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Orchids in the Open: Understanding Biodiversity Beyond Madagascar's Forests

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ABSTRACT

Aim: Orchids make up 8% of Madagascar's vascular plant species richness and are typically associated with the island's forests. Yet most of the island is covered by open ecosystems, long dismissed as degraded. This perception has contributed to their neglect, limiting our understanding of species ecology and hindering conservation action in this global biodiversity hotspot. Using orchids, we provide a novel understanding of plant diversity patterns across Madagascar's ecosystems.

Location: Madagascar.

Methods: We assessed the ecosystem attribution of the 884 orchid species of Madagascar among closed (forest) and open (grassy, marsh, rocky outcrop, scrub) ecosystems. We analysed the taxonomic composition, richness, environmental niche, geographic patterns, phenology, and collection patterns of orchids using a mix of herbarium, publication, and iNaturalist data.

Results: We find that 31% of Madagascar's orchid species occur in open ecosystems, with 17% restricted to them. These species match closed-ecosystem species in degree of endemism to Madagascar (~85%) but are associated with higher elevations, fire, and pronounced precipitation seasonality, and are distributed particularly in the grassy Central Highlands, a region historically undervalued ecologically compared to humid forests. Temporally, open-ecosystem specialist orchids exhibit strongly synchronous, brief wet-season flowering, unlike the more diffuse flowering observed throughout the year in forests.

Conclusions: We reveal a distinct component of Madagascar's orchid flora, demonstrating that open-ecosystem species represent high endemism and ecological specialisation, with implications for understanding biogeography and conservation planning across tropical landscapes. These results provide an evidence base for open ecosystem conservation and suggest that other taxa may also be under-represented in our understanding of Madagascar's open-ecosystem biodiversity. Re-evaluating open ecosystems can uncover overlooked dimensions of species diversity and ecological function, informing more balanced conservation strategies across contrasting ecosystems.

ABSTRACT

Objectif: Les orchidées représentent 8% de la richesse spécifique des plantes vasculaires de Madagascar et sont généralement présentes dans les forêts de l'île. Pourtant, la majeure partie de l'île est couverte d'écosystèmes ouverts, longtemps considérés comme dégradés. Cette perception a contribué à leur faible connaissance, limitant notre compréhension de l'écologie de leurs

espèces et entravant les actions de conservation dans cette zone à forte biodiversité. En prenant les orchidées comme modèle, nous apportons une vision nouvelle sur les patrons de diversité végétale à travers les écosystèmes de Madagascar.
Localisation: Madagascar.
Méthodes: Nous avons évalué la répartition de 884 espèces d'orchidées de Madagascar, distribuées entre écosystèmes fermés (forêts) et ouverts (milieux herbacés, marais, rochers, fourrés). Nous avons analysé la composition taxonomique, la richesse spécifique, la niche environnementale, les patterns géographiques, la phénologie et l'échantillonnage des orchidées à partir de données issues d'étiquettes d'herbier, de publications et d'observations disponibles sur la plateforme iNaturalist.
Résultats: Nous montrons que 31% des espèces d'orchidées de Madagascar sont présentes dans des écosystèmes ouverts, dont 17% sont strictement restreintes à ces écosystèmes. Ces espèces présentent un taux d'endémisme de Madagascar comparable à celui des espèces des écosystèmes fermés (~85%), mais elles sont associées à des altitudes plus élevées, au feu et à une saisonnalité marquée des précipitations. Elles sont particulièrement réparties dans les Hautes Terres, région centrale herbeuse, une zone historiquement sous-échantillonnée sur le plan écologique par rapport aux forêts humides. Sur le plan temporel, les orchidées spécialistes des écosystèmes ouverts présentent une floraison fortement synchrone et brève pendant la saison humide, contrairement à la floraison plus diffuse observée tout au long de l'année des orchidées de forêt.
Conclusions: Nous mettons en évidence une composante distincte de la flore des orchidées de Madagascar, montrant que les espèces des écosystèmes ouverts se caractérisent par un fort endémisme et une spécialisation écologique marquée, avec des implications pour la compréhension de la biogéographie et la planification de la conservation à travers les paysages tropicaux. Ces résultats fournissent une base empirique pour la conservation des écosystèmes ouverts et suggèrent que d'autres taxons pourraient eux aussi être sous-représentés dans notre compréhension de la biodiversité des écosystèmes ouverts de Madagascar. Réévaluer les écosystèmes ouverts peut révéler des dimensions négligées de la diversité spécifique et du fonctionnement écologique, et ainsi éclairer des stratégies de conservation plus adaptées entre écosystèmes contrastés.

1 | Introduction

Orchids are among the world's most popular and best-studied plant groups due to their iconic floral displays, and are found across almost all terrestrial ecosystems, from dry alpine grasslands to humid lowland rainforests (Djordjević and Tsiftsis 2022; Pérez-Escobar et al. 2024). In Madagascar, Orchidaceae is the most species-rich plant family with over 900 species, representing 8% of the island's vascular plant species (Antonelli et al. 2022; Droissart et al. 2023). Although orchids are best known for their remarkable diversity across Madagascar's forests (Cribb and Hermans 2009), some studies have highlighted them as potentially important for understanding open ecosystems—habitats whose origins and ecology remain debated (Bond et al. 2008; Silander Jr. et al. 2024). The functional adaptations of orchids to different environments—such as growth form, fire tolerance via belowground bud storage, and flowering seasonality—and their high ecological specialisation (Lamont and Downes 2011; Zhang et al. 2018; Djordjević and Tsiftsis 2022; Taylor et al. 2021) make orchids a useful group to address questions about plant diversity patterns across Madagascar's ecosystems.

Tropical and sub-tropical open ecosystems and their biodiversity are underappreciated and underrepresented in science, policy and management, with priority given to forests (Silveira et al. 2022; Pilon et al. 2025), a bias that shapes both conservation priorities and how biodiversity patterns are interpreted. Meanwhile, biomes dominated by open ecosystems cover almost 60% of the world's vegetated area (Dinerstein et al. 2017) with distinct biota directly supporting over a billion livelihoods (Lehmann and Parr 2016; Ryan et al. 2016). Madagascar's stark environmental gradients and diverse ecosystems (Moat and Smith 2007) have fascinated biologists for the last two centuries. The closed ecosystems of eastern humid forest, western dry forest, and spiny thickets containing famous plants such as Darwin's Orchid (*Angraecum sesquipedale*) are globally renowned. Among open ecosystems, rocky outcrops, such as in the iconic Tsingy, have also captured scientific and conservation attention (Raharimahefa 2012; Rabarimanarivo et al. 2019). In contrast, the extensive tropical and montane grasslands, Tapia savannas, marshes, and high-elevation scrubs are rarely connected with Madagascar's nature, with narratives of ecosystems as products of human colonisation and transformation (Perrier de la Bâthie 1921; Kull 2000). Given that orchids have adapted to most terrestrial ecosystems globally over evolutionary timescales, if all ecosystems—both closed and open—in Madagascar are natural and not the result of recent human action, one would expect to find orchid species in all of Madagascar's ecosystems.

Open and closed ecosystems are shaped by different processes with consequent differences in ecosystem function and dynamics (Bond 2019; Keith et al. 2022). In many closed ecosystems, the canopy limits light penetration to the ground year-round, impacting microclimates, litter layers, and plant recruitment (Rüger et al. 2009; Balandier et al. 2022). This is not the case in tropical dry forests for the period when they are deciduous, but in open ecosystems, woody cover is generally low, allowing light to reach the ground year-round, with plants recruiting in open sunlit conditions. An ecosystem can be deterministically open in areas with soils absent or unsuitable for woody growth, or in climate too dry or too cold (Bond 2019). However, the distribution of many open ecosystems is not determined by climate and soils, but is rather driven through interactions among climate, soils, disturbance, plant adaptations, and life history strategies (Asner et al. 2009; Warman and Moles 2009; Staver et al. 2011). Since megafaunal extinctions, disturbance in Madagascar has been

primarily in the form of cattle grazing and fire (Johnson 2009; Solofondranohatra et al. 2020). Fire had been naturally present in the mosaic landscapes of grasslands and shrublands even before human arrival on the island (Razafimanantsoa et al. 2024). In contrast, intact closed ecosystems suppress fires through positive feedbacks involving microclimates and litter accumulation supported by high tree cover (Hoffmann et al. 2012).

