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環境因子與競爭對台灣無尾目群集的影響

Effects of Environmental Variables and Competition on Anuran Communities in Taiwan

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國立臺灣大學（碩）博士學位論文
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環境因子與競爭對台灣無尾目群集的影響
Effects of Environmental Variables and Competition on Anuran Communities in Taiwan

本論文係吳安妮君（學號R11B44001）在國立臺灣大學生態學與演化生物學研究所完成之碩士學位論文，於民國114年7月23日承下列考試委員審查通過及口試及格，特此證明

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中文摘要

群集組成受到決定性機制（如環境篩選與競爭）以及隨機性機制（如擴散與生態漂變）的共同影響。理解這些機制的相對貢獻，對於預測生物多樣性如何回應環境變遷至關重要。由於蛙類具有複雜的生活史，並依賴同時依賴水域與陸域環境，因此對環境變化特別敏感。儘管在熱帶與亞熱帶地區，群集組成機制受到越來越多的關注，但對於島嶼（如臺灣）中這些機制（如環境篩選及競爭）的運作方式及其在時間尺度下的變化，目前仍所知有限。本研究使用臺灣兩棲類資料庫中自 2005 年至 2021 年間，於 3,534 個樣區進行的標準化調查資料，探討臺灣蛙類群集組成的機制及其時空變化。我們運用典範對應分析（Canonical Correspondence Analysis, CCA）評估物種與環境因子的關係，並進行共現分析（co-occurrence analysis）以探討物種間的共域關係（如潛在的競爭）。分析分別針對整體期間（2005–2021）與兩個五年子時期（2005–2009 與 2017–2021）進行，以揭示時間變化趨勢。CCA 結果顯示，溫度、濕度與微棲地結構是影響物種組成的主要環境因子，支持環境篩選為重要機制。然而，這些變數的解釋力隨時間而下降：2005–2009 年的總解釋變異為 36.93%，而 2017–2021 年為 17.31%，整體期間僅為 9.91%。這可能反映出環境擾動增加、棲地同質化，或近期資料中噪音增多等問題。部分物種在不同時期維持穩定的環境關聯，例如斯文豪氏赤蛙固定出現在溪流環境，而長腳赤蛙偏好低溫環境；另一些物種，如黑眶蟾蜍與莫氏樹蛙，則顯示其環境關聯性隨時間出現變化，可能與環境變遷有關。我們亦檢測到環境條件的時序變化：2005–2009 年間樣區層級的平均溫度為 24.66˚C，至 2017–2021 年間下降了 1.37˚C（具統計顯著性），而相對濕度則顯著上升。儘管微棲地類別的變化主要反映分類系統的調整，這些氣候變化仍可能影響物種與環境之間的關係。共現分析結果顯示，正向物種共域關係（物種同時出現）在所有時期皆較為常見，佔整體與近期期間中物種配對的 60–65%；而早期（2005–2009）則有較高比例的隨機關係（43%），顯示該時期群集結構較鬆散。拉都希氏赤蛙、腹斑蛙與布氏樹蛙等物種在各時期皆與多數其他物種呈現正向共現，而莫氏樹蛙與梭德氏赤蛙則常與其他物種呈現負向共現，可能反映出棲位差異或競爭排除。整體而言，我們的研究結果強調了：

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1) 環境篩選與正向的物種共域關係（而非許多先前研究所指出的競爭）所扮演的角色；2) 無尾目群集組成的時間變化； 3) 環境變化對物種與環境的關係及物種間共域關係的影響。本研究凸顯了長期生態資料對於偵測群集層級受環境改變的重要性，並透過強調保護棲地異質性與監測物種動態變化的必要性，為未來在氣候與土地利用持續變遷下的保育工作提供參考方向。

關鍵字：生物與環境間的關係、生物間共域模式、環境變化、長期生態監測、典範對應分析

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Abstract

Community assembly is shaped by both deterministic processes, such as environmental filtering and competition, and stochastic forces like dispersal and ecological drift. Understanding the relative contributions of these processes is essential for predicting biodiversity responses to environmental change. Anurans are particularly sensitive to such changes due to their complex life cycles and dependence on both aquatic and terrestrial habitats. However, despite increasing recognition of community assembly mechanisms in tropical and subtropical ecosystems, relatively little is known about how these processes (e.g., environmental filtering and competition) operate in island systems such as Taiwan, and how they change over time. In this study, we investigated anuran community assembly mechanisms in Taiwan and its temporal change using a standardized dataset from the Taiwan Amphibian Database, covering 3,534 survey sites between 2005 and 2021. We applied Canonical Correspondence Analysis (CCA) to evaluate species–environment relationships and co-occurrence analysis to explore species–species co-occurrence associations (e.g., potential competition). Analyses were conducted for the entire study period (2005–2021) and two five-year sub-periods (2005–2009 and 2017–2021) to examine temporal changes. The CCA results indicated that temperature, humidity, and microhabitat structure were key environmental variables shaping species composition, supporting the role of environmental filtering. However, the explanatory power of environmental variables declined over time, with the 2005–2009 period explaining 36.93% of variation in species distribution, compared to 17.31% in 2017–2021 and only 9.91% in the full dataset. This decline may reflect increasing environmental disturbance, homogenization of habitat conditions, or noise in more recent data. Some species showed consistent environmental associations across

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time periods, such as *Odorrana swinhoana* with running water and *Rana longicrus* with low temperatures. Others, like *Duttaphrynus melanostictus* and *Zhangixalus moltrechti*, shifted their associations over time, possibly in response to changing environmental conditions. Temporal changes in environmental conditions were also detected. Between 2005–2009 and 2017–2021, site-level mean temperature decreased significantly by 1.37°C, while relative humidity increased slightly but significantly. While the change in microhabitat composition was largely attributed to classification system updates, these environmental changes likely contributed to shifts in species–environment relationships. Co-occurrence analysis revealed that positive associations between species co-occurrence were consistently more common than negative ones, accounting for 60–65% of species pairs in the full and recent periods. In contrast, the earlier period (2005–2009) had a higher proportion of random associations (43%), suggesting a less structured community. Species like *H. latouchii*, *N. adenopleura*, and *P. braueri* consistently exhibited strong positive co-occurrence patterns, while species such as *Z. moltrechti* and *R. sauteri* showed high levels of negative co-occurrence, potentially reflecting niche differentiation or competitive exclusion. Overall, our findings highlight 1) the role of environmental filtering and positive species co-occurrence associations—rather than competition, as suggested by many previous studies, 2) dynamic shifts in anuran community composition over time, and 3) the effect of environmental change on species–environment associations and co-occurrence relationships. The study underscores the importance of long-term ecological data for detecting community-level responses and informs future conservation efforts by emphasizing the need to preserve habitat heterogeneity and monitor shifting species dynamics under ongoing climate and land-use change.

Keywords: Species-environment relationships, species co-occurrence patterns, environmental change, long-term ecological monitoring, Canonical Correspondence analysis

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Chapter 1 Introduction

1.1 Processes of community assembly

The processes of community assembly have long been an interesting topic for ecologist to discuss (Cody and Diamond 1975, Connor and Simberloff 1979). The structure of ecological communities is influenced by a combination of non-random (deterministic) and random (stochastic) processes (Zhou and Ning 2017). Deterministic processes—including environmental filtering and biotic interactions like competition—act predictably by selecting species based on their traits and interactions. In contrast, stochastic processes involve randomness, such as dispersal events and ecological drift. For instance, wetlands with stable hydrology exhibit community assembly patterns shaped by predictable environmental constrains, while more dynamic sites are influenced by stochasticity (Daniel et al. 2019). Although deterministic and stochastic are both important community assembly processes, this study will focusing on deterministic factors because they provide mechanistic understanding necessary for predicting community dynamics and informing conservation management (Zhou and Ning 2017). In the process of deterministic, environmental filtering has emerged as a foundational concept: abiotic conditions acting as a filter that allows only species with compatible traits to persist in a particular habitat (Kraft et al. 2015). For example, fish in a subtropical lake, environmental filtering strongly drives community assembly during dry season: species tolerant of low-water, high-temperature, and oxygen-stress conditions dominate the niche. (Chen et al. 2022). A further example can be found in how tropical land-use change influences community assembly based on species traits. In logged forests, beetle and bird communities exhibit trait clustering, signaling strong environmental filtering. Conversion to oil palm leads to random trait patterns, indicating

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loss of filtering mechanisms (Waddell et al. 2020). In Arctic epibenthic invertebrates along the Chukchi Sea shelves showed strong functional trait alignment—body size, feeding/living habits, movement mode, larval development—with these abiotic factors (Sutton et al. 2021). These provides unambiguous evidence that environmental filtering is an important mechanism in community assembly.

