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Habitat heterogeneity drives fern species diversity in Bilar, Bohol, Philippines using Hill numbers

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Abstract. *Lanzaderas MAA, Saldom MJ, Baldos AP. 2026. Habitat heterogeneity drives fern species diversity in Bilar, Bohol, Philippines using Hill numbers. Biodiversitas 27 (2): d270237. https://doi.org/10.13057/biodiv/d270237.* Ferns are ecologically vital components of tropical ecosystems, yet remain underrepresented in biodiversity assessments. This study applied the Hill numbers framework to evaluate the α-diversity of ferns across four habitat types: forest area, hilly terrain, open area, and riparian zone in Bilar, Bohol, Philippines. A total of 24 plots (10 m x 10 m each) were established, with three quadrats per habitat type in each barangay, covering an aggregate area of 2,400 m^2. From these plots, we recorded 2,033 individual ferns representing 19 species. Species richness (q = 0) was highest in hilly terrain (13 species), followed by forest area (10), riparian zone (10), and open area (6). At q = 1 and q = 2, the effective numbers of species indicated comparable diversity between hilly terrain, forest area, and riparian zone, while open area showed significantly lower evenness and dominance ($p<0.05$). *Nephrolepis cordifolia* and *Christella acuminata* were the most widespread and abundant taxa, whereas *Diplazium esculentum* occurred exclusively in riparian zone, underscoring microhabitat specificity. The application of Hill numbers provided a more comprehensive and scale-independent understanding of fern diversity than traditional indices, capturing differences in both species richness and evenness. These findings emphasize that structurally and topographically complex habitats sustain higher effective species numbers. The study advocates prioritizing heterogeneous landscapes in conservation and restoration programs to enhance ecological resilience and safeguard fern diversity in fragmented tropical forests.

Keywords: Bohol, Pteridophytes, fern diversity, habitat types, Hill numbers

INTRODUCTION

Biodiversity underpins the stability and resilience of ecosystem, influencing its functions, recovering it from disturbance, and delivering its vital services to nature and people (Buot and Buhay 2022). Despite its global importance, biodiversity continues to decline at unprecedented rates due to land-use change, habitat degradation, and climate change (Díaz et al. 2019). This loss is most alarming in tropical regions, which harbor the world's highest concentrations of biological diversity yet face escalating anthropogenic pressures. Monitoring biodiversity across ecological gradients is thus essential for informing conservation strategies and understanding spatial variation in ecosystem responses (Socolar et al. 2016).

Among the diverse biotic components of tropical forests are ferns (Division Pteridophyta) - spore-bearing vascular plants often overlooked despite their ecological importance. These ancient lineages, which trace their evolutionary history back hundreds of millions of years (Huang et al. 2019), occupy a broad range of environments from shaded understories to disturbed open areas (Alcala et al. 2019). Ferns contribute to nutrient cycling, influence microclimatic conditions, and can inhibit invasive species (Dai et al. 2020). Some species, such as *Dicranopteris dichotoma* (Thunb.) Bernh, improve soil fertility and facilitate tree regeneration (Aros-Muarin et al. 2021), while tree ferns like *Cyathea smithii* Hook.f. create microsites that enhance seedling establishment by moderating temperature and moisture (Liu et al. 2022). Their sensitivity to environmental variation makes ferns useful indicators of habitat quality and disturbance (Abas 2017). Ferns' unique chemistry also offers bioprospecting potential, serving as a valuable source of novel bioactive compounds (Cao et al. 2017; Dvorakova et al. 2024).

Despite their ecological importance, ferns remain underrepresented in tropical ecological studies, which often prioritize trees and commercially valuable taxa (delos Angeles et al. 2025). This bias has left many areas, including parts of the Philippines, with incomplete and outdated records of fern diversity. The Philippines hosts ~1,100 fern species in 144 genera and 39 families (Pelser et al. 2011; Magtoto and Austria 2017), and ethnobotanical studies highlight their cultural and medicinal value (Nuneza et al. 2021; Juliasih and Adnyana 2023). On Bohol Island, surveys are still largely based on early collections by Hugh Cuming in the 1840s (Smith 1841) and a karst forest inventory by Barcelona et al. (2006) reporting 169 fern and fern ally species. Recent inventories from other Philippine sites indicate that additional taxa likely remain undocumented, reinforcing the need for site-specific studies to address regional knowledge gaps (Coritico and Amoroso 2020; Galope-Obemio et al. 2022; Rufila et al. 2022).

