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ORIGINAL RESEARCH

Influence of habitat attributes on terrestrial orchid communities across a tropical forest recovery gradient

Benjamin J. Crain[1] · Melissa K. McCormick[1] · Lawrence W. Zettler[2] · Julian Dendy[3] · Christian P. Giardina[4] · Amanda Uowolo[4] · Susan Cordell[4] · Dennis F. Whigham[1]

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Abstract
Understanding drivers of plant diversity and distributions is critical for their conservation, particularly among changing environments. While plants' responses to disturbances are relatively well-studied, in-depth analyses of how they respond to habitat recovery are surprisingly scarce. This is particularly true for one of the most diverse, sensitive, and threatened plant families: the Orchidaceae. To address this knowledge gap, we evaluated the diversity and distribution of terrestrial orchid species within a recovering tropical forest landscape in the Republic of Palau. We tested the hypotheses that orchid abundance, richness, and diversity vary across a forest successional gradient and that orchid species exhibit specificity and/or fidelity to particular tree species. Surveys yielded distribution data for 23 orchid species and General Linear Models revealed that habitat type and tree abundance, diversity, and size significantly affected orchid abundance. Habitat type and tree abundance also affected orchid richness and diversity. Indicator analysis showed that only two orchid species were significantly associated with individual tree species. The local landscape-scale study established that orchid communities varied across habitats and that mature forests had greater orchid abundance, richness, and diversity. Interestingly, tree abundance had a stronger influence on orchid communities than tree diversity, tree size, or specific tree species. The study demonstrated that orchids can occupy a range of successional habitats and indicated that reservation strategies paired with restoration efforts utilizing various tree species for reforestation will benefit orchid communities over potentially shorter timeframes than might occur without active management.

Keywords Conservation · Micronesia · Orchidaceae · Plant diversity · Reforestation · Republic of Palau

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Extended author information available on the last page of the article

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Introduction

The recent United Nations Convention on Biological Diversity (COP 16) re-emphasized the global significance of habitat loss and highlighted the need to prioritize the environment and improve conservation efforts for global and local biodiversity, including for plant species and their habitats (CBD 2024; Medellin 2024). Although numerous studies document global scale patterns of forest habitat loss and recovery (*e.g.*, Hansen et al. 2010; Hansen et al. 2013; Dubayah et al. 2020; Hansen et al. 2021), detailed studies examining how local biodiversity dynamics recover following disturbances are equally necessary. Without assessments across a range of scales, it will be difficult to develop effective protocols that enhance global and local plant biodiversity conservation.

Among most forested habitats, non-woody plant communities are critical components of biodiversity, and among all plant families, the Orchidaceae is a major contributor to overall diversity, especially in the tropics. With at least 28,000 species (Givnish et al. 2015), the Orchidaceae is one of the largest families of flowering plants, with representatives occurring in all major types of terrestrial habitats (Pridgeon et al. 1999–2014). From a conservation standpoint, the orchid family is especially important because nearly half of all species whose conservation status has been assessed are threatened or endangered, and all species in the family are of conservation concern (Swarts and Dixon 2017; CITES 2022), primarily as a result of human activities (Crain and Tremblay 2014; Christenhusz and Byng 2016; IUCN 2017; Swarts and Dixon 2017; Fay 2018; Wraith and Pickering 2018). This is particularly the case in many tropical forests, where orchid abundance is high and forests are being exploited at an alarming rate (Fay 2018; Phillips et al. 2020). Orchids are also ecologically significant because they are sensitive indicators of environmental disturbances (Akhalkatsi et al. 2014; Collins and Brundrett 2015; Crain and Tremblay 2017). Due to their sensitivity, they may have the potential to serve as indicators of the impacts of disturbances or the benefits of recovery efforts. These factors clearly make orchids important subjects for ecological research geared towards biodiversity preservation.

Orchids' abundances, diversity levels, and distributions, hinge on multiple factors characterizing their individual habitats including microclimatic conditions, vegetation types, soil or host tree characteristics, the presence of suitable mycorrhizal fungi, and appropriate pollinators (Hietz et al. 2006; McCormick and Jacquemyn 2014; Crain and Tremblay 2017; Crain and Fernández 2020; Li et al. 2021). All of these factors can be influenced by local habitat conditions, including the level of habitat disturbance (Djordjević and Tsiftsis 2022; Besi et al. 2023a; Martin-Forés et al. 2022). While several orchid studies demonstrate that disturbances are detrimental to orchid species (Crain and Tremblay 2017; Crain et al. 2019; Zettler et al. 2019), other studies have shown that disturbances can have a favorable effect on certain orchids via reduced competition with other plants, easier access to space, and a greater abundance of light resources (Hernandez-Pérez and Solano 2015; Djordjević et al. 2020a). Consequently, there is a critical need to determine how variable habitat attributes across forest loss and recovery gradients influence orchid communities to help guide conservation and restoration efforts.

Several regional studies examine the influence of habitat attributes on orchids, including variables related to habitat disturbance or loss (Bulafu et al. 2007; Huang et al. 2008; Souza

Rocha and Luiz Waechter 2010; Štípková et al. 2017; Crain and Fernández 2020; Juiling et al. 2020; Saavedra and Pitogo 2020; Kusumastuti and Suratman 2021). Most focus on how broad scale landscape characteristics relate to orchid abundance, diversity, and distribution. Interestingly, regional studies from tropical as well as from temperate regions reveal that orchids can inhabit disturbed, recovering, or mixed-use forests, suggesting that disturbed habitats may be viable, yet potentially overlooked habitats for sustaining orchid diversity (Solis-Montero et al. 2005; Tsiftsis et al. 2008; Solano-Gómez et al. 2016; Crain and Fernández 2020; Djordjević et al. 2020a, b).

