# Land use and climate shape amphibian multidimensional diversity and conservation in a coffee agroforestry landscape, Western Ghats

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**Running Head:** Coffee, climate and amphibians

## Abstract

Shade coffee agroforests are potential refuges for biodiversity in human-modified tropical landscapes. However, biodiversity is influenced by coffee cultivation methods and climates, both of which vary widely and are increasingly dynamic. One significant but understudied dynamic is the shift in cultivated species from arabica (*Coffea arabica*) to robusta (*C. canephora*), which alongside deforestation and climate change, is reshaping global coffee landscapes. We compared land uses (secondary rainforest, arabica coffee, robusta coffee) and climate zones (coffee in wet vs. dry zones) for amphibian abundance, community composition, multidimensional diversity (taxonomic, functional, phylogenetic), and ecologically-sensitive and conservation-priority species in India's Western Ghats mountains. We sampled amphibians using line transects (total 12.9 km), collected primary and secondary data on 12 functional traits, geographic distributions, threat status, phylogeny, and estimated multidimensional diversity (Hill-Chao numbers q=0-2) and species occurrence probabilities across land uses and climate zones. While overall amphibian abundance and richness (q=0) were similar across land uses and climates, the secondary rainforest had distinct community composition, higher multidimensional diversity (q=1, 2), and higher occurrence probabilities of stream breeding and threatened-endemic species than coffee. Amphibian multidimensional diversity (q=1, 2) was generally higher in arabica than robusta coffee in both climate zones, and alongside stream breeding and threatened-endemic species was lower in dry than wet zones. Our findings suggest that arabica-to-robusta conversion and climate drying can diminish amphibian multidimensional diversity, and underscore the value of safeguarding and restoring forests and streams for conserving ecologically-sensitive and conservation priority species in changing coffee landscapes.

## Keywords
biodiversity; tropical forest; human-modified landscape; functional diversity; phylogenetic diversity; threatened species; trait-based filtering

## 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; Arroyo-Rodríguez et al., 2020; Wies et al., 2021). 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 identify emerging threats and opportunities, and help design biodiversity-friendly tropical production systems and HMLs.

Shade coffee agroforests are a production system of particular significance for biodiversity conservation (Jha et al., 2014). This is partly because coffee, which is among the most highly traded agricultural commodities, 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 (Perfecto et al., 1996; Manson et al., 2024) and important refuges for biodiversity in HMLs (Bhagwat et al., 2008). However, coffee cultivation encompasses a 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 (Moguel & Toledo, 1999; De Beenhouwer et al., 2013; Perfecto et al., 2019). Studies consistently associate such intensification with reduced diversity and abundance across a range of taxa in coffee agroforests (Philpott et al., 2008; Ibarra-Isassi et al., 2021; Monge et al., 2022). 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) (Jha et al., 2014; Chang et al., 2018; Perfecto et al., 2019; González-Orozco et al., 2024).

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 (Jha et al., 2014; FAO, 2025). 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.

Biodiversity patterns across land use types 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 (Kehoe et al., 2015; Newbold et al., 2015; Cordier et al., 2021; Davison et al., 2021). 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 offer insights into the ecological and evolutionary processes that underlie community responses to land use change (Cadotte et al., 2011; Flynn et al., 2011; Díaz et al., 2013; 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; Uchida et al., 2019; Sfair et al., 2022). Importantly, the effects of land use change can differ across diversity indicators and levels of community organization (Thompson et al., 2016; Chapman et al., 2018; Graham et al., 2019; Albaladejo-Robles et al., 2023; Jithin et al., 2025). This underscores the importance of considering multiple dimensions of diversity and responses at multiple levels of community organization while investigating biodiversity patterns and correlates across land uses and designing conservation interventions in production systems and HMLs.

We examine amphibian communities across land uses and climate zones 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 ability, narrow distributional ranges accompanied by high endemism make amphibians particularly sensitive to variation in habitat quality and climate (Becker et al., 2010; Botts et al., 2013; Frishkoff et al., 2015; Nowakowski, Watling, et al., 2017). Globally and within the Western Ghats, amphibians are a highly threatened vertebrate group, with limited coverage from existing protected areas and exposure to multiple interacting environmental threats, particularly from land use and climate change (Hof et al., 2011; Nori et al., 2015; Luedtke et al., 2023; 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 (Harvey et al., 2021; Rathod & Rathod, 2013; Sankararaman et al., 2021).

Our study examines whether and how differences in land use (tropical secondary 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) correlate with 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 do amphibian abundance, community composition, multidimensional diversity, ecologically-sensitive functional groups, and conservation-priority species (hereafter, amphibian indicators) vary with land use? We hypothesized that structural simplification, reduced environmental heterogeneity, and fewer resources and niches would result in amphibian indicators reducing from rainforest to coffee agroforests, and within coffee, from relatively more densely shaded arabica to robusta agroforests (Perfecto & Vandermeer, 2008; Wanger et al., 2010; Murrieta-Galindo, López-Barrera, et al., 2013). Second, we ask: how do amphibian indicators in coffee agroforests vary with climate (rainfall zone)? We hypothesized that lower rainfall would translate to higher desiccation stress and filter amphibian communities, resulting in lower values of amphibian indicators in the dry zone compared to the wet zone coffee (Da Silva et al., 2012; Ochoa-Ochoa et al., 2019; Murray et al., 2021). 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 et al., 2022).

## 2 METHODS

### 2.1 Study Area

The study was conducted in the Western Ghats mountains of peninsular India, a global biodiversity hotspot (Fig. 1a). With over 253 amphibian species, nearly 94% of which are endemic to the region and 50% classified as threatened by the IUCN, the Western Ghats is considered an important globally threatened amphibian landscape (Luedtke et al., 2023; Deepak & Dinesh, 2024). 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. 1c). 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 (MAP) varies from 2,000 mm to 4,000 mm along an east–west gradient (Fig. 1c), with the majority of rainfall occurring during the southwest monsoon (June–September). Mean annual temperature ranges from 20.6° C to 22.5° C (Fick & Hijmans, 2017). 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. 1c). This 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. 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).

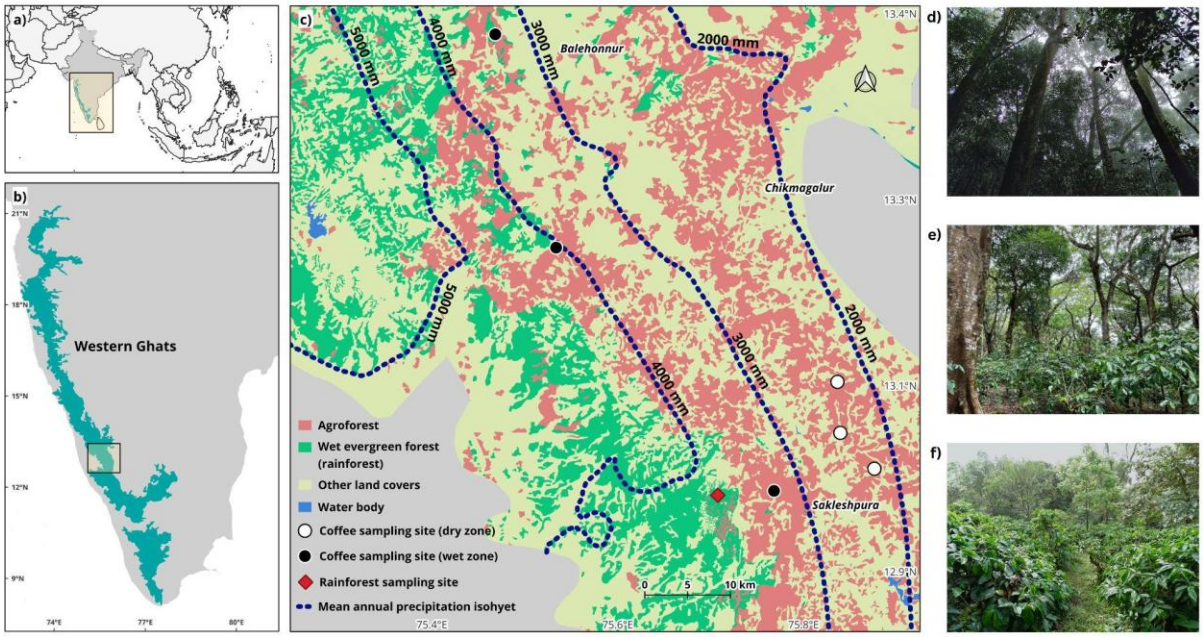


**Figure 1:** Maps showing (a) the location of the study region in peninsular India, (b) the study area in the Western Ghats, a global biodiversity hotspot and (c) the study area with key land cover types, mean annual precipitation isohyets, and sampling locations marked. The

‘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, highly 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). Representative photographs of d) secondary tropical rainforest, e) shade arabica coffee, and f) shade robusta coffee land uses from the study area are provided

In the Western Ghats, coffee agroforests overlap with sites with high conservation value (i.e., higher threatened and endemic species: 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). Both arabica and robusta coffee are largely grown under shade tree canopies in this region, typically as shade polycultures comprising multiple native and non-native tree species, but often and increasingly as shade monocultures of non-native *Greviella robusta* (Osuri et al., 2025). 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.; Garcia et al., 2010).

### 2.2 Amphibian sampling

We surveyed amphibians in six polyculture shade coffee agroforest sites and one secondary tropical rainforest site in the study area (Table S1). We selected large (≥50 ha) agroforests that cultivated both arabica and robusta coffee in segregated zones. Three agroforests were situated in the wet zone (MAP: 3,000 mm – 4000 mm) towards the western limit of coffee cultivation in the region, and the other three were situated in the dry zone (MAP: 2000 mm – 3000 mm) towards the eastern limit of coffee cultivation (Fig. 1c). Mean annual temperature did not differ between the wet and dry zones (wet zone: 22.0° C; dry zone: 21.9° C). All selected sites were associated with the same regional species pool, as verified from occurrence records on GBIF (*GBIF*, 2026), but the spread and inter-site distances varied based on the availability of suitable agroforests and access permits from landowners. All dry zone sites were located south of 13.3° N to avoid sampling biogeographically distinct regions north of this latitude in this zone; this contributed to the lower inter-site distances in this zone compared to the wet zone. 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 rainforest, 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 secondary forest sample is likely to yield lower (i.e., conservative) estimates of rainforest amphibian diversity and conservation indicators (Vallan, 2000; Thompson & Donnelly, 2018; Juárez-Ramírez et al.,

2024). No reference sites were available in the highly deforested dry zone where any remaining forests are highly fragmented and degraded. Pilot surveys confirmed the presence of lentic habitats in all sites. Lotic habitats were present in the rainforest and in highly reduced and degraded form in wet zone coffee sites, but largely absent from coffee sites in the dry zone.

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. Transects were located at random along straight lines that followed narrow harvest paths in coffee and animal trails in the rainforest. Transects were spaced a minimum of 150 m and up to 1 km apart within each site to maintain sampling independence. 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 (Biju et al., 2014; Gururaja et al., 2014; Dahanukar et al., 2016; Garg et al., 2021; Bisht et al., 2021). A single species belonging to the *Minervarya* genus remained unidentified to the species level and was recorded as *Minervarya* sp.1, 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 the overstory structure of the coffee agroforests and the secondary rainforest. In 150 m $\times$ 20 m plots established along each transect, we identified all trees (DBH $\geq$ 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: partial overlap; 2: substantial overlap but with a few openings; and 3: full overlap with no sky visible) as described by 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.

### 2.3 Functional traits, phylogenetic tree, and conservation status data

For each amphibian species in our study, we collected data on 12 functional traits that are associated with sensitivity to habitat modification and frequently included in amphibian functional diversity estimation (Table S3; Cortés-Gómez et al., 2016; Riemann et al., 2017; Dehling & Dehling, 2021). These include morphological (snout-to-vent length (SVL), head length, head width, femur length, tibia length, eye diameter, finger and toe disc width),

ecological (foot webbing, microhabitat use and skin type) and life-history traits (breeding strategy). Morphological traits were estimated from measurements of 3-8 adult males per species from the rainforest and coffee agroforests (using a Mitutoyo digital vernier caliper with 0.01 mm least count). Species-level estimates for morphological traits were obtained by averaging measurements across individuals within each species. For nine species that were not measured in the field, morphological traits were collated from species descriptive accounts (Biju et al., 2014; Gururaja et al., 2014; Dahanukar et al., 2016). For ecological and 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). All but two species – *Duttaphrynus melanostictus* and *Uperodon taprobanicus* – were endemic to the Western Ghats. 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' from the function *get_tree()* using '*rtrees*' package (Li, 2023).

### 2.4 Data analysis

To check whether detectability differed between land use types and climate zones, 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. S1), 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 from 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 (five land use type and climate zone combination) to estimate coverage-based rarefied taxonomic, functional, and phylogenetic diversity (TD, FD, and PD) based on Hill-Chao number orders q = 0, q = 1, and q = 2 in iNEXT.3D package (Chao & Jost, 2012; Chao et al., 2021). Taxonomic diversity was calculated using the species abundance by treatment 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, breeding strategy and skin type. We excluded head length, head width, femur length, tibia length, eye diameter as these were strongly correlated (Spearman's $r \geq 0.8$) 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. S2). Hill-Chao numbers (Hill numbers) of order q = 0 represent the observed richness of species, functional groups, and lineages, while order q = 1 (a generalized measure of Shannon entropy) incorporates species relative abundances, reflecting the diversity of common species, functional groups, and lineages, and order q = 2 (a generalization 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-Chao numbers of order q = 1 and q = 2 enable more robust comparisons of multidimensional 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 treatment.

#### *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 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; 6 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 affected model convergence. We modelled the presence-absence of species using a 'probit' link function with land use and climate zone combination as a 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 signal in species' response to land use change and climate zone. 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 four Markov Chain Monte Carlo (MCMC) chains with default priors and 500 posterior samples per chain, a thinning interval of 10,000, and a burn-in of 2,500,000 iterations, resulting in 2,000 posterior samples in total. We assessed model convergence using the effective sample size (ESS = 2,000) and the potential scale reduction factor (PSRF < 1.05; Gelman & Rubin, 1992). 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 $\beta$-coefficients with posterior probabilities ≥ 95% as strongly supported. We also predicted the species occurrence probabilities from the posterior samples. Finally, we computed $\beta$-coefficient means and 95% CIs across species grouped by breeding strategy (Lotic, Lentic, Terrestrial), body size (Small, Medium, and Large), and conservation priority (High, Medium, Low).

For the first question assessing amphibian indicators across land uses, we made comparisons between rainforest, arabica, and robusta coffee in the wet zone (rainforest vs. arabica-wet vs. robusta-wet), and only arabica and robusta coffee in the dry zone (arabica-dry vs. robusta-dry), where suitable rainforest sites were unavailable. No comparisons are made between rainforest in the wet zone and coffee in the dry zone. For the second question assessing amphibian indicators between climate zones, we compared arabica and robusta coffee in the wet zone to their counterparts in the dry zone (arabica-wet vs. arabica-dry and robusta-wet vs. robusta-dry).

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). We interpreted differences in treatment means as reflecting the direction and magnitude of differences in amphibian indicators, with the degree of non-overlap between 95% confidence intervals (CIs) indicating the consistency and reliability of those estimates (Nakagawa & Cuthill, 2007; Cumming, 2009). For any pair of land use-climate zone combinations, we interpreted highly similar means and highly overlapping 95% CIs as no difference, dissimilar means and partly overlapping 95% CIs as moderately consistent differences, and dissimilar means with completely non-overlapping 95% CIs as high differences.

All analyses were performed in R version 4.5.1 (R Core Team, 2025) using RStudio (Posit 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

As expected, the secondary rainforest had considerably higher canopy cover, tree density, and tree species richness than coffee agroforests, and canopy cover was higher in arabica than robusta coffee, based on visual inspection of means and 95% confidence intervals overlain on the half-violin plots (Fig. 2; Table S5). Tree basal area did not differ consistently between rainforest and coffee, nor did tree density and species richness differ consistently across coffee crop types and climate zones (Fig. 2; Table S5).

