UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

FACULTAD DE ESTUDIOS SUPERIORES IZTACALA
ECOLOGÍA

DESARROLLO DE HERRAMIENTAS ANALÍTICAS DE DIVERSIDAD FENOLÓGICA, PERIÓDICA Y BETA TEMPORAL: ESTUDIO DE CASO DE LA COMUNIDAD DE ANFIBIOS DEL ÁREA DE PROTECCIÓN DE FLORA Y FAUNA DE NAHÁ, CHIAPAS.

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

DANIEL JOAQUÍN SÁNCHEZ OCHOA

TUTOR PRINCIPAL DE TESIS:
DR. HIBRAIM ADÁN PÉREZ MENDOZA, FES IZTACALA

COMITÉ TUTOR:
DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA, FES IZTACALA
DRA. PATRICIA KOLEFF OSORIO, CONABIO

LOS REYES IZTACALA, TLALNEPANTLA, ESTADO DE MÉXICO, ENERO 2023.

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UNAM POSGRADO

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FACULTAD DE ESTUDIOS SUPERIORES IZTACALA

OFICIO CPCB/1139/2022

ASUNTO: Oficio de Jurado

M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **26 de septiembre de 2022** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **SÁNCHEZ OCHOA DANIEL JOAQUIN** con número de cuenta **307160847** con la tesis titulada **“Desarrollo de herramientas analíticas de diversidad fenológica, periódica y beta temporal: estudio de caso de la comunidad de anfibios del área de protección de flora y fauna de Nahá, Chiapas.”,** realizada bajo la dirección del **DR. HIBRAIM ADAN PÉREZ MENDOZA,** quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
“POR MI RAZA HABLARÁ EL ESPÍRITU”
Ciudad Universitaria, Cd. Mx., a 06 de diciembre de 2022

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

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ÍNDICE

Resumen

El estudio de la variación espacial y temporal de los patrones de diversidad es esencial para el entendimiento de los patrones y conservación de las especies y las comunidades en un planeta de constante cambio. Las especies evolucionan de diferentes formas sobre el eje espacial y temporal, siendo las variaciones ambientales las que determinan en mayor medida estos cambios. Particularmente, la variación temporal del ambiente asociado hace que los patrones temporales de las especies sean diversos. Actualmente no hay ninguna medida que resuma en un solo valor de buena manera los patrones de diversidad temporal de las comunidades. Particularmente, el nicho temporal de las especies opera de diferentes formas, haciendo que haya diferentes niveles de análisis. En primera instancia, la repartición temporal y la periodicidad de las especies (entendida como la frecuencia de ocurrencia de especies) y de sus procesos biológicos dentro de una comunidad ocurre de manera diferencial. Por otro lado, la heterogeneidad temporal de las comunidades se refiere a cuál es el número de comunidades únicas a lo largo del tiempo. De esta manera se propusieron tres nuevas medidas de diversidad, asociadas a diferentes atributos comunitarios: (1) diversidad fenológica, (2) diversidad periódica y (3) diversidad β temporal. Uno de los objetivos principales de la tesis es desarrollar tres medidas con un marco teórico para ayudar a su comparabilidad e interpretación. De manera general, las tres medidas se construyeron a partir del análisis de series de tiempo y los números de Hill, las cuales representan de forma adecuada: (1) el número efectivo de curvas fenológicas en la comunidad, (2) el número efectivo de curvas periódicas en la comunidad y (3) el número efectivo de comunidades únicas en el tiempo. Todas las medidas fueron probadas con simulaciones donde se varió la riqueza de especies y su abundancia relativa y con datos reales de campo. De manera general, las tres medidas fueron consistentes en su funcionalidad con las otras medidas de diversidad basadas en los números de Hill. Por lo tanto, las tres medidas proveen una forma interpretable y comparable de diversos atributos temporales, haciendo notar así mismo su fácil replicabilidad en otros taxones y series de datos temporales de diferentes resoluciones. Finalmente, las medidas propuestas tienen implicaciones en la teoría ecológica, y aplicaciones en planes de manejo de áreas de conservación y monitoreo de la biodiversidad, entre otros.

Abstract

The study of the spatial and temporal variation in diversity patterns has become essential for the understanding and conservation of species and communities in a world of constant change. Species activities vary tremendously over space and time, and environmental variation plays a major role in shaping variation in activity patterns. Environmental variation along temporal axes generates diversity in the temporal patterns of species. There currently is no measure that effectively summarizes the temporal attributes of communities. The properties of the temporal niches of species are multifarious, and this requires different types of analysis. Variation in the temporal distribution and periodicity of species can affect variation in the biological processes within communities. The temporal heterogeneity of communities directly regulates the uniqueness of communities over time. Three new diversity measures were proposed to summarize different community traits: (1) phenological diversity, (2) periodical diversity, and (3) temporal β diversity. The main objective of this work was to develop three measures with a robust theoretical framework that can be easily compared and interpreted. We constructed the measures based on time series analysis and Hill numbers theory. These new measures characterize (1) the effective number of phenological curves in a community (PE), (2) the effective number of periodic curves in a community (PeD), and (3) the effective number of unique communities over time (TβD). All measures were tested with simulations where the species richness and relative abundance of species were varied as well as with empirically collected field data. In general, these three measures were consistent with other Hill numbers measures. These measures thus provide an effective approach for measuring various temporal traits of communities in an interpretable and comparable manner that is widely applicable to other taxa and time series data sets with various resolutions. The proposed measures have the potential to contribute to the development of ecological theory, management of conservation areas, biodiversity monitoring, between others.

CAPÍTULO I

INTRODUCCIÓN

Desarrollo de herramientas analíticas de diversidad fenológica, periódica y beta temporal: estudio de caso de la comunidad de anfibios del área de protección de flora y fauna de Nahá, Chiapas.

El estudio de la variación de la biodiversidad es central para la teoría ecológica de comunidades (McGill et al. 2006; Willis et al. 2007). En general el principal objetivo de los estudios de diversidad es entender la distribución espacial y temporal de las especies en el planeta y a su vez, conocer cuál es su relación con las variables ambientales, sea cual sea el nivel de estudio (e.g. genética, específica, funcional). Esto tiene implicaciones importantes en el entendimiento de los patrones biogeográficos, funcionalidad del ecosistema, la resiliencia, así como con los servicios ecosistémicos que la biodiversidad nos aporta, así como su correcto manejo y conservación.

La biodiversidad no presenta los mismos patrones a lo largo del planeta y mucho menos responde a los mismos factores (Kerr 2001; Irigoien et al. 2004; Ceballos y Ehrlich 2006; Kerswell 2006; Hughes et al. 2021). De esta manera, fue necesario desarrollar medidas de las diferencias de los sistemas biológicos para comparar e interpretar los procesos que subyacen en la diversidad y distribución de las especies (Izsák y Papp 2000; Buckland et al. 2005; Lamb et al. 2009). Así, desde el desarrollo de las primeras medidas de diversidad (Shannon 1948; Simpson 1949), se ha logrado analizar los patrones y procesos de la distribución y abundancia de las especies; sin embargo, el marco teórico de las medidas de diversidad son en su mayoría con un enfoque espacial (Koleff y Gaston 2002; Buckland et al. 2005; Baselga et al. 2012; De Cáceres et al. 2013; Magurran et al. 2019; Féret y de Boissieu 2020). De manera contraria, el análisis temporal ha sido poco explorado teórica y matemáticamente, ya que el tiempo es una variable compleja que dificulta el entendimiento de los cambios de la biodiversidad bajo este eje (Magurran et al. 2019).

La falta de medidas adecuadas que resuman los patrones temporales de la biodiversidad se debe a varios factores. La primera es que medir cualquier atributo a través del tiempo resulta ser arduo en términos de esfuerzo de muestreo. Por otro lado, la propia naturaleza de los datos genera en la mayoría de los casos variables discretas (dependiendo del objeto de estudio y su escala temporal de los ciclos de vida), debido a que el esfuerzo de muestreo pocas veces es continuo, generando vacíos de información entre muestreos (Bradshaw y Spies 1992; Jung y Tremayne 2003; Tuljapurkar y Haridas 2006; Mondal y Percival 2010). Otro problema particular, que es inherente a los datos temporales o series de tiempo, es que resulta complicado analizar mediciones que no provienen de entidades independientes y que generan en la mayoría de los casos autocorrelación temporal, siendo los sitios cercanos (temporalmente hablando) los más auto correlacionados, respecto a los lejanos (Tuljapurkar y Haridas 2006). Si bien, la falta de independencia de los datos propicia que los análisis no sean simples, haciendo que el análisis se vuelva más difícil cuando las respuestas de las dinámicas comunitarias no dependen solamente de las condiciones ambientales abióticas, sino también de interacciones entre las especies.

Por tal motivo, la forma en la que se ha estudiado la diversidad temporal ha tenido un intenso debate sobre cuál es la mejor manera para evaluar y estimar la diversidad de las comunidades en el tiempo. Sin ahondar demasiado en el tema, las medidas o índices más usados están relacionadas con aproximaciones espaciales (Capítulo IV) (Engen et al. 2011; Baselga 2012; Legendre y Gauthier 2014; Lamy et al. 2015; Legendre 2019), y ninguna se basa en los números de Hill, que son los más aceptados en la actualidad (Hill 1973; Jost 2006a). A diferencia de los índices de Shannon y Simpson, los números de Hill tienen mayor comparabilidad e interpretación ya que éstas incluyen el peso relativo de la abundancia de las especies (Jost 2006a, b; Chao y Chiu 2016). Por otro lado, ninguna de las medidas propuestas considera los problemas antes mencionados al trabajar con las series de tiempo. Esto también propicia que el tiempo se entienda como una variable más, carente de atributos intrínsecos.

El tiempo opera en las comunidades en diferentes niveles. El primer atributo temporal está relacionado con la variación de los eventos biológicos que ocurren en las especies y que ha sido estudiado a partir de la fenología (Paranjpe and Sharma 2005; Hudson 2010; Pau et al. 2011; Denny et al. 2014). De igual manera, no hay una medida que resuma la diversidad de patrones fenológicos dentro de una comunidad. El segundo atributo temporal está relacionado con la frecuencia en la ocurrencia de los eventos biológicos en las especies (Koenig y Liebhold 2005; Benincà et al. 2015; Tonkin et al. 2017a; Laje et al. 2018). Esto está asociado en mayor medida a la periodicidad resultante de habitar un planeta que se rige por eventos cíclicos, ya que, de manera general, el planeta experimenta periodicidad debido a los patrones de translación y rotación. El estudio de la periodicidad ha sido muy puntual para conocer ciertos patrones; sin embargo, tampoco se tiene una medida que resuma la diversidad de patrones periódicos. Finalmente, el atributo temporal que más se ha desarrollado para su estudio ha sido la variación de las comunidades en el tiempo, remitiéndose a los cambios y la heterogeneidad de la riqueza y abundancia relativa de las especies, ligándose directamente con los conceptos de la diversidad β (Legendre y Gauthier 2014; Legendre 2019).

La tesis se centra en desarrollar tres medidas de diversidad temporal que consideren el análisis de series de tiempo bajo una perspectiva de números de Hill: 1) diversidad fenológica (Capítulo II), 2) diversidad periódica (Capítulo III) y 3) diversidad β temporal (Capítulo IV). Finalmente, estas medidas se ponen a prueba con datos de campo de riqueza y abundancia de una comunidad de anfibios en Nahá, Chiapas, donde se hizo un muestreo de cuatro meses durante la temporada de lluvias (Capítulo V). De esta manera se espera que las medidas propuestas, en primera instancia, sean la base para poder comparar atributos temporales comunitarios de una forma confiable, robusta y fácilmente interpretable. Así, poder contribuir al entendimiento de procesos ecológicos como la diferenciación del nicho temporal dentro de las comunidades, así como mejorar el entendimiento de los patrones biogeográficos, funcionalidad del ecosistema, y finalmente para generar propuestas de manejo, monitoreo y conservación de las especies.

Hipótesis

El marco teórico que hay sobre la medición de la diversidad temporal muestra que las medidas actuales no son comparables entre sí. Esto se debe a que ninguna medida está basada en los números de Hill y no toman en cuenta los atributos de las series de tiempo. Por lo tanto, esta investigación plantea la hipótesis de que al integrar el análisis de series de tiempo y los números de Hill permitirá una mayor comparabilidad entre los estudios de diversidad temporal de las comunidades.

CAPÍTULO II

Quantifying phenological diversity: a framework based on Hill numbers theory

(Publicado en PeerJ) Daniel Sánchez-Ochoa, Edgar J. González, Maria del Coro Arizmendi,
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Quantifying phenological diversity: a framework based on Hill numbers theory

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ABSTRACT

Background. Despite the great concern triggered by the environmental crisis worldwide, the loss of temporal key functions and processes involved in biodiversity maintenance has received little attention. Species are restricted in their life cycles by environmental variables because of their physiological and behavioral properties; thus, the timing and duration of species' presence and their activities vary greatly between species within a community. Despite the ecological relevance of such variation, there is currently no measure that summarizes the key temporal aspects of biological diversity and allows comparisons of community phenological patterns. Here, we propose a measure that synthesizes variability of phenological patterns using the Hill numbers based attribute diversity framework.

Methods. We constructed a new phenological diversity measure based on the aforementioned framework through pairwise overlapping distances, which was supplemented with wavelet analysis. The Hill numbers approach was chosen as an adequate way to define a set of diversity values of different order q, a parameter that determines the sensitivity of the diversity measure to abundance. Wavelet transform analysis was used to model continuous variables from incomplete data sets for different phenophases. The new measure, which we call Phenological Hill numbers (PD), considers the decouplings of phenophases through an overlapping area value between pairs of species within the community. PD was first tested through simulations with varying overlap in phenophase magnitude and intensity and varying number of species, and then by using one real data set.

Results. PD maintains the diversity patterns of order q as in any other diversity measure encompassed by the Hill numbers framework. Minimum PD values in the simulated data sets reflect a lack of differentiation in the phenological curves of the community overtime; by contrast, the maximum PD values reflected the most diverse simulations in which phenological curves were equally distributed over time. PD values were consistent with the homogeneous distribution of the intensity and concurrence of phenophases over time, both in the simulated and the real data set.

Discussion. PD provides an efficient, readily interpretable and comparable measure that summarizes the variety of phenological patterns observed in ecological communities. PD retains the diversity patterns of order q characteristic of all diversity measures encompassed by the distance-based Hill numbers framework. In addition, wavelet transform analysis proved useful for constructing a continuous phenological curve. This methodological approach to quantify phenological diversity produces simple and intuitive values for the examination of phenological diversity and can be widely applied to any taxon or community's phenological traits.

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INTRODUCTION

The biodiversity crisis involves the loss of species and their functions from all ecosystems worldwide (*Chen & Shen, 2017*). The loss of key temporal functions and processes involved in biodiversity maintenance is a major component of biodiversity loss (*Lamy et al., 2015*; *Cardinale et al., 2012*; *Youngflesh et al., 2021*). Despite the great concern triggered by this crisis, a measure for summarizing the diversity of temporal patterns in communities has received little research (*Legendre & Gauthier, 2014*; *Legendre, 2019*). Phenology is defined as the study of the timing of recurring biological events, their variation within and among species, and the biotic and abiotic agents responsible for the initiation, duration, and end of such events (*Paranjpe & Sharma, 2005*; *Liang & Schwartz, 2009*; *Lieth, 1974*; *Denny et al., 2014*). The term phenology also refers to the timing of recurrent biological events themselves (*i.e.,* phenological patterns) (*Hudson, 2010*; *Wolkovich, Cook & Davies, 2014*; *Cohen, Lajeunesse & Rohr, 2018*). Under this latter conceptualization, phenology has been interpreted as an expression of the environmental responses of organisms over time. Species are generally restricted in their life cycle by environmental variables because of their physiological and behavioral traits. Consequently, the timing and duration of phenophases (*e.g.*, the distinguishable portion or aspect of an organism's life cycle) vary greatly among species within a community (*Angus & Moncur, 1977*; *Bunting, 1975*; *Visser & Both, 2005*; *Cleland et al., 2007*; *Stange & Ayres, 2010*; *Gompper et al., 2016*; *Horne, 2017*; *Tonkin et al., 2017*; *Eisenhauer et al., 2018*; *Li et al., 2018*). Despite the high degree of variation in phenophases among species in a community and the ecological significance of this variation, a measure summarizing the diversity in the timing of biological events in communities is still lacking.

Given the differences in the types of phenological events, variation within species, and life histories, approaches for measuring phenology are many-fold, which makes generalizing phenology complex (*i.e.,* depending on their life cycle and whether they are unitary or modular; *Vuorisalo & Tuomi, 1986*). Phenological data come in numerous forms, and the phenophases of organisms are often measured using presence/absence data and intensity or abundance counts of distinguishable biological processes or activities displayed by individuals in a particular timeframe (*e.g.*, growing, feeding, courtship, mating, breeding). Non-sessile organisms may respond rapidly to environmental variation by altering their behavior and activity patterns over time; in addition, capture and handling may be required to distinguish the phenophases of these organisms (*e.g.*, *Tang et al, 2016*; *Marra et al., 2005*; *García-Cobos, Crawford & Ramírez-Pinilla, 2020*). By contrast, in most modular and sessile organisms (mostly plants but also sessile animals, particularly benthic ones), phenophases are easily distinguishable among individuals along their life cycle, such as flowering, leaf abscission, and budding (*Denny et al., 2014*).

Phenological patterns can be studied at different biological levels of organization, including individuals, populations, and communities (*Denny et al., 2014*). The study of phenology at the individual level usually involves analyses of the relationship between phenological events and environmental cues (*e.g.*, *Marchand et al., 2020*). However, environmental relationships have also been examined at the population level, and synchronicity indices have been developed to analyze the variation in the timing of phenophases among individuals within a single population or between populations (*e.g.*, *Hodges & Doraiswamy, 1979*; *Kharouba et al., 2018*; *Ghosh et al., 2020*; *Michel et al., 2020*; *Félix-Burruel et al., 2021*). At the community level, synchronicity measures have been used to explore the degree of overlap in the timing of phenophases among few species or functional groups (*e.g.*, *Heithaus, 1979*; *Herrero, 2003*; *Bartomeus et al., 2013*; *Corredor, 2020*; *McDevitt-Galles et al., 2020*; *Ramakers, Gienapp & Visser, 2020*). Some community-level phenological studies have used descriptive approaches to analyze species phenophases and explore the environmental drivers of phenological patterns (*Slagsvold, 1977*; *Ovaskainen et al., 2013*). Phenology has been widely studied, but there is currently no measure that permits comparisons between communities to be made. Therefore, a measure is necessary for summarizing the temporal axis of biological diversity is needed to facilitate comparisons of phenologies between communities and generate new ecological questions.

Within-community phenological variation can be summarized based on the magnitude of the decouplings between the phenophases displayed by different species within a community, including their timing, duration and intensity. Thus, a measure of the differences among the phenological patterns might be indirectly correlated with the biotic interactions that shape phenological patterns (*Walker & Chapin, 1987*; *Thorn et al., 2020*; *Visser & Both, 2005*; *Cleland et al., 2007*; *Stange & Ayres, 2010*; *Inouye, Ehrlén & Underwood, 2019*; *Gompper et al., 2016*; *Horne, 2017*; *Tonkin et al., 2017*; *Eisenhauer et al., 2018*; *Li et al., 2018*), improving our understanding of how species or communities respond to both biotic and abiotic environmental cues (*Losey & Denno, 1999*; *McKinney & Goodell, 2011*; *Bertness et al., 2014*; *Chuine & Régnière, 2017*). Such a measure that incorporates phenological shifts between species and indirectly involves positive and negative interspecific interactions due to temporal niche overlap can provide insight into processes of facilitation or limitation based on the afforementioned decouplings in the phenophases of co-occurring species (*Bergamo et al., 2018*; *Hegland et al., 2009*; *Jönsson et al., 2009*; *Forrest & Miller-Rushing, 2010*). Given that diversity measures summarize key ecological aspects of communities, they are the basis for improving our understanding of more complex and specific ecological phenomena such as the large-scale consequences of climate change on communities (*Pau et al., 2011*; *Pérez-Ramos et al., 2020*; *Alp et al., 2016*).

Here, we develop a novel measure that summarizes a key aspect of temporal biological diversity: phenological Hill numbers (PD). We define PD as the variety of phenological patterns observed in ecological communities over a defined time period. Accordingly, PD reflects the distribution of temporal niches of the species occurring in the community and capture its relationship with the environment (including the indirect responses to biological interactions).

MATERIAL AND METHODS

We constructed our phenological diversity measure using the Hill numbers-based attribute diversity framework (*Chiu & Chao, 2014*; *Chao, Chiu & Jost, 2014*) for phenological intensity/abundance data. Although this framework is based on pairwise overlapping distance, long-termphenologicalsamplingoftenproducesinformationgapsintheestimates of discrete variables and results in abrupt changes over time. This inconvenience can be solved through wavelet transform analysis, which is a reliable approach for predicting values to fill these gaps and model a continuous variable (*Jung & Tremayne, 2003*; *Tuljapurkar & Haridas, 2006*; *Wei, 2006*; *Bradshaw & Spies, 1992*; *Frick, Grossmann & Tchamitchian, 1998*; *Mondal & Percival, 2010*).