There are also studies on orchid abundances, diversity levels, and distributions at local scales but most focus on either tropical epiphytic orchids (e.g., Ackerman and Moya 1996; Hietz et al. 2006; Mújica et al. 2013; Wiegand et al. 2013; Besi et al. 2019; Raventós et al. 2021; Mirioba et al. 2024) or temperate terrestrial orchids (Collins et al. 2005; Coates et al. 2006; Pellegrino and Bellusci 2014). There is a paucity of studies, however, examining how disturbances impact terrestrial orchids in the tropics, despite their diversity, susceptibility, and in some cases their perceived value (Hinsley et al. 2018). In one example, Bergman et al. (2006) documented that an understory terrestrial orchid in Puerto Rico, *Wullschlaegelia calcarata*, required decades to recover following a 1936 hurricane. Almost 50 years later, the species was still absent from sites that had been heavily disturbed (<20% canopy cover remaining) but was more abundant in sites that were minimally disturbed. In another pair of studies from peninsular Malaysia, Besi et al. (2019, 2023b) found low numbers of terrestrial orchids in logged forests, but also noted that some species occurred in unlogged fragments within these disturbed forests. Clearly, terrestrial orchid species resiliency in tropical forests following disturbances and across recovery stages is an important component to consider in orchid conservation planning, especially in light of projected ecological changes that will likely be exacerbated by climate change over the next century.

Here we examine the distribution, abundance, and diversity of terrestrial orchid species across a steep habitat disturbance gradient within a recovering tropical forest setting. Our objective was to determine how habitat attributes across a forest recovery gradient influence the distribution, abundance, and diversity of terrestrial orchid species. Specifically, we tested the hypotheses that orchid abundance, richness, and diversity vary along a recovery gradient, as represented by habitats with no or few trees ranging to forested habitats with differing tree abundances, sizes, and diversity levels. We also tested the hypothesis that terrestrial orchid species preferentially co-occur with particular tree species and exhibit significant specificity and/or fidelity to them. Our expectations were that orchid abundance, richness, and diversity would be greater in more mature and diverse forest habitats as these patterns have been observed in previous orchid studies in other locations in the tropics (Morales-Linares et al. 2022; Besi et al. 2023a; Mirioba et al. 2024). We also expected that certain orchids would tend to occur in proximity to specific tree species as significant positive associations between terrestrial orchids and specific tree species have been documented elsewhere in the tropics (Bergman et al. 2006). In testing these hypotheses, our goal was to better understand the ecology of terrestrial orchid communities in the tropics to inform efforts to sustain them in a landscape complex undergoing recovery.

Methods

Study site

The study was conducted in the Republic of Palau, a critical component of the Polynesia/Micronesia Global Biodiversity Hotspot (*sensu* Myers et al. 2000; Fig. 1; Online Resource 1). Palau is an insular nation within the Caroline Island group of Micronesia and consists of ca. 586 islands (Hillmann Kitalong 2008). Most of the islands are rather small in area and relatively low in elevation as they are formed from raised coral and calcareous/coralline limestone (Cole et al. 1987). Four of the islands are of volcanic origin however, including Babeldaob, which is the largest in the country (Cole et al. 1987). Babeldaob has moderate relief, with elevations ranging from sea level to a maximum of ca. 215 m (Hillmann Kitalong 2008). Palau has a tropical wet climate with a mean annual temperature of ca. 27 °C and a mean annual rainfall of ca. 3.7 m. A dry period occurs between January and April (Cole et al. 1987; Donnegan et al. 2007; Hillmann Kitalong 2008). Recent studies show that over 80% of the country is forested, with the majority covered by lowland tropical forest (Donnegan et al. 2007; Hillmann Kitalong 2008).

Our focal site was in the Ngardok Nature Reserve, one of Palau's most important protected areas (PAN 2022), in Melekeok State on Babeldaob Island. The chosen setting was historically forested, but portions of the area were converted to agriculture nearly a century ago (Dendy et al. 2022). Since agriculture was abandoned following World War II, the site has been passively recovering for several decades, with recovery periodically disrupted by wildfires. Because of its lengthy disturbance and recovery history, the reserve contains a

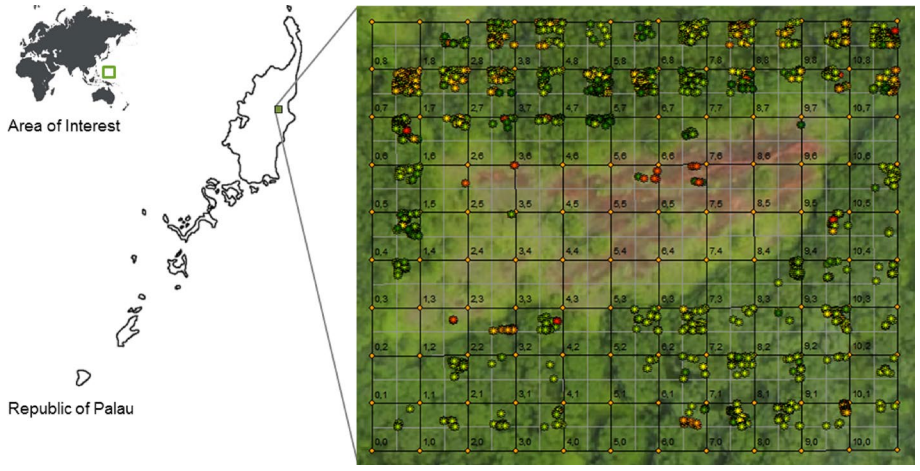


Fig. 1 Map of the Ngardok ForestGEO plot in the Ngardok Nature Reserve, Melekeok State, Babeldaob Island, Republic of Palau, highlighting the documented distribution of terrestrial orchids across the site. The black gridlines delineate the boundaries of the individual 20 m × 20 m quadrats on the site (identified by coordinate numbers in the lower left corners representing column number followed by row number beginning on the southwest corner of the plot). Light grey gridlines delineate the boundaries of the four individual 10 m × 10 m subquadrats within each quadrat (a-d, beginning at the lower left and moving counter clockwise around the quadrat). Colored markers indicate the location of terrestrial orchids on the plot with markers of different colors indicating individual species

complex mosaic of habitat types, ranging from disturbed sites with few or no trees to mature forests (Fig. 2a; Online Resource 1).

