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Plant clonality in a soil-impoverished open ecosystem: insights from southwest Australian shrublands

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- **Background and Aims** Clonality is a key life-history strategy promoting on-spot persistence, space occupancy, resprouting after disturbance, and resource storage, sharing and foraging. These functions provided by clonality can be advantageous under different environmental conditions, including resource-paucity and fire-proneness, which define most mediterranean-type open ecosystems, such as southwest Australian shrublands. Studying clonality–environment links in underexplored mediterranean shrublands could therefore deepen our understanding of the role played by this essential strategy in open ecosystems globally.
- **Methods** We created a new dataset including 463 species, six traits related to clonal growth organs (CGOs; lignotubers, herbaceous and woody rhizomes, stolons, tubers, stem fragments), and edaphic predictors of soil water availability, nitrogen (N) and phosphorus (P) from 138 plots. Within two shrubland communities, we explored multivariate clonal patterns and how the diversity of CGOs, and abundance-weighted and unweighted proportions .of clonality in plots changed along with the edaphic gradients.
- **Key Results** We found clonality in 65 % of species; the most frequent were those with lignotubers (28 %) and herbaceous rhizomes (26 %). In multivariate space, plots clustered into two groups, one distinguished by sandy plots and plants with CGOs, the other by clayey plots and non-clonal species. CGO diversity did not vary along the edaphic gradients (only marginally with water availability). The abundance-weighted proportion of clonal species increased with N and decreased with P and water availability, yet these results were CGO-specific. We revealed almost no relationships for unweighted clonality.
- **Conclusions** Clonality is more widespread in shrublands than previously thought, and distinct plant communities are distinguished by specific suites (or lack) of CGOs. We show that weighting belowground traits by aboveground abundance affects the results, with implications for trait-based ecologists using abundance-weighting. We suggest unweighted approaches for belowground organs in open ecosystems until belowground abundance is quantifiable.

Key words: Aridity, clonal growth organs, open shrubby ecosystems, fine-scale edaphic gradients, kwongan, lignotuber, rhizome.

INTRODUCTION

Clonality in plants, especially its evolutionary and ecological role, has been widely examined in relatively nutrient-rich grassy landscapes (Herben *et al.*, 2014; Herben and Klimešová, 2020; Bartušková *et al.*, 2021; Ottaviani *et al.*, 2021). Studies on clonality have focused on the importance of clonal growth organs (CGOs; e.g. rhizomes, stolons; Klimešová *et al.*, 2019) as essential strategies for promoting plant regeneration and fine-scale space occupancy where resources can then be foraged and potentially shared across interconnected ramets (Klimešová *et al.*, 2019, 2021*a*). The role of clonality in plant communities that have assembled under vastly different evolutionary and environmental conditions, such as those offered by disturbance-prone and open shrubby ecosystems, remains largely underexplored (Ottaviani *et al.*, 2020; Klimešová *et al.*, 2021*a*). Yet, in these ecosystems, clonality can be seen as an effective strategy allowing plants to cope with soil resource paucity and recurrent fires (He *et al.*, 2011). In fact, some clonal organs, such as rhizomes, often bear buds and can store carbohydrates, which can boost resprouting after biomass removal caused by disturbance (Pausas *et al.*, 2018; Klimešová *et al.*, 2019).

The hyper-diverse mediterranean-type shrublands in southwest Australia occur on old and stable landscapes experiencing prolonged climatic and landscape stability and predictable fire regimes (Pate and Beard, 1982; Hopper and Gioia, 2004; Mucina and Wardell-Johnson, 2011). These open shrubby ecosystems have experienced limited soil rejuvenation and slow yet relentless soil eluviation, and as a result they have undergone extreme soil impoverishment (Peltzer *et al.*, 2010). The seasonal lack of water (Hnatiuk and Hopkins, 1980; Groom *et al.*, 2000) and low levels of crucial nutrients, especially soil phosphorus (P), affect trait selection and species distribution (Laliberté *et al.*, 2012; Lambers, 2014). For example, various P-acquisition and P-use efficiency strategies exist in these shrublands (see Veneklaas, 2022); many proteoid species exude acid from their roots to access occluded P (Lambers *et al.*, 2013, 2022). Further, lignotubers or serotinous seeding life-history strategies promote regeneration via bud-bank (sprouting) or seeds (seeding) after a fire (He *et al.*, 2011; Lamont and Downes, 2011). Information on species-level fire response traits indicative of clonality is abundant (e.g. Pate *et al.*, 1990; Pausas and Verdú, 2005; He *et al.*, 2011). Nevertheless, few studies focused on these shrublands (He *et al.*, 2011) or trait databases (Falster *et al.*, 2021) have explicitly included traits associated with clonality.