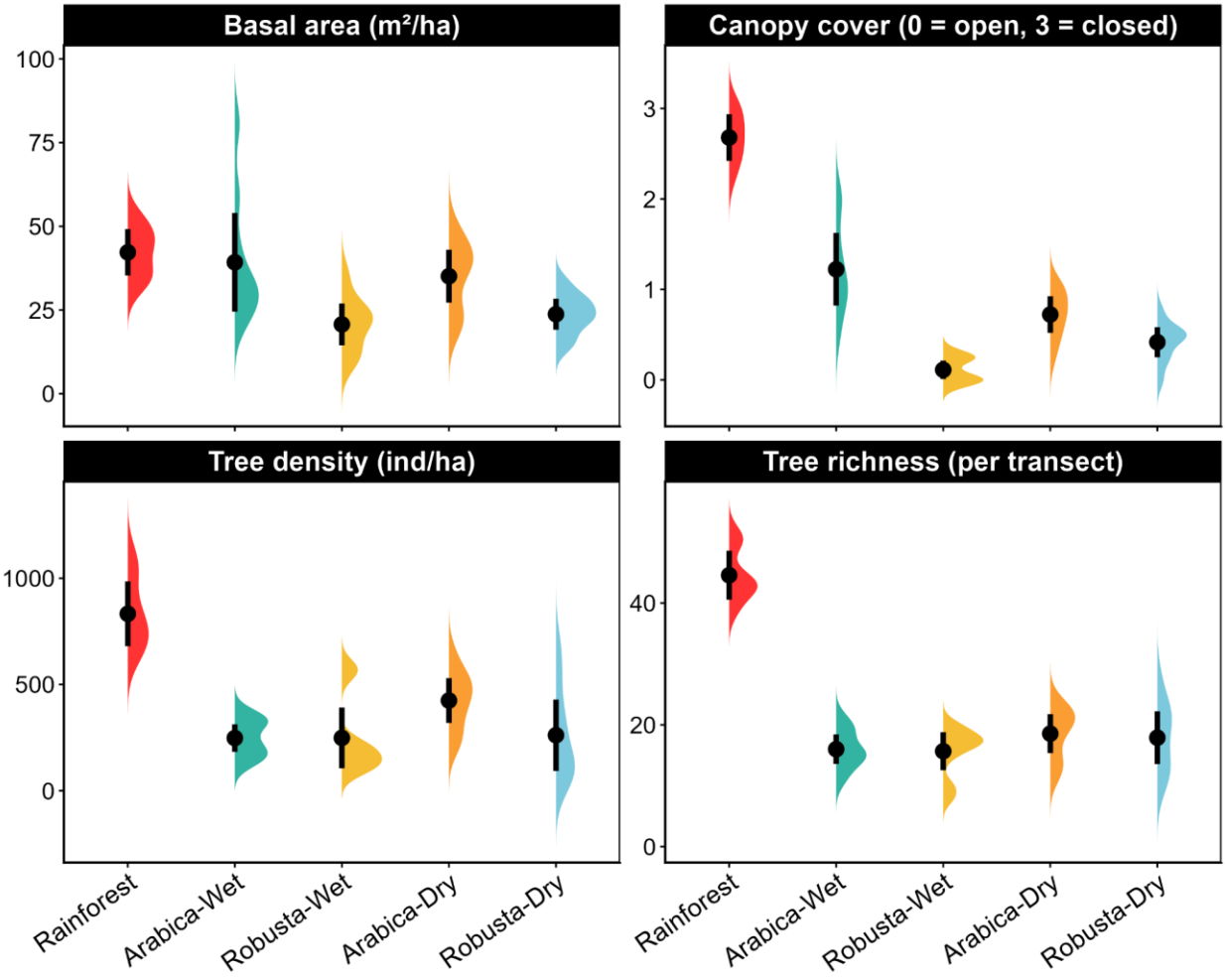


Figure 2: Half-violin plots showing the distribution of overstorey structural attributes across the five land use-climate zone combinations, including basal area ($m^2$ $ha^{-1}$), canopy cover (ordinal scale: 0-3) tree density (trees $ha^{-1}$), and tree species density (species per transect). Black points denote group means with error bars representing 95% confidence intervals

We recorded a total of 2,185 adult amphibian 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. S3). In rainforests, *Clinotarsus curtipes* (16%),

*Raorchestes glandulosus* (14%), and *R. hassanensis* (11%) were most abundant. 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. 3a; Table S6). Among the 14 genera recorded (Fig. S2), *Minervarya* was not detected in rainforests, while *Micrixalus* was absent from coffee agroforests.

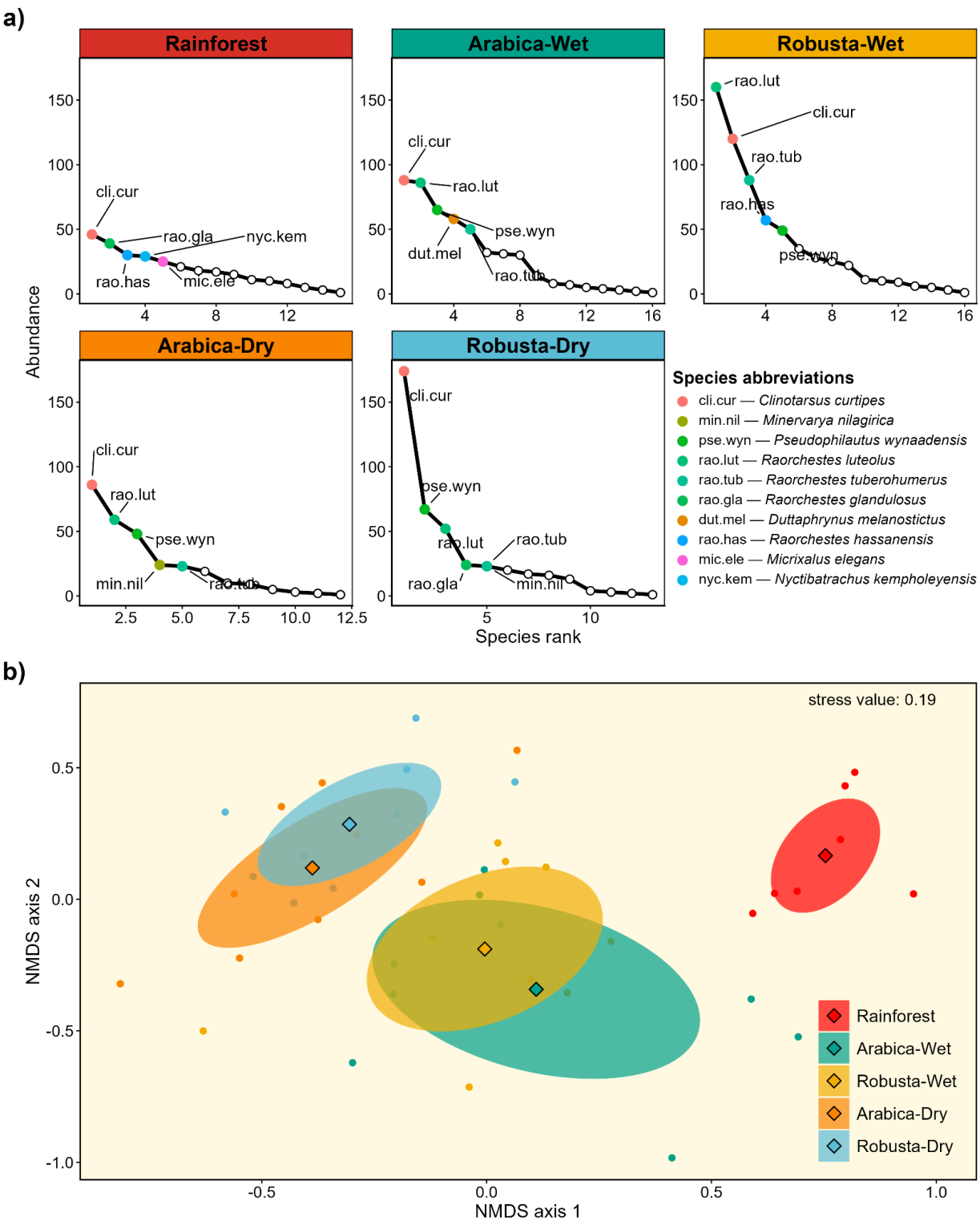


Figure 3: a) Rank–abundance curves illustrating patterns of dominance and evenness in amphibian assemblages across the five land use-climate zone combinations. b) NMDS plot based on the Bray-Curtis dissimilarity matrix of transects (points), illustrating differences in

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 and composition

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. S4). 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. S4). The rainforest, wet zone coffee, and dry zone coffee harbored taxonomically distinct amphibian communities (Fig. 3b; 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. 3b; PERMANOVA $R^2 = 0.01$, $p = 0.89$).

### 3.2 Taxonomic, functional, and phylogenetic diversity

TD, FD, and PD at Hill number order q = 0 (i.e., richness) varied widely and did not differ consistently across land use-climate zone combinations, inferred from the substantial overlaps of estimated 95% CIs of these indicators across combinations (Fig. S5). At the order q = 1 (Hill-Shannon), and q = 2 (Hill-Simpson), TD, FD, and PD were highest in the rainforest, while arabica coffee was either higher or no different from robusta coffee within climate zones depending on the diversity dimension (Fig. 4). In the wet zone, arabica FD and PD were higher than robusta, with complete non-overlaps or partial overlaps of 95% CIs suggesting high to moderate consistency of these differences (Fig. 4). In the dry zone, TD, FD, and PD were higher in arabica than robusta coffee with a moderate level of consistency (Fig. 4). Between climate zones, excluding robusta FD and PD at q = 2, all three diversity dimensions were higher in wet than dry zone coffee with high to moderate levels of consistency (Fig. 4).

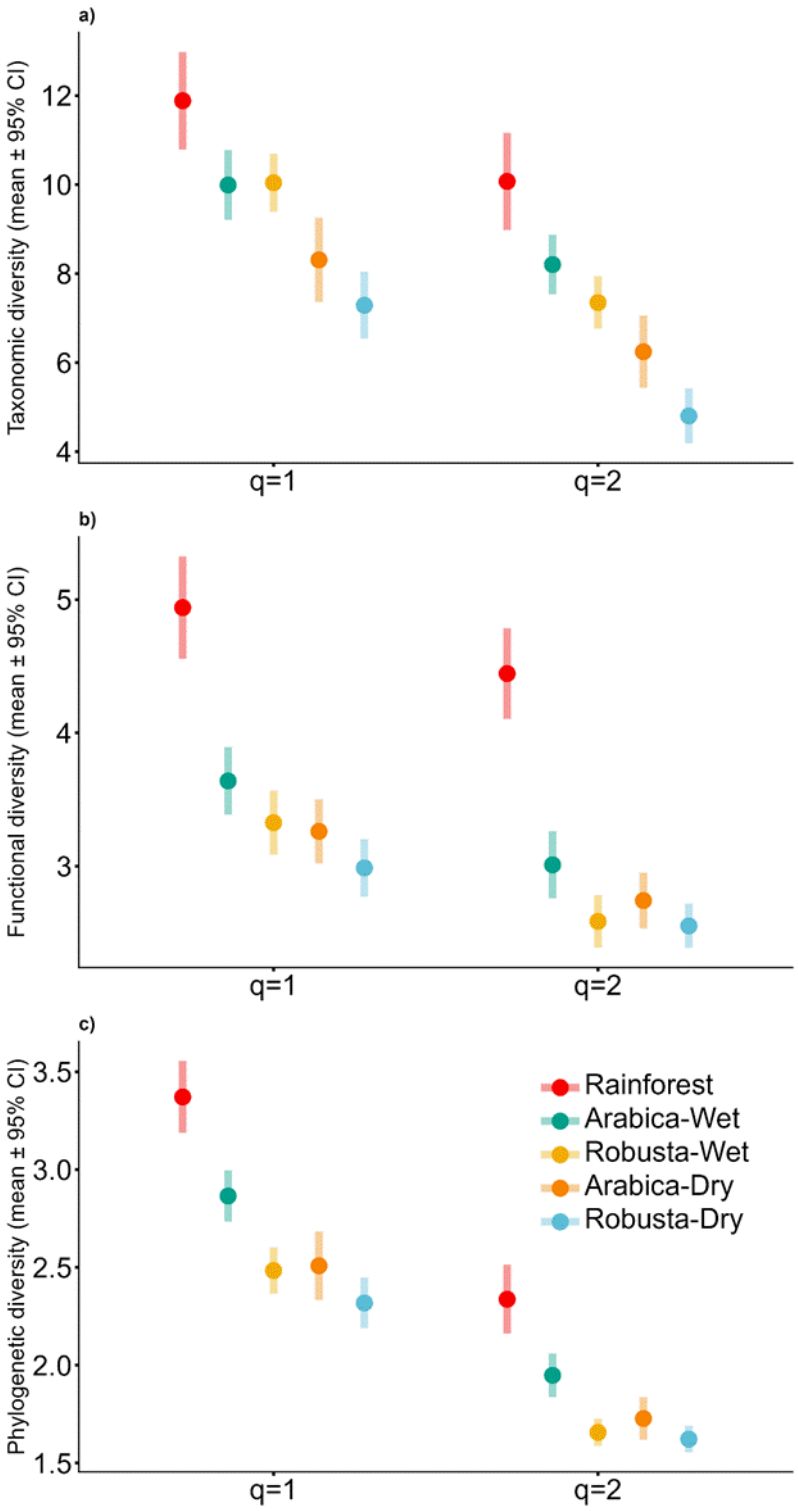


Figure 4: Abundance-based amphibian a) taxonomic, b) functional and c) phylogenetic Hill-Shannon (q = 1) and Hill-Simpson (q = 2) diversity across land use types and climate zones (at 98% sampling coverage). Points and bars represent estimated means and 95% confidence intervals, respectively

### 3.3 Species and species-group responses

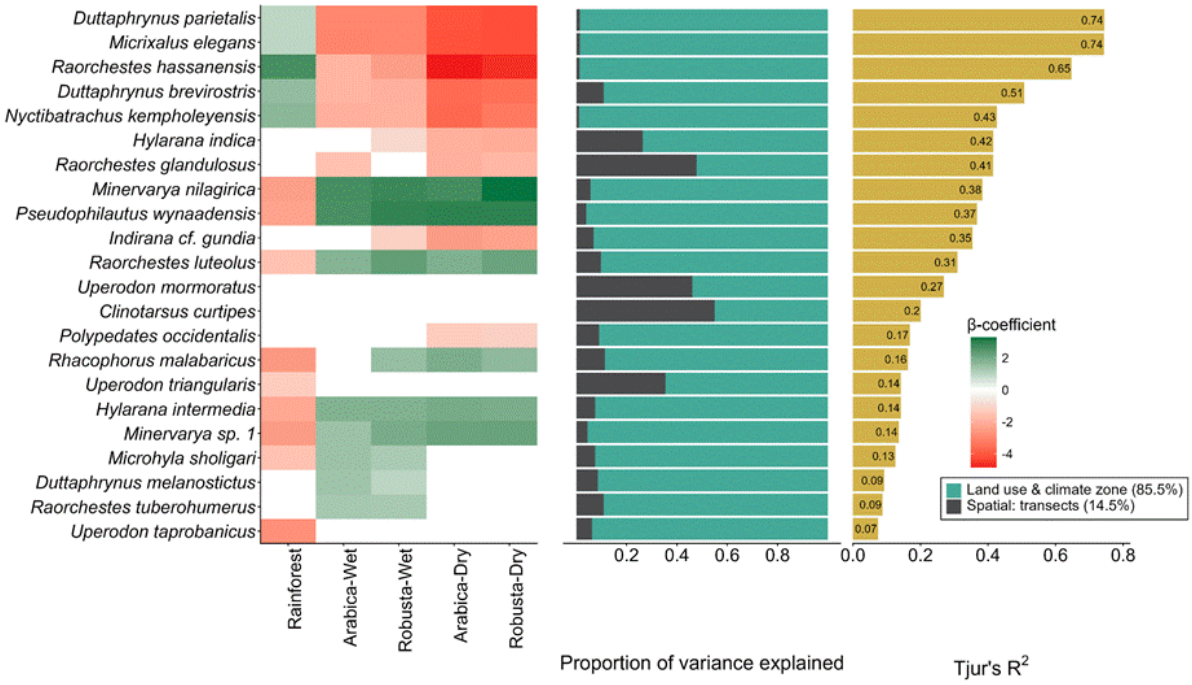


Figure 5: Result from the HMSC model-estimated species response (*β*-coefficients) to land use types and climate zones (left). Green and red colours indicate statistically supported positive and negative responses respectively, the variance partitioning plot illustrating the variance explained by predictors (middle) and Tjur's $R^2$ indicating the model fit for each species. Species are arranged from highest to lowest Tjur's $R^2$

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. 5). We found no phylogenetic signal in species response to land uses and climate zones ($\rho$ = 0.07, 95% credible interval: 0–0.49). The rainforest had higher *β*-coefficient values (untransformed occurrence probabilities) of *Raorchestes hassanensis*, *Duttaphrynus parietalis*, *D. brevirostris,* and *Micrixalus elegans*, suggesting that these species are forest "specialists" (Fig. 5; Fig. S6). 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. 5; Fig. S6). 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. 5; Fig. S6).