Plant species have evolved to the divergent conditions in open and closed ecosystems across the tropics (Simon et al. 2009; Maurin et al. 2014), and some are generalist and can thrive in various environments or colonise biome boundaries. Species in closed ecosystems generally lack substantive adaptations to fire (Scheper et al. 2021), whereas those in open ecosystems often possess traits related to persistence, recovery or avoidance of fire (Whitman et al. 2011; Zizka et al. 2014; Vorontsova and Rakotomalala 2021). Many open-ecosystem orchids, mostly tuberous geophytes, exhibit obligate or facultative fire-stimulated flowering, and in South Africa this often occurs within 4 months after fire (Lamont and Downes 2011). Orchids have also adapted to the different vertical ecosystem structures. In closed ecosystems, there is ample habitat for epiphytes and shade-tolerant terrestrials such as mycoheterotrophs (Leake 1994; Zhang et al. 2018). Meanwhile, most diversity in open ecosystems is terrestrial or lithophytic, tolerating high light and wind exposure (Bardot-Vaucoulon et al. 2022; Hermans and Rajaovelona 2022). The light niche occupied by orchid species is hence diverse and complex across ecosystems, limited not only to light intensity but also quality related to reflection and selective absorption, with species-specific impacts on vegetative growth or flowering (Zhang et al. 2018; Wang et al. 2019; Djordjević et al. 2020). Moreover, as orchids in closed ecosystems are usually epiphytes, the competition for light, nutrients, and water differs from that of terrestrial plants (Werner and Homeier 2024). On islands, geophytic orchids become proportionally more abundant than epiphytes with increasing seasonality (Taylor et al. 2021), reflecting their resilience to wider temperature ranges, colder temperatures or lower precipitation (Howard et al. 2019). As open ecosystems are often characterised by high precipitation seasonality, orchid phenology likely tracks both seasonal vegetation growth and fire timing (Liu et al. 2022). Orchid distributions are further shaped by complex local moisture, soil, and temperature conditions and multi-level structural differences, as shown in studies from closed (e.g., Djordjević et al. 2020; Pica et al. 2024; Crain et al. 2025) and open ecosystems (e.g., Djordjević et al. 2016; Slaviero et al. 2016).

Principal features of open ecosystems, such as canopy openness and recurrent fire, have often been interpreted as signs of habitat degradation in Madagascar (Perrier de la Bâthie 1927; Perrier de la Bâthie 1928; Kull 2000). Views on Madagascar's open ecosystems are divergent, from a product of deforestation over the past 1000 years (Joseph et al. 2021), in comparison to natural origins over evolutionary timescales (Bond et al. 2008; Solofondranohatra et al. 2020; Razafimanantsoa et al. 2024). However, regardless of the pre-colonisation extent of open ecosystems, there is also an unanswered question of whether extant open ecosystems are currently species-rich (Vorontsova et al. 2016; Solofondranohatra et al. 2020) or species-poor (Styger et al. 2007), considering unknown diversity patterns (Antonelli et al. 2022) and many species yet to be discovered in Madagascar (Ondo et al. 2024). Efforts to understand open ecosystems are further inhibited by biases in sampling (Silander Jr. et al. 2024). Much of the institutional focus of 20th-century botanical research in Madagascar was on forests (Vorontsova et al. 2021), with dedicated work on open ecosystems gaining momentum only more recently (Rabarivola et al. 2019; Rasaminirina and Larridon 2023). Open ecosystems have also been long neglected in conservation, poorly represented in protected areas (Cribb and Hermans 2015; Ralimanana et al. 2022), in contrast with forests (From et al. 2005; Droissart et al. 2023; Silander Jr. et al. 2024).

Here, we studied the environments, geography, phenology, and collection patterns of orchids through the lens of ecosystem types in Madagascar. After classifying species as open-ecosystem specialist (OE), closed-ecosystem specialist (CE), or mixed-ecosystem generalist (ME), we tested four primary hypotheses:

H1. *Orchids are found across a range of open ecosystems in Madagascar, with a proportion of specialist (OE) and generalist (ME) species, and with a substantial component of this richness predicted to be endemic.*

H2. *OE species occupy a distinct environmental niche from CE species.*

H3. *OE species have a distinct phenology with a short flowering season and a high synchronisation of flowering.*

H4. *Sampling effort, discovery of species over time, and age of records differ between species of open and closed ecosystems.*

2 | Methods

2.1 | Study System

There is a variety of open ecosystems *sensu* Bond (2019) recognised in Madagascar. Grasslands cover most of the Central Highlands, dominated by C_4 grasses regularly burning in the dry season, interspersed with patches of gallery forests (closed ecosystems) in the valleys and lee of hillsides (Lehmann et al. 2022). Granitic inselbergs and other rocky outcrops are found across grassy highlands, and extensive outcrops, such as tsingy, along the western coast. Scrub habitats of ericaceous shrublands are common at higher elevations (Silander Jr. et al. 2024) and dry open shrublands are present on sandy, low-nutrient soils and along the coast. Tapia savannas (or woodlands), named after Tapia (*Uapaca bojeri*), are found in the highlands of central and southwestern Madagascar (Kull and Birkinshaw 2022). Among Madagascar's open ecosystems, some better-studied areas of open-ecosystem orchid diversity include Andringitra (Perrier de la Bâthie 1927; Rabetaliana et al. 1999), and Itremo (Rakotonasolo et al. 2025). Closed ecosystems in Madagascar include humid and sub-humid forest formations, littoral forests, mangroves, as well as dry forests and spiny thickets (Moat and Smith 2007). They form homogeneous formations, but are also interspersed in fine mosaics with open ecosystems, especially across the Central Highlands.

2.2 | Data

2.2.1 | Species List

Orchidaceae is a cosmopolitan flowering plant family of close to 30,000 species worldwide (Govaerts et al. 2021), with most richness concentrated in the tropics. A list of Orchidaceae species in Madagascar was compiled using the World Checklist of Vascular Plants and extracted using the *rWCVPdata* R package (Govaerts et al. 2021). Only native species with accepted names were retained. We excluded hybrids and included subspecies and varieties within their respective species. Additionally, species missing from *rWCVPdata*, for example, due to their very recent description, were added from POWO (2024), returning a final list of 920 species. We classified species as endemic if they only occurred in Madagascar.

2.2.2 | Ecosystem and Growth Form Assignment

Ecosystem classification of each species (Table 1) was determined based on a comparative review of descriptions from herbarium specimens from Kew Herbarium (K) accessed in person and through the Kew Data Portal (Royal Botanic Gardens, Kew 2025), and some specimens from Muséum National d'Histoire Naturelle (P), Missouri Botanical Garden Herbarium (MO), Herbier de Tananarive (TAN) accessed through Tropicos (2025) and JSTOR Global Plants (JSTOR 2024); checklists (Hermans et al. 2007; Cribb and Hermans 2009; Rakotonasolo et al. 2025); journal publications (Andriamihaja et al. 2023; Bosser 2015; Cribb et al. 2011, 2012; Fischer et al. 2009; Hermans 2020a, 2020b; Hermans et al. 2017, 2020a, 2020b, 2020c, 2021a, 2021b, 2021c, 2021d, 2022, 2025, Hermans and Cribb 2014; Hermans and Rajaovelona 2019; Hervouet et al. 2014; Hervouet and Hermans 2022; Huang et al. 2018; Pace 2020); GBIF descriptions (GBIF.org 2024); and iNaturalist (2024) images. Each species was assigned to one of the ecosystem specialisation categories of OE, ME and CE. If a species was found only in open-ecosystem types (e.g., grassland and rocky outcrop), we refer to it as an open-ecosystem specialist (OE). If a species was found only in closed-ecosystem types (e.g., humid forest), it was marked as a closed-ecosystem specialist (CE). If a species was found across both open- and closed-ecosystem types (e.g., grassland and dry forest), it was marked as mixed-ecosystem (ME), that is, generalist. The final open-ecosystem types used included grassy, rocky outcrop, scrub and marsh. Among closed ecosystems, we only further distinguished two ecosystem types—humid forests (if referred to as 'humid', 'wet', or 'evergreen') and dry forests, which were used in supplementary analyses. Admittedly, the classifications used here are not final, and likely some species may shift ecosystem specialisation categories in the future as we continue to better understand the ecology of habitats in Madagascar. We assigned ecosystem classification to 884/920 species. The ecosystem could not be determined for 36 species due to incomplete information available, for example, dubious identifications, missing location and ecosystem description, or lost type specimens, and we removed those species from further analyses.

Additionally, each species was assigned a growth form based on checklists (Hermans et al. 2007; Cribb and Hermans 2009), POWO (2024) and GIFT (Denelle et al. 2023). Growth forms were divided into epiphyte (including climbers), terrestrial (i.e., geophyte), and lithophyte (Figure S2). Although the epiphyte–geophyte contrast has been widely emphasised in orchid research (Taylor et al. 2021; Djordjević et al. 2022), we also distinguish lithophytes here due to their common occurrence in Madagascar and their ecological relevance in open ecosystems. Growth form classifications are non-exclusive, and some species are classified in each of the three forms. Species are referred to as obligate tree-epiphytes if they are classified as epiphytes only.

The resulting ecosystem and growth form assignment is in Data S1.

