literature (Table 1); and (d) intraspecific trait variability relates more strongly to niche widths than to species-mean traits, with positive effects of intraspecific trait variation on niche widths.

2 | MATERIALS AND METHODS

2.1 | Study region and study species

The CFR is characterized by a Mediterranean-type climate, with cool, wet winters and hot, dry summers, and has highly leached, nutrient-deficient soils (Allsopp, Colville, & Verboom, 2014). The dominant vegetation types are sclerophyllous, fire-prone shrublands, which are often dominated by members of the Proteaceae family (Rebelo, 2001). Proteaceae of the CFR show high functional diversity and are model organisms for ecological research (Schurr, Esler, Slingsby, & Allsopp, 2012). Within the global spectrum of plant functional traits, Proteaceae species exhibit conservative nutrient use and reproduce from relatively large, nutrient-rich seeds (Díaz et al., 2016; Lamont & Groom, 2013).

We studied 26 Proteaceae species of the genera *Protea* and *Leucadendron* (including ‘non-sprouters’ without fire-protected buds and ‘resprouters’ with fire-protected buds) that are serotinous (= brady-sporous) and have a fire-linked life cycle (Treurnicht et al., 2016: fig. 1a). These species form long-lived canopy-stored seed

banks (but no persistent soil seed banks), retaining seeds in woody, fire-proof cones for several years until fire (Lamont, Maitre, Cowling, & Enright, 1991). Fire triggers seed release and dispersal, and the recruitment of new individuals is generally confined to the first few years after fire. Fire is also the major source of adult mortality and strongly reduces the canopy size of surviving resprouters (Treurnicht et al., 2016). Consequently, Proteaceae populations typically establish as stands of uniformly sized individuals. This fire-driven life cycle allows the direct quantification of key demographic rates (fecundity, recruitment and adult fire survival) that span the entire life cycle of the study species, describes how demographic rates change with post-fire age and implicitly accounts for variation in plant growth and size (e.g., Lamont et al., 1991; Treurnicht et al., 2016).

2.2 | Measurement of leaf, plant-architectural and seed traits across species’ geographical ranges

We measured 11 functional traits from 26 plant species, constituting major leaf, plant-architectural and seed traits, which comprise the LHS scheme (Westoby, 1998), but also included other leaf, plant-architectural and seed traits (Westoby & Wright, 2006). We measured these traits for between eight and 22 populations per species (Supporting Information Table S1), totalling 305 populations and 1,220 individual plants across the study species. Trait sampling sites corresponded to (population-level) geographical locations of a set of demographic study sites (Figure 2a) from Treurnicht et al. (2016). For each sampled population, we randomly selected three adult plants (for dioecious *Leucadendron* species, three plants per sex) and measured four leaf traits [SLA, leaf width, leaf longevity and leaf nitrogen (N) content], four plant-architectural traits (plant height, wood density, ramification index and resprouting ability) and three seed traits (seed mass, seed N content and seed N:P ratio). Resprouting ability is a dichotomous trait that varies only between species (Rebelo, 2001). Leaf and seed nutrient traits were measured on samples pooled for each population. All other traits were measured at the individual level, following standard protocols (Supporting Information Appendix S1).

2.3 | Range-wide demographic data and responses to environmental gradients

Data on variation in key demographic rates (fecundity, recruitment and adult fire survival) were collected across the geographical ranges of the study species (Figure 2a). The total fecundity of an adult plant since the last fire (the size of individual canopy seed banks) was determined as the product of total closed cones per plant and the number of fertile seeds per cone. This measures the total seed output of a plant per fire interval, given that the plant would burn shortly after sampling. Per capita post-fire seedling recruitment (the ratio between post-fire recruits and pre-fire adults that are visible as skeletons) and adult fire survival (proportion of post-fire surviving adults among all pre-fire adults) was measured in recently