There is no global consensus on where clonal life-history strategies are most advantageous for promoting plant regeneration and fine-scale space occupancy. Several authors have observed that clonal modes of plant reproduction are more prevalent in low-nutrient environments compared to sexual pathways (e.g. Jónsdóttir and Watson, 1997; Pennings and Callaway, 2000), whereas others predict the opposite (e.g. Gardner and Mangel, 1999; Fu *et al.*, 2010). Ecologists typically examine shifts in the type, frequency and distribution of clonal modes of reproduction on the wet and nutrient-rich ends of possible edaphic gradients (e.g. temperate grasslands). For example, rhizomes are rare on undeveloped stony soils in the arctic (Klimešová *et al.*, 2012); sprouting from roots is uncommon in aquatic communities but tends to prevail among perennial weeds of agricultural land (Sosnová *et al.*, 2010; Klimešová and Martínková, 2022). Annual and stoloniferous plants tend to prefer nutrient-rich habitats, with rhizomatous plants being in the middle and non-clonal perennials at the nutrient-poor end of the gradient (Klimešová and Herben, 2021). This relationship can be associated with rapid biomass turnover and nutrient cycling in productive environments (Klimešová *et al.*, 2018). While clonality is a relatively universal feature of plants occurring in most terrestrial ecosystems, the type of CGO and frequency distributions may differ depending on local edaphic factors. Therefore, more observational studies investigating the relationship between CGO diversity and their frequency distribution along fine-scale edaphic gradients in open ecosystems, particularly from shrublands, will deepen our understanding of clonality.

Methods linking traits and edaphic gradients at the community level are manifold (e.g. Ackerly and Cornwell, 2007; Bernard-Verdier *et al.*, 2012). Most standard approaches use community-weighted means to analyse the relationship between species traits (such as CGOs) and edaphic variables (Peres-Neto *et al.*, 2017; Zelený, 2018). The use of weighting relies on the assumption that the effect of individual species on ecosystem functioning is related to their abundance in the community (Grime, 1998); however, mainly the aboveground appearance of species are used as weighting factors. Whether this approach is most accurate for CGOs, which are primarily located belowground (Klimešová *et al.*, 2019), is a legitimate question, especially where the contribution of biomass to above- and belowground organs is not equal (Ottaviani *et al.*, 2020). For example, within shrublands, biomass allocated into the aboveground compartment can be up to five times smaller than the belowground counterpart (Low and Lamont, 1990). This 5 : 1 ratio changes depending on the species (Bowen, 1991), type of CGO (Low and Lamont, 1990) and the species' position in the landscape (Enright and Lamont, 1992). Therefore, alternative methodological approaches use unweighted trait values (e.g. Klimešová, *et al.*, 2021*b*) – while these results are less tied to overall ecosystem function, they are still informative of trait–environmental links.

Here, we analyse how the diversity of CGOs and their frequency change between plant communities along with key fine-scale soil gradients of water availability and nutrient status in one mediterranean-type open shrubby ecosystem in southwest Australia (Tsakalos *et al.*, 2018, 2019). Specifically, we set out to: (1) explore the multivariate clonal patterns across communities and how they change along with fine-scale edaphic gradients. We expect that the floristic communities will also be identifiable by distinct CGO (or lack of) fingerprints; (2) reveal how the diversity of CGOs and the proportion of clonality change along gradients. We expect the diversity of CGOs and the proportion of clonality to increase with reduced soil nitrogen (N), P and water availability. Plants should be better able to cope in these long-term stable, harsh conditions by having multiple ways of conserving, sharing and using resources between interconnected ramets; (3) inspect if individual CGOs show contrasting responses to different edaphic gradients. We expect herbaceous CGOs (i.e. herbaceous rhizomes and tubers, stolons, stem fragments) typified by rapid growth and reduced longevity to be more common in resource-rich soils than long-lived woody CGOs (i.e. lignotubers and woody rhizomes) because biomass turnover and nutrient cycling are generally quicker in productive environments; and (4) examine whether the CGO–edaphic gradient relationships are affected by the choice of abundance weighting. We expect that abundance transformations will reveal different CGO–soil trends; this choice is critical in open ecosystems because of the unknown biomass species scaling relationships between above- and belowground organs.

METHODS

Study area

The studied shrublands share several unifying features (including high species richness and turnover, low nutrient status of soils) with other globally recognized editerranean-type vegetation shrubland types, such as *fynbos* (South Africa) and some types of *matorral* (California, Chile, Western Mediterranean) and especially the species-rich Eastern Mediterranean *phrygana* (e.g. Rundel *et al.* 2016). Such shrublands are also found in regions outside the winter-rainfall regions (e.g. in Mexico: *mexical*, Verdú *et al.*, 2003; *campos rupestre*, Mucina 2018; New Caledonia: *maquis minier*, Pillon *et al.*, 2021), invariably on nutrient-poor soils (see Mucina and Wardell-Johnson, 2011). The study area, 1210 km^2 in area, is found on Iluka Resource's Ltd Pty mining tenement located around the township of Eneabba (29°49′S, 115°16′E), ~280 km north of Perth, Western Australia. The study area consists of sandy plains (~85 % of the study area), laterite-capped hillocks (~10 %) and minor drainage lines (~5 %) (Playford *et al*., 1976; Mory, 1994). Based on species co-occurrence patterns, the vegetation has been classified into two major community groups (sandy and clayey shrubland), with a soil texture and coupled exchangeable cation gradients (Tsakalos *et al*., 2018). The sandy shrubland is widespread and occurs on sandy soils with low exchangeable cations, while the clayey shrubland is more spatially constrained (wet depressions) and is typical of clay-enriched or clayey soils with higher exchangeable cation content. The sandy shrubland is species-rich and includes diagnostic species such as *Alexgeorgea nitens* (Restionaceae), *Banksia attenuata* (Proteaceae), *Callitris acuminata* (Cupressaceae) and *Verticordia grandis* (Myrtaceae). The clayey shrubland has a lower species richness and includes diagnostic species such as *Melaleuca concreta*, *M. urceolaris*, *Thryptomene mucronulata* (all Myrtaceae) and *Conostylis prolifera* (Haemodoraceae). Classification of a species–trait data set featuring response traits linked to water relationships, carbon balance, nutrition acquisition and fire response revealed two functional communities also distributed along with the previously identified sand–clay soil texture and coupled exchangeable cation gradient (Tsakalos *et al*., 2019).

