Crop species and climate shape amphibian communities and conservation significance of coffee agroforests in the Western Ghats

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Abstract

Shade coffee agroforests are recognized as refuges for biodiversity and potential allies in conservation across the human-modified tropics. However, biodiversity is strongly influenced by coffee cultivation methods and climates, both of which vary widely and are increasingly dynamic. In this context, one significant but understudied change is the shift in cultivated species from arabica (*Coffea arabica*) to robusta (*C. canephora*) coffee, which alongside continued deforestation and climate change, is reshaping present and future coffee landscapes globally. We examined the effects of land use (rainforest, arabica coffee, robusta coffee) and climate (coffee in wet vs. dry zones) on amphibian abundance, community composition, multidimensional diversity (taxonomic, functional, phylogenetic), and ecologically-sensitive and conservation-priority species in India's Western Ghats mountains—a global biodiversity hotspot and threatened amphibian landscape. We sampled amphibians along line transects (total 12.9 km), collected primary and secondary data on species functional traits (12 traits), geographic distributions, conservation threat status, and phylogenies, and estimated multidimensional diversity (Hill numbers $q = 0\text{-}2$) and species occurrence probabilities using joint species distribution models across land uses and climate zones. While overall abundance and richness ($q = 0$) were roughly similar across land uses and climates, the rainforest had distinct amphibian community composition, higher multidimensional diversity ($q = 1$ and 2), and higher occurrence probabilities of lotic (stream-breeding) and conservation-priority (threatened and endemic) species. Amphibian multidimensional diversity ($q = 1$ and 2) was generally higher in arabica compared to robusta coffee in both climate zones and decreased alongside lotic and conservation-priority species from wet to dry zones. Our results highlight that while coffee agroforests can sustain substantial numbers and varieties of amphibians, arabica-to-robusta conversions and climate drying can diminish multidimensional diversity, and securing and restoring remnant forests and streams is essential for conserving threatened, endemic, and ecologically-sensitive amphibian species in changing coffee landscapes.

1. INTRODUCTION

Biodiversity and its conservation share a complex relationship with agricultural and agroforestry production systems in the tropics. On one hand, the expansion of production systems over the past century has been a leading driver of tropical deforestation and biodiversity loss (Gibbs et al., 2010; IPBES, 2019). Today, most tropical biodiversity hotspots lack extensive forest cover and are instead dominated by human-modified landscapes (HMLs) comprising mosaics of production systems interspersed with other land uses including remnant natural ecosystems (Gardner et al., 2009). On the other hand, while intact tropical forests are exceptional and irreplaceable for biodiversity, production systems can represent last refuges for a large proportion of biodiversity in landscapes that are already heavily deforested (Bhagwat et al., 2008; Gibson et al., 2011). For this reason, HMLs and production systems are presently widely recognized as key allies to formal protected areas for securing the future of tropical biodiversity (Gardner et al., 2010; Arroyo-Rodríguez et al., 2020). However, tropical HMLs can be highly dynamic as deforestation, land use change, and intensification of production practices continue alongside, and sometimes in response to, a changing climate (Steffan-Dewenter et al., 2007; Mantyka-pringle et al., 2012; Oakley & Bicknell, 2022; Hylander et al., 2024). Investigating biodiversity responses to these ongoing changes can help identify emerging threats and opportunities, and design biodiversity-friendly tropical production systems and HMLs.

Shade coffee agroforests are a production system of particular significance for biodiversity conservation. This is partly because coffee, which is among the most highly traded commodities globally, is cultivated across many of Earth's most biodiverse and threatened tropical forest regions (Hardner & Rice, 2002). This is also because coffee agroforests maintain a shade tree canopy that often comprises multiple native species, which makes them among the more biodiversity-friendly agroforestry systems (Manson et al., 2024; Perfecto et al., 1996), and important refuges for biodiversity in HMLs (Bhagwat et al., 2008). However, coffee cultivation encompasses large variation and high dynamism in production practices, and spans wide climate gradients (14°C to 26°C mean annual temperature and <1000 mm to >4000 mm mean annual precipitation), both of which can modulate coffee agroforests' potential as biodiversity refuges (Caudill et al., 2014; Ovalle-Rivera et al., 2015). A key concern for biodiversity conservation is the suite of ongoing changes in the ways coffee is cultivated (Jha et al., 2014; Perfecto et al., 2019). One major axis of change is the intensification of cultivation practices, characterized by the widespread replacement of traditional and polyculture-shade agroforests by monoculture-shade and unshaded systems, and increased application of chemical inputs (De Beenhouwer et al., 2013; Moguel & Toledo, 1999; Perfecto et al., 2019). Studies consistently show that such intensification reduces diversity and abundance across a range of taxa in coffee agroforests (Ibarra-Isassi et al., 2021; Monge et al., 2022; Philpott et al., 2008). Another important axis of change—but one that is far less studied—is the global shift in crop species from *Coffea arabica* (arabica coffee) to *C. canephora* (robusta coffee) (Chang et al., 2018; González-Orozco et al., 2024; Jha et al., 2014; Perfecto et al., 2019).

Arabica and robusta coffee together comprise nearly all the coffee that is traded commercially, with an annual production of 11.2 Mt and an estimated extent of c. 122,000 km^2 (FAO, 2025).

The respective market shares of the two coffee species have, however, been changing substantially over recent decades. While robusta coffee production has doubled since the 1960s to attain around 45% of the global total, the dominance of arabica coffee has correspondingly declined from 80% to 55% over the same period (FAO, 2025; Jha et al., 2014). Reasons for this transition include robusta requiring less shade and potentially being less vulnerable to pests than arabica, which alongside other factors such as higher yields and lower labor requirements, underlie its displacement of the latter in global coffee production (Garcia et al., 2010; Harvey et al., 2021). Furthermore, models predict that climate change could drive geographic shifts in areas suitable for coffee cultivation, accompanied by contractions in the extent of arabica-suitable areas, and expansions of robusta-suitable areas (Bunn et al., 2015; Magrach & Ghazoul, 2015; Schroth et al., 2015). Together, these studies suggest that the conversion of tropical forests to coffee agroforests, and conversion from arabica to robusta cropping systems, are significant contemporary and future land transitions. It is crucial to understand, therefore, whether and how these transitions impact biodiversity and shape conservation opportunities and challenges under various climate settings in coffee-growing regions.

How land use change alters biodiversity can be examined through various lenses. The most widely used is the taxonomic lens, which focuses on variation in species richness, diversity and composition of communities, and/or abundances of focal species, across multiple land uses (Cordier et al., 2021; Davison et al., 2021; Kehoe et al., 2015; Newbold et al., 2015). Many recent studies, however, highlight the limitations of a singular taxonomic focus and emphasize the advantages of examining additional dimensions such as the variety of functional traits (functional diversity) and evolutionary lineages (phylogenetic diversity) represented within communities (Cavender-Bares et al., 2009; Devictor et al., 2010; Mouillot et al., 2013; Tinoco et al., 2018). Considering these additional dimensions can enable incorporating ecosystem functioning and evolutionary history into conservation strategies, and improve our understanding of the ecological and evolutionary processes that underlie community responses to land use change (Cadotte et al., 2011; Díaz et al., 2013; Flynn et al., 2011; Gross et al., 2017). Species functional and phylogenetic traits are also useful, alongside attributes such as range size (Cooper et al., 2008; Waldock et al., 2020) and conservation threat status (Sodhi et al., 2008), to detect land use impacts of ecological and conservation significance at finer levels of community organization, such as sensitive functional groups, evolutionarily distinct lineages, and endangered species (Faith, 2008; Newbold et al., 2018; Nowakowski et al., 2018; Sfair et al., 2022; Uchida et al., 2019). Importantly, the effects of land use change can differ across diversity indicators and levels of community organization (Albaladejo-Robles et al., 2023; Chapman et al., 2018; Graham et al., 2019; Jithin et al., 2025; Thompson et al., 2016). This underscores the importance of considering multiple dimensions of diversity and responses at multiple levels of community organization while investigating land use impacts and designing conservation interventions in production systems and HMLs.

We examine the influence of land use and climate on amphibian communities in India’s Western Ghats mountains—a globally significant biodiversity hotspot (Myers et al., 2000), threatened amphibian landscape (Luedtke et al., 2023), and coffee-growing region (Murugan et al., 2022). The combination of a complex biphasic lifecycle, endothermy, strong microhabitat affinities, limited thermal and desiccation tolerance, low dispersal, narrow distributional ranges accompanied by high endemism, make amphibians particularly sensitive to habitat and climatic variation (Becker et al., 2010; Botts et al., 2013; Frishkoff et al., 2015; Nowakowski, Watling, et al., 2017a). At both global and Western Ghats scales, amphibians are a highly threatened vertebrate group with inadequate coverage from existing protected areas and multiple environmental stressors acting (Luedtke et al., 2023; Nori et al., 2015; Steigerwald et al., 2024). Production systems such as coffee, therefore, take on exceptional importance as potential refuges, and transformations within such systems can be highly consequential for amphibian conservation (Hegde et al., 2019; Rathod & Rathod, 2013; Sankararaman et al., 2021).

Our study examines whether and how land use (tropical rainforest vs arabica coffee vs robusta coffee) and climate (wet zone: 3,000–4,000 mm annual rainfall vs dry zone: 2,000–3,000 mm annual rainfall) influence amphibian abundance, species composition, taxonomic, functional and phylogenetic diversity, and occurrences of ecologically-sensitive functional groups and conservation-priority species in the Western Ghats. We considered ecologically-sensitive species to include those that breed in flowing water (lotic: (Almeida-Gomes & Rocha, 2015; Bolochio et al., 2020), terrestrial breeders including species exhibiting direct-development (Loyola et al., 2008; Nowakowski et al., 2018), and small-bodied species (Sheridan et al., 2022; Tracy et al., 2010). We consider species that are endemic to the Western Ghats and classified as threatened by the IUCN to be of higher conservation priority than non-threatened and widely distributed species. We ask two specific questions. First, how does land use influence amphibian abundance, community composition, multidimensional diversity, ecologically sensitive functional groups, and conservation priority species (hereafter, amphibian indicators)? We hypothesized that increasing structural simplification leading to reduced environmental heterogeneity and fewer resources and niches would reduce amphibian indicators from rainforest to arabica to robusta coffee (Gardner, Barlow, et al., 2007; Murrieta-Galindo, López-Barrera, et al., 2013; Perfecto & Vandermeer, 2008). Second, we ask: how does climate (rainfall zone) influence amphibian indicators in coffee agroforests? We hypothesized that lower rainfall would translate to higher desiccation stress and filter amphibian communities, resulting in lower values of amphibian indicators in dry zone compared to wet zone coffee (Da Silva et al., 2012; Murray et al., 2021; Ochoa-Ochoa et al., 2019). Across hypotheses we note, however, that biodiversity responses to tree-based agroforestry systems can be less pronounced and more variable than responses to treeless land uses, and that alternative outcomes including no differences across land uses and climate zones, and higher values of certain indicators in coffee than forests, are realistic possibilities (Cervantes-López & Morante-Filho, 2024).

2 METHODS

2.1 Study Area

The study was conducted in the Western Ghats mountains of peninsular India, a global biodiversity hotspot (Fig. S1b). With over 232 amphibian species, nearly 70% of which are endemic to the region and 50% classified threatened by the IUCN, the Western Ghats is considered an important globally threatened amphibian landscape (Luedtke et al., 2023). The focal study area was located in the *Malenadu* region of the central Western Ghats, spanning Hassan and Chikmagalur districts, Karnataka State (12.9°–13.4°N, 75.5°–75.9°E; Fig. S1c). The landscape is characterised by undulating terrain at elevations ranging from 800 to 1,100 m above sea level (asl), with isolated peaks reaching up to 1,400 m asl. Mean annual precipitation varies from 2,000 mm to 4,000 mm along an east–west gradient (Figure S1c), with the majority of rainfall occurring during the southwest monsoon (June–September). Mid elevation wet evergreen forests characterized by the canopy tree species *Mesua ferrea* and *Palaquium ellipticum* represent the predominant potential natural vegetation type (Pascal, 1986). Once extensive across the study area, these forests have largely been replaced by privately-owned coffee agroforests over the past two centuries, and are presently restricted to a few mostly fragmented and degraded remnants on State-protected or privately-owned lands (Fig. S1c). The coffee-growing landscape is flanked by ~1,500 km^2 of State-protected low-elevation wet-evergreen forests on its west, and on its east by open agriculture and highly fragmented and degraded remnants of moist-deciduous forest on State-protected and privately-owned lands. The study area is home to many range-restricted and evolutionarily distinctive amphibian species including *Micrixalus kottigeharensis* (VU), *Indirana gundia* (NT), *Nyctibatrachus grandis* (EN), and *Raorchestes hassanensis* (NT).