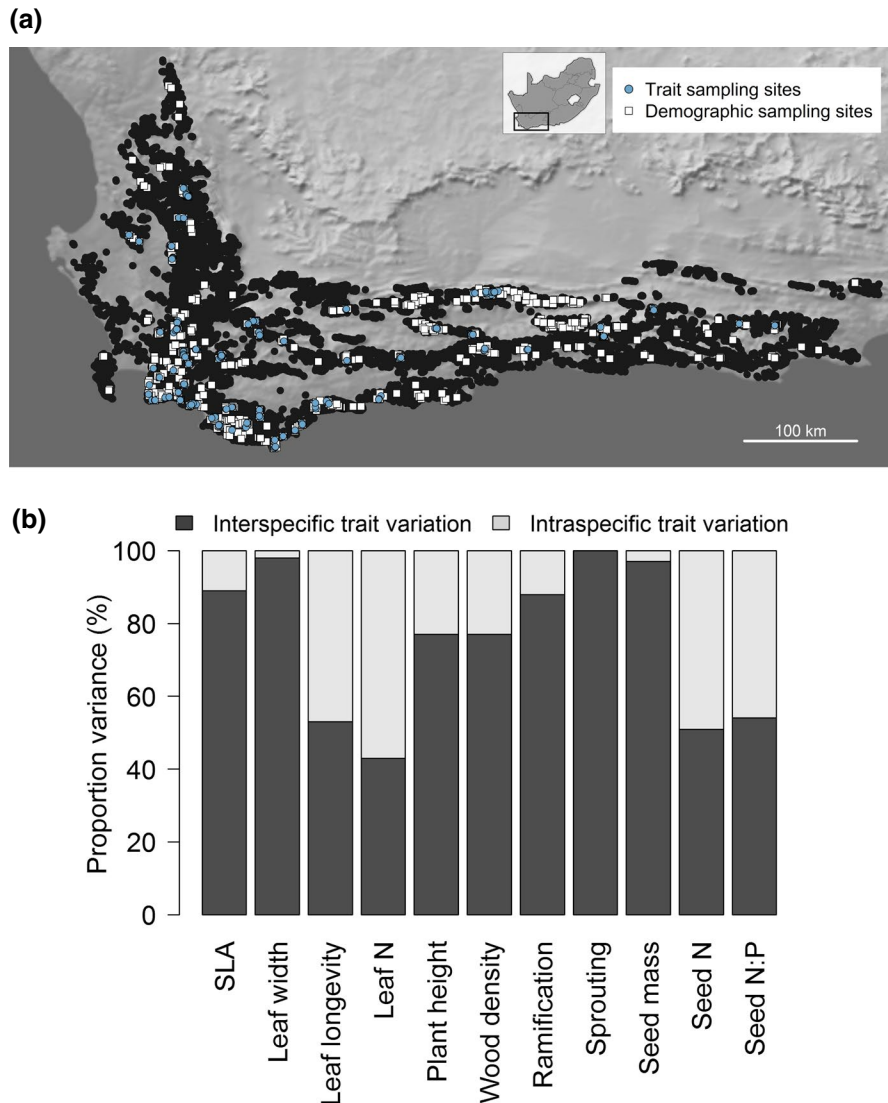


FIGURE 2 (a) Map of trait sampling sites (blue circles) that corresponded to a set of demographic study sites (white squares) from Treurnicht et al. (2016) for 26 Proteaceae species in the Cape Floristic Region (CFR; South Africa). The black area indicates the geographical distribution of the entire Proteaceae family in the CFR study region (Rebello, 2001). (b) Range-wide trait variation between species and populations (inter- and intraspecific variation, respectively) in 11 functional traits, including major leaf, plant-architectural and seed traits. The bar graph shows variance components estimated by trait-specific linear mixed effect models (see Materials and Methods and Table 1) [Colour figure can be viewed at wileyonlinelibrary.com]

burnt populations. Sampled populations covered the major environmental gradients within the geographical range of each species and the variation in population density. In total, the demographic data comprised 3,617 population-level records for the 26 study species (for species-specific sample size, see Supporting Information Table S2; for a full description of the demographic sampling, see Treurnicht et al., 2016).

Species-specific demographic responses to environmental gradients were analysed with hierarchical demographic response models (Pagel et al., 2019) that explain intraspecific variation in per-capita fecundity $\mu.fec(E,T,D)$, per-seed establishment rate $\pi.est(E,D)$ and adult fire survival probability $\pi.surv(E,T,D)$ as functions of four climatic-edaphic covariates (E), the length of the fire interval (T) and population density (D). Climatic-edaphic variables (E) included: (a) a

summer month aridity index (hereafter, "aridity", in millimetres per degree Celsius; based on De Martonne, 1926); (b) mean daily minimum winter temperature (T_{min} ; in degrees Celsius); (c) mean daily maximum summer temperature (T_{max} ; in degrees Celsius); and (d) an index of soil nutrient status ["soil fertility"; from low fertility (0) to high fertility (10); for details, see Supporting Information Table S3]. The response of each demographic rate to the different environmental variables $k = 1 \dots K$ was described by a multiplication of Gaussian curves of the form $\exp[-(E_k - opt_k)^2 / (2sig_k^2)]$, where mean parameters opt_k describe the optima and corresponding variance parameters sig_k^2 describe the width of the response curve. Depending on whether the optima of these Gaussian responses lie within the observed environmental range or not, the responses can be unimodal or monotonic. Demographic responses were estimated for all three demographic rates of each study

species, except that responses of adult fire survival rates to environmental variation were modelled for resprouter species only (because non-sprouters have low fire survival, with very little intraspecific variation; Treurnicht et al., 2016). Further details on the model structure, formulation of density dependence and Bayesian parameter estimation are provided by Pagel et al. (2019).