Within the Ngardok Nature Reserve, a four-hectare permanent forest dynamics monitoring plot was established as part of the Smithsonian Institution's Forest Global Earth Observatory network (ForestGEO) (Condit et al. 2014; Fig. 1; Online Resource 1). The plot was divided into 99 quadrats, each of which measured 20 m × 20 m in size. Each quadrat was subdivided into four 10 m × 10 m subquadrats. The plot encompassed a gradient of six habitats: badlands, savannas, woody savannas, fernlands, forest edges, and mature forest (Online Resource 1). We were keen to utilize ForestGEO data and methodologies to support a highly structured inventory of terrestrial orchids and to test hypotheses about orchid communities. Accordingly, the site characteristics of the Ngardok plot were ideal for examining non-woody plant communities amidst the dynamics of a recovering tropical forest and offered a unique opportunity to analyze terrestrial orchid diversity and dynamics in Palau and Micronesia based on habitat attributes (Condit et al. 2014; Anderson-Teixeira et al. 2015; Chang et al. 2015; Spicer et al. 2022).

Orchids in Palau

The orchid family is one of the most diverse and inimitable components of plant diversity in Palau. Recent estimates show that over 80 orchid species occur in the country, including numerous rare endemics (Hillmann Kitalong and Uesugi 2017), but ongoing surveys indicate that the number may be substantially larger (*e.g.*, Crain 192 US, Crain 200 US; Crain et al. personal observation). Regardless, the orchid flora of Palau is considerably diverse for the country's size. For comparison, the nearby Federated States of Micronesia and Guam have an estimated 62 and 29 species respectively, while the geographically iso-

Fig. 2 **(a)** A landscape view of the Ngardok ForestGEO research plot highlighting the mixture of habitat types ranging from disturbed areas (bottom right) to mature forests (left and center) and **(b–d)** selected orchid species documented on the site: *Crepidium setipes*, *Spathoglottis micronesiaca*, and *Peristylus palawensis*

lated Hawaiian Islands have only three native species, despite each of these Pacific island groups being larger in area than Palau (Canfield 1980; ESRI 2018b). Of all Palau's orchids, approximately one third are terrestrial species, which is in line with global estimates for the family (Swarts and Dixon 2009).

Field surveys and data collection

We sampled the northeast subquadrat (10 m × 10 m) within each of the 99 quadrats (20 m × 20 m) in the Ngardok plot, thereby ensuring that surveys covered all six habitat types on the site. At the northeast corner of each subquadrat, GPS coordinates were recorded, and elevation was documented. We used a total count method to quantify the number of individual orchids within each 100 m^2 subquadrat. Each subquadrat was surveyed by counting terrestrial orchids along 10 m transects that were distributed at 1 m intervals, ensuring we were able to observe all orchids present. Each orchid encountered was identified to species using field guides, published species descriptions, and herbarium records (*e.g.*, Hillmann Kitalong and Uesugi 2017 and references therein). Species nomenclature for each orchid was verified through searches on the Plants of the World Online database (RBGK 2019). Unidentifiable species were identified to genus, or in rare cases, listed as unknown species. Some orchids can be both terrestrial and epiphytic, *e.g.*, *Dipodium fevrellii*, and accordingly, only individuals that occurred on the forest floor were tallied. The locations of individual orchids were mapped manually in the field based on their position relative to the subquadrat boundary markers and to the locations of documented trees on the site. Clonal species were counted as separate individuals if they were separated by more than 30 cm. For each orchid encountered, the identity of each of the four nearest neighboring trees (one in each of the four cardinal directions surrounding the orchids) was recorded.

The orchid distribution maps from the field surveys were digitized in the laboratory using ArcGIS 10.3 (ESRI 2018a) to create a georeferenced point layer shapefile showing the distribution of terrestrial orchids across the Ngardok plot. Once the point layer for orchids was created, geographic coordinates (decimal degrees) for each individual were quantified with the Calculate Geometry tool (ESRI 2021). The orchid distribution layer was then combined in an ArcGIS map with a shapefile denoting the distribution of quadrat and subquadrat boundaries on the plot. Subsequently, a point layer detailing the distribution of trees on the plot was added to the orchid distribution map. Data on the attributes of trees (*e.g.*, species, diameter) nearest individual orchids were incorporated in the orchid data set.

Orchid community and habitat metrics

We used the georeferenced orchid distribution data first to quantify orchid richness (total number of species) and orchid abundance (total number of individuals) across the entire Ngardok plot. Skewness of the species distribution profile was calculated to evaluate the overall asymmetry of the species abundance measures (Estill and Cruzan 2001).

Local orchid abundance (number of individuals), richness (number of species), and orchid diversity (effective species number; Jost 2006, 2019) were quantified for each individual subquadrat. We also used the Ngardok ForestGEO survey data to quantify site specific attributes related to the six habitat types for each subquadrat (Online Resource 1). We initially tallied tree abundance (total number of individuals) on each subquadrat. We then

quantified tree species richness (number of species) and tree diversity, measured as effective species number (Jost 2006, 2019). In addition, we used survey data to calculate median and maximum tree size (DBH), and basal area of tree stem cover (cm^2/m^2). Lastly, we recorded the overall habitat type that characterized each subquadrat (Online Resource 1).

Generalized linear models

Generalized Linear Models (GLMs) were used to evaluate the effects of habitat attributes on terrestrial orchid community metrics. Prior to running the GLMs, we examined the data for potential collinearity among predictor variables. We used Spearman's correlation analysis because some predictor variables were not normally distributed (*e.g.*, count data for number of trees and tree species). If predictor variables were strongly correlated (correlation coefficients ≥ 0.7; Taylor 1990; Evans 1996; Rafter et al. 2003; Dormann et al. 2013), only one of the pair was included in the GLM analyses (Online Resource 1). We then generated a series of GLM models for each response variable and selected final models based on optimization of Akaike information criterion (AIC) values. The basic model formulation was:

$$g(y_i) = \alpha + \beta_n x_{ni} + \varepsilon_i \quad (1)$$

where g is the relevant link function, y_i is one of our abundance, richness, or diversity measures on subquadrat i, α is the intercept (set to zero in our models), the various β values are coefficients to be estimated, $\boldsymbol{x_{ni}}$ is a vector of subquadrat characteristics, and ϵ_i the site-specific unobservable contribution. GLMs were employed because our response variables exhibited non-normal distributions (all p-values for Shapiro's tests for normality < 0.05; Hahn and Ohyama 2024) and we selected the appropriate model family and link function based on the specific type of response variable in each model (Table 1a; Ford 2022; Hahn and Ohyama 2024).