2.2.3 | Occurrence Data

Occurrence data were obtained from the Global Biodiversity Information Facility (GBIF), Droissart et al. (2023), Royal Botanic Gardens, Kew & Kew Madagascar. GBIF data (GBIF.org 2024) were downloaded on 29th November 2024 using the *rgbif* R package (Chamberlain and Boettiger 2017; Chamberlain et al. 2025), retaining only preserved specimens. The Droissart et al. (2023) dataset with unrestricted locality data was shared directly by the authors. Human observation data were only included from iNaturalist (2024), with the exact location data shared directly by Royal Botanic Gardens, Kew & Kew Madagascar, as most of the publicly available data for Orchidaceae have reduced accuracy to protect sensitive taxa. We excluded occurrences with >5 km positional accuracy. Across all datasets, we excluded cultivated species; records with dubious or missing coordinates; records with dubious identifications (for instance, 8939 records from shade houses without clearly identifiable fertile specimens were removed, mostly of CE species); and records identified only at the family or genus level. The names were then matched to the taxonomic backbone of Plants of the World Online using the *rWCVP* R package (Brown et al. 2023), merging information from subspecies and varieties to the species level. Afterwards, data were cleaned using the *CoordinateCleaner* R package (Zizka et al. 2019) to remove duplicates (comparing records rounded at five decimal places) and occurrences outside of Madagascar. The final occurrence dataset consisted of 14,963 records for 862 species. The geolocated data are not available with this publication to protect sensitive taxa; data can only be obtained directly from the data providers.

2.2.4 | Environmental Data

In advance of the analyses on species' environmental niche and habitat suitability, we selected six environmental variables related to disturbance and climate which we considered important to plant species distribution in the context of Madagascar—mean yearly burned area, elevation, mean diurnal range, isothermality, annual precipitation, and precipitation seasonality (Table 2). All variables were standardised individually on a scale from 0 to 1 for the analyses. To assess collinearity between variables, we used the absolute value of the correlation coefficient (|r|) with a threshold for exclusion of $|r|>0.7$ indicating high correlation (Dormann et al. 2013). None of the pairs of variables was highly correlated (Figure S3).

TABLE 1 | The classification used for assigning ecosystem types and corresponding ecosystem categories to each species. The distinction between open and closed ecosystems follows Bond (2019).

Ecosystem category	Ecosystem type	IUCN classification	Description (Madagascar's context)
Open	Grassy	T4.2 Pyric tussock savannas T6.5 Tropical alpine grasslands and herbfields	Ecosystems with a grass-dominated ground layer characterising grasslands, savannas & Tapia woodlands (characterised by *Uapaca bojeri* trees); grasses are shade-intolerant; usually, fire-prone C_4 grasses, but also C_3 grasses mostly at higher elevations (Bloesch et al. 2002); distinct dry season. Tapia woodlands have been previously described as a form of grassy ecosystem, floristically and functionally different from adjacent forests (Solofondranohatra et al. 2018). They are fire-adapted ecosystems where different tree species display fire adaptations (Rasoafaranaivo 2005). The density of woody species and the canopy cover in Tapia woodlands are driven by the fire return interval, with frequent fire promoting canopy openness. As Tapia and savanna were used interchangeably with grassland, often clearly pointing to the same ecosystem and with 72% Tapia species and 75% savanna species classified as grassland species (Figure S1), we merged Tapia, savanna and grassland into a 'grassy' category. For example, grassland; prairie; savanna; sclerophyllous (Tapia) woodland in Imamo, Col des Tapia, Itremo, and Isalo.
	Rocky outcrop	T3.4 Young rocky pavements, lava flows and screes T3.1 Seasonally dry tropical shrublands*	Ecosystems with sparse lithophytic (rupicolous) vegetation; they have limited extent and are usually located within grasslands or scrublands, providing refuge from fire (Hermans and Rajaovelona 2022); subjected to direct light and wind exposure (Bardot-Vaucoulon et al. 2022). For example, exposed rocks of inselbergs in Andringitra; rock outcrops in the limestone tsingy. *Note that some rocky outcrops may be better described under the 3.1 than the 3.4 category in the IUCN classification. Here, we split the rocky outcrop and scrub ecosystems due to their distinctiveness in botanical descriptions.
	Scrub	T3.1 Seasonally dry tropical shrublands MT2.1 Coastal shrublands and grasslands	Dominated by shade-intolerant ericoid shrubs; sandy low-nutrient soils; usually at high elevations but also in coastal lowlands (dry, deciduous scrub); fires are present but not frequent—usually at decadal-scale intervals (Silander Jr. et al. 2024; Hackel et al. 2025). For example, montane *Philippia* scrubland (Andringitra, Ambohitantely or Isalo); coastal scrub.
	Marsh	TF1.4 Seasonal floodplain marshes	Seasonally inundated ecosystems dominated by graminoids (grasses and sedges); open-canopy ecosystems with few or no trees. For example, marsh; wet grassland; peatland
Closed	Humid forest	T1.1 Tropical/Subtropical lowland rainforests T1.3 Tropical/Subtropical montane rainforests	Closed-canopy forest in a warm tropical climate with high annual rainfall; species are fire-intolerant; fire is rare and usually is a result of drought or human modification. For example, humid evergreen forest; moist semi-deciduous forest; shaded rocks in forests.
	Dry forest	T1.2 Tropical/Subtropical dry forests and thickets	Multilayered closed canopy of mostly deciduous tree species; rainfall 400–1400 mm, with a pronounced dry season > 6 months (Gautier et al. 2022); in an undisturbed ecosystem, the ground layer is usually sparse and herbaceous cover is discontinuous (Armstrong and Goodman 2022). For example, dry deciduous forest; dry spiny forest.

Note: Individual ecosystem types (Table 1) were grouped using the Ecosystem Functional Groups of the IUCN Global Ecosystem Typology 2.1 (Keith et al. 2022) and informed by the historical classifications compiled by Gautier et al. (2022) to account for the inconsistencies of describing the same ecosystem. These broad ecosystem types are often used in the context of orchids in Madagascar (Cribb and Hermans 2009).

TABLE 2 | Variables used for analysing the environments of orchids.

Environmental variable	Code	Description	Source
Mean yearly burned area	Fire	Many open-ecosystem species have fire adaptations (Lamont and Downes 2011; Midgley and Bond 2013), with fire promoting the diversity of fire-adapted flora while filtering out disturbance-intolerant species typical for closed ecosystems (Wieczorkowski et al. 2024). We expected OE species to be more abundant in areas experiencing fire than CE species. To achieve a normal distribution of Fire in the analyses, we applied a fourth root transformation.	Received from authors of Phelps et al. (2022), derived from Giglio et al. (2018)
Elevation	Elev	Elevation is repeatedly found to structure the patterns of orchid diversity (Ackerman et al. 2007; Djordjević et al. 2022; Lussu et al. 2024). It is also used as a proxy of mean annual temperature, which affects plant ecology and distribution (Zanne et al. 2018), as the two variables are highly correlated ($\|r\| > 0.9$).	NASA Shuttle Radar Topography Mission (2013)
Mean diurnal range	T_Diu_R	Calculated as (Mean of monthly (max temp—min temp)). The mean diurnal range is related to species' tolerance to temperature fluctuation and has been found to be a correlate of species elevation range sizes (Gallou et al. 2023). We expected most OE species to be commonly tolerant of high temperature ranges typical of open landscapes, in contrast with humid forests where daily temperature varies less.	WorldClim (Fick and Hijmans 2017) [T_Diu_R: bio2, T_Seas: bio3, P_Ann: bio12, P_Seas: bio15]. Many of the specimens are much older than the bioclimatic variables (average for the years 1970–2000); however, the broad patterns should remain the same.
Isothermality	T_Iso	Calculated as (Temperature Diurnal Range/Temperature Annual Range) (×100). Isothermality has been suggested to be important in tropical and insular environments (Nix 1986); in the tropics, it can largely influence plant species distributions as species differ by their tolerance of larger vs. smaller temperature fluctuations within a day relative to the year (Huang et al. 2021).	
Annual precipitation	P_Ann	Precipitation and its seasonality are key to structuring seasonally dry ecosystems (Lehmann et al. 2011). The highest annual precipitation should also be correlated with the distribution of humid forest species.	
Precipitation seasonality	P_Seas		

2.3 | Analyses

Data processing, visualisation and analyses were conducted in R (R Core Team 2022) using the following packages: *ape* (Paradis and Schliep 2019), *circular* (Agostinelli and Lund 2024), *DHARMa* (Hartig 2024), *eulerr* (Larsson 2024), *factoextra* (Kassambara and Mundt 2020), *FSA* (Ogle et al. 2023), *ggcorrplot* (Kassambara 2023), *ggVennDiagram* (Gao and Dusa 2024), *ggridges* (Wilke 2024), *gridExtra* (Auguie 2017), *pairwiseAdonis* (Arbizu 2017), *patchwork* (Pedersen 2024), *raster* (Hijmans 2023), *readxl* (Wickham and Bryan 2023), *rnaturalearth* (Massicotte and South 2023), *rnaturalearthdata* (South et al. 2024), *sf* (Pebesma 2018; Pebesma and Bivand 2023), *terra* (Hijmans 2024), *tidyterra* (Hernangómez 2023), *tidysdm* (Leonardi et al. 2024), *tidyverse* (Wickham et al. 2019), *V.PhyloMaker2* (Jin 2024), *vegan* (Oksanen et al. 2022), and *writexl* (Ooms 2024). The order of analyses is structured along the hypotheses.