Phenology as a continuous variable: wavelet time series analysis

Wavelet transform detects the frequency spectrum of discrete time series data and fits a smoothed curve to them (*Schmidt & Skidmore, 2004*; *Sifuzzaman, Islam & Ali, 2009*). This analysis is based on the comparison of the similarity between a scaling function (which can be stretched, shrunk, and shifted in time) and the original time series (*Torrence & Compo, 1998*). With these comparisons, a matrix is constructed that contains the fits of the scaling function to the time series, in which the total sum of each column in the matrix produces the smoothed curve. In the case of phenological data, we can use such a smooth curve as an approximation to a continuous phenological pattern, in which the abrupt changes caused by sampling effort and protocol are smoothed out, in line with the assumption that phenophases start and finish gradually rather than abruptly (Fig. 1).

Wavelet transform analyses require specifying two parameters. The first parameter is the scaling function. The most common scaling functions are Morlet, Paul, DOG, Biorthogonal and Mexican hat, and these differ mainly from each other in the signal resolution calculation (*González-Nuevo et al., 2006*; *Singh, Singh & Sharma, 2011*). For our purposes, the Morlet scaling function is preferable, as it is optimal for data that cannot be directly interpreted, and time series with unknown frequencies and scales (*Percival & Walden, 2000*). The second parameter is the attenuation threshold (τ), which determines the phenological curve steepness. Values close to 0 translate into a highly smoothed curve; conversely, values approaching infinity translate into a wiggly curve, similar to the raw time series data. A value of 2 is used as a standard for wavelet analysis in mathematics software (*e.g.*, Matlab and wavScalogram R package). Wavelet analysis must be performed on the discrete phenological curve or time series of each studied species in the community; thus, the number of total smoothed phenological curves that must be calculated equals the number of species in the community (*S*).

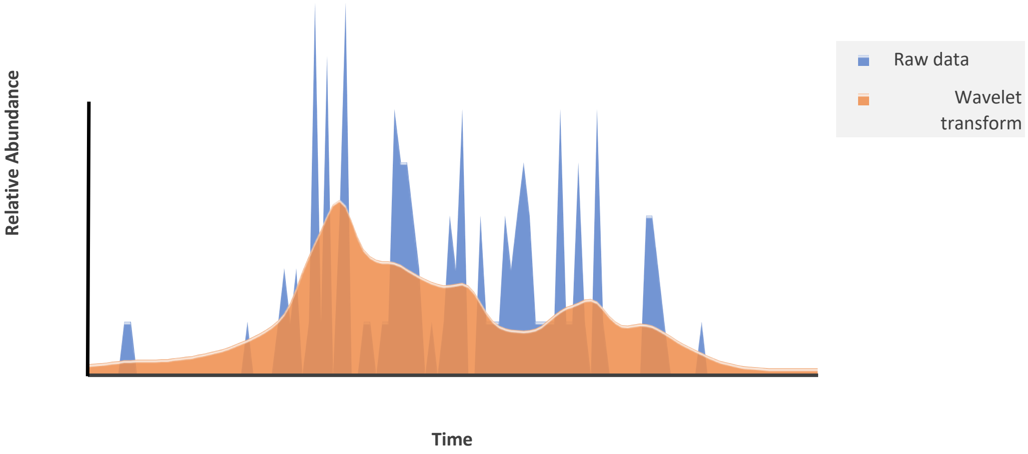

Figure 1 Comparison of two phenological curves for the same data set. The blue curve represents the raw data, and the red curve represents the smoothed phenological curve through the wavelet transform.

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Quantifying Phenological Hill numbers (PD)

Our phenological diversity measure is based on the Hill numbers-based attribute diversity framework (*Jost, 2007*; *Chiu & Chao, 2014*; *Chao, Chiu & Jost, 2014*). Hill numbers are a set of metrics that have two major advantages over other diversity indices:(1)the interpretation of the diversity values are consistently the same, and (2) the sensitivity regarding abundant and rare species or traits can be regulated with a parameter (*q*). This *q* parameter directly determines the sensitivity of the diversity measure (^{q}D) to the relative abundances of species occurring in the community. Although *q* can take any non-negative real number, ecologists typically consider three values: 0, 1 and 2 (*Chao, Chiu & Jost, 2014*). When $q = 0$, the relative abundance of species is overlooked, and the measure simply represents *S* (*i.e.,* $^{0}D = S$). When $q = 1$, *S* is weighted by the proportions of the species abundances and can be interpreted as the effective number of species equally abundant within an assemblage, which is equivalent to exp(*H*) *(i.e.,* the exponent of Shannon's entropy; *Jost, 2006*). Finally, when $q = 2$, the diversity values favor the most abundant species, and the less abundant or rare species are almost not accounted for; consequently, ^{2}D can be roughly interpreted as the effective number of dominant or the most abundant species in the community (*Jost, 2006*). In addition, Hill numbers are consistent with basic diversity concepts like evenness and dominance (*Chiu & Chao, 2014*; *Chao, Chiu & Jost, 2014*). Additionally, Hill numbers are expressed in intuitive units of effective number of species, and they can be directly compared across orders of *q* to gain information on the dominance, community traits and comparisons among different species assemblages. Finally, Hill numbers theory can be generalized to taxonomic, phylogenetic, and functional diversities (*Chiu & Chao, 2014*; *Chao, Chiu & Jost, 2014*; *Chao et al., 2019*). Here, we use this framework to measure PD in a community.

Phenological diversity assessment through the species-pairwise distance framework

The measure that we present here is based on a pairwise overlapping distance, following the same logic by *Chao et al. (2014)* in developing their functional diversity measure under the assumption that each species has specific phenological curves (*Chao, Chiu & Jost, 2014*; *Chao et al., 2019*). The distance we used is based on the Morisita-Horn index modified to measure the amount of overlap between pairs of phenological curves (*Luna-Nieves et al., 2022*). Let O_{ij} be the pairwise overlapping distance between the continuous phenological curves of the *i*-th and *j*-th species, defined as

$$o_{ij} = 1 - \frac{2^{\mathrm{R}}\, z_i(t) z_j(t)\, dt}{\mathrm{R}\ z_i(t)_2 dt + \mathrm{R}\ z_j(t)_2 dt} \qquad (1)$$

where z_i and z_j are the smoothed continuous-over-time phenological curves of species *i* and *j*, respectively and the integral is calculated over the studied time interval. O_{ij} ranges in the [0, 1] interval, with $O_{ij} = 1$ when curves fully overlap (Fig. 2C), and $O_{ij} = 0$ when curves show no overlap (Fig. 2A). When completely overlapping in time (Fig. 2C), the species belong to the same phenological group; when they partially overlap, they partially belong to the same phenological group (Fig. 2B). A third case corresponds to the scenario in which the phenological curves do not overlap (Fig. 2A), which represents the existence of completely different phenological groups.

Therefore, our approach to measuring phenological diversity is based on the pairwise overlap distance measured through the Morisita-Horn index (*Horn, 1966*; *Garratt & Steinhorst, 1976*).

Considering that both deterministic and stochastic variables contribute to the phenomena regulating phenology, similar phenological curves between pairs of species might suggest that they have similar environmental requirements, a common response to the same environmental cues, or similar evolutionary constraints. By contrast, dissimilar phenological curves suggest that the species have different environmental requirements or might simply reflect historical competitive displacement between species (*Slagsvold, 1977*; *Baselga, Gómez-Rodríguez & Lobo, 2012*). As the phenological curves may vary among time in position and shape. The overlapping area of the phenophase curves between pairs of species over the entire time series can provide an indirect and prospective measure of the interactions between phenophases only in the time frame measured. Because our framework of phenological diversity is based on the approach of "attributediversity'' (*Chao, Chiu & Jost, 2014*; *Chao et al., 2019*), which is a robust extension of Hill numbers, it can be applied to measure species traits and their diversity in orders of *q*. Within this framework, phenological Hill numbers (PD) can thus be interpreted as the pairwise phenological distance between species (in units of equally abundant and distinct species with distinct phenological group) occurring in an assemblage within the time interval over which it was measured.

To construct our phenological diversity measure we need to consider a standardizing factor: sum of the relative overlap of phenological curves, denoted as *Q*. This factor is

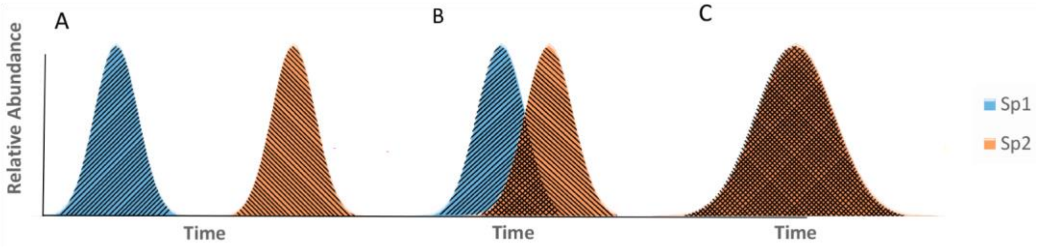

Figure 2 Theoretical overlap scenarios between pairs of phenological curves. (A) Non-overlapping phenological curves. (B) Phenological curves partially overlapping. (C) Fully overlapping phenological curves (the blue curve is behind the orange curve), species 1, species 2.

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calculated as follows (*Chao, Chiu & Jost, 2014*; *Chao et al., 2019*):

$$Q = \sum_{i=1}^{S} \sum_{j=1}^{S} O_{ij} p_i p_j, \qquad (2)$$

where O_{ij} is calculated as in Eq. (1), and p_i is the relative intensity or abundance of the phenological event measured on species *i,* defined as

$$p_i = \frac{\int z_i(t)dt}{\sum_{j=1}^{S} \int z_j(t)\,dt}. \qquad (3)$$

Finally, the phenological Hill numbers of order *q*, ${}^{q}PD$, is calculated as

$$ {}^{q}PD = \left[\sum_{i=1}^{S}\sum_{j=1}^{S}\frac{o_{ij}}{Q}(p_ip_j)^{q}\right]^{\frac{1}{2*(1-q)}}. \tag{4} $$

Given that when $q = 1$ the exponent $\frac{1}{2*(1-q)}$ is undefined, we decided to use the same approach as *Chiu & Chao (2014)*. Therefore,

$$ {}^{1}PD = \exp\left(-\frac{1}{2}\sum_{i=1}^{S}\sum_{j=1}^{S}\frac{o_{ij}}{Q}p_ip_j\log(p_ip_j)\right). \tag{5} $$

Simulations and field data

To illustrate the utility of ${}^{q}PD$, we generated simulated data sets reflecting different community scenarios and applied our measure to these and one additional real data sets. Although these simulations are unlikely to occur in nature, they provide a glimpse into a real community phenological pattern (Fig. 3). Simulations vary in several community traits, such as: the degree of overlap, differential or even in intensity, and total number of species (*i.e., S*) (Fig. 3).

As previously explained, ${}^{q}PD$ values represent the ‘‘phenological Hill numbers’’ and thus quantify the diversity of different phenological curves in a given assemblage. The contribution of the phenological curve of each species is considered unique and equally distinct from each other; thus, ${}^{q}PD$ values always range from >0 (Fig. 3) to the total number of phenological curves measured (*S*, when there is no overlap at all between them).

Therefore, phenological Hill numbers values have lower values when q increases.

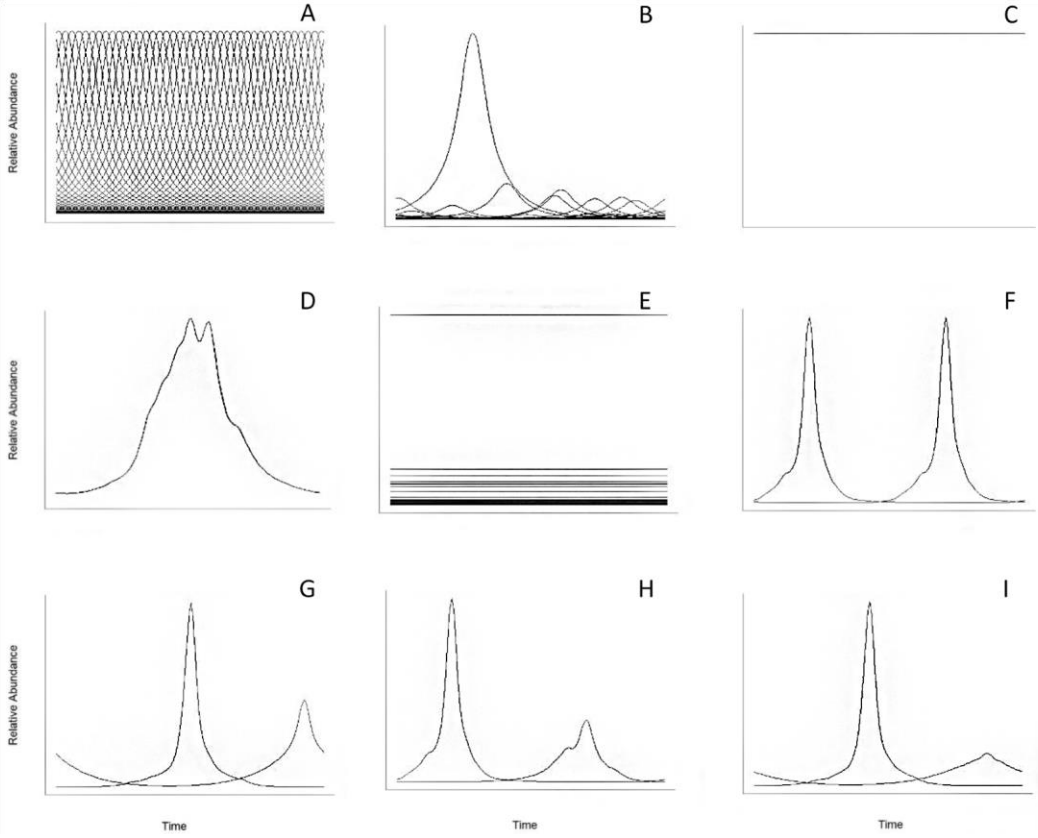

Figure 3 **Graphs of the tested phenological diversity simulations.** (A) S= 40, all species are equally distributed over time and the abundances are equal; (B) S= 40, all species are equally distributed over time and the abundances are unequal; (C) S= 40, all species are present all the time without abundance variation and abundances are equal; (D) S= 40, all species are present all the time with abundance variation and abundances are equal; (E) S= 40, all species are present all the time without abundance variation and abundances are unequal; (F) S= 2, species equally distributed over time with equal abundance; (G) S= 2, species not equally distributed over time with equal abundance; (H) S= 2, species equally distributed over time with unequal abundances; (I) S= 2, species not equally distributed over time with unequal abundances. A, B, C, D and E are modifications of the Madagascar amphibian community dataset.

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In addition to the simulated data sets, we performed an analysis of ${}^{q}PD$ based on field data for the breeding phenological activity of an amphibian community from Madagascar (Fig. 4; S=40; time period = 360 days; frequency = daily; *Heinermann et al., 2015*).

All analyses were performed in R v. 4.1.2 (*R Core Team, 2021*) using the DescTools (*Signorell et al., 2020*) and wavScalogram (*Benítez, Bolós & Ramírez, 2010*) packages. We provide the script for calculating the phenological diversity measure in the Supplementary Material.

RESULTS

${}^{q}PD$ values are illustrated as phenological Hill numbers profiles in Fig. 5. As expected, there is a tendency to decrease as q increases in cases with abundance variation (Fig. 5), and there is no decreasing pattern in simulations a, c, d, e, f, g, h and i. The absence of a decreasing

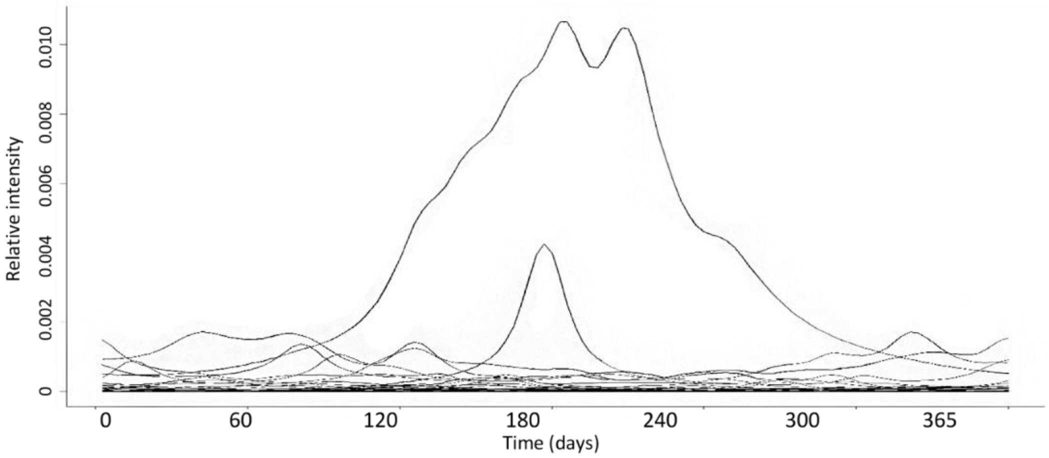

Figure 4 Wavelet transformed data of 120 sample points of an amphibian community in Madagascar over one year. Each line represents one phenological curve, S = 40.

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pattern in these simulations corresponds to null variation in the intensity and overlapping area among species (Fig. 3).

The minimum values in simulations c and d reflect the lack of differentiation in the community phenological curves over time (Figs. 3C, 3D and 6B). The ^{q}PD values were consistent with the homogeneous distribution of the intensity and concurrence of phenophases over time. The most diverse simulation was case a (Fig. 5A), where 40 species occur once in the year and the intensities of phenological curves are equal. By contrast, simulations c, d, e were the least diverse; with values of 0, where species occur all year-round with no differential phenophase intensities. Likewise, simulations f, g, h and i have low ^{q}PD values because only two phenological curves were analyzed (Fig. 5C), and variation in the intensity and timing of the phenophases is apparent and the distance between two curves must be between 0 and 1 (Fig. 3). For simulations c, d and e (Fig. 5B), the distribution of the overlapping area among all phenological curves was the same. Overall, these results confirm that phenophase intensity is a phenological trait that directly affects ^{q}PD values.

Figure 4 show the data for the phenological Hill numbers of the Madagascar amphibian community. ^{0}PD for Madagascar was 47.5 (S=40 species, 120-time sample points). There was a decreasing pattern as q increased, with ^{2}PD values being reduced to 8.4.

DISCUSSION

Here, we propose a phenological diversity measure based on time series analysis and Hill numbers diversity theory that provides an efficient, readily interpretable and comparable measure that summarizes a key aspect of temporal biological diversity, namely the mean variety of phenological patterns observed in ecological communities. An initial step in developing our phenological diversity measure involves transforming data sets that are incomplete due to information gaps. Wavelet transform analysis proved useful for constructing a continuous phenological curve. Several studies have recommended the use of

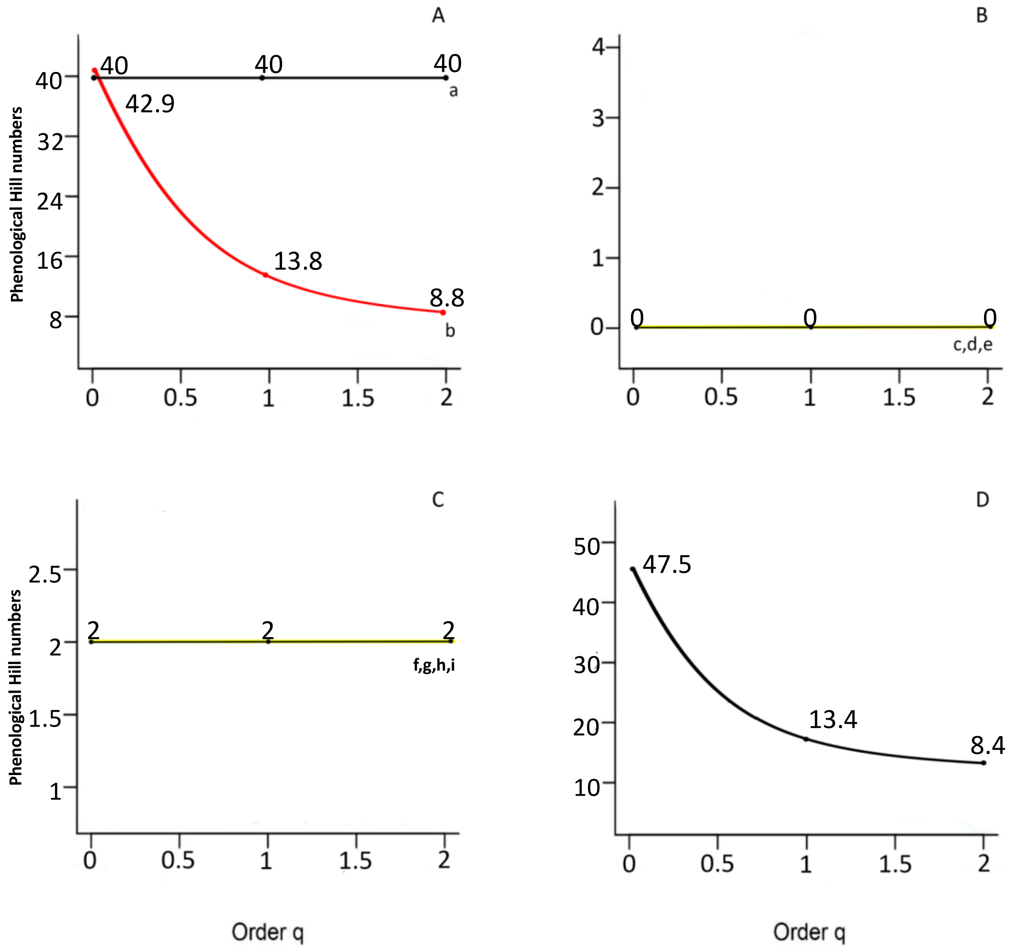

Figure 5 **Phenological Hill numbers profiles as functions of *q* (0 *q* 2) for simulated (A-I) data and real data sets (amphibian community from Madagascar).** (A) Case a, all species are equally distributed over time and have equal abundances; case b, all species are equally distributed over time and have unequal abundances. (B) Case c, all species are present all the time without abundance variation and equal abundances; case d, all species are present all the time with abundance variation among time but species present equal abundances; case e, all species are present all the time without abundance variation and unequal abundances. (C) Case f, species equally distributed over time with equal abundances; case g, species not equally distributed over time with equal abundances; case h, species equally distributed over time with unequal abundances; case i, species not equally distributed over time with unequal abundances. (D) Real data sets from Madagascar. Cases a, b, c, d, and e in (A) and (B) are modifications of the data from the amphibian community in Madagascar.