Data collection and collation

We use species compositional, soil and trait data sets featured in Tsakalos *et al.* (2018, 2019, 2020). The plot data collation details are given in Tsakalos *et al.* (2018). The availability of soil data sampled and analysed at the plot level (n = 189; each of 100 m^2 in size) served as the limiting factor in selecting and constructing balanced compositional and trait data sets. A preliminary inspection of the soil and compositional properties led to the removal of 51 marginal plots. These were considered disturbed – proximal to paddocks and containing edaphic variables deviating from those expected in natural systems (such as $P > 50$ mg kg^{-1}: Singh and Gilkes, 1991; bulk density < 1.1: Bache *et al*., 2008) and containing species associated with younger dune systems linked to exposed limestone. We used 138 plots positioned in the sandy (119) and clayey (19) shrubland communities for all further analyses. We used soil data on bulk density (g cm^{-3}; proxy for water availability, with an inverse relationship), total N (%; N) and total P (mg kg^{-1}; P), which captured a spatially representative subset of the survey area to form our environmental data set (for soil sampling and chemical extraction details, refer to Tsakalos *et al*., 2018).

We created a CGO database by scoring six (one main organ type per species) nominal CGO trait categories (i.e. lignotubers, herbaceous and woody rhizomes, stolons, tubers, stem fragments) and recognizing the absence of clonality (i.e. non-clonal) as an additional category, for all 463 species present within the 138 plots (Supplementary Data Table S1). Clonality is the potential capacity to produce multiple rooting units (ramets), which may become independent when the connection with the parent plant is lost. We combined new field observations (i.e. ~25 % of the 463 species) made during the peak (spring) flowering season of 2019 and 2020 with our DRYAD database (Tsakalos *et al*., 2020) and information from the FloraBase database (Western Australian Herbarium, 1998−) to establish the presence or absence of clonal traits. When we used the FloraBase database, we assigned trait values using information from specimens near the study area. With a few exceptions, the applied classification system of CGOs followed the concepts and nomenclature of standard protocols (Klimešová *et al*., 2019). Our rhizomatous traits differed in two ways. First, we did not distinguish where their growth originated (i.e. above- or belowground) because we did not have such information. Second, we have distinguished CGO classes for herbaceous and woody rhizomes because of the differences in their longevity and ability to produce vertical stems (Pausas *et al*., 2018). Our tuber CGO is a large category and encompasses Klimešová *et al*.'s (2019) tubers and bulbs and includes a combination of (herbaceous) stem tubers, root tubers and bulbs. Lastly, we have classified lignotubers (including xylopodium; see Pausas *et al*., 2018) as a CGO because lignotubers have the potential to become independent rooting units (ramets), as observed in several *Banksia* species (Proteaceae; see also Millar *et al*., 2010) in our study area. A selection of CGOs is presented in Fig. 1, and a description of their general morphological characteristics and ecological relevance is given in Table 1.

We constructed weighted and unweighted trait matrices. Specifically, we calculated the weighted trait values by summing the cover of all species within a given CGO and dividing it by the total projected cover of all species in each plot (Garnier *et al*., 2004). Then, we calculated the unweighted trait values as the proportion of all species with a given CGO in each plot. Our decision to use both matrices was simple; weighting aligns with Grime's (1998) mass ratio hypothesis, which states that the functional effect of a given species is proportional to its relative contribution to the total biomass of the community. In contrast, the unweighted logic suggests that even a species with low abundance or biomass can be a good indicator of environmental conditions. Hence these two matrices may provide complementary insights into the functioning of the vegetation (Zelený, 2018). Additionally, because we work on a mediterranean-type open shrubby ecosystem where plants allocate biomass conspicuously into belowground CGOs, weighted and unweighted means can yield different results (Ottaviani *et al*., 2020).

Data analyses

We used R 4.1.2 (R Core Team, 2021) and several packages reported below to conduct all analyses.