Besides environmental filtering, another common deterministic mechanism is competition, which has been widely recognized as a key ecological force structuring species composition and distribution (Das Gupta and Pinno 2018). For example, in tropical and subtropical regions, Anolis lizard assemblages demonstrate that competition intensity increases with ecological similarity, while intraspecific competition remains dominant, highlighting competition's role in niche differentiation (Thonis and Akçakaya 2024). Similarly, tropical arboreal ant communities display spatial segregation consistent with competitive exclusion, where dominant species create distinct territorial mosaics (Camarota et al. 2016). Collectively, these examples underscore the pervasive influence of competition in shaping animal community structure across diverse taxa and tropical to subtropical ecosystems.

1.2 Community assembly mechanisms in anurans

Ecological studies on anuran communities have indicated that both environmental filtering and competition play significant roles in shaping species composition, although the relative importance of each mechanism can vary depending on ecological contexts. Previous studies found that in tropical and subtropical regions, environmental filtering is often identified as a primary force structuring community. For example, research conducted in Madagascar and

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Borneo demonstrated that habitat characteristics like pond heterogeneity, vegetation cover, and stream morphology significantly influence species composition (Keller et al. 2009, Mausberg et al. 2023). Similarly, investigations in southeastern Brazil and along elevational gradients in subtropical areas found climatic and habitat factors to be key determinants of species richness and turnover (Prado and Rossa-Feres 2014).

Competition, however, has also been recognized as an important assembly mechanism. Under brackish water environments, intensified interspecific competition was documented between *Bufo bufo* and *B. calamita* (Gómez-Mestre and Tejedo 2002). Additionally, different ecological contexts within anuran communities may invoke different assembly mechanisms; for instance, one study reported that arboreal species exhibited patterns shaped by both environmental filtering and competition, whereas terrestrial species were predominantly structured by environmental filtering, with competitive interactions being prominent in smaller pond habitats (Ramalho et al. 2021). Another study identified competition as a significant factor influencing species' responses to habitat drying (Thurman and Garcia 2019). These findings collectively indicate that anuran community assembly involves complex interactions among various ecological factors, underscoring the need for continued research to better understand these dynamics.

1.3 Key environmental variables shaping community composition

As human activities reshape the environment at an alarming rate, it is critical to identify which key environmental variables will drive changes in community composition. Across diverse ecosystems, clear patterns have emerged showing that shifts in microhabitats and other

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environmental variables are among the most potent drivers of biotic reorganization. For instance, while regional bird species richness in northern lower Michigan remained stable over five decades, profound turnover in species composition reflected deterministic responses to habitat change, such as forest succession and urban expansion (Parody et al. 2001). In alpine grasslands, experiments manipulating warming, precipitation, and grazing intensity demonstrated pronounced shifts in soil microbial communities in response to altered moisture and nutrient levels—conditions directly shaped by anthropogenic influence (Zhang et al. 2016). In aquatic ecosystems, altered rainfall and temperature regimes have been tied to changes in amphibian populations (Parris 2004). Meanwhile, in temperate wetlands, shifts in precipitation and temperature have reorganized anuran assemblages, with breeding patterns and community structure tightly linked to pool availability and seasonal climate variation (Ospina et al. 2013). Collectively, these examples demonstrate that temporal changes in key environmental variables can indeed alter species composition across different taxa, potentially shifting community dominance, diversity, and ecosystem function. They also highlight the importance of long-term monitoring and research, as changes in community assembly mechanisms and composition driven by environmental shifts can only be accurately detected and predicted through extended observation and analysis.

1.4 Environmental changes and community assembly in Anuran

It is important to study environmental change impact on anuran communities because of the reasons:

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1) Environmental change affects species from many different aspects, for example, it modifies temperature, precipitation patterns, hydrological cycles, and habitat structure – altering species distribution, survival rate, behavior, phenology, and inter- and intraspecific interactions (Chen et al. 2011, Bellard et al. 2012). For example, rising temperatures have driven poleward and elevational range shifts in numerous taxa and advanced breeding phenology by several days per decade, while altered rainfall regimes can shrink or fragment suitable habitats, reducing population connectivity and resilience (Hellmann et al. 2012, Walpole et al. 2012). Ecological specialist may face a higher risk under environmental change due to narrow niche breadth, physiological sensitivity, and limited dispersal capacity; for instance, anurans depend on precise hydroperiods and microhabitats for breeding and metamorphosis—altered hydrology reduces pond permanence, disrupts larval development, and can desynchronize breeding cues (Colles et al. 2009, Ruthsatz et al. 2018). Moreover, because anurans occupy both aquatic and terrestrial stages, shifts in water availability or microclimate may disconnect life-history stages, exacerbating mortality at metamorphosis.

2) Approximately 41% of amphibian species face the risk of extinction. (IUCN 2022). Amphibians are widely regarded as one of the most vulnerable animal groups due to their elevated risk of extinction (Navas and Otani 2007). Numerous studies have highlighted the impacts of environmental change on the behavior, physiology, and seasonal activity of anurans. For instance, in Canada, early spring-breeding species like the wood frog (*Lithobates sylvaticus*), spring peeper (*Pseudacris crucifer*), and northern leopard frog (*L. pipiens*) have been documented to initiate their calling activity earlier in recent years (Walpole et al. 2012); In North America, wood frogs have shown shifts toward earlier breeding times and smaller adult body sizes in response to warming climates (Sheridan et al. 2018). Additionally, environmental change

and declining pond water levels may exacerbate disease susceptibility (Beecher 2006), leading to population declines. Overall, these findings support the conclusion that environmental change has significant impacts on anurans, though the magnitude and direction of these effects vary by species (Ficetola and Maiorano 2016).

1.5 Knowledge gaps

Despite extensive research into species-environment relationships and species co-occurrence patterns, several important gaps remain. First, the majority of research on anuran species-environment relationships and co-occurrence patterns has been conducted in Neotropical regions, leaving gaps in our understanding of these relationships within Asian ecosystems, particularly in subtropical island contexts. For example, in Taiwan, there is limited understanding of how anuran community relate to environmental variables. Second, most existing studies do not incorporate long-term datasets or analyze data across distinct time periods, limiting insights into potential temporal changes in species-environment associations and co-occurrence relationships—a critical gap under rapidly shifting climate and land-use patterns. Third, key environmental factors influencing changes in species composition remain poorly characterized. Addressing these gaps will be essential for better predicting amphibian responses to ongoing environmental changes.

1.6 Aims and objectives

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1) To evaluate the role of environmental filtering in annual community assembly, we applied Canonical correspondence analysis (CCA) across three time periods (2005-2021, 2005-2009, and 2017-2021) to identify which environmental variables associate with species composition and whether these associations vary over time.

2) To assess the role of species co-occurrence relationships, we conducted a co-occurrence analysis and examined potential temporal variation.

Chapter 2 Materials and Methods

2.1 Data

Species occurrence and environmental data were obtained from the Taiwan Amphibians Database, which compiles standardized amphibian survey records collected between 2005 and 2021. This dataset includes records of all anuran species in Taiwan (*Buergeria otai, B. robusta, Bufo bankorensis, Duttaphrynus melanostictus, Fejervarya limnocharis, Hoplobatrachus chinensis, Hyla chinensis, Hylarana latouchii, Limnonectes fujianensis, Kurixalus eiffingeri, K. idiootocus, Microhyla heymonsi, Nidirana adenopleura, Odorrana swinhoana, Pelophylax fukienensis, Polypedates braueri, P. megacephalus, Rana longicrus, R. sauteri, Sylvirana guentheri, Zhangixalus moltrechti, Z. taipeianus, Z. aurantiventris, Rhinella marina, N. shyhhuangi, A. catesbeiana, M. butleri, K. berylliniris, Kaloula pulchra, Eleutherodactylus planirostris* and *F. cancrivora*), as well as site-level measurements of temperature, humidity, and microhabitats determined through visual assessment during fieldwork.