Figure 1: a) The study area comprising shade coffee agroforests and pockets of remnant forests in the Western Ghats, India, and representative photographs of b) wet evergreen forest, c) shade arabica coffee, and d) shade robusta coffee land uses from the study area

In the Western Ghats, coffee agroforests overlap with sites with high conservation value (i.e higher endemism and diversity: Das et al., 2006). *Coffea arabica* (arabica coffee) and *C.*

canephora (robusta coffee) are the two main types of coffee grown in the Hassan and Chikmagalur Districts with arabica spanning c. 77,380 ha and robusta c. 63,840 ha (*Coffee Board of India*, 2024). In line with global and regional trends reported elsewhere (Chang et al., 2018), robusta cultivation is on the rise in these districts with a 37% increase in extent from 2006 to 2024, while arabica extent decreased by 6% over the same period (Coffee Board of India, 2024). One key factor contributing to these opposing trends is the replacement of arabica by robusta coffee, which is an ongoing transition evident across multiple coffee agroforests in the landscape (first author, pers. obs.).

2.2 Amphibian sampling

We surveyed amphibians in six shade coffee agroforests and one tropical rainforest site in the study area. We selected large (≥40 ha) agroforests that cultivated both arabica and robusta coffee in segregated zones (Table S1). Three agroforests were situated in the wet zone (3,000mm – 4000 mm mean annual precipitation) towards the western limit of coffee cultivation in the region and the other three were situated in the dry zone (2000 mm – 3000 mm mean annual precipitation) towards the eastern limit of coffee cultivation (Fig. S1c). Mean annual temperature did not differ between the wet and dry zones. The reference rainforest was located in a private property in the Kadamane village, Hassan District, situated in the wet zone. This 1,600 ha secondary forest, selectively logged and used for shade coffee cultivation until the 1980s and now protected, resembles lightly disturbed tropical rainforests in structure (Nandakumar et al., 2024), and is among the last remaining relatively intact rainforests in the coffee-growing landscape. While sampling more rainforest sites would have been ideal had suitable ones been available, we reason that our sample from a single fragment is likely to yield lower (i.e., conservative) estimates of rainforest amphibian diversity and conservation indicators (Vallan, 2000; Juárez-Ramírez et al., 2024).

Amphibians were sampled using line transects of 150 m length across terrestrial (including riparian) habitats. We marked six transects in each of the six agroforests (three each in arabica and robusta blocks) and seven in the rainforest, for a total of 43 transects. Each transect was sampled twice in 2023 during the monsoon season (June–September) when amphibian activity and detectability are at their highest, resulting in a total effort of 12.9 km walked across sites. Transects were surveyed after dark between 18:30 and 01:00 hrs by three trained observers moving at a consistent pace. The primary observer (first author) walked along the center of each transect, detecting amphibians through direct visual encounters and/or auditory cues (Rödel & Ernst, 2004). Two accompanying observers assisted by identifying species and measuring the perpendicular distance for each detection on either side of the transect line, using a laser distance meter (Leica Geosystems Disto D2 4.0). Photographs of unidentified amphibians were taken and later identified based on published keys (S. Biju et al., 2014; S. D. Biju et al., 2014; Bisht et al., 2021; Dahanukar et al., 2016; Garg et al., 2021). A single species belonging to the *Minervarya* genus remained unidentified to the species level and was recorded as *Minervarya* sp., and a single species from the *Indirana* genus was identified as *Indirana* cf. *gundia* based on morphology and geographic distribution (Dahanukar et al., 2016). We followed the Amphibian Species of the World database for taxonomy (Frost, 2026).

Alongside amphibians, we sampled vegetation plots to describe overstory structure of the coffee agroforests and rainforests. In 150 m × 20 m plots established along each transect we identified all trees (DBH ≥ 10cm) to the species level and measured their diameter at breast height (DBH, cm) and height (m). Tree measurements were used to estimate tree density and basal area, scaled to a hectare (m^2 ha^{-1}). Tree species density was calculated as the number of tree species recorded per transect. Additionally, we assessed canopy cover through visual estimation using a four-point ordinal scale (0: no overlap of neighboring tree canopies; 1: canopies of neighboring trees partially overlap; 2: overlap of neighboring tree canopies but with a few openings; and 3: substantial overlap of neighboring tree canopies with no sky visible) as described in (Raman et al., 1998). Canopy cover was scored every 50 m along the length of each plot, from which we estimated average canopy cover at the transect level. Structural variables summarized by land use and climate zone are presented in Fig. S2. We also recorded various other structural and floristic attributes but do not present details here as they were not considered in the present study, and will be reported elsewhere.

2.3 Functional traits, phylogenetic tree and conservation status data

For each species in our study, we collected data on 12 functional traits associated with responses to habitat modification and frequently considered in estimates of amphibian functional diversity (Table S3). These include the morphological traits snout-to-vent length (SVL), head length, head width, femur length, tibia length, eye diameter, finger and toe disc width, and life-history traits - microhabitat use, breeding strategy, foot webbing, and skin type (Cortés-Gómez et al., 2016; Dehling & Dehling, 2021; Riemann et al., 2017). The morphological traits were estimated from measurements of 3-8 adult males per species from the rainforest (using a Mitutoyo digital vernier caliper with 0.01 mm least count). Species-level estimates for morphological traits were obtained by averaging over measured individuals within each species. For nine species that were not measured in the field, morphological traits were collated from species descriptive accounts (Dahanukar et al., 2016; Garg & Biju, 2016; Biju et al., 2014; Garg & Biju, 2021; Gururaja et al., 2014). For categorical life-history traits, information was extracted from species descriptive accounts on the India Biodiversity Portal (Vattakaven et al., 2016) and corroborated through consultation with experts (<name redacted for review>, pers. comm). Amphibians were grouped into tertiles based on SVL: the lowest 33% SVL species were labeled Small (≤2.7 cm), the highest 33% labeled Large (≥4.6 cm), and the intermediate 33% labeled Medium (2.8 cm to 4.5 cm).

We divided amphibian species into conservation priority groups using a three-level classification based on species endemism and IUCN threat status. Species that are both endemic to the Western Ghats and listed as threatened or near-threatened (CR, EN, VU, NT) by the IUCN were classified as High-priority, Western Ghats' endemics that were not IUCN-threatened as Medium-priority, and species that were neither endemic nor IUCN-threatened as Low-priority (note: all threatened or near-threatened species of the Western Ghats are endemic to the region). The average extent of occurrence (EOO) of high-priority (9 species) was 12,188 km², while medium-priority (17 species) EOO averaged 68,484 km², and low-priority species (2 species) ranged over 6,000,000 km² (IUCN, 2025; GeoCAT; https://geocat.iucnredlist.org). Species trait and conservation priority classifications are provided in Table S3 and S4.

We derived a time-calibrated phylogenetic tree for the amphibians in our study by pruning a recent global amphibian phylogenetic tree (Portik et al., 2023). Missing species *(Duttaphrynus microtympanum, Polypedates occidentalis, Uperodon triangularis, and Minervarya sp. 1*) in the phylogenetic tree were grafted to their closest relative using the scenario 'random_below_basal' in the function *get_tree()* using the R package rtrees (Li, 2023).

2.4 Data analysis

To check whether detectability differed between habitat types, we first pooled all adult amphibian detections across transects within rainforest, arabica-wet, robusta-wet, arabica-dry, and robusta-dry and plotted histograms of detection distances. We found that the land use types and climate zones had very similar histograms of detection distances (Fig. S3), indicating similar community-wide detection probabilities across land uses and climate zones. Based on this, we pooled data across detection distances within each transect for subsequent analyses.

2.4.1 Abundance and community composition

We compared overall amphibian abundance (individuals per transect) across land uses and climate zones using means and bootstrapped 95% CIs. We compared the taxonomic community composition across land uses and climate zones using non-metric multidimensional scaling (NMDS) based on Bray-Curtis dissimilarity index using the *metaMDS()* function in the vegan package (Oksanen et al., 2001). We subsequently ran Permutational Multivariate Analysis of Variance (PERMANOVA) using the *adonis()* function in the vegan package to test for differences in community composition between land use types and across climate zones.

2.4.2 Taxonomic, functional, and phylogenetic diversity

We used amphibian species abundance data pooled to the treatment level to estimate coverage-based rarefied taxonomic, functional, and phylogenetic diversity (TD, FD, and PD) of each land use in wet and dry zones based on Hill number orders $q = 0$, $q = 1$, and $q = 2$ in iNEXT.3D package (Chao et al., 2021; Chao & Jost, 2012). Taxonomic diversity was calculated using the species abundance by habitat matrix. To compute functional diversity, we first compiled a species-by-trait matrix comprising 7 uncorrelated traits. We retained SVL, finger disk width, toe disc width, microhabitat, foot webbing and life-history traits breeding strategy and skin type. We excluded head length, head width, femur length, tibia length, eye diameter as these were strongly correlated (Spearman's $r \geq 0.9$) with at least one of the retained traits (Table. S2). We computed pairwise species dissimilarities using Gower's distance with *gowdis* function in the FD package (Laliberté & Legendre, 2010). Phylogenetic diversity was calculated as the effective number of equally divergent lineages using the time-calibrated phylogenetic tree (Fig. S4). Hill numbers of order $q = 0$ represent the observed richness of species, functional groups, and lineages, while order $q = 1$ (a generalised measure of Shannon entropy) incorporates species relative abundances, reflecting the diversity of common species, functional groups, and lineages, and order $q = 2$ (a generalisation of Simpson entropy) gives higher weightage to dominant species, emphasizing the diversity of the most abundant species, functional groups, and lineages (Chao et al., 2014, 2021). By placing less emphasis on rare species, Hill numbers of orders q = 1 and q = 2 enable more robust comparisons of multiple dimensions of diversity between land use types and climate zones (Chao et al., 2021). We standardized TD, FD, and PD estimates to the minimum observed sample coverage (98%) to ensure unbiased estimation (Roswell et al., 2021), and estimated means and 95% CIs for each habitat.

2.4.3 Species and species-group responses

We used Hierarchical Modelling of Species Communities (HMSC)—a joint species distribution modeling framework based on Bayesian inference—to investigate individual species responses to the land use types and climate zones (Ovaskainen et al., 2017). We constructed the model using species occurrence (presence/absence) data at the transect level (43 transects with data pooled across two temporal replicates). The final occurrence dataset included 22 species; 7 species (*Pedostibes tuberculosus, Micrixalus kottigeharensis, Nyctibatracus sylvaticus, Duttaphrynus microtympanum, Rhacophorus lateralis and Minervarya mysorensis)* were excluded from the analysis as they occurred in less than 5% of the transects and affect model convergence. We modelled the presence-absence of species using a ‘probit’ link function with land use type as fixed effect (rainforest as the intercept) and the spatial coordinates of the geographic centroid of each transect as a random effect to account for spatial autocorrelation. In addition, we incorporated species phylogeny into the model to check for potential phylogenetic signals in species responses to habitat change. We chose to model presence-absence instead of abundance data because the skewed and zero-inflated nature of our abundance data prevented model convergence under the currently implemented ‘Poisson’ and ‘log-normal Poisson’ distributions in the ‘Hmsc’ package (Tikhonov et al., 2020).

We ran 4 Markov Chain Monte Carlo (MCMC) chains, each with a total of 7,500,000 iterations. The first 2,500,000 iterations of each chain were discarded as initial burn-in. From the remaining iterations, we retained every 10,000th sample, resulting in 500 posterior samples per chain and a total of 2,000 posterior samples across the four chains. We assessed model convergence using the effective sample size (ESS) and the potential scale reduction factor (PSRF). To evaluate the explanatory power of the model, we used the Tjur R^2 statistic. To assess the effects of land use type and climate zone on species occurrence, we considered β-coefficients with posterior probabilities ≥ 95% as strongly supported. Finally, we computed β-coefficient means and 95% CIs across species grouped by breeding strategy (Lotic, Lentic, Terrestrial), body size (Large, Medium and Small), and conservation priority (High, Medium, Low).

We base our analyses and inferences on comparing estimated means and 95% confidence intervals (CIs) of amphibian indicators across land uses and climate zones, and largely avoid statistical and significance testing (Cumming, 2009). For any two treatments, we interpret differences in means as conveying the direction and strength of differences in amphibian indicators between those treatments, and the absence of or low overlap between the 95% CIs as indicating the consistency and reliability of the estimated differences in amphibian indicators (Cumming, 2009; Nakagawa & Cuthill, 2007). For question 1 (land use effects), we focused on comparisons between rainforest, arabica-wet, and robusta-wet, and between arabica-dry and robusta-dry. For question 2 (climate effects), we compared arabica-wet to arabica-dry and robusta-wet to robusta-dry.

All analyses were performed using R statistical software version 4.5.1 (R Core Team, 2025). The study was approved by the internal research ethics committee of <redacted for review> with the permit number <redacted for review>. No specimens were collected during the surveys, and all efforts were made to minimize disturbance to amphibians, other wildlife and their habitats.