Full-size DOI: 10.7717/peerj.13412/fig-5

time series analysis in ecological and forestry studies (*Senf et al., 2017*; *Li & Wu, 1995*; *Dale & Mah, 1998*; *Cho & Chon, 2006*; *Cazelles et al., 2008*). This approach has been used for specific purposes such as population dynamics, disease transmission, and animal migration (*Cho & Chon, 2006*; *Cazelles et al., 2008*). Thus, incorporating time series in the study of phenology enhances our understanding of phenological diversity in communities, as it captures the continuous nature of phenology. A recent study using the Fourier transform showed that this tool can be used to detect periodical patterns in phenological cycles in longterm data (*Bush et al., 2017*), and this approach performed better than circular statistics (*Morellato, Alberti & Hudson, 2010*). However, these two approaches have not been used to model continuous phenological data. Likewise, we demonstrated that time series analysis can be used to model a continuous phenological curve from discrete or not fully continuous data; thus, there is a need to develop more robust theory aside from Fourier's approach given that phenological patterns are not unimodal (*e.g.*, empirical orthogonal function, wavelets or Hilbert-Huang method; *Cho & Chon, 2006*; *Cazelles et al., 2008*; *Bowman & Lees, 2013*; *Huang, 2014*). Limitations of Fourier's approach are primarily related to the information features of multi-scale functions at dominant intensities through the time series; in other words, Fourier analysis only provides information on the periods but not on their distribution over time. Consequently, Fourier transform is less applicable than wavelet analysis to nonlinear, nonstationary transient and scale-dependent phenomena such as natural processes characterized by high variability (*Cees, 1999*; *Li & Wu, 1995*). The specific advantage of wavelet analysis is that it considers the frequency of each time interval in the time series from small to large scales, which enables a more accurate calculation of nonlinear and nonstationary variables, such as phenological processes. As described in the Methods section, two parameters need to be specified: the scaling function and the attenuation threshold (τ). The scaling function relates to the nature of the time series data and the approach of the wavelet transform (*Cazelles et al., 2008*). Scaling functions are numerous and each one has a specific use. We used the Morlet function because of the lack of predictability in the biological data related to phenological traits (*Percival & Walden, 2000*) and its capacity for high-frequency resolution (*Cazelles et al., 2008*). The Daubechies scaling function is used in variables with fractal sequences or even in signal discontinuities (*Akansu, Haddad & Çaglar, 1993*). The Mexican hat scaling function is used in seismic signal patterns where variables show strong changes in the beginning and decrease over time (*Zhou & Adeli, 2003*). The latter features in temporal data are not observed in phenological information and therefore the use of these scaling functions is not warranted for this purpose.

The τ parameter reflects the rate of occurrence or disappearance of phenological traits over time. In nature, phenological processes generally occur gradually and continuously rather than abruptly and discretely; however, because of logistic restrictions, we are generally limited to collecting discrete records of phenological patterns. For example, the flowering of some cacti can occur in a single night (*Petit, 2001*), whereas the flowering of many tropical rainforest tree species tends to be gradual (*Newstrom, Frankie & Baker, 1994*; *Brown & Hopkins, 1996*). Regardless of the community, both examples take place in a continuous manner and are time scale-dependent. Therefore, the phenological curve slope can be adjusted depending on the nature of the phenological process, which directly affects the area of overlap of the pairwise distance and, consequently, how the phenological processessharetimeintheentirecommunity.Althoughthestandardvalueofusexploration of different approaches for defining τ to accurately describe the phenology of species is necessary given variability in the time and duration of phenophases among species. Until he standard value of 2 be used to permit comparisons to be made among different systems and studies. Changes in τ might modify ^{q}PD values but not the diversity patterns in order of q. Future research on the standardization of values is needed to increase the comparability of results (see Materials and Methods for explanation; *Percival & Walden, 2000*).

The Morisita-Horn index was found to be appropriate for measuring the pairwise overlapping distance between phenological curves (*Luna-Nieves et al., 2022*). There are two other widely accepted measures (or metrics) of overlap between curves: the Jaccard overlap index (*Smith,* *Solow & Preston, 1996*; *Yue & Clayton, 2005*) and the Szymkiewicz-Simpson overlap coefficient (*Ramos-Guajardo, González-Rodríguez & Colubi, 2020*); however, these indices do not represent the intensity and the proportion of overlap of phenological curves. The Jaccard overlapping area index only accounts for the overlapping area of both samples but ignores the area outside of the overlapping area. The Szymkiewicz-Simpson index is based on the overlapping area and the area of the smaller phenological curve. Unlike these two indices, the Morisita-Horn Index is calculated by including both the overlapping and non-overlapping areas, thus making it a better tool for our purposes (*Yue & Clayton, 2005*). The temporal overlap of phenological curves over time reflects the temporal niche similarity between species and provides insight into the existence and magnitude of interactions such as competition, mutualism, and facilitation (*Kochmer & Handel, 1986*; *Murdoch et al., 2002*; *Hodgson et al., 2011*; *Bergamo et al., 2018*; *Lane et al., 2018*; *Donohue, 2005*).

The proposed measure of phenological diversity is an extended application of the principle of Hill numbers used to measure phylogenetic (*Chao, Chiu & Jost, 2010*) and functional diversity (*Chiu & Chao, 2014*; *Chao, Chiu & Jost, 2014*; *Scheiner et al., 2017*). The main advantage of our measure is its ability to provide a more objective and easy-tointerpret way for comparing the mean variety of phenological patterns observed across different studies (*Chiu & Chao, 2014*). Our approach retains the diversity patterns of order q as the rest of diversity measures encompassed by the Hill numbers framework does. In ecological terms, the phenological Hill numbers values can be interpreted as a quantification of the mean different ways in which the community displays phenological curves over time. When $q = 0$, the measure represents the mean number of phenological curves included in the analysis (richness) as long as they do not overlap. If they do, this number is reduced to 0 when they are all identical because the distance between phenological curves is zero. When $q > 0$, the phenological curves shared by increasingly larger numbers of species are assigned higher weight in determining the phenological Hill numbers values. In practice, this means that phenological curves that are highly similar to each other in terms of time and intensity are grouped together, which ultimately translates into the mean effective number of phenological curves. Thus, regardless of the value of q, higher values of phenological Hill numbers represent a more heterogeneous arrangement and lower temporal overlap in the phenological curves within a community.

The simulations we performed represent the behavior of extreme scenarios of phenological Hill numbers. Results show that differences in intensity, overlapping area and variation in the number of phenological curves determine the values of phenological Hill numbers because this measure is directly linked to both variations in these variables and q values (*Chao, Chiu & Jost, 2014*). Specifically, the highest ${}^{q}PD$ values correspond to data on phenophases evenly distributed over time, as has been shown in other diversity studies (*e.g.*, *De Bello et al., 2009*); this result is related to the degree of species evenness in the community and reflects the degree of concurrence in the phenological curves (Figs. 3A, 3B). Likewise, the lowest ${}^{q}PD$ values correspond to the lowest degree of variation in the intensity of phenological curves and the constant presence of all phenological curves over time; from a biological perspective, there is no heterogeneity in this case, and all species have the same intensity in their phenological curves and occur in the same timeframe (Figs. 3C, 3D, 3E). When the intensity of phenological curves varies and the concurrence of curves remains constant (*e.g.*, Fig. 3A *vs.* Figs. 3B and 3C, or 3D *vs.* 3E), ${}^{q}PD$ values decrease when *q* increases, demonstrating that the measure is sensitive to the intensity of the different phenological curves. We also demonstrate that ^qPD values are closely related to the number of phenological curves measured (Fig. 3C). Therefore, our framework does provide a reliable measure of a key community attribute under different phenological scenarios. Phenological curves are constructed through signal processing by wavelet analysis and intensity or abundance data is needed; thus, our approach do not consider the presence/absence data frames and a modification of our framework must be developed due to the nature of binary data.

^qPD can be successfully evaluated in In the case of the Madagascar amphibians data set, we calculated a maximum ^0PD value of 47.5 for a group of 40 species monitored over time. As *q* increases, the effective number of the phenological curves became greatly reduced, implying that there are few ways in which phenological curves can occur when abundance is assigned more weight in estimating ^qPD. In other words, there are between a mean of 13 ($q = 1$) or 8 ($q = 2$) distinct ways in which species partition their activity temporally throughout the studied year. This can be explained by the fact that amphibian activity is highly tied to rainfall patterns, and several species respond similarly to this factor (see *Heinermann et al., 2015*). Some amphibian species occur continuously throughout the year, whereas others only do so during a short period in the rainy season, throughout the entire rainy season, in the cold dry season, or under hot dry conditions. Overall, our analysis provided a robust measure that summarizes the diversity of these patterns. Nevertheless, ^0PD values (47.5) are slightly larger than taxonomic diversity (40) because $Q < 1$. Thus, the distance measure used in this framework can alter diversity values but not the overall patterns.

The proposed method correctly incorporates the proportion of overlapping area and the intensity of phenological curves, making our phenological diversity measure consistent with the Hill numbers unified framework(*Chao, Chiu & Jost, 2014*;*Chao et al., 2019*).Moreover, the proposed framework enables any phenological phenomenon to be examined with any set of taxa at the community level. Nevertheless, two assumptions require consideration:

(1) long time series data lead to a better modeling of continuous phenological curves (more than 25 is recommended) (*Chamoli, Bansal & Dimri, 2007*; *Cazelles et al., 2008*), and (2) our analysis assumes, due wavelet analysis, that phenology is a cyclical phenomenon and does not fit systems with non-cyclic patterns (*Percival & Walden, 2000*).

There is a need for more studies to examine phenological patterns, including long-term studies based on records of community phenological diversity patterns, to enhance our understanding of the environmental cues that underlie the structure of communities in different environments and how species share the temporal dimension in infra and supra annual scales, especially regarding the impacts of climate change and the problems associated with the increasing mismatch between phenophases of interacting species (*Pau et al., 2011*; *Pérez-Ramos et al., 2020*; *Rafferty et al., 2013*; *Morente-López et al., 2018*; *Renner & Zohner, 2018*). Specifically, our measure only summarizes the variability of a temporal trait of communities, and it should be tested and correlated with different environmental variables and phenophase measurements at different time frames and different taxonomic levels to further improve our understanding of the factors underlying the phenological patterns displayed by groups of species. Thus, our approach provides a new tool for measuring a single temporal attribute (PD) of communities and the correlations of this attribute with environmental variables can provide important insights that could aid conservation, restoration and management programs. Time series analysis should also be conducted under the assumption that the phenological data can be cyclical or not cyclical over time. Finally, we emphasize that ${}^{q}PD$ is suitable for the analysis of massive datasets associated with the collection of phenological time series data and with any phenological process within a community.

CONCLUSIONS

The phenological Hill numbers framework presented here produces simple and intuitive values for phenological diversity evaluation and thus can be widely applied to any taxon or community phenological traits using long-term data. Therefore, our measure has the properties of other diversity frameworks, and comparisons among studies using this same measure are possible. Phenological Hill numbers has important implications for the design of conservation and restoration programs that consider species and community patterns for the long-term persistence of biodiversity and *ad hoc* management.

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ADDITIONAL INFORMATION AND DECLARATIONS

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Competing Interests

The authors declare there are no competing interests.

Author Contributions

- Daniel Sánchez-Ochoa conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Edgar J. González conceived and designed the experiments, performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.
- Maria del Coro Arizmendi conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Patricia Koleff conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Raúl Martell-Dubois conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Jorge A. Meave conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.
- Hibraim Adán Pérez-Mendoza conceived and designed the experiments, performed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Data Availability

The following information was supplied regarding data availability:

The code for all simulations and analysis and the phenological curves are available in the Supplemental Files.

The data from Madagascar amphibian community is available at DOI 10.1080/00222933.2015.1009513.

Supplemental Information

Supplemental information for this article can be found online at http://dx.doi.org/10.7717/peerj.13412#supplemental-information.

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CAPÍTULO III

An analytical method based on the Hill numbers framework for assessing diversity in the periodicity of ecological communities.

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(Sometido a Oecologia)

An analytical method based on the Hill numbers framework for assessing diversity in the periodicity of ecological communities

On the title page, include name(s) of author(s), the affiliation(s) of the author(s), and the e-mail address, telephone and fax numbers of the corresponding author. A declaration of authorship is required to be included as a footnote on the title page.)

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Abstract

Understanding spatial and temporal diversity patterns is essential for the conservation of species and communities in a changing world. Species evolve in various ways over spatial and temporal axes, and this change is regulated principally by environmental variation. The environmental variation associated with a seasonal world constrains the vital processes of species to be periodical. Despite the ecological significance of such temporal variation, there is currently no measure that summarizes the periodical aspects of biological diversity and allows comparisons between communities of their temporal patterns. Periodical diversity refers to the number of different periodical patterns of a community. Here, we aimed to develop a measure of periodical diversity of biological processes in a robust mathematical framework to enhance our understanding of the ecological and evolutionary processes underlying periodical community patterns. We constructed a periodical Hill numbers diversity measure based on wavelet transform analysis and a phenological overlap index. This measure, which we name periodical diversity (PeD), expresses this attribute in terms of Hill numbers of order *q*, with maximum values representing communities with the most diverse periodical curves. We tested PeD with (1) four simulations varying in the magnitude of periodical patterns, the number of periodical patterns, and species richness, and (2) two real data sets. PeD values were consistent with the richness/abundance relationship in both the simulated and empirical data sets, where periodical diversity is reduced when unequal abundance of species occurs. Therefore, PeD provides an easily interpretable and comparable measure that summarizes the variety of periodical patterns in a vital process among the species within a community, irrespective of the vital process or taxon under study.

Key words: Periodic patterns, time series analysis, Overlap Index, Hill numbers, community

Introduction

Understanding spatial and temporal diversity patterns is essential for the conservation of species and communities in a changing world (CITAS). Species evolve in various ways over spatial and temporal axes, and this change is regulated principally by environmental variation (CITAS). Several metrics have been developed to quantify the diversity of species and traits within communities in an effort to understand these patterns (Shannon 1948; Simpson 1949; Jost 2007a; Chiu and Chao 2014; Chao et al. 2019a). One underexplored dimension of diversity is the temporal axis. The periodicity of biological processes, such as metabolism, growth, reproduction, behavior, and migration, is an inevitable product of our seasonal world (Gwinner 1981; Laje et al. 2018; White and Hastings 2020; Oita et al. 2021; Schmitt et al. 2021). Periodicity is a trait of the temporal axis that is defined as a sequence of discrete, evenly spaced events measured in units of time. The activities of humans are often based on the periodicity of astronomical phenomena (e.g., a year being the time it takes for the Earth to revolve around the sun), whereas the perception of time by organisms can vary and is likely tied to both biotic and abiotic factors (Péron et al. 2016; Laje et al. 2018), which increases the difficulty of understanding this temporal property.

The periodical pattern of a species biological process is related to its temporal niche (Hut et al. 2012), and the abiotic cues of habitats are the main factors shaping the periodical patterns of species (Knop et al. 2018). For example, zooplankton and phytoplankton exhibit diurnal periodical patterns related to changes in light, nutritional resources, and tides generated by the tilted axis of Earth’s rotation; from a biological standpoint, this is associated with the trophic interactions and biological processes related to daily variation in solar energy and primary productivity (Perissinotto and McQuaid 1992; Keitt 2008; Ahmed et al. 2022). They also exhibit monthly patterns related to tides, wave oscillations, and nocturnal light intensity generated by lunar phases that prompt plankton migrations (Last et al. 2016). Finally, there are also annual patterns related to the seasonality derived from the Earth's movement around the sun, which results in changes on an annual scale (Carey et al. 2015).

Aside from the obvious influence of abiotic factors on the periodical patterns of a species, periodicity is also affected by interactions with other species (Benincà et al. 2015). Although sympatric species often avoid overlapping their temporal niches, some species are capable of coexisting temporally with others (Marinho et al. 2020). Thus, environmental variables (biotic and abiotic) have been used to explain species periodicity, which generates a high degree of variation in periodical patterns among species, populations, and communities (Cazelles et al. 2008). Thus, periodical diversity is an important emergent property of a community because it is closely related to the temporal niche (Meszéna et al. 2006; Bronstein 2009).

Periodical changes have rarely been measured at the community level (Allen et al. 2006); the few studies that have been conducted to date have revealed strong seasonal dynamics of particular species. Moreover, no formal measurement of periodical diversity from a community perspective has been developed. The composition of communities tends toward stability, and changes, modifications, or perturbations can push communities to a variety of stable states (Ives et al. 2003; Molina-Montenegro 2008; Gonze et al. 2018; Hastings et al. 2018). These alternative stable states are not completely determined by environmental cues, and there is evidence that non-linear interactions among species directly affect the periodical patterns of species in communities (Heinermann et al. 2015; Engen et al. 2017; White and Hastings 2020). Little is known regarding the evolution of periodical patterns among species and the diversity in periodic patterns within and between communities (Sabo and Post 2008; Bar-Joseph et al. 2012). Because two communities can have similar abundance and richness values but different periodicity patterns, a measure that summarizes the diversity in the periodicity of biological processes could provide insightful information on the causes underlying the temporal distribution of the vital processes of organisms in nature and permit comparisons at the community level. Measurements of periodical diversity also have important implications for the development of monitoring plans. Knowledge of the patterns of periodical diversity in an area can be used to optimize the temporal sampling of communities such that the efficiency of sampling is maximized. For example, if sampling is concentrated in periods corresponding to the least common multiple, more species will be sampled with less effort than if sampling were focused in periods that were not based on analysis of periodical patterns.

A unique and reliable way of measuring the intensity of periodical patterns is to use a time series analysis approach (Bradshaw and Spies 1992; Bradshaw and Holzapfel 2007; Cazelles et al. 2008; Jackson 2009). Periodical information can be extracted easily from time series data and can be used to calculate a continuous periodical model that considers all the periodic patterns that a species can show in a particular site and time (Dale and Mah 1998; Percival and Walden 2000; Mondal and Percival 2010). Among the statistical techniques developed to analyze periodical patterns, wavelet analysis is a useful tool for spectral analysis that has been developed to study time series data that presents non-stationary and periodical behaviors (Cazelles et al. 2008). Wavelet analysis can be used to calculate variation in the amplitude of a signal varying in periodicity and time; wavelet analysis can thus be used to identify different periodical patterns in a time series of a particular biological process (Cazelles et al. 2008; Tonkin et al. 2017b; Roberts and Mannion 2019). Hence, a measure of periodical diversity based on Hill numbers theory can be developed by calculating periodic models for each species in a community through the use of a distance-based approach, as has been done previously with functional (Chiu and Chao 2014; Chao et al. 2019a) and phenological diversity (Sánchez-Ochoa et al. 2022). The goal of this study was to develop a measure of periodical diversity of such biological processes that varies with time, based on a robust mathematical framework to enhance our understanding of the ecological and evolutionary processes underlying periodical community patterns. We calculated periodical patterns using wavelet analysis and calculated diversity using the Hill numbers framework.

Materials and Methods

Our periodical diversity measure is based on the Hill numbers diversity framework (Chao et al. 2014a; Chiu and Chao 2014) and time series signal processing approaches to decompose raw data into a periodical function (Cazelles et al. 2008). Wavelet transform analysis is used to quantify the different periodic components of species patterns (Percival and Walden 2000; Cho and Chon 2006; Cazelles et al. 2008). This analysis considers the frequency spectrum of the time series data of each species in the community and estimates a new temporal function of period vs. signal temporal intensity called the wavelet or periodical function (Percival and Walden 2000; Cazelles et al. 2008). Each signal of each species is considered a unique trait that contributes to the diversity values. The diversity measure is based on the Hill numbers pairwise distance framework. The species that share similar periodical patterns contribute less to diversity values and vice versa.