The study site, Taiwan, is a subtropical island and spanning a latitudinal range from approximately 21.9°N to 25.3°N and exhibits high topographic complexity, with elevations ranging from sea level to nearly 4,000 meters. This geographic and elevational variation gives rise to a wide range of climatic conditions—from tropical lowlands to temperate mountain forests—positioning Taiwan as a biodiversity hotspot with notable levels of endemism. Amphibian habitats in Taiwan range from lowland wetlands and agricultural landscapes to pristine mountain streams and forests, providing a wide array of ecological niches.

A total of 3,534 survey sites were included in the analysis, the locations are showed in *Fig. 1 a)*. Surveys were conducted by trained volunteers following a consistent general protocol, which involved visual and auditory detection of amphibians. Observations were made between approximately 30 minutes after dawn and midnight. In each survey, observers documented both the occurrence and the number of individuals for every amphibian species detected. Auditory detection was based on species recognition by ear. However, survey effort was not standardized across volunteer groups, and the number of visits per site varied and was not recorded in a consistent manner. Microhabitats were visually classified in the field. Note that the classification system for microhabitat changed in 2014, please see *Table 1* for more details.

Data were cleaned prior to analysis to remove erroneous entries, including values with 0% relative humidity, temperatures exceeding 50 °C, empty microhabitat descriptions, and records missing location or date information. For the temporal comparison, we used data from the entire period (2005–2021), as well as two-time windows: 2005–2009 and 2017–2021. Only sites with data available in both of these periods were included in temporal comparisons (*Fig. 1 b)*). Prior to the Canonical Correspondence Analysis, we excluded datapoints with microhabitat type accounted for less than 1%.

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2.2 Species filtering and microhabitat classification

To minimize small-sample bias we discarded species represented by < 1000 individuals in the 2005–2021 dataset (*Zhangixalus aurantiventris*, *Rhinella marina*, *Nidirana shyhhuangi*, *Aquarana catesbeiana*, *Microhyla butleri*, *Kurixalus berylliniris, Kaloula pulchra*, *Eleutherodactylus planirostris* and *Fejervarya cancrivora*), leaving *Polypedates megacephalus* as the only exotic species retained for analysis. The microhabitats were classified into 32 different categories as showed in *Table 1*. All data handling and ordinations were performed in R 4.4.3 (Team 2021) using dplyr 1.1.1 for filtering and vegan 2.6-4 for CCA.

2.3 Methods to examine species-environment relationships

Understanding the species-environmental relationships remains a central goal in ecology. We applied Canonical Correspondence Analysis (CCA) (ter Braak 1986) —a direct gradient analysis that relates community composition to environmental variables using constrained ordination. CCA does not rely on trait or phylogenetic data and is well suited to long-term, observational datasets like ours. CCA was conducted separately for three time periods: 2005–2009, 2017–2021, and 2005-2021. For data from 2005-2021, the independent variables include temperature, humidity, year and microhabitat, and for data from 2005-2009 and 2017-2021, the independent variables include temperature, humidity, and microhabitat.

Species abundance data were Hellinger-transformed using the ‘decostand()’ function from the vegan package to reduce the influence of zeros and skewed distributions. Temperature

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and humidity were log-transformed and microhabitat was treated as a categorical covariate. Ordination plots were created using ‘ordiplot()’ to visualize species–environment relationships.

2.4 Testing temporal changes in environment and microhabitat composition

To evaluate whether temperature and humidity significantly differed between two time periods (2005-2009 and 2017-2021), we applied generalized linear mixed-effect models (GLMMs) to the combined dataset using the lme4 and glmmTMB packages in R version 4.4.3. We first imported two separate environmental datasets corresponding the two time periods. A categorical variable ‘time_period’ was added to each dataset to indicate the sampling period, and the two datasets were merged. Humidity was linearly rescaled to fit the (0, 1) interval using a simple transformation, enabling modeling with a beta distribution. The variable ‘location’ (site) was included as a random effect to account for repeated measurements within the same site across years. For temperature analysis, the fixed effect ‘time_period’ captured the difference in mean temperature between the two sampling periods, while the random intercept for location controlled for site-level variation. Model summaries were obtained using ‘summary()’ and significance of the fixed effect was assessed via ‘anova()’ using type II Wald qui-square tests. Because humidity values were bounded between 0 and 1 after rescaling, we used a beta regression mixed model with a logit link. this model was fit using the ‘glmmTMB()’ function from the ‘glmmTMB’ package.

To evaluate whether microhabitats were significantly different across two time periods, we applied Bayesian multinomial logistic regression model using the brms package in R 4.4.3. The model specification treated microhabitats as a categorical response variable without assigning a reference category, allowing for symmetric treatment of all habitat types. Posterior inference was based on Markov Chain Monte Carlo sampling, using 4 chains with 1000 iterations per chain. We inspected the posterior distributions of the category-specific regression coefficients to assess how predictors influenced the selection of each microhabitat. A microhabitat type was considered significantly different in its association with a covariate if the 95% credible interval (CI) of the corresponding posterior estimate did not include zero.

2.5 Methods to examine species co-occurrence patterns

To understand the co-occurrence patterns between species and the temporal changes in co-occurrence patterns, we also applied co-occurrence analysis, which infers non-random associations between species across sites (Ulrich et al. 2012). Co-occurrence patterns—whether two species are found together more or less often than expected by chance—can provide indirect evidence of biotic interactions, with aggregation suggesting shared habitat preference, and segregation potentially indicating competitive exclusion.

To conduct pairwise co-occurrence analysis, we used the cooccur package. Species matrices were binarized (presence–absence), transposed, and formatted as required. Species pairs with significantly more or fewer co-occurrences than expected under random assembly ($p < 0.05$) were interpreted as evidence of potential biotic interactions. In the resulting co-occurrence plots, significant positive associations (species that co-occur more often than expected, possibly

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due to shared environmental preferences or facilitation) were visualized in blue, while significant negative associations (species that co-occur less often than expected, potentially due to competitive exclusion) were shown in yellow.

Although co-occurrence analysis only reveals patterns of species co-occurrence and does not directly infer species-species interactions, it provides an alternative approach to examining how environmental and biotic factors may shape community structure when experimental data or trait information is unavailable. Analyses were performed in R 4.1.2 using the cooccur package (Griffith et al. 2016).

Chapter 3 Results

3.1 2005-2021 CCA results: species relationships with environmental variables

We used CCA to understand the relationships between environmental variables and species distribution. The CCA results from 2005-2021 show that the total explained variance was 9.91%, with CCA 1 accounting for 36.58% and CCA 2 for 20.01% of the variation (*Fig. 2*). Species generally had diverse niches (e.g., temperature, humidity, and microhabitats). Regarding temperature, some species fell along the temperature axis. The population density of *Ho. chinensis*, *S. guentheri*, *D. melanostictus*, *F. limnocharis*, *P. braueri* and *N. adenopleura* correlated with high temperature; however, the population density of *Z. taipeianus*, *K. eiffingeri*, *R. longicrus*, *B. bankorensis*, *R. sauteri,* and *O. swinhoana* was correlated with low temperature. Regarding humidity, the axis is shorter compare to temperature, *N. adenopleura*, *P.*

megacephalus, *P. fukienensis*, *K. idiootocus*, and *Hy. chiensis* are correlated with low humidity, the species like *H. latouchii, O. swinhoana*, *B. bankorensis*, *B. otai, B. robusta,* and *R. sauteri* were correlated with higher humidity. Regarding microhabitats, species generally associated with different microhabitats, although some types (e.g., short grass, artificial field, shore of still water) showed similar effect on species density.

The CCA results showed both consistent and inconsistent results with field observations. Consistently, arboreal species *Hy. chinensis, Z. moltrechti* and *K. idiootocus* was associated with microhabitat of vegetation; *R. sauteri* was reportedly found at higher latitude, consistent with its association with low temperature in the CCA; and *O. swinhoana* was reportedly correlated with stream or creak in the field, consistent with running water in the CCA. Inconsistently, some arboreal species (e.g., *B. otai* and *Z. taipeianus*) are not correlate with vegetation types; species in family Ranidae reportedly correlated with aquatic habitat (Solomampianina and Molnár 2011), but this correlation was not revealed for the species *R. longicrus* .