Traditional diversity indices, such as species richness, provide a basic measure of biodiversity but fail to capture variation in species abundance and dominance (Schwalm et al. 2016). Fern communities, like many plant assemblages, are typically characterized by a few dominant species and numerous rare ones - patterns that simple richness metrics cannot fully describe. The Hill numbers framework offers a more integrative and statistically coherent approach to quantifying diversity. Adjusting the parameter q allows the weighting of rare (q = 0), common (q = 1), and dominant species (q = 2), thereby unifying richness, evenness, and dominance into a single continuum (Jost 2006; Chao et al. 2023). This approach reveals subtle diversity gradients that may be obscured by conventional indices, providing deeper insight into how habitat structure and disturbance shape community composition.

This study aims to assess and compare fern species diversity across four natural habitat types—forest area, hilly terrain, open area, and riparian zone—in the Municipality of Bilar, Bohol, Philippines. Specifically, it applies the Hill numbers framework to determine how fern richness, evenness, and dominance vary across habitat gradients. We hypothesize that structurally complex habitats, such as forests and hilly terrain, support higher effective species diversity than open and riparian areas. The findings are expected to contribute to more comprehensive understanding of fern community dynamics in tropical landscapes and to inform evidence-based biodiversity conservation and restoration initiatives.

MATERIALS AND METHODS

Study area

Field assessments were conducted in Barangay (Brgy.) Owac and Brgy. Yanaya, Bilar, Bohol, Philippines, located approximately at 9º41'N, 124º8'E, and 9°42′N, 124°06′E, respectively (Figure 1). Mean elevation ranges from 304 to 386 meters above sea level (m asl). Bohol experiences a tropical climate, primarily classified as Type IV under the PAGASA (2022) system, indicating rainfall is more or less evenly distributed throughout the year. Bohol has experienced extensive historical deforestation and habitat fragmentation, with only a fraction of its original limestone and lowland forests remaining (Aureo et al. 2020; Aureo and Decena 2023). These remnant forests, including portions within and adjacent to the Rajah Sikatuna Protected Landscape (RSPL), harbor high biodiversity and endemic species, making them critical areas for ecological and conservation studies

Establishment of plots

The study covered four habitat types—forest area, hilly terrain, open area, and riparian zone—forming a heterogeneous landscape that shapes fern distribution and diversity. Forest and hilly habitats within RSPL are relatively undisturbed, legally protected secondary forests (Proclamation No. 287, s. 2000): the forest area has a closed canopy (15-20 m) that maintains shaded, moist microclimates favorable to ferns, while the hilly terrain supports diverse assemblages due to elevation- and slope-driven microclimatic variation. In contrast, the open area and riparian zone outside RSPL are more disturbed by clearing, small-scale cultivation, and vegetation removal; the open area is grass-dominated and favors sun-tolerant early successional ferns, whereas the riparian zone retains moist, humid conditions along streams that support hydrophilic species. Overall, these habitats represent a protection-disturbance gradient from intact RSPL forests to modified areas outside, explaining spatial variation in fern diversity across Bilar.