Calculation of periodical patterns: wavelet time series analysis

Although there are several types of time series analysis (e.g., Fourier transform and orthogonal function) (Morellato et al. 2010; Bush et al. 2017), they are not well suited to describe time series that show non-stationary behavior in their amplitude and work better for stationary variables with a unique dominant period (Torrence and Compo 1998; Sabo and Post 2008; Sifuzzaman et al. 2009), a phenomenon that is not frequently observed in most species biological processes. Wavelet transform analysis calculates a wavelet function (W_x) that represents the intensity of a periodical signal by detecting and decomposing the frequency patterns in a time series (Percival and Walden 2000; Cazelles et al. 2008). This is achieved through the comparison between a time series and a mother function (φ), which can be transformed by changes in scale (a), and position (τ) in time (t). $\varphi(t)$ for each scale (a) and position (τ) is calculated as:

$$\varphi_{a,\tau}(t) = \frac{1}{\sqrt{a}} \varphi^* \left(\frac{t-\tau}{a}\right), \qquad \text{eqn 1}$$

where φ is a specific mother function (e.g., Morlet, Daubechies, Coiflets, Biorthogonal, Mexican hat; Gonzalez et al., 2006; Singh, Singh & Sharma, 2011). Thus, the wavelet transform of a time series $x(t)$ with a given mother function is expressed as:

$$W_x(a,\tau) = \frac{1}{\sqrt{a}} \int_{-\infty}^{+\infty} x(t)\, \varphi^* \left(\frac{t-\tau}{a}\right) dt = \int_{-\infty}^{+\infty} x(t)\, \varphi_{a,\tau}(t) dt. \qquad \text{eqn 2}$$

Thus, $W_x(a,\tau)$ represents the contribution of a to the time series data at time $\boldsymbol{\tau}$. The wavelet transform can be described as the cross correlation of the abundance of a species or the intensity of a species' biological process with a particular mother function with different scales at different times ($\boldsymbol{\tau}$). A good match between the mother function and the time series produces a large positive value of the transformed wavelet; in turn, a weak match results in low values of the transformed wavelet (Percival and Walden 2000; Cho and Chon 2006; Cazelles et al. 2008). Selecting the appropriate mother function is important for two reasons: it provides the basis for the cross correlation, and the results change significantly among mother functions (Cazelles et al.

2008). Here, we selected the Morlet mother function because it is optimal for data with unknown frequencies and scales and is sensitive to small changes (CITA). The wavelet transform analysis must be performed on the time series dataset of each species in the community. Thus, the number of total wavelet functions (period vs. intensity) curves equals species richness (*S*).

Interpreting periodic curves

The periodic curve is a model calculated from a signal analysis of a variable recorded over time that is influenced by the temporal autocorrelation and frequencies of the time series itself (Percival and Walden 2000; González-Nuevo et al. 2006). With ecological data, wavelet analysis produces a continuous curve that indicates the intensity or power (*y*-axis; related with the intensity of the periodical patterns of the measured species) of the periodic (*x*-axis) signals of a biological process in a species. The units of this curve are a combination of the intensity (abundance) and periodicity of the measured process, with higher values of the wavelet model in periods located further to the right of the *x*-axis and lower periods to the left. We present a periodical pattern for illustrative purposes in Figure 1, assuming that species can have overlapping periodic patterns that do not overlap over time. In other words, two species can present similar or equal periodical patterns (e. g. species that breed once per year), but do not show temporal overlap (same species occur at different times of year).

Quantifying periodical diversity (PD) through Hill numbers

The Hill numbers attribute diversity framework proposed by Chao, Chiu & Jost (2014) is the basis of our periodical diversity measure, which is based on the Hill numbers theory (Hill 1973). Hill numbers have advantages over other diversity measures because the values are highly comparable between studies. Principally, this is because Hill numbers take to account the relative sensitivity to species richness and abundance, and can be modified by varying the parameter q. This parameter can be any non-negative real number; however, ecologists generally use the values 0, 1, and 2, as they have straightforward biological interpretations (Chao et al. 2014a, 2019a). When $q = 0$, species richness is the only community attribute considered, and the relative abundance of each species is overlooked (i.e., ${}^0D = S$). When $q = 1$, species richness is weighted by species abundance; thus, ${}^1D$ can be interpreted as the effective number of common species in the community assemblage. When $q = 2$, only the most abundant species are considered, and the less abundant or rare species are not accounted for; thus, ${}^2D$ is interpreted as the effective number of dominant species in the community (Jost 2006b). Aside from the ease of interpretation, the main advantage of Hill numbers is that they can be directly compared across studies. In addition, the application of the Hill numbers theory has already been generalized to phylogenetic, functional (Chao et al. 2014a, 2019a) and phenological diversities (Sánchez-Ochoa et al. 2022). We use this mathematical approach to measure periodical diversity in a community.

Periodical diversity through the species pairwise distance framework

Our periodical diversity measure requires computing the distance between the periodical patterns of species pairs, which is similar to how phylogenetic diversity is measured as described in Chao *et al*. (2014). Under the assumption that each time series produces a periodical function, the pairwise overlapping area is used as the distance measure (Chao *et al.*, 2014; Chao *et al.*, 2019). The Morisita-Horn index can be used to measure the overlapping area of two variables over a given time period; in our case, it measures the total overlap between pairs of periodical curves. To use this index as a distance between periodical patterns, we must use its additive complement (Luna-Nieves et al., 2022). Thus, the pairwise periodical distance can be defined as

$$d_{ij} = 1 - \frac{2\int z_i(p)z_j(t)dp}{\int z_i(p)^2dp + \int z_j(t)^2dp} \qquad \text{eqn 3}$$

where z_i and z_j are the periodical curves of species *i* and *j*, respectively. d_{ij} ranges between 0 and 1; if the periodical curves fully overlap, $d_{ij} = 0$, and when periodical curves show no overlap, $d_{ij} = 1$. The overlap of the periodical patterns of two species does not necessarily indicate concurrence in time of the measured process. In other words, as previously mentioned, two species can have the same periodical patterns (e.g. year-round breeding activity), but the process does not occur at the same time (e.g. one breeds in the winter and the other breeds in the summer). Therefore, our approach for measuring periodical diversity is based exclusively on the pairwise periodical distance measured through the Morisita-Horn index (Horn 1966; Garratt & Sterinhorst, 1976).

A standardizing factor is needed to calculate our periodical diversity measure. The relative intensity of overlap of periodical curves is denoted by *Q.* The *Q* parameter combines the overlapped area of the periodical curves between the *i*th and *j*th periodical curves and the intensity of the measured processes (Chao et al. 2014a, 2019b; Chiu and Chao 2014) (eqn 4),

$$Q = \sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij}\, p_i p_j, \qquad \text{eqn 4}$$

where p_i is the relative intensity of the *i*th periodical curve and is defined as

$$p_i = \frac{\int z_i(t)dt}{\sum_{j=1}^{S}\int z_j(t)dt}. \qquad \text{eqn 5}$$

Therefore, integrating all these elements, the periodical diversity of order of *q* is defined as:

$$^{q}PeD = \left[\sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij}\left(\frac{p_i p_j}{Q}\right)^{q}\right]^{\frac{1}{2(1-q)}}. \qquad \text{eqn 6}$$

When q = 1, the $\frac{1}{2(1-q)}$ exponent is undefined, and the following formula is used instead:

$$^{1}PeD = \left[exp\left(\sum_{i=1}^{S}\sum_{j=1}^{S} d_{ij}\left(\frac{p_i p_j}{Q}\right)\log\frac{p_i p_j}{Q}\right)\right]. \qquad \text{eqn 7}$$

Periodical diversity values quantify the effective number of periodical patterns in a community. Thus, the contribution of the periodic curve of each species is considered unique and equally distinct from each other, generating a periodical Hill numbers value higher than 0 to around S, depending on the distances in the pairwise overlapping areas.

Simulations and field data

To exemplify the utility of the periodical diversity measure, we simulated data sets that varied in the periodicity, abundance, and richness patterns under a 40-species community scenario; we also evaluated our periodical diversity measure with two empirical datasets. Although the scenarios in our simulations are unlikely to occur in nature, they exemplify extreme cases that demonstrate the robustness of our measure (Figures 2 and 3). The first, second, third, and fourth simulations correspond to a community with 40 species with different total abundances that together present different periodical patterns (Figure 2A and 2B), a community with 40 equally abundant species that present different periodical patterns (Figure 2C and 2D), a community with 40 non-equally-abundant species that together present 20 different periodical patterns (Figure 3A and 3B), and a community with 20 non-equally-abundant species that together present 20 different periodical patterns, respectively. Finally, the two field data sets correspond to an amphibian community from Madagascar (Figure 4A and Figure 5; S = 40; study period = 360 days; frequency of sampling = daily) (Heinermann et al. 2015) and a long-term database of a benthic community in Chesapeake

Bay, USA (Figure 4B and Figure 6; S = 66; time period = 24 years, frequency of sampling = yearly; Chesapeake Bay Foundation, 2020).

All analyses were performed in R Studio (2020) using the DescTools (Asem, 2020) and wavScalogram (Benítez et al. 2010) packages. We provide the script for calculating the phenological diversity measure in the Supplementary Material.

Results

There is a tendency for the periodical Hill number values to decrease as q increases (Figure 6 and 7. However, there is no decreasing pattern in the second simulation (Figure 2C and 2D) because the patterns of species abundance with time are the same in the community (Figure 2C). Periodical diversity values are shown in Figures 5 and 6. The highest values of periodical diversity were obtained with simulations 1 and 3 (Figure 2A-2B and 3A-3B), both of them being cases with 40 species having different abundances. Simulation 4 was the least diverse and corresponds to the dataset with 20 species. Finally, simulation 2 shows null variation in values and corresponds to the data set with 40 species with different periodical patterns and the same abundance. In general, abundance and number of species directly affect periodical diversity values, and this is reflected in the results of each simulation (Figure 7).

Figure 8A shows the data for the periodical diversity of the Madagascar amphibian community and Chesapeake Bay macro benthic community. ${}^{0}PeD$ for Madagascar was 45.15 (S = 40 species, 120 time points); for Chesapeake, ${}^{0}PeD$ was 67.71 (S = 66, 24 time points). In both cases, the q profile maintains a decreasing pattern as q increased, with q = 1 values reduced to 15.19 for Madagascar and 15.92 for Chesapeake Bay; finally, with q = 2, values reduced to 9.06 and 9.25 for Madagascar and Chesapeake Bay, respectively (Figure 8A and 8B). Thus, the Chesapeake Bay data show more abrupt changes than the Madagascar data in the ^{q}PeD profiles.

Discussion

The periodical Hill numbers framework provides a reliable and interpretable measure of periodical diversity. This framework employs different analyses to obtain an accurate periodical diversity measurement (wavelets, Morisita-Horn index, and Hill numbers). Several studies have proposed the use of time series analysis for period or frequency calculations in ecological and biological time series (Li and Wu 1995; Dale and Mah 1998; Cho and Chon 2006; Tonkin et al. 2017b). However, to our knowledge, no previous study has proposed the use of time series analysis to measure diversity based on frequency time series data. In our case, we used wavelet analysis due to the nature of biological processes, which are nonlinear, non-stationary, and dependent on other variables or natural processes, which generates high variability in these processes (Dale and Mah 1998; Cazelles et al. 2008). Wavelet analyses are useful for this kind of continuous and non-stationary data; other time series analyses, such as Fourier transform or empirical orthogonal functions, cannot be used for these types of data (Cazelles et al. 2008).

Our periodical diversity measure is an extended application of the principle used in phylogenetic (Chao et al. 2014a), functional (Chao et al. 2019a) and phenological diversity (Sánchez-Ochoa et al. 2022). In our case, the pairwise distance between periodical curves was measured through the additive complement of the POI measure (Luna-Nieves et al. 2022), an application of the Morisita-Horn index (Horn, 1966). Because of this, the weighting between richness and abundance is maintained as the order of q changes. Likewise, all overlapping measures that exist, particularly Morisita-Horn and the POI integration and conversion, are more appropriate than other overlapping measures because they both consider the overlapping and non-overlapping areas in our particular framework, which accounts for the importance of the absences in temporary niche theory (Sánchez-Ochoa et al. 2022).

Our periodical diversity measure permits comparisons across different studies. When q = 0, the values represent the total number of completely distinct and unique periodical curves in the community. When q > 0, the periodical diversity values give more importance to species with higher intensities in their periodical curve, which corresponds to species showing greater importance in terms of periodical curves in the community and thus represents the number of periodical curves best represented in the community.

The simulations developed in this study exemplify different scenarios of periodical patterns in a community. The periodical diversity simulations display a variety of abundances/intensities, species richness, and periodical patterns; this measure thus behaves as other diversity Hill number measures (Chiu and Chao 2014; Chao and Chiu 2016; Ohlmann et al. 2019). The highest values of periodical diversity correspond to a simulation that presents different periodical patterns measured in 40 species; this result shows that the measure is directly related to the number of periodical curves tested considering their appearance over time (Figure 7A and 5C). The next simulation with higher periodical values corresponds to the periodical patterns of an evenly abundant species; this result is closely related to the species evenness in the community and reflects the lack of heterogeneity in the abundances or intensity of the species regardless of their frequency patterns (Chiu and Chao 2014). Finally, the lowest periodical diversity values correspond to the lowest periodical curves tested (*S* = 20) and show almost half of the values of the first and second simulations, as it occurs with all diversity indices (Gering et al. 2003); this shows that our measure is closely related to the number of periodical curves measured. Therefore, our framework is a reliable measure of a (poorly explored) community temporal attribute such as periodicity.

The periodical Hill numbers diversity measure was also evaluated on field data. For the Madagascar amphibian's dataset, the periodical diversity of order 0 was 45.15, indicating that there are 45 different, unique periodical patterns in the community. As *q* increases, the effective mean periodical diversity is reduced to 9.06 with *q* = 2. Thus, there are nine dominant periodical patterns; in other words, there are nine periodical patterns that stands out in the community. To determine which environmental variables drive these patterns, a specific study is needed. The resolution of sampling is different and the sampling periodicity differs; periodical patterns can occur on a yearly or biannual scale, or even on a multi-year scale such as the patterns of the ENSO oscillation and solar patterns. We hypothesize that a diurnal, weekly, monthly, and annual cycles are represented among these patterns. Otherwise, the design of the sampling regime might also affect at least one of the observed periodical patterns. A similar result was observed for the Chesapeake macrobenthos community. The periodical diversity was 67.71 when *q* = 0, indicating a mean of nearly 68 different, unique periodical patterns in this community. As in the previous field data case, there are approximately nine common or overly common periodical patterns that are dominant over the others. The environmental variables that potentially affect these organisms are associated with annual rain patterns, wind patterns, oceanic currents and hurricanes (Heinermann et al. 2015). Other analyses could be used to disentangle the causes underlying these periodical diversity values. Something important to highlight is that the time resolution of the sampling effort probably affects the results, and different periodical diversity patterns could be observed under different sampling designs. This also occurs with other diversity measures (CITAS). The resolution of the sampling effort alters the diversity values; thus, sampling effort should be based on the objectives of the research (Jarzyna and Jetz 2018).

Our results show that the periodical Hill number diversity framework was appropriately incorporated in our periodical diversity measure, thus exhibiting properties similar to those of the Hill numbers, which are comparable and intuitive (Chao et al. 2014a, 2019a; Chiu and Chao 2014). Furthermore, this measure enables any periodical phenomena to be analyzed. However, this measure is not free of shortcomings. Time resolution and sampling effort affect the precision in estimating periodical patterns. This occurs because the periodical calculations of wavelet analysis are limited, as this analysis is unable to measure a period greater than $T/2$ and smaller than the minimum sampling interval. Thus, with a higher resolution in sampling effort and long time series data, signals of periodical patterns are more robust, and the calculation of periodical Hill numbers is more reliable. Moreover, the proposed framework can be examined with any taxa at the community level.

Finally, the most important contribution of our Hill numbers-based periodical diversity measure is that it enhances our understanding of how species periodical patterns respond to cyclical phenomena on Earth (Cho and Chon 2006; Pau et al. 2011; Tonkin et al. 2017a). There is no information on which species are more capable of dealing with environmental changes through alterations in their periodical patterns, and several hypotheses are worth considering. For example, species with short periodical patterns would be expected to deal better with some environmental changes than species with long periodical patterns, as they often require particular environmental conditions to display the process of interest (CITA). From a physiological perspective, species with more restrictions in their activity periods may be more capable and better adapted to waiting for favorable environmental conditions than species that depend on particular environmental cues (Sinervo et al. 2010). There is likely a tradeoff between a species' ability to resist environmental changes and the preferred periodical pattern of activity of a species; that is, the more that a species is capable of resisting environmental change, the more likely the periodical pattern of a species is to change. Additional data are needed to confirm this possibility. Finally, it is important to emphasize that periodical diversity has direct application to monitoring and conservation plans because the measure would provide the necessary information to refine the sampling effort based on periodical patterns of species. Likewise, this could be improved if the phenological diversity is considered (Sánchez-Ochoa et al. 2022). Thus, this increase the efficiency of sampling limiting the sampling effort in periods where a greater number of species are recorded.

More studies based on our periodic diversity measure are needed to examine periodical patterns in a community context, understand the environmental cues underlying periodical processes, and gain further insight into how natural selection shapes the temporal distribution of species and the degree to which the periodical patterns of species are affected by environmental changes (*e.g.* Koenig and Liebhold 2005). Of course, our measure needs to be tested with other time series data (even massive biological datasets) at different time frames and taxonomic levels to increase its applicability and to clarify the effects of sampling effort and species detectability on measurements of periodical diversity. Thus, we suggest to use our periodical diversity as a complementary measure for any study of the temporal variation in community diversity.

Conclusions

Our Hill numbers-based periodic diversity measure provides a reliable and intuitive approach for evaluating the diversity of periodical patterns in any ecological community. The framework has the same properties of other Hill numbers-based trait diversity measures (such an account of both richness and species abundance) and thus permits comparisons among biological communities, irrespective of taxon or length of the time series. Our analysis should enhance the design and monitoring and conservation plans and in our understanding of the evolution of periodicity patterns in communities.

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Declarations

All authors conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft; DJSO, HAPM and EJG performed the experiments, prepared figures and/or tables, DJSO and EJG analyzed the data; all authors provide editorial advice.

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Conflicts of interest/Competing interests

The authors declare there are no competing interests and all authors consent for publication.

Availability of data and material

The data for analysis are cited in the text

Code availability

The code for analysis is available in the Supplemental Files

Authors' contributions

Daniel Sánchez-Ochoa conceived and designed the experiments, performed the experiments, analyzed the data, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

Maria del Coro Arizmendi conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Patricia Koleff conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Raúl Martell-Dubois conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Jorge A. Meave conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Hibraim Adán Pérez-Mendoza conceived and designed the experiments, authored or reviewed drafts of the paper, and approved the final draft.

Christopher Akcali Kemal contributed to the discussion section, authored or reviewed drafts of the paper, enhanced the style of the writing, and approved the final draft.

Edgar J. González conceived and designed the experiments, performed the experiments, prepared figures and/or tables, authored or reviewed drafts of the paper, and approved the final draft.

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Figure 1. **Periodogram**. Representation of periodicities of a single variable. The *x*-axis represents the periods on the scale from which samples were collected. The *y*-axis represents the power of the signal; higher values indicate greater intensity of the period calculated.

Figure 2. **Graphs of the tested community simulations**. (A) $S = 40$, all species present different periodical patterns and unequal abundance; (B) representation of all periodical patterns of the simulation on panel A; (C) $S = 40$, all species present different periodical patterns and equal abundance; (D) representation of all periodical patterns of the simulation on panel C.

Figure 3. **Graphs of the tested community simulations**. (A) $S = 40$, with only 20 different periodical patterns with non-equal abundance; (B) representation of all periodical patterns of the simulation on panel A; (C) $S = 20$, all species present different periodical patterns with unequal abundance; (D) representation of all periodical patterns of the simulation on panel C.

Figure 4. **Temporal patterns for the Madagascar and Chesapeake Bay macrobenthos communities.** (A) $S = 40$, with all species having unequal abundances; (B) $S = 66$ representation of all temporal patterns of Chesapeake field data.

Figure 5. **Periodical patterns for all species of the Malagasy amphibian community data.**

Figure 6. **Periodical patterns for all species of the Chesapeake macrobenthos community data.**

Figure 7. **Periodical Hill numbers profiles as functions of q (0 ≤ q ≤ 2) for simulated data.** (A) Case with 40 species presenting different periodical patterns and unequal abundance; (B) case with 40 species presenting different periodical patterns and equal abundance; (C) case with 40 species with only 20 different periodical patterns with unequal abundance; (D) case with 20 species presenting different periodical patterns with unequal abundance

Figure 8. **Periodical Hill numbers profiles as functions of q (0 ≤ q ≤ 2) for real data sets.** (A) Madagascar amphibian community, $S = 40$; (B) macrobenthic community from Chesapeake Bay, $S = 66$.