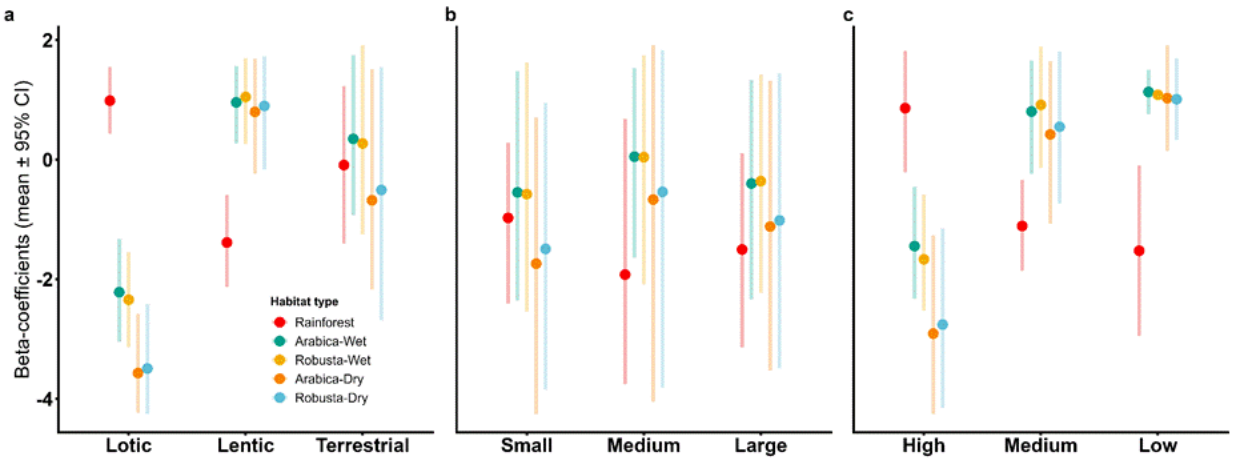


Figure 6: Untransformed occurrence probabilities (*β*-coefficients), derived from the HMSC model, grouped by (a) breeding strategy, (b) body size, and (c) conservation-priority. Points and error bars represent estimated means and 95% confidence intervals of each land use and climate zone.

*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. 6a). None of the breeding strategies showed any difference between arabica and robusta coffee in either wet or dry zone (Fig. 6a). Occurrence probabilities of lotic and terrestrial breeders (but not lentic breeders) showed small decreases on average from arabica-wet to arabica-dry and robusta-wet to robusta-dry, but with large overlaps in 95% CIs (Fig. 6a).

Body size showed no clear association with any land use type and climate zones, with substantial overlap in 95% CIs across all size classes (Fig. 6b).

Interestingly, high conservation-priority species showed consistently higher values in rainforests, while medium and low conservation-priority species showed higher *β*-coefficients in coffee agroforests than rainforests (with 95% CIs partially overlapping; Fig. 6c). None of the conservation priority groups showed any differences between arabica and robusta coffee in either wet or dry zone (Fig. 6c). 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. 6c).

## 4. DISCUSSION

Our study examined patterns of amphibian multidimensional diversity, community composition, and species occurrences across secondary tropical rainforest and arabica and robusta coffee agroforests under relatively wet versus dry climate contexts in India's Western Ghats. We found that while both arabica and robusta coffee can match or surpass secondary 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 high conservation-priority species than either coffee system in the wet zone (representative rainforest sites were unavailable for a similar comparison in the dry zone). We also found that arabica generally harbors higher amphibian multidimensional diversity than robusta coffee. Multidimensional diversity and occurrences of lotic and high conservation-priority species in both arabica and robusta tend to decrease from wetter to drier zones of coffee cultivation. These findings suggest that land use change from rainforest to coffee, and the transition from arabica to robusta coffee, can have significant negative implications for amphibian multidimensional diversity, community composition, and conservation, which could be amplified under a drying climate.

The relatively less-disturbed secondary rainforest in our study harbored a distinct amphibian community with 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 in the wet zone. The substantially higher multidimensional diversity (q = 1 and 2) in the rainforest than coffee despite the land uses not differing consistently in amphibian abundances and species richness aligned with previous findings (Juárez-Ramírez et al., 2024). One factor underlying this pattern is that amphibian species abundances in the secondary 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 (Wanger et al., 2010; Chao et al., 2021); by contrast, amphibian species abundances in both coffee systems—especially robusta—were highly skewed (Fig. 3a). Another factor could be the asymmetries in winner-loser replacements across land uses with “losers” from forest to coffee being more functionally and phylogenetically unique—for example, lotic breeding and evolutionarily ~60 million year old *Nyctibatrachus* spp. and *Micrixalus* spp. (Roelants et al., 2004)—than the “winners” (lentic breeding *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). While secondary forests cannot substitute for irreplaceable primary forests as biodiversity refuges (Gardner et al., 2007; Gibson, 2011), our findings suggest that the former can nevertheless contribute meaningfully to sustaining amphibian multidimensional diversity and ecologically-sensitive and conservation-priority groups. Recognizing and restoring such forests could play a key role alongside safeguarding irreplaceable primary forests in amphibian conservation strategies for coffee producing landscapes (Gardner et al., 2007; Juárez-Ramírez et al., 2024).

While coffee agroforests had lower multidimensional diversity and reduced occurrences of high conservation-priority species, they 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 (Scheffers et al., 2013; Nowakowski, Watling, et al., 2017), the persistence of these sensitive groups suggests the coffee agroforests are effective to some extent at maintaining relatively suitable understory habitats, breeding sites,

and microclimates for these groups (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 and old secondary rainforests for conserving amphibians in mosaic production landscapes (Murrieta-Galindo, González-Romero, et al., 2013; Pinzón et al., 2025).

In agreement with previous research (Murray et al., 2021; Nowakowski, Thompson, et al., 2017), the guild of lotic breeding species, including the *Micrixalus* and *Nyctibatrachus* genera which are considered among the most threatened in the entire Indomalayan biogeographic region (Re:wild et al., 2023), declined sharply from rainforest to arabica and robusta coffee. Lotic breeding species are known to disperse and forage terrestrially during the wet season (Sankararaman & Miller, 2024), and their declines from rainforest to coffee are possibly associated with corresponding reductions in high quality lotic habitats (Bolochio et al., 2020; Coleman et al., 2024). We observed that streams and associated riparian habitats were relatively numerous and intact in the rainforest compared to coffee agroforests, where they are often modified for water supply and storage, and exploited for rocks and large boulders, which are crucial lotic habitats (Rajiv et al., 2025; Fig. S7). While we did not systematically sample streams in this study, opportunistic searches failed to detect the presence of any forest-affiliated lotic species in coffee agroforest streams. Apart from this, the relatively closed canopy of the rainforest potentially fosters more suitable microclimates for sensitive lotic species than coffee agroforests. In contrast to lotic breeding species, lentic breeders such as *Minervarya* spp. and *Rhacophorus malabaricus* were encountered more frequently in coffee agroforests than the rainforest, consistent with previous research identifying this guild as being less sensitive to land use change (Mendenhall et al., 2014; Nowakowski, Thompson, et al., 2017). Previous studies and our own observations suggest that the high availability of lentic breeding sites including artificial irrigation ponds and seasonal ephemeral pools along roadsides could play a role in sustaining a diverse and abundant community of lentic amphibians in coffee agroforests (Sankararaman et al., 2021; Fig. S8). Given that many amphibian species exhibit biphasic life cycles and breeding strategy is a key trait associated with species responses to land use change (Becker et al., 2007; Bickford et al., 2010; Almeida-Gomes & Rocha, 2015), understanding the interplay between terrestrial and aquatic habitat attributes and their relative contributions to shaping amphibian communities in HMLs is an important topic for further study.

Arabica and robusta coffee sustained similar amphibian abundances but the former generally exhibited greater multidimensional diversity (particularly functional and phylogenetic diversity at $q = 2$ and $q = 1$) within climate zones. These patterns suggest that while 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. Our findings largely resemble those of Chang et al., (2018), who reported little difference in bird abundances between arabica and robusta coffee but lower diversity and abundance of sensitive functional groups in the latter agroforestry system. 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: rainforest, arabica coffee, robusta coffee (Fig. 2, Fig. 4). This suggests that differences in habitat structure and management could

be associated with amphibian community patterns across land uses (Brüning et al., 2018; Hernández-Ordóñez et al., 2019; Torralvo et al., 2022), highlighting the need for research examining variation in habitat structure and management within and across arabica and robusta systems, amphibian species-habitat relationships, and implications for conservation policies and interventions. In addition to canopy cover and other overstory attributes that are generally the focus of biodiversity-friendly coffee agroforestry (Manson et al., 2024), such research must consider practices affecting the understory and litter layers, which represent crucial amphibian microhabitats (Wanger et al., 2009; Rakotozafy et al., 2025).

Amphibian indicators in arabica and robusta coffee varied markedly across climate zones, with coffee in the dry zone exhibiting lower multidimensional diversity, reduced occurrence probabilities of lotic, terrestrial breeders (with moderate 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*). Several amphibian indicators decreased nearly as strongly from wet and dry zone coffee as they did from rainforest to wet zone coffee. The above pattern is unlikely to be an artefact of the wet zone coffee sites lying further apart than the dry zone ones 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. S9 for occurrence-based estimates of taxonomic, functional, and phylogenetic diversity in wet versus dry zones). The observed reductions in amphibian multidimensional diversity, ecologically-sensitive and conservation-priority groups from wet to dry zone coffee, despite no corresponding simplification of overstory structure, align with previous studies and suggest that increased climate stress could be filtering amphibian communities in the drier sites (Alves-Ferreira et al., 2025; Da Silva et al., 2012; Murray et al., 2021; Torralvo et al., 2022). Our results also highlight potential emerging threats from climate drying to amphibian multidimensional diversity, lotic and terrestrial breeders, and high conservation-priority species in coffee agroforests (Loyola et al., 2008; Jansen et al., 2009; Hoffmann et al., 2021; Le Galliard et al., 2021; Wu et al., 2024; Alves-Ferreira et al., 2025). Several climate models project increasing drying, alongside increasing variability and extreme events, in many coffee-growing regions including the Western Ghats (Murugan et al., 2022; Dhara et al., 2025), Brazil (Gomes et al., 2020), Vietnam (Anh Dinh et al., 2025), Ethiopia (Moat et al., 2017) and Puerto Rico (Fain et al., 2018). Given that tropical amphibians have narrow thermal tolerance margins (Sunday et al., 2014; Nowakowski, Watling, et al., 2017), and most species including those associated with terrestrial strata depend on moist microhabitats for reproduction, promoting management practices that maintain favourable microhabitats and restoring forest and riparian refuges might be especially important for sustaining amphibian-friendly coffee agroforestry under drier and warmer climates (Lin, 2007; González-del-Pliego et al., 2020; Sankararaman & Miller, 2024). In coffee-producing landscapes that occupy “middle” elevations (800 m to 1400 m asl) in the Western Ghats, such interventions could also facilitate climate-induced upward range shifts that are predicted for a wide suite of amphibian species (Marathe et al., 2025).

Collectively, our results 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. First, we find that secondary tropical rainforests can harbor significant amphibian multidimensional diversity and conservation value in coffee producing landscapes. As climate and market trends amplify the threat of deforestation by coffee cultivation (Bunn et al., 2015; Magrach & Ghazoul, 2015; Schroth et al., 2015), recognizing and ecologically restoring secondary forest patches—for example, on uncultivated lands and discontinued coffee fields—could play a key role alongside the protection of irreplaceable primary rainforest remnants for sustaining conservation in coffee producing landscapes. Second, the transition from arabica to robusta coffee agroforests that feature simplified overstory structure can strengthen trait-based environmental filtering and diminish the potential of coffee agroforests to harbor diverse amphibian communities. While biodiversity-friendly farming initiatives tend to focus mainly on overstory management, amphibians are also likely to respond strongly to how understories and lotic habitats are managed (Wanger et al., 2009; Luría-Manzano et al., 2024). Future research to identify coffee agroforest habitat attributes and management practices that matter most for amphibians, including threatened and ecologically sensitive groups such as lotic breeders, can help broaden the coverage of biodiversity-friendly coffee farming standards (Iverson et al., 2019). In this regard, while we discuss the simplification of overstory structure as a potential threat arising from the arabica to robusta coffee transition, certain other attributes of robusta agroforestry including relatively lower pesticide use than arabica (Chang et al., 2018) and strong dependence on biotic interactions such as insect-mediated pollination (Crane & Walker, 1984) could present conservation opportunities that need to be explored. Finally, amphibian multidimensional diversity and conservation value of coffee agroforests can decrease substantially from wetter to drier regions, plausibly in association with increasing environmental stress. This illuminates climate drying as a potential threat, and elevates the significance of securing and restoring hospitable microclimates, streams and associated riparian habitats for sustaining amphibian conservation in rapidly evolving coffee production landscapes.

**REFERENCES**


Albaladejo-Robles, G., Böhm, M., & Newbold, T. (2023). Species life-history strategies affect population responses to temperature and land-cover changes. Global Change Biology, 29(1), 97–109. https://doi.org/10.1111/gcb.16454

Almeida-Gomes, M., & Rocha, C. F. D. (2015). Habitat loss reduces the diversity of frog reproductive modes in an Atlantic forest fragmented landscape. Biotropica, 47(1), 113–118. https://doi.org/10.1111/btp.12168

Alves-Ferreira, G., Heming, N. M., Talora, D., Keitt, T. H., Solé, M., & Zamudio, K. R. (2025). Climate change is projected to shrink phylogenetic endemism of Neotropical frogs. Nature Communications, 16(1), 3713. https://doi.org/10.1038/s41467-025-59036-2

Anh Dinh, L., Aires, F., & Rahn, E. (2025). Climate change impacts on Robusta coffee production in Vietnam. Environmental Research Letters, 20(11), 114059. https://doi.org/10.1088/1748-9326/ae14d1

Arroyo-Rodríguez, V., Fahrig, L., Tabarelli, M., Watling, J. I., Tischendorf, L., Benchimol, M., Cazetta, E., Faria, D., Leal, I. R., Melo, F. P., & others. (2020). Designing optimal human-modified landscapes for forest biodiversity conservation. Ecology Letters, 23(9), 1404–1420. https://doi.org/10.1111/ele.13535

Barlow, J., Gardner, T. A., de Jesus da Silva Araujo, I., Avila-Pires, T. C. S., Bonaldo, A. B., Costa, J., Esposito, M. C., Ferreira, L. V., Hawes, J. E., Hernández, M. I. M., Hoogmoed, M. S., Leite, R. N., Lo-Man-Hung, N. F., Malcolm, J. R., Martins, M. L. B., Mestre, L. A. M., Martins, M. B., R. Miranda-Santos, A. L. Nunes-Gutjahr, … Peres, C. A. (2007). Quantifying the biodiversity value of tropical primary, secondary, and plantation forests. Proceedings of the National Academy of Sciences of the United States of America, 104(47), 18555–18560. https://doi.org/10.1073/pnas.0703333104

Becker, C. G., Fonseca, C. R. C., Fonseca, C., Haddad, C. F. B., Batista, R. F., & Prado, P. I. (2007). Habitat split and the global decline of amphibians. Science, 318(5857), 1775–1777. https://doi.org/10.1126/science.1149374