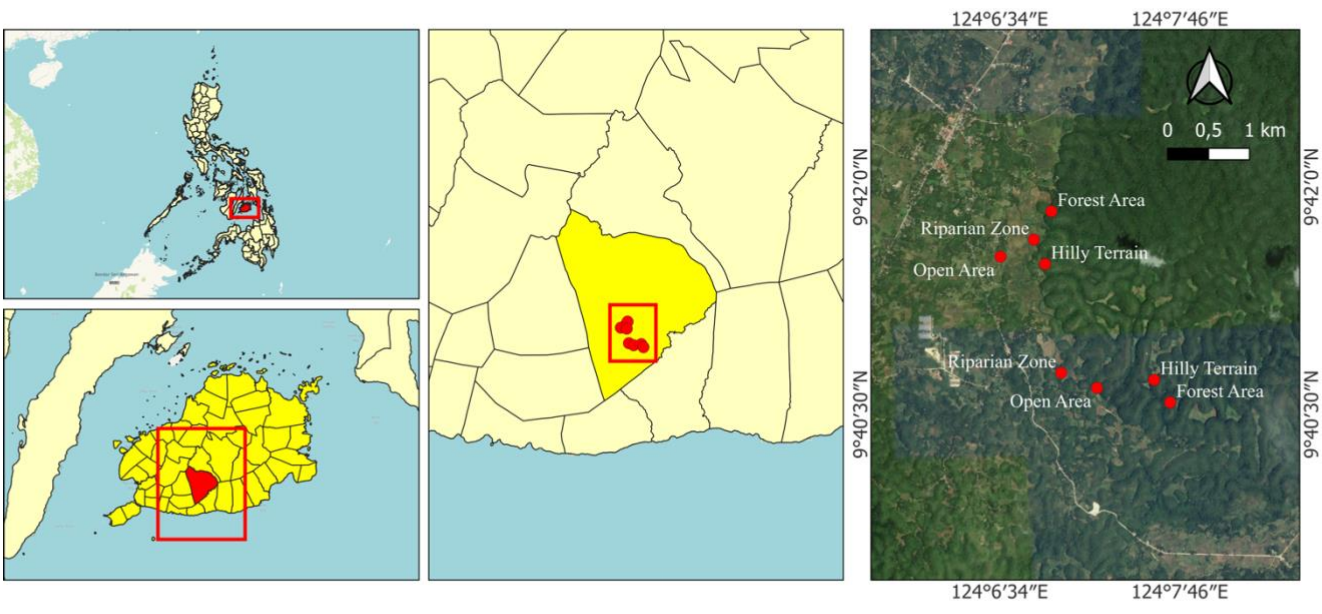

Figure 1. Map of the study area showing the four sampled habitat types: forest area, hilly terrain, open area, and riparian zone in Bilar, Bohol, Philippines

Three 10 m × 10 m quadrats were established per habitat type in each barangay, yielding 24 plots that covered 2,400 m², following Saro et al. (2022). Although 100 m spacing was initially planned, limited patch size required the three quadrats within each habitat to be placed contiguously, which may have increased spatial autocorrelation and reduced fine-scale within-habitat variation; however, this adjustment enabled consistent sampling in small or fragmented patches while still capturing dominant microhabitats. Ferns were documented via purposive sampling in areas with clear fern presence and distinct habitat features, and identified using Co's Digital Flora. Sampling occurred from January to February 2025 (dry season), when site access was most feasible.

Data analysis

Data were processed and analyzed in R (R Core Team 2022) using Hill numbers, which express diversity as the "effective number of species" and unify richness, Shannon, and Simpson indices while differing in how they weight rare versus common species (Hill 1973; Jost 2006). Alpha diversity was estimated with iNEXT (Hsieh et al. 2016) using q = 0 (species richness), q = 1 (exponential Shannon), and q = 2 (inverse Simpson), representing the same general framework with different rarity scaling (Chao et al. 2023). Species richness is most sensitive to rare species and sample size, whereas Hill-Shannon and Hill-Simpson place more weight on common species and are less sampling-sensitive (Roswell et al. 2020; Chao et al. 2023). Unidentified taxa were retained as distinct OTUs because they were morphologically distinguishable, ensuring diversity estimates captured observed variation and avoiding underestimation of richness or distortion of evenness.

We used a fixed sample coverage of 95% to allow unbiased comparisons of fern species diversity across habitat types (Monge-Gonzales et al. 2019). A non-overlapping 95% confidence interval guarantees statistical differences at a level of 5% (whether interpolated or extrapolated; Chao et al. 2023). Figures were generated using *ggplot* and *ggiNEXT* in the R program.

RESULTS AND DISCUSSION

Fern species composition across habitat types

We recorded a total of 2,033 individual fern specimens in the study area, representing 19 species distributed across 10 families and 12 genera. Among these, one species remains unidentified. Across the four habitat types surveyed, hilly terrain recorded the highest number of fern species (n = 13), followed by forest area (n = 10), riparian zone (n = 10), and open area (n = 6). Within the forest area, ten species were observed, including three epiphytic species occurring on tree stems and seven terrestrial species on the forest floor. The hilly terrain exhibited twelve ground-dwelling species and one epiphytic species. All six species recorded in the open area were found on the ground. The riparian zone supported 10 terrestrial species, with no epiphytes observed. The hilly terrain accounted for the highest relative abundance of ferns, comprising approximately 40% of all recorded individuals, while in term of microhabitat, tree stem contributed fewer compared to ground in both the forest area and hilly terrain (Table 1).