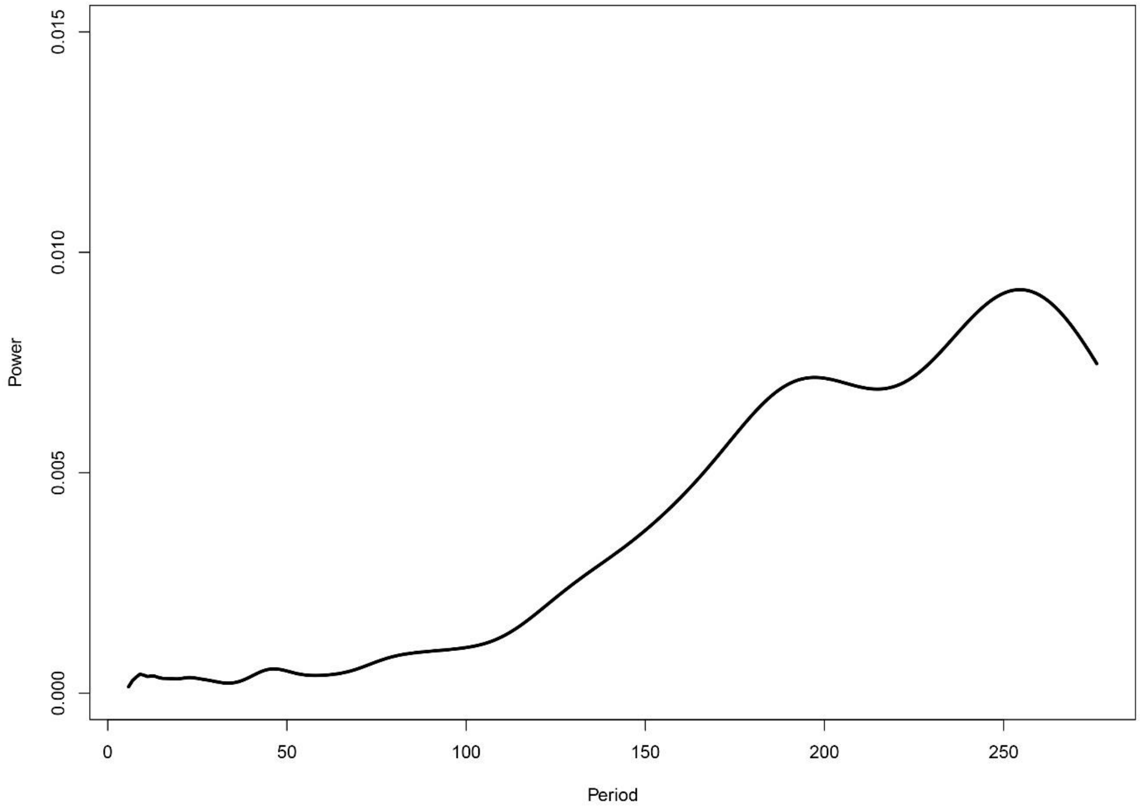

Figure 1. **Periodiogram**. Representation of periodicities of a single variable. Axis x represent the periods in the scale of time of the sampling effort. Axis y represent the power of the signal; higher values are the intensity of the period calculated.

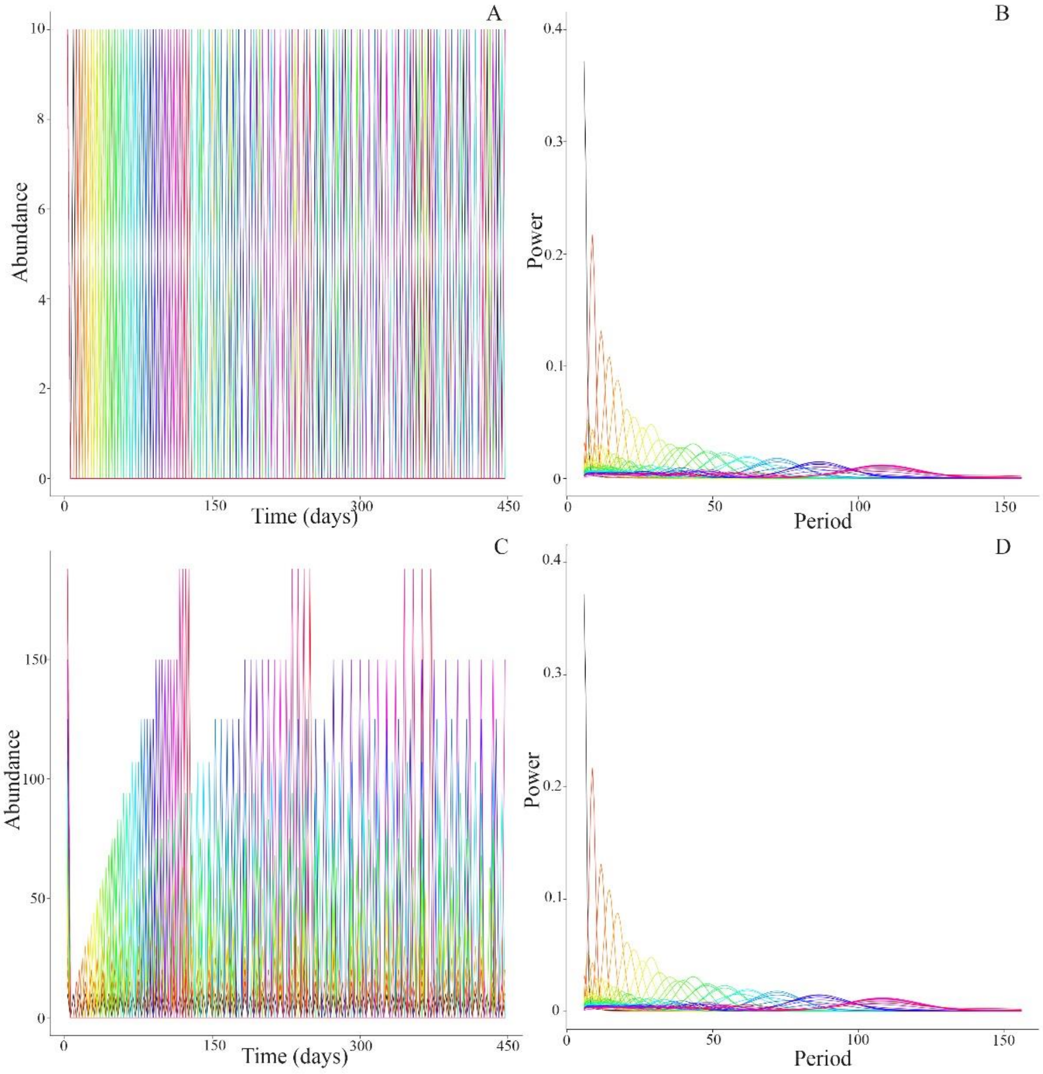

Figure 2. **Graphs of the tested PeD simulations**. (A) *S* = 40, all species present different periodical patterns and non-equal abundance; (B) representation of all periodical patterns of simulation on panel A; (C) *S* = 40, all species present different periodical patterns and equal abundance; (D) representation of all periodical patterns of simulation on panel C.

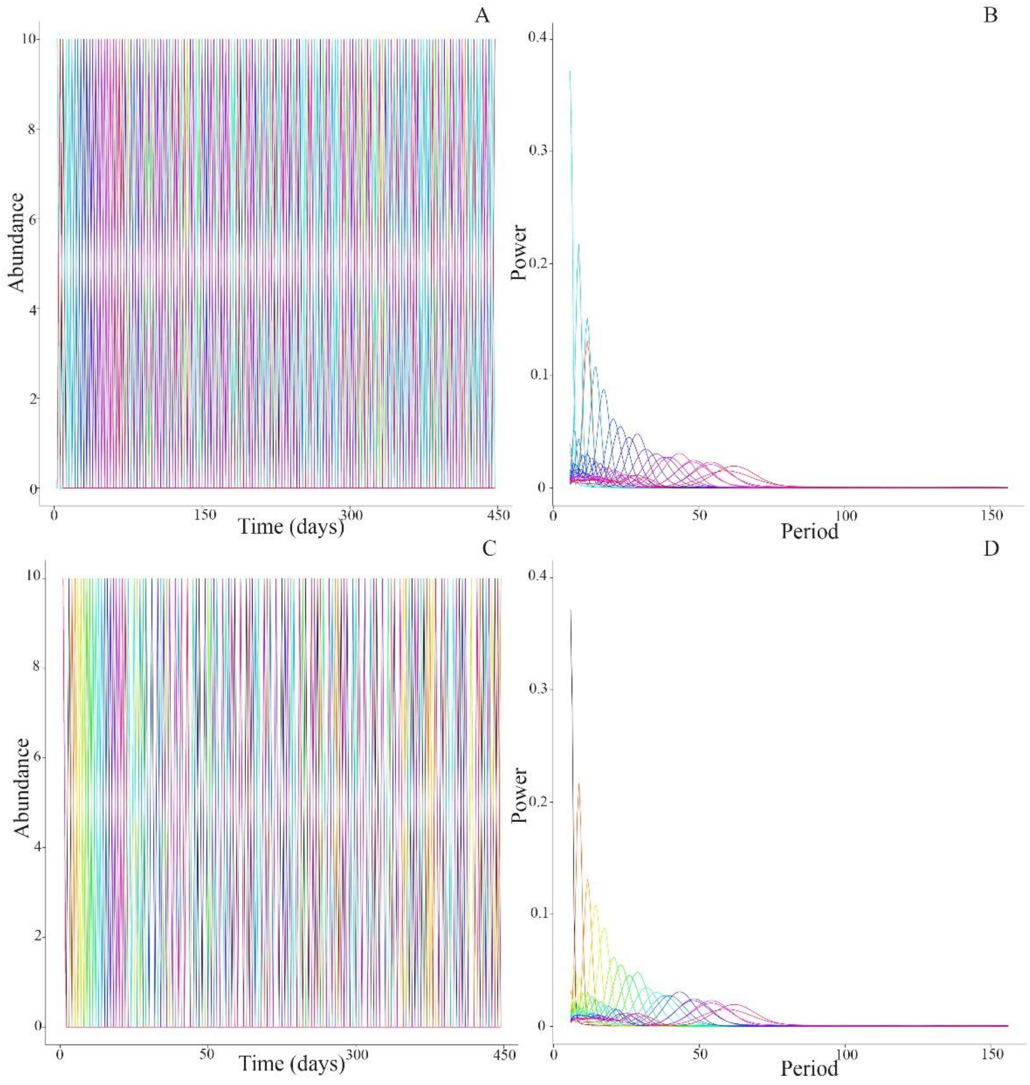

Figure 3. **Graphs of the tested PeD simulations**. (A) *S* = 40, there are only 20 different periodical patterns with non-equal abundance; (B) representation of all periodical patterns of simulation on panel A; (C) *S* = 20, all species present different periodical patterns with non-equal abundance; (D) representation of all periodical patterns of simulation on panel C.

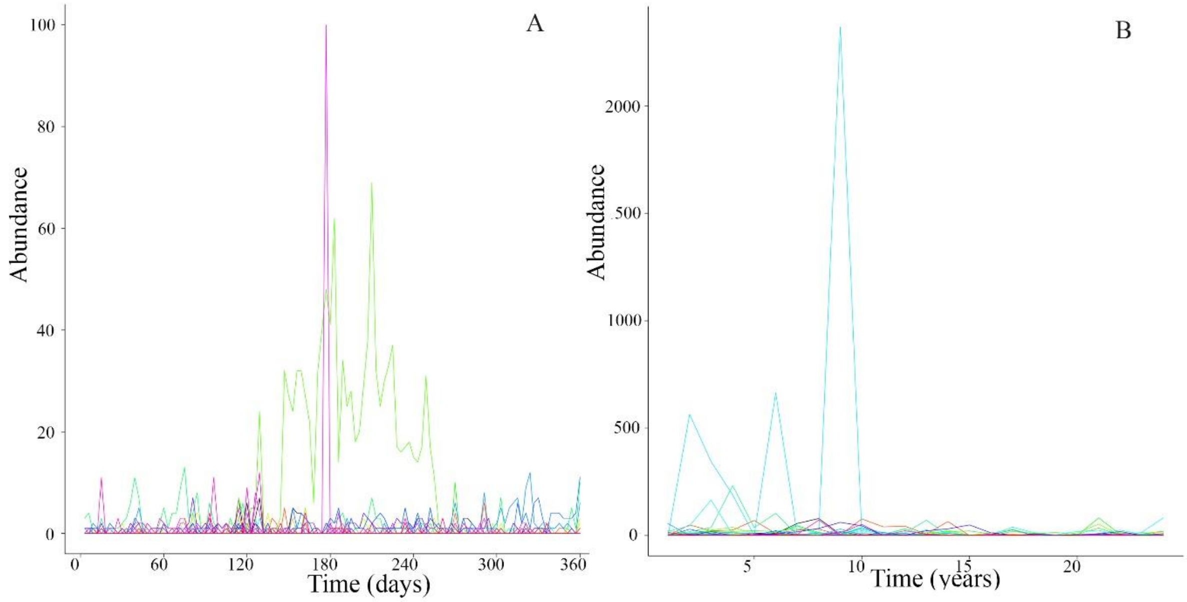

Figure 4. **Temporal patterns for the Madagascar and Chesapeake Bay macrobenthos data.** (A) *S* = 40, with all species having unequal abundances; (B) *S* = 66 representation of all temporal patterns of Chesapeake field data.

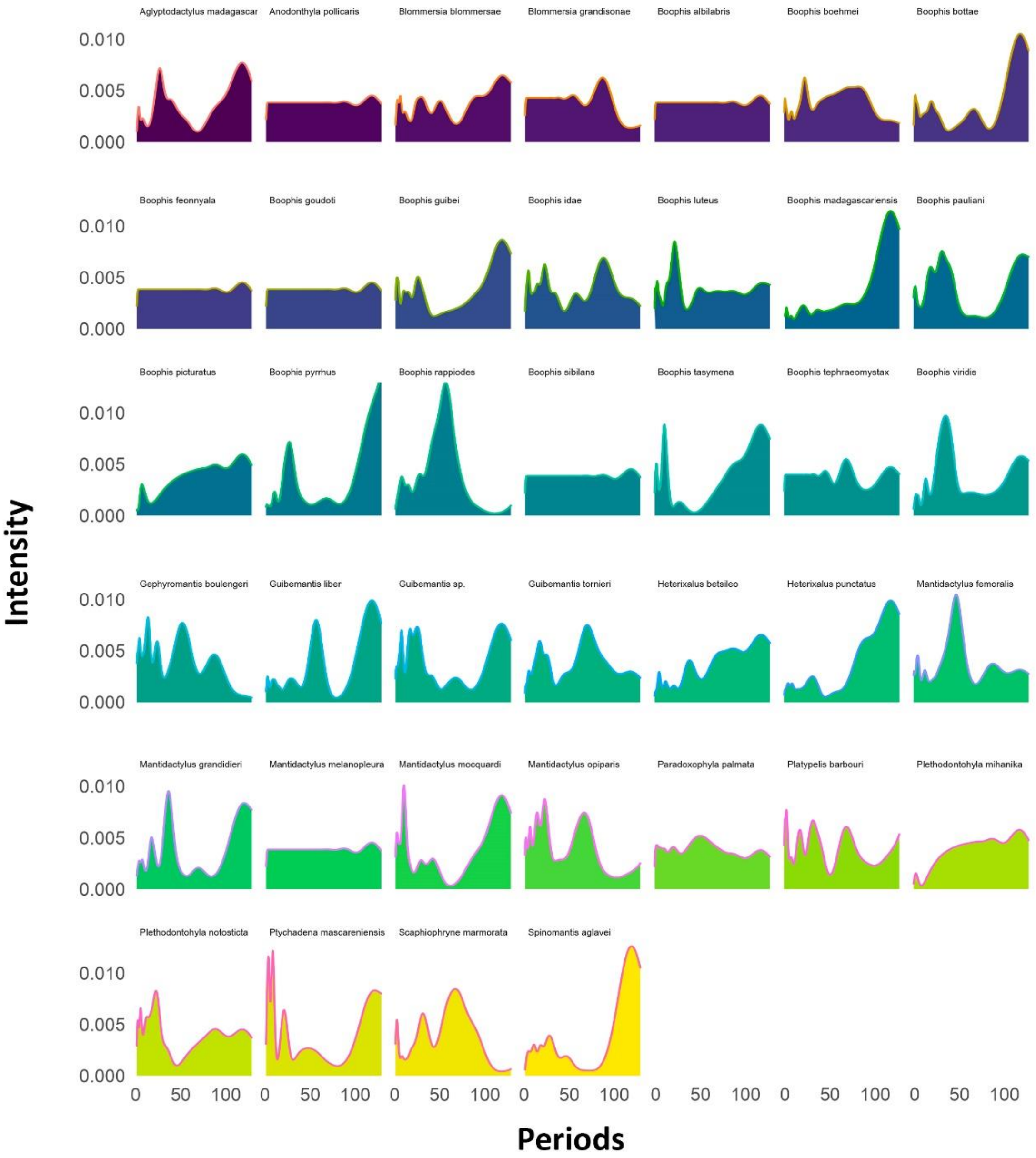

Figure 5. **Periodical patterns for all species of the Malagasy amphibian community data.**

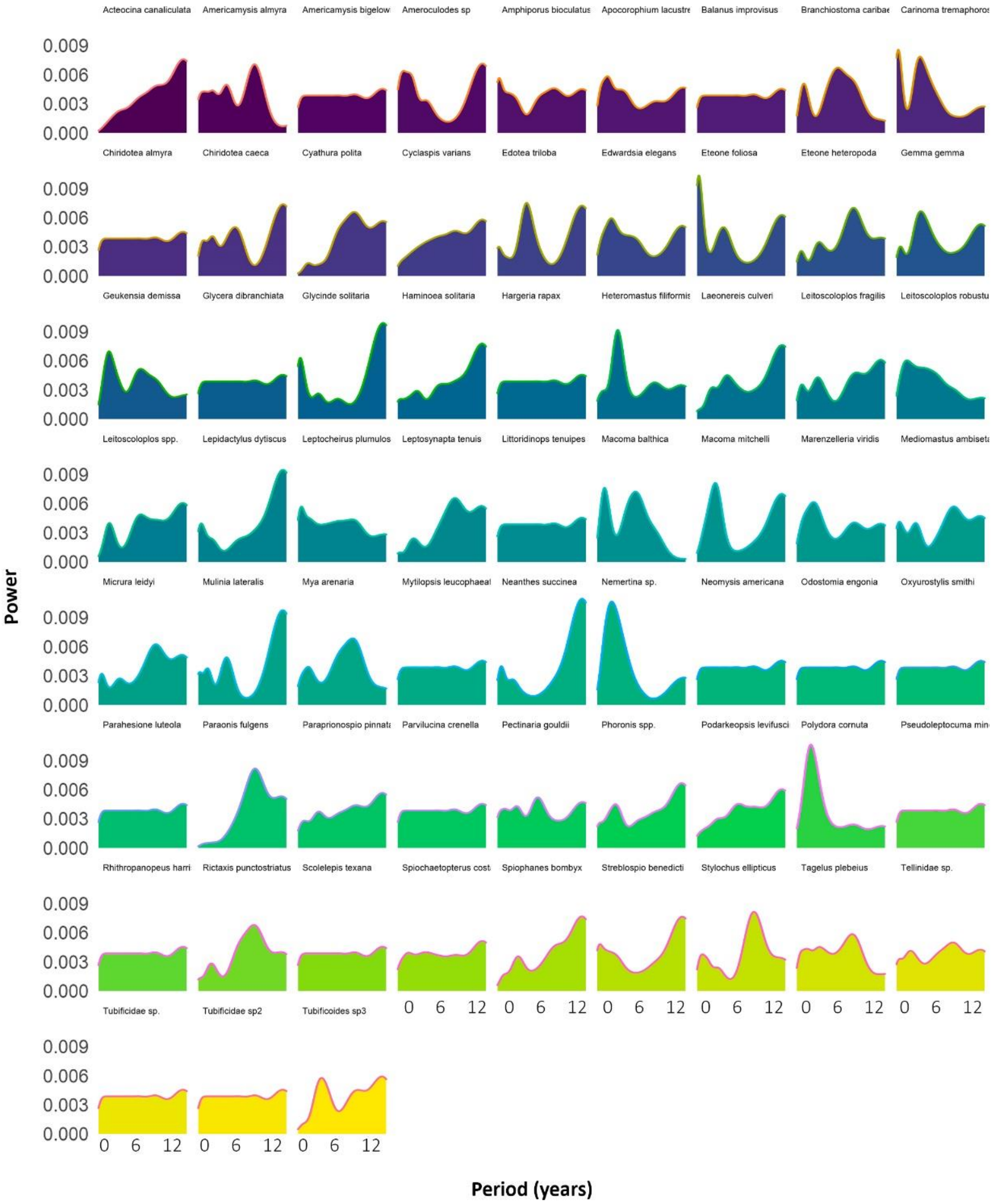

Figure 6. **Periodical patterns for all species of the Chesapeake macrobenthos community data.**