3. RESULTS

We recorded a total of 2,185 adult individuals representing 28 species and 14 genera from 43 transects across the five land use and climate combinations. The overall numbers of species recorded in rainforest, arabica-wet, robusta-wet, arabica-dry, and robusta-dry were 18,19, 20, 16 and 17 respectively (Fig. S5). In rainforests, *Clinotarsus curtipes* (16%), *Raorchestes glandulosus* (14%), and *R. hassanensis* (11%) were most common. Arabica–wet was dominated by *C. curtipes (18%)*, *R. luteolus* (17%), and *Pseudophilautus wynaadensis* (13%), and robusta–wet was dominated by *R. luteolus* (24%), *C. curtipes* (18%), and *R. tuberohumerus* (13%). In arabica–dry, the abundant species were *C. curtipes* (28%), *R. luteolus* (19%), and *P. wynaadensis* (15%), while robusta–dry sites had higher abundances of *C. curtipes* (39%), *P. wynaadensis* (15%), and *R. luteolus* (12%). Overall, the three most abundant species across land use types and climate zones accounted for 66% of total detections (Fig. S5; Fig. S6). All but two species – *Duttaphrynus melanostictus* and *Uperodon taprobanicus* – were endemic to the Western Ghats. Among the seven clades represented in the phylogeny (Fig. S4), the *Minervarya* clade was not detected in rainforests, while the *Micrixalus* clade was not detected in the coffee agroforests. The rainforest, wet-zone coffee, and dry-zone coffee harbored taxonomically distinct amphibian communities (Fig. 2; PERMANOVA $R^2 = 0.34$, $p < 0.01$), while arabica and robusta coffee showed considerable overlap of community composition within their respective climate zones (Fig. 2; PERMANOVA $R^2 = 0.01$, $p = 0.89$).

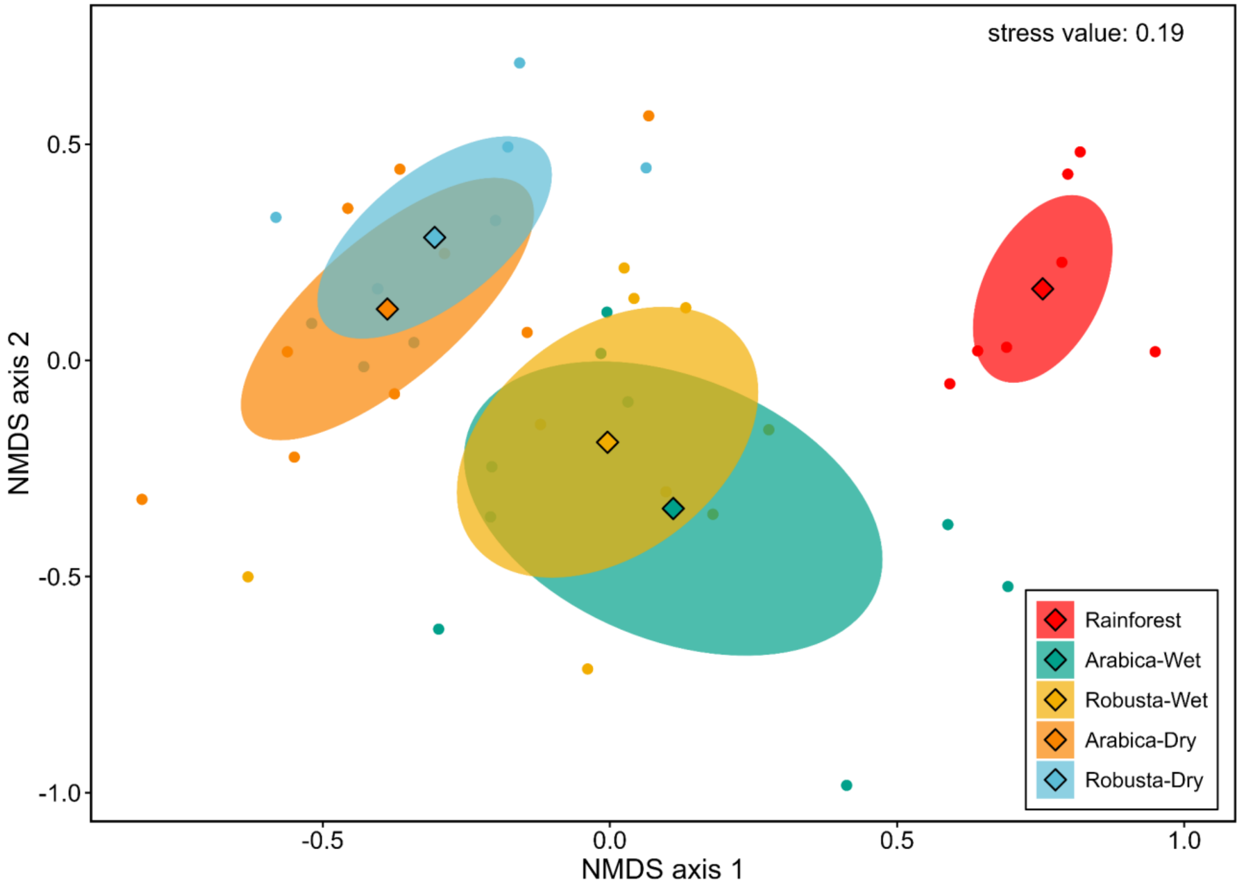

Figure 2: NMDS plot based on the Bray-Curtis dissimilarity matrix of transects (points), illustrating differences in taxonomic composition between land use types and climate zones. 95% confidence interval ellipses are depicted around the centroids (diamond) of each cluster

3.1 Amphibian abundance

Mean amphibian abundance was higher in robusta-wet (mean = 73.1; 95% CI: 43.0–108.0) than arabica-wet (mean = 54.4; 95% CI: 24.7–88.9) and rainforest (mean = 40.4; 95% CI: 30.8–51.1), and in robusta-dry (mean = 49.3; 95% CI: 36.6–65.8) than arabica-dry (mean = 34.4; 95% CI: 25.0–45.9), but large overlaps in 95% CIs suggest that abundances did not differ consistently across land uses (Fig. S7). Similarly, robusta and arabica coffee in the wet zone had greater mean amphibian abundances but large overlaps in 95% CIs compared to their counterparts in the dry zone (Fig. S7).

3.2 Taxonomic, functional, and phylogenetic diversity

TD, FD, and PD at Hill number order q = 0 (i.e., richness) varied widely and, based on considerable overlaps of estimated 95% CIs, did not differ consistently between the rainforest and arabica and robusta coffee in the wet and dry zones (Fig. S8). At the order q = 1 (Hill-Shannon), and q = 2 (Hill-Simpson), TD, FD, and PD were consistently highest in the rainforest (Fig. 3). Differences in TD, FD, and PD between the two coffee land uses ranged from none (i.e., zero to small differences in means with large 95% CIs overlaps within a given climate zone), and higher in arabica than robusta with moderate consistency (moderately higher means in arabica than robusta with partially overlapping 95% CIs within a climate zone), to consistently higher in arabica than robusta (substantially higher means in arabica than robusta with non-overlapping 95% CIs within a climate zone). Wet zone TD at q = 1 exhibited the first pattern (no difference), wet zone FD and dry zone TD, FD, and PD at q = 1, and wet zone TD and dry zone TD, FD, and PD at q = 2 were moderately higher in arabica, and wet zone PD at q = 1, wet zone FD and PD at q = 2, and dry zone TD at q = 2 were consistently higher in arabica than robusta (Fig. 3). Comparisons of arabica and robusta coffee across wet and dry zones showed a similar range of responses from no difference (robusta FD and PD at q = 2), and moderately higher in the wet zone (arabica and robusta FD, and robusta PD at q = 1, and arabica FD at q = 2), to consistently higher in the wet zone (arabica and robusta TD and arabica PD at q = 1 and 2; Fig 3).

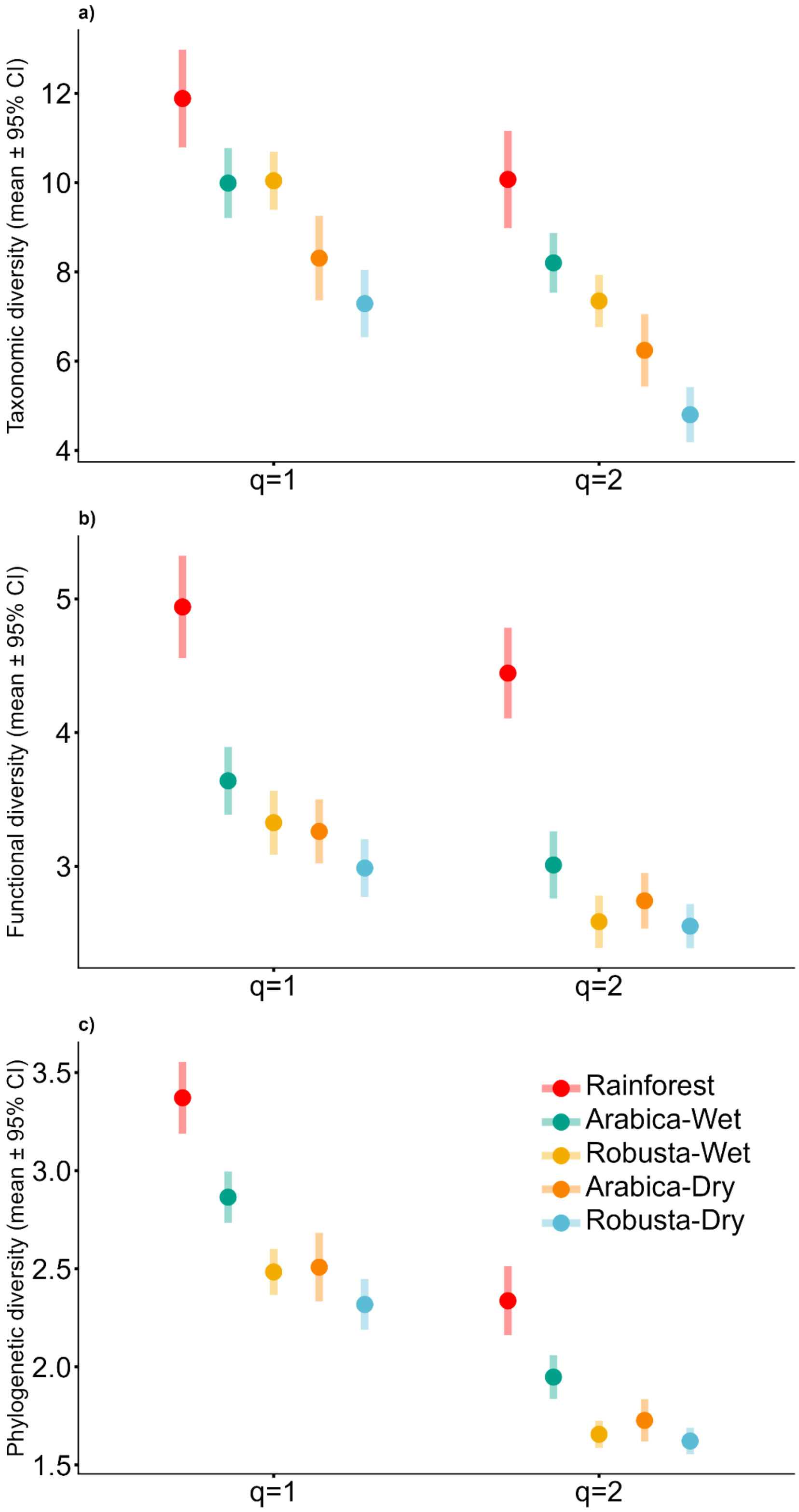

Figure 3: Abundance based amphibian a) taxonomic, b) functional and c) phylogenetic Hill-Shannon (q = 1) and Hill-Simpson (q = 2) diversity across land use types and climate zones (at

98% sampling coverage). Points and bars represent estimated means and 95% confidence intervals, respectively

3.3 Species and species-group responses

The mean explanatory power of the converged HMSC occurrence (presence/absence) model indexed using species Tjur's R^2 estimates was 0.33 (range: 0.07 - 0.74). Land use type and climate zone explained most (85.5%) of the variation in species occurrences while the spatial configuration of transects accounted for 14.5% of the variation (Fig. 4). We found no phylogenetic signal in species response to land uses and climate zones (ρ = 0.07, 95% CI: 0–0.49).

The rainforest had higher β-coefficient values (untransformed occurrence probabilities) of *Raorchestes hassanensis*, *Duttaphrynus parietalis*, *D. brevirostris,* and *Micrixalus elegan*s, suggesting that these species are forest specialists (Fig. 4; Fig. S9). By contrast, several "generalist" species showed little variation in β-coefficients across land use types and climate zones (e.g., *Uperodon* spp., *Clinotarsus curtipes*), or β-coefficient increases from forest to coffee (e.g., *Raorchestes luteolus*, *Psuedophilautus wynaadensis*, *D. melanostictus, R. tuberohumerus, Hylarana intermedia*, *Minervarya* spp.; Fig. 4; Fig. S9). Within coffee, a few species had higher β-coefficients in arabica than robusta coffee (e.g., *Indirana* cf. *gundia*), and in wet-zone than dry-zone coffee (*Polypedates occidentalis, R. hassanensis*, *N. kempholeyensis*; Fig. 4; Fig. S9).