Abundance and dominance of fern species

The heatmap (Figure 2) illustrates distinct abundance patterns of fern species across the four habitat types in Bilar, Bohol. Rather than being evenly distributed, fern assemblages display clear contrasts between widespread generalist species and habitat specialists.

Nephrolepis cordifolia (L.) C.Presl emerged as the most dominant and widely distributed species, occurring abundantly across all habitats, particularly in forest area and hilly terrain. Similarly, *Selaginella plana* (Desv. ex Poir.) Hieron. showed high abundance in these two habitats, indicating a broad ecological tolerance and adaptability to varying microclimatic conditions. In contrast, species such as *Diplazium esculentum* (Retz.) Sw. and *Lygodium circinnatum* (Burm.f.) Sw. were largely confined to riparian zone, reflecting their preference for moist, shaded environments. Hilly terrain and forest area supported the densest fern populations, with several overlapping species, suggesting structurally complex and favorable conditions for fern establishment. Meanwhile, open area and riparian zone hosted fewer species, though the latter harbored unique taxa not found elsewhere. The presence of an unidentified "Miscellaneous 1" species with moderate abundance in multiple habitats further suggests potential undiscovered diversity within the study area. Overall, the heatmap reveals that fern distribution is shaped by both habitat heterogeneity and species-level ecological strategies, distinguishing generalists like *N. cordifolia* from specialists restricted to specific environments.

Table 1. Number of fern species, individuals, and relative abundance (%) recorded across different habitat types in Bilar, Bohol, Philippines. Relative abundance indicates the proportion of individuals in each habitat relative to the total count (N = 2,033)

Habitat types/ microhabitat	No. of species	No. of individuals	Relative abundance
Forest area	10	322	15.84
Ground (terrestrial)	7	304	14.95
Tree stem (epiphytes)	3	18	0.89
Hilly terrain	13	826	40.63
Ground (terrestrial)	12	825	40.58
Tree stem (epiphytes)	1	1	0.05
Open area	6	461	22.68
Riparian zone	10	424	20.86
Total	19	2,033	100.00

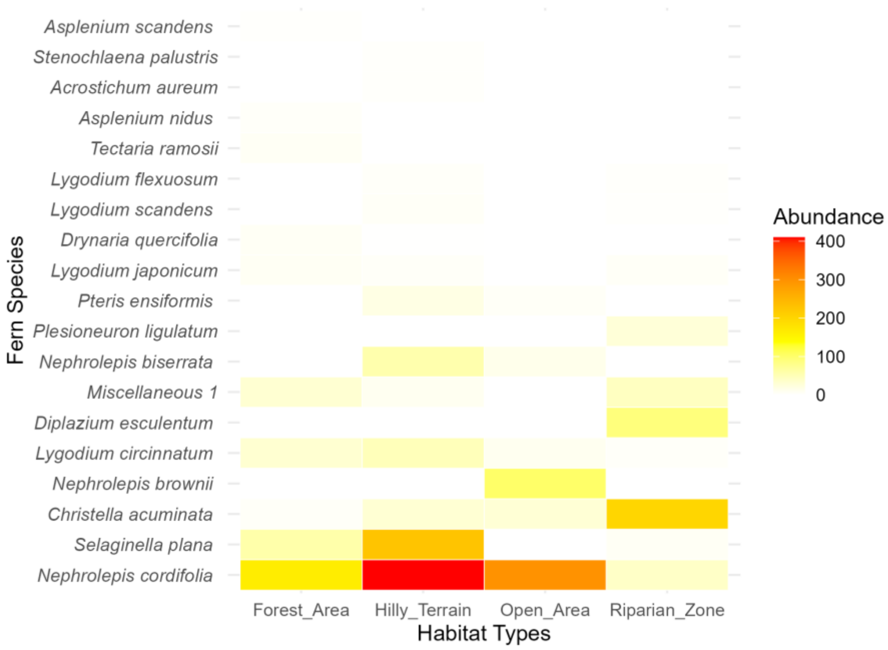

Figure 2. Heatmap illustrating the abundance of fern species across four habitat types. Each cell represents the observed number of individuals per species-habitat combination. The color gradient corresponds to abundance levels, with lighter shades indicating lower counts and darker red shades representing higher abundance (up to >400 individuals). Species are arranged along the vertical axis according to their observed frequency across habitats, highlighting differences in species dominance and habitat preference