Clonality patterns across shrubland communities

We explored multivariate CGO patterns using non-metric multidimensional scaling (NMDS) ordinations and used permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) to support our visual interpretations. We made two NMDS ordinations based on species pairwise trait dissimilarity calculated using a modified Gower distance measure from our weighted and unweighted trait matrices (GAWDIS R package; de Bello *et al*., 2021). This modified distance measure ensured that the final dissimilarity was a product of the even effect of clonal and non-clonal traits. The PERMANOVAs used 10^4 permutations and Bonferroni-corrected P-values for multiple comparisons (Borcard *et al*., 2018) to assess the relationship between functional composition and the traits, fine-scale

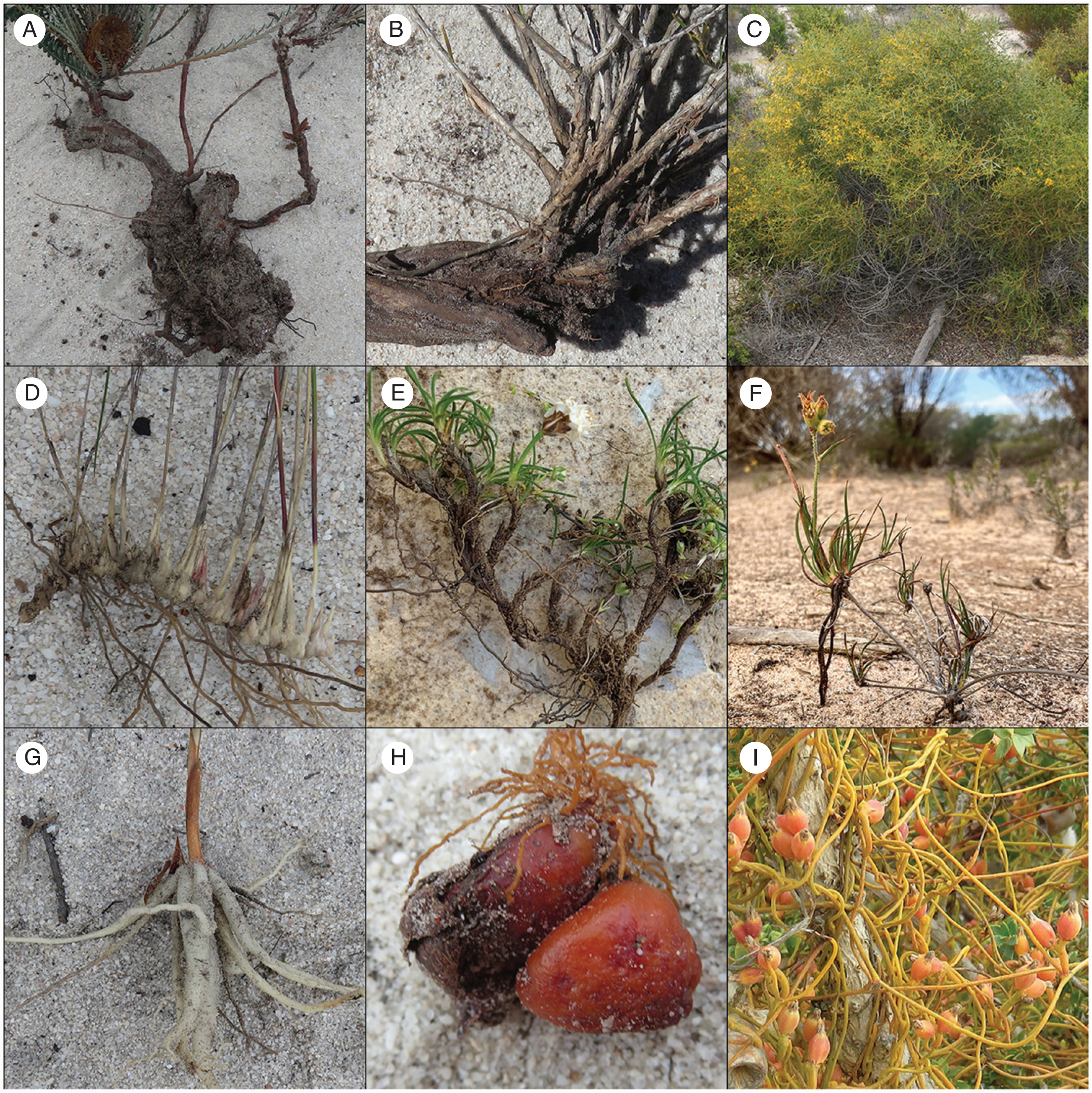

Fig. 1. Examples of plant species and their CGOs from Eneabba shrublands, Western Australia: (A–B) lignotubers of *Banksia dallanneyi* (Proteaceae) and *Eremaea asterocarpa* (Myrtaceae); (C) a woody rhizome of *Acacia rostellifera* (Fabaceae); (D–E) herbaceous rhizomes of *Amphipogon turbinatus* (Poaceae) and *Laxmannia sessiliflora* (Asparagaceae); (F) stolons of *Conostylis prolifera* (Haemodoraceae); (G–H) tubers of *Burchardia congesta* (Colchicaceae) and *Drosera magna* (Droseraceae); (I) detachable stem fragments of *Cassytha flava* (Lauraceae).

edaphic gradients, and sandy and clayey communities. We fitted all significant ($P \leq 0.05$) *post hoc* vectors on the NMDS ordination (vegan R package; Oksanen *et al*., 2020).