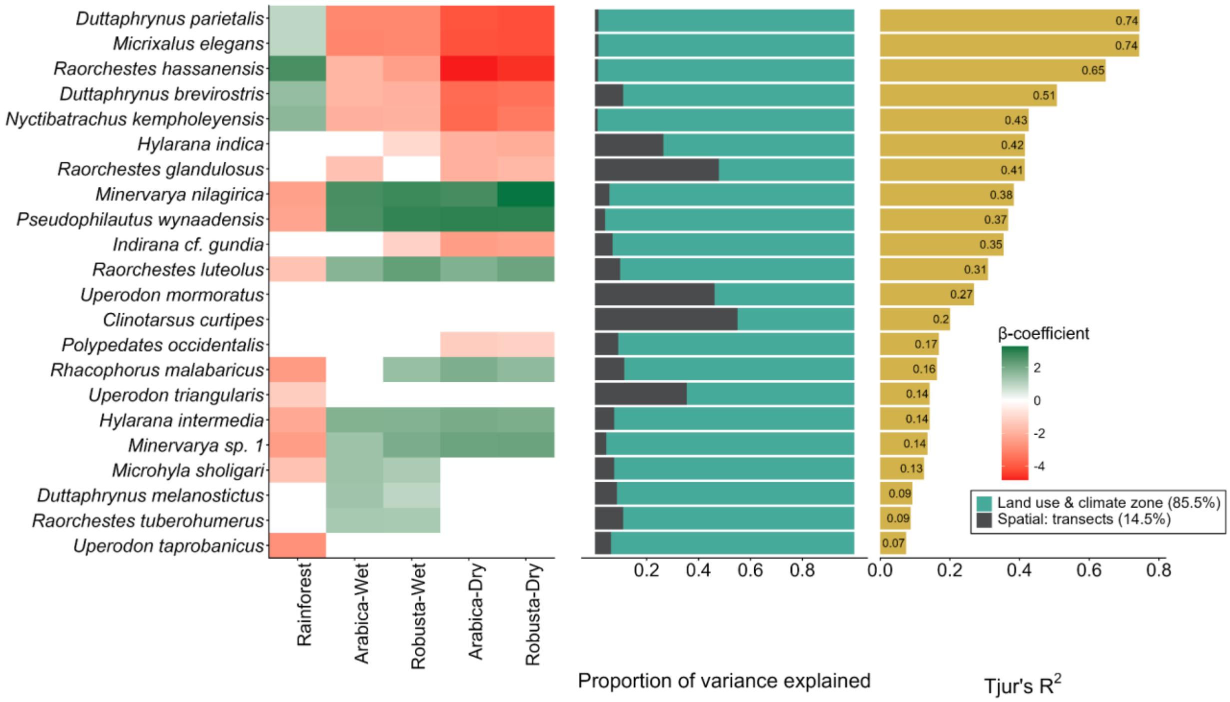

Figure 4: Result from the HMSC model-estimated species response (β-coefficients) to land use types and climate zones (left). Green and red colours indicate statistically supported positive

and negative responses respectively, the variance partitioning plot illustrating the variance explained by predictors across species (middle) and Tjur's R^2 indicating the model fit for each species

β-coefficients of lotic breeding species were substantially and consistently highest in the rainforest, while those of lentic breeders were lower in rainforest (with 95% CIs partially overlapping) than all other land uses, and occurrence probabilities of terrestrial breeders did not differ between rainforest, arabica-wet, and robusta-wet (Fig. 5a). None of the breeding strategies showed any differences between arabica and robusta coffee in either wet or dry zone (Fig. 5a). Lotic and terrestrial (but not lentic) breeder occurrence probabilities showed small decreases on average from arabica-wet to arabica-dry and robusta-wet to robusta-dry, but with large overlaps in 95% CIs suggesting low consistency and reliability of these patterns (Fig. 5a).

Amphibian species *β*-coefficients showed no clear associations with body size. Arabica and robusta coffee had higher average *β*-coefficients than forests for medium- and large-bodied amphibians, and arabica and robusta in the dry zone had lower average average β coefficients than their counterparts in the wet zone, but all comparisons were associated with large overlaps in 95% CIs and accordingly low consistency and reliability in differences (Fig. 5b)

β-coefficients of high conservation priority species were substantially and consistently highest in the rainforest, while those of medium and low conservation priority species were lower in rainforest (with 95% CIs partially overlapping) than coffee (Fig. 5c). None of the conservation priority groups showed any differences between arabica and robusta coffee in either wet or dry zone (Fig. 5c). High (but not medium and low) conservation priority species occurrence probabilities showed small decreases on average from arabica-wet to arabica-dry and robusta-wet to robusta-dry, but with large overlaps in 95% CIs suggesting low consistency and reliability of these patterns (Fig. 5c).

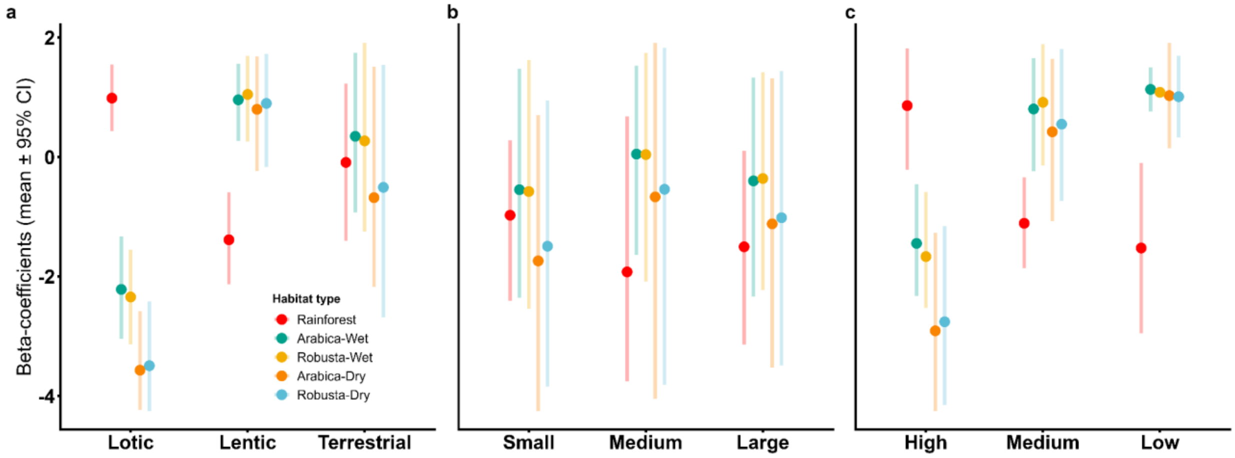

Figure 5: Untransformed occurrence probabilities (*β*-coefficients), derived from the HMSC model, grouped by (a) breeding strategy, (b) body size, and (c) conservation priority. Bars and error bars represent estimated means and 95% confidence intervals across species within each group

DISCUSSION

Findings from our study suggests that land use change from tropical rainforest to coffee, and from arabica to robusta coffee can have several implications for amphibian multidimensional diversity, community composition, and conservation. We found that while both arabica and robusta coffee can match or surpass tropical rainforests for amphibian abundance and multidimensional (taxonomic, functional, and phylogenetic) richness ($q = 0$), the rainforest harbored distinct community composition, higher multidimensional Hill-Shannon ($q = 1$) and Hill-Simpson ($q = 2$) diversity, and higher occurrences of lotic (stream-breeding) and conservation-priority species than either coffee crop type. We also found that arabica generally harbors higher amphibian multidimensional diversity than robusta coffee, and multidimensional diversity and occurrences of lotic and conservation-priority species in both arabica and robusta tend to decrease from wetter to drier zones of coffee cultivation.

In line with previous studies (Trimble & Van Aarde, 2014; Nowakowski et al., 2018; Juárez-Ramírez et al., 2024), the rainforest in our study harbored a distinct amphibian community harboring a greater variety of functional types and evolutionary lineages and a greater representation of ecologically sensitive lotic and high conservation-priority (threatened and endemic) species than arabica and robusta coffee. The substantially higher multidimensional diversity ($q = 1$ and 2) in rainforest than coffee despite the land uses not differing consistently in amphibian abundances and species richness was also consistent with previous findings (Juárez-Ramírez et al., 2024). One factor underlying this pattern is that amphibian species abundances in the rainforest were more evenly distributed, thus enabling a wider representation of species, traits, and evolutionary lineages among abundant ($q = 1$) and dominant ($q = 2$) species (Chao et al., 2021); by contrast, amphibian species abundances in both coffee systems—especially robusta—were highly skewed (Fig. S6). Another factor could be asymmetries during winner-loser replacements across land uses with "losers" in the forest-coffee transition being more functionally and phylogenetically unique—for example, lotic and evolutionarily ~70 million year old *Nyctibatrachus* spp. and *Micrixalus* spp. (Roelants et al., 2004)—than the "winners" (lentic *Microhyla sholigari*, *Minervarya* spp., *Uperodon mormoratus*, *Uperodon taprobanicus*) that replace them in coffee (Greenberg et al., 2018; Lourenço-de-Moraes et al., 2020; Pyron, 2018; Torralvo et al., 2022). Collectively, these results highlight the exceptional and irreplaceable value of remnant tropical rainforests for sustaining amphibian multidimensional diversity, certain ecologically sensitive groups, and conservation in coffee-growing landscapes (Gardner, Ribeiro-Junior, et al., 2007; Juárez-Ramírez et al., 2024).

While lotic-breeding species declined sharply from rainforest to arabica and robusta coffee, lentic-breeding species, which previous studies have shown to be less vulnerable to land use change (Mendenhall et al., 2014; Nowakowski, Thompson, et al., 2017), displayed the opposite pattern. This contrasting pattern is likely explained by the increased availability of lentic breeding habitats in the form of artificial irrigation ponds and seasonal ephemeral pools along roadsides (Sankararaman et al., 2021), while the stream and riparian habitats of lotic breeders are typically exploited and degraded for water supply, construction materials, and expanding area under coffee cultivation (Bolochio et al., 2020; Coleman et al., 2024).

Both coffee crop types appeared relatively hospitable for species of moderate conservation priority (endemic to the Western Ghats but not threatened) and ecologically sensitive terrestrial breeders and small-bodied species. Given the vulnerability of terrestrial reproduction and small body size to desiccation (Nowakowski, Watling, et al., 2017b; Scheffers et al., 2013), the persistence of these sensitive groups suggests the role of shade tree overstories and coffee bushes in maintaining relatively hospitable understory habitats, breeding sites, and microclimates for these sensitive groups in coffee agroforests (Scheffers et al., 2014; Monroe et al., 2017; González-del-Pliego et al., 2020; Burrow & Maerz, 2022). Together, these results highlight the potential for coffee agroforests to complement remnant rainforests for conserving amphibians in mosaic production landscapes (Murrieta-Galindo, González-Romero, et al., 2013; Pinzón et al., 2025).

Arabica and robusta coffee sustained similar amphibian abundances but the former generally exhibited greater multidimensional diversity (functional and phylogenetic more than taxonomic and q = 2 and 1 more than q = 0) across climate zones. These patterns largely resemble the findings of (Chang et al., 2018) who reported little difference in bird abundances between arabica and robusta coffee but lower diversity and abundances of sensitive functional groups in the latter crop type. Including rainforest, the three land use types rank in the same order for amphibian multidimensional diversity as they do for habitat structural variables such as canopy cover and basal area: rainforest, arabica coffee, robusta coffee (Fig. 3, Fig. S2). This pattern aligns with the hypothesis that increasing structural simplification operates as an environmental filter on amphibian communities (Brüning et al., 2018; Hernández-Ordóñez et al., 2019; Torralvo et al., 2022), and suggests that relatively structurally complex arabica might be more effective than robusta coffee at sustaining amphibian multidimensional diversity, although both appear equally ineffective at buffering losses of lotic and high conservation priority species. At the same time, other management attributes—for example, relatively low pesticide use (Chang et al., 2018)—could play a role in enabling robusta coffee to sustain high overall amphibian abundances. Thus, while continued deforestation and a transition from arabica to robusta coffee might not diminish amphibian numbers, it could erode the diversity of species, functional types, and lineages, and lead to other detrimental outcomes for amphibian conservation in coffee-growing regions.