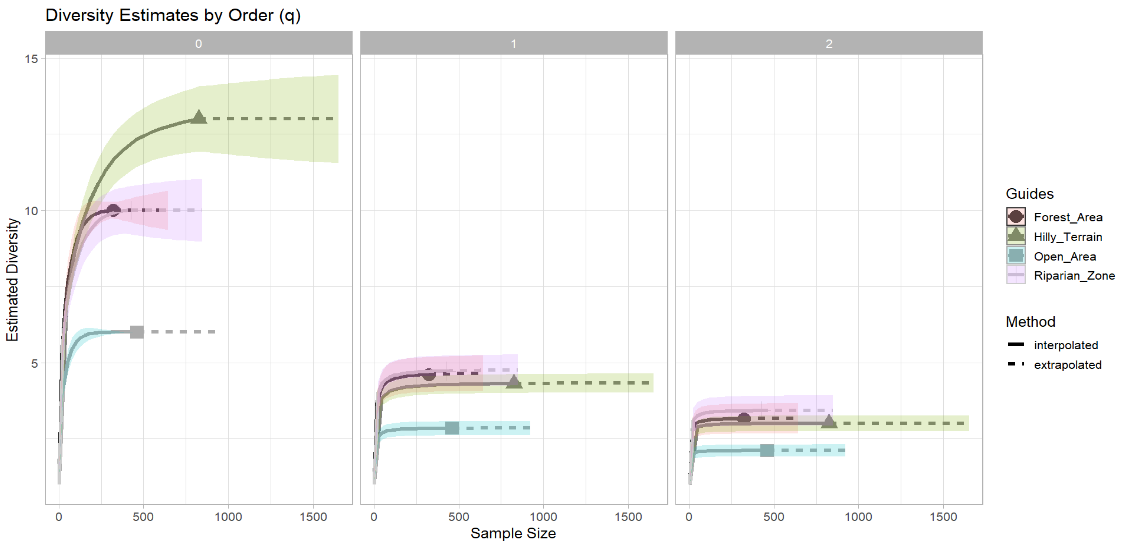

Figure 3. The interpolation (solid lines) and extrapolation (dashed lines) curves for species richness (q=0), Shannon (q=1), and Simpson diversity (q=2) of the habitat types. Shaded areas are the 95% confidence interval

Fern diversity across habitat types based on Hill numbers

The multi-panel plot in Figure 3 displays diversity estimates by order (q) for four different habitat types: forest area, hilly terrain, open area, and riparian zone, across varying sample sizes. The solid lines indicate interpolated diversity values, while the dashed lines represent extrapolated values, with the shaded regions denoting 95% confidence intervals. At an order of q=0 (species richness), hilly terrain exhibits the highest estimated diversity, at roughly 13 species. Forest area and riparian zone also show considerable diversity, plateauing around 10 species. In contrast, open area consistently demonstrates the lowest diversity, asymptote at around 6 species. The confidence interval in hilly terrain is wider at higher sample sizes, particularly during extrapolation, indicating greater uncertainty in their total species richness estimates compared to the other habitat types. Moreover, the sampling curves reached a clear plateau with extrapolation, implying that further sampling in this area would likely not discover new species.

At q=1 (Shannon diversity), which incorporates species abundance alongside richness, we observe, as anticipated, that the overall estimated diversity values are lower than those for q=0. In this context, forest area, hilly terrain, and riparian zone exhibit comparable diversity estimates, peaking in the range of 4.5 to 5.0 effective species. Open area consistently retains its position as the least diverse, stabilizing around 2.5 effective species. Notably, the sampling curves for all habitat types generally display saturation, suggesting that our current sampling effort is largely adequate for capturing the majority of the diversity in this particular order.

At q=2 (Simpson diversity), which emphasizes dominant species, we observe a further reduction in estimated diversity values. Interestingly, at this order, the three habitat types - forest area, hilly terrain, and riparian zone - exhibit remarkably similar and relatively low diversity, clustering tightly between 3.0 and 3.5 effective species. Consistent with earlier observations, open area maintains its position as having the lowest estimated effective diversity across all study sites. The diminished disparities among these habitat types at q=2 suggest that while their overall species count (q=0) and evenness (q=1) might differ, the actual number of highly abundant species remains quite comparable across these diverse environments. Furthermore, the sampling curves for q=2 appear to have reached asymptotes, strongly indicating that further sampling efforts would likely not yield significant alterations in our current estimates of dominant species diversity.