2.3.1 | H1: Diversity and Endemism

To assess species diversity across ecosystems, we calculated total species richness per each of the three ecosystem

specialisation categories (OE, ME, CE) and per four open-ecosystem types (grassy, marsh, rocky outcrop, scrub). The endemicity rate was calculated as the number of species endemic to Madagascar divided by the total species richness in a given ecosystem specialisation category. The results are presented using area-proportional Euler diagrams to compare species richness and endemism to Madagascar across ecosystem specialisation categories, and then using a Venn diagram to compare species richness across four open-ecosystem types. The ecosystem attribution and growth forms were summarised for each of 11 tribes and displayed on a tribe-level cladogram generated using the phylogeny compiled by Jin and Qian (2019) based on the GBOTB phylogeny for seed plants (Smith and Brown 2018). An accurate genus-level phylogeny was not yet available at the time of writing due to the unresolved phylogenetic position of multiple Orchidaceae genera. We additionally calculated the richness across ecosystems, excluding strict tree-epiphytic species as they are expected to be largely exclusive to closed ecosystems.

2.3.2 | H2: Environmental Distribution

To assess the environmental niches across ecosystem specialisation categories, occurrence data for each species were first thinned at 1 km to reduce the bias of sampling closely positioned populations of the same species, and then we filtered out records for which any value for the six environmental variables was missing. The final dataset used included 10,846 records for 862 species. To understand the environmental preferences of OE, ME and CE species, we first plotted the occurrence densities of the three groups for each of the six environmental variables. To assess differences between the ecosystem specialisation categories, we used a Kruskal-Wallis test followed by Dunn's (1964) test of multiple comparisons with the Bonferroni correction due to the non-normal distribution of environmental variables. Then, we evaluated the association of OE, ME and CE species with environmental variables using a principal component analysis (PCA). Biplots were used to visualise the first and second PCs, with a visualisation of the second and third PC in Figure S4. We also ran separate PCAs for individual ecosystem types (Figure S5). We quantified differences in environmental niches among ecosystem-specialisation categories using PERMANOVA based on a Bray-Curtis distance matrix, which we calculated for the values of all environmental variables for each species occurrence. A global model tested differences among all three categories simultaneously, followed by a pairwise test to resolve differences between specific category pairs.

Based on environmental parameters extracted at species occurrence locations, we analysed habitat suitability for OE, ME and CE species using SDM methodology. To reduce spatial autocorrelation, the occurrences (14,963 records for 862 species) were first split by ecosystem specialisation category, then spatially thinned by retaining at most one record per 30″ raster cell, and subsequently enforcing a minimum distance of 10 km between records (OE: 309 records for 82 spp.; ME: 491 records for 99 spp.; CE: 567 records for 241 spp.; note that occurrences in each group were thinned for the entire group, regardless of the species identity). Pseudo-absences were generated at a 3:1 ratio to presences, with a minimum 10 km distance from both presences and each other. All six environmental variables were used as predictors. Models were trained using Maxent, Random Forest (rf), and Extreme Gradient Boosting (gbm) algorithms. Model performance was evaluated using five-fold spatial cross-validation. Final models were selected for each algorithm based on the Boyce Index (≥ 0.5), and the ensemble prediction was computed as the mean suitability across selected models. Metrics of the final models are reported in Table S2, and their hyperparameter configurations are provided in Table S3.

2.3.3 | H3: Phenology

To assess species phenology across ecosystems, we assessed the number of flowering events per month (i.e., the number of unique georeferenced occurrence records collected during each month), the length of the flowering season per species, and flowering synchronisation. The date of occurrence, expressed as a day of year ranging from 1 to 365, was used as a substitute for the date of the flowering event, as specimens are almost exclusively collected (or photographed, in the case of iNaturalist) when flowering to allow identification to the species level. The total number of flowering events for OE, ME and CE species was calculated for each month and displayed on a circular plot using the dates of occurrence records where available (OE: 1349 records for 117 spp.; ME: 3367 records for 121 spp.; CE: 7684 records for 497 spp.).

2.3.3.1 | Flowering Season. Using the flowering event data, we analysed whether the flowering season length (in days) differs across ecosystem specialisation categories. Only species with at least four observations on different days of the year (D) were used to reduce the risk of underestimating the flowering season length for species with few observations (OE: 940 records for 63 spp.; ME: 2460 records for 96 spp.; CE: 5654 records for 293 spp.). To quantify the length of the flowering season for each species, we calculated the shortest circular span of observed flowering days within a year. This approach accounts for flowering periods spanning across the end and beginning of the calendar year (e.g., from December into January). For each species, we sorted the observed flowering days in ascending order and computed the differences (*gaps*) between each pair of consecutive days. We then included the circular gap (c)—the number of days between the last and first observation across the year boundary:

$$c = 365 - (\max\ (D) - \min\ (D)) \tag{1}$$

where c is the circular gap, max (D) is the last observed flowering day in a calendar year, and min (D) is the first observed flowering day.

The largest gap in the flowering calendar was assumed to represent the non-flowering period. Therefore, the length of the flowering season (f; the shortest continuous span of flowering activity) was estimated by subtracting the largest gap from the total number of days in the year:

$$f = 365 - \max\ (\text{gaps}, c) \tag{2}$$

where f is the length of the flowering season, and max (gaps, c) is the largest gap in the flowering calendar.

This method ensures that flowering seasons that wrap around the year-end are correctly captured. A linear model was then used to compare the flowering season length between OE, ME, and CE species by modelling the flowering season length as a function of ecosystem specialisation category, using a normal distribution, interpreted using R^2 value and a p-value (p) with a significance threshold of 0.05.

2.3.3.2 | Synchronisation. To assess flowering synchronisation, we followed Texier et al. (2018) to calculate the synchronisation coefficient (r), which captures both the duration and consistency of flowering patterns (Hamann 2004). The coefficient ranges from 0 (complete asynchrony, that is, events evenly spread across the year) to 1 (perfect synchrony, where all events occur on the same date each year), indicating the regularity with which flowering occurs over time. Only species with at least four observations were used (OE: 1266 records for 67 spp.; ME: 3323 records for 99 spp.; CE: 7358 records for 312 spp.), as species with very low sample sizes may produce unreliable results.

Each flowering event was converted into an angular value (θ_i) between 0 and 2π radians, scaled such that January 1st corresponds to 0 and December 31st to 2π. For each species, we calculated the mean flowering angle (Φ)—representing the average flowering time—as the angle of the resultant vector formed by summing daily vectors weighted by the number of flowering events per day (n_i). The length of this vector, relative to the total number of events, gives the synchronisation coefficient (r), which reflects how tightly flowering events are clustered around the mean date.

The components of this mean vector were calculated as:

$$x = \sum_{i=1}^{k} n_i \cos(\theta_i) \tag{3}$$

$$y = \sum_{i=1}^{k} n_i \sin(\theta_i) \tag{4}$$

where k is the number of unique days of the year with at least one flowering observation, n_i is the number of flowering events on day i, and θ_i is the angular value (in radians) representing that day of the year, scaled from 0 to 2π. The values x and y are the horizontal and vertical components of the mean flowering vector.

The mean flowering angle (Φ) was then computed as:

$$\Phi = \operatorname{atan2}(y, x) \tag{5}$$

where Φ is the mean flowering angle (in radians), that is, the direction of the mean flowering vector, computed from the directional components x and y derived in Equations (3) and (4). Negative values of Φ were shifted by adding 2π to express mean flowering angles on the interval $[0, 2\pi]$.

The mean flowering day ($\bar{D}$) was then calculated as:

$$\bar{D} = \frac{\Phi}{2\pi} \times 365 \tag{6}$$

where $\bar{D}$ is the mean flowering day for a species, obtained by converting mean flowering angle (Φ) to an equivalent day of the year, rounded to the nearest day, with values of 0 reassigned to day 365.

The synchronisation coefficient (r) was calculated as the normalised length of the mean vector:

$$r = \frac{\sqrt{x^2 + y^2}}{\sum_{i=1} n_i} \tag{7}$$

where r is the synchronisation coefficient (or mean resultant length), the numerator is the length of the mean vector, and the denominator is the total number of flowering events across the year.

To evaluate whether flowering synchronisation differed between ecosystem specialisation categories (OE, ME, CE), we used a Kruskal-Wallis test, followed by Dunn's (1964) test for pairwise comparisons with Bonferroni correction. To estimate the proportion of species exhibiting a significantly distinct flowering season (i.e., whether r is significantly greater than 0), we applied the Rayleigh test (Batschelet 1981). As the Rayleigh test has reduced power at low sample sizes, potentially failing to detect synchrony in species with few observations (Figure S6), the true number of species flowering synchronously may still be underestimated, even though we restricted our analysis to those with at least four observations. We considered species to be highly synchronous if $r \geq 0.75$ and $p < 0.05$ for the Rayleigh test (Texier et al. 2018).

Using the same data and methodology, we repeated the process of calculating the synchronisation coefficient at the community level (i.e., combining the observations across species) for each ecosystem specialisation category.