Amphibian indicators in arabica and robusta coffee were strongly influenced by climate zone, with coffee in the dry zone exhibiting lower multidimensional diversity, reduced occurrence probabilities of lotic, terrestrial-breeding (with less certainty), and high conservation-priority species, and the replacement of threatened and endemic rainforest affiliated species (e.g., *R. hassanensis*, and *I.* cf. *gundia*) by widely-distributed generalists (e.g., *U. taprobanicus*). The above pattern is unlikely to be an artefact of the wet zone coffee sites lying further apart than the dry zone ones (Fig. S1) because according to our HMSC model, land use and climate zone (85.5%) had far stronger influence than transect spatial locations (14.5%) on amphibian species occurrences (also see Fig. S10 for occurrence-based estimates of taxonomic, functional, and phylogenetic diversity in wet versus dry zones). Our findings align with previous studies that associate climate stress with environmental filtering, declines of lotic, terrestrial-breeding and other ecologically-sensitive amphibian species, and increases in wide-ranging desiccation-tolerant species (Da Silva et al., 2012; Murray et al., 2021; Torralvo et al., 2022). The divergence in amphibian indicators between wet and dry zone coffee qualitatively—and in some cases also quantitatively (e.g., arabica phylogenetic diversity at q = 1)—resembled divergences between rainforest and coffee within the wet zone. These stark differences between wet and dry zone coffee illustrate the importance of incorporating climate and other environmental contexts into biodiversity assessments and conservation planning for coffee and other land use systems that span wide environmental gradients (Harvey et al., 2021). These results also highlight potential future risks to amphibian multidiversity and to the conservation of lotic- and terrestrial-breeding as well as endemic species in coffee agroforests arising from climate drying (Alves-Ferreira et al., 2025; Hoffmann et al., 2021; Jansen et al., 2009; Le Galliard et al., 2021; Loyola et al., 2008; Wu et al., 2024), which some climate models suggest is likely, alongside increasing variability and extreme events, in several coffee-growing regions including the Western Ghats (Dhara et al., 2025; Murugan et al., 2022), Brazil (Gomes et al., 2020), Vietnam (Anh Dinh et al., 2025), Ethiopia (Moat et al., 2017) and Puerto Rico (Fain et al., 2018).

Collectively, our findings offer a few key insights for biodiversity and conservation in the face of ongoing and predicted changes to coffee production systems in the Western Ghats and other tropical biodiversity hotspots. Our study builds evidence that the transition from arabica to structurally simplified robusta coffee agroforestry represents a growing conservation challenge (Chang et al., 2018; Jha et al., 2014), especially when accompanied by climate drying which can amplify multidimensional biodiversity loss and declines of threatened and ecologically sensitive species. At the same time, robusta cultivation is known to require less pesticide use than arabica at present (Chang et al., 2018) and depend more on biotic interactions such as insect-mediated pollination (Crane & Walker, 1984), highlighting the need and opportunity for research examining potential synergies and tradeoffs between biodiversity and robusta coffee production across contrasting agroforest management and climate settings. Our findings also underscore the critical value of remnant natural ecosystems for biodiversity in production landscapes (Barlow et al., 2007; Gibson et al., 2011; Thompson & Donnelly, 2018), and challenges for conservation as market- and climate-driven shifts in coffee drive further deforestation (Magrach & Ghazoul, 2015; Bunn et al., 2015; Laderach et al., 2011; Schroth et al., 2014). While there already exists a substantial body of policy and financial instruments for sustainable and biodiversity-friendly coffee (Iverson et al., 2019; Wright et al., 2024), innovations are needed that introduce or strengthen incentives for retaining structurally complex arabica agroforestry systems (Guillemot et al., 2018) promoting ethical and biodiversity-friendly management practices in robusta coffee. In addition, efforts should focus on safeguarding forest remnants, streams and associated riparian habitats, and other high value ecosystems and microhabitats during geographic expansion and realignment of coffee cultivation, and restoring degraded ecosystems in rapidly evolving coffee production landscapes.

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Appendix/Supplementary Material

Crop species and climate shape amphibian communities and conservation significance of coffee agroforests in the Western Ghats

This file includes

TABLES

Table S1: Amphibian sampling sites, spatial location, cultivated area, effort, and number of detections (sight and call)

Table S2: Functional traits measured across adult males in this study following the protocols from Cortés-Gómez et al., (2016)

TABLE S3: Functional trait values of amphibian species recorded during the study. Morphological measurements (cm) were obtained from 3–8 adult male individuals per species and for 9 species traits were collated from existing species descriptive accounts

TABLE S4: Conservation priority classification based on species threat status from IUCN (threatened - NT, VU, EN, CR) and endemism. Estimated extent of occurrence for each species was obtained from the IUCN database and for few missing species estimated from the GeoCAT toolkit.

FIGURES

Figure S1: Maps showing (a) the location of the study region in peninsular India, (b) the study area in the Western Ghats, a global biodiversity hotspot and (c) the study area with key land cover types, mean annual precipitation isohyets, and sampling locations marked. The Agroforest class primarily comprises shade coffee, with small pockets of tea and forestry plantations. The Other land covers class mainly represents open agriculture, montane grasslands, degraded forests, and unclassified areas. Blue dashed lines represent mean annual precipitation isohyets (2000–5000 mm). Land cover data were derived from Renard et al., (2010). Mean annual precipitation data were extracted from the Worldclim dataset (Fick & Hijmans, 2017).

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Figure S5: Amphibian species and their individual abundance across land uses and climate zones recorded in the study area, central Western Ghats. The heat map displays the square-root transformed abundance values for improved visual interpretation.

Figure S6: Rank–abundance curves illustrating patterns of dominance and evenness in amphibian assemblages across land uses and climate zones. Species are color-coded with corresponding names shown in the legend below. Numbers in the figure indicate the rank of respective species.

Figure S7: Amphibian abundance per transect (mean ± 95% CI) across land uses and climate zones with the points representing the observed raw amphibian counts recorded in each transect within each habitat.

Figure S8: Functional, phylogenetic and taxonomic richness of amphibians across land uses and climate zones, measured using Hill number at q=0 at 99% sampling coverage. Points and bars represent estimated means and 95% confidence intervals, respectively.

Figure S9: Predicted probabilities of occurrence from the MCMC samples of HMSC model for 22 amphibian species across land use and climate zones.

Figure S10: Incidence-based amphibian taxonomic, functional and phylogenetic Hill-Shannon (q = 1) and Hill-Simpson (q = 2) diversity across habitats (at 96% sampling coverage). Points and bars represent estimated means and 95% confidence intervals, respectively

Table S1: Amphibian sampling sites, spatial location, area, effort, and number of detections (sight and call)

Sampling site code	Latitude, Longitude	Category	Area (ha)	No. of transects	No. of temporal replicates	Effort (km)	Mean elevation (m)	Visual detections	Aural detections
Site1	12.93686, 75.71824	Wet-Coffee	~250	6	2	1.8	950	736	36
Site2	13.42797, 75.41824	Wet-Coffee	~200	6	2	1.8	1050	216	8
Site3	13.19851, 75.48372	Wet-Coffee	~120	6	2	1.8	1080	113	22
Site4	12.932191, 75.657758	Wet-Rainforest	~1600	7	2	2.1	1000	228	55
Site5	12.96071, 75.82627	Dry-Coffee	~150	6	2	1.8	980	128	28
Site6	12.99924, 75.78964	Dry-Coffee	~80	6	2	1.8	980	327	13
Site7	13.05416, 75.7865	Dry-Coffee	~80	6	2	1.8	1030	244	10

Table S2: Functional traits measured across adult males in this study following the protocols described in Cortés-Gómez et al., (2016)

Functional traits	Data description	Functional meaning	References	Remarks
SVL	Continuous	Habitat use, physiological tolerance	Ribeiro et al., 2017; Dehling & Dehling, 2021; Riemann et al., 2017	Correlated (r > 0.8), but retaining this trait as this is a representative trait for other morphological traits
Terminal disk diameter *(third finger, fourth toe)*	Continuous	Climbing, adhesion and vertical niche	Riemann et al., 2017; Dehling & Dehling, 2021	
Head length	Continuous	Size of food items	Hernández-Ordóñez et al., 2019	Highly correlated (r > 0.8) with SVL, head width, eye diameter, tibia and femur length
Head width	Continuous	Size of food items	Alvarez-Grzybowska et al., 2020; Dehling & Dehling, 2021	Highly correlated (r > 0.8) with SVL, head length, eye diameter, tibia and femur length
Eye diameter	Continuous	Habitat use, activity, prey detection and breeding	Alvarez-Grzybowska et al., 2020	Moderately correlated

Tibia and femur length	Continuous	Habitat use, horizontal niche	Cortes-Gomez et al., 2016; Riemann et al., 2017	Highly correlated (r > 0.8) with SVL, head length, eye diameter, head width
Foot Webbing	Ordinal - extensive; medium; rudimentary	Swimming, climbing structures	Riemann et al., 2017; Hernández-Ordóñez et al., 2019; Dehling & Dehling, 2021	
Skin type	Nominal - rough; granular; smooth; tuberculated	Desiccation tolerance	Alvarez-Grzybowska et al., 2020; Hernández-Ordóñez et al., 2019	
Breeding strategy	Nominal - lotic; lentic; direct development	Breeding habitat use, reproductive strategy	Ribeiro et al., 2017; Alvarez-Grzybowska et al., 2020	
Adult microhabitat use	Nominal - arboreal; shrub; aquatic; semiaquatic; terrestrial; fossorial	Habitat use	Hernández-Ordóñez et al., 2019; Dehling & Dehling, 2021	

TABLE S3: Functional trait values of amphibian species recorded during the study. Morphological measurements (cm) were obtained from 3–8 adult male individuals per species and for 9 species traits were collated from existing species descriptive accounts

Species	**SVL**	**Head length**	**Head width**	**Femur length**	**Tibia length**	**Eye diameter**	**Finger disc**	**Toe disc**	**Breeding strategy**	**Microhabitat**	**Foot webbing**	**Skin type**
Clinotarsus curtipes	5.48	2.31	2.14	2.72	2.52	0.68	0.13	0.13	lentic	terrestrial	medium	smooth
Duttaphrynus brevirostris	4.64	14.40	1.67	1.82	1.88	0.53	0.00	0.00	lentic	terrestrial	rudimentary	rough
Duttaphrynus melanostictus	5.40	1.85	2.10	2.31	1.97	0.57	0.00	0.00	lentic	terrestrial	rudimentary	rough
Duttaphrynus microtympanum	4.40	1.39	1.78	2.00	1.76	0.48	0.00	0.00	lentic	terrestrial	rudimentary	rough
Duttaphrynus parietalis	8.10	2.69	3.48	3.55	3.10	0.79	0.00	0.00	lentic	terrestrial	rudimentary	rough
Indirana cf. *gundia*	2.27	0.95	0.83	1.29	1.43	0.32	0.06	0.07	terrestrial	terrestrial	medium	tuberculated
Hylarana indica	4.94	1.92	1.65	2.69	2.90	0.54	0.13	0.14	lotic	semiaquatic	medium	smooth
Hylarana intermedia	3.92	1.58	1.18	1.94	2.01	0.45	0.14	0.12	lentic	semiaquatic	medium	smooth
Micrixalus elegans	1.47	0.52	0.49	0.79	0.79	0.18	0.03	0.10	lotic	aquatic	medium	smooth
Micrixalus kottigeharensis	2.29	0.83	0.66	1.24	1.26	0.23	0.10	0.12	lotic	aquatic	medium	granular
Microhyla sholigari	1.82	0.50	0.56	0.92	1.02	0.16	0.01	0.01	lentic	semiaquatic	rudimentary	smooth
Minervarya mysorensis	4.12	1.44	1.46	2.32	2.38	0.47	0.04	0.04	lentic	semiaquatic	rudimentary	tuberculated

Minervarya nilagirica	4.68	1.62	1.63	2.57	2.74	0.54	0.00	0.00	lentic	semiaquatic	rudimentary	tuberculated
Minervarya sp.1	3.16	1.18	1.19	1.51	1.51	0.37	0.00	0.00	lentic	semiaquatic	rudimentary	tuberculated
Nyctibatrachus kempholeyensis	2.27	0.71	0.90	1.18	1.12	0.25	0.07	0.08	lentic	aquatic	medium	granular
Nyctibatrachus sylvaticus	3.23	1.25	1.41	1.58	1.43	0.35	0.08	0.11	lotic	aquatic	medium	granular
Pedostibes tuberculosus	3.98	1.12	1.23	1.26	1.61	0.44	0.23	0.14	lotic	arboreal	extensive	tuberculated
Polypedates occidentalis	5.5	1.87	1.68	2.96	2.9	0.59	0.35	0.32	lentic	arboreal	extensive	
Pseudophilautus wynaadensis	2.70	1.05	1.08	1.50	1.47	0.38	0.14	0.13	terrestrial	shrub	rudimentary	smooth
Raorchestes glandulosus	2.33	0.96	0.99	1.28	1.20	0.33	0.13	0.14	terrestrial	shrub	rudimentary	smooth
Raorchestes luteolus	2.74	1.00	1.01	1.43	1.37	0.37	0.15	0.15	terrestrial	shrub	rudimentary	smooth
Raorchestes hassanensis	3.21	1.10	1.38	1.80	1.69	0.46	0.23	0.19	terrestrial	shrub	rudimentary	smooth
Raorchestes tuberohumerus	1.93	0.60	0.70	0.99	0.93	0.26	0.11	0.11	terrestrial	shrub	rudimentary	smooth
Rhacophorus lateralis	3.29	1.04	1.05	1.72	1.74	0.41	0.18	0.16	lentic	arboreal	extensive	smooth
Rhacophorus malabaricus	6.95	2.20	2.45	3.85	3.90	0.75	0.55	0.45	lentic	arboreal	extensive	smooth