2.4 | Demographic niche characteristics

Combining the response curves of all three demographic rates, we then predicted variation of intrinsic (low-density) population growth rates (r_0) along environmental gradients. Based on the fire-driven life cycle of our study species, the expected population size N after a fire interval of length T can be calculated as the sum of adult survivors and new recruits that establish after a fire:

$$N_{t+T} = N_t \times \pi.\text{surv}(\mathbf{E}, T, D) + N_t \times p.\text{fem} \times \mu.\text{fec}(\mathbf{E}, T, D) \times \pi.\text{est}(\mathbf{E}, D),$$

where the parameter $p.\text{fem}$ specifies the average proportion of female individuals (only for the dioecious *Leucadendron* species). To calculate r_0 , we set all density variables to zero and first calculated the rate of change in population size per fire interval:

$$\lambda_0(\mathbf{E}, T) = \frac{N_{t+T}}{N_t} = \pi.\text{surv}(\mathbf{E}, T) + \mu.\text{fec}(\mathbf{E}, T) \times \pi.\text{est}(\mathbf{E}) \times p.\text{fem}.$$

The intrinsic population growth rate (r_0) was then calculated on an annual basis as:

$$r_0(\mathbf{E}, T) = \frac{\log[\lambda_0(\mathbf{E}, T)]}{T}.$$

From the predicted r_0 in the five-dimensional niche space (constituting four climatic–edaphic variables in \mathbf{E} and fire interval T), we then derived the following characteristics of species' niches (see Figure 1). Niche optima per environmental dimension were determined from the combination of environmental conditions for which r_0 is maximal. We identified the niche optimum by numerical global optimization (using the box-constraint quasi-Newton method; function 'optim' in R v.3.1.0). The global maximum population growth rate (r_{max}) of each species was calculated as the value of r_0 at this environmental optimum. Niche widths in each environmental dimension were determined as the range of each environmental variable for which r_0 is positive when all other environmental variables are set to their optimal values. The Supporting Information (Table S4) provides a complete overview of the estimated niche characteristics and posterior standard deviations. Given that individual demographic rates were estimated from natural communities and incorporate effects of interspecific biotic interactions, the estimated niches ($r_0 > 0$) represent the realized niche (or "post-interactive" niche; *sensu* Hutchinson, 1978).

2.5 | Trait variation and trait-niche analyses

We first quantified trait variation between species and populations (inter- and intraspecific variation, respectively) and then investigated how species-mean trait values and intraspecific trait variation related to species' niche characteristics. Niche characteristics were scaled, and quantitative trait values (excluding resprouting ability) were \log_{10} -transformed and scaled to ensure comparability across analyses. Resprouting ability ('Sprouting') was a binary variable (zero: non-sprouter; one: resprouter).

To test the first hypothesis of whether the 11 traits vary more between than within species, we partitioned trait variance into variation between species and populations across species geographical ranges (inter- and intraspecific variation, respectively). To this end, we fitted a linear mixed effect model for each trait (R package "lme4"; Bates, Maechler, Bolker, & Walker, 2015) that contained nested random effects of populations within species (except for nutrient traits, for which only a random effect of species was included because samples were pooled at the population level; see Supporting Information Appendix S1). Furthermore, to address hypotheses 2 and 3 of how species-mean traits relate to niche characteristics, we examined associations between species-mean trait values and r_{max} , and between niche optima and widths for each environmental dimension. We used phylogenetic generalized least squares (PGLS) regression with a Brownian correlation structure (R packages: "nmls", Pinheiro, Bates, DebRoy, & Sarkar, 2015 and "ape", Paradis, Claude, & Strimmer, 2004) determined by an ultrametric phylogenetic tree (Supporting Information Figure S1). For each niche characteristic and environmental dimension, we applied automated model selection that uses the sample size-corrected Akaike information criterion (AICc; Burnham & Anderson, 2002) to rank alternative models that represented all possible combinations of explanatory trait variables (using R package "MuMIn"; Barton, 2016). We calculated an AICc-weighted marginal average of all models with $\Delta\text{AICc} < 10$ (Burnham & Anderson, 2002). This provides a robust basis for evaluating the effect sizes of multiple variables (Grueber, Nakagawa, Laws, & Jamieson, 2011). For these averaged models, we then evaluated overall model fit as the proportion of variance explained by trait effects (R^2 ; following Ives, 2018) and considered the effect size of each trait as the corresponding standardized regression coefficient. Specifically, to address our fourth hypothesis of how intraspecific trait variability relates to niche widths, we quantified the dependence of niche widths on intraspecific trait variation from alternative model analyses using the between-population standard deviation per trait as predictor variables. As above, we used automated model selection and model averaging to evaluate the overall model fit and effect sizes of intraspecific trait variation on niche widths, and compared these with the overall model fit and effects of species-mean traits on niche widths.