Indicator analysis

To determine if the distribution of orchid species was linked to the presence of individual tree species, we conducted an analysis to identify significant indicator species in terms of individual orchid species' associations with specific site groups based on tree species (Dufrêne and Legendre 1997; De Cáceres and Legendre 2009; Djordjević et al. 2016, 2020a). For the indicator analysis, we developed a community data matrix with tree distribution data from the sampled area of the plot as individual sites and the orchid distribution data as our species of interest. We tallied which individual trees were paired with individual orchid species as nearest neighbors and then created a vector to describe the classification of sites (*i.e.*, individual trees) into site groups (*i.e.*, tree species). Indicator value indices (*IndVal*) were calculated as the product of two measures: (*A*) specificity and (*B*) fidelity (also referred to as sensitivity). *A* is defined as the frequency of the species in the target site group divided by the sum of the frequencies over all groups. *B* is defined as the relative frequency of occurrence of the species inside the target site group (Dufrêne and Legendre 1997; De Cáceres and Legendre 2009). The "multipatt*"* function in the "indicspecies" package in R was used for the analysis (De Cáceres and Legendre 2009). Statistical significance of the indicator values was evaluated by a randomization procedure with 999 permutations to test the null

Table 1 Features and results of generalized linear models (GLMs) analyzing the effects of habitat attributes on Orchid communities on individual subquadrats of the Ngardok nature reserve ForestGEO plot. (a) parameters and overall results of the individual GLM models for each response variable. (b) details on each of the β coefficients for each of the predictor variables included in each model

(a)	Response variable: y_i	Model Family	Link Function	Model p-value	Pseudo R^2	AIC
	Orchid Abundance	Poisson	Log	<0.01	0.46	2695.5
	Orchid Richness	Poisson	Log	<0.01	0.32	311.3
	Orchid Diversity	Gamma	Log	<0.01	0.29	177.1

(b)	Response variable: y_i	Badlands (SE)	Savanna (SE)	Woody Savanna (SE)	Shaded Fernlands (SE)	Forest Edge (SE)	Forest (SE)	Number of Trees (SE) × 10^{-3}	Median Tree DBH (SE)	Tree Diversity (SE) × 10^{-2}	Elevation in Meters (SE) × 10^{-3}
	Orchid Abundance	−13.83 (440.10)	1.53 (0.22)***	0.65 (0.32)*	−13.5 (340.20)	4.48 (0.16)***	4.50 (0.16)***	8.33 (0.56)***	−0.12 (0.02)***	−6.71 (0.46)***	−2.57 (3.51)
	Orchid Richness	−16.84 (1993.00)	−0.08 (0.67)	−1.40 (0.90)	−16.67 (1544.00)	1.61 (0.59)**	1.44 (0.59)	8.05 (2.05)***	−0.11 (0.01)	−2.30 (1.69)	−4.67 (12.58)
	Orchid Diversity	0.11 (0.23)	0.18 (0.11)	0.05 (0.13)	0.21 (0.21)	0.57 (0.17)**	0.54 (0.17)**	5.98 (1.65)***	−0.06 (0.03)	NA	NA

[a]Note that intercepts (α) in all models were set to zero. Pseudo R^2 values were calculated using McFadden's formula. AIC values are shown for each of the final models; no other model configurations produced significantly lower AIC values. Beta coefficients (β) in the table are followed by standard errors (SE) in parentheses. Values listed as 'NA' in the table indicate variables not included in final models based on AIC values. *Indicates a p-value of <0.05, **is <0.01, and ***is <0.001 for each predictor variable

hypothesis of no association between an orchid species and a tree species. Orchid species with significant indicator values at $p \leq 0.05$ were considered to be associated with specific tree species. Lastly, we reviewed each component of the *IndVal* (*A* and *B*) to determine if significant associations were due to specificity, fidelity, or both.

Results

Terrestrial orchids on the Ngardok ForestGEO plot

The surveyed portions of the Ngardok forest dynamics monitoring plot collectively had 2,672 individuals of terrestrial orchids representing 23 species (Figs. 1–3). Mean abundance of individuals per species over the entire plot was ~116 (SD = 237.88). The most abundant species was *Crepidium setipes* (Fig. 2b) with 944 individuals, followed by *Platylepis hosokawae* ($n = 615$), *Crepidium kerstingianum* ($n = 472$), *Cleisostoma porrigens* ($n = 185$), and *D. fevrellii* ($n = 133$). The remaining 18 species all had fewer than 100 individuals, and their abundances ranged from 56 individuals (*e.g.*, *Appendicula reflexa*) to a single individual (*e.g.*, *Spathoglottis micronesiaca*; Fig. 2c). Overall, the distribution of species abundances was highly right skewed ($g_1 = 2.65$, $p < 0.01$), indicating that a few species were common while the majority were much rarer (Fig. 3).

The abundance of orchids was variable across the Ngardok plot (Fig. 1). One subquadrat had 198 individuals and seven subquadrats had more than 100 individuals. There were no orchids in 31 of the 99 subquadrats. Overall, the number of individuals per subquadrat averaged ca. 27 (SD = 40.03).

Terrestrial orchid species richness and diversity also varied across the plot (Fig. 1). On average, individual subquadrats had ca. two terrestrial orchid species (SD = 2.18), but one subquadrat had nine species and 16 subquadrats had five or more species. The mean effective species number was 1.65 (SD = 0.98) with the most diverse subquadrat having an effective species number of 4.97.