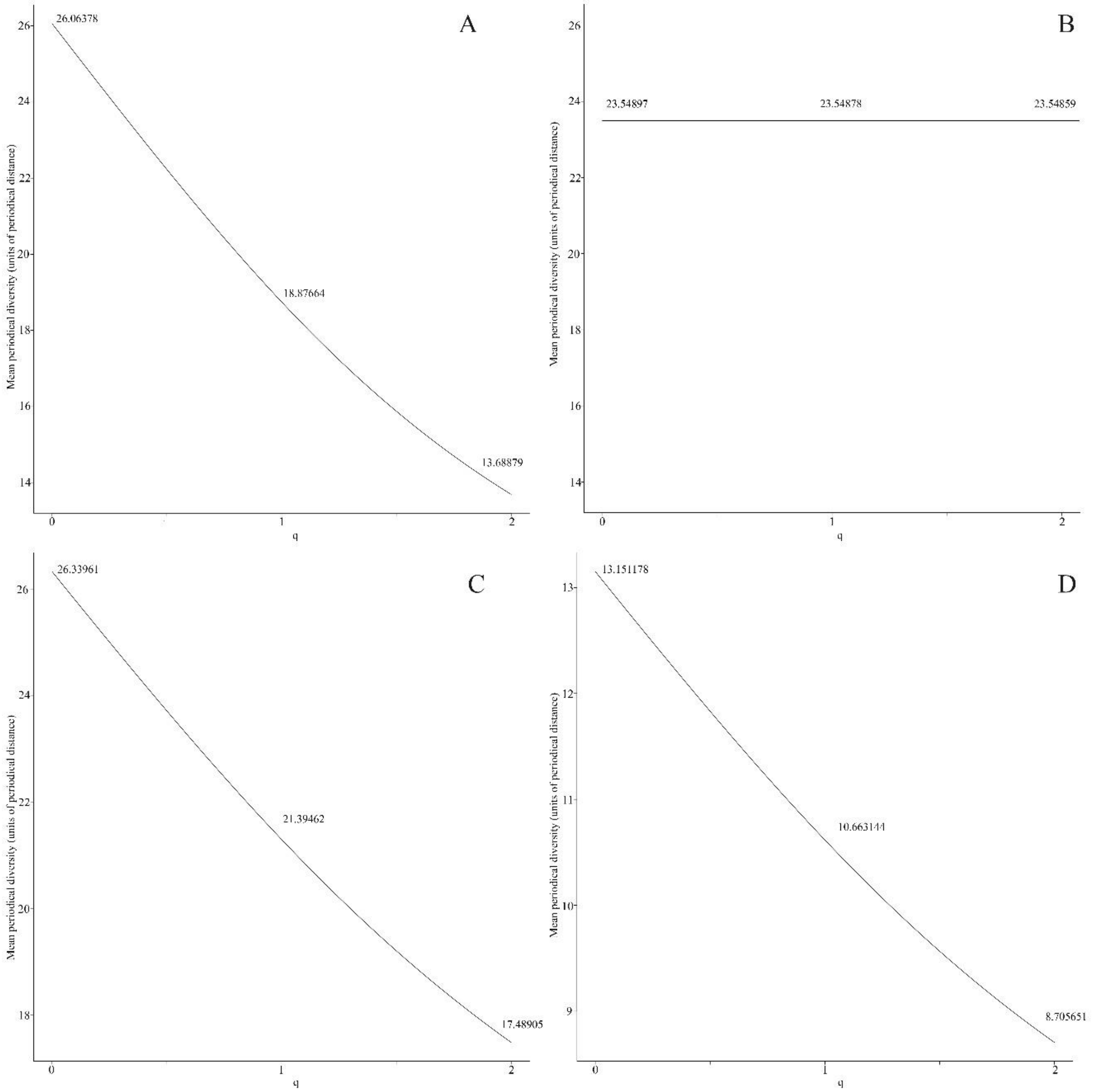

Figure 7. **Periodical Hill numbers profiles as functions of q (0 ≤ q ≤ 2) for simulated data.** (A) Case with 40 species present different periodical patterns and non-equal abundance; (B) case with 40 species present different periodical patterns and equal abundance; (C) case where with 40 species with only 20 different periodical patterns with non-equal abundance and (D) case with 20 species present different periodical patterns with non-equal abundance

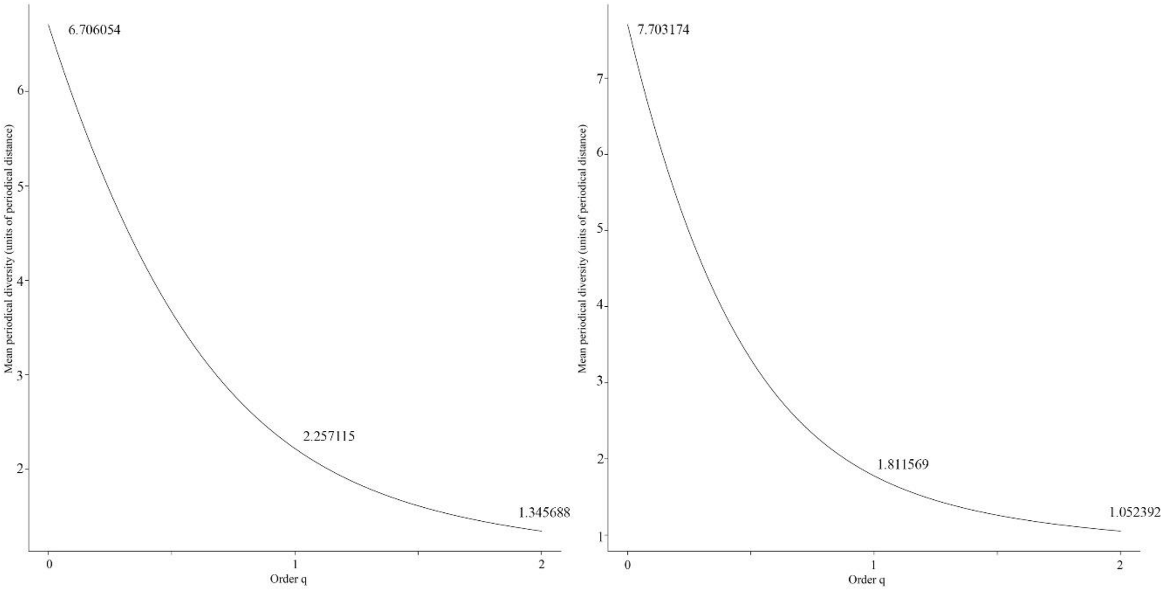

Figure 8. **Periodical Hill numbers profiles as functions of q (0 ≤ q ≤ 2) for real data sets.** (A) Amphibian community from Madagascar, *S* = 40; (B) macrobenthic community from Chesapeake Bay, *S* = 66.

CAPÍTULO IV

Capturing temporal heterogeneity of communities: a temporal β-diversity based on Hill numbers and time series analysis

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(En revisión en Ecological Informatics)

Capturing temporal heterogeneity of communities: a temporal β-diversity based on Hill numbers and time series analysis

Key-words: biodiversity, Hill numbers, species turnover, time series analysis, wavelet transform analysis.

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TA: We developed a novel measure to summarize a key aspect of heterogeneity biological diversity: the temporal β diversity as the effective number of completely different communities over sampling period.

Abstract

Beta-diversity is a term used to refer to the heterogeneity in the composition of species through space or time. Despite a consensus on the advantages of measuring β-diversity using data on species abundances through Hill numbers, we still lack a measure of temporal β-diversity based on this framework. In this paper, we present the mathematical basis for a temporal β-diversity measure, based on both signal processing and Hill numbers theory through the partition of temporal γ-diversity. The proposed measure was tested in four hypothetical simulated communities with species varying in temporal concurrence and abundance and two empirical data sets. The values of each simulation reflected community heterogeneity and changes in abundance over time. In terms of γ-diversity, *q*-values are closely related to total richness (S) and show a negative exponential pattern when they increase. For α-diversity, *q*-value profiles were more variable than γ-diversity, and different decaying patterns in α-diversity can be observed among simulations. Temporal β-diversity shows different patterns, which are principally related to the rate of change between γ- and α-diversity. Our framework provides a direct and objective approach for comparing the heterogeneity of temporal community patterns; this measure can be interpreted as the effective number of completely different unique communities over the sampling period indicating either a larger variety of community structures or higher species heterogeneity through time. This method can be applied to any ecological community that has been monitored over time.

Introduction

We live in a biodiverse world were species changes along space and time (Williams et al. 1997; Mittermeier and Rylands 2017). The different forms of biodiversity have been studied using different mathematical, statistical and information system approaches (Purvis and Hector 2000; Koleff and Gaston 2002). The principal goal of all measures is to characterize variation in biodiversity across different spatial and temporal scales (Humphries et al. 1995; Yoccoz et al. 2001; Fischer et al. 2010). The regional component of biodiversity (γ diversity) contains the inter-site differences (β diversity) between local richness of species (α diversity). Thus, the study of γ, α and β diversity provides values that can predict changes diversity (Crist and Veech 2006; Jost 2007b, 2010; Veech and Crist 2010; Anderson et al. 2011; Baselga 2012). γ, α and β diversities are thus a group of key concepts for understanding the changes in species over landscape, and their applications are wide and include species dispersion, hotspot regionalization, reserve design, and clarification of the complementarity of the composition of species; it is thus one of the most important concepts of ecological theory (Koleff and Gaston 2002; Halffter and Moreno 2005; Ferrier et al. 2007; Baselga 2012; Chao et al. 2016; Mittermeier and Rylands 2017; Tonkin et al. 2017b; Féret and de Boissieu 2020; Fortin et al. 2020).

The concepts of γ, α and β diversity revolves around the understanding of biodiversity patterns. In general, γ and α diversity are different mathematically and similar conceptually but not in scale, being α diversity focused at local and γ at regional. Otherwise, the concept of β-diversity revolves around the heterogeneity of species. The concept of γ diversity is simply the total number of species on a region. α diversity measures attach various definitions influenced by different assumptions of the species diversity, in general there are 2 main analytical groups, the ones related with absence presence data and the based abundance data. Contrary, β diversity measures use different mathematical contexts, concepts and frameworks. Nevertheless, there are two main analytical approaches for measuring β-diversity. The first one is the decomposition approach, in which β-diversity is calculated based on the segregation of γ-diversity and α-diversity components; the second one includes differentiation or variance measures derived from the total similarity of a pairwise community abundance matrix (Tuomisto 2010). Both approaches allow different hypotheses related to the processes driving species distribution and diversity patterns to be tested (Koleff and Gaston 2002; Koleff 2005; Jost 2006a; Tuomisto 2010; Baselga 2012). Differentiation measures are based on similarity-dissimilarity analysis, and the central idea is to assess changes in community structure from a sampling unit to another across different spatial, environmental, or temporal scales (Yue and Clayton 2005; Engen et al. 2011; Chao et al. 2014a). Therefore, the differentiation approach can be used to address questions related to gains or losses of species among spatial or temporal scales and changes in their proportion among sites (Chao et al. 2014a; Chao and Chiu 2016). In general, these last approaches involve community turnover and nestedness models, most of which are based on pairwise differences in space, time, or the environment (Baselga 2012).

The decomposition β-diversity approach is based on the overall component of diversity (γ-diversity) and its relationship to within-community local diversities (α-diversity). Under this approach, raw data are not directly used because the decomposition approach depends on the calculation of α-diversity, except when α = S. In general, this approach captures community variation for an entire set of sampling units that do not require exact species identities because it is based on the calculation of α-diversity (Jost 2007a; Chao and Chiu 2016). Consequently, this approach can be used to address questions related to the heterogeneity and the number of unique species in the communities in a landscape, or to the proportion of species that are not shared among all sampling units. Several multiplicative and additive algorithms can be used under this approach, but all of them are based on the relationship between α- and γ-diversities (Jost 2007a; Baselga et al. 2012; Chao et al. 2019b). Although there is much discussion about what measure is optimal for a given objective or purpose, it has been suggested that both approaches could provide complementary insights that contribute to the advancement of community theory (Chao and Chiu 2016; Moreno et al. 2018). However, the temporal axis of β-diversity has been less explored than the spatial axis, and even some authors have pointed out the lack of reliable temporal frameworks and measures (Koleff and Gaston 2002; Magurran et al. 2019).

The approaches and frameworks for measuring temporal γ, and α diversity are related with the common spatial measures as Simpson, Shannon ad Jaccard index (Shannon, 1948; Simpson, 1949; Jost, 2006b; Chung, Miasojedow, Startek, & Gambin, 2019). There is a unique temporal α diversity approach based on Hill numbers theory (Chao et al., 2021). This measure is the most robust and counts for the effective number of equally abundant species, and also can be applied for species traits (Chao et al., 2021). However, β-diversity measures are diverse and framework development is still lacking (Magurran et al. 2019). Engen proposed to calculate bivariate correlations among community assemblages (Engen et al. 2011). Later, Baselga proposed the β_{TUR} and β_{NES} measures. These indexes are the most used temporal β diversity measures because they permit the use of presence/absence data, information that can be easily obtained with low sampling effort (Baselga 2012). Legendre used Moran´s Eigenvector Map analysis (MEMs) to calculate the positive and negative correlations among time points in community samples (Legendre and Gauthier 2014b). Finally, the temporal β-diversity index was proposed to measure changes in species composition between adjacent time points (Legendre 2019). In general, all the proposed measures are similar to spatial diversity measures. These measures of temporal α and β-diversity are accessible, but the outputs of these measures are not completely comparable between studies, with exception with Chao et al (2021). The temporal β-diversity measures are more related to correlation measures, and the species composition among time points has been calculated using various approaches. Although all measures are quite robust to different traits and approaches, they are not immune to many of the problems associated with spatial β diversity measures. The main shortcomings associated with these measures include their tendency to generate misunderstandings of temporal traits and overlook data independence assumptions. Generally, most temporal biodiversity measurements are based on a sequence of data points indexed along a temporal axis. The data points are literally consecutive measurements of biodiversity of the same area over a time interval, which permits changes to be tracked over time. The assembly of biodiversity observations obtained by repeated measurements over time has certain peculiarities (Parzen 1961; Cho and Chon 2006; Bar-Joseph et al. 2012). Time series are normally characterized with information gaps created by sampling effort, which usually results in discrete variables. The amount of missing information will be determined by the time intervals between samples (Cho and Chon 2006; Cazelles et al. 2008). Any approach for estimating diversity from a temporal perspective has been developed via consideration of the aforementioned assumptions (Legendre and De Cáceres 2013; Legendre 2019). Temporal diversity analysis has been conducted based on time-correlation analysis and time-to-time relatedness analysis of communities; consequently, comparisons among current studies of temporal diversity are not possible (Engen et al. 2011) , except for α diversity (Chao et al. 2021). Thus, a robust temporal β-diversity analysis should be consider the above-mentioned time series assumptions relating to the gaps in the database

(Percival and Walden 2000; Cho and Chon 2006; Inouye et al. 2019). The major problem with this assumption is that ecological processes are considered to occur discretely, which is not true, moreover, species into a community present variation in their abundance changes. This assumption are effectively accounted through wavelet transform analysis, which includes the frequency estimators and provide a reliable approach for predicting gaps in the data to model a continuous variable (Mondal and Percival 2010). In light of these considerations, Hill numbers diversity theory integrated with time series analysis might provide a robust approach for overcoming the lack of comparability in current temporal measures. Hill numbers are a group of diversity metrics that have various advantages in the interpretation of diversity values principally because their units are consistent, which makes them duplicable and comparable among studies.

Hill numbers are a group of parametric measures used to measure diversity based on the modification of the *q* parameter (Jost 2007a; Tuomisto 2010), which determines the sensitivity of the measure to the relative abundance of species and can take any value ≥ 0 (Jost 2007a). Hill numbers denote the effective number of species in the community and have been shown to be reliable for characterizing several community traits (e.g., taxonomic, functional and phylogenetic diversity; Liebhold, Koenig, & Bjørnstad, 2004). The advantage of the Hill numbers approach is that results derived from it usage are more robust, comparable, and interpretable measures compared to other diversity index approaches because Hill numbers are direct diversity values (Chao et al. 2014a, 2016; Chao and Chiu 2016; Ohlmann et al. 2019).

A measure of temporal diversity based on Hill numbers and time series analysis that captures the heterogeneity of diversity through time could provide a more promising strategy for assessing this important biodiversity component, similar to the way in which spatial diversity measures have become comparable among studies (Jost 2007a, b). We expect that this measures will enhance estimates of temporal γ and α diversity, and have a new temporal β that allows interpretable comparisons among studies, considering the ecological processes as a continuous variable. In addition, the measures could be used to characterize temporal diversity patterns and thus provide insights into the temporal dynamics of communities; information on temporal compositional shifts can shed on light on the status of communities and the effects of environmental variables on temporal species heterogeneity (Chao et al. 2019b; Legendre 2019; Magurran et al. 2019).

Materials and Methods

Temporal patterns as a continuous variable: temporal diversity data preparation

We developed our temporal α, γ and β-diversity measures based on the wavelet transform analysis (Schmidt and Skidmore 2004; Sifuzzaman et al. 2009; Tonkin et al. 2017a) and the Hill numbers diversity approach (Hill 1973; Jost 2007a; Chao and Chiu 2016). Our proposed temporal diversity measures were developed specifically for the decomposition approach. By considering the gaps associated with variation in sampling effort, wavelet time series analysis was used to fill gaps in abundance information through an estimated continual abundance curve, and this permits the distance-based Hill numbers diversity measure to be used (Chao and Chiu 2016), with the area under the curve as the basis of the pairwise distance measure. Wavelet transform analyze the frequency spectrum of a discrete time series data, fitting a modeled smoothed curve. The analysis compares (through convolutions) the raw data with a scaling function which can be shrunk, stretched and shifted in time. Finally, a matrix is constructed with all the fitting values in which the sum of the columns results on the new modeled curve (Figure 1).

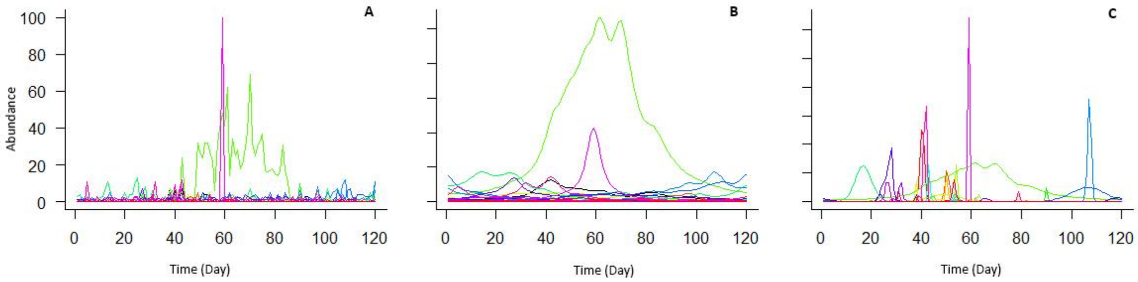


Figure 1. Comparison of same data set of abundance patterns of a Malagasy amphibian community. (A) representation of the raw data, (B) wavelet transformed data with τ = 2, and (C) wavelet transformed data with adjusted τ values. Each color represents a species (S = 40; N = 120 days).

τ – the rate of change of species abundances over continuous time

Biological processes occur gradually and continuously, however in most cases they are discreetly recorded due to sampling. However, there are differences in rates of change in the occurrence and abundance changes of species. For example, groups of species that have a high response to environmental changes often have abrupt changes in their abundance (such as amphibians, reptiles and insects). On the contrary, there are organisms in which changes in abundance occur in a more attenuated pattern (such as plant communities). Being more specific, within these generalities, it is true that each species has its particularities of the temporal variation, thus, τ is a variable that considers this biological aspect (Figure 1). Wavelet analysis typically assigns a value of

2 to the rates of change in modeled phenomena through time. Given that rates of change in the abundance of species through time are not equivalent due to variation in the traits of species, unique values of this parameter should be assigned to each species to account for this variation. Wavelet analysis allows interpolation of a continuously modelled abundance curve; however, unlike the common use of wavelet analysis, this analysis for our purpose requires the specification of the attenuation threshold ($\boldsymbol{\tau}$), a parameter that controls for the rate of continuous change in the occurrence of species in the community. In other words, $\boldsymbol{\tau}$ determines the slope (i.e., the speed) at which species abundance or species intensity changes through time (Li and Wu 1995; Percival and Walden 2000). For example, there are communities where some species display faster rates of appearance with respect to others (Rossman et al. 2016), i.e., depending on its intrinsic natural history traits, each species can potentially exhibit their own rate of change in abundance through time (Ehrlén and Morris 2015). Thus, a fixed parameter value (usually 2 in most analyses) is not an appropriate assumption, and a more objective value is needed for each species (Dale and Mah 1998; Torrence and Compo 1998; Sifuzzaman et al. 2009). In this way, a correct fixed $\boldsymbol{\tau}$ must consider the resolution (sampling time interval), the total sampling effort (T), and the steepness of the abundance changes in the raw data. In this regard, the rate of change in the abundance of species over time and the accuracy of the data sampled are important. If time series data have a high resolution, $\boldsymbol{\tau}$ will be weighted highly according to the rate of change in the abundance of each species; otherwise, when time series data have low resolution, $\boldsymbol{\tau}$-values will highly weight the new abundance curve calculated with wavelet transform analysis. Here, we propose, for a given *i* species, a value of

$$\tau_i = (\tau_{\max} - \tau_{\min})\delta_i + \tau_{\min}, \qquad \text{eqn. 1}$$

where

$$\tau_{\max} = (T-1)^{\frac{T}{T+1}}, \qquad \text{eqn. 2}$$

$\tau_{\max}$ corresponds to a constant of the maximum value that τ_i can take in the analyzed community, $\tau_{\min} = 2$, $\tau_{\min}$ corresponds to the constant minimum threshold that τ_i can take.