3 | RESULTS

3.1 | Range-wide inter- and intraspecific trait variation

Interspecific trait variation generally exceeded intraspecific trait variation across the geographical ranges of our 26 study species. Ten of the 11 functional traits varied more between than within species (Figure 2b; Table 1; Supporting Information Figure S2). Leaf N was the only trait for which intraspecific variation across species geographical ranges exceeded interspecific variation (57%; Figure 2b). We generally found relatively weak correlations both among species-mean traits and intraspecific trait variation (pairwise Spearman correlation coefficients never exceeded 0.64; Supporting Information Figure S3), and the study species were well dispersed in trait space (Supporting Information Figure S4).

3.2 | Interspecific variation in niche characteristics

The estimated r_{\max} ranged from 0.28 to 1.53 for the study species (mean: 0.74; Supporting Information Table S4). Niche optima in each environmental dimension also varied substantially between species; for example, T_{\min} optima ranged from -1.73 to 9.65 °C, which corresponds to 95% of the total range in T_{\min} across the study region. Interspecific variation in other niche optima covered between 65 and 100% of the environmental variation in the study region (Supporting Information Tables S3 and S4). Likewise, niche widths in each environmental dimension varied substantially between species. The range of environments for which individual species showed positive population growth covered between 21.5% (aridity; *Leucadendron modestum*) and 100% (aridity: *Protea laurifolia*; and soil

fertility: 14 species) of the total environmental range in the study region (Supporting Information Tables S3 and S4).

3.3 | Effects of species-mean traits on r_{\max} and niche optima

Species-mean traits explained a limited amount ($R^2 = 0.27$) of the overall variation in r_{\max} compared with other niche characteristics, and no single trait had a significant effect (Figures 3 and 4). In contrast, species-mean traits explained substantial proportions of the interspecific variance in niche optima (mean R^2 across all environmental dimensions = 0.57; range: 0.45–0.68; Figure 3b). Niche optima for aridity ($R^2 = 0.65$) and T_{\min} ($R^2 = 0.68$) increased with SLA and seed mass but decreased with seed N:P (Figure 5a). The T_{\min} optima additionally decreased with plant height (Figure 5a). Niche optima for fire interval ($R^2 = 0.56$) depended exclusively on resprouting ability (i.e., optimal fire intervals were shorter for resprouters than for non-sprouters; Figure 5a). These relationships between species-mean traits and niche optima generally matched trait–environment associations reported in the literature; seven of the eight significant effects that we found corresponded to these expectations (Table 1; Figure 5a).

3.4 | Effects of species-mean traits and intraspecific trait variation on niche widths

Species-mean traits generally explained considerable proportions of the interspecific variance in niche widths (mean $R^2 = 0.66$; range: 0.55–0.78; Figure 3c). Niche widths for T_{\min} ($R^2 = 0.71$) increased with leaf longevity and resprouting ability, whereas T_{\max} widths ($R^2 = 0.64$) increased with wood density only (Figure 5b). The niche