3.2 2005-2009 CCA results: species relationships with environmental variables

The CCA results from 2005–2009 was showed in *Fig. 3*. The results showed that the total explained variance was 36.93%, with CCA 1 accounting for 38.62% and CCA 2 for 21.49% of the variation. Regarding temperature, many species were distributed along the temperature axis. *Ho. chinensis, D. melanostictus, F. limnocharis, M. heymonsi,* and *S. guentheri* were correlated with high temperature; while *K. eiffingeri*, *Z. moltrechti, Z. taipeianus, L. fujianensis, O. swinhoana,* and *B. bankorensis* were associated with low temperature. Regarding humidity, *Z.*

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moltrechti, *K. taipeianus, K. eiffingeri, L. fujianensis* and *O. swinhoana* showed a correlation with high humidity; *Ho. chinensis, B. robust,* and *R. sauteri* were correlated with low humidity. Regarding microhabitat, *S. guentheri* associated with short grass; *K. eiffingeri* correlated with building; *B. robusta* correlated with vegetation types of bush.

The CCA results showed both consistent and inconsistent patterns compared with field observations. Consistently, species such as *Z. taipeianus* and *R. longicrus* have been reported as winter breeders (Kam et al. 1995, Chang et al. 2014), and were associated with low temperature in this study. However, many species like *K. eiffingeri, Z. moltrechti* and *Z. taipeianus* were found in man-made structures like buildings and the slope of the ditch.

3.3 2017-2021 CCA results: species relationships with environmental variables

The CCA results from 2017–2021 showed that the total explained variance was 17.31%, with CCA 1 accounting for 34.26% and CCA 2 for 16.82% of the variation (*Fig. 4*). Temperature, humidity, and microhabitats were all important factors affecting species distribution. Regarding temperature, *H. latouchiti, R. sauteri, S. guentheri, N. adenopleura* were correlated with high temperature; while *F. limnocharis, B. bankorensis, D. melanostictus, Z. moltrechti,* and *P. megacephalus* were correlated with low temperature Regarding humidity, the patterns were less obvious, *P. braueri, Z. moltrechti,* and *P. megacephalus* showed weak correlation with low humidity; *P. fukienensis, R. longicrus, L. fujianensis,* and *O. swinhoana* showed correlation with high humidity. Regarding microhabitats, majority of the microhabitats were clustered in the center of the plot and cannot well distinguish species from different microhabitat, still *P. fukienensis* and *Ho. chinensis* were correlated with river wider than 5 meters; species like *N. adenopleura* and *O. swinhoana* were correlated with microhabitat around temperate still water.

The CCA results showed both consistent and inconsistent patterns compared to field observations. Consistently with field observation, *Z. moltrechti, B. bankorensis,* and *R. longicrus* were correlated with lower temperature; *O. swinhoana* was correlated with running water; arboreal species tend to correlated with low humidity. Inconsistent with conventional field observations, most of the species did not show clear patterns correlated with certain microhabitat types, for example, species in family Ranidae like *R. longicrus* were not correlated with water body; species prefer lower temperature like *R. sauteri* did not correlated with lower temperature; and arboreal species like *Z. moltrechti, B.otai,* and *P. megacephalus* did not correlated with the microhabitat of vegetation types.

3.4 Comparison between 2005-2009 and 2017-2021 CCA results

Species generally showed different relationships with environmental factors between the two time periods. For instance, *H. latouchii* correlated with still water and showed weak correlation with lower temperature during 2005-2009, however, during 2017-2021, it did not show clear correlations with microhabitats and was positively correlated with higher temperature. During 2005-2009, *L. fujianensis* correlated with still water; while during 2017-2021, it did not show clear correlation with certain microhabitat; *D. melanostictus* was correlated with higher temperature during 2005-2009, but correlated with lower temperature during 2017-

2021. During 2005-2009, *Z. moltrechti* was correlated with high humidity and the microhabitat of artificial slope, while during 2017-2021, it was correlated with lower humidity and did not show clear correlation pattern with microhabitat.

A few species showed consistency between the two time periods. For example, *B. bankorensis* and *R. longicrus* was correlated with lower temperature; *S. guentheri* correlated with higher temperature and temperate still water during 2005-2009, and during 2017-2021, it correlated with higher temperature and both temperate and permanent still water.

3.5 Environmental change between 2005-2009 and 2017-2021

To evaluate whether shifts in community composition were associated with temporal variations in temperature and humidity, we employed generalized linear mixed models (GLMMs), incorporating time period (2005–2009 vs. 2017–2021) as a fixed effect and treating sampling site as a random effect. The model estimated a mean temperature of 24.66 °C in 2005–2009, which declined by 1.37 °C in 2017–2021 (p-value < 0.05, *Table 2*), indicating a statistically significant decrease in mean temperature. Similarly, mean relative humidity increased from 78.14% in 2005–2009 to 78.90% in 2017–2021 (p-value < 0.05, *Table 3*), demonstrating a significant rise in humidity. These shifts in temperature and humidity between the two periods suggest that altered environmental conditions may have contributed to the observed changes in species distributions. Regarding microhabitat type, these two periods did not differ significantly after considering the microhabitat re-classification (*Table 4*).

3.6 Results of co-occurrence analyses

The co-occurrence analysis results of 2005-2021, 2005-2009, and 2017-2021 were showed in Fig. 5, Fig. 6, and Fig. 7, respectively, and the overall percentage of each scenario is showed in *Table 5*. Overall, the results from 2005–2021 showed that positive species relationships were more common than negative ones, with 139 positive (60%), 69 negative (30%), and 23 random (10%) relationships. Certain species exhibited clear co-occurrence patterns. For example, although 30% of all species pairs had negative co-occurrence relationships, *R. sauteri*, *Z. moltrechti*, and *P. megacephalus* showed even higher proportions of non-co-occurrence with other species, at 62%, 52%, and 57%, respectively. In contrast, *H. latouchii*, *N. adenopleura*, *P. braueri*, and *K. eiffingeri* tended to have more positive associations with other species, with 90%, 86%, 81%, and 81% of their pairings being positive, respectively.

The results from 2005–2009 showed a similar pattern to those from 2005–2021. More species pairs exhibited positive than negative co-occurrence relationships. However, the proportion of random relationships was the highest among the three time periods, with 71 positive (37%), 38 negative (20%), and 81 random (43%) relationships. During this period, *P. megacephalus* had not yet been introduced to Taiwan, and *B. otai* had not been distinguished from *B. choui*, making direct comparisons challenging. Compared to the average proportion of species pairs with positive co-occurrence relationships, *H. latouchii*, *L. fujianensis*, and *K. idiootocus* showed higher positive co-occurrence rates, at 63%, 63%, and 68%, respectively. Unlike the results from 2005–2021, there were fewer species with a high percentage of negative co-occurrence relationships, with *D. melanostictus, F. limnocharis, Ho. chinensis,* and *Z. moltrechti* each showing 37% negative associations. Some species had notably high percentages

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of random co-occurrence relationships, such as *Hy. chinensis* (68%), *M. heymonsi* (63%), and R. longicrus (84%).

The 2017–2021 results were similar to those from 2005–2021, with 150 positive (65%), 60 negative (26%), and 21 random (9%) co-occurrence relationships. 26% of species pairs exhibited negative associations, and *P. megacephalus*, *R. sauteri*, and *Z. moltrechti* had higher percentages of non-co-occurrence with other species, at 48%, 57%, and 48%, respectively. Meanwhile, *H. latouchii*, *N. adenopleura*, and *P. braueri* continued to show strong positive associations, with 95%, 86%, and 81% positive co-occurrence rates, respectively.

3.7 Temporal changes in co-occurrence relationships

The results for 2005–2021 and 2017–2021 were similar, with positive relationships accounting for 60% and 65%, negative relationships for 30% and 26%, and random relationships for 10% and 9%, respectively. While the 2005–2009 period also exhibited more positive than negative species associations, it stood out for having a significantly greater proportion of random pairwise relationships than the other two time periods.

Some species showed consistent co-occurrence patterns over time. For instance, *H. latouchii, L. fujianensis, K. idiootocus*, and *N. adenopleura* maintained positive relationships with most other species across both the 2005–2009 and 2017–2021 periods. However, the species most associated with negative co-occurrence relationships varied between time periods. During 2005–2009, *D. melanostictus, F. limnocharis, Ho. chinensis*, and *Z. moltrechti* had the highest proportions of negative co-occurrences, whereas in 2017–2021, the species were *P. megacephalus*, *R. sauteri*, and *Z. moltrechti*.