Discussion

Species composition and habitat specificity

The distribution of fern species across the four habitat types in Bilar, Bohol, reflects clear ecological differentiation driven by variations in microclimate, substrate, and disturbance intensity. Species richness was highest in hilly terrain, suggesting that topographic complexity creates diverse microsites varying in light, moisture, and soil depth, conditions favorable for a wider range of fern taxa. In contrast, open area supported fewer species, consistent with the reduced structural heterogeneity and higher exposure characteristic of disturbed landscapes (Alcala et al. 2019; delos Angeles et al. 2020).

Patterns of abundance indicate a gradient between generalist and habitat-specialist species. *N. cordifolia*, the most abundant taxon, occurred across all habitats, underscoring its broad ecological tolerance and ability to thrive in both shaded and sunlit environments. Its dominance, particularly in hilly terrain and open area, is consistent with its known resilience to disturbance and capacity to colonize rocky or well-drained slopes (Zou et al. 2024). Conversely, *S. plana* and *Christella acuminata* (Houtt.) Holttum exhibited restricted distributions, showing strong preferences for moist and semi-shaded habitats. These species' abundance in hilly terrain and riparian zone, respectively, reflects niche specialization shaped by hydrological and microclimatic stability (Xu et al. 2018).

Several taxa, including *D. esculentum*, *Plesioneuron ligulatum* (C.Chr.) Holttum, and *Nephrolepis brownii* (Desv.) Hovenkamp & Miyam., were confined to specific habitats, indicating strong habitat specificity. The occurrence of *D. esculentum* exclusively in riparian zone highlights its reliance on consistently high soil moisture, as previously documented in tropical Asia (Peligro 2021; Negi and Kanwal 2024). In contrast, *N. brownii* and *Pteris ensiformis* (Burm.f), dominant in open area, are characteristic of disturbed and high-light environments (Beltrán et al. 2020). Rare species such as *Stenochlaena palustris* (Burm.f), *Asplenium scandens* Blume, and *Acrostichum aureum* L. occurred at low abundance and narrow habitat ranges, likely reflecting microhabitat constraints or competitive exclusion by dominant taxa (Tuomisto et al. 2003). The observed composition suggests that fern assemblages in Bilar are structured by both environmental filtering and disturbance-mediated selection. The coexistence of widespread generalists and habitat-restricted specialists highlights the ecological importance of maintaining a mosaic of habitat conditions to sustain fern diversity across tropical landscapes.

Hill numbers reveal diversity patterns

The analysis of Hill numbers offers a comprehensive view of fern diversity across the four habitat types by incorporating not only species counts but also their relative abundances. At the level of q = 0 (species richness), which represents the total number of species without considering their abundance, both forest area and hilly terrain exhibited the highest estimated diversity. These results align with ecological principles, suggesting that structurally complex and environmentally stable habitats, such as mature forests and topographically varied hills, support more species due to their wider range of microhabitats and resource niches (Bita-Nicolae and Dhyani 2025). Comparable trends have been reported in forests of the Philippines, where elevation gradients and slope variation promote fern diversity by enhancing spatial heterogeneity in light, temperature, and soil conditions (Coritico et al. 2020; De Villa and Lagat 2024). The continued upward trajectory of the extrapolated curves for these habitats further suggests that additional sampling could reveal more species, underscoring their high biodiversity potential.

In contrast, open area consistently showed the lowest species richness. Its exposure to intense sunlight, greater temperature fluctuations, and frequent disturbance likely limit the establishment of moisture-dependent and shade-loving taxa. This dominance of a few hardy species mirrors findings from roadside and exposure-gradient studies in the Philippines, where increased radiation and soil desiccation reduce evenness and filter out sensitive species (Perida et al. 2023). Meanwhile, riparian zone, though richer than open area, is subject to dynamic hydrological disturbances such as fluctuating water levels. These conditions favor adaptable and stress-tolerant species but can constrain overall richness (Sarmiento et al. 2022; Titisari et al. 2025).