2.3.4 | H4: Sampling Patterns—Sampling Effort and Temporal Patterns of Collections

To compare the differences in sampling patterns between ecosystem specialisation categories, we used the sampling effort, the discovery of species over time, and the age of records. For the sampling effort, the total number of occurrence records per species was used as a proxy. We acknowledge that the sampling effort can be confounded with rarity. To understand the discovery of species across ecosystems through time and the temporal patterns of collections, we plotted the cumulative percentage of species per year of first publication and the cumulative percentage of occurrence records per year. We predicted that: (1) most OE species would be described later than CE species; and (2) OE species' records would be more recent than those of CE species. Only species endemic to Madagascar

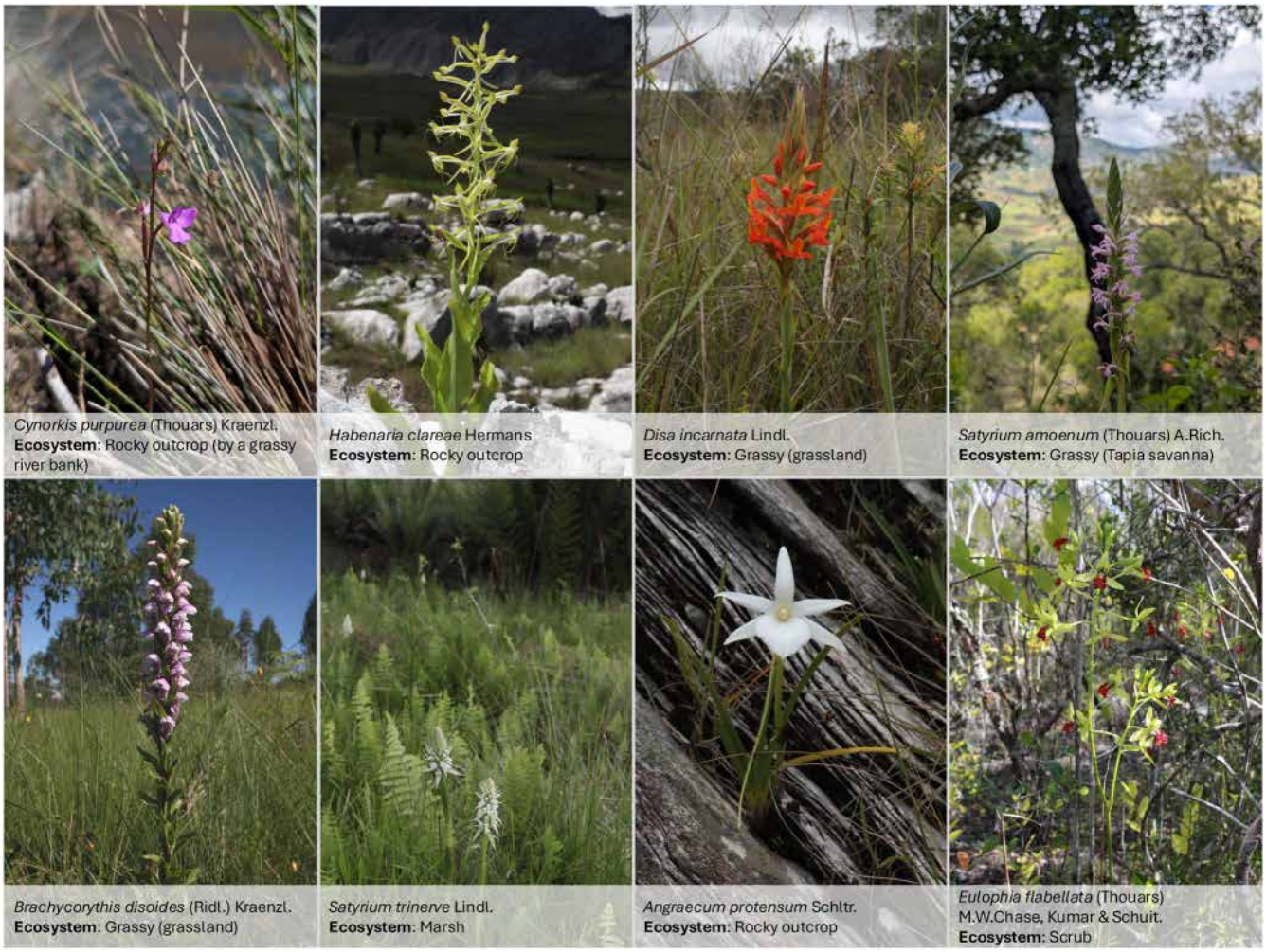

FIGURE 1 | Orchids in open ecosystems of Madagascar. Photographs by J. Hermans and J. D. Wieczorkowski.

were used in the context of species discovery to assess research history in Madagascar. Due to the non-normal distribution of sampling effort, year of first publication and year of observation, we used a Kruskal-Wallis test followed by Dunn's (1964) test of multiple comparisons with the Bonferroni correction to assess whether they differ between ecosystem specialisation categories. We additionally use the year 2000 as a threshold for comparison of temporal patterns, where we predicted changes in research practices in the 21st century, considering the increasing recognition of open ecosystems as natural systems (Silander Jr. et al. 2024).

3 | Results

3.1 | Diversity Across Ecosystems

We assigned ecosystem classifications (Table 1) to 884 orchid species, among which 146 are exclusively in open ecosystems (OE species), 127 in both open and closed ecosystems (mixed-ecosystem—ME species), and 611 exclusively in closed ecosystems (CE species) (Figure 1, Figure 2A). Species occurring in open ecosystems (273 spp.), that is, including specialists (OE) and generalists (ME), were (non-exclusively) in rocky outcrops (142 spp.), grassy ecosystems (i.e., grasslands, savannas, Tapia; 136 spp.), scrubs (88 spp.) and marshes (75 spp.) (Figure 2B). The rate of endemicity to Madagascar was 86% for OE and 85% for CE species (Figure 2A).

Of 146 OE species, the three tribes Orchideae, Cymbidieae, and Vandeae contained 95% of species richness (Figure 2C). Genera specialist to open ecosystems were only within Orchideae and include *Brachycorythis*, *Disa*, *Platycoryne*, and *Satyrium*. Orchideae contained a genus near-endemic to Madagascar, *Tylostigma* (8 spp.), predominantly found in open ecosystems (marshes), and two species in both marshes and forests (*T. nigrescens* and *T. filiforme*). OE species were mostly terrestrial (Orchideae, Cymbidieae), and some lithophytic (mostly Vandeae). ME species spanned all growth forms, with most in Vandeae and Orchideae. CE species were predominantly epiphytes, with 75% of all species across Vandeae and Malaxideae. If obligately tree-epiphytic species were excluded, there were 234 spp. within open ecosystems (sum of OE and ME), and 280 spp. in closed (CE and ME).