Chapter 4 Discussion

4.1 Overall results

To identify species-environment relationships and species-species co-occurrence relationships, this study employed CCA to investigate species-environment relationships and used co-occurrence analyses to explore species interactions in anuran communities in Taiwan. The CCA results revealed clear patterns of niche differentiation among anurans; the co-occurrence analyses showed more positive than negative associations between species pairs during all 3 time periods, while the percentage of random relationships was higher between 2005-2009.

4.2 Variability in CCA Explanatory Power

The total explained variance of the CCA was relatively low across all periods, particularly for the full dataset from 2005–2021, which accounted for only 9.91% of the total variance. This suggests that species distribution patterns may be shaped by additional unmeasured environmental or biotic factors, such as interspecific competition or historical land use legacies, that were not captured in the analysis. Notably, the CCA conducted for the period 2005–2009 explained a much higher proportion of variance (36.93%) compared to 2017–2021

(17.31%). Since the number of data points in 2005–2009 was smaller than in 2017–2021, this could imply that the data from 2017–2021 contained more noise. The difference may also reflect stronger environmental filtering or more stable environmental gradients in earlier years, whereas more recent conditions may have become increasingly disturbed, homogeneous, or stochastic—possibly due to ongoing urbanization, environmental change, or shifts in land management. Another potential explanation for the lower explanatory power, especially in the full dataset, is methodological: although microhabitat was included as an important variable, rare habitat types accounting for less than 1% of observations were removed, yet more than ten microhabitat types still remained in the analysis. This may have introduced noise or redundancy, limiting the CCA's ability to detect clear species–environment relationships. Together, these factors suggest that both ecological and methodological considerations influenced the explanatory power of the CCA over time.

4.3 Temporal dynamics of species-environment relationships

By analyzing anuran community data spanning 16 years, we identified clear temporal changes in environmental variables and their influence on species–environment relationships. For example, between 2005–2009 and 2017–2021, mean temperature significantly decreased, and humidity increased. The effects of these environmental changes on species–environment associations varied among species: some species, such as *Zhangixalus moltrechti* and *Odorrana swinhoana*, showed consistent associations with specific environmental variables (e.g., low temperature and running water, respectively), while others, like *Nidirana adenopleura*, shifted their associations with environmental variables between the two periods. While the mechanisms

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driving these shifts remain unclear, our findings suggest that temperature, humidity, and land use change are likely involved, echoing their reported influences on community composition over time (Murray et al. 2021). These temporal dynamics of community assembly and associated environmental variables highlight the value and necessity of long-term ecological studies, which provide critical insights for biodiversity monitoring and landscape-level conservation planning.

4.4 The inconsistency of CCA results with field observation

The CCA results across different periods demonstrated both consistent and inconsistent patterns when compared to field observations. Consistently, certain species' associations matched expected ecological patterns. For example, the arboreal species *Hy. chinensis*, *Z. moltrechti*, and *K. idiootocus* were associated with vegetation-rich microhabitats in the 2005–2021 dataset; *R. sauteri* showed a preference for low-temperature environments, consistent with its high-altitude distribution; and *O. swinhoana* was associated with running water habitats. Similarly, winter-breeding species such as *Z. taipeianus* and *R. longicrus* correlated with lower temperatures in both the 2005–2009 and 2017–2021 datasets. In 2017–2021, consistent results also included *Z. moltrechti*, *B. bankorensis*, and *R. longicrus* associating with lower temperatures, and *S. guentheri* with warmer habitats and still-water environments.

However, several inconsistencies were also evident. Arboreal species such as *B. otai, Z. taipeianus*, and *P. megacephalus* did not show expected correlations with vegetation types. Similarly, although members of the Ranidae family are generally associated with aquatic habitats (Solomampianina and Molnár 2011), species like *R. longicrus* and *B. bankorensis* did not exhibit strong correlations with water bodies in some time periods. Notably, the expected association

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between *O. swinhoana* and running water was absent in the 2017–2021 results, and *R. sauteri*, typically associated with cooler temperatures, was instead correlated with warmer habitats during that period.

These discrepancies may stem from several factors. Methodologically, although we excluded microhabitat types contributing less than 1% of observations, there are still many different microhabitats, which might affect the CCA results. Additionally, by assigning a single dominant (modal) microhabitat per site may still overlook ecologically meaningful variation—particularly for species that rely on patchy or transitional habitats. This simplification, though necessary to reduce noise and avoid overparameterization, may obscure fine-scale species–habitat associations. Moreover, limitations inherent to CCA—such as its assumption of unimodal responses and insensitivity to complex or nonlinear ecological interactions—may hinder its ability to detect true ecological patterns. Furthermore, environmental variables beyond temperature, humidity, and broad microhabitat categories—such as canopy cover, soil moisture, or predator abundance—may also be important drivers of species distributions but were not included in the analysis. To better capture species–environment relationships, future studies could incorporate finer-scale environmental metrics and consider complementary analytical approaches, such as generalized additive models or hierarchical modeling.

4.5 Temporal shifts in species co-occurrence patterns

The co-occurrence analyses revealed notable temporal changes in species–species relationships across the periods 2005–2009 and 2017–2021. While positive co-occurrence relationships dominated in all periods, their proportion increased over time—from 37% in 2005–

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2009 to 65% in 2017–2021—accompanied by a decline in random associations. This trend suggests that species distributions might have become more spatially overlapping in recent years, potentially due to increasing environmental changes or shared responses to changing environmental conditions. Some species exhibited consistent co-occurrence patterns across time. For example, *H. latouchii*, *N. adenopleura*, and *P. braueri* maintained strong positive associations with most other species in both time periods. In contrast, species showing consistently high levels of negative associations—such as *R. sauteri*, *Z. moltrechti*, and *P. megacephalus*—tended to co-occur with fewer species, possibly reflecting distinct habitat preferences or niche specialization.

Interestingly, the species associated with negative co-occurrence relationships shifted between time periods. During 2005–2009, species like *D. melanostictus, F. limnocharis, Ho. chinensis*, and *Z. moltrechti* exhibited the highest rates of non-co-occurrence. However, by 2017–2021, this pattern had shifted to include *P. megacephalus*, *R. sauteri*, and *Z. moltrechti*. This turnover suggests that species-species interactions may be changing over time, possibly influenced by environmental changes, species introductions, or anthropogenic disturbances. Overall, the temporal increase in positive co-occurrence relationships may reflect greater habitat sharing or reduced niche segregation, while the shifting identity of negatively associated species underscores the dynamic nature of species interactions in response to changing environments. These results highlight the importance of long-term monitoring to capture fluctuations in community assembly and species coexistence patterns.

4.6 Conservation implications

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This study provides valuable insights for conservation planning by highlighting how species–environment relationships and species associations have changed over time. The CCA results revealed that temperature, humidity, and microhabitat are important factors shaping anuran community composition, though their explanatory power has declined in recent years. This weakening of environmental associations suggests that habitat conditions may have become more homogeneous or disturbed, potentially due to anthropogenic pressures. Nevertheless, some species maintained consistent preferences—such as *O. swinhoana* with running water or arboreal species with low humidity—indicating the continued relevance of specific habitat features for certain taxa.

The co-occurrence analyses from 2005–2021 showed that more species pairs exhibited positive rather than negative associations, suggesting a tendency toward aggregation rather than exclusion. This, together with the species-specific environmental associations observed in CCA, highlights the importance of maintaining or restoring a diverse array of habitat types that can support a wide range of ecological niches and promote species coexistence.

Therefore, conservation efforts should prioritize habitat heterogeneity—including the preservation of variance microhabitats—to sustain functionally rich and resilient anuran communities. Species with strong and consistent environmental preferences may serve as ecological indicators, while shifts in species–environment relationships could serve as early warning signs of community-level disturbance or environmental change.

4.7 Study limitations

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There are several limitations to this study. First, our analysis did not include functional trait or phylogenetic information, both of which are commonly applied in past research to enhance insights into community assembly mechanisms (Spasojevic and Suding 2012, Braun and Lortie 2024). Integrating functional traits and phylogenetic information can let us have a better understanding of how competition and evolutionary history participated in the formation of species community. This omission is primarily due to the incompleteness, inaccuracy, and coarse resolution of existing functional trait datasets for anurans in Taiwan. Many of our study species are either missing from these datasets or have trait records – such as habitat preferences—that do that align with field observations.