Becker, C. G., Fonseca, C. R. C., Fonseca, C., Haddad, C. F. B., & Prado, P. I. (2010). Habitat split as a cause of local population declines of amphibians with aquatic larvae. Conservation Biology, 24(1), 287–294. https://doi.org/10.1111/j.1523-1739.2009.01324.x

Bhagwat, S. A., Willis, K. J., Birks, H. J. B., & Whittaker, R. J. (2008). Agroforestry: A refuge for tropical biodiversity? Trends in Ecology & Evolution, 23(5), 261–267. https://doi.org/10.1016/j.tree.2008.01.005

Bickford, D., Ng, T. H., Qie, L., Kudavidanage, E. P., & Bradshaw, C. J. A. (2010). Forest Fragment and Breeding Habitat Characteristics Explain Frog Diversity and Abundance in Singapore. Biotropica, 42(1), 119–125. https://doi.org/10.1111/j.1744-7429.2009.00542.x

Biju, S. D., Garg, S., Mahony, S., Wijayathilaka, N., Senevirathne, G., & Meegaskumbura, M. (2014). DNA barcoding, phylogeny and systematics of Golden-backed frogs (Hylarana, Ranidae) of the Western Ghats-Sri Lanka biodiversity hotspot, with the description of seven new species. https://doi.org/10.1163/18759866-08304004

Biju, S.D., Garg, S., Gururaja, K., Shouche, Y., & Walujkar, S. A. (2014). DNA barcoding reveals unprecedented diversity in Dancing Frogs of India (Micrixalidae, Micrixalus): A taxonomic revision with description of 14 new species. Ceylon Journal of Science (Biological Sciences), 43(1), 37. https://doi.org/10.4038/cjsbs.v43i1.6850

Bisht, K., Garg, S., Sarmah, A. N. D. A., Sengupta, S., & Biju, S. D. (2021). Lost, forgotten, and overlooked: Systematic reassessment of two lesser-known toad species (Anura, Bufonidae) from Peninsular India and another wide-ranging northern species. Zoosystematics and Evolution, 97(2), 451–470. https://doi.org/10.3897/zse.97.61770

Bolochio, B. E., Lescano, J. N., Cordier, J. M., Loyola, R., & Nori, J. (2020). A functional perspective for global amphibian conservation. Biological Conservation, 245, 108572. https://doi.org/10.1016/j.biocon.2020.108572

Botts, E. A., Erasmus, B. F. N., & Alexander, G. J. (2013). Small range size and narrow niche breadth predict range contractions in South African frogs: Niche breadth and range contractions in South African frogs. Global Ecology and Biogeography, 22(5), 567–576. https://doi.org/10.1111/geb.12027

Brüning, L. Z., Krieger, M., Meneses-Pelayo, E., Eisenhauer, N., Ramirez Pinilla, M. P., Reu, B., & Ernst, R. (2018). Land-use heterogeneity by small-scale agriculture promotes amphibian diversity in montane agroforestry systems of northeast Colombia. Agriculture, Ecosystems & Environment, 264, 15–23. https://doi.org/10.1016/j.agee.2018.05.011

Bunn, C., Läderach, P., Ovalle Rivera, O., & Kirschke, D. (2015). A bitter cup: Climate change profile of global production of Arabica and Robusta coffee. Climatic Change, 129(1–2), 89–101. https://doi.org/10.1007/s10584-014-1306-x

Burrow, A., & Maerz, J. (2022). How plants affect amphibian populations. Biological Reviews, 97(5), 1749–1767. https://doi.org/10.1111/brv.12861

Cadotte, M. W., Carscadden, K., & Mirotchnick, N. (2011). Beyond species: Functional diversity and the maintenance of ecological processes and services: Functional diversity in ecology and conservation. Journal of Applied Ecology, 48(5), 1079–1087. https://doi.org/10.1111/j.1365-2664.2011.02048.x

Caudill, S. A., Vaast, P., & Husband, T. P. (2014). Assessment of small mammal diversity in coffee agroforestry in the Western Ghats, India. Agroforestry Systems, 88(1), 173–186. https://doi.org/10.1007/s10457-013-9664-3

Cavender-Bares, J., Kozak, K. H., Fine, P. V., & Kembel, S. W. (2009). The merging of community ecology and phylogenetic biology. Ecology Letters, 12(7), 693–715. https://doi.org/10.1111/j.1461-0248.2009.01314.x

Cervantes-López, M. de J., Andresen, E., Hernández-Ordóñez, O., Mora, F., Reynoso, V. H., & Arroyo-Rodríguez, V. (2022). Lightly-harvested rustic cocoa is a valuable land cover for amphibian and reptile conservation in human-modified rainforest landscapes. Journal of Tropical Ecology, 38(5), 312–321. https://doi.org/10.1017/S0266467422000219

Chang, C. H., Karanth, K. K., & Robbins, P. (2018). Birds and beans: Comparing avian richness and endemism in arabica and robusta agroforests in India’s Western Ghats. Scientific Reports, 8(1), 3143. https://doi.org/10.1038/s41598-018-21401-1

Chao, A., Chiu, C.-H., & Jost, L. (2014). Unifying species diversity, phylogenetic diversity, functional diversity, and related similarity and differentiation measures through Hill numbers.

Annual Review of Ecology, Evolution, and Systematics, 45(1), 297–324. https://doi.org/10.1146/annurev-ecolsys-120213-091540

Chao, A., Henderson, P. A., Chiu, C.-H., Moyes, F., Hu, K.-H., Dornelas, M., & Magurran, A. E. (2021). Measuring temporal change in alpha diversity: A framework integrating taxonomic, phylogenetic and functional diversity and the iNEXT. 3D standardization. Methods in Ecology and Evolution, 12(10), 1926–1940. https://doi.org/10.1111/2041-210X.13682

Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: Standardizing samples by completeness rather than size. Ecology, 93(12), 2533–2547. https://doi.org/10.1890/11-1952.1

Chapman, P. M., Tobias, J. A., Edwards, D. P., & Davies, R. G. (2018). Contrasting impacts of land-use change on phylogenetic and functional diversity of tropical forest birds. Journal of Applied Ecology, 55(4), 1604–1614. https://doi.org/10.1111/1365-2664.13073

Coffee Board of India. (2024). https://coffeeboard.gov.in/ (accessed 4 April 2026)

Coleman, D. W., Wood, R. J., & Healey, M. (2024). Frogs and flows: Using life-history traits and a systematic review to establish water-dependent functional groups for stream frogs in New South Wales, Australia. Ecohydrology, 17(3), e2643. https://doi.org/10.1002/eco.2643

Cooper, N., Bielby, J., Thomas, G. H., & Purvis, A. (2008). Macroecology and extinction risk correlates of frogs. Global Ecology and Biogeography, 17(2), 211–221. https://doi.org/10.1111/j.1466-8238.2007.00355.x

Cordier, J. M., Aguilar, R., Lescano, J. N., Leynaud, G. C., Bonino, A., Miloch, D., Loyola, R., & Nori, J. (2021). A global assessment of amphibian and reptile responses to land-use changes. Biological Conservation, 253, 108863. https://doi.org/10.1016/j.biocon.2020.108863

Cortés-Gómez, Á. M., Ramírez-Pinilla, M. P., & Urbina-Cardona, N. (2016). Protocol for the measurement of functional traits in amphibians. In functional ecology as an approach to the study, management and conservation of Biodiversity: Protocols and Applications (pp. 126–179).

Crane, E., & Walker, P. (1984). Pollination directory for world crops.

Cumming, G. (2009). Inference by eye: Reading the overlap of independent confidence intervals. Statistics in Medicine, 28(2), 205–220. https://doi.org/10.1002/sim.3471

Da Silva, F. R., Almeida-Neto, M., Do Prado, V. H. M., Haddad, C. F. B., & De Cerqueira Rossa-Feres, D. (2012). Humidity levels drive reproductive modes and phylogenetic diversity of amphibians in the Brazilian Atlantic Forest. Journal of Biogeography, 39(9), 1720–1732. https://doi.org/10.1111/j.1365-2699.2012.02726.x

Dahanukar, N., Modak, N., Krutha, K., Nameer, P. O., Padhye, A. D., & Molur, S. (2016). Leaping frogs (Anura: Ranixalidae) of the Western Ghats of India: An integrated taxonomic review. Journal of Threatened Taxa, 8(10), 9221–9288. https://doi.org/10.11609/jott.2532.8.10.9221-9288

Das, A., Krishnaswamy, J., Bawa, K. S., Kiran, M. C., Srinivas, V., Kumar, N. S., & Karanth, K. U. (2006). Prioritisation of conservation areas in the Western Ghats, India. Biological Conservation, 133(1), 16–31. https://doi.org/10.1016/j.biocon.2006.05.023

Davison, C. W., Rahbek, C., & Morueta-Holme, N. (2021). Land-use change and biodiversity: Challenges for assembling evidence on the greatest threat to nature. Global Change Biology, 27(21), 5414–5429. https://doi.org/10.1111/gcb.15846

De Beenhouwer, M., Aerts, R., & Honnay, O. (2013). A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. Agriculture, Ecosystems & Environment, 175, 1–7. https://doi.org/10.1016/j.agee.2013.05.003

Deepak, P., & Dinesh, K. (2024). Status of amphibian diversity in the Western Ghats. In biodiversity hotspot of the Western Ghats and Sri Lanka (pp. 219–239). Apple Academic Press.

Dehling, D. M., & Dehling, J. M. (2021). Elevated alpha diversity in disturbed sites obscures regional decline and homogenization of amphibian diversity (p. 2021.09.21.461266). bioRxiv. https://doi.org/10.1101/2021.09.21.461266

Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: The need for integrative conservation strategies in a changing world. Ecology Letters, 13(8), 1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x

Dhara, C., Deshpande, A., Roxy, M. K., Dalpadado, P., & Shrestha, M. S. (2025). A post-AR6 update on observed and projected climate change in India. PLOS Climate, 4(11), e0000724. https://doi.org/10.1371/journal.pclm.0000724

Díaz, S., Purvis, A., Cornelissen, J. H. C., Mace, G. M., Donoghue, M. J., Ewers, R. M., Jordano, P., & Pearse, W. D. (2013). Functional traits, the phylogeny of function, and ecosystem service vulnerability. Ecology and Evolution, 3(9), 2958–2975. https://doi.org/10.1002/ece3.601

Fain, S. J., Quiñones, M., Álvarez-Berríos, N. L., Parés-Ramos, I. K., & Gould, W. A. (2018). Climate change and coffee: Assessing vulnerability by modeling future climate suitability in the Caribbean island of Puerto Rico. Climatic Change, 146(1), 175–186. https://doi.org/10.1007/s10584-017-1949-5

Faith, D. P. (2008). Threatened species and the potential loss of phylogenetic diversity: Conservation scenarios based on estimated extinction probabilities and phylogenetic risk analysis. Conservation Biology, 22(6), 1461–1470. https://doi.org/10.1111/j.1523-1739.2008.01068.x

Fick, S. E., & Hijmans, R. J. (2017). WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. International Journal of Climatology, 37(12), 4302–4315. https://doi.org/10.1002/joc.5086

Flynn, D. F., Mirotchnick, N., Jain, M., Palmer, M. I., & Naeem, S. (2011). Functional and phylogenetic diversity as predictors of biodiversity–ecosystem-function relationships. Ecology, 92(8), 1573–1581. https://doi.org/10.1890/10-1245.1

Food and Agriculture Organization of the United Nations. (2025). FAO. https://www.fao.org/home/en (accessed 4 April 2026)

Frishkoff, L. O., Hadly, E. A., & Daily, G. C. (2015). Thermal niche predicts tolerance to habitat conversion in tropical amphibians and reptiles. Global Change Biology, 21(11), 3901–3916. https://doi.org/10.1111/gcb.13016

Frost, D. R. (2026). Amphibian Species of the World: An Online Reference. https://amphibiansoftheworld.amnh.org/ (accessed 4 April 2026)

Garcia, C. A., Bhagwat, S. A., Ghazoul, J., Nath, C. D., Nanaya, K. M., Kushalappa, C. G., Raghuramulu, Y., Nasi, R., & Vaast, P. (2010). Biodiversity conservation in agricultural landscapes: Challenges and opportunities of coffee agroforests in the Western Ghats, India. Conservation Biology, 24(2), 479–488. https://doi.org/10.1111/j.1523-1739.2009.01386.x

Gardner, T. A., Barlow, J., Chazdon, R. L., Ewers, R. M., Harvey, C. A., Peres, C. A., & Sodhi, N. S. (2009). Prospects for tropical forest biodiversity in a human-modified world. Ecology Letters, 12(6), 561–582. https://doi.org/10.1111/j.1461-0248.2009.01294.x

Gardner, T. A., Barlow, J., Sodhi, N. S., & Peres, C. A. (2010). A multi-region assessment of tropical forest biodiversity in a human-modified world. Biological Conservation, Conserving Complexity: Global Change and Community-Scale Interactions, 143(10), 2293–2300. https://doi.org/10.1016/j.biocon.2010.05.017

Gardner, T. A., Ribeiro-Junior, M. A., Barlow, J., Ávila-Pires, T. C. S., Hoogmoed, M. S., & Peres, C. A. (2007). The value of primary, secondary, and plantation forests for a Neotropical Herpetofauna. Conserv. Biol., 21. https://doi.org/10.1111/j.1523-1739.2007.00659.x

Garg, S., Suyesh, R., Das, S., Bee, M., & S D, B. (2021). An integrative approach to infer systematic relationships and define species groups in the shrub frog genus Raorchestes, with description of five new species from the Western Ghats, India. PeerJ, 9, e10791. https://doi.org/10.7717/peerj.10791

GBIF. (2026). Home Page. Available from: https://www.gbif.org. (accessed 20 June 2026)

Gelman, A., & Rubin, D. B. (1992). Inference from iterative simulation using multiple sequences. Statistical Science, 7(4), 457–472. https://doi.org/10.1214/ss/1177011136

Gibbs, H. K., Ruesch, A. S., Achard, F., Clayton, M. K., Holmgren, P., Ramankutty, N., & Foley, J. A. (2010). Tropical forests were the primary sources of new agricultural land in the 1980s and 1990s. Proceedings of the National Academy of Sciences, 107(38), 16732–16737. https://doi.org/10.1073/pnas.0910275107

Gibson, L., Lee, T. M., Koh, L. P., Brook, B. W., Gardner, T. A., Barlow, J., Peres, C. A., Bradshaw, C. J. A., Laurance, W. F., Thomas E. Lovejoy, Lovejoy, T. E., & Sodhi, N. S. (2011). Primary forests are irreplaceable for sustaining tropical biodiversity. Nature, 478(7369), 378–381. https://doi.org/10.1038/nature10425

Gomes, L. C., Bianchi, F. J., Cardoso, I. M., Fernandes, R. B. A., Fernandes Filho, E. I., & Schulte, R. P. (2020). Agroforestry systems can mitigate the impacts of climate change on coffee production: A spatially explicit assessment in Brazil. Agriculture, Ecosystems & Environment, 294, 106858. https://doi.org/10.1016/j.agee.2020.106858

González-del-Pliego, P., Scheffers, B. R., Freckleton, R. P., Basham, E. W., Araújo, M. B., Acosta-Galvis, A. R., Medina Uribe, C. A., Haugaasen, T., & Edwards, D. P. (2020). Thermal tolerance and the importance of microhabitats for Andean frogs in the context of land use and climate change. Journal of Animal Ecology, 89(11), 2451–2460. https://doi.org/10.1111/1365-2656.13309

González-Orozco, C. E., Porcel, M., Byrareddy, V. M., Rahn, E., Cardona, W. A., Velandia, D. A. S., Araujo-Carrillo, G. A., & Kath, J. (2024). Preparing Colombian coffee production for climate change: Integrated spatial modelling to identify potential robusta coffee (Coffea canephora P.) growing areas. Climatic Change, 177(4), 67. https://doi.org/10.1007/s10584-024-03717-2

Graham, S. I., Kinnaird, M. F., O'Brien, T. G., Vågen, T.-G., Winowiecki, L. A., Young, T. P., & Young, H. S. (2019). Effects of land-use change on community diversity and composition are highly variable among functional groups. Ecological Applications, 29(7), e01973. https://doi.org/10.1002/eap.1973