Relationships between CGO diversity and fine-scale edaphic gradients

We quantified the relationship between the edaphic gradients (i.e. bulk density, Total N, and Total P) and clonal diversity (i.e. number of CGOs; categorical variable; range: 2–6) using analysis of variance across the means of different groups (i.e. ANOVA). We visually checked all ANOVA test assumptions and applied non-parametric testing as required. Parametric instances used classic ANOVAs and *post hoc* Tukey honestly significant difference (HSD) testing. Non-parametric instances used Welch ANOVAs and *post hoc* Games Howell testing. Because we established the plots across two major community groups (Tsakalos *et al*., 2018), we applied ANOVA testing to data subsets involving all plots, sandy or clayey plots,

Table 1. *Clonal growth organs, their general morphological characteristics, ecological relevance and key references*

Clonal growth organs	General morphological characteristics	Main functions	Reference
Lignotubers	Thickened woody shoot and root bases	Carbohydrate, bud and mineral storage used for sprouting after disturbance (mainly fire in kwongan)	Herath and Lamont (2009); Rusch *et al.* (2011)
Herbaceous rhizomes	Belowground fleshy or fibrous rooting stems	As above, plus foraging and sharing of resources between ramets	Pate and Beard (1982); Herath and Lamont (2009); Sosnová *et al.* (2010); Pausas *et al.* (2018); Klimešová *et al.* (2019)
Woody rhizomes	Belowground woody rooting stems	As above except they are slower growing with a lower colonization ability	
Stolons	Aboveground (often prostrate) rooting stems	Foraging and sharing of resources; space occupancy	Pausas *et al.* (2018); Klimešová *et al.* (2019)
Tubers	Belowground storage organs combining stem, root and leaf origin	Carbohydrate, bud and mineral storage; clonal multiplication producing new ramet(s) able to replace parent plants following disturbance or death	Pate *et al.* (1990); Klimešová and Klimeš (2007); Klimešová *et al.* (2019)
Stem fragments	Aboveground rooting detached fragments, which are shed from parent plants	Space occupancy; rapid exploration and exploitation of soil resources	Klimešová *et al.* (2019)
Non-clonal plants	Perennial or annual plants lacking any specialized belowground organs as well as the capacity for adventitious rooting	-	-

separately. We sourced all functions from the rstatix R package (Kassambara, 2020).

We applied a Jonckheere–Terpstra's One-sided Monotonic Trend Test (Terpstra, 1952) to inspect how trait diversity changes along bulk density, N and P edaphic gradients. The Jonckheere–Terpstra test (DescTools R package; Signorell *et al.*, 2019) is a non-parametric test for ordered differences among classes (i.e. clonal diversity, namely the number of CGOs). The method tests for differences between group medians but incorporates information regarding whether the order of the groups is meaningful (e.g. Chelli *et al.*, 2022).

Relationships between weighted CGOs, unweighted CGOs and fine-scale edaphic gradients

We examined the relationships between the abundance-weighted and unweighted trait matrices and the environmental predictors using beta regression models (betaregs) and generalized mixed-effects models (GLMERs). We included the community type as a random effect in both models to account for data non-independence (i.e. plots nested within two distinct community types). We created a betareg to model each weighted CGO against the environmental predictors (glmmTMB R package; Brooks *et al.*, 2017). We created a GLMER using a binomial log-link distribution to model each unweighted CGO against the environmental predictors (lme4 R package; Bates *et al.*, 2015). In both models, we accounted for species richness. We used beta distribution modelling for the weighted data because the cover is a continuous variable between 0 and 1 and does not meet the requirement of a binomial distribution required by GLMERs (Zuur *et al.*, 2009). We calculated the variance explained by the fixed effects (predictors) and fixed plus random effects (i.e. marginal and conditional R^2, respectively) for each model (MuMIn R package; Barton, 2020).

RESULTS

Potentially clonal species represented 65 % of the 463 shrubland species. The distribution of the CGO types was disproportionate, with species having lignotubers (28 %) or herbaceous rhizomes (26 %) being the most abundant. Tubers (5 %), woody rhizomes (4 %), stolons (2 %) and stem fragments (<1 %) were the least abundant CGOs. The number of species (i.e. species diversity) and number of CGOs (i.e. CGO diversity) averaged across all 138 plots was 45 and five, respectively. On average, 77 % of the species in a plot were clonal (min = 33 %, max = 94 %). The average aboveground cover of all species across all plots was 15 % (min = 4 %, max = 25 %); the combined cover of clonal species was 12 % and of non-clonal species was 3 %.

Clonality patterns across shrublands

Visual inspection of the non-overlapping 95 % ellipses based on confidence intervals suggests that the two floristically derived major community groups are well defined also from a clonal perspective (Fig. 2) . PERMANOVA significantly ($P \le 0.001$) supported this observation from both weighted ($r^2 = 0.223$) and unweighted ($r^2 = 0.396$) analyses. Non-clonal species explained the highest proportion ($r^2 = 0.954$), followed by lignotubers ($r^2 = 0.676$), herbaceous rhizomes ($r^2 = 0.600$) and stolons ($r^2 = 0.188$) of the significant ($P \le 0.001$) weighted CGO–compositional variance relationships. Species with woody rhizomes explained the highest proportion ($r^2 = 0.680$), followed by lignotubers ($r^2 = 0.589$), herbaceous rhizomes ($r^2 = 0.353$) and not being clonal ($r^2 = 0.261$) of the significant ($P \le 0.001$) unweighted CGO–compositional variance relationships. Clonal species were more prevalent in sandy rather than clayey shrublands. In the weighted analysis of the environmental variables, PERMANOVA identified bulk density as a significant driver of the multivariate clonal patterns. Sandy shrubland contained soils with higher bulk