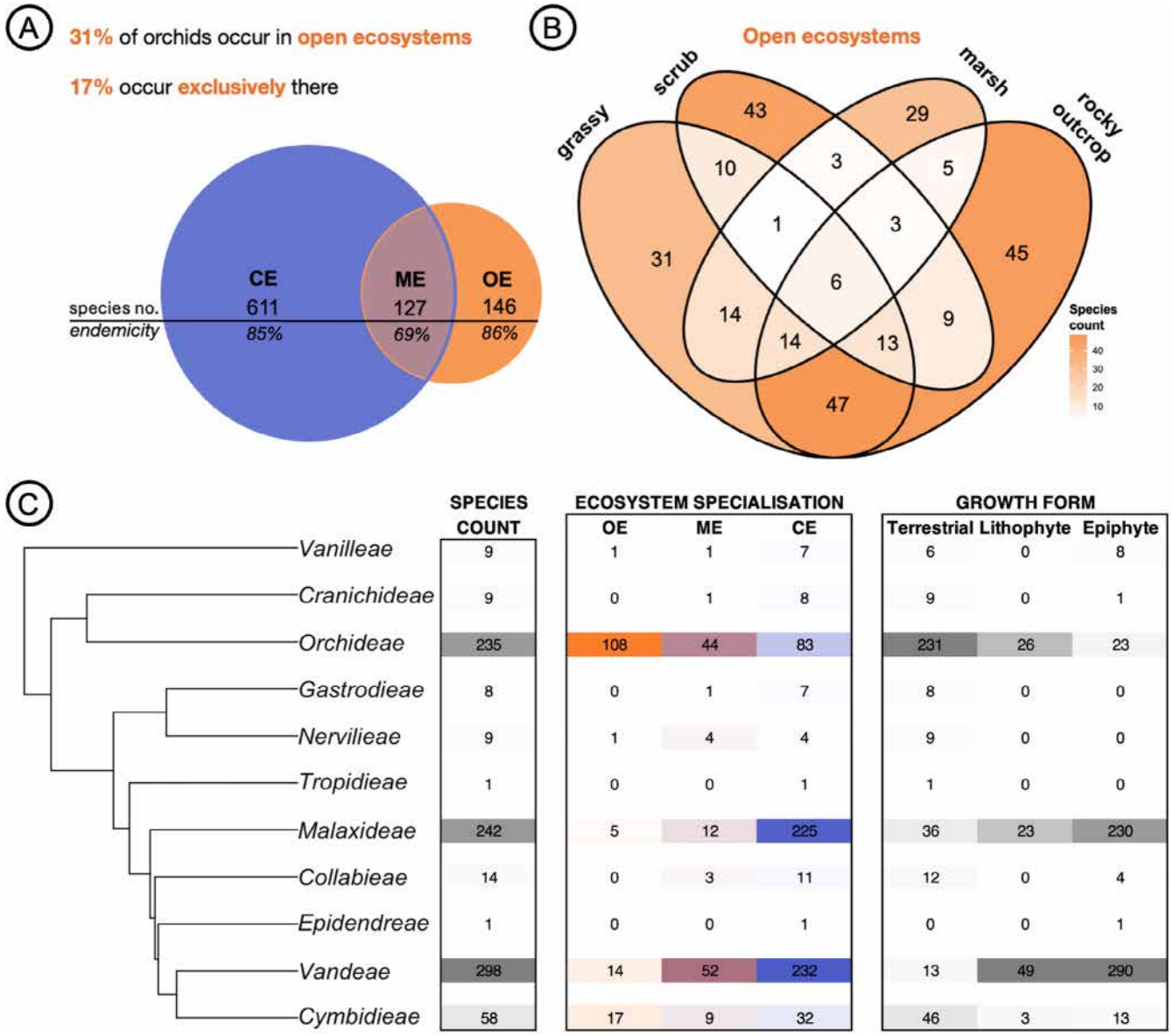

FIGURE 2 | Orchid diversity in Madagascar. (A) Euler diagram depicting the number of species in each category of open-ecosystem specialist (OE), mixed-ecosystem (ME), and closed-ecosystem specialist (CE) species. Assignment of ecosystem specialisation categories was possible for 884 out of 920 species. There are 273 species that occur exclusively (OE) or non-exclusively (ME) in open ecosystems. (B) Venn diagram depicts the overlaps across classifications of individual open-ecosystem types for 273 species. (C) Tribe-level cladogram of Orchidaceae native to Madagascar, along with the total species count per tribe and with corresponding growth form and ecosystem specialisation classifications (using data for 884 spp.). Numbers indicate the number of species per tribe. Colour shading is scaled individually for each column, with the highest value in a column given the highest colour intensity. Ecosystem specialisation categories are exclusive, with species occurring in both open and closed ecosystems noted under ME. Growth form classifications are non-exclusive, and the same species may occur in any combination of the three forms.

3.2 | Environmental Distribution

OE species were found in areas with the highest elevations, fire activity, diurnal temperature range, and precipitation seasonality and the lowest annual precipitation, while CE species were at the opposite end of the spectrum, and ME species in the middle (Figure 3A, Table S1). CE species are more widely environmentally distributed than OE, occupying most of the environmental space characterised by high annual precipitation (Figure 3B), with some of the spread determined by the differences between dry and humid forests (Figure S5). OE, CE, and ME species occupy substantively different environments (PERMANOVA $p < 0.05$, Table S1, Figure 3B), with CE-OE comparison having the largest effect size ($R^2 = 6.0\%$), suggesting the greatest, although still low, distinction in environmental space.

The relative habitat suitability map shows the broad geographic patterns of environmental suitability for each ecosystem specialisation category (Figure 3C). OE species were predominantly found in the Central Highlands, extending from the southernmost to the northernmost high-elevation

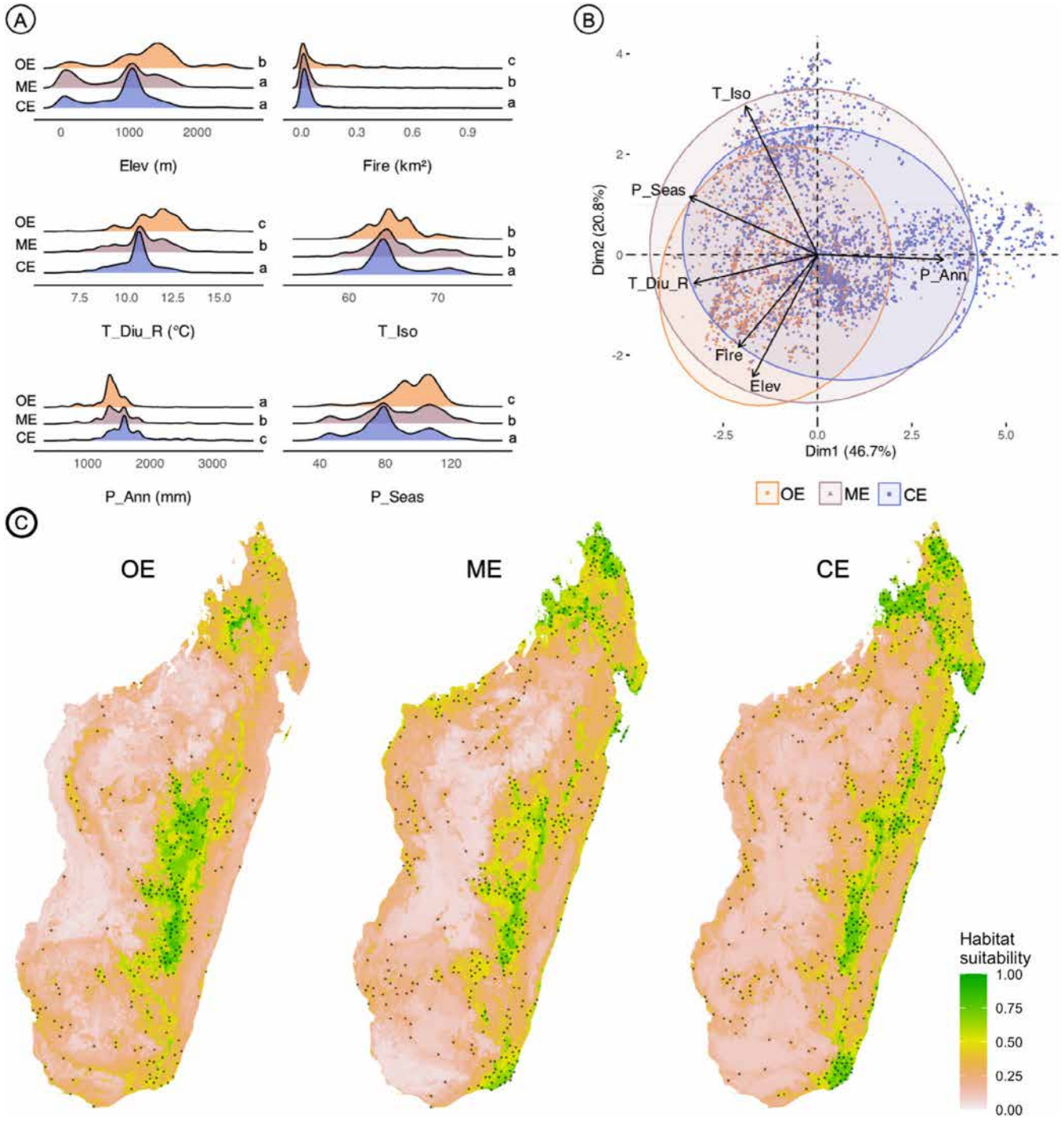

FIGURE 3 | Environmental distribution of open-ecosystem specialist (OE), mixed-ecosystem (ME), and closed-ecosystem specialist (CE) species. (A) Density plots display occurrences across six environmental gradients of elevation, fire, temperature diurnal range, isothermality, annual precipitation and precipitation seasonality. The occurrence dataset used totalled 10,857 observations for 861 species. Letters indicate groups with significant differences according to the Dunn test (Table S1), with the group with the lowest value starting from 'a'. (B) Principal component analysis shows a multidimensional space for all Orchidaceae occurrences using the six variables. Each ellipse captures the area in which 95% of the individuals from a given ecosystem specialisation group are expected to fall. The first three components account for 80.5% of the variation. The first component is driven by precipitation variables and temperature diurnal range, the second by isothermality and elevation, and the third by fire. PERMANOVA results indicated significant differences in environmental niches between the three groups ($p < 0.001$). (C) Relative habitat suitability for OE, ME and CE species. We used 309 occurrences of OE species, 491 occurrences of ME species, and 567 occurrences of CE species, which are all marked as black dots on corresponding plots. All six environmental variables were used as predictors.