Greenberg, D., Palen, W., Chan, K., Jetz, W., & Mooers, A. (2018). Evolutionarily distinct amphibians are disproportionately lost from human-modified ecosystems. Ecology Letters. https://doi.org/10.1111/ele.13133

Gross, N., Bagousse-Pinguet, Y. L., Liancourt, P., Berdugo, M., Gotelli, N. J., & Maestre, F. T. (2017). Functional trait diversity maximizes ecosystem multifunctionality. Nature Ecology & Evolution, 1(5), 0132. https://doi.org/10.1038/s41559-017-0132

Gururaja, K. V., Dinesh, K. P., Priti, H., & Ravikanth, G. (2014). Mud-packing frog: A novel breeding behaviour and parental care in a stream dwelling new species of Nyctibatrachus (Amphibia, Anura, Nyctibatrachidae). Zootaxa, 3796(1), 33–61. https://doi.org/10.11646/zootaxa.3796.1.2

Hardner, J., & Rice, R. (2002). Rethinking green consumerism. Scientific American, 286(5), 88–95. https://doi.org/10.1038/scientificamerican0502-88

Harvey, C. A., Pritts, A. A., Zwetsloot, M. J., Jansen, K., Pulleman, M. M., Armbrecht, I., Avelino, J., Barrera, J. F., Bunn, C., García, J. H., Isaza, C., Munoz-Ucros, J., Pérez-Alemán, C. J., Rahn, E., Robiglio, V., Somarriba, E., & Valencia, V. (2021). Transformation of coffee-growing

landscapes across Latin America. A review. Agronomy for Sustainable Development, 41(5), 62. https://doi.org/10.1007/s13593-021-00712-0

Hernández-Ordóñez, O., Santos, B. A., Pyron, R. A., Arroyo-Rodríguez, V., Urbina-Cardona, J. N., Martínez-Ramos, M., Parra-Olea, G., & Reynoso, V. H. (2019). Species sorting and mass effect along forest succession: Evidence from taxonomic, functional, and phylogenetic diversity of amphibian communities. Ecology and Evolution, 9(9), 5206–5218. https://doi.org/10.1002/ece3.5110

Hof, C., Araújo, M. B., Jetz, W., & Rahbek, C. (2011). Additive threats from pathogens, climate and land-use change for global amphibian diversity. Nature, 480(7378), Article 7378. https://doi.org/10.1038/nature10650

Hoffmann, E. P., Williams, K., Hipsey, M. R., & Mitchell, N. J. (2021). Drying microclimates threaten persistence of natural and translocated populations of threatened frogs. Biodiversity and Conservation, 30(1), 15–34. https://doi.org/10.1007/s10531-020-02064-9

Hylander, K., Nemomissa, S., Fischer, J., Zewdie, B., Ayalew, B., & Tack, A. J. M. (2024). Lessons from Ethiopian coffee landscapes for global conservation in a post-wild world. Communications Biology, 7(1), 714. https://doi.org/10.1038/s42003-024-06381-5

Ibarra-Isassi, J., Handa, I. T., Arenas-Clavijo, A., Escobar-Ramírez, S., Armbrecht, I., & Lessard, J.-P. (2021). Shade-growing practices lessen the impact of coffee plantations on multiple dimensions of ant diversity. Journal of Applied Ecology, 58(5), 919–930. https://doi.org/10.1111/1365-2664.13842

IPBES. (2019). Global assessment report on biodiversity and ecosystem services of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services. Zenodo. https://doi.org/10.5281/zenodo.6417333

Iverson, A. L., Gonthier, D. J., Pak, D., Ennis, K. K., Burnham, R. J., Perfecto, I., Ramos Rodriguez, M., & Vandermeer, J. H. (2019). A multifunctional approach for achieving simultaneous biodiversity conservation and farmer livelihood in coffee agroecosystems. Biological Conservation, 238, 108179. https://doi.org/10.1016/j.biocon.2019.07.024

Jansen, M., Schulze, A., Werding, L., & Streit, B. (2009). Effects of extreme drought in the dry season on an anuran community in the Bolivian Chiquitano region. Salamandra, 45, 233–238.

Jha, S., Bacon, C. M., Philpott, S. M., Ernesto Méndez, V., Läderach, P., & Rice, R. A. (2014). Shade Coffee: update on a disappearing refuge for biodiversity. BioScience, 64(5), 416–428. https://doi.org/10.1093/biosci/biu038

Jithin, V., Rane, M., Watve, A., & Naniwadekar, R. (2025). Orchards and paddy differentially impact rock outcrop amphibians: Insights from community-and species-level responses. Ecological Applications, 35(1), e3058. https://doi.org/10.1002/eap.3058

Juárez-Ramírez, M. C., Lira-Noriega, A., Manson, R. H., Nori, J., & Pineda, E. (2024). Assessing the potential role of different land covers for conserving threatened amphibian diversity in a human-modified tropical mountain landscape. Biological Conservation, 299, 110790. https://doi.org/10.1016/j.biocon.2024.110790

Kehoe, L., Kuemmerle, T., Meyer, C., Levers, C., Václavík, T., & Kreft, H. (2015). Global patterns of agricultural land-use intensity and vertebrate diversity. Diversity and Distributions, 21(11), 1308–1318. https://doi.org/10.1111/ddi.12359

Laderach, P., Lundy, M., Jarvis, A., Ramirez, J., Portilla, E. P., Schepp, K., & Eitzinger, A. (2011). Predicted impact of climate change on coffee supply chains. In W. Leal Filho (Ed.), The economic, social and political elements of climate change (pp. 703–723). Springer Berlin Heidelberg. https://doi.org/10.1007/978-3-642-14776-0_42

Laliberté, E., & Legendre, P. (2010). A distance-based framework for measuring functional diversity from multiple traits. Ecology, 91(1), 299–305. https://doi.org/10.1890/08-2244.1

Le Galliard, J.-F., Rozen-Rechels, D., Lecomte, A., Demay, C., Dupoué, A., & Meylan, S. (2021). Short-term changes in air humidity and water availability weakly constrain thermoregulation in a dry-skinned ectotherm. PLOS ONE, 16(2), e0247514. https://doi.org/10.1371/journal.pone.0247514

Li, D. (2023). rtrees: An R package to assemble phylogenetic trees from megatrees. Ecography, 2023(7), e06643. https://doi.org/10.1111/ecog.06643

Lin, B. B. (2007). Agroforestry management as an adaptive strategy against potential microclimate extremes in coffee agriculture. Agricultural and Forest Meteorology, 144(1–2), 85–94. https://doi.org/10.1016/j.agrformet.2006.12.009

Lourenço-de-Moraes, R., Campos, F. S., Ferreira, R. B., Beard, K. H., Solé, M., Llorente, G. A., & Bastos, R. P. (2020). Functional traits explain amphibian distribution in the Brazilian Atlantic Forest. Journal of Biogeography, 47(1), 275–287. https://doi.org/10.1111/jbi.13727

Loyola, R., Becker, C. G., Kubota, U., Haddad, C. F. B., Fonseca, C., Fonseca, C. R. C., & Lewinsohn, T. M. (2008). Hung Out to Dry: Choice of priority ecoregions for conserving threatened Neotropical anurans depends on life-history traits. PloS One, 3(5), 8. https://doi.org/10.1371/journal.pone.0002120

Luedtke, J. A., Chanson, J., Neam, K., Hobin, L., Maciel, A. O., Catenazzi, A., Borzée, A., Hamidy, A., Aowphol, A., Jean, A., Sosa-Bartuano, Á., Fong G., A., De Silva, A., Fouquet, A., Angulo, A., Kidov, A. A., Muñoz Saravia, A., Diesmos, A. C., Tominaga, A., … Stuart, S. N. (2023). Ongoing declines for the world's amphibians in the face of emerging threats. Nature, 622(7982), 308–314. https://doi.org/10.1038/s41586-023-06578-4

Luría-Manzano, R., Serrano, F. C., Böhm, M., Sawaya, R. J., Haddad, C. F. B., & Martins, M. (2024). Tadpoles in lotic waters, habitat specialization, and human population density lead tree frogs (Hylinae) to higher extinction risk. Biological Conservation, 290, 110439. https://doi.org/10.1016/j.biocon.2023.110439

Magrach, A., & Ghazoul, J. (2015). Climate and pest-driven geographic shifts in global coffee production: Implications for Forest Cover, Biodiversity and Carbon Storage. PloS One, 10(7), e0133071. https://doi.org/10.1371/journal.pone.0133071

Manson, S., Nekaris, K. A. I., Nijman, V., & Campera, M. (2024). Effect of shade on biodiversity within coffee farms: A meta-analysis. Science of The Total Environment, 914, 169882. https://doi.org/10.1016/j.scitotenv.2024.169882

Mantyka-pringle, C. S., Martin, T. G., & Rhodes, J. R. (2012). Interactions between climate and habitat loss effects on biodiversity: A systematic review and meta-analysis. Global Change Biology, 18(4), 1239–1252. https://doi.org/10.1111/j.1365-2486.2011.02593.x

Marathe, A., Vijayakumar, S. P., Torsekar, V., Dinesh, K. P., Pal, S., Srikanthan, A., & Shanker, K. (2025). Range and elevation predict responses to climate change in frogs and lizards in the Western Ghats biodiversity hotspot of peninsular India. bioRxiv. https://doi.org/10.1101/2025.04.10.648234

Mendenhall, C. D., Frishkoff, L. O., Santos-Barrera, G., Pacheco, J., Mesfun, E., Quijano, F. M., Ehrlich, P. R., Ceballos, G., Daily, G. C., & Pringle, R. M. (2014). Countryside biogeography of Neotropical reptiles and amphibians. Ecology, 95(4), 856–870. https://doi.org/10.1890/12-2017.1

Moat, J., Williams, J., Baena, S., Wilkinson, T., Gole, T. W., Challa, Z. K., Demissew, S., & Davis, A. P. (2017). Resilience potential of the Ethiopian coffee sector under climate change. Nature Plants, 3(7), 17081. https://doi.org/10.1038/nplants.2017.81

Moguel, P., & Toledo, V. M. (1999). Biodiversity conservation in traditional coffee systems of Mexico. Conservation Biology, 13(1), 11–21. https://doi.org/10.1046/j.1523-1739.1999.97153.x

Monge, O., Dullinger, S., Fusani, L., & Schulze, C. H. (2022). Taxonomic, functional and phylogenetic bird diversity response to coffee farming intensity along an elevational gradient in Costa Rica. Agriculture, Ecosystems & Environment, 326, 107801. https://doi.org/10.1016/j.agee.2021.107801

Monroe, K. D., Collazo, J. A., Pacifici, K., Reich, B. J., Puente-Rolón, A. R., & Terando, A. J. (2017). Occupancy and abundance of Eleutherodactylus frogs in coffee plantations in Puerto Rico. Herpetologica, 73(4), 297–306. https://doi.org/10.1655/Herpetologica-D-16-00089

Mouillot, D., Graham, N. A. J., Villéger, S., Mason, N. W. H., & Bellwood, D. R. (2013). A functional approach reveals community responses to disturbances. Trends in Ecology & Evolution, 28(3), 167–177. https://doi.org/10.1016/j.tree.2012.10.004

Murray, A. H., Nowakowski, A. J., & Frishkoff, L. O. (2021). Climate and land-use change severity alter trait-based responses to habitat conversion. Global Ecology and Biogeography, 30(3), 598–610. https://doi.org/10.1111/geb.13237

Murrieta-Galindo, R., González-Romero, A., López-Barrera, F., & Parra-Olea, G. (2013). Coffee agrosystems: An important refuge for amphibians in central Veracruz, Mexico. Agroforestry Systems, 87, 767–779. https://doi.org/10.1007/s10457-013-9595-z

Murrieta-Galindo, R., López-Barrera, F., González-Romero, A., & Parra-Olea, G. (2013). Matrix and habitat quality in a montane cloud-forest landscape: Amphibians in coffee plantations in central Veracruz, Mexico. Wildlife Research, 40(1), 25–35. https://doi.org/10.1071/WR12076

Murugan, M., Alagupalamuthirsolai, M., Ashokkumar, K., Anandhi, A., Ravi, R., Rajangam, J., Dhanya, M. K., & Krishnamurthy, K. S. (2022). Climate change scenarios, their impacts and implications on Indian cardamom-coffee hot spots; one of the two in the world. Frontiers in Sustainable Food Systems, Volume 6-2022. https://www.frontiersin.org/journals/sustainable-food-systems/articles/10.3389/fsufs.2022.1057617

Myers, N., Mittermeier, R. A., Mittermeier, C. G., da Fonseca, G. A. B., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. Nature, 403(6772), Article 6772. https://doi.org/10.1038/35002501

Nakagawa, S., & Cuthill, I. C. (2007). Effect size, confidence interval and statistical significance: A practical guide for biologists. Biological Reviews, 82(4), 591–605. https://doi.org/10.1111/j.1469-185X.2007.00027.x

Nandakumar, R., Kumar, V. S., Karthick, V., & Osuri, A. M. (2024). Woody debris removal modifies carbon stocks and soil properties in a fragmented tropical rainforest. Biotropica, 56(2), e13304. https://doi.org/10.1111/btp.13304

Newbold, T., Hudson, L. N., Contu, S., Hill, S. L., Beck, J., Liu, Y., Meyer, C., Phillips, H. R., Scharlemann, J. P., & Purvis, A. (2018). Widespread winners and narrow-ranged losers: Land use homogenizes biodiversity in local assemblages worldwide. PLoS Biology, 16(12), e2006841. https://doi.org/10.1371/journal.pbio.2006841

Newbold, T., Hudson, L. N., Hill, S. L. L., Contu, S., Lysenko, I., Senior, R. A., Börger, L., Bennett, D. J., Choimes, A., Collen, B., Day, J., De Palma, A., Díaz, S., Echeverria-Londoño, S., Edgar, M. J., Feldman, A., Garon, M., Harrison, M. L. K., Alhusseini, T., … Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. Nature, 520(7545), 45–50. https://doi.org/10.1038/nature14324

Nori, J., Lemes, P., Urbina-Cardona, N., Baldo, D., Lescano, J., & Loyola, R. (2015). Amphibian conservation, land-use changes and protected areas: A global overview. Biological Conservation, 191, 367–374. https://doi.org/10.1016/j.biocon.2015.07.028

Nowakowski, A. J., Frishkoff, L. O., Thompson, M. E., Smith, T. M., & Todd, B. D. (2018). Phylogenetic homogenization of amphibian assemblages in human-altered habitats across the globe. Proceedings of the National Academy of Sciences, 115(15). https://doi.org/10.1073/pnas.1714891115

Nowakowski, A. J., Thompson, M. E., Donnelly, M. A., & Todd, B. D. (2017). Amphibian sensitivity to habitat modification is associated with population trends and species traits. Global Ecology and Biogeography, 26(6), 700–712. https://doi.org/10.1111/geb.12571

Nowakowski, A. J., Watling, J. I., Whitfield, S. M., Todd, B. D., Kurz, D. J., & Donnelly, M. A. (2017). Tropical amphibians in shifting thermal landscapes under land-use and climate change. Conservation Biology, 31(1), 96–105. https://doi.org/10.1111/cobi.12769

Oakley, J. L., & Bicknell, J. E. (2022). The impacts of tropical agriculture on biodiversity: A meta-analysis. Journal of Applied Ecology, 59(12), 3072–3082. https://doi.org/10.1111/1365-2664.14303

Ochoa-Ochoa, L. M., Mejía-Domínguez, N. R., Velasco, J. A., Marske, K. A., & Rahbek, C. (2019). Amphibian functional diversity is related to high annual precipitation and low precipitation seasonality in the New World. Global Ecology and Biogeography, 28(9), 1219–1229. https://doi.org/10.1111/geb.12926

Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Borman, T., Carvalho, G., Chirico, M., De Caceres, M., … Weedon, J. (2001). vegan: community ecology package (p. 2.7-3) [Dataset]. https://doi.org/10.32614/CRAN.package.vegan

Osuri, A. M., Kumar, V. S., Dutta, V., Vidwath, S. M., Cariappa, K. M., Purnesh, C. D., & Shetty, S. (2025). Shade coffee agroforests as native plant sources for restoration. Journal of Applied Ecology, 62(6), 1330–1336. https://doi.org/10.1111/1365-2664.70046

Ovalle-Rivera, O., Läderach, P., Bunn, C., Obersteiner, M., & Schroth, G. (2015). Projected shifts in Coffea arabica suitability among major global producing regions due to climate change. PloS One, 10(4), e0124155. https://doi.org/10.1371/journal.pone.0124155

Ovaskainen, O., Tikhonov, G., Norberg, A., Guillaume Blanchet, F., Duan, L., Dunson, D., Roslin, T., & Abrego, N. (2017). How to make more out of community data? A conceptual framework and its implementation as models and software. Ecology Letters, 20(5), 561–576. https://doi.org/10.1111/ele.12757

Pascal, J.-P. (1986). Explanatory booklet on the forest map of South India. Sheets: Belgaum-Dharwar-Panaji, Shimoga, Mercara-Mysore. Institut français de Pondichéry.