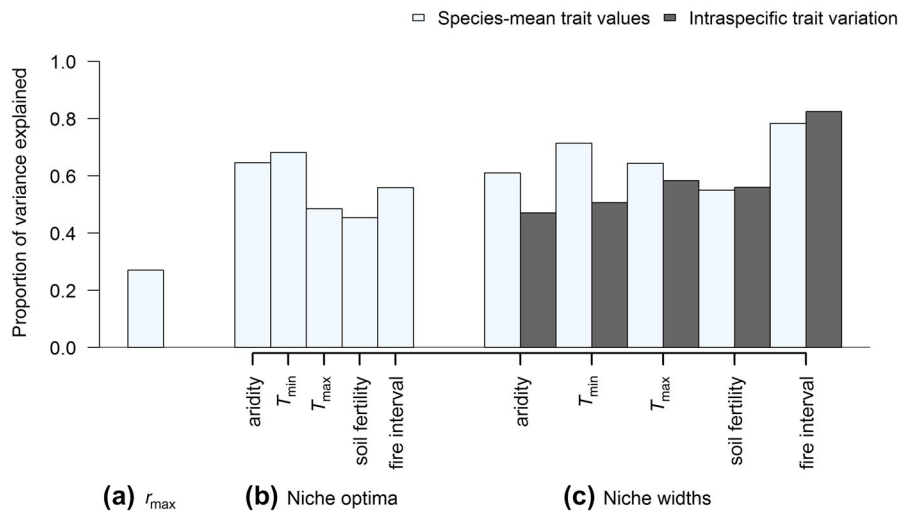


FIGURE 3 Proportion of variance explained (R^2) by species-mean trait values (light blue bars) and intraspecific trait variation (grey bars) for three niche characteristics of (a) r_{\max} , in addition to (b) niche optima and (c) niche widths in five major environmental dimensions for the 26 Proteaceae study species. Niche optima and widths were defined along environmental gradients of climate (aridity, T_{\min} and T_{\max}), soil fertility and fire interval (for details, see Supporting Information Table S3). The R^2 values are from phylogenetic generalized least square average models ($\Delta AICc < 10$) [Colour figure can be viewed at wileyonlinelibrary.com]

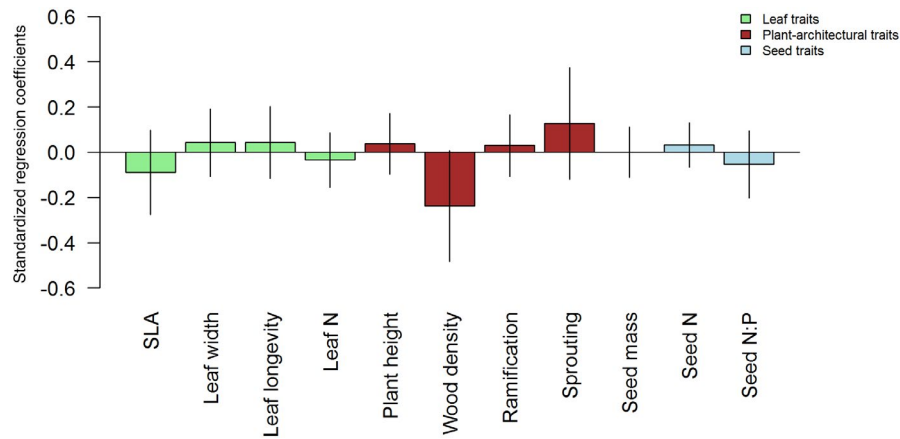


FIGURE 4 Effects of species-mean trait values on the global maximum population growth rate (r_{max}) for 26 Proteaceae species. Bars are standardized regression coefficients with associated errors (whiskers) of 11 functional traits from phylogenetic generalized least squares averaged models ($\Delta AICc < 10$). Resprouting ability ('Sprouting') is a dichotomous variable (zero: non-sprouter; one: resprouter) [Colour figure can be viewed at wileyonlinelibrary.com]