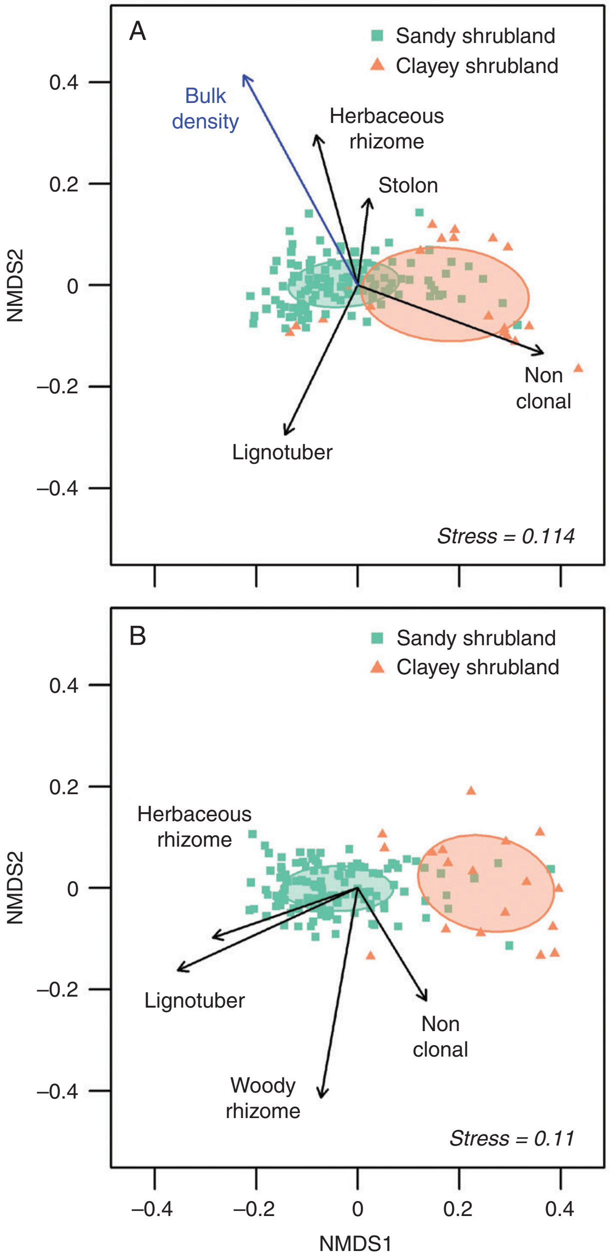

FIG. 2. Two-dimensional NMDS ordination based on community-weighted (A) and unweighted means (B). The shaded hulls represent 95 % ellipses based on confidence intervals encapsulating sandy and clayey shrubland communities. We superimposed significant ($P \leq 0.05$) CGOs (black) and environmental variables (blue) as vectors identified by PERMANOVA. Stress values of the ordination indicate a good fit of the two-dimensional scaling (i.e. <0.2).

density ($r^2 = 0.065$) than clayey shrubland. We detected no environmental drivers from the unweighted analysis.

Relationships between CGO diversity and fine-scale edaphic gradients

CGO diversity within a plot increased significantly with species richness for all plots and sandy and clayey plots separately (Supplementary Data Fig. S1). Jonckheere–Terpstra permutational testing revealed marginal increases in diversity along the bulk density gradient across all plots and for sandy shrubland separately (Fig. S2, Jonckheere–Terpstra's $P \leq 0.05$). We did not observe any significant patterns in CGO diversity along N or P gradients (Figs S3 and S4).

Relationships between weighted and unweighted CGOs and fine-scale edaphic gradients

The community-weighted mean of clonal species increased with bulk density and N and decreased with P (Fig. 3A–C). In soils with lower bulk density, the species with herbaceous rhizomes increased. In contrast, species with woody rhizomes decreased (Fig. 3A). A similar pattern occurred for N, and we also observed a significant increase in lignotuberous species (Fig. 3B). Weighted clonality decreased with increasing P (Fig. 3cC); herbaceous and woody rhizomatous species mirrored this pattern. Most of the models' variability was accounted for by the random effect associated with community type (marginal r^2: 0.03–0.14; conditional r^2: 0.09–1.21). In the unweighted analyses, the woody rhizomes decreased with increasing N (Fig. 3D–F). We did not detect other significant CGO–soil trends using the unweighted data. Supplementary Data Tables S2 and S3 provide complete summary statistics of the models.

DISCUSSION

We provide a newly created dataset containing information on clonality and six related organs for 463 shrubland species – an unprecedented achievement for resource-poor, fire-prone open shrubby ecosystems (see Tavşanoğlu and Pausas, 2018 for fire-related traits in the Mediterranean Basin). By analysing clonal patterns in the studied hyper-diverse shrublands, we obtained insights into what contributes to functionally defining different plant communities, which aligned with previous classifications based on floristics and other traits informing on different functional axes (resource economics, fire response; Tsakalos *et al.*, 2018, 2019). We contextualize our findings by offering eco-evolutionary and biogeographical hints of what could be behind the relationships (or lack thereof) between CGOs and key fine-scale edaphic factors relevant to open ecosystems on old, stable and soil-impoverished landscapes.