The equation

$$\delta_i = (d_i - \min_i(d_i))/(\max_i(d_i) - \min_i(d_i)), \qquad \text{eqn. 3}$$

represents the rescaling factor between 0 -1 of d_i, or the derivative that biologically refers to the rate of change where

$$d_i = \frac{1}{T}\int \left|\frac{d^2 z_i(t)}{dt^2}\right| dt, \qquad \text{eqn. 4}$$

d_i corresponds to the mean concavity of absolute values of the species abundance; in other words, d_i is the average steepness of the changes in species abundances between consecutive samples in time. Finally, $z_i(t)$ represents the raw abundance of the *i*th-species for each time, whereas *T* represents the total number of sampling times.

Each τ_i value integrates the rate of abundance change of each species based on the observations and the maximum number of sampling points of the study. The scaling function used for the wavelet analysis was the Morlet scaling function, which is optimal for data with unknown frequencies and scales, and data that cannot be directly interpreted (Percival and Walden 2000).

Temporal* β *diversity: effective number of distinct communities over time

For our temporal β-diversity measure, we replaced the discrete abundance vectors by abundance or intensity curves derived from the wavelet time series analysis. We modified the equations from Chao & Chiu (2014) (eqn. 5), so that the relative abundance values (z_i) represent the abundance curves of the *i*-th species. To estimate temporal β-diversity through the multiplicative component (γ/α), we first need to calculate temporal γ-diversity and temporal α-diversity. To calculate γ-diversity of order *q* ($^qDT\gamma$), we used the relative abundance of species in the community (z_{i+}/z_{++}; $i = 1, 2, \ldots, S$), where $z_{i+} = \int_T z_i(t)dt$ is the total area of abundance of *i-th* species, and $z_{++} = \sum_{i=1}^{S} \int_T z_i(t)dt$ is the total sum of the area abundance of all species. Consequently, γ-diversity of order *q* is defined as

$$ {}^{q}DT_{\gamma T} = \left\{ \sum_{i=1}^{S} \left(\frac{z_{i+}}{z_{++}} \right)^{q} \right\}^{\frac{1}{(1-q)}}, \qquad \text{eqn. 5} $$

and when *q* = 1 as

$$ {}^{1}DT_{\gamma T} = \exp\left\{ -\sum_{i=1}^{S} \frac{z_{i+}}{z_{++}} \log\left(\frac{z_{i+}}{z_{++}} \right) \right\}, \qquad \text{eqn. 6} $$

The temporal γ-diversity is interpreted as the “effective number of species in the entire community through time” or the species richness when q > 0. For temporal α-diversity we applied the same set of measures and definitions proposed by Chao & Chiu (2014) but on a temporal scale. In this sense, temporal α-diversity represents “the effective number of species per time unit” or the “mean effective number of species per time unit”, and defined by:

$$ {}^{q}DT_{\alpha T} = \frac{1}{T} \left\{ \sum_{i=1}^{S} \int_T \left(\frac{z_i(t)}{z_{++}} \right)^{q} dt \right\}^{\frac{1}{(1-q)}}, \qquad \text{eqn. 7} $$

and when q = 1, as:

$$^{1}DT_{\alpha T} = \exp\left\{-\sum_{i=1}^{S}\int_{T}\left(\frac{z_i(t)}{z_{++}}\right)\log\left(\frac{z_i(t)}{z_{++}}\right)dt - \log(T)\right\}. \qquad \text{eqn. 8}$$

Finally, the multiplicative temporal β-diversity can be calculated as:

$$^{q}D_{\beta_T} = {}^{q}DT_{\gamma T}/{}^{q}DT_{\alpha T}\ , \qquad \text{eqn. 9}$$

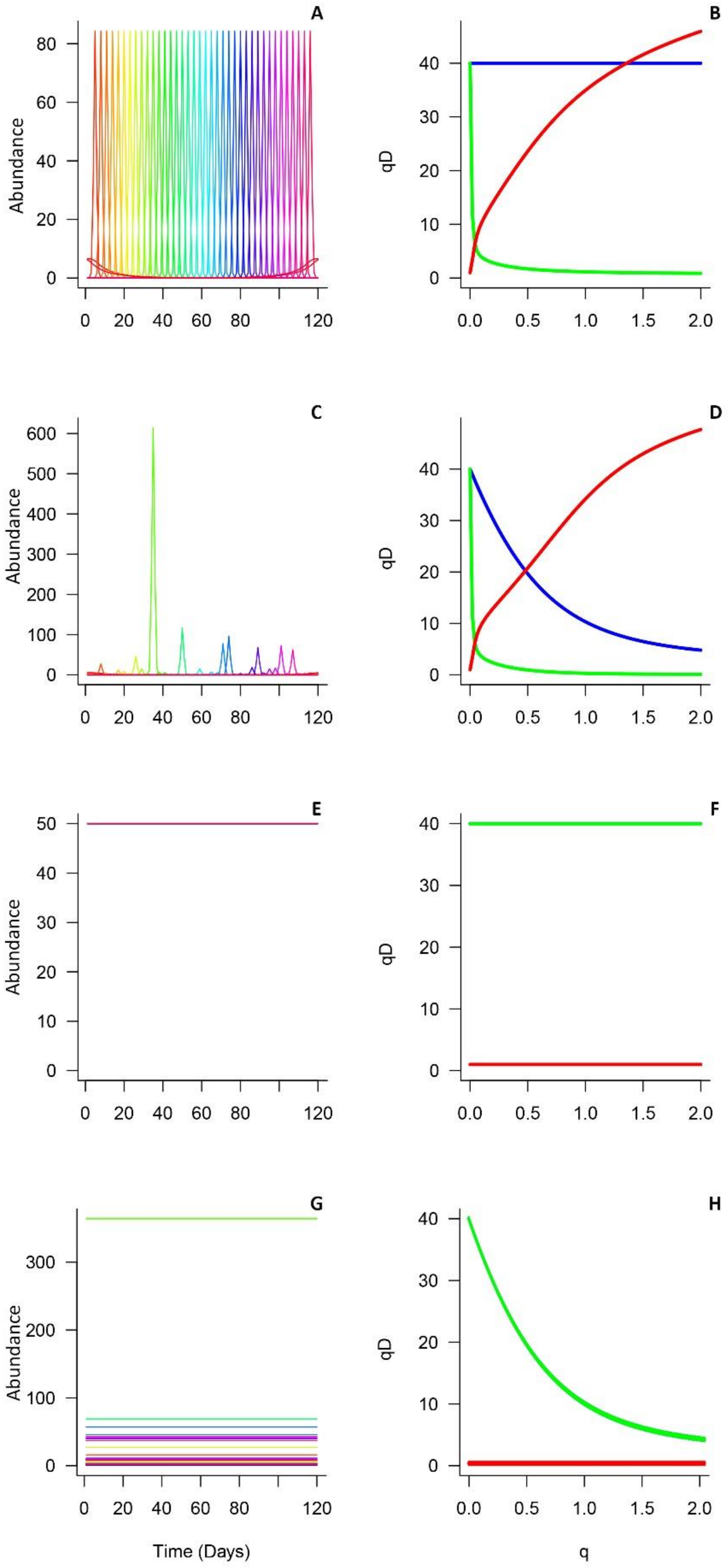
This value can be interpreted as “effective number of completely different unique communities over the sampling period”. The contribution of species heterogeneity among communities is based on changes in the rate of whole community richness and the mean community changes at each sampling point. Temporal α- and γ-diversities always range from > 0 to S and decrease as q increases; temporal β-diversity ranges from 1 (when q = 0) to infinite.

To illustrate the use and utility of this measure of temporal β-diversity, we performed simulations varying the abundance and heterogeneity of species richness. In addition, we performed two extra analyses based on field data of an amphibian community from Madagascar (S = 40; time period = 360 days; frequency = daily; Heinermann et al., 2015) and a macro-benthic community from Chesapeake Bay (S = 66; *time period* = 24 years, frequency = yearly; Chesapeake Bay Foundation, 2020).

We used R Studio with the DescTools (Asem, 2020) and wavScalogram (Benítez, Bolós & Ramírez, 2010) packages. The script for the temporal β-diversity calculation can be found in Appendix 1.

Results

Patterns of temporal α- and γ-diversity were similar to those suggested by other diversity measures based on Hill numbers, which was consistent with expectation. The values of each simulation reflected community heterogeneity and changes in abundance over time. In terms of γ-diversity, *q*-values are closely related to total richness (S) and show a negative exponential pattern when they increase, except when species abundances are constant over time. For α-diversity, *q*-values profiles are more variable than for γ-diversity, and different decaying patterns in α-diversity can be observed among simulations (Figure 1). Whenever *q* increases, if there are differences in abundance, α-diversity values display a decaying pattern (Figures 1B, 1D and 1H), causing temporal β-diversity to show different patterns, as observed in the analyses based both on simulations and field data (Figures 1 and 2). Otherwise, the absence of a decreasing pattern in Figures 1 and 3 reflects the null variation in both species richness and abundances in the simulated data. The minimum values of β-diversity are always 1 and in general they increase as *q* increases, except in those cases where γ- and α- diversities do not change (i.e., Figure 1F and 1H). The most variable β-diversity pattern is shown in Figures 1B and 1D, where species are equally distributed over time, which corresponds to the most heterogeneous community in terms of species changes over time. For the Malagasy amphibian community, temporal β-diversity shows high values near *q* = 0 and then stabilizes as *q* increases; by contrast, β-diversity shows a nearly constant increasing pattern as *q* increases in the Chesapeake Bay macro-benthic community.


A
Abundance
0
20
40
60
80
0
20
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B
qD
0
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0.0
0.5
1.0
1.5
2.0
C
Abundance
0
100
200
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500
600
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20
40
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80
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D
qD
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E
Abundance
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40
60
80
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F
qD
0
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30
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0.5
1.0
1.5
2.0
G
Abundance
0
100
200
300
0
20
40
60
80
120
Time (Days)
H
qD
0
10
20
30
40
0.0
0.5
1.0
1.5
2.0
q

Figure 2. Graphs showing temporal γ-, α-, and β-diversity profiles as functions of q ($0 \leq q \leq 2$): (A) simulated data where species are equally distributed over time and abundance patterns are identical, representing a situation where each species can be found at any specific time. (B) Temporal γ- (blue line), α- (green line) and β-diversity (red line) profiles of panel A. (C) Simulated data where species are equally distributed over time and abundances are unequal. (D) Temporal γ- (blue line), α- (green line) and β-diversity (red line) profiles of panel C. (E) Simulated data where species are present all the time without abundance variation and equal abundances. (F) Temporal γ- (blue line), α- (green line) and β-diversity (red line) profiles of panel E. (G) Simulated data where species are present all the time without abundance variation and unequal abundances. (H) Temporal γ- (blue line), α- (green line) and β-diversity (red line) profiles of panel G.

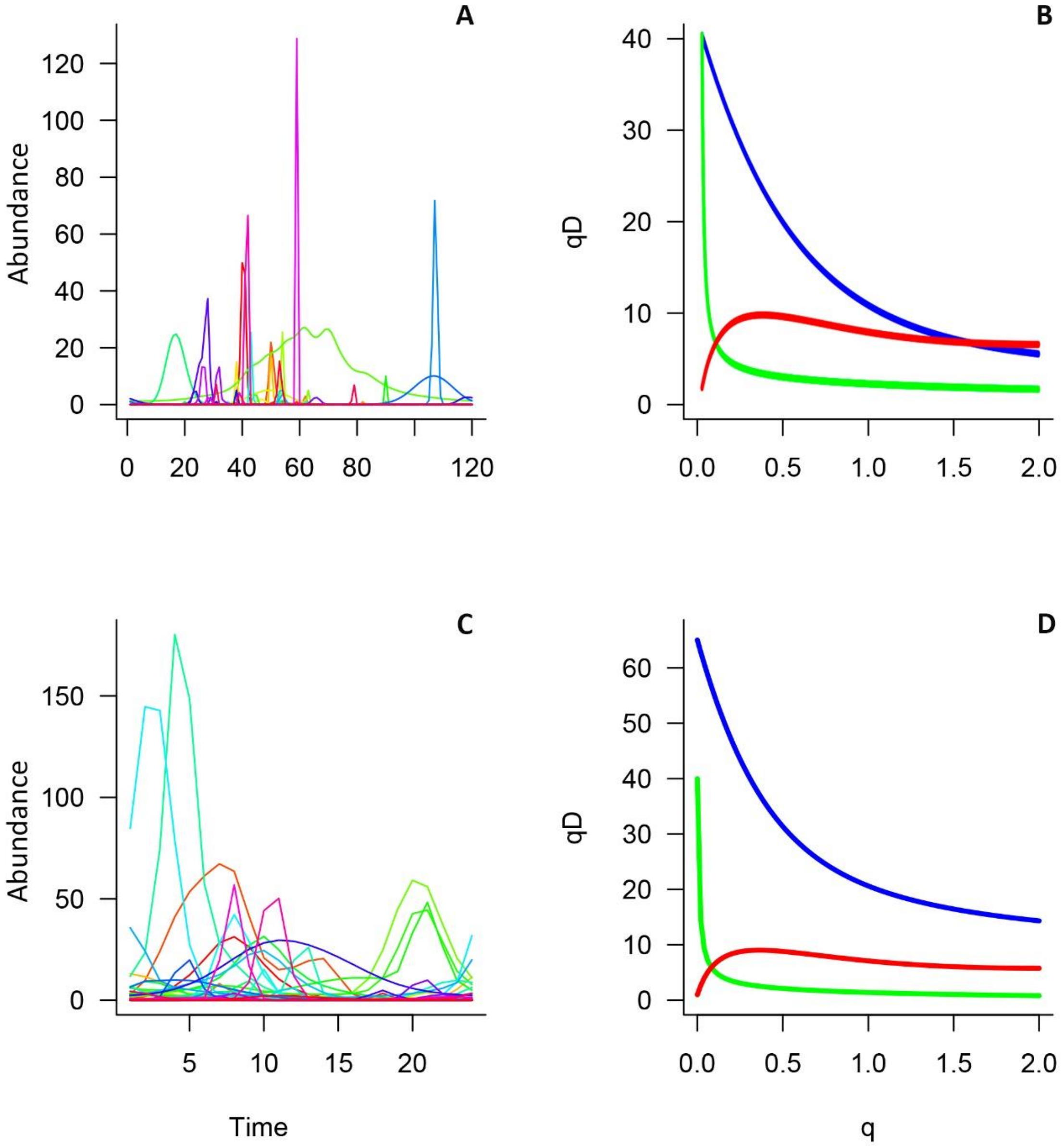

Figure 3. Graphs showing the temporal γ-, α- and β-diversity profiles as functions of q (0 ≤ *q* ≤ 2) for an amphibian community from Madagascar. (A) Wavelet transform distribution of species throughout time for the amphibian community from Madagascar (S = 40). (B) Temporal γ- (blue line), α- (green line) and β-diversity (red line) profiles of panel A. (C) Wavelet transform

distribution of species throughout time for the macro benthos community from Chesapeake Bay (S = 66). (D) Temporal γ- (blue line), α- (green line) and β-diversity (red line) profiles of panel C.

Discussion

Here, we propose a temporal γ, α and β-diversity measures based on time series analysis and Hill numbers diversity theory that provides an interpretable, efficient and comparable tool to characterize temporal community heterogeneity. The use of wavelet analysis for developing a temporal diversity framework enhanced the robustness of the results and circumvents sampling effort-related problems (Sifuzzaman et al. 2009; Mondal and Percival 2010). To perform this analysis, we approximate the abundance time series data to simulate a continuous abundance curve as in other studies (Li and Wu 1995; Dale and Mah 1998; Cazelles et al. 2008; Senf et al. 2017). One of the major challenges associated with temporal diversity analysis, especially β-diversity measures, is the failure of datasets to meet the assumptions of time series data because current measures do not consider sampling resolution patterns and time frequency characteristics (Legendre and De Cáceres 2013; Legendre and Gauthier 2014a; Legendre 2019), and wavelet analysis can overcome this difficulty. Other studies have shown that time series analysis is an effective way to analyze data collected from ecological and forestry studies (Dale and Mah 1998; Sebastian et al. 2019) for several purposes such as population dynamics, disease transmission, animal migration and phenology (Li and Wu 1995; Dale and Mah 1998; Schmidt and Skidmore 2004; Shuai et al. 2018; Zhang et al. 2019; Wu et al. 2020; Nourani et al. 2021). For our purpose, wavelet analysis provides an effective method for modelling a continuous abundance curve under the assumption that species abundance changes occur gradually rather than abruptly at different scales. Nevertheless, there are two assumptions to considerate in wavelet analysis transform related with sampling effort: Overall, (1) equidistant temporal sampling and (2) long time series data conduct to a better modeled curves. It is possible to analyze data based on repeatedly sampling effort, depending on the question and life cycle of organisms, otherwise other time series analysis perspectives as Hilbert Huang approach should be better, but this perspective has not been used for ecological data. Likewise, is recommended that 25 is the minimum number of sampling temporal points necessary to wavelet analysis, nevertheless here we performed an example with 24 sampling points (Chesapeake microbenthic community) (Chamoli et al. 2007; Cazelles et al. 2008). There is no systematic assessment for that assumption and there is a need to test it with high resolution data, removing and reducing random sampling points.

Temporal changes in the abundance, conspicuousness or biological processes of species vary among all species in communities. Wavelet analysis through the τ parameter partially takes into account this variation. Mathematically, the τ parameter controls the slope of the modeled curve, but this parameter is not modified in conventional wavelet analysis (Li and Wu 1995; Torrence and Compo 1998; Sifuzzaman et al. 2009). Biologically, the τ parameter reflects the rate of change in the occurrence and abundance of species; this prompted us to assign an objective τ-value for each species in the studied community. In this way, the τ-parameter directly relates to the rate of change in the abundance of each species and the total sampling points. In our study, τ-values near 2 imply that the analyzed species have abundance patterns similar to those modeled by wavelet analysis, and species with higher τ-values have simulated abundance curves that resemble the mode (statistics) of the raw data. Likewise, this idea suggests that the probability of detection or occurrence of species is a parameter that should be considered in all diversity studies, and the recorded frequencies of species are an artifact of species´ actual frequencies and their detection probabilities. The imperfect detection of species is important to consider to obtain high quality estimates of the size of ecological populations (MacKenzie and Kendall 2002; Wintle et al. 2005; Banks-Leite et al. 2014). This stems from the fact that the signals of species are underestimated when they are present but not detected. Various situations can lead to underestimates in the signals of species (Li and Wu 1995; Cazelles et al. 2008; Marion et al. 2018), and a correction in the detection in the abundance curves in our analysis could refine the overlapping area and $\boldsymbol{\tau}$ calculation; nevertheless, imperfect detectability also varies with time.

For temporal α diversity, was possible to use the perspective of Chao 2016 (Chao and Chiu 2016), however it is not the same as that proposed in 2021 (Chao et al. 2021). Firstly, the already existing measure accounts for the effective number of equally abundant species and here, temporal α diversity accounts to the mean effective number of species seen per sampling unit. The differences between measures are mainly associated with the model construction, however, we considered the 2016 Chao's perspective because it was a framework built to bridge the two β diversities approaches. On the other hand, this perspective indirectly takes into account the detection of organisms since it considers the average number of species seen per sample. Thus, this perspective is more sensitive to average changes in the number of species from sample to sample. Thus, this perspective is more sensitive to average changes in the number of species from sample temporal points. At the same time temporal α diversity values when $q = 0$ will be equal to those of temporal γ diversity when $q = 0$. This is mainly due to the fact that the calculation of the continuous curve of abundance through wavelet assigns a value close to zero in the probability of encountering the species over time. In this sense, in this measure we are assuming that the species have imperfect detectability, and could be registered at any time, variating in four axes (species traits, spatial variation, temporal variation and sampling characteristics; (Guillera-Arroita 2017). This has received a lot of attention at population and community level (Chen et al. 2013; Banks-Leite et al. 2014; Kellner and Swihart 2014; Rossman et al. 2016); however, some studies have pointed out the need to include imperfect detectability on biodiversity surveys (Boulinier et al. 1998; Kellner and Swihart 2014). Future research on the standardization of values is needed to improve the comparability of results, without excluding low detectability or rare species. From our experience, link function, $\boldsymbol{\tau}$ parameter, or even a cutoff value could be options where the diversity values could be better adjusted, however, with the change of these variables, diversity patterns remain unchanged.