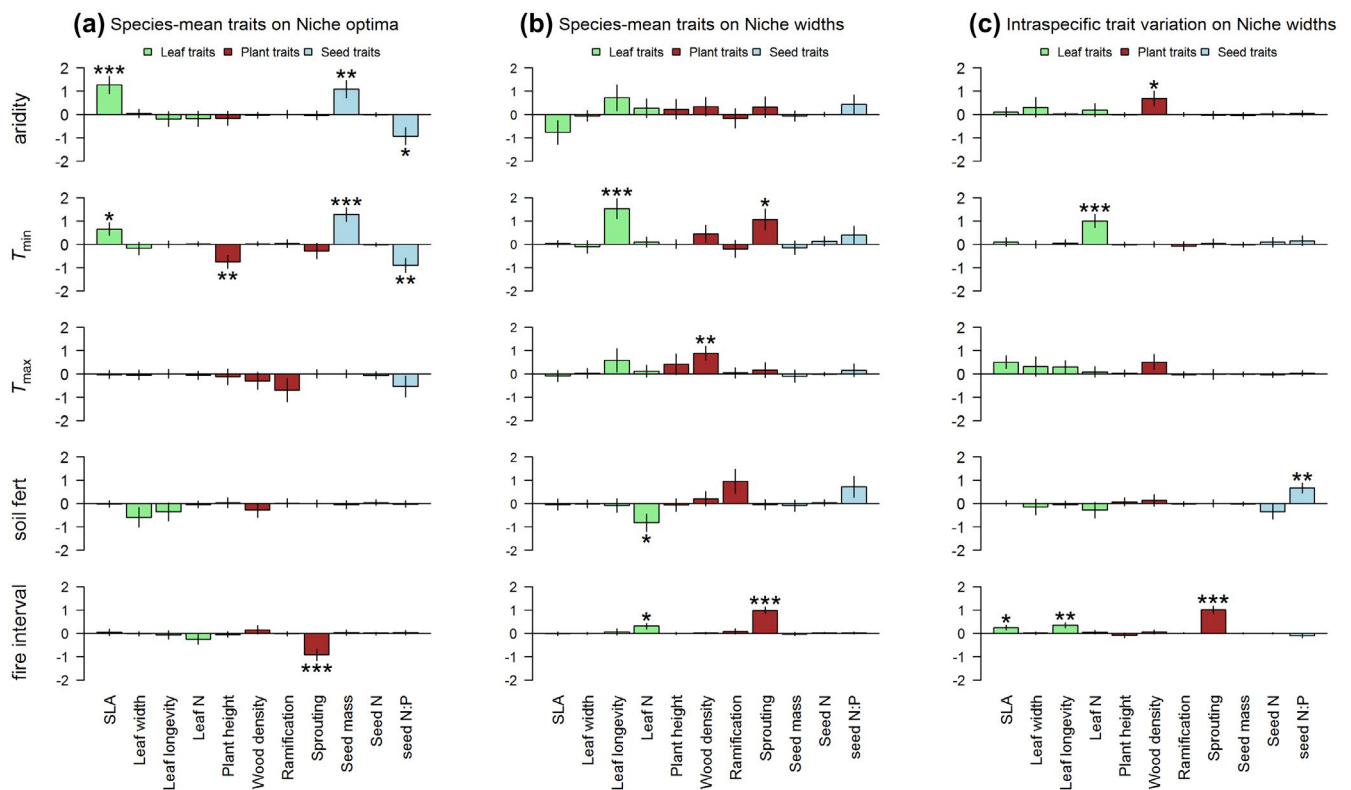


FIGURE 5 Effects of 11 functional traits (leaf traits = green bars; plant-architectural traits = maroon-brown bars; seed traits = light blue bars) on Hutchinsonian niche characteristics (i.e., niche optima and widths along different environmental dimensions) for 26 Proteaceae species: (a,b) species-mean trait values on niche optima and widths, respectively, and (c) intraspecific trait variation on niche widths. Bars are standardized regression coefficients with associated errors (whiskers) from phylogenetic generalized least squares averaged models ($\Delta AICc < 10$). Asterisks denote levels of significance (* $p < .05$; ** $p < .01$; *** $p < .001$). Niche optima are the values for which population growth is maximal, whereas niche widths are the environmental range for which population growth is positive along environmental gradients of climate (aridity, T_{min} and T_{max}), soil fertility and fire interval (see Figure 1 and Materials and Methods). Resprouting ability ('Sprouting') is a dichotomous variable (zero: non-sprouter; one: resprouter) [Colour figure can be viewed at wileyonlinelibrary.com]

widths for soil fertility ($R^2 = 0.55$) decreased with leaf N. Fire niche widths ($R^2 = 0.78$) were broader for species with resprouting ability compared with non-sprouters, and increased with leaf N (Figure 5b).

Niche widths were also well explained by intraspecific trait variation (mean $R^2 = 0.59$; range: 0.47–0.83; Figure 3c). Importantly, all significant effects of intraspecific trait variation on niche widths

were positive, meaning that species with greater intraspecific trait variation had wider niches (Figure 5c). Niche widths for aridity ($R^2 = 0.47$) and T_{\min} ($R^2 = 0.51$) depended on intraspecific variation in wood density and leaf N, respectively (Figure 5c). Soil fertility widths ($R^2 = 0.56$) were explained by intraspecific variation in seed N:P, and fire niche widths ($R^2 = 0.83$) were determined by resprouting ability, leaf longevity and SLA (Figure 5c).

4 | DISCUSSION

In this study, we related inter- and intraspecific trait variation across species' geographical ranges to demographically derived Hutchinsonian niche characteristics (r_{\max} , and niche optima and widths along environmental dimensions) of 26 plant species. We found varying support for the four hypotheses that we tested. In agreement with our first hypothesis, trait values generally varied more between than within the study species (Figure 2b). Our second hypothesis was partially supported since species-mean traits were associated with a limited amount of the variation in r_{\max} ; however, mean traits showed stronger associations with niche optima along environmental gradients. Furthermore, these individual associations corresponded well to trait–environment associations described in the literature (Table 1), which supported our third hypothesis. Finally, although intraspecific trait variability did not relate more strongly to niche widths than species-mean traits (Figures 3 and 5), intraspecific trait variability consistently increased species' niche widths, thus partly confirming our fourth hypothesis.