Second, we attempted to include functional traits in the JSDM. However, due to the large size of our dataset, the computational load was too high, and the model failed to complete the analysis within a feasible time frame. This limitation restricted our ability to assess the role of trait-mediated processes in shaping community structure.

Third, to reduce multicollinearity and improve model stability, we simplified land-use data and assigning a single dominant (modal) land-use type to each site. While this approach was necessary for computational feasibility, it may have overlooked important but less dominant habitat features, potentially leading to an incomplete representation of habitat heterogeneity and affecting the accuracy of species–habitat associations in the CCA.

Fourth, spatial sampling was uneven across regions and time periods. Only a small number of sites had survey data from both 2005–2009 and 2017–2021, with just one site in southern Taiwan and three in central Taiwan. The majority of long-term survey sites were

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concentrated in northern Taiwan, which may introduce spatial bias and limit the generalizability of our findings to other regions.

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Appendix

Table 1 Classification of microhabitats. An asterisk (*) indicates categories used only prior to 2014 that cannot be merged into the post-2014 classification system.

Habitat types	Microhabitats	Abbreviation
草地	短草	short_grass
草地	高草	tall_grass
樹木	灌木	veg_bush
樹木	底層	veg_bottom
樹木	果園*	veg_fruit
樹木	竹子	veg_bamboo
樹木	喬木	veg_arbor
人造區域	-	art
人造區域	建物	art_building
人造區域	邊坡*	art_slope
人造區域	乾溝	art_dry_ditch
人造區域	步道	art_trail
人造區域	車道	art_road
人造區域	空地	art_field
靜止水域	岸邊	still_shore

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靜止水域	水溝*	still_ditch
靜止水域	植物	still_plant
靜止水域	水域	still_water
靜止水域	旱田*	still_dry
暫時性靜止水域	水域	temp_still_water
暫時性靜止水域	水田*	temp_still_paddy
暫時性靜止水域	岸邊	temp_still_shore
暫時性靜止水域	植物	temp_still_plant
暫時性靜止水域	植物	temp_still_plant_puddle
暫時性靜止水域	-	temp_still
永久性靜止水域	水域	per_still_water
永久性靜止水域	岸邊	per_still_shore
永久性靜止水域	植物	per_still_plant
永久性靜止水域	-	per_still
流動水域	河流 > 5m	run_w_river
流動水域	河流 < 5m	run_s_river
流動水域	山澗瀑布	run_waterfall

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Table 2 GLMM results for temperature

Predictor	**Estimate (β)**	**SE**	**df**	**t-value**	**p-value**
Intercept (2005–2009)	24.6591	0.1157	11463.3316	213.05	< 0.001
Time period (2017–2021 vs 2005–2009)	-1.3754	0.1255	11464.7173	-10.96	< 0.001

Table 3 GLMM results for humidity

Predictor	**Estimate (β)**	**SE**	**z-value**	**p-value**
Intercept (2005–2009)	1.27117	0.02013	63.14	< 0.001
Time period (2017–2021 vs 2005–2009)	0.04462	0.02174	2.05	< 0.05

Table 4 Bayesian multinomial logistic regression model results for humidity

	Estimate	**l-95% CI**	**u-95% CI**
art_building	0.99	-0.89	1.91
art_dry_ditch	0	-1.5	1.48
art_field	0.73	-0.35	1.38
art_road	-0.67	-1.82	0.95
art_slope	0.48	-1.42	1.85

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art_trail	-0.13	-1.41	1.57
per_still	0.16	-1.57	1.95
per_still_plant	0.35	-1.8	1.78
per_still_shore	0.51	-0.75	1.76
per_still_water	-0.03	-1.93	1.7
run_s_river	-0.14	-1.17	0.68
run_w_river	-0.21	-1.12	1.07
run_waterfall	0.27	-1.34	1.93
short_grass	-0.43	-1.36	0.83
still_ditch	-1.41	-1.86	-0.79
still_dry	0.45	-0.34	1.51
still_plant	0.03	-1.97	1.9
still_shore	-0.45	-1.02	0.47
still_water	0.1	-1.35	1.94
tall_grass	0.08	-0.68	1.77
temp_still	0.57	-0.53	2.02
temp_still_paddy	0.79	-1.96	1.93

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temp_still_plant	-1.09	-1.98	0.07
temp_still_plant_puddle	0.87	0.38	1.8
tempstillshore	0.03	-1.3	1.6
temp_still_water	1.17	0.47	1.92
veg_arbor	0.4	-0.72	1.67
veg_bamboo	-0.01	-1.54	1.7
veg_bottom	-0.32	-0.93	0.96
veg_bush	-0.48	-1.96	1.53
veg_fruit	0.21	-0.72	1.96

Table 5 Overall results of co-occurrence analyses

	Positive relationships	Random relationships	Negative relationships
2005-2021	139 (60%)	23 (10%)	69 (30%)
2005-2009	71 (37%)	81 (43%)	38 (20%)
2017-2021	150 (65%)	21 (9%)	60 (26%)

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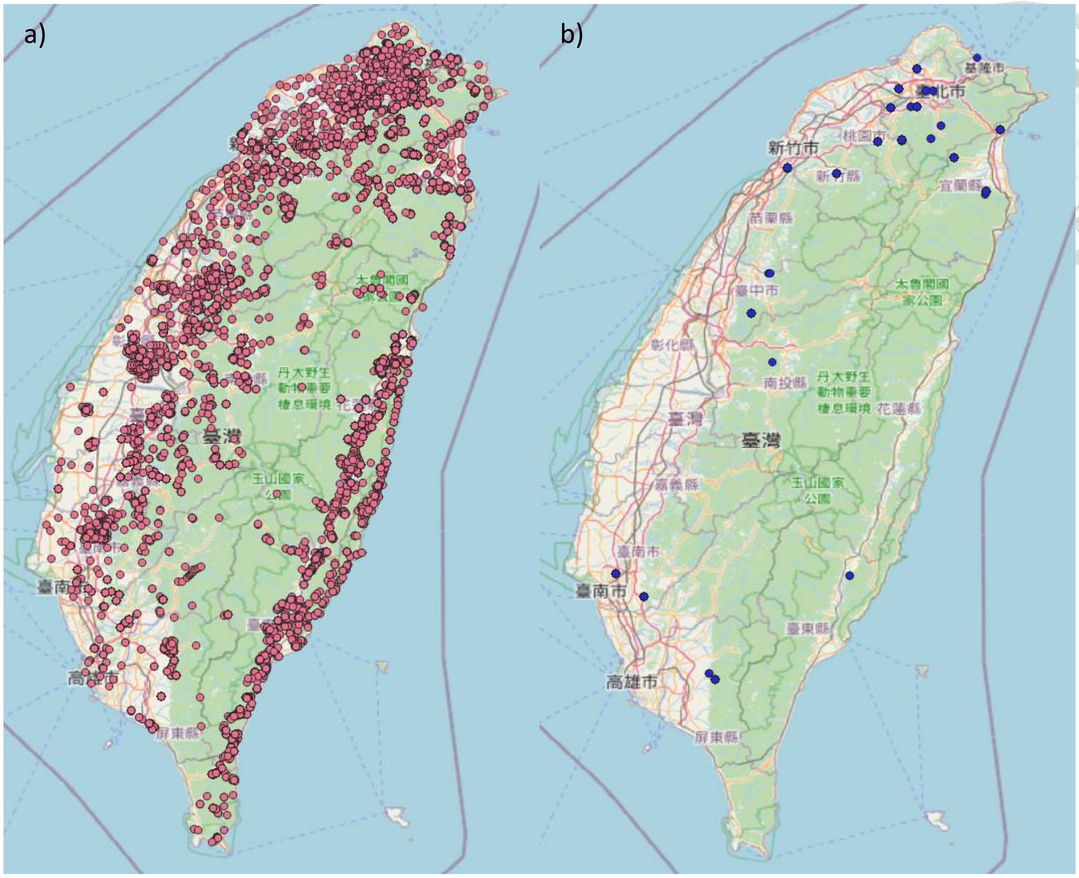