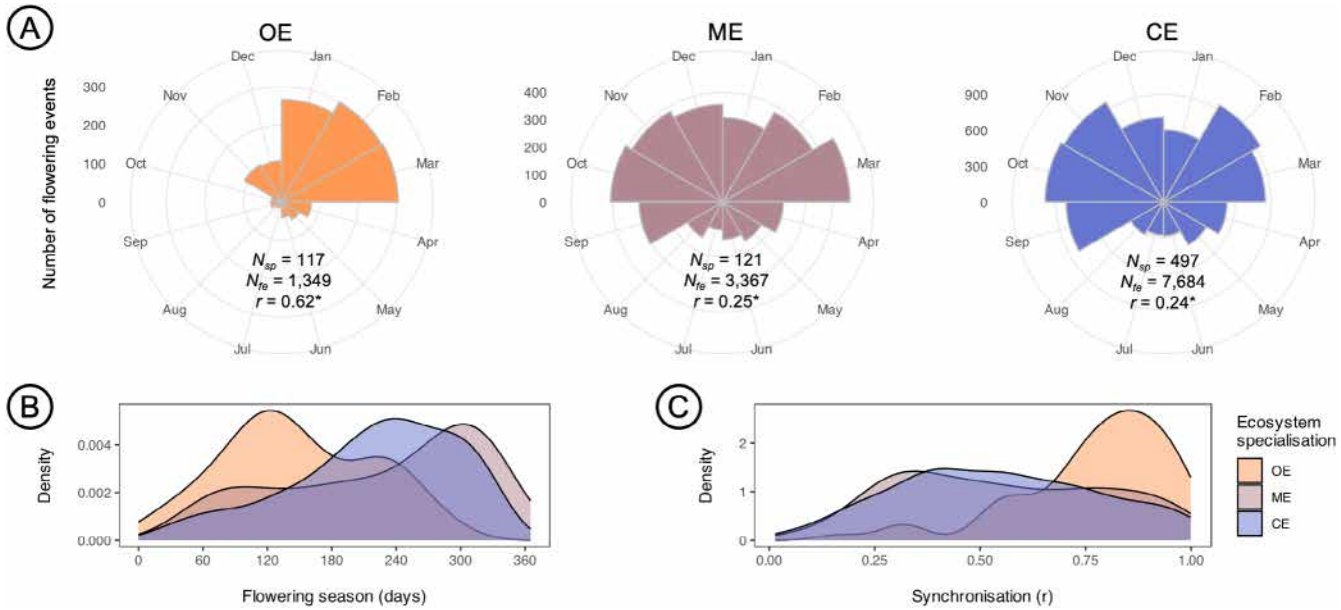

FIGURE 4 | Phenological patterns of open-ecosystem specialist (OE), mixed-ecosystem (ME), and closed-ecosystem specialist (CE) species. (A) Number of flowering events per month. N_{sp} is the total number of species. N_{fe} is the total number of flowering events. r is the synchronisation coefficient calculated across all species, with * indicating significant values (<0.05). (B) Length of flowering season (days) per species, which refers to the minimum period in a year when a given species is found flowering. It is calculated as the minimum number of consecutive days needed to connect all recorded flowering dates for a species, using a circular (radial) year scale. Only species with observations on at least four different days of the year were included; N_{sp}: 63 (OE), 96 (ME), 293 (CE). (C) Synchronisation of flowering events per species. Only species with at least four observations were included; N_{sp}: 67 (OE), 99 (ME), 312 (CE).

areas, with low suitability in the west. CE species showed high suitability along the eastern side of the Central Highlands—where they strongly overlapped with OE species—and along the eastern coast and in the north. ME species exhibited an intermediate suitability pattern, combining features of both OE and CE patterns—present across the Central Highlands, the eastern coast, and the north.

3.3 | Phenology

Flowering in OE species was concentrated between January–March, while CE and ME species flowered more broadly throughout the year, though with fewer flowering events typically recorded between May and August (Figure 4A). Flowering season of OE species was significantly shorter (149 days) than of CE (220 days) or ME species (225 days) (Figure 4B, Table S1). Flowering synchronisation (r) at the community level (i.e., across all flowering events) was equal to 0.62 for OE, compared to 0.25 for ME and 0.24 for CE. At the species level, flowering synchronisation was significantly highest among OE species (Figure 4C, Table S1, $p<0.001$), with flowering seasonality detected for 86.6% of OE, 69.7% of ME, and 61.9% of CE species. Highly synchronous flowering ($r\geq0.75$ and Rayleigh $p<0.05$) was detected for 62.7% of OE, 28.3% of ME and 20.8% of CE species. Full results on phenological characteristics of each species are in Data S2.

3.4 | Sampling Patterns

Sampling effort per species was higher for ME (30.7±3.3) than OE (12.0±1.4) and CE (15.2±1.1) species ($p<0.001$), with no statistical difference between OE and CE ($p=1$) (Figure 5A, Table S1). Among OE species, 49.3% had <5 records and none had >100 records, compared to 44.8% and 2.3% respectively among CE species. Species discovery happened on average later for CE (1950±1.8) than OE (1941±4.3) and ME (1937±4.2) species ($p=0.01$, Table S1), although with proportionally more OE (23.2%) than CE (20.4%) species published since 2000 (Figure 5B). The age of records was significantly older for OE (1988±0.9) than CE (2001±0.3) and ME (2000±0.5) species ($p<0.001$, Table S1), and with 40.8% of OE records predating 2000 compared to only 21.2% and 24.4% for CE and ME respectively (Figure 5C).

4 | Discussion

4.1 | Diversity and Endemism

Madagascar's open ecosystems harbour a diverse and unique orchid flora—an important contribution to ongoing efforts to move beyond simple 'natural versus anthropogenic' narratives and toward a fuller, ecologically-informed understanding of biodiversity and disturbance regimes in these systems (Phelps et al. 2025). We found that one-third of orchid species in Madagascar inhabit open ecosystems, with 149/275 species occurring exclusively in open ecosystems. Open-ecosystem orchids are mostly terrestrial, geophytic species, while some are lithophytes. Closed-ecosystem orchid richness is higher (739 spp.), largely composed of tree epiphytes. When analyses exclude obligate tree epiphytes, the disparity in richness diminishes, with 236 species in open and 279 in closed ecosystems. Although Madagascar is already a globally renowned hotspot for orchid endemism (Vitt et al. 2023), our attention needs to

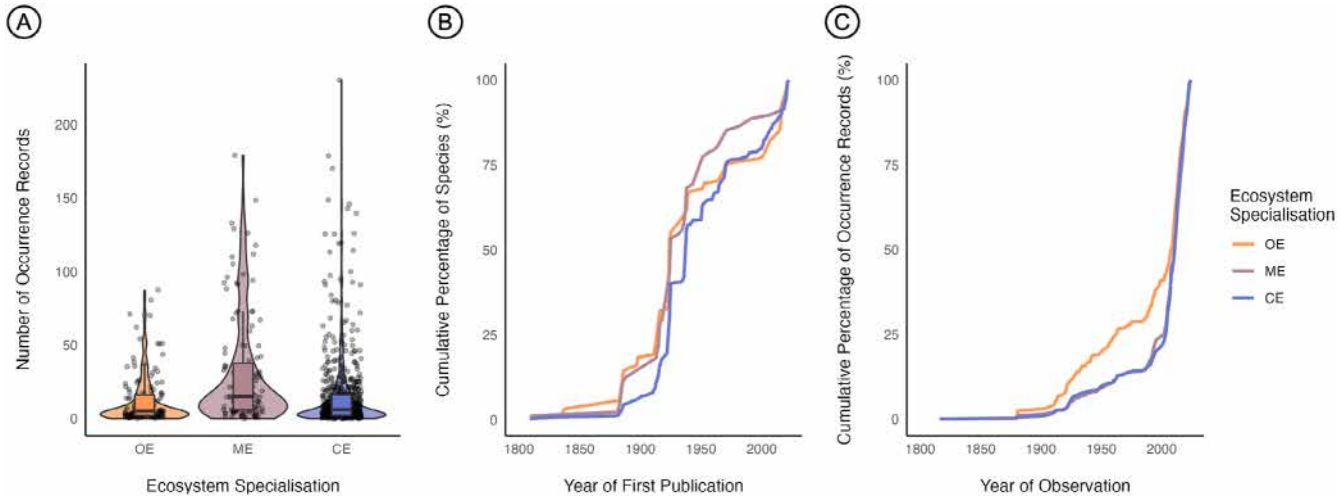

FIGURE 5 | Sampling patterns for open-ecosystem specialist (OE), mixed-ecosystem (ME), and closed-ecosystem specialist (CE) species. (A) Sampling effort—number of occurrence records per species. (B) Species discovery—cumulative percentage of species' first publications across the past > 200 years. (C) Age of records—cumulative percentage of all occurrence records. For (A) and (C), 14,963 records for 862 species were used. For (B), only species endemic to Madagascar were used (733 spp.).

extend beyond its famous forests. A forest-first framing can make forests the default baseline for interpreting biodiversity and conservation value, obscuring high-value open-ecosystem floras and contributing to their under-prioritisation in conservation planning. Orchid species in both open and closed ecosystems exhibit an equally high level of endemism to Madagascar (~85%)—a remarkably elevated value among the world's islands (Schrader et al. 2024)—underscoring Madagascar's importance for urgent conservation prioritisation (Kier et al. 2009).