Clonality in shrublands is more widespread than previously predicted

The observed proportions of potential clonality in shrubland plant species ranged between 37 and 65 %. This range depends on how clonality is defined; our lower bound (37 %) follows Klimešová *et al.* (2019), whereas our upper bound (65 %) includes lignotubers as a potential CGO (Millar *et al.*, 2010). Our upper estimate seems relevant in mediterranean-type shrublands because lignotubers are bud-bearing and storage organs that may lead to potentially independent rooting units through organ fragmentation (as observed in *Banksia* species; Millar *et al.*, 2010). Studies from other mediterranean-type shrublands to compare are scarce. However, research featuring

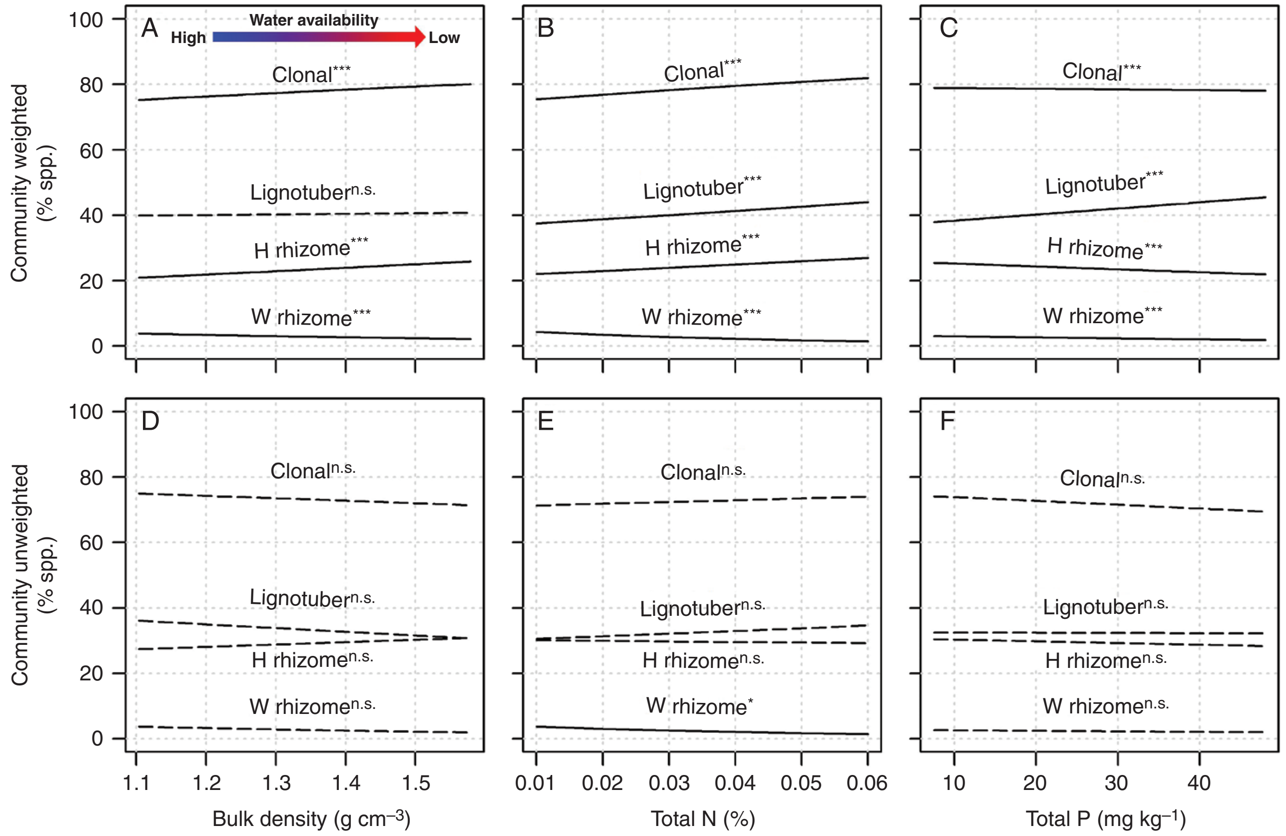

FIG. 3. Relationship between community-weighted (A–C) and unweighted (D–F) means of the three most abundant CGOs (lignotubers, herbaceous [H] and woody [W] rhizomes) with (A, D) bulk density (an inverse proxy for water availability), (B, E), total N and (C, F) total P. Regression lines are reported. n.s., Non-significant; $*P > 0.05$; $***0.05 < P < 0.001$.

Mediterranean shrublands of Sardinia (Italy) found that about half of the species are clonal (Campetella *et al.*, 2019), which aligns with our findings.

Global estimates of clonal species span 53–79 % in central Europe, 39 % in China, 46 % in Great Britain and 3.3–26.7 % in Australia – see Klimešová *et al.* (2021*a*) for an overview. Around the latitude of our study site, Zhang *et al.* (2018) predicted mean clonality was ~5 % (ranging from 0 to 20 %). However, in this study, we identified clonality for a considerably higher proportion of species. This stresses the need for detailed field studies to examine plant clonality in regions and biomes less studied from this perspective.