Perfecto, I., Jiménez-Soto, M. E., & Vandermeer, J. (2019). Coffee landscapes shaping the Anthropocene: Forced simplification on a complex agroecological landscape. Current Anthropology, 60(S20), S236–S250. https://doi.org/10.1086/703413

Perfecto, I., Rice, R. A., Greenberg, R., & Van der Voort, M. E. (1996). Shade coffee: A disappearing refuge for biodiversity: Shade coffee plantations can contain as much biodiversity as forest habitats. BioScience, 46(8), 598–608. https://doi.org/10.2307/1312989

Perfecto, I., & Vandermeer, J. (2008). Biodiversity conservation in tropical agroecosystems: A new conservation paradigm. Annals of the New York Academy of Sciences, 1134(1), 173–200. https://doi.org/10.1196/annals.1439.011

Philpott, S. M., Arendt, W. J., Armbrecht, I., Bichier, P., Diestch, T. V., Gordon, C., Greenberg, R., Perfecto, I., Reynoso-Santos, R., Soto-Pinto, L., & others. (2008). Biodiversity loss in Latin American coffee landscapes: Review of the evidence on ants, birds, and trees. Conservation Biology, 22(5), 1093–1105. https://doi.org/10.1111/j.1523-1739.2008.01029.x

Pinzón, J., Aceros, L., Reu, B., Ramírez-Pinilla, M. P., & Ernst, R. (2025). Matrix-protection rather than protected area conservation can safeguard multilevel amphibian diversity in Colombian agroforestry systems. Agriculture, Ecosystems & Environment, 386, 109559. https://doi.org/10.1016/j.agee.2025.109559

Portik, D. M., Streicher, J. W., & Wiens, J. J. (2023). Frog phylogeny: A time-calibrated, species-level tree based on hundreds of loci and 5,242 species. Molecular Phylogenetics and Evolution, 188, 107907. https://doi.org/10.1016/j.ympev.2023.107907

Posit team. (2025). RStudio: Integrated Development Environment for R [Computer software]. Posit Software, PBC. http://www.posit.co/

Pyron, R. A. (2018). Global amphibian declines have winners and losers. Proceedings of the National Academy of Sciences, 115(15), 3739–3741. https://doi.org/10.1073/pnas.1803477115

R Core Team. (2025). R: A language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Rajiv, N., Sankararaman, V., & Ramachandran, V. (2025). Surviving the Patchwork: Habitat Preferences of a Threatened Amphibian in a Fragmented Tropical Landscape. Ecology and Evolution, 15(12), e72785. https://doi.org/10.1002/ece3.72785

Rakotozafy, L. M. S., Tobler, U., Randriamanantena, R., Rasataharifaly, K. S., Andrianarimisa, A., & Martin, D. A. (2025). Lurking in the leaves: How large native trees and leaf litter promote amphibian diversity in Malagasy agroforests. Journal of Applied Ecology. https://doi.org/10.1111/1365-2664.70191

Raman, T. R. S., Rawat, G. S., & Johnsingh, A. J. T. (1998). Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. Journal of Applied Ecology, 35(2), 214–231. https://doi.org/10.1046/j.1365-2664.1998.00297.x

Rathod, S., & Rathod, P. (2013). CEPF Western Ghats special series: Amphibian communities in three different coffee plantation regimes in the Western Ghats, India. Journal of Threatened Taxa, 4404–4413. https://doi.org/10.11609/JoTT.o3054.4404-13

Re:wild, Synchronicity Earth, & IUCN SSC Amphibian Specialist Group. (2023). State of the World's Amphibians: The Second Global Amphibian Assessment. Re:wild. https://www.iucn-amphibians.org/wp-content/uploads/sites/4/2023/10/SOTWA-final-10.4.23.pdf

Renard, Q., Ramesh, B., G, M., & Pélissier, R. (2010). Data paper: High-resolution vegetation cover data for the Southern Western Ghats of India. Head of Ecology Department; Institut Français de Pondichéry. https://hal.science/hal-00481614

Riemann, J. C., Ndriantsoa, S. H., Rödel, M.-O., & Glos, J. (2017). Functional diversity in a fragmented landscape—Habitat alterations affect functional trait composition of frog assemblages in Madagascar. Global Ecology and Conservation, 10, 173–183. https://doi.org/10.1016/j.gecco.2017.03.005

Rödel, M.-O., & Ernst, R. (2004). Measuring and monitoring amphibian diversity in tropical forests. I. An evaluation of methods with recommendations for standardization. Ecotropica, 10(1), 1–14.

Roelants, K., Jiang, J., & Bossuyt, F. (2004). Endemic ranid (Amphibia: Anura) genera in southern mountain ranges of the Indian subcontinent represent ancient frog lineages: evidence

from molecular data. Molecular Phylogenetics and Evolution, 31(2), 730–740. https://doi.org/10.1016/j.ympev.2003.09.011

Roswell, M., Dushoff, J., & Winfree, R. (2021). A conceptual guide to measuring species diversity. Oikos, 130(3), 321–338. https://doi.org/10.1111/oik.07202

Sankararaman, V., Dalvi, S., Miller, D. A., & Karanth, K. K. (2021). Local and landscape characteristics shape amphibian communities across production landscapes in the Western Ghats. Ecological Solutions and Evidence, 2(4), e12110. https://doi.org/10.1002/2688-8319.12110

Sankararaman, V., & Miller, D. (2024). Life-history traits govern the habitat use of diverse amphibian assemblages in an agroforest landscape matrix. Animal Conservation, 27(1), 86–97. https://doi.org/10.1111/acv.12882

Scheffers, B. R., Brunner, R. M., Ramirez, S. D., Shoo, L. P., Diesmos, A., & Williams, S. E. (2013). Thermal buffering of microhabitats is a critical factor mediating warming vulnerability of frogs in the Philippine biodiversity hotspot. Biotropica, 45(5), 628–635. https://doi.org/10.1111/btp.12042

Scheffers, B. R., Edwards, D. P., Diesmos, A., Williams, S. E., & Evans, T. A. (2014). Microhabitats reduce animal's exposure to climate extremes. Global Change Biology, 20(2), 495–503. https://doi.org/10.1111/gcb.12439

Schroth, G., Läderach, P., Blackburn Cuero, D. S., Neilson, J., & Bunn, C. (2015). Winner or loser of climate change? A modeling study of current and future climatic suitability of Arabica coffee in Indonesia. Regional Environmental Change, 15(7), 1473–1482. https://doi.org/10.1007/s10113-014-0713-x

Sfair, J. C., Lososová, Z., Chytrý, M., & de Bello, F. (2022). Functional rarity and evolutionary uniqueness of threatened species across different scales and habitats in a Central European flora. Journal of Applied Ecology, 59(10), 2542–2552. https://doi.org/10.1111/1365-2664.14255

Sheridan, J. A., Mendenhall, C. D., & Yambun, P. (2022). Frog body size responses to precipitation shift from resource-driven to desiccation-resistant as temperatures warm. Ecology and Evolution, 12(12), e9589. https://doi.org/10.1002/ece3.9589

Sodhi, N. S., Bickford, D., Diesmos, A. C., Lee, T. M., Koh, L. P., Brook, B. W., Sekercioglu, C. H., & Bradshaw, C. J. A. (2008). Measuring the meltdown: Drivers of global amphibian extinction and decline. Plos One, 3(2), e1636. https://doi.org/10.1371/journal.pone.0001636

Steffan-Dewenter, I., Kessler, M., Barkmann, J., Bos, M. M., Buchori, D., Erasmi, S., Faust, H., Gerold, G., Glenk, K., Gradstein, S. R., Guhardja, E., Harteveld, M., Hertel, D., Höhn, P., Kappas, M., Köhler, S., Leuschner, C., Maertens, M., Marggraf, R., … Tscharntke, T. (2007). Tradeoffs between income, biodiversity, and ecosystem functioning during tropical rainforest conversion and agroforestry intensification. Proceedings of the National Academy of Sciences, 104(12), 4973–4978. https://doi.org/10.1073/pnas.0608409104

Steigerwald, E., Chen, J., Oshiro, J., Vredenburg, V. T., Catenazzi, A., & Koo, M. S. (2024). Microreserves are an important tool for amphibian conservation. Communications Biology, 7(1), 1177. https://doi.org/10.1038/s42003-024-06510-0

Sunday, J. M., Bates, A. E., Kearney, M. R., Colwell, R. K., Dulvy, N. K., Longino, J. T., & Huey, R. B. (2014). Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. Proceedings of the National Academy of Sciences, 111(15), 5610–5615. https://doi.org/10.1073/pnas.1316145111

Thompson, M. E., & Donnelly, M. A. (2018). Effects of secondary forest succession on amphibians and reptiles: A review and meta-analysis. Copeia, 106(1), 10–19. https://doi.org/10.1643/CH-17-654

Thompson, M. E., Nowakowski, A. J., & Donnelly, M. A. (2016). The importance of defining focal assemblages when evaluating amphibian and reptile responses to land use. Conservation Biology, 30(2), 249–258. https://doi.org/10.1111/cobi.12637

Tikhonov, G., Opedal, Ø. H., Abrego, N., Lehikoinen, A., De Jonge, M. M. J., Oksanen, J., & Ovaskainen, O. (2020). Joint species distribution modelling with the r-package Hmsc. Methods in Ecology and Evolution, 11(3), 442–447. https://doi.org/10.1111/2041-210X.13345

Tinoco, B. A., Santillán, V. E., & Graham, C. H. (2018). Land use change has stronger effects on functional diversity than taxonomic diversity in tropical Andean hummingbirds. Ecology and Evolution, 8(6), 3478–3490. https://doi.org/10.1002/ece3.3813

Torralvo, K., de Fraga, R., Lima, A. P., Dayrell, J., & Magnusson, W. E. (2022). Environmental filtering and deforestation shape frog assemblages in Amazonia: An empirical approach assessing species abundances and functional traits. Biotropica, 54(1), 226–238. https://doi.org/10.1111/btp.13053

Tracy, C. R., Christian, K. A., & Tracy, C. R. (2010). Not just small, wet, and cold: Effects of body size and skin resistance on thermoregulation and arboreality of frogs. Ecology, 91(5), 1477–1484. https://doi.org/10.1890/09-0839.1

Trimble, M. J., & Van Aarde, R. J. (2014). Amphibian and reptile communities and functional groups over a land-use gradient in a coastal tropical forest landscape of high richness and endemicity. Animal Conservation, 17(5), 441–453. https://doi.org/10.1111/acv.12111

Uchida, K., Hiraiwa, M. K., & Cadotte, M. W. (2019). Non-random loss of phylogenetically distinct rare species degrades phylogenetic diversity in semi-natural grasslands. Journal of Applied Ecology, 56(6), 1419–1428. https://doi.org/10.1111/1365-2664.13386

Vallan, D. (2000). Influence of forest fragmentation on amphibian diversity in the nature reserve of Ambohitantely, highland Madagascar. Biological Conservation, 96(1), 31–43. https://doi.org/10.1016/s0006-3207(00)00041-0

Vattakaven, T., George, R. M., Balasubramanian, D., Réjou-Méchain, M., Muthusankar, G., Ramesh, B. R., & Prabhakar, R. (2016). India Biodiversity Portal: An integrated, interactive and participatory biodiversity informatics platform. Biodiversity Data Journal, 4, e10279. https://doi.org/10.3897/BDJ.4.e10279

Waldock, C. A., De Palma, A., Borges, P. A., & Purvis, A. (2020). Insect occurrence in agricultural land-uses depends on realized niche and geographic range properties. Ecography, 43(11), 1717–1728. https://doi.org/10.1111/ecog.05162

Wanger, T. C., Saro, A., Iskandar, D. T., Brook, B. W., Sodhi, N. S., Clough, Y., & Tscharntke, T. (2009). Conservation value of cacao agroforestry for amphibians and reptiles in South-East Asia: Combining correlative models with follow-up field experiments. Journal of Applied Ecology, 46(4), 823–832. https://doi.org/10.1111/j.1365-2664.2009.01663.x

Wanger, T. C., Iskandar, D. T., Motzke, I., Brook, B. W., Sodhi, N. S., Clough, Y., & Tscharntke, T. (2010). Effects of Land-Use Change on Community Composition of Tropical Amphibians and

Reptiles in Sulawesi, Indonesia. Conservation Biology, 24(3), 795–802. https://doi.org/10.1111/j.1523-1739.2009.01434.x

Wies, G., Nicasio Arzeta, S., & Martinez Ramos, M. (2021). Critical ecological thresholds for conservation of tropical rainforest in Human Modified Landscapes. Biological Conservation, 255, 109023. https://doi.org/10.1016/j.biocon.2021.109023

Wu, N. C., Bovo, R. P., Enriquez-Urzelai, U., Clusella-Trullas, S., Kearney, M. R., Navas, C. A., & Kong, J. D. (2024). Global exposure risk of frogs to increasing environmental dryness. Nature Climate Change, 14(12), 1314–1322. https://doi.org/10.1038/s41558-024-02167-z

Supplementary Material for

# Land use and climate shape amphibian multidimensional diversity and conservation in a coffee agroforestry landscape, Western Ghats

*This file includes*

**TABLES**

**Table S1:** Amphibian sampling sites, spatial location, area, effort, and number of visual and acoustic detections.

**Table S2:** Functional traits measured across adult males in this study following the protocols of 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 (https://geocat.iucnredlist.org).

**Table S5**: Summary of overstorey structural attributes across the five land use and climate zone combinations, including basal area ($m^2\ ha^{-1}$), tree density (trees $ha^{-1}$), tree species richness (number of species per transect), and canopy cover (ordinal scale: 0-3). Values are presented as mean ± SD for each habitat type.

**Table S6:** Abundance-based ranks of amphibian species recorded across rainforest and coffee agroforest land use types in a coffee agroforestry landscape, Western Ghats. Values in each cell represent rank (number of individuals recorded).

**FIGURES**

**Figure S1:** The distribution of detection distance (kernel density curves) of amphibians across land use and climate zones

**Figure S2:** Rooted phylogenetic tree of all amphibian species recorded in the study landscape of the central Western Ghats, India, derived from Portik et al., (2023). The phylogeny includes 14 genera 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

**Figure S3:** Amphibian species and their individual abundance recorded across land uses and climate zones from the study area in central Western Ghats, India

**Figure S4:** Amphibian abundance per transect (mean ± 95% CI) across land uses and climate zones with the points representing the observed raw amphibian counts in each transect

**Figure S5:** 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 S6:** Predicted occurrence probabilities of 22 amphibian species across land use and climate zones, derived from posterior samples of the HMSC model.

**Figure S7:** A degraded stream section in a wet coffee agroforest site, showing exposed bedrock, overgrown vegetation, and reduced water flow during the monsoon.

**Figure S8:** Artificial lentic breeding habitats in coffee agroforests. Cemented storage tanks beneath the shade tree canopy retain rainwater and leaf litter during the monsoon (a), providing suitable aquatic habitat for tadpole development, particularly for foam-nesting tree frogs (b). Larger irrigation ponds act as breeding sites for species such as *Minervarya* spp. and *Clinotarsus curtipes* (c).