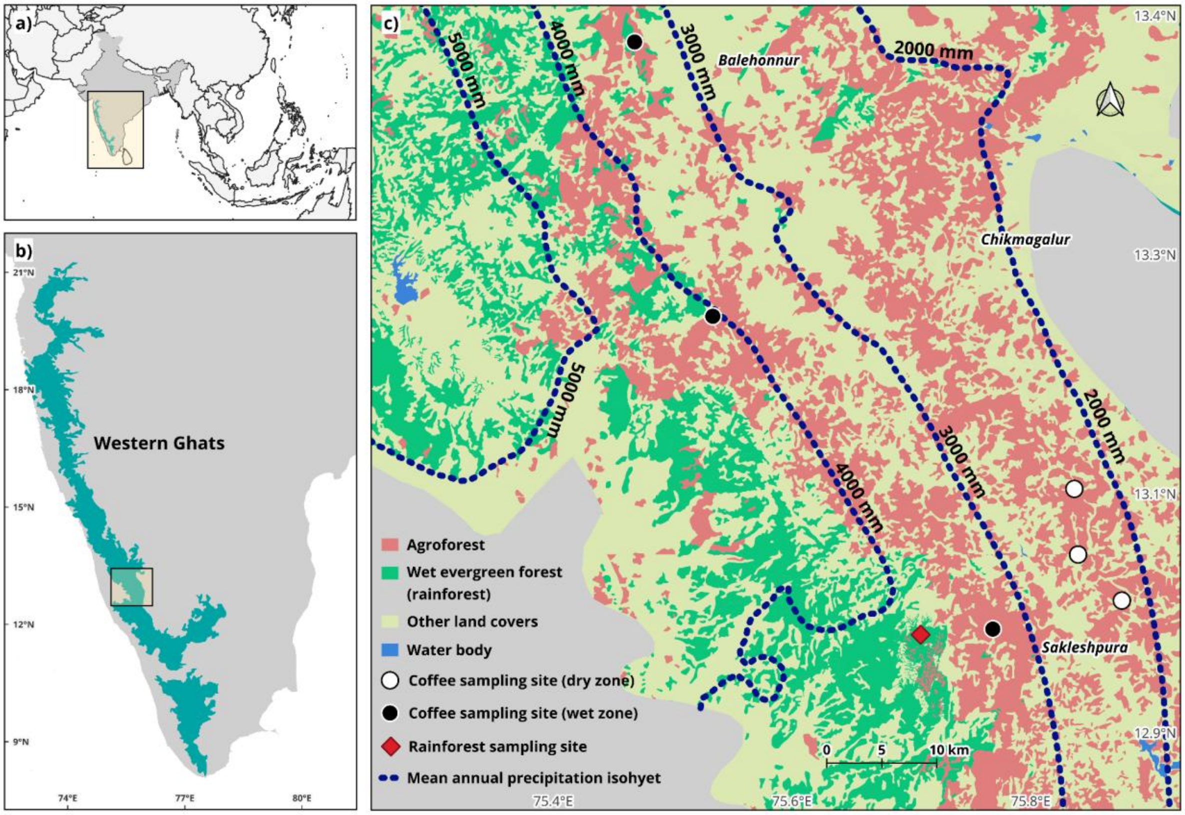
Uperodon mormoratus	3.57	0.84	1.11	1.40	1.26	0.28	0.18	0.10	lentic	terrestrial	medium	granular
Uperodon taprobanicus	4.85	1.09	1.36	1.80	1.53	0.39	0.20	0.00	lentic	terrestrial	rudimentary	granular
Uperodon triangularis	3.61	0.91	1.27	1.65	1.37	0.30	0.15	0.00	lentic	terrestrial	rudimentary	smooth

TABLE S4: Conservation priority classification based on species threat status from IUCN (threatened - NT, VU, EN, CR) and endemism. Estimated extent of occurrence for each species was obtained from the IUCN database and for few missing species estimated from the GeoCAT toolkit.

Species	**IUCN 2025**	**Threat status**	**Endemism**	**EOO_km²**	**Conservation priority**
Clinotarsus curtipes	LC	non-threatened	endemic	179673.40	medium
Duttaphrynus brevirostris	VU	threatened	endemic	11589.51	high
Duttaphrynus melanostictus	LC	non-threatened	non-endemic	9344377.75	low
Duttaphrynus microtympanum	LC	non-threatened	endemic	26654.00	medium
Duttaphrynus parietalis	LC	non-threatened	endemic	44600.33	medium
Indirana cf. *gundia*	NT	threatened	endemic	22439.00	high
Hylarana indica	LC	non-threatened	endemic	24999.40	medium
Hylarana intermedia	LC	non-threatened	endemic	26037.00	medium
Micrixalus elegans	VU	threatened	endemic	8355.41	high
Micrixalus kottigeharensis	VU	threatened	endemic	8201.04	high
Microhyla sholigari	LC	non-threatened	endemic	32252.00	medium

Minervarya mysorensis	LC	non-threatened	endemic	43919.00	medium
Minervarya nilagirica	LC	non-threatened	endemic	84736.00	medium
Minervarya sp.1	LC	non-threatened	endemic	NA	medium
Nyctibatrachus kempholeyensis	LC	non-threatened	endemic	54185.00	medium
Nyctibatrachus sylvaticus	EN	threatened	endemic	2276.50	high
Pedostibes tuberculosus	LC	non-threatened	endemic	107615.60	medium
Polypedates_occidentalis	LC	non-threatened	endemic	78865	medium
Pseudophilautus wynaadensis	LC	non-threatened	endemic	93682.22	medium
Raorchestes glandulosus	VU	threatened	endemic	11659.11	high
Raorchestes luteolus	LC	non-threatened	endemic	28060.62	medium
Raorchestes hassanensis	NT	threatened	endemic	13261.00	high
Raorchestes tuberohumerus	LC	non-threatened	endemic	73670.31	medium
Rhacophorus lateralis	VU	threatened	endemic	15203.03	high
Rhacophorus malabaricus	LC	non-threatened	endemic	83797.65	medium
Uperodon mormoratus	LC	non-threatened	endemic	113000.44	medium
Uperodon taprobanicus	LC	non-threatened	non-endemic	2794359.72	low
Uperodon triangularis	NT	threatened	endemic	16705.00	high

FIGURES



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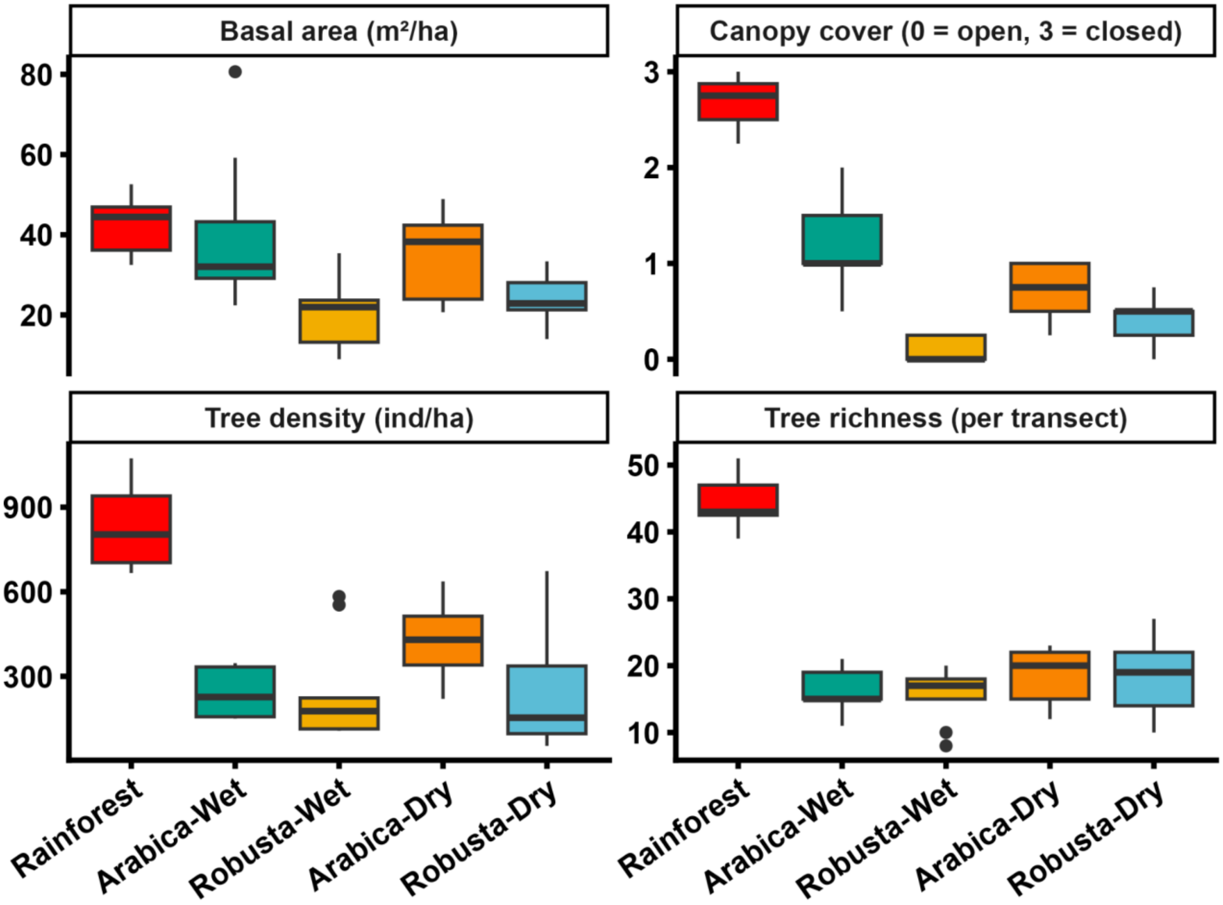

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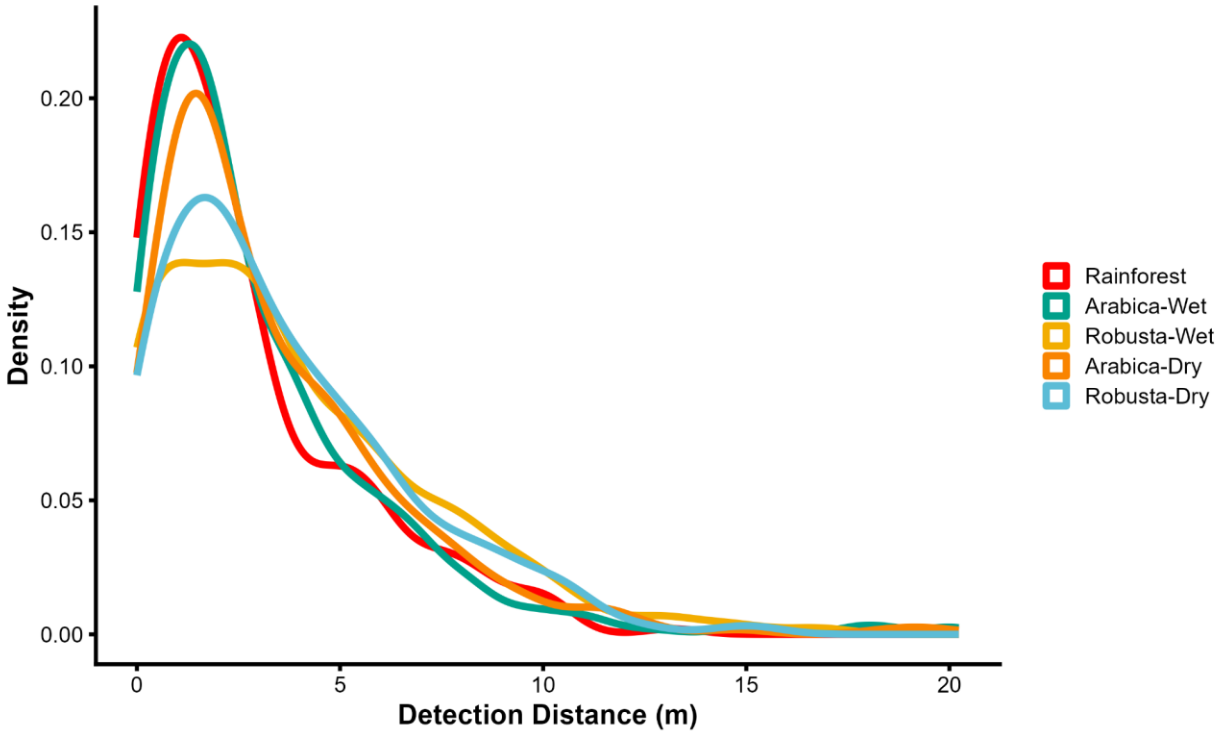


Figure S3: The distribution of detection distance (kernel density curves) of amphibians across habitat types, with less variation observed among habitats.