Fig. 1 a) Study sites from 2005-2021. b) Study sites from 2005-2009 and 2017-2021

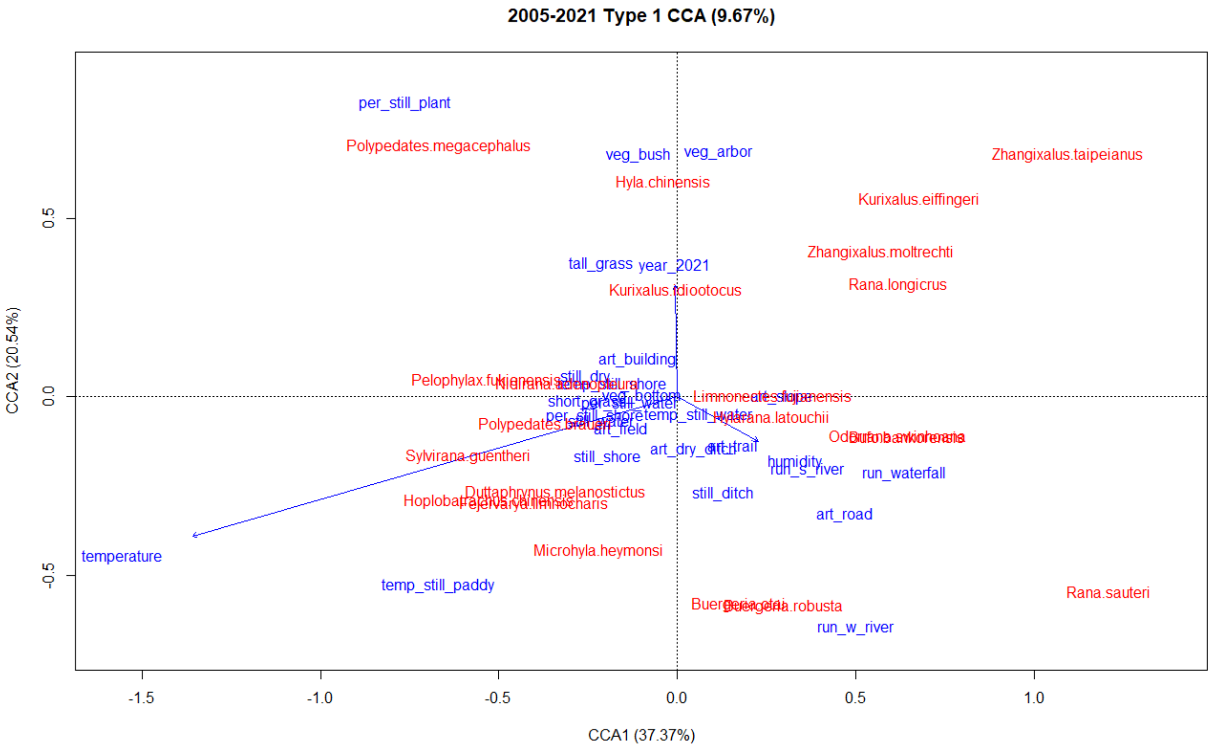

Fig. 2 CCA results biplot during 2005-2021.

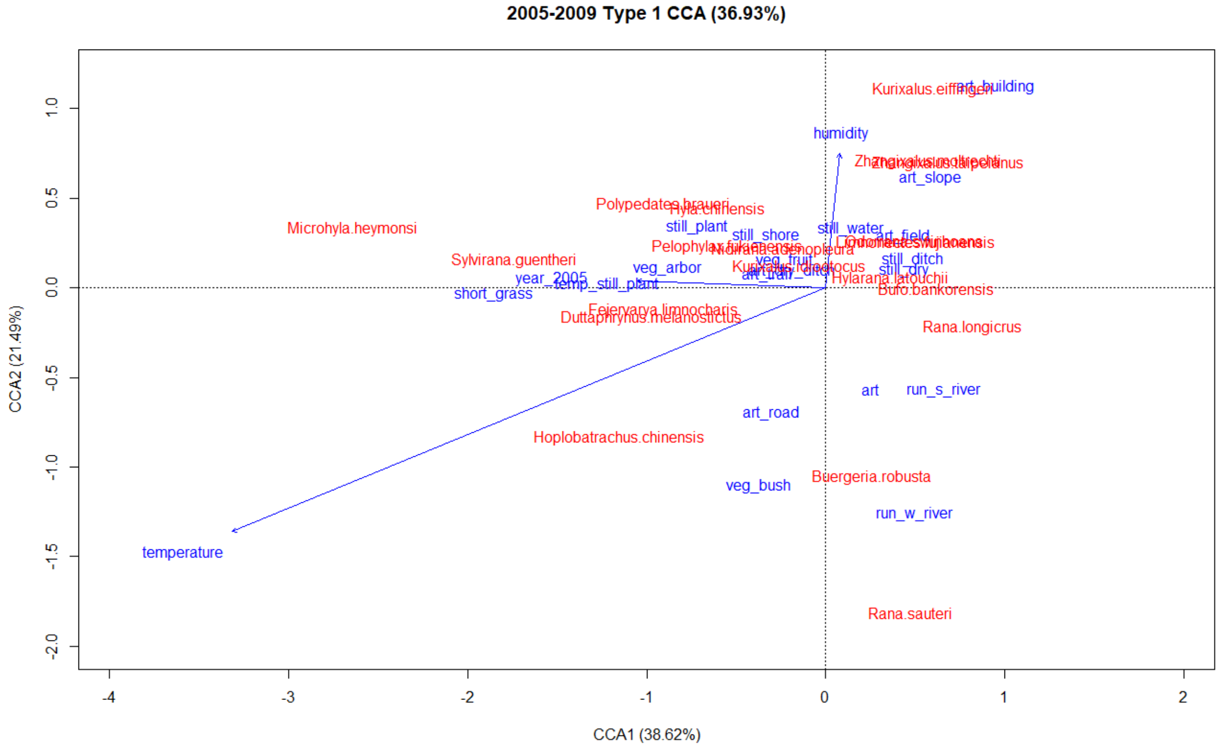

Fig. 3 CCA results biplot during 2005-2009.

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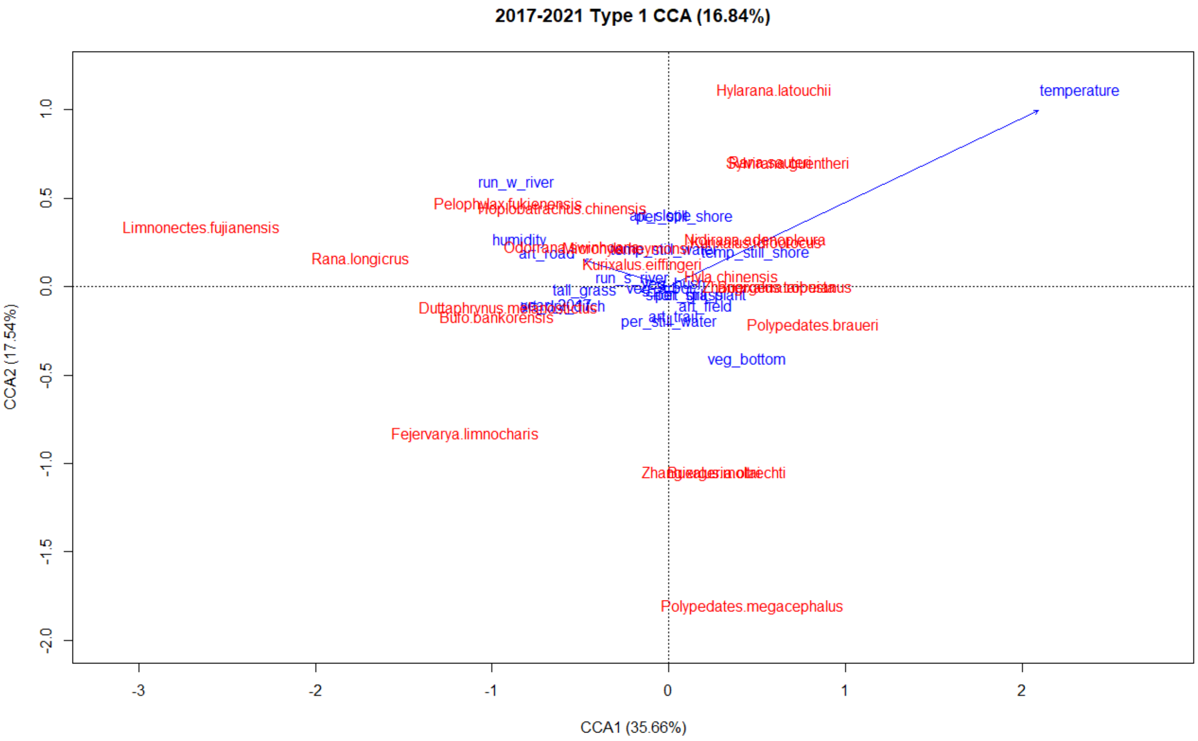

Fig. 4   CCA results biplot during 2017-2021.