Relationships between orchids and habitat attributes

Considerable differences were noted in orchid community metrics among the six habitat types on the Ngardok plot (Fig. 4). Forest and forest edge habitats had the greatest numbers of individuals ($\bar{x} = 41.2$, SD = 44.5 and $\bar{x} = 39.2$, SD = 43.0 respectively; Fig. 4a). Savanna and woody savanna habitats had fewer orchids ($\bar{x} = 3.1$, SD = 6.6 and $\bar{x} = 1.0$, SD = 2.8 respectively). No orchids were found in badland or shaded fernland habitats. Orchid richness (Fig. 4b) was also highest in forest edge and forest habitats ($\bar{x} = 3.1$, SD = 2.9 and $\bar{x} = 3.0$, SD = 2.0 respectively). Savanna and woody savanna habitats had fewer species ($\bar{x} = 0.6$, SD = 0.9 and $\bar{x} = 0.2$, SD = 0.4 respectively). Orchid diversity exhibited a similar pattern (Fig. 4c), with forested subquadrats having the largest effective orchid species number ($\bar{x} = 2.0$, SD = 1.1) followed closely by forest edges ($\bar{x} = 1.8$, SD = 1.1), then savanna ($\bar{x} = 1.1$, SD = 0.2), and woody savanna habitats ($\bar{x} = 1.0$, SD = 0.0).

GLMs provided a mechanism for assessing the specific relationships between the variation in terrestrial orchid community metrics and habitat attributes across individual subquadrats on the Ngardok plot (Table 1). The final GLM model selections and the co-variates

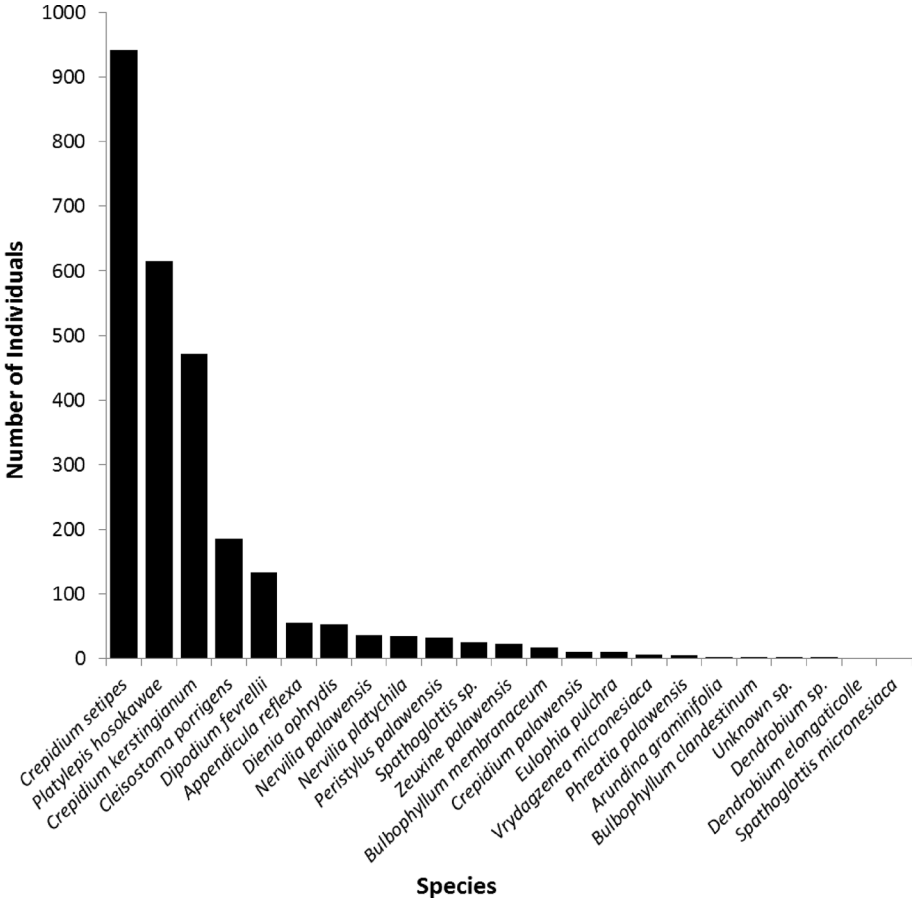


Fig. 3 Histogram showing the abundance of the 23 individual terrestrial orchid species documented across the Ngardok ForestGEO plot

that were included in the analyses were based on minimizing AIC values; as a result covariates were included or excluded from models if it resulted in a significant reduction in AIC values. Overall, the three GLM models that were chosen (Table 1a) were highly significant and had good predictive capacity; Pseudo R^2 estimates in these models were above generally accepted thresholds for goodness of fit ($\geq$0.2–0.4 is considered acceptable; Hensher and Johnson 2018).

The GLMs revealed that habitat type (β_1) was significantly related to orchid abundance, richness, and diversity (Table 1b). Specifically, forest edge habitats were positively related with all three metrics and forest habitats had a positive relationship with abundance and diversity but not richness. Savanna and woody savanna habitats were positively associated with abundance, but to a lesser degree than forest or forest edge habitats. The number of trees on a given subquadrat also had significant positive relationships with orchid abundance, richness, and diversity. Median tree size and tree diversity were negatively related to orchid abundance. Badland and shaded fernland habitats, as well as the elevation of individual subquadrats were not related to any of the orchid metrics.

The indicator analysis showed that among the 23 orchid species on the Ngardok plot, only two were significantly related to individual tree species. *Nervilia palawensis* exhibited a significant relationship with *Calophyllum pelewense* (Clusiaceae; $IndVal = 0.59$, $p < 0.03$). Assessment of the individual components of *IndVal* showed that specificity ($A = 0.70$) had a larger impact on the relationship than fidelity ($B = 0.50$). *Cleisostoma porrigens* was associated with *Premna serratifolia* (Lamiaceae; $IndVal = 0.58$, $p < 0.03$). Assessment of the individual components of *IndVal* in this case revealed that specificity ($A = 0.34$) had much less of an impact on the relationship than fidelity ($B = 1.00$). No other terrestrial orchids had statistically significant associations with individual tree species.