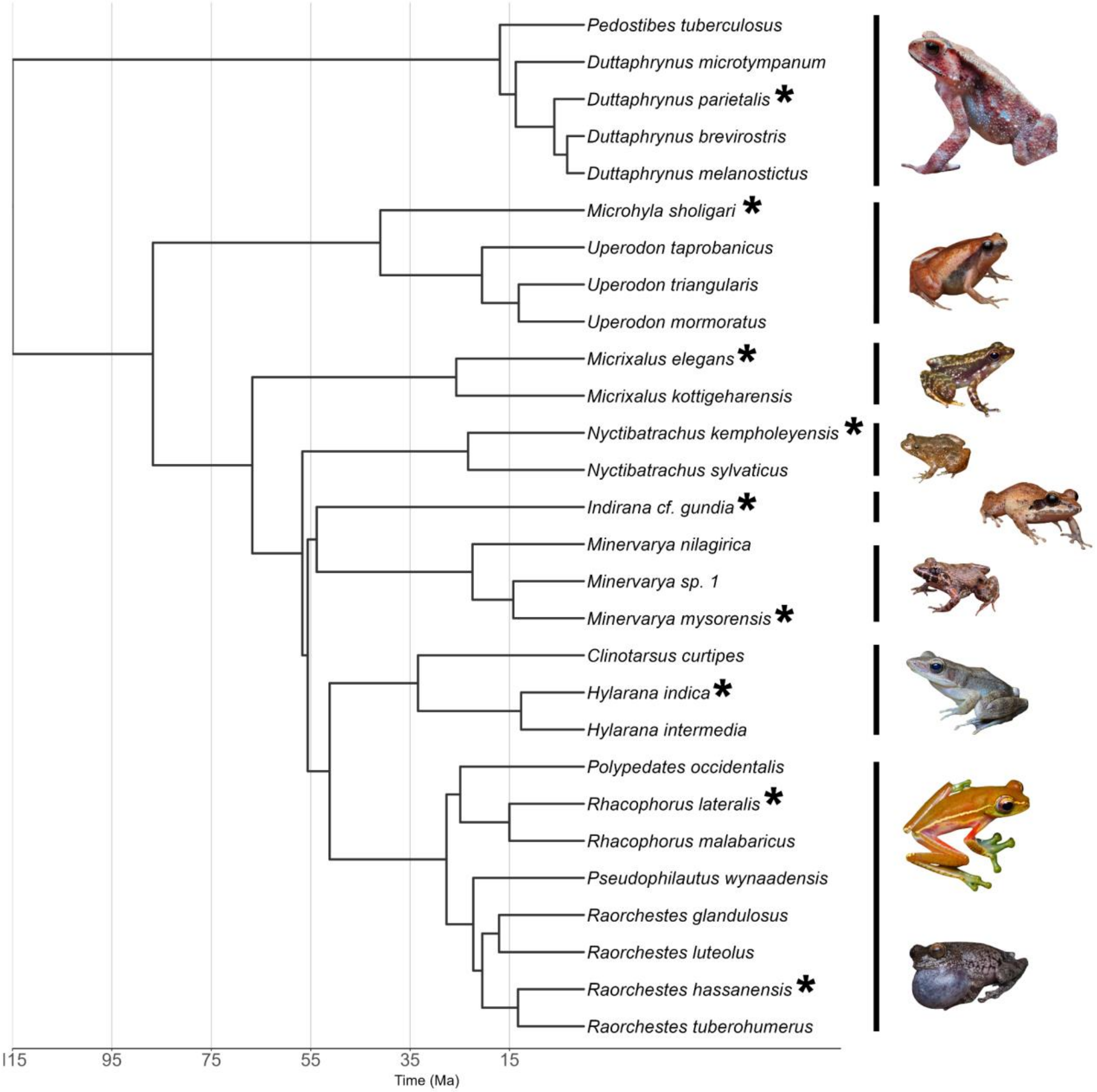
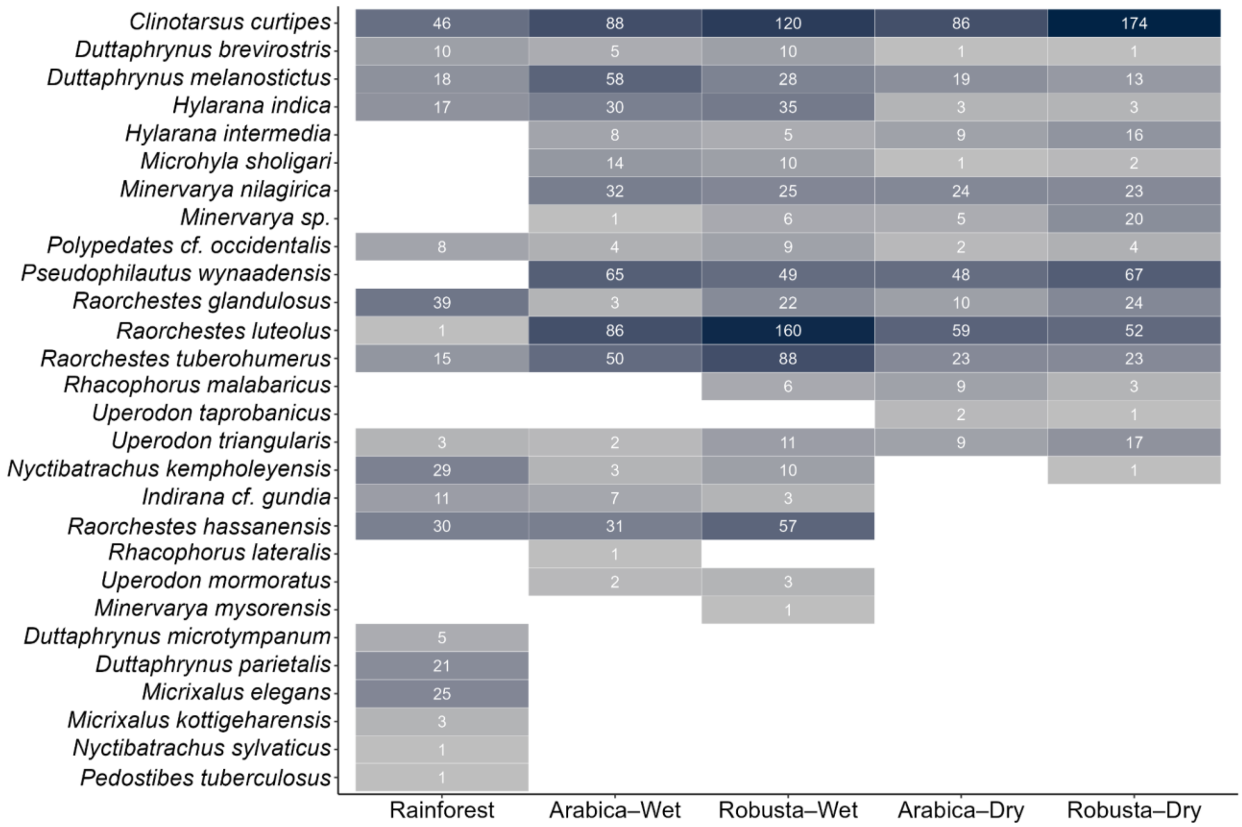


Figure S4: Rooted phylogenetic tree derived from Portik et al., (2023) of amphibian species recorded in the study landscape of the central Western Ghats, India. The phylogeny includes species from eight families: Bufonidae, Microhylidae, Micrixalidae, Nyctibatrachidae, Ranixalidae, Dicroglossidae, Ranidae, and Rhacophoridae. The x-axis represents time in millions of years (Ma). Asterisks (*) indicate species for which images are provided



	Rainforest	Arabica–Wet	Robusta–Wet	Arabica–Dry	Robusta–Dry
Clinotarsus curtipes	46	88	120	86	174
Duttaphrynus brevirostris	10	5	10	1	1
Duttaphrynus melanostictus	18	58	28	19	13
Hylarana indica	17	30	35	3	3
Hylarana intermedia		8	5	9	16
Microhyla sholigari		14	10	1	2
Minervarya nilagirica		32	25	24	23
Minervarya sp.		1	6	5	20
Polypedates cf. occidentalis	8	4	9	2	4
Pseudophilautus wynaadensis		65	49	48	67
Raorchestes glandulosus	39	3	22	10	24
Raorchestes luteolus	1	86	160	59	52
Raorchestes tuberohumerus	15	50	88	23	23
Rhacophorus malabaricus			6	9	3
Uperodon taprobanicus				2	1
Uperodon triangularis	3	2	11	9	17
Nyctibatrachus kempholeyensis	29	3	10		1
Indirana cf. gundia	11	7	3		
Raorchestes hassanensis	30	31	57		
Rhacophorus lateralis		1			
Uperodon mormoratus		2	3		
Minervarya mysorensis			1		
Duttaphrynus microtympanum	5				
Duttaphrynus parietalis	21				
Micrixalus elegans	25				
Micrixalus kottigeharensis	3				
Nyctibatrachus sylvaticus	1				
Pedostibes tuberculosus	1				

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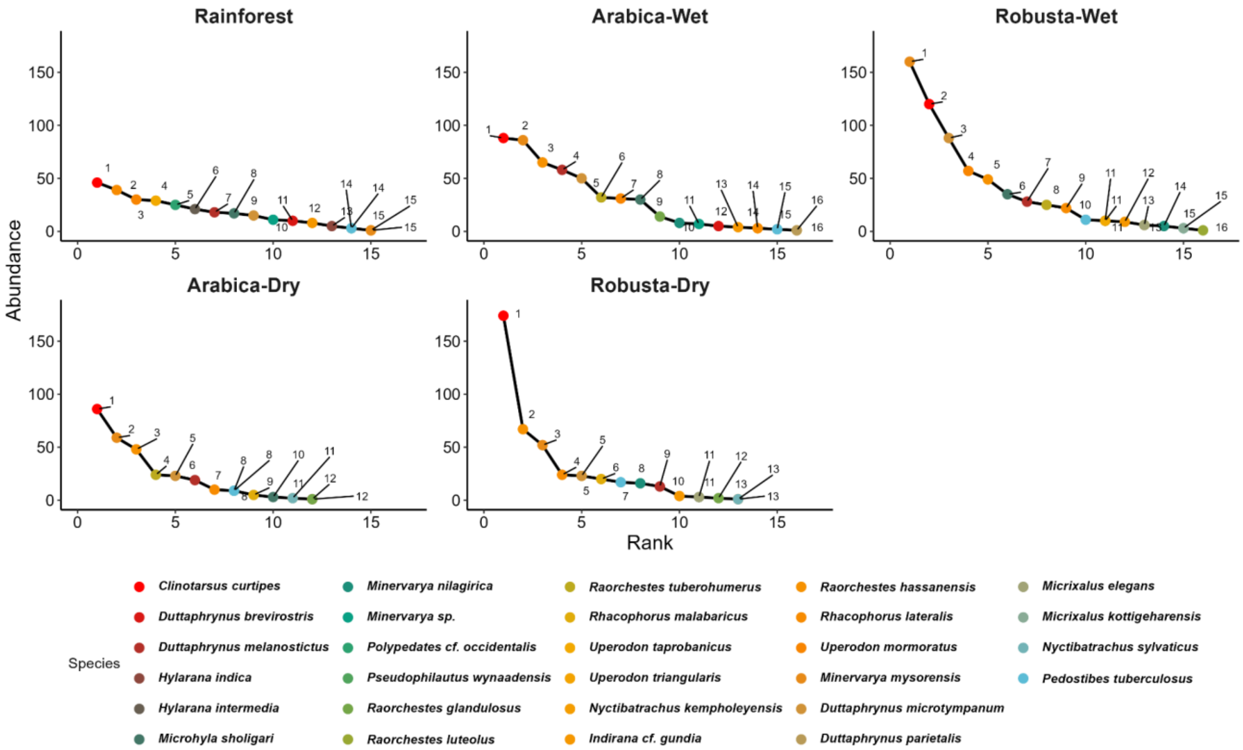