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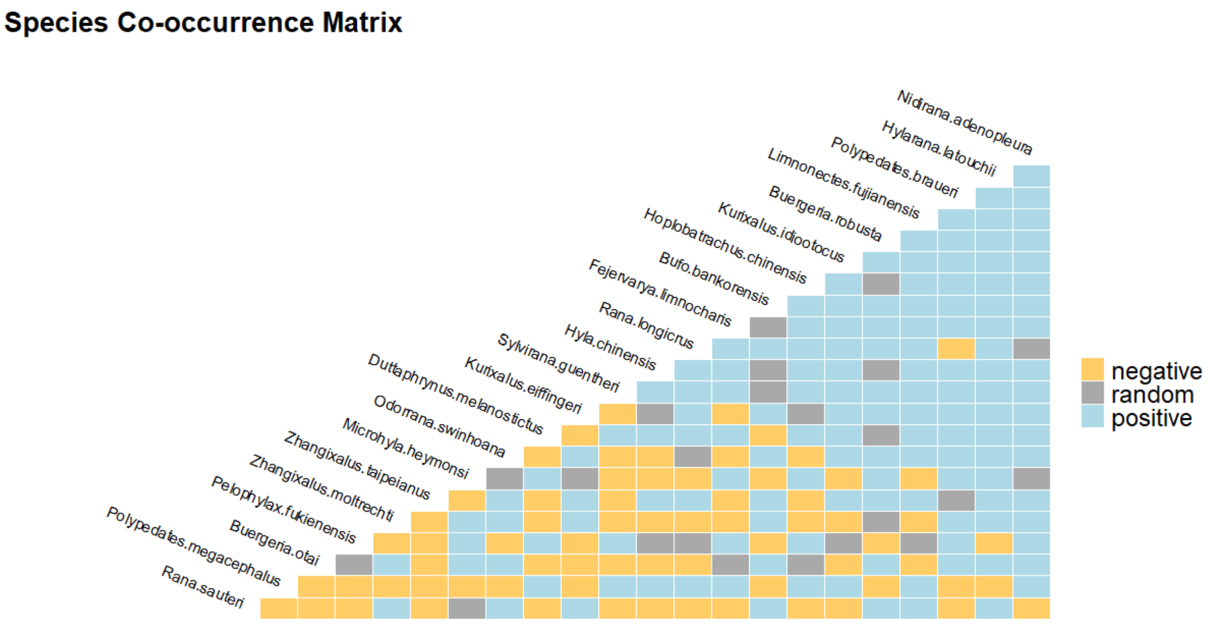

Fig. 5 Co-occurrence analysis results of 2005-2021.

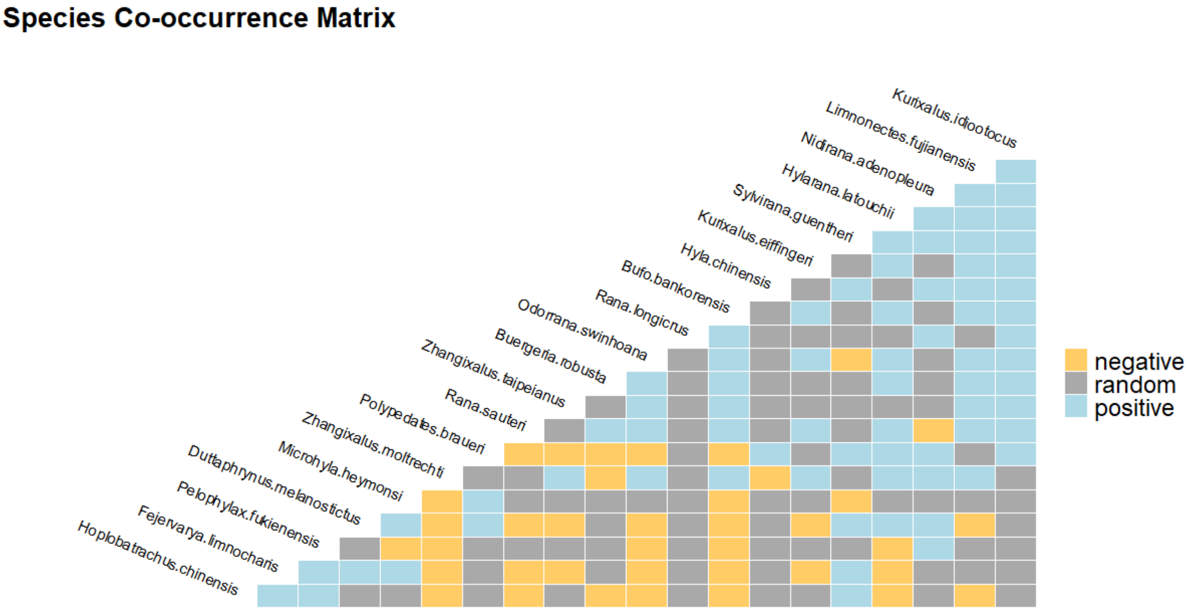

Fig. 6 Co-occurrence analysis results of 2005-2009.

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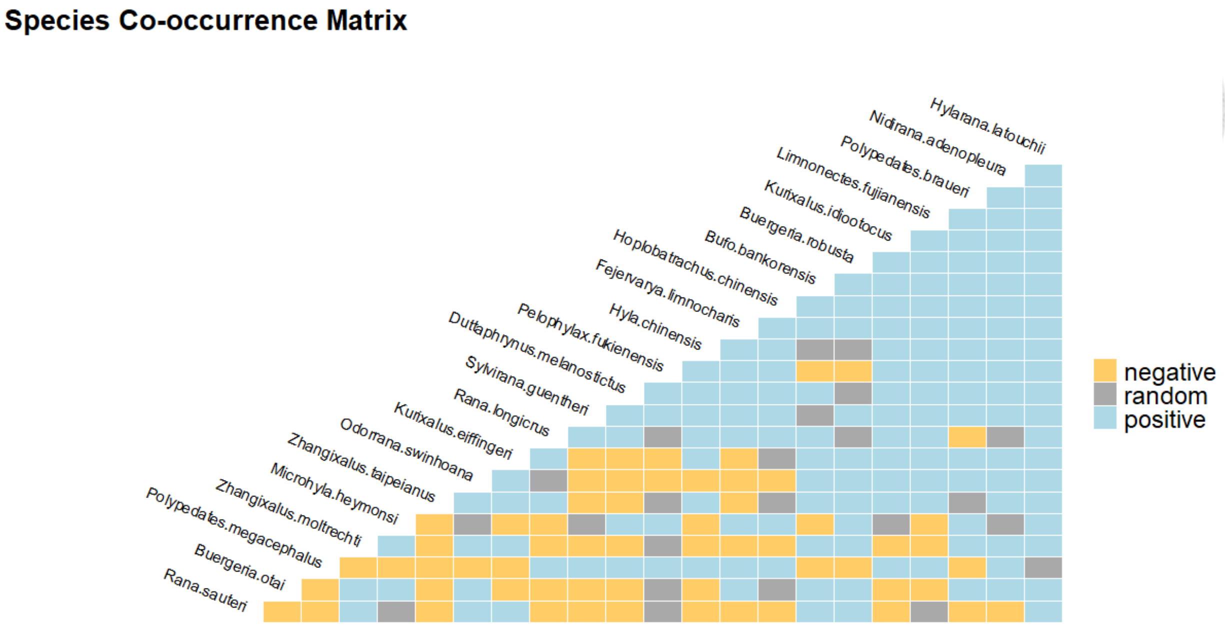

Fig. 7 Co-occurrence analysis results of 2017-2021.

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