Our study, which included 11 leaf, plant-architectural and seed traits, showed that relatively few traits were associated with any given niche characteristic, often with strong effects. Notably, mean trait values of Westoby's (1998) LHS scheme (SLA, plant height and seed mass) were related to niche optima along climatic gradients of aridity and T_{\min} . The consistent positive effects of seed mass in aridity and T_{\min} optima are likely attributed to the strong climatic controls of post-fire seedling recruitment in our study species (Treurnicht et al., 2016). The seemingly counter-intuitive positive effect of SLA on the aridity optimum might be driven, in part, by temperature; thinner, narrower leaves have a thinner boundary layer that limits water loss and facilitates cooling by increasing transpiration rates (Yates, Verboom, Rebelo, & Cramer, 2010). Moreover, SLA is a highly context-dependent trait, and climate–leaf size relationships are not necessarily universal (e.g., Adler et al., 2014; Wright et al., 2017). In contrast, climatic niche widths were determined by traits beyond the LHS scheme: T_{\min} widths were associated with higher leaf longevity (a resource-conservation strategy; Westoby, 1998) and resprouting ability (conferring tolerance to stressful conditions; Clarke et al., 2013), whereas T_{\max} widths were defined by denser wood (allowing species to persist in a wider range of temperature conditions; Chave et al., 2009; Messier et al., 2017; Reich, 2014). Furthermore, greater intraspecific variation in wood density and leaf N increased the aridity and T_{\min} niche widths, respectively.

Overall, our trait-based perspective on the Hutchinsonian niches of species suggests that the functional relevance (i.e., link to demographic performance; Violle et al., 2007) of any trait depends on the environmental gradient under consideration and that, in turn, each niche characteristic is associated with a relatively small set of traits among those considered in our study.

Our findings demonstrate how individual traits are related to Hutchinsonian niches as an integrative measure of demographic performance along environmental gradients. The clear trait–niche relationships that we detected are likely to have arisen because we used trait and demographic data collected from the same geographical location (Salguero-Gómez et al., 2018), covered species' entire geographical ranges and derived niche characteristics from a performance measure (r_0) that integrates demographic rates across the full life cycle of our study species. We thus estimated niche characteristics that summarize demographic responses to the full range of environments experienced by a species. Trait-based studies of Hutchinsonian niches thus have great potential to advance the emerging fields of functional population ecology (Adler et al., 2014; Salguero-Gómez et al., 2018) and functional biogeography (Violle et al., 2014). Complementary to our approach, it seems rewarding for functional ecology to resolve trait relationships for individual demographic rates (e.g., Visser et al., 2016) and examine how multiple traits and their interactions influence fitness (Blonder et al., 2018; Messier et al., 2017; Pistón et al., 2019).

We examined the effects of traits on characteristics of the realized Hutchinsonian niche. Although our estimates of realized niches (and the underlying intrinsic population growth rates) account for intraspecific density dependence (Ehrlén & Morris, 2015), they do not explicitly resolve interspecific interactions. The detected trait–niche relationships thus represent trait effects of how intrinsic population growth responds to the abiotic environment in the absence of interacting species (the fundamental niche) and interspecific interactions (the difference between the realized and fundamental niches). It will be exciting to disentangle these two components of the realized niche in future investigations. To this end, it will be necessary to examine how range-wide variation in population growth rate is jointly affected by the traits and density of co-occurring competitors. Traits are known to affect how intra- and interspecific competition alters individual demographic rates (e.g., basal area growth of individual trees; Kunstler et al., 2016). This suggests, for example, that traits also explain competitive effects on the more integrative measure of population growth. Such integrative analyses conducted in a controlled common-garden environment (Kraft, Godoy, & Levine, 2015) revealed that differences in traits between species determine both the strength of forces leading to competitive exclusion and stabilized coexistence (Kraft et al., 2015). Repeating such analyses across large-scale environmental gradients should yield new insights into how trait spectra shape interspecific competition, niches and species coexistence at large spatial scales (Alexander, Diez, Hart, & Levine, 2016; Hart, Usinowicz, & Levine, 2017).

Global climate change is progressing rapidly, with disproportionate impacts on biodiversity, and the trait–niche relationships that we found provide insights into the potential responses of functional diversity to ongoing environmental change. In particular, the CFR biodiversity hotspot is experiencing shorter fire intervals, in addition to hotter and drier conditions (Wilson, Latimer, & Silander, 2015) known to cause local species loss (Slingsby et al., 2017). The niche optima at lower fire intervals and the wider fire niches of our resprouter species implies a lower vulnerability to both shorter and more variable fire return intervals compared with non-sprouters. This can be attributed to the high fire survival rates of resprouters (Treurnicht et al., 2016) and their ability to recover rapidly after fire (Clarke et al., 2013). In contrast, semelparous non-sprouters rely on successful reproduction at the time of fire and may face the risk of immaturity at short fire intervals and senescence at long fire intervals (Treurnicht et al., 2016 and references therein). We also found that resprouters tend to have wider T_{\min} niches, which corresponds to evidence that resprouters are generally more resistant to climatic stress (Clarke et al., 2013). For non-sprouters, investment in leaf N (high leaf N promotes fast growth; Wright et al., 2004) and greater intraspecific variation in SLA and leaf longevity seem to promote wider fire niches. Fast-growing non-sprouters may thus be able to buffer against frequent fires if their populations are able to respond via leaf trait plasticity.