**Figure S9:** 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 visual and acoustic detections.

| Sampling site code | Latitude, Longitude | Category | Arabica area (ha) | Robusta area (ha) | Total area (ha) | No. of transects | No. of temporal replicates | Total effort (km) | Mean elevation (m) | Visual detections | Acoustic detections |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Site1 | 12.93686, 75.71824 | Wet-Coffee | ~90 | ~110 | ~200 | 6 | 2 | 1.8 | 950 | 750 | 36 |
| Site2 | 13.42797, 75.41824 | Wet-Coffee | ~65 | ~55 | ~120 | 6 | 2 | 1.8 | 1050 | 216 | 8 |
| Site3 | 13.19851, 75.48372 | Wet-Coffee | ~60 | ~60 | ~120 | 6 | 2 | 1.8 | 1080 | 116 | 22 |
| Site4 | 12.932191, 75.657758 | Wet-Rainforest | -nil- | -nil- | ~1600 | 7 | 2 | 2.1 | 1000 | 228 | 55 |
| Site5 | 12.96071, 75.82627 | Dry-Coffee | ~60 | ~90 | ~150 | 6 | 2 | 1.8 | 980 | 128 | 28 |
| Site6 | 12.99924, 75.78964 | Dry-Coffee | ~125 | ~125 | ~250 | 6 | 2 | 1.8 | 980 | 329 | 13 |
| Site7 | 13.05416, 75.7865 | Dry-Coffee | ~25 | ~30 | ~55 | 6 | 2 | 1.8 | 1030 | 246 | 10 |

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

| Functional traits | Data description | Functional meaning | References | Remarks |
|---|---|---|---|---|
| **Snout-to-vent length (SVL)** | Continuous | Habitat use, physiological tolerance | Ribeiro et al., 2017; Dehling & Dehling, 2021; Riemann et al., 2017 | Highly correlated with other morphological traits (r > 0.8) but retained as a representative trait |
| **Terminal disk diameter** *(third finger and 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; terrestrial (including direct development) | Breeding habitat use, reproductive strategy | Murray et al., 2021; 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 diameter | Toe disc diameter | 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 | lotic | 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 | lotic | 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 | smooth |
| *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 (https://geocat.iucnredlist.org).

| **Species** | **IUCN threat status** | **Threat category** | **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 |

**Table S5**: Summary of overstorey structural attributes across the five land use and climate zone combinations, including basal area ($m^2\ ha^{-1}$), tree density (trees $ha^{-1}$), tree species richness (number of species per transect), and canopy cover (ordinal scale: 0-3). Values are presented as mean ± SD for each habitat type.

| **Overstorey variables** | **Rainforest** (mean ± SD) | **Arabica-Wet** (mean ± SD) | **Robusta-Wet** (mean ± SD) | **Arabica-Dry** (mean ± SD) | **Robusta-Dry** (mean ± SD) |
|---|---|---|---|---|---|
| **Basal area** ($m^2\ ha^{-1}$) | 42.23 ± 7.48 | 39.25 ± 19.16 | 20.70 ± 8.11 | 35.09 ± 10.25 | 23.75 ± 6.02 |
| **Tree density** (trees $ha^{-1}$) | 832.86 ± 164.78 | 247.78 ± 84.34 | 248.52 ± 186.10 | 424.44 ± 136.85 | 261.11 ± 218.49 |
| **Tree species richness** (per transect) | 44.57 ± 4.35 | 16.00 ± 3.16 | 15.67 ± 4.06 | 18.56 ± 4.16 | 17.89 ± 5.64 |
| **Canopy cover** (ordinal scale: 0-3) (per transect) | 2.68 ± 0.28 | 1.22 ± 0.52 | 0.11 ± 0.13 | 0.72 ± 0.26 | 0.42 ± 0.22 |

**Table S6:** Abundance-based ranks of amphibian species recorded across rainforest and coffee agroforest land use types in a coffee agroforestry landscape, Western Ghats. Values in each cell represent rank (number of individuals recorded).

| Species | Rainforest | Arabica-Wet | Robusta-Wet | Arabica-Dry | Robusta-Dry |
|---|---|---|---|---|---|
| *Clinotarsus curtipes* | 1 (46) | 1 (88) | 2 (120) | 1 (86) | 1 (174) |
| *Duttaphrynus brevirostris* | 11 (10) | 12 (5) | 11 (10) | 12 (1) | 13 (1) |
| *Duttaphrynus melanostictus* | 7 (18) | 4 (58) | 7 (28) | 6 (19) | 9 (13) |
| *Duttaphrynus microtympanum* | 13 (5) | - | - | - | - |
| *Duttaphrynus parietalis* | 6 (21) | - | - | - | - |
| *Hylarana indica* | 8 (17) | 8 (30) | 6 (35) | 10 (3) | 11 (3) |
| *Hylarana intermedia* | - | 10 (8) | 14 (5) | 8 (9) | 8 (16) |
| *Indirana* cf. *gundia* | 10 (11) | 11 (7) | 15 (3) | - | - |
| *Micrixalus elegans* | 5 (25) | - | - | - | - |
| *Micrixalus kottigeharensis* | 14 (3) | - | - | - | - |
| *Microhyla sholigari* | - | 9 (14) | 11 (10) | 12 (1) | 12 (2) |
| *Minervarya mysorensis* | - | - | 16 (1) | - | - |
| *Minervarya nilagirica* | - | 6 (32) | 8 (25) | 4 (24) | 5 (23) |
| *Minervarya sp.1* | - | 16 (1) | 13 (6) | 9 (5) | 6 (20) |
| *Nyctibatrachus kempholeyensis* | 4 (29) | 14 (3) | 11 (10) | - | 13 (1) |
| *Nyctibatrachus sylvaticus* | 15 (1) | - | - | - | - |
| *Pedostibes tuberculosus* | 15 (1) | - | - | - | - |
| *Polypedates occidentalis* | 12 (8) | 13 (4) | 12 (9) | 11 (2) | 10 (4) |
| *Pseudophilautus wynaadensis* | - | 3 (65) | 5 (49) | 3 (48) | 2 (67) |
| *Raorchestes glandulosus* | 2 (39) | 14 (3) | 9 (22) | 7 (10) | 4 (24) |
| *Raorchestes hassanensis* | 3 (30) | 7 (31) | 4 (57) | - | - |
| *Raorchestes luteolus* | 15 (1) | 2 (86) | 1 (160) | 2 (59) | 3 (52) |
| *Raorchestes tuberohumerus* | 9 (15) | 5 (50) | 3 (88) | 5 (23) | 5 (23) |
| *Rhacophorus lateralis* | - | 16 (1) | - | - | - |
| *Rhacophorus malabaricus* | - | - | 13 (6) | 8 (9) | 11 (3) |
| *Uperodon mormoratus* | - | 15 (2) | 15 (3) | - | - |
| *Uperodon taprobanicus* | - | - | - | 11 (2) | 13 (1) |
| *Uperodon triangularis* | 14 (3) | 15 (2) | 10 (11) | 8 (9) | 7 (17) |

**FIGURES**

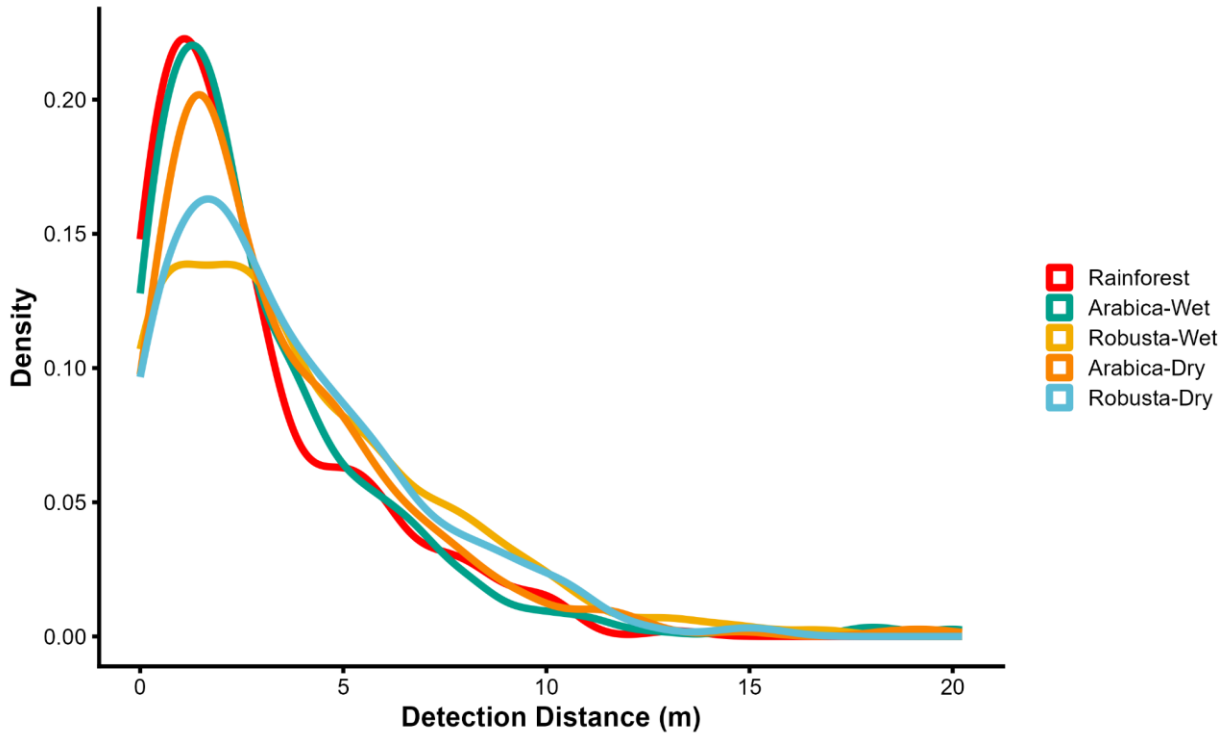


**Figure S1:** The distribution of detection distance (kernel density curves) of amphibians across land use and climate zones

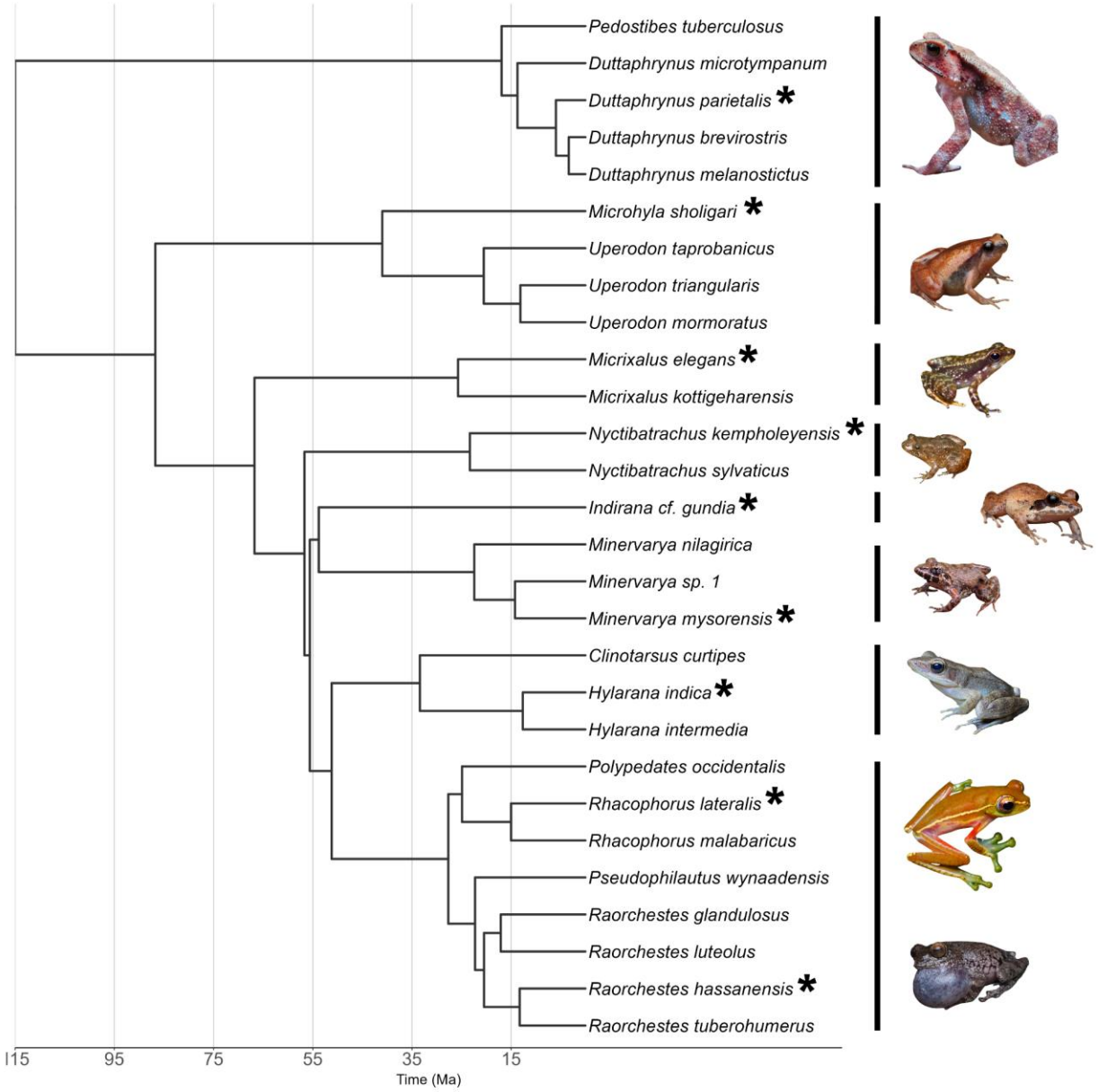


**Figure S2:** Rooted phylogenetic tree of all amphibian species recorded in the study landscape of the central Western Ghats, India, derived from Portik et al., (2023). The phylogeny includes 14 genera from eight families: Bufonidae, Microhylidae, Micrixalidae, Nyctibatrachidae, Ranixalidae, Dicroglossidae, Ranidae, and Rhacophoridae. The x-axis represents time in millions of years (Ma). Asterisks (*) indicate species for which images are provided

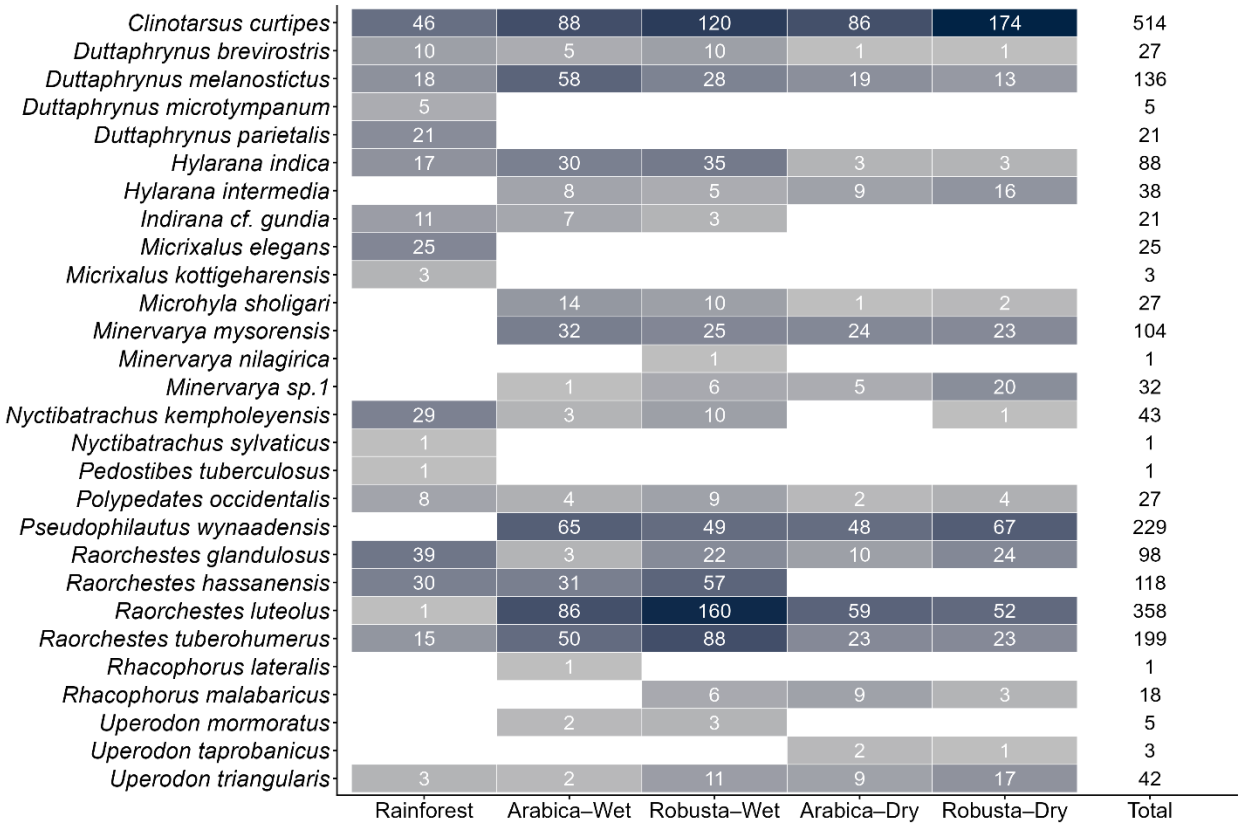


**Figure S3:** Amphibian species and their abundance recorded across land uses and climate zones from the study area in central Western Ghats, India