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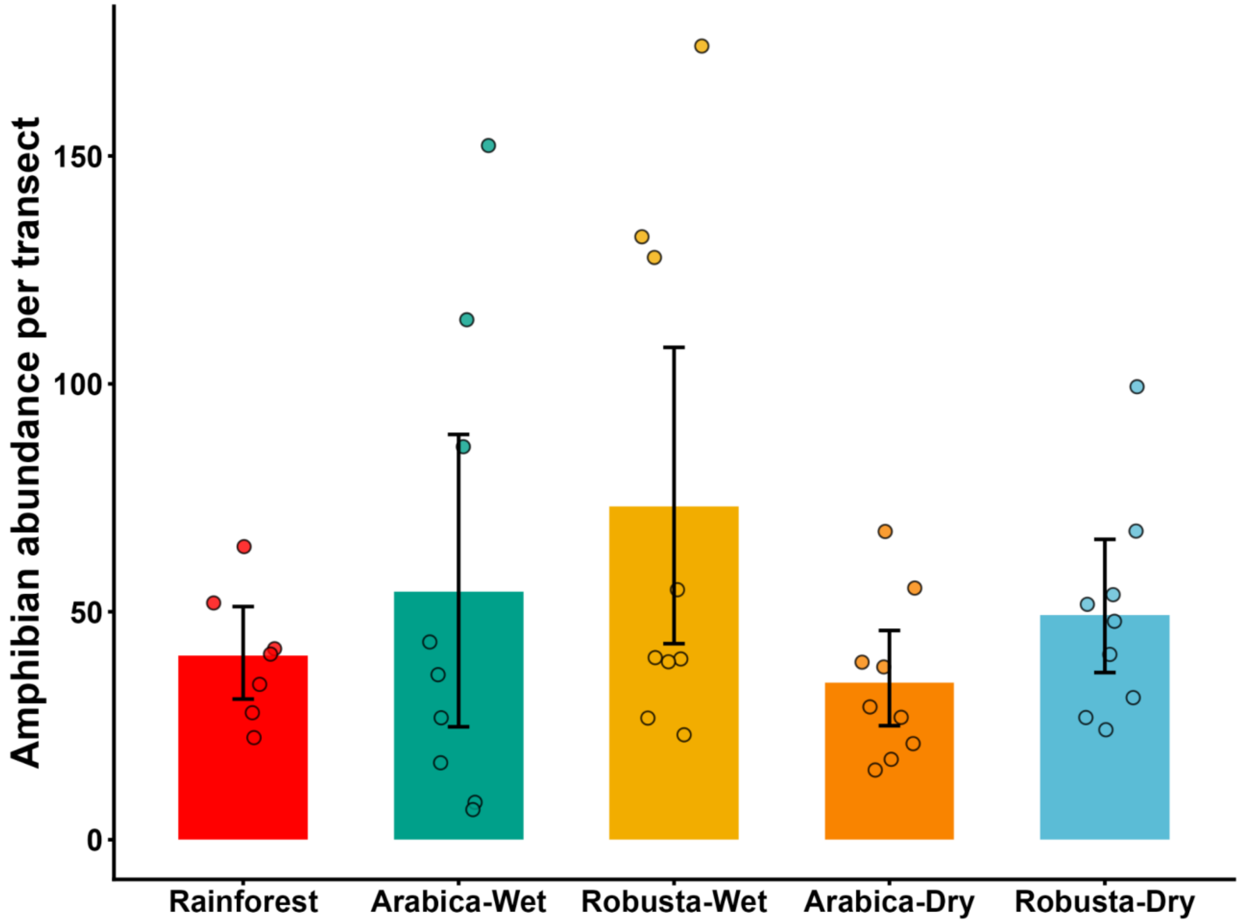

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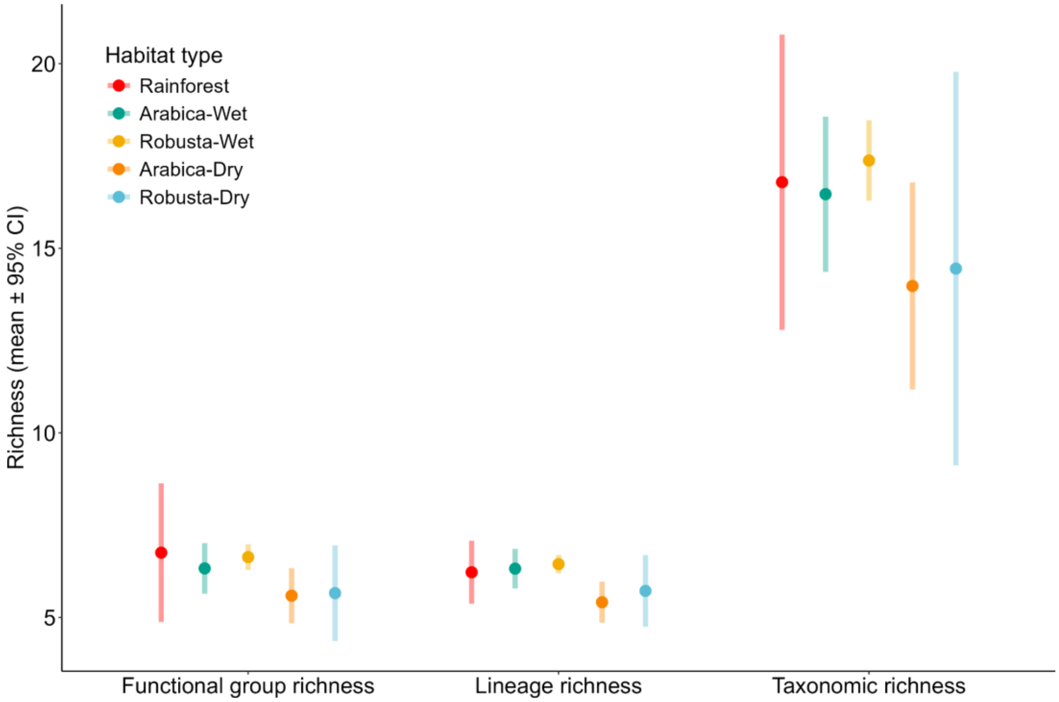

Figure S8: Functional, phylogenetic and taxonomic richness of amphibians across land uses and climate zones, measured using Hill number at q=0 at 99% sampling coverage. Points and bars represent estimated means and 95% confidence intervals, respectively.

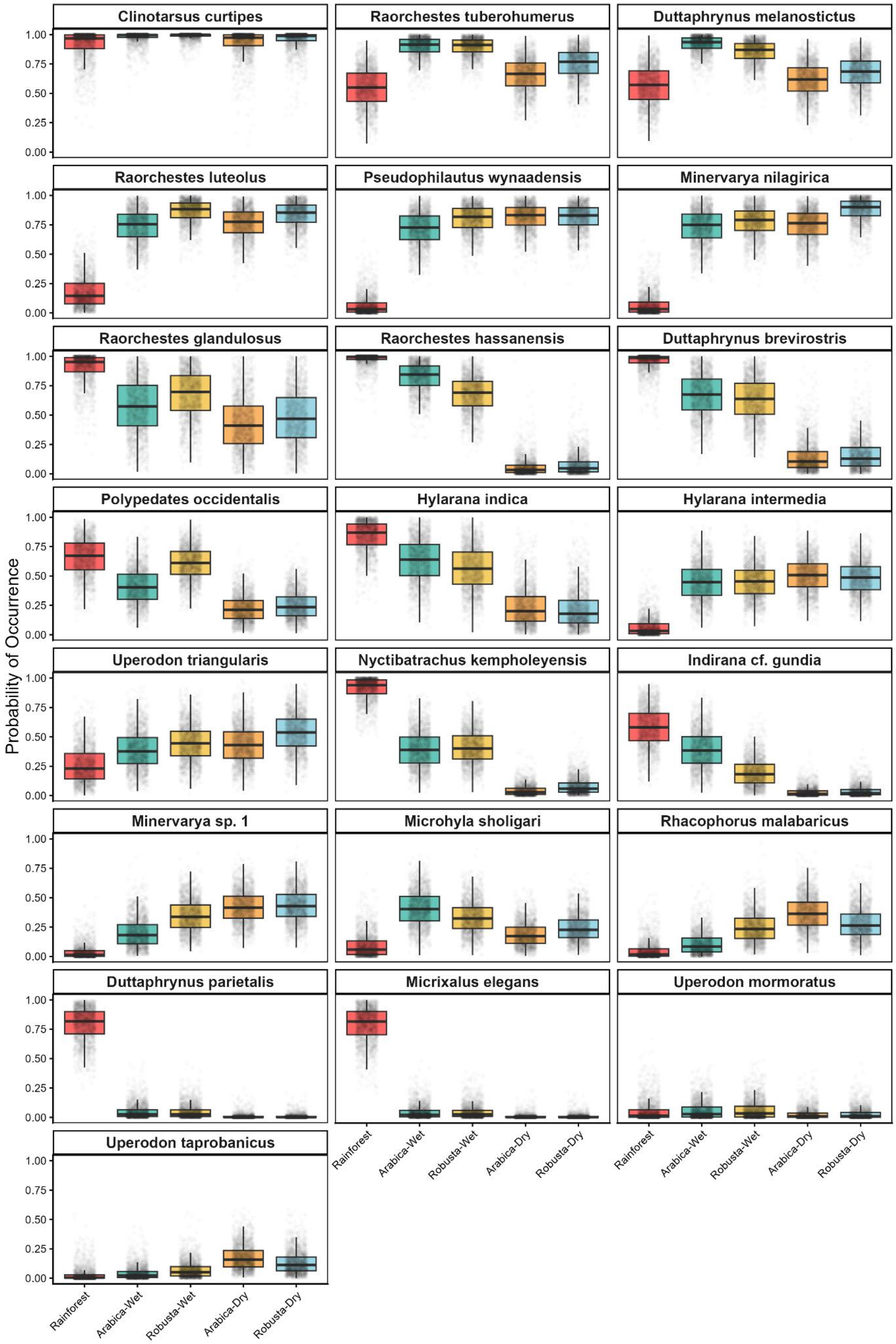

Figure S9: Predicted probabilities of occurrence from the MCMC samples of HMSC model for 22 amphibian species across land use and climate zones.

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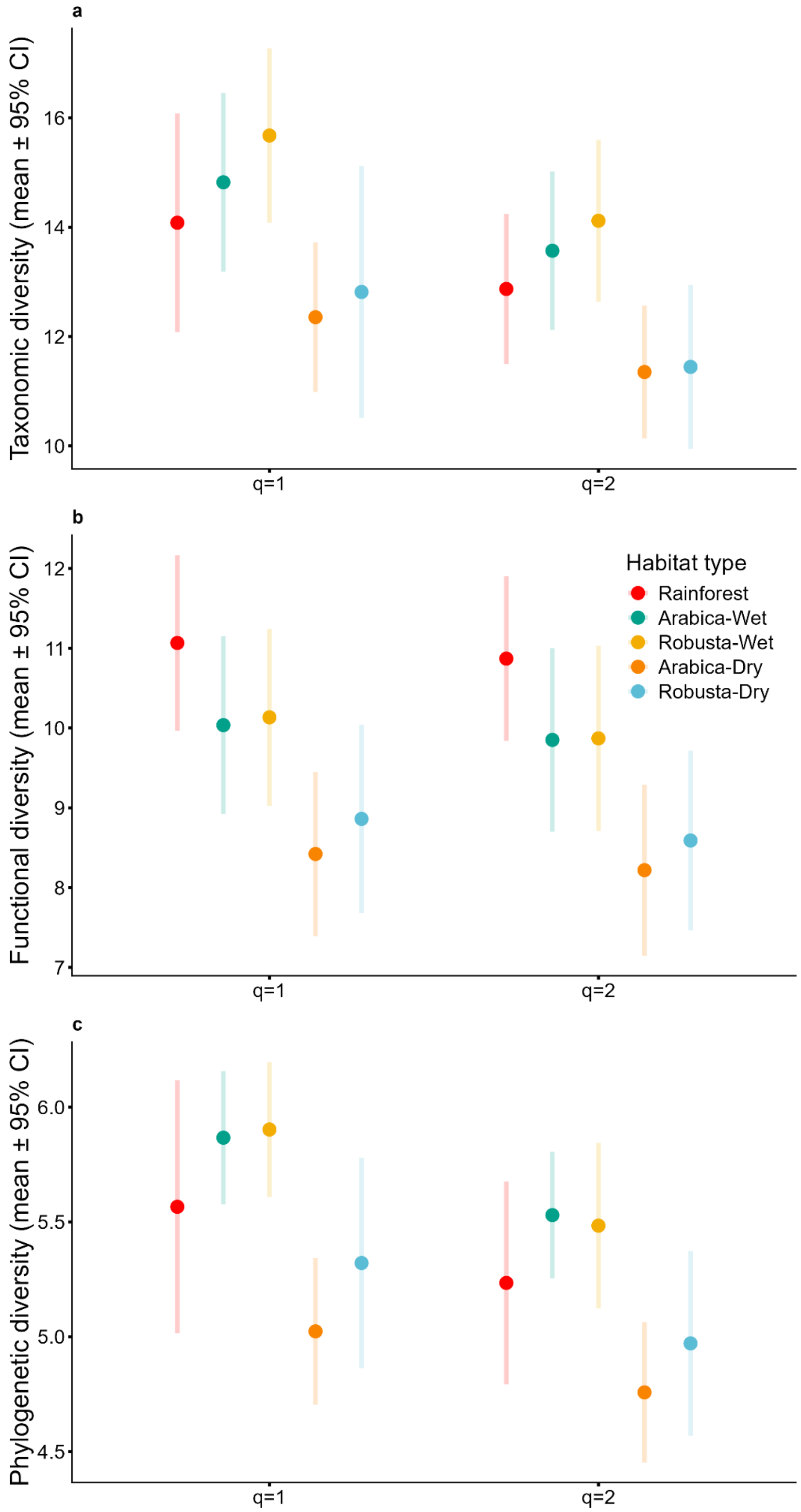

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47 **Figure S10:** Incidence-based amphibian taxonomic, functional and phylogenetic Hill-Shannon

(q = 1) and Hill-Simpson (q = 2) diversity across habitats (at 96% sampling coverage). Points and bars represent estimated means and 95% confidence intervals, respectively

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