Clonality patterns across shrublands

Our analyses have confirmed that the two main communities previously identified based on floristic composition (Tsakalos *et al.*, 2018) and other functional trait axes (Tsakalos *et al.*, 2019) are also distinguished by distinct clonal patterns (Fig. 2). Specifically, a higher diversity and proportion of herbaceous rhizomatous and lignotuberous species characterize sandy shrubland, whereas non-clonal species distinguish clayey shrubland. These communities remain consistently defined from a clonal viewpoint irrespective of the choice of weighting, indicating that previous classifications were robust.

The choice of weighting impacted the ability to detect edaphic drivers of the community (clonal) composition. Bulk density marginally explains the variability in the functional CGO trait space using abundance weighting (Fig. 2Aa). Sosnová *et al.* (2010) suggest that the low resistance of wet soils is advantageous for rooting, rhizome penetration, stem fragmentation and fine-scale space occupancy. However, this model does not seem appropriate for our shrublands since all sites occur on uncompacted sandy soils where mechanical soil resistance is low (Henderson *et al.*, 1988; Tsakalos *et al.*, 2018), and clonal species may thrive under such circumstances and play important functional roles (e.g. resource foraging and sharing, soil stabilization/protection from erosion; Yu *et al.*, 2008). However, caution is necessary when making such inferences because no edaphic drivers contributed to explaining the unweighted functional trait space (Fig. 2B). Yet, we should also be careful about directly equating bulk density with soil water availability and mechanical soil resistance. The correlations are correct, but bulk density also correlates with cation exchange capacity (due to higher clay content), a critical nutritional factor in the studied nutrient-impoverished soils (Tsakalos *et al.*, 2018).

Relationships between clonality and fine-scale edaphic gradients

The finding that drier (and sandier) plots contained higher CGO diversity and an overall higher aboveground abundance-weighted proportion of clonal species may indicate that clonality provides an ecological advantage in mediterranean-type shrublands (Supplementary Data Fig. S2; Fig. 3A, B). Sharing limited resources among interconnected ramets may constitute an effective strategy for plants in seasonally dry and disturbance-prone open ecosystems to overcome arid periods (Pennings and Callaway, 2000). The studied shrublands rely on prolonged summer access to water deep in the soil profile and short-term pulses of water in the shallow soil profile (corresponding with bulk density measurements) associated with mediterranean-type winter rainfall events (Zencich *et al*., 2002). CGOs with woody structures are long-lived and can occur deep in the soil profile (>5 m; Low and Lamont, 1990), where access to deep water sources may be less responsive to short-term changes in water availability. In contrast, herbaceous rhizomes are short-lived, often occur in shallow soils and thus are more responsive to seasonal changes in water availability. Additionally, this pattern may be related to rapid biomass turnover and nutrient cycling observed in other wet and productive environments (Klimešová *et al*., 2018). However, this result is challenged by that obtained for the unweighted mean (no relationships), which calls for caution when making such ecological inferences.

The contrasting patterns revealed for clonality (weighted mean) along soil N vs. P gradients indicate that clonality can be differentially advantageous depending on the nutrient analysed (Fig. 3B, C, E, F). In the P-impoverished southwest Australian shrublands, one of the nutrient-poorest regions worldwide (Hopper and Gioia, 2004), clonality may only provide an ecological advantage under limiting P conditions. Here, eco-evolutionary pressures (i.e. long-term stability and predictability of fire proneness and chronic resource scarcity; see Mucina and Wardell-Johnson, 2011) may have selected potentially adaptive clonal strategies (He *et al*., 2011). The decrease in clonality with increasing P may also be a by-product of toxicity (Lambers *et al*., 2022). Although P toxicity is a widespread feature of many proteaceous species endemic to the southwest Australian region (Shane *et al*., 2004; Lambers *et al*., 2013), our research suggests that it may be of profound importance to other non-proteoid rhizomatous species too.

CONCLUSIONS

Together with bringing insights into the role of clonality in open shrubby ecosystems, our research comes with drawbacks, opening avenues for further studies. Most importantly, we advocate developing more accurate proxies of species-level belowground abundance, which could be related to different aboveground organs, traits and functions (Ottaviani *et al*., 2020). DNA-based methods (Pärtel *et al*., 2012), such as real-time PCR (Herben *et al*., 2018), can determine both species' presence and their relative abundance in soil samples; however, their implementation is still far from routine. Finally, the clonal traits included here are all categorical and qualitative, based on the proportion of clonal species and type of CGOs. Future studies may measure continuous and quantitative clonal traits, such as lateral spread (see Cornelissen *et al*., 2014) or the number of offspring produced yearly, ideally including intraspecific variability. All these developments may provide a deeper understanding of the relationship between clonality and the environment in open ecosystems.

SUPPLEMENTARY DATA

Supplementary data are available online at https://academic.oup.com/aob and consist of the following. Table S1: Database of the species, their CGO status and corresponding reference collated from Eneabba, Western Australia. Figure S1: Graphics of the species richness grouped according to the CGO. Figure S2: Graphics of the soil bulk density grouped according to the CGO diversity. Figure S3: Graphics of the soil N grouped according to the CGO diversity. Figure S4: Graphics of the soil P grouped according to the CGO diversity. Table S2: Beta regression modelling of the water availability, N and P on the weighted shrubland data. Table S3: Generalized linear mixed-effects modelling of the water availability, N and P on the abundance of unweighted shrubland data.

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