Discussion

Characteristics of terrestrial orchid communities

The goal of this study was to determine how habitat attributes across a forest recovery gradient in the Ngardok Nature Reserve influence the distribution, abundance, and diversity of terrestrial orchid species and to determine if they are dependent on specific tree species so that effective conservation strategies can be established. The 23 terrestrial orchid species on the Ngardok ForestGEO plot represented ca. 25% of Palau's known orchid diversity, demonstrating that the reserve has substantial conservation value for the Polynesia/Micronesia global biodiversity hotspot. The orchid species distribution profile (Fig. 3) was in line with other orchid studies where a few species are common while the majority tend to be rare (Koopowitz et al. 1993; Crain and Tremblay 2014).

From a conservation ecology viewpoint, it was intriguing that the species occurring most frequently on the plot were endemics (*C. setipes*, *P. hosokawae*, *C. kerstingianum*) while others were less common despite having larger global distributions (*e.g. Dienia ophrydis*, *Eulophia pulchra*), or in some cases, being highly disturbance prone and abundant elsewhere (*e.g.*, *Spathoglottis* spp., *Arundina graminifolia*). One possible explanation for the abundance of *C. setipes*, *P. hosokawae*, *C. kerstingianum* is their growth habits; they are clonal and produce ramets, thus resulting in higher numbers of shoots. However, *A. graminifolia* and species in the genus *Spathoglottis*, which are found in great abundance at many sites across Palau, are not clonal, indicating that growth habit is not the sole mechanism contributing to species' abundances.

Another possible explanation for these patterns could be due to the distribution and abundance of orchid mycorrhizal fungi (McCormick et al. 2018). For example, if the most common orchids (*e.g. C. setipes*, *P. hosokawae*, and *C. kerstingianum*) form mycorrhizal associations with a variety of fungi, or those that are abundant or widespread across the Ngardok plot, it could explain their overall abundance as compared to less common species that occur in similar habitats (*e.g.*, *D. ophrydis* and *E. pulchra*), but might interact with specific fungal symbionts or those that are less abundant or less widely distributed. Detailed analyses of Palauan orchids' mycorrhizal associations, their distribution, and abundance, verified by in vitro symbiotic germination trials, should help clarify the role they might play in determining orchids' overall distribution and abundance across the Ngardok plot. More broadly, previous research on mycorrhizal associations on 45 ForestGEO plots (including Ngardok) showed that latitudinal patterns of tree beta-diversity were strongly related to

Fig. 4 Number of individual orchids, orchid species, and effective orchid species occurring on individual subquadrats characterized by the different habitat types covering the Ngardok Nature Reserve ForestGEO plot (median, minimum, maximum, and upper and lower quartiles). See Online Resource 1 for details on how habitat types are characterized. Note that while the median number of orchids was greatest on subquadrats characterized as forest edge, mean number of orchids was greatest on subquadrats characterized as forest. Additionally, while median number of orchid species was the same for subquadrats characterized as forest and forest edge, the mean number was greatest on subquadrats characterized as forest edge

associations with arbuscular mycorrhizal fungi (Zhong et al. 2021). In future work, the ForestGEO network could provide a similarly powerful laboratory for examining how mycorrhizal associations influence orchid diversity over large scales.

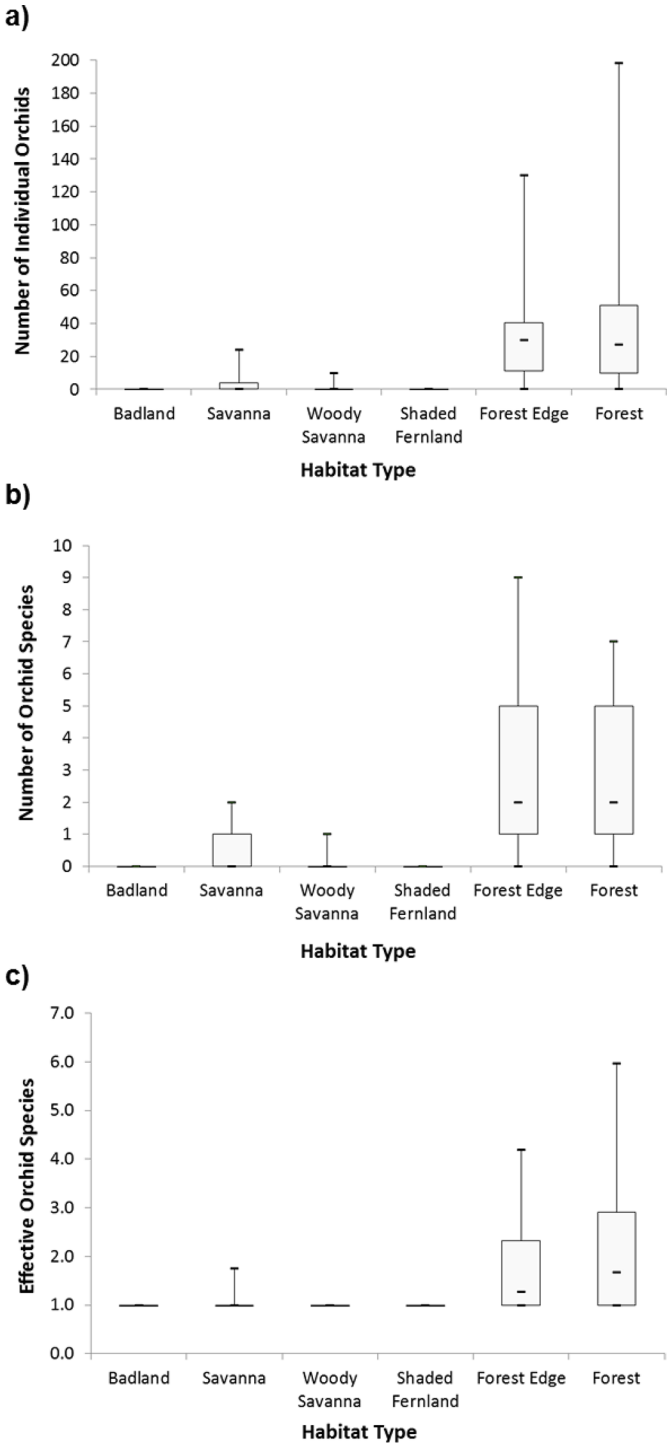
The role of local habitat for sustaining terrestrial orchids across a forest recovery gradient

Orchids were distributed distinctly across the six habitats that composed the Ngardok plot. Thus we rejected the null hypothesis that orchid abundance, richness, and diversity are uniform across the surveyed forest recovery gradient. When considering the differing habitat types on the plot (Online Resource 1), the stark differences among forests and forest edges versus savannas and woody savannas or badlands and shaded fernlands, offered clear evidence that forest conservation, and where needed, forest recovery helps to sustain orchid communities.