At q = 1 (Shannon diversity), which accounts for both richness and evenness, the pattern shifts slightly. Forest area, hilly terrain, and riparian zone displayed comparable diversity estimates, suggesting balanced distributions among common and moderately abundant species. The near-saturation of the q = 1 curves implies adequate sampling coverage and indicates that community composition is well represented (Chao et al. 2023). The overlap of diversity values among habitats further suggests that stable microclimates promote coexistence through reduced competitive exclusion (O'Brien and Escudero 2021).

At q = 2 (Simpson diversity), which gives greater weight to dominant species and is less influenced by rare taxa, the diversity curves converge across all habitats. This convergence indicates that while total richness and evenness differ, the number of highly dominant species remains comparable. The asymptotic nature of these curves implies that further sampling would not substantially alter dominance-based diversity estimates. Such convergence reflects a key ecological principle: across contrasting environments, similar processes such as environmental filtering or competitive interactions shape the success of dominant species (Crawford et al. 2021; Bita-Nicolae and Dhyani 2025). The observed balance in q = 2 values across habitats suggests that no single species overwhelmingly outcompetes others, consistent with reports from lowland tropical forests where resource partitioning and microhabitat variability maintain multiple co-dominant species (Monge-González et al. 2021).

Conservation implications

This study underscores the crucial role of environmental heterogeneity in maintaining fern diversity within tropical landscapes. While riparian zones provide stable hydrological conditions and forested areas offer shade and microclimatic buffering, it is the structural complexity of hilly terrains characterized by varying slope, aspect, and soil conditions that most strongly enhances fern richness and evenness. Similar findings by Cicuzza and Mammides (2022) emphasize that habitat heterogeneity, rather than forest cover alone, drives total fern species richness. The results from Bilar, Bohol, therefore, reaffirm that conservation strategies must move beyond a simple forest–non-forest dichotomy and instead prioritize areas exhibiting high microhabitat variability.

The integration of Hill numbers provided a more nuanced understanding of biodiversity patterns by simultaneously accounting for species richness, evenness, and dominance. This framework revealed that habitats with intermediate disturbance and greater topographic complexity (e.g., hilly terrain) tend to sustain both diverse and balanced fern communities. Such findings support Jost's (2006) argument that Hill numbers offer a unified and interpretable measure of ecological diversity that facilitates meaningful cross-habitat comparisons.

From management perspective, these results underscore that sustaining a mosaic of habitat types such as riparian buffers, hilly terrains, and forest interiors is essential to maximizing fern diversity and maintaining ecosystem resilience. The distinct assemblages observed across habitats reveal that conserving a single habitat form would overlook a substantial portion of fern biodiversity. Thus, habitat heterogeneity should be viewed as a cornerstone of forest restoration and monitoring programs, ensuring that ecological complexity and microhabitat diversity are preserved. Integrating quantitative biodiversity metrics, such as Hill numbers, into land-use planning can further enhance conservation decisions by capturing both species richness and abundance patterns. Recognizing ferns as sensitive indicators of forest health can strengthen ecosystem-based management, guiding more inclusive and adaptive conservation strategies in tropical landscapes.

In conclusion, this study demonstrates that habitat heterogeneity strongly structures fern assemblages in Bilar, Bohol, and that Hill numbers provide a clear, scale-independent way to compare diversity across habitat gradients. Across 24 plots (10 m × 10 m; 2,400 m²), 2,033 individuals representing 19 fern species were recorded from four habitat types, with hilly terrain supporting the highest richness (q = 0; 13 species), followed by forest area and riparian zone (10 species each), while open areas were consistently species-poor (6 species). When abundance was incorporated (q = 1) and dominance was emphasized (q = 2), forest area, hilly terrain, and riparian zone converged to broadly comparable effective species numbers, indicating that differences among these habitats are driven primarily by rare species and evenness rather than by shifts in the dominant core of the community; open areas remained the least diverse across all orders. Species-level patterns further reinforced microhabitat filtering, with widespread generalists (e.g., *Nephrolepis cordifolia*) occurring across habitats, while some taxa showed strong habitat specificity, including *Diplazium esculentum* restricted to riparian conditions. From a management perspective, the results argue for conserving and restoring landscape mosaics that retain topographic and structural complexity—particularly hilly and forested habitats—alongside riparian buffers, because protecting only single habitat type would miss a substantial fraction of local fern diversity.

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