Identifying the functional determinants of species niches is essential for improving predictions of climate-driven range shifts (Estrada et al., 2016; Evans et al., 2016). Trait-based approaches of species niches that span entire geographical ranges should promote an understanding of how traits determine range limits. For example, intraspecific trait variation that defines climatic niches may reflect the ability of species to cope with climate change (Estrada et al., 2016). Given that we found that greater intraspecific trait variation in wood density, leaf longevity and seed N:P extends niche widths, an important next step is to determine whether range-wide variation in these traits arises from genetic differentiation or phenotypically plastic responses to environmental gradients (Fajardo & Siefert, 2019; Sides et al., 2014; Violle et al., 2012; Yang et al., 2018). Experimental evidence for a few of our study species indicates that leaf traits are, to some extent, phenotypically plastic, but the degree of plasticity varies between both species and populations (Akman, Carlson, & Latimer, 2018; Carlson & Holsinger, 2012). Studying the relative importance of adaptive differentiation and phenotypic plasticity for trait variation is also essential for predicting biotic responses to environmental change, because species with wide niches owing to genetic differentiation could be susceptible to environmental change, whereas species with wide niches owing to phenotypic plasticity may better tolerate environmental change *in situ* (Benito Garzón, Robson, & Hampe, 2019).

Overall, we found a distinct, largely non-overlapping set of traits that were associated with different niche characteristics. Moreover, traits were generally not strongly correlated (Supporting Information Figure S4). This posits that species may be able to shift their niches and trait values independently along different environmental axes

(Holt, 2009). Hence, should a single environmental variable change, diversity in the relevant trait should decrease, but with little effect on other traits. Collectively, an understanding of the tolerance and capacity of populations and species to respond to future environmental change, the spectrum of environmental conditions in relationship to the tolerance limits of species, and the magnitude of trait plasticity is urgently needed to improve assessments of global changes in biodiversity (e.g., Benito Garzón et al., 2019). Our approach, linking traits and demographically derived niches, is complementary to the recent development of physiological niche models that predict range dynamics (e.g., Higgins et al., 2012; Kearney & Porter, 2009). Once demographic niche estimates are available for a larger number of species and physiological niche models are refined, it will be exciting to see how these tools can supplement relatively simple trait–demography correlations. This would allow testing for more complex relationships between traits and niche characteristics and would facilitate the development of process-based SDMs for many species (Evans et al., 2016).

ACKNOWLEDGMENTS

We thank private landowners and reserve managers for access to field sites; conservation organizations for research permits (CapeNature: AAA0028-AAA005-00213; Eastern Cape Parks: CRO91/12CR; SANPARKS: Agulhas National Park). We thank Barbara Seele, Justine Rudman, Francois Burger and Reinaert van der Merwe for assistance with collecting and processing trait data, and Katharina Mayer and Bianca Goetjes for assistance in processing nutrient samples. This research was funded by the German Research Foundation (DFG) grants: SCHU 2259/5-1 and SCHU 2259/3-3 to F.M.S. M.T. was also supported by the National Research Foundation - South African Environmental Observation Network (NRF-SAEON's) Professional Development Programm, the Claude Leon Foundation (www.leonfoundation.co.za/) and Stellenbosch University (South Africa). The authors declare no conflict of interests.

DATA ACCESSIBILITY

All data (trait data, demographic niche estimates and phylogeny for the study species) can be found in the Figures and Supporting Information. Additionally, trait data are contained in FYNBASE, available from the TRY Plant Trait Database (<https://www.try-db.org/de/Datasets.php>)

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BIOSKETCH

Martina Treurnicht is a plant ecologist with a research focus on studying the relationships between species performance and environmental variation as a basis for understanding biodiversity responses to ongoing global change. In light of this, she often uses large-scale demographic and trait-based approaches across multiple species and biogeographical gradients (for more, see <https://fynbosser.wordpress.com/>).

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Treurnicht M, Pagel J, Tonnabel J, Esler KJ, Slingsby JA, Schurr FM. Functional traits explain the Hutchinsonian niches of plant species. *Global Ecol Biogeogr*. 2020;29:534–545. <https://doi.org/10.1111/geb.13048>