On badland habitats several factors likely prevented orchid establishment. The complete lack of canopy cover and presence of bare soil resulted in micro-climates and substrate conditions that are not conducive for most of Palau's terrestrial orchids. Similar findings have been documented for other tropical terrestrial orchids on disturbed sites (Bergman et al. 2006; Besi et al. 2019). Shaded fernlands were also inhospitable to orchids, but unlike badland sites, fernlands have a deep (often well over 1 m thick), dense, and uniform mat of *Dicranopteris linearis* (Gleicheniaceae), which likely limited orchid establishment. Studies have shown that other plants begin to appear in these habitats only when tree canopies begin to develop in later successional stages, causing the thick fern mats to decline (Russell et al. 1998; Yang et al. 2021).

Both savanna and woody savanna habitats share some features with shaded fernlands, including at least 50% fern cover, but the presence of trees and a decrease in fern cover provided appropriate niches for certain orchids to become established. Both habitats had statistically significant positive relationships with orchid abundance. The presence of some tree cover, including at least one potentially large tree ($\geq$5 cm DBH) in each habitat, appeared to be sufficient for suppressing fern cover and providing small patches of suitable orchid habitat, especially for species tolerant of disturbances such as *A. graminifolia* and *Spathoglottis* spp. The presence of species that are less disturbance prone, including *Nervilia platychila*, *P. hosokawae*, and *C. porrigens* in the savanna and/or woody savanna habitats suggests that the presence of even minimal tree cover can provide some suitable habitat for various terrestrial orchids.

Most terrestrial orchids occurred within forest and forest edges, however. Forests were the most abundant habitat the Ngardok plot, and along with forest edges these habitats covered approximately two thirds of its area. The most common species (*C. setipes*, *P. hosokawae*, and *C. kerstingianum*; Fig. 3) were found almost exclusively in these habitats,


a)
Number of Individual Orchids
200
180
160
140
120
100
80
60
40
20
0
Badland
Savanna
Woody Savanna
Shaded Fernland
Forest Edge
Forest
Habitat Type
b)
Number of Orchid Species
10
9
8
7
6
5
4
3
2
1
0
Badland
Savanna
Woody Savanna
Shaded Fernland
Forest Edge
Forest
Habitat Type
c)
Effective Orchid Species
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Badland
Savanna
Woody Savanna
Shaded Fernland
Forest Edge
Forest
Habitat Type

potentially explaining their overall abundance. Each of these locally common orchids is characterized by thin fleshy leaves as well as fleshy stems and appears to be best suited to humid shady environments. Other species from these genera outside of Palau are noted to occur in similar humid and shady habitats (Stewart 1996; Usmadi et al. 2023), but very little is known about their ecology in terms of specific habitat requirements and potential specificity. The analysis of orchids at the subquadrat level using GLM models also highlighted significant positive relationships between those two habitats and overall orchid abundance, richness, and diversity, further indicating that they are the most important habitats for sustaining orchid species in the plot.

Interestingly, orchid richness and diversity had stronger associations with forest edge than forest habitats. This is in accord with other studies showing that forest edges of a variety of forest types sustain greater richness or diversity levels for a wide array of organismal groups (*e.g.*, Duelli et al. 2002; Malonza et al. 2011; Addo-Fordjour and Owusu-Boadi 2016). Edges have also been shown to be important habitats for orchids in particular (Hernandez-Pérez and Solano 2015; Parra Sánchez et al. 2016; Djordjević et al. 2020a). As has been documented in other orchid studies, this is a likely consequence of greater variation in local conditions in edge habitats, allowing different orchid species to thrive outside of forest cores (Parra Sánchez et al. 2016; Djordjević et al. 2020a). This may especially true for drought tolerant species and for those adapted to higher light levels (Hernandez-Pérez and Solano 2015; Djordjević et al. 2020a). Additionally, greater orchid pollinator richness levels have been found in edge habitats in at least one instance (Nemésio and Silveira 2006), potentially supporting a greater diversity of orchids in these habitats as a result.

In contrast, forest habitats had higher orchid abundance, most likely due to the presence of clonal species (*e.g.*, *Crepidium* spp., *Platylepis* spp.) and species that appear strictly limited to mature forest habitats (*e.g.*, *Peristylus palawensis* [Fig. 2d], *Vrydagzenea micronesiaca*, *Nervilia palawensis*). The presence of the forest specialist species is also a likely contributing factor for the significant association between forest habitat and orchid diversity but not richness.

Another possible explanation for orchid communities' affinity for forest and forest edge habitats is the potential impact of more mature vegetation cover on mycorrhizal fungi that are necessary for recruitment on the Ngardok plot. Wall et al. (2020) suggested that it can take decades before fungal communities that orchids depend on recover following disturbance. With fungal recovery supporting recovery of understory vegetation (Koziol and Bever 2016, 2017; Koziol et al. 2018; Liu et al. 2021), this might also explain the limited distribution of orchids among the more disturbed habitat types as compared to forests and forest edges.