Open-ecosystem species richness is concentrated in grassy ecosystems, followed by rocky outcrops, high-elevation and coastal scrubs, and marshes. While rocky outcrops have received some recognition for their unique species diversity (Rabarimanarivo et al. 2019), the broad distribution of species richness across diverse open ecosystems highlights the need for research attention and a deeper understanding of the links between biodiversity and ecological processes. Ecosystems such as scrub and Tapia have long been considered vulnerable to fire and degraded whenever the woody canopy is sparse (Silander Jr. et al. 2024; Hackel et al. 2025). However, recent research is changing our perspective on their relationship with fire (Solofondranohatra et al. 2018). The key woody species in these systems are adapted to fire, such as through thick protective bark, leathery leaves resisting burning, and epicormic sprouting in *Uapaca bojerii* trees in Tapia (Kull and Birkinshaw 2022), or high flammability in *Erica* spp. in scrub (Perrier de la Bâthie 1927; Gil-Romera et al. 2019; Hackel et al. 2025). Many orchids are found in these flammable ecosystems, pointing to their potential adaptation to fire. Some species are confirmed to flower in recently burned areas, such as *Benthamia herminioides* in ericaceous scrub (Cribb and Hermans 2009). Open-ecosystem orchids typically have underground tubers, which are protected from fire and then resprout (e.g., *Cynorkis flexuosa*), or fire-resistant pseudobulbs (e.g., *Eulophia rutenbergiana*) (Cribb et al. 2005). In South Africa, the genus *Disa* (in Madagascar specialised to open ecosystems) has a long evolutionary history linked to the first appearance of a flammable grassy biome (Bytebier et al. 2010). However, others, such as *Angraecum* spp., are vulnerable to grassland fires and are restricted to rocky outcrops which rarely burn (Whitman et al. 2011; Rajaovelona et al. 2020). We also find diverse marsh orchids, including *Tylostigma*, a near-endemic Orchideae genus that is predominantly associated with open ecosystems. Together, these examples suggest that open-ecosystem occupancy may reflect both pre-adapted colonists and within-island ecological divergence, which will require explicit phylogenetic and biogeographic analyses to disentangle. Madagascar's open ecosystems are thus home to a wide variety of species with unique adaptations to thrive in open habitats.

4.2 | Environments

Species of open and closed ecosystems occupy distinct environmental niches, although with areas of overlap. The key distinction between them is driven by elevation, where OE species are found at the highest elevations across grasslands, scrubs and rocky inselbergs, with a similar gradient found in temperate systems (Djordjević et al. 2022). OE species are also more tolerant of higher daily temperature variability, similar to temperate orchids with which they share functional adaptation (tuberous storage organs) and close phylogenetic relationship (Orchideae) (Freudenstein and Rasmussen 1999; Djordjević and Tsiftsis 2022). Meanwhile, many tropical orchids tend to be sensitive to low temperatures and temperature variability (Zhang et al. 2018), characterising Madagascar's closed ecosystems of humid forests, but not the few dry forest species. Considering the environments characterising open-ecosystem orchids, we find their diversity to be mostly distributed in the highlands of the centre, south and north of the island, and some across the coastal open scrub and grassy ecosystems (Figure 3C). The concentration of orchid diversity in the Central Highlands is similar to the pattern seen for grasses (Nanjarisoa et al. 2017; Antonelli et al. 2022) and sedges (Rasaminirina et al. 2026). The highest overlap between OE and CE species is also in the Central Highlands (Figure 3C), characterised by seasonal rainfall and fire patterns, and fine-scale mosaics of vegetation from open flammable grasslands on the hills

to humid gallery forests in the river valleys (Lehmann et al. 2022). Therefore, in these environments, multiple species coexist within a bioclimatic space, though fine-scale distributions are difficult to distinguish without precise coordinates and microclimatic data. Despite this overlap, microhabitat conditions vary markedly, enabling the coexistence of species with contrasting functional traits and differing light and moisture requirements.

4.3 | Phenology

Ecosystem seasonality drives OE orchids to flower over a short, highly synchronised period during the wet season, starting in November and peaking across January–March. Evidence on the phenology of herbaceous plants in tropical open ecosystems has been scarce, although some studies pointed to flowering concentrated in the wet season (Batalha and Mantovani 2000; Arruda et al. 2021). In the seasonally dry open ecosystems of the Central Highlands, rains allow plant growth from December to April, followed by seasonal dryness and plant curing enabling fire from May to November (Alvarado et al. 2018), and the flowering period for OE orchids mirrors that ongoing cycle. Fire-stimulated flowering has not been comprehensively assessed in Madagascar, but has been observed across southern African OE species of *Disa*, *Satyrium* and *Eulophia*, also abundant in Madagascar (Lamont and Downes 2011). Recent work from Australia shows that fire effects on terrestrial orchids are highly season-specific, with vulnerability governed by whether burns overlap with critical stages of tuber development (Thomsen et al. 2024). Disentangling the effects of water availability and fire-stimulated cues would require targeted experiments (e.g., controlled exposure to fire cues versus watering) and long-term population monitoring that relates flowering timing to local fire events and rainfall patterns. Among CE epiphytic orchids in tropical rainforests, flowering has been previously linked to increases in moisture availability, flowering at the beginning of and during the main rainy season, although on the community level, flowering occurs throughout the year (Texier et al. 2018). Here, we find that the flowering of CE species has low synchronisation at the community level ($r = 0.24$) and is asynchronous for 38% of species, especially across humid forests of little seasonality in rainfall and temperature. Our phenological comparison has broad implications for tropical ground-layer surveys, where open ecosystems may be chronically under-surveyed due to flowering seasonality. In the wet season, field sites are difficult to access, but sampling outside of this period would underestimate the richness—especially in open ecosystems. Thus, biodiversity assessments must align field work with ecosystem-specific phenology.

4.4 | Sampling Patterns

Most records for OE orchids come from the Central Highlands, as for many taxonomic groups (Antonelli et al. 2022), and therefore partly reflect the distribution of main sampling localities, with consequences for record age and the apparent timing of species discovery. However, even within the Central Highlands, the sampling is spatially uneven. Many open grassy landscapes have few collections, likely linked to an assumed lack of native vegetation, with the collections skewed toward a few protected areas (Lowry II et al. 2018). The west of Madagascar has been poorly sampled for all vascular plants (Qian et al. 2021), while there are grassy ecosystems that have received little study and attention (Lehmann et al. 2022). It is unclear if low species richness across orchids and other plants in these regions is accurate or a symptom of few collections. Moreover, half of the OE species have fewer than five geolocated records, and few species are well-sampled, limiting inference on distributions and threats. Although we found no difference in sampling effort between ecosystems, much understanding of species distributions in open ecosystems relies disproportionately on old specimens. The earlier description and collection of OE than CE species may be related to the fact that known OE species are mostly distributed in the Central Highlands, close to where most of the population lives. Interpretation of species distributions can be further biased by recent land-use change (Vieilledent et al. 2018; Ralimanana et al. 2022), as the high rates of land conversion in the last 25 years mean that species may no longer occur in some of the areas where they were historically recorded. This further underscores the need for improved sampling in Madagascar's open ecosystems, particularly as a greater proportion of OE than CE species have been described since 2000. For instance, *Cynorkis prehsleri* was recently discovered in an unprotected grassland alongside a road and is only known from a few subpopulations (Hermans 2020a). While forest orchids have mobilised initiatives such as shade houses and seed banks (Stévart et al. 2019), similar attention is needed for open ecosystems.

5 | Conclusion

A view of open ecosystems as anthropic products risks losing the unique biodiversity that remains poorly understood. In contrast to the extensive attention given to forest loss (Morelli et al. 2020), the extent and impact of open ecosystem loss remain largely undocumented in Madagascar. The protection of open ecosystems in Madagascar is low (Ralimanana et al. 2022), and few protected areas contain large areas of grassy ecosystems (Alvarado et al. 2014; Silander Jr. et al. 2024). While Madagascar's forests are a well-known hotspot of plant diversity, its open ecosystems are also home to a unique terrestrial and lithophytic orchid flora. This suggests that other, less-studied taxa may also be under-represented in our understanding of Madagascar's open landscapes. Open ecosystems are underappreciated habitats of endemic plant diversity in Madagascar, requiring research, protection, and appropriate management.

Author Contributions

J.D.W. and C.E.R.L. conceived and designed the study. J.D.W. compiled the dataset of ecosystem classifications with inputs from L.R.R. and J.H. J.D.W. performed the analyses. J.D.W. wrote the manuscript. C.E.R.L. and A.Z. provided supervision. All authors reviewed and commented on the manuscript, and accepted the final version.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The dataset with ecosystem assignments is uploaded with the submission (Data S1). The geolocated data are available from GBIF (https://doi.org/10.15468/dl.t8uqks), Royal Botanic Gardens, Kew & Kew Madagascar (https://www.inaturalist.org/projects/zavamaniry-gasy-plants-of-madagascar), and Droissart et al. (2023). Royal Botanic Gardens, Kew & Kew Madagascar, and Droissart et al. (2023) have restricted locality data to maintain confidentiality concerning the exact location of threatened orchid species; complete data can be requested directly from the providers. Code used in all analyses is available at https://doi.org/10.5281/zenodo.18662870.

Peer Review

For transparency, the peer review documents associated with this article are available at https://doi.org/10.1111/ddi.70172.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Data S1:** Supporting Information. **Data S2:** Supporting Information. **Data S3:** Supporting Information.