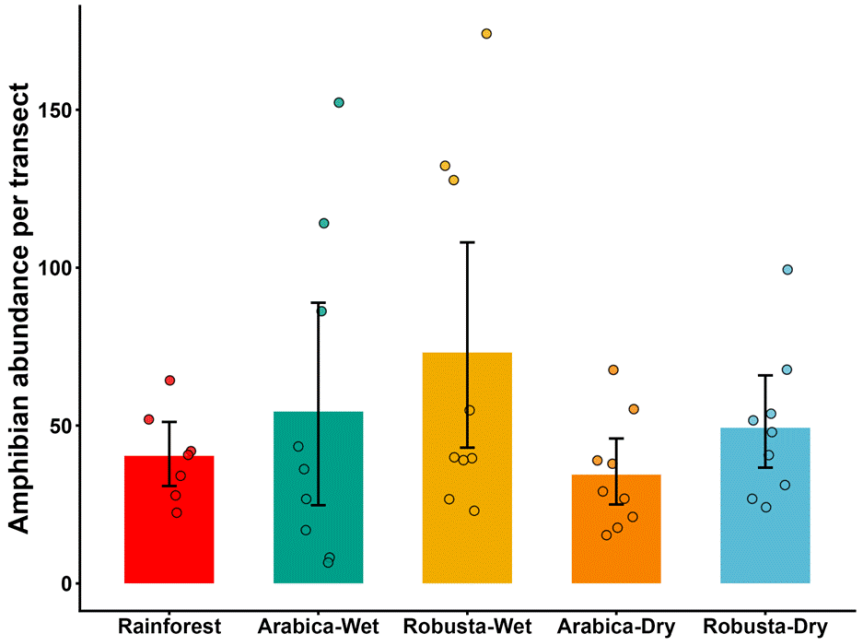


**Figure S4:** Amphibian abundance per transect (mean ± 95% CI) across land uses and climate zones with the points representing the observed raw amphibian counts in each transect

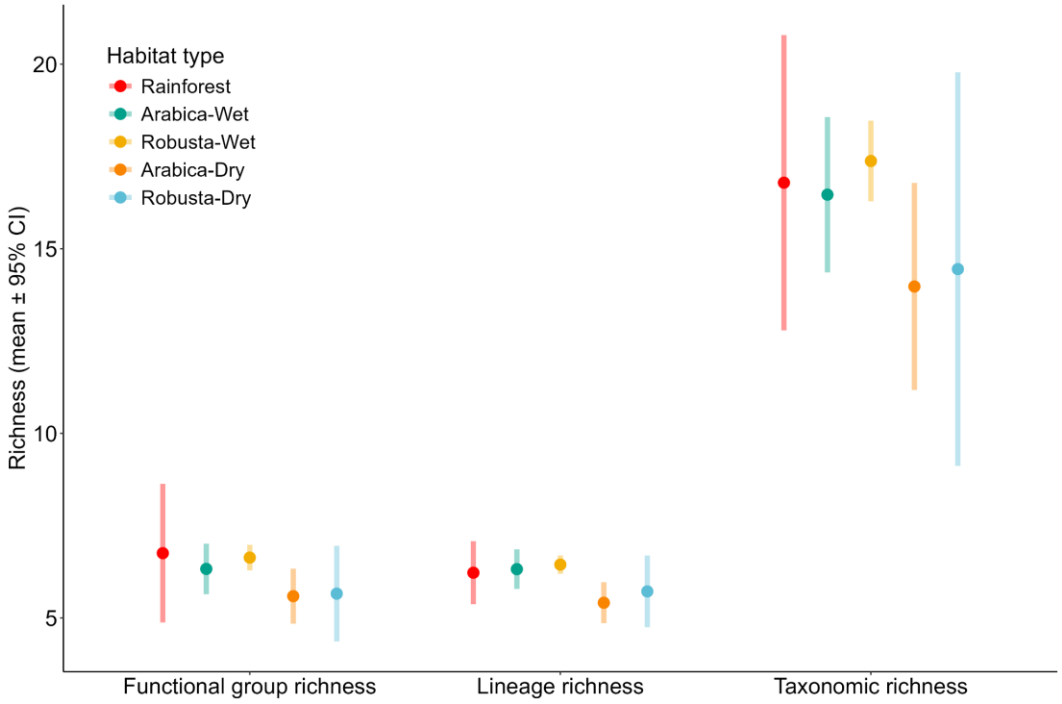


**Figure S5:** Functional, phylogenetic and taxonomic richness of amphibians across land uses and climate zones, measured using Hill number at q=0 at 99% sampling coverage. Points and bars represent estimated means and 95% confidence intervals, respectively

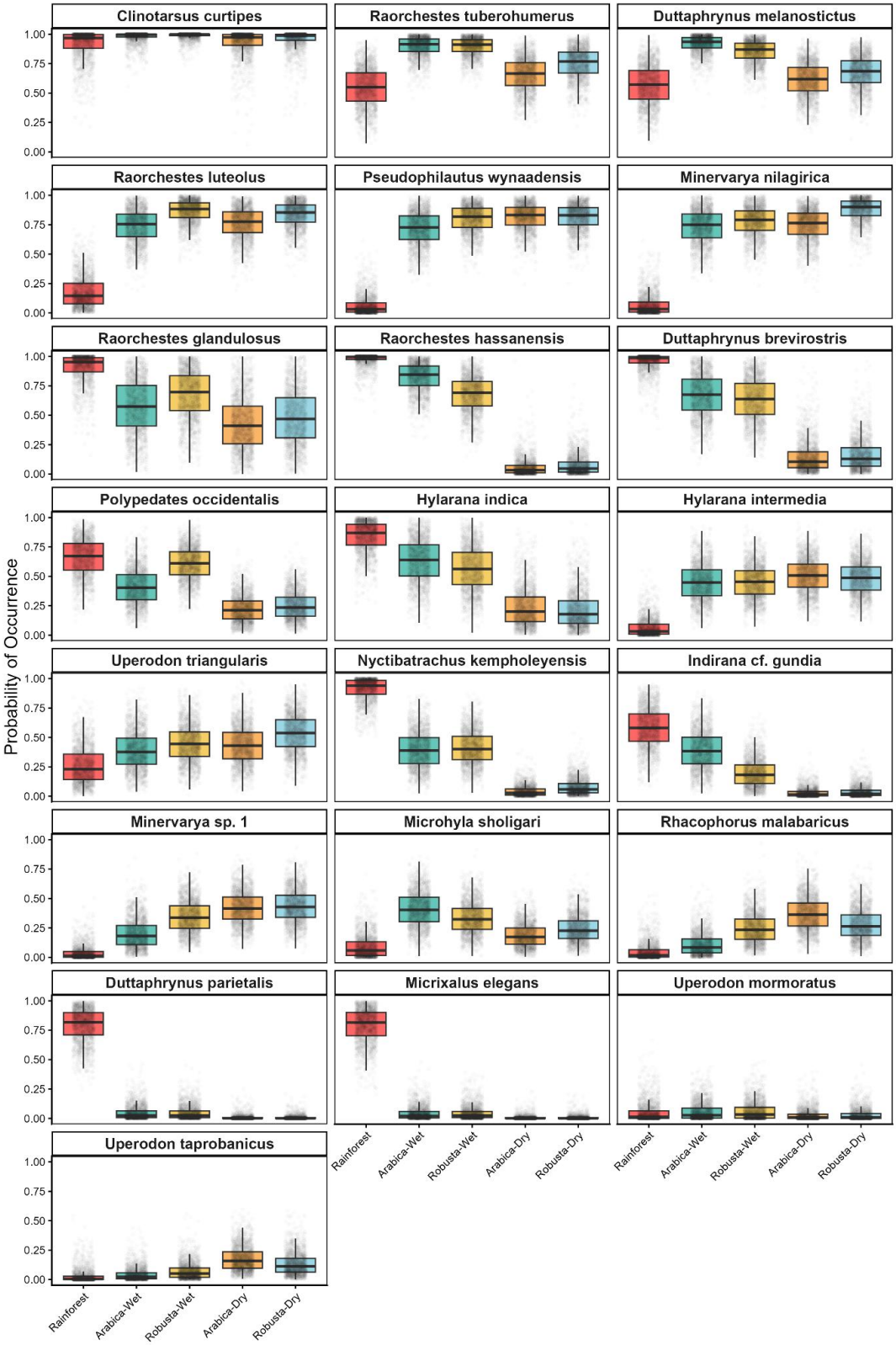


**Figure S6:** Predicted occurrence probabilities of 22 amphibian species across land use and climate zones, derived from posterior samples of the HMSC model

**Figure S7:** A degraded stream section in a wet coffee agroforest site, showing exposed bedrock, overgrown vegetation, and reduced water flow during the monsoon


**Figure S8:** Artificial lentic breeding habitats in coffee agroforests. Cemented tanks beneath the shade tree canopy retain rainwater and leaf litter during the monsoon (a), providing suitable aquatic habitat for tadpole development, particularly for foam-nesting tree frogs (b). Large irrigation ponds act as breeding sites for species such as *Minervarya* spp. and *Clinotarsus curtipes* (c)

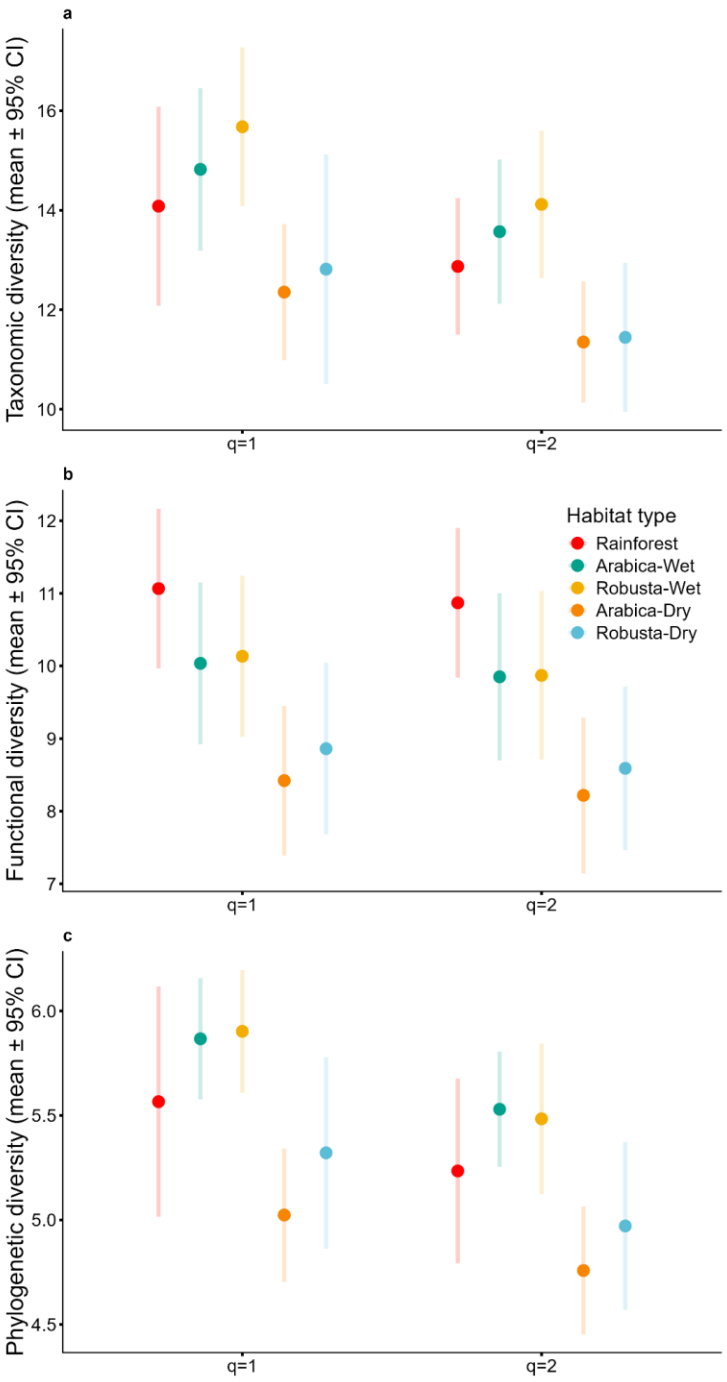


**Figure S9:** Incidence-based amphibian taxonomic, functional and phylogenetic Hill-Shannon (q = 1) and Hill-Simpson (q = 2) diversity across habitats (at 96% sampling coverage). Points and bars represent estimated means and 95% confidence intervals, respectively

## REFERENCES


1. Alvarez-Grzybowska, E., Urbina-Cardona, N., Córdova-Tapia, F., & García, A. (2020). Amphibian communities in two contrasting ecosystems: Functional diversity and environmental filters. Biodiversity and Conservation, 29, 2457–2485.

2. Cortés-Gómez, Á. M., Ramírez-Pinilla, M. P., & Urbina-Cardona, N. (2016). Protocol for the measurement of functional traits in amphibians. In Functional Ecology as an Approach to the Study, Management and Conservation of Biodiversity: Protocols and Applications (pp. 126–179).

3. Dehling, D.M., Dehling, J.M. Elevated alpha diversity in disturbed sites obscures regional decline and homogenization of amphibian taxonomic, functional and phylogenetic diversity. Sci Rep 13, 1710 (2023). https://doi.org/10.1038/s41598-023-27946-0

4. Díaz-García, J. M., Pineda, E., López-Barrera, F., & Moreno, C. E. (2017). Amphibian species and functional diversity as indicators of restoration success in tropical montane forest. Biodiversity and Conservation, 26(11), 2569–2589. https://doi.org/10.1007/s10531-017-1372-2

5. Hernández-Ordóñez, O., Santos, B. A., Pyron, R. A., Arroyo-Rodríguez, V., Urbina-Cardona, J. N., Martínez-Ramos, M., Parra-Olea, G., & Reynoso, V. H. (2019). Species sorting and mass effect along forest succession: Evidence from taxonomic, functional, and phylogenetic diversity of amphibian communities. Ecology and Evolution, 9(9), 5206–5218.

6. Murray, A. H., Nowakowski, A. J., & Frishkoff, L. O. (2021). Climate and land-use change severity alter trait-based responses to habitat conversion. Global Ecology and Biogeography, 30(3), 598–610. https://doi.org/10.1111/geb.13237

7. Portik, D. M., Streicher, J. W., & Wiens, J. J. (2023). Frog phylogeny: A time-calibrated, species-level tree based on hundreds of loci and 5,242 species. Molecular Phylogenetics and Evolution, 188, 107907. https://doi.org/10.1016/j.ympev.2023.107907

8. Ribeiro, J., Colli, G. R., Batista, R., & Soares, A. (2017). Landscape and local correlates with anuran taxonomic, functional and phylogenetic diversity in rice crops. Landscape Ecology, 32(8), 1599–1612. https://doi.org/10.1007/s10980-017-0525-8

9. Riemann, J. C., Ndriantsoa, S. H., Rödel, M.-O., & Glos, J. (2017). Functional diversity in a fragmented landscape—Habitat alterations affect functional trait composition of frog assemblages in Madagascar. Global Ecology and Conservation, 10, 173–183.