Considering specific habitat attributes, the number of trees on individual subquadrats had the strongest relationships with terrestrial orchid abundance, richness, and diversity; greater tree numbers had a positive influence on each orchid metric. The functional connection between the number of trees and orchids is likely a consequence of increased shading, a factor that has been shown to benefit orchids (Besi et al. 2019; Djordjević et al. 2020a). A related successional factor in the Ngardok plot is that as tree density increases in previously disturbed areas, fern abundance decreases, and leaf litter and humus increase to the potential benefit of terrestrial orchids (Russell et al. 1998; Besi et al. 2019; Yang et al. 2021). The same transition from fern dominated habitats to forested habitats may also be more conducive to the establishment of the mycorrhizal communities that orchids depend

on for recruitment (Bergman et al. 2006; Martos et al. 2009). From a conservation outlook, this finding suggests that tree replanting efforts on disturbed sites should have a significant positive impact on developing terrestrial orchid communities.

At the same time, median tree size as well as tree diversity on individual subquadrats both exhibited negative relationships with terrestrial orchid abundance. The negative association with tree size suggests that more mature trees with greater basal cover and canopy closure may not bolster local population growth for all orchid species, potentially due to effects of canopy closure and even direct limitation of understory space when very large trees occupy a subquadrat (Huang et al. 2008; Parra Sánchez et al. 2016; Djordjević et al. 2020a). The negative effect of tree diversity on orchid abundance is in accord with other studies showing that greater tree diversity leads to more closed canopies that potentially limit terrestrial herbaceous plant communities including orchids (Djordjević et al. 2020a; McCormick et al. 2022; Zheng et al. 2022). Again, from a conservation position, this suggests that reforestation efforts could be impactful on developing terrestrial orchid communities even at relatively early stages or with limited tree diversity levels.

Although we observed a negative association between orchids and tree size and diversity, it is possible that this is a result of confounding variables such as light levels or dispersal limitations that were not assessed in this study. Previous studies have revealed that increasing tree size and diversity positively influences orchid communities (Morales-Linares et al. 2022). Accordingly, it is important to note that greater tree sizes and diversity could have significant positive influences on other aspects of terrestrial orchid community development and persistence in Palau, for example by increasing mycorrhiza or pollinator diversity (Kottke et al. 2008; Antonini et al. 2017). However, given the logistical and scientific constraints on seed collection, propagation, and use of diverse tree species in restoration efforts in Palau, it is noteworthy that a selection of more readily available tree species can still be utilized to the benefit of terrestrial orchid communities.

The finding that tree diversity was negatively associated with terrestrial orchid abundance and had no significant influence on richness or diversity was supported by the indicator analysis that showed little connection between the presence of individual orchid species and specific tree species. While two species of orchids and trees exhibited significant relationships with each other, these were largely consequences of the overall rarity of one of the members of each species pair. For example, the tree species, *C. pelewense*, was only documented 16 times on the entire Ngardok plot, and only two times on our survey sites. Although, *N. palawensis* occurred in proximity to one of those tree occurrences, the orchid also occurred in proximity to five other tree species, suggesting that the relationship could be attributed more to the rarity of the tree than to species specificity or fidelity. Similarly, *C. porrigens* was linked to the tree species *P. serratifolia* which only occurred 15 times on the plot and only one time on the survey site. Thus, while this single occurrence led to a significant *IndVal* measure, the orchid species occurred with 29 other tree species on the plot, again suggesting that the relationship was more a relic of rarity as opposed to true ecological specificity or fidelity. Accordingly, we rejected the hypothesis that terrestrial orchid species preferentially occur in proximity to specific tree species. From a conservation standpoint, this again highlights the greater importance of reforestation efforts overall, versus the potential need to plant specific tree species to support terrestrial orchids on the Ngardok Nature Reserve.

Conclusions

The quantification of terrestrial orchids on the Ngardok ForestGEO forest dynamics monitoring plot establishes the value of the framework for understanding controls of orchid distribution, abundance, and diversity, with enormous potential to extend this work to other ForestGEO sites in both tropical and temperate locations. The occurrence of a species-rich terrestrial orchid community on the Ngardok plot also demonstrates the importance of the reserve from a biodiversity conservation standpoint at local, national, and regional scales and as part of the greater Polynesia/Micronesia Global Biodiversity Hotspot. The presence of a diverse orchid community, which includes several species that are rare and/or endemic to Palau, highlights the potential for recovering tropical forest habitats to provide substantial conservation benefits if properly protected and managed. In a broader context, the fact that terrestrial orchid communities have colonized and/or persisted on the Ngardok plot highlights the rewards of reservation conservation strategies, even in the absence of pristine habitats or active restoration activities (Rosenzweig 2003). At the same time, our results indicate that reforestation efforts to restore disturbed sites should also serve to bolster the benefits of reserves in this diversity hotspot. Accordingly, understanding forest recovery patterns and the resulting effects will assuredly improve the design of global and local biodiversity conservation targets and agendas to have the greatest impact on the largest number of species, including for terrestrial orchid communities.

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Author contributions All authors contributed to the study conception and design. Material preparation and orchid data collection were performed by B.C., M.M., and L.Z. Tree data collection was performed by J.D. and A.U. Analyses were performed by B.C. The main draft of the manuscript was written by B.C. and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Data availability The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Competing interests The authors declare no competing interests.

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performed by B. Crain, M. McCormick, and L. Zettler. Tree data collection was performed by J. Dendy and A. Uowolo. Analyses were performed by B. Crain. The first draft of the manuscript was written by B. Crain and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.

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Authors and Affiliations

Benjamin J. Crain[1] · Melissa K. McCormick[1] · Lawrence W. Zettler[2] · Julian Dendy[3] · Christian P. Giardina[4] · Amanda Uowolo[4] · Susan Cordell[4] · Dennis F. Whigham[1]

✉ Benjamin J. Crain
bcrainium@yahoo.com

[1] North American Orchid Conservation Center, Smithsonian Environmental Research Center, Edgewater, MD 21037, USA

[2] Orchid Recovery Program, Illinois College, Jacksonville, IL 62650, USA

[3] USDA Forest Service, Forest Inventory and Analysis, Pacific Northwest Research Station, Corvallis, OR 97331, USA

[4] USDA Forest Service, Institute of Pacific Island Forestry, Pacific Southwest Research Station, Hilo, HI 96720, USA