The temporal β-diversity measure proposed here is a decomposition Hill numbers approach adopted from the scheme developed by Chao and Chiu (2014), which is based on the relationship between γ- and α-diversities in a community. Given the great variation in β-diversity decomposition methods, other decomposition approximations could also be tested using the same approach; our γ- and α-diversity calculations would be the same as the theoretical framework and can be easily linked to other perspectives (Ricotta and Marignani 2007; Chao et al. 2019b). β-diversity can be analyzed through a distance-based approach; however, the Chao and Chiu framework was mainly constructed to establish a link between both β-diversity approaches (Chao and Chiu 2016) and a temporal β-distance-based approach to complement our measure, including time series transformation of the same data (Podani et al. 2013; Chao et al. 2016). Likewise, other temporal β diversity frameworks, such as those of Baselga and Legendre (Baselga 2012; Legendre 2019), have demonstrated the value of using multiple measures of β diversity, but the utility of using multiple measures ultimately depends on the hypothesis tested (Anderson et al.

2011). However, the interpretation of these other measures requires caution because some refer to the concepts of turnover and others to variation (as our measure), but the interpretability is maintained under the Hill numbers framework. Otherwise, the most used measures of β diversity (Jaccard and Sorensen) (Jaccard, 1912; Sorensen, 1948; González, n.d.; Chao, Chazdon, & Shen, 2005; Baselga, 2012) and even α diversity (Shannon and Simpson) (Whittaker and Whittaker 1972) do not have a unifying structure that facilitates interpretation and comparison (Jost 2006a, 2010).

Thus, the principal advantage of our framework is that the proposed temporal β-diversity measure provides a more direct and objective approach for comparing the heterogeneity of temporal community patterns. In this context, temporal γ-diversity is defined as the "effective number of species throughout the entire studied time period", temporal α-diversity as the "mean effective number of species at each time", and temporal β-diversity as the "effective number of completely different unique communities over the sampling period". In general, γ- and α- *q* profiles are consistent across estimated spatial diversity patterns (Ohlmann et al. 2019); however, *q*-profiles related to β-diversity do not show a consistent pattern. Specifically, temporal α-diversity only reflects an expected outcome rather than the reality indicated by the sampling measurements; thus, a completeness analysis could improve the robustness of the results for both temporal γ- and α-diversity as has been shown in other studies of diversity patterns (E 1999; Sørensen et al. 2002; Williams et al. 2006). For temporal β-diversity, overestimations were observed in simulations, especially in cases where several species were equally distributed, as temporal β-diversity values are higher than *S* (the number of species) when $q = 2$. A high temporal β-diversity indicates a high number of unique communities throughout the sampling period and thus temporal heterogeneity in the activity of species within the community. Nevertheless, our measure is not suitable for indicating the moments where unique communities are occurring, but other measures can be used to provide this information, such as Legendre's TBI (Temporal Beta Index) (Legendre 2019). Thus, we show here that the use of different frameworks provides complementary information and that the use of each measure is not mutually exclusive.

Despite differences in the taxonomic group, species richness, and temporal resolution among field studies, temporal β-diversity can be measured using these data. Although we expected asymptotic behaviors, we observed different temporal β-diversity patterns in the two data sets examined. In the Malagasy amphibian community, we observed that the temporal β-diversity *q*-profile shows high values when *q* is between 0 and 1, and the profile shows an asymptotic pattern. The rate of change in the α-diversity *q*-profile largely determines the heterogeneity of the community (temporal β-diversity) because α- and γ-diversity values are divergent. For example, few species of amphibians are commonly observed per sampling occasion or per unit of time; in other words, few species are recorded during each sampling event, and the species observed continuously vary as has been documented in other studies (Tanadini and Schmidt 2011; Heinermann et al. 2015; Asad et al. 2020). This result has direct implications for our understanding of the heterogeneity of communities through time as well as for conservation and monitoring actions because some community traits through spatial and temporal scales exhibit divergent patterns (Renner et al. 2018; Rowan et al. 2020). Thus, to understand the temporal relations as spatial perspectives of γ, α and β diversity is to analyze several data sets. It is true that the relation between spatial γ and α diversities largely determines spatial β diversity, something that we also suspect occurs in temporal diversity. From a temporal view, probably there is a linear correlation between temporal γ and α diversity, resulting in a constant and low temporal β diversity values. Thus if temporal α diversity (mean number of species per time) present low values per unit of time, temporal β diversity should be higher, resulting a temporarily diverse community (Koleff and Gaston 2002; Lawton 2008). Communities that show high temporal heterogeneity in composition require conservation or monitoring plans in which sampling effort is high in frequency, so that the range of environmental variation that can occur at a site is sampled; however, the reason for the need for a high sampling frequency is not solely because of temporal variation in the composition of communities but also because of variation in the detectability of species as aforementioned (Veech et al. 2016). However, low temporal α-diversity values do not prove that some species do not occur in the studied unit; rather, it is likely that features of the environment affect their conspicuousness as several studies have shown (Wintle et al. 2005; Tanadini and Schmidt 2011; Asad et al. 2020) or even undergo short-distance migrations (Jenni and Kéry 2003; Boyle 2011; Visser 2017). All of these assumptions directly relate to other ecological processes such as interactions and phenological patterns because the occurrence of some species depends directly on the presence of other species (MacKenzie and Kendall 2002); for example, the common interactions between flowering plants and pollinator life cycles (Bucharova et al. 2022; Fisogni et al. 2022), as well as interactions between predators prey (Posey and Hines 1991; Walls and Williams 2001; Coghlan et al. 2022) or parasites and host (Holt 1972). In this way, patterns of temporal β diversity between different functional groups require comparison to determine whether the temporal β diversity of one group predicts the temporal β diversity of another group; our measure permits these comparisons to be made and other hypotheses to be tested. Finally, in the case of the Chesapeake Bay macro-benthic community, we observed that the *q*-profile of the temporal β-diversity increases without reaching an asymptote; thus, temporal β-diversity values are likely higher than the one presented (8.17) and a higher sampling resolution or a longer time window could alter these results; ultimately, it is likely that this community is more heterogeneous through time. This demonstrates the need for more studies that estimate temporal β diversity using different levels of sampling effort or conducting analyses at different time scales to understand the effect of scale on temporal β diversity patterns, as other studies have shown that scale affects diversity patterns in other ecological axes (Loreau 2000; Papatheodorou et al. 2004; Jarzyna and Jetz 2018).

The implementation of our new temporal-diversity measure is needed to advance our understanding of community temporal species changes and its heterogeneity and how this could become a tool for the optimization of time and resources in management plans and community monitoring programs. Otherwise, understanding of temporal ecological patterns and their relationships with environmental cues could generate new questions related to temporal community changes and how communities are affected by this poorly explored axis. It would also be interesting to know whether temporal β-diversity responds similarly to spatial measures of temporal α- and γ-diversities. Finally, we emphasize that the temporal diversity measure proposed here is suitable for the analysis of any taxonomic level, community and temporal scale. Therefore, if we have a long time series data of species abundance, we are able to compare between years, seasons or any periodical perspective; always taking into account the wavelet limitations aforementioned or our own sampling resolution. Finally, this proposal looks for establish a baseline (principally for β diversity), for analyze temporal diversity.

Conclusions

The analysis of temporal diversity is crucial for understanding the temporal distribution of species assemblages and the uniqueness and heterogeneity of species in communities. As the collection of long-term data increases, appropriate temporal analytical methods are needed to improve our understanding of temporal community patterns. Our temporal diversity framework produces intuitive, comparable and simple values for assessing species heterogeneity over time. Our measure has the same properties of other γ, α and β-diversity measures and can be applied to mid- and long-term community data sets available for any taxon even on disturbed ecosystems. Temporal α-, β- and γ-diversities have important implications for the temporal design of community monitoring, conservation and restoration programs.

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Conflict of Interest statement

There is no conflict of interest for any author

Author contributions

D.S-O., E.G., M.C.A, P.K., J.M and H.P. conceived the ideas and design of the study; D.S-O, E.G. and R.M-D. designed the methodological framework; D.S-O. obtained the data; D.S-O and E.G. analyzed the data; D.S-O, E.G. and H.P. wrote the manuscript. All authors contributed critically to the development of the ideas, approaches and draft, and gave final approval for publication.

Data Availability

Malagasy amphibian community data available from the paper 10.1080/00222933.2015.1009513 (Heinermann et al. 2015) and Chesapeake Bay macro-benthic community data available from page https://www.chesapeakebay.net/what/downloads/baywide_benthic_database

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CAPÍTULO V

Temporal diversity of six amphibian communities in the Lacandon jungle of southern Mexico

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(Artículo sin someter)

"Temporal diversity of six amphibian communities in the Lacandon jungle of southern Mexico"

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Abstract

Introduction

With the continually increasing rate of global change, organisms, communities, and ecosystems are changing on their temporal biological process on increasingly narrow temporal scales (Hansen et al. 2001; Pincebourde et al. 2016; Kroeker et al. 2020). This has generated increased interest in quantifying biological changes across short scales (Hutchings and Baum 2005; Prober et al. 2012; Goertzen et al. 2022). Previous studies have documented various changes in different organization levels. Species experience physiological and behavioral changes affecting the population dynamics, , phenotypic variation, species distribution, , variation un disease resistance, affecting directly the ecosystem structure and function (Danovaro and Gambi 2002; Bernhardt-Römermann et al. 2015; Barnagaud et al. 2017; Delgado-Baquerizo et al. 2019).

Biological diversity is a trait of ecological communities that can respond in various ways to environmental changes (Vallan 2002; Bonecker et al. 2013; Zeglin 2015; de Resende et al. 2021). However, the biological changes through time is not fully understood because of the difficulty of measuring temporal variations in community patterns, which requires sustained sampling effort which can be difficult, particularly for those working in the countries exhibiting the highest diversity rates. Biological diversity at large scales decreases when the environments changes to the point of exceeding the range of conditions that organisms can tolerate (Harley et al. 2012; Harrison 2020), and increases when environmental changes create new niches that species can occupy (San Roman and Wagner 2021). Likewise,biotic interactions throughout the changes of spatial and temporal mismatches affect diversity patterns in communities (Vellend 2008). Thus, the biological diversity constantly changes in response to several biotic and abiotic factors, and to understandthe effects of climate change requires quantifying temporal changes in diversity species over different timescales (Montoya and Raffaelli 2010).

Organisms respond in various ways to environmental change. Sessile organisms are generally restricted to responding to environmental change via phenotypic plasticity (Palmer et al. 2012), whereas mobile organisms can also respond to environmental change by dispersing to new environments (if there are not physical barriers) or by altering their behavior (Mattysen 2012). Ectothermic organisms provide suitable systems for understanding how biotic and abiotic factors can affect temporal diversity on narrow temporal scales given that they are highly sensitive to environmental change and typically respond by modifying their behavior (Ceron et al. 2020).

Amphibians in particular provide great systems for examining the effects of temporal variation of species diversity in response to environmental variables and competition dynamics (Bruzgul et al. 2005; Alford and Richards 1999). In general, amphibians respond directly to spatial and temporal variation in water availability, humidity, and temperature to meet their metabolic requirements (Buckley and Jetz 2007; Gouveia et al. 2019). Amphibians are highly dependent on water availability because of their permeable skin and the structure of their eggs; thus, the environment, especially humidity, precipitation, and temperature, has a major effect on their physiology and activity (Kirlin et al. 2006; da Silva et al. 2012).

Here, we quantified the temporal diversity of amphibian communities in the Lacandon jungle of southeastern Mexico during the rainy season. Specifically, we quantified three components of temporal diversity to characterize amphibian diversity patterns during the rainy seasonpatterns: 1) the distribution of species through time (phenological diversity), 2) the diversity of periodical patterns of species through time (periodical diversity), and 3) the heterogeneity in diversity through time (temporal beta diversity). We then quantified the relative importance of temperature and humidity on the temporal diversity measures to determine the degree to which each variable explains the diversity patterns of the amphibian community.

Materials and Methods

Study area

The study was conducted in the Natural Protected Area of Nahá, located in the northern Lacandon jungle in southern Mexico (16° 58´ 34.77´´ N and 91° 34´54.15´´ W; Figure 1). The area features primary and secondary growth forests with a transition between temperate cloud forests to tropical rain forests. This protected area (38.5 km^2) is completely surrounded by pastures and agricultural lands. The climate is tropical and humid with mild temperatures, and the wet season runs from June to November (CONANP, 2006).

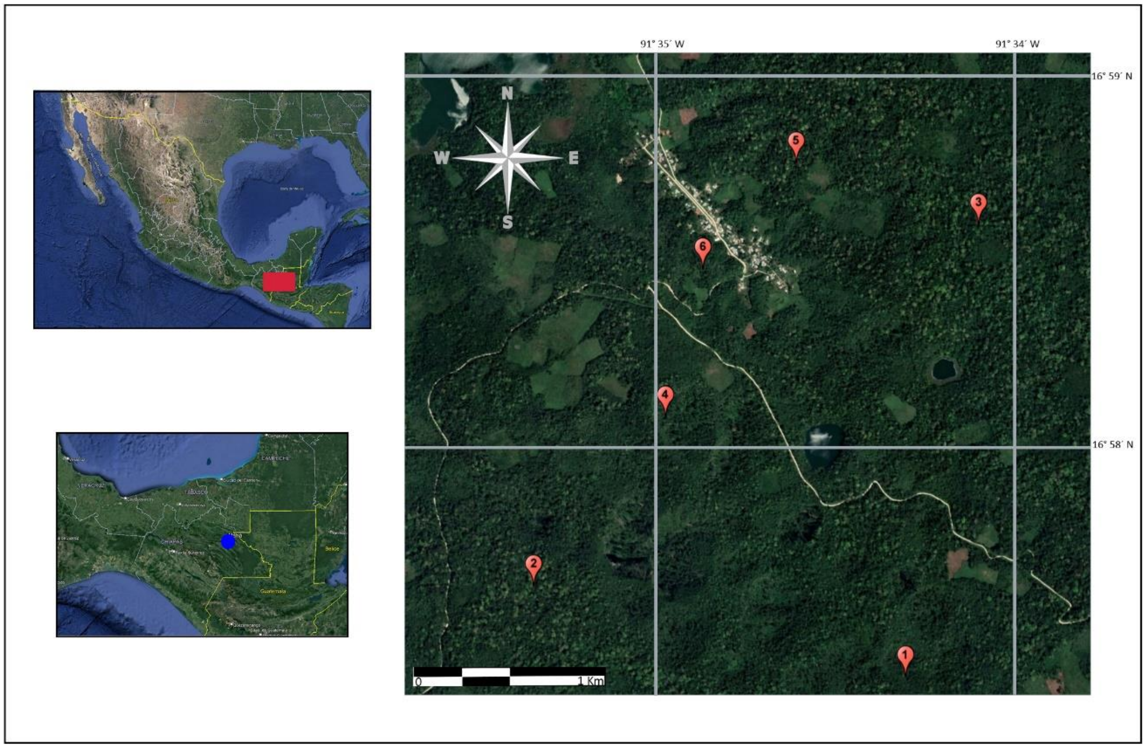

Figure 1. Location of the six communities sampled during the rainy season.

Sampling methods

We delimited six permanent plots (2500 m^2) in the Natural Protected Area and sampled amphibians from July to November 2019 (Table 1). All surveys were conducted from 10 minutes after sundown (which corresponds to the peak of amphibian activity at our sites based on our personal experience) for either two hours (in the event that no amphibians were observed) or until the entire plot had been sampled by all observers. Sampling was conducted by four persons with flashlights and all amphibian species and their abundances were recorded. Amphibians that could be easily recognized were not disturbed; amphibians that required handling for identification (e.g., members of the *Craugastor* genus) were released at their site of capture shortly after detection. To avoid the same individuals from being countedmore than once, each sampler was made aware of each encounter with an amphibian by other samplers while sampling. The temperature and humidity of each site were measured using data loggers (HOBO UA-001-64; measurements taken every 15 min) during the study.Relative humidity (RH), mean daily temperature (MT), higher temperature (LT), lower temperature (HT), relative humidity variation (SDRH), and temperature variation (SDT) was measured on data loggers.

Temporal diversity measures

To characterize temporal diversity, we used measures based on a recently developed framework employing the Hill numbers approach. Phenological diversity (PD) the diversity in the distribution of species through time, was estimated following Sánchez-Ochoa et al. (2022). Periodical diversity (PeD) was estimated as described in Sánchez-Ochoa (unpublished manuscript), and temporal beta diversity (TBD) was performed as described in Sánchez-Ochoa (unpublished manuscript). Because the temporal diversity measures are quantifiedin orders of q, the results were represented with profiles of these orders. Thus, the$q$ profile of each temporal diversity measure was correlated with local richness to determine whether there was a positive or a negative relationship between each measure with the number of species of each site. Moreover, we evaluated the correlation between temporal diversity measures with environmental variables using a multimodel approach. We used four different null models (gaussian, log-gaussian, gamma andlog-gamma) to determine if the data could be explained by randomness and also tested the relation with environmental variables and diversity values. We used Akaike Information Criterion (AIC) to select the best supported models. We also analyzed the phenological diversity of the most common species (*Bolitoglossa rufescens*, *Craugastor chac*, *C. loki*, *C. laticeps*, *Gastrophryne elegans*, and *Smilisca baudini*) across sites to evaluate the consistency in the temporal patterns of each species.

Table 1. Characteristics of the study sites +.

Site	Geographic coordinates	Elevation (m a.s.l.)	Water body type	Distance to urban area (m)
1	16°57.397 N 91°34.324 W	953	Absent	1,400
2	16°96.385 N 91°59.277 W	978	Absent	2,147
3	16°58.468 N 91°34.321 W	1042	Absent	580
4	16°58.103 N 91°35.119 W	922	Ephemeral	829
5	16°58.556 N 91°34.544 W	932	Permanent	236
6	16°58.494 N 91°34.858 W	908	Ephemeral	110

Results

We recorded a total of 25 amphibian species (γ, $q = 0$) from 114 sampling events. A total of seven species were recorded in site 1; nine in site 2; 12 in site 3; 10 in site 4; 11 in site 5 and 15 in site 6 (Table 2). Changes in the overall amphibian abundance curve mirrored changes in rainfall patterns (Figure1). There was high diversity in the temporal and periodical patterns of amphibian species (Figures 2 & 4). Overall amphibian community temporal diversity is shown in Table 2 and Figure 5. As expected, PD, PeD, and the γ and α components decreased with increasing *q*. PD values higher than *S* (30.81), which indicates a high degree of segregation in the temporal patterns of species in the study, result in a high effective number of phenological curves, around 31. Values of PeD were slightly lower than those of *S* (23.37); however, the effective number of periodical curves was still close to *S*. PD and PeD values were near 10 when *q* = 2; thus, there were approximately 10 effective phenological and periodical patterns in the amphibian community. β diversity continually increased and reached 65.57, which indicates a high degree of heterogeneity in the amphibian community.

The temporal and periodical records of each site are shown in Figure 6. In general, the diversity patterns of the community varied among sites. The PD *q* profiles are shown in Figure 7. The PeD *q* profiles are shown in Figure 8 and the TBD and γ and α component q profiles are shown in Figure 9. The values of the aforementioned measures are shown in Table 3. In general, the PD, PeD, and TBD patterns were similar, but the magnitude of the changes in *q* profiles varied among sites. Some were less diverse than others when abundance was taken into account (*q* = 2). Site 6 had the highest values of all temporal measures, including a higher effective number of phenological and periodical patterns and higher heterogeneity with time.

Environmental variables are shown in Table 4. Temperatures ranged between 14.41 to 30.31 °C, with a mean and standard deviation of 20.91 ± 0.06 °C. MHR ranged from 93.55 and 98.14 mm. There was greater variation in relative humidity than in temperature. The only relationship with an AIC value lower than that from the null model was between PeD and SDT. (Figure 10). The complete model selection based on AIC is listed in supplementary section S1. The phenological diversity values of the most common species among sites were greater than 1, which indicated different temporal patterns. The values of the species ranged from 6.19 to 15.28 for q = 0; and 3.97 to 11.73 for q = 1; and 3.34 to 11.36 for q = 2. The values and the temporal patterns are shown in supplementary section S2.

Finally, the values of PD in order of q (0, 1 and 2) for the most frequent species among sites varied. The PD values for species observed in at least five sites were as follows: *Bolitoglossa rufescens*, 6.89 (q = 0), 4.7 (q = 1) and 3.93 (q = 2); *Craugastor chac*, 6.19 (q = 0), 3.97 (q = 1) and 3.34 (q = 2); *Craugastor loki*, 6.12 (q = 0), 5.5 (q = 1) and 5.07 (q = 2); *Craugastor laticeps*, 6.76 (q = 0), 4.74 (q = 1) and 3.73 (q = 2); *Gastrophryne elegans*, 7.26 (q = 0), 5.28 (q = 1) and 4.45 (q = 2); and *Smilisca baudini*, 15.28 (q = 0), 11.73 (q = 1) and 11.36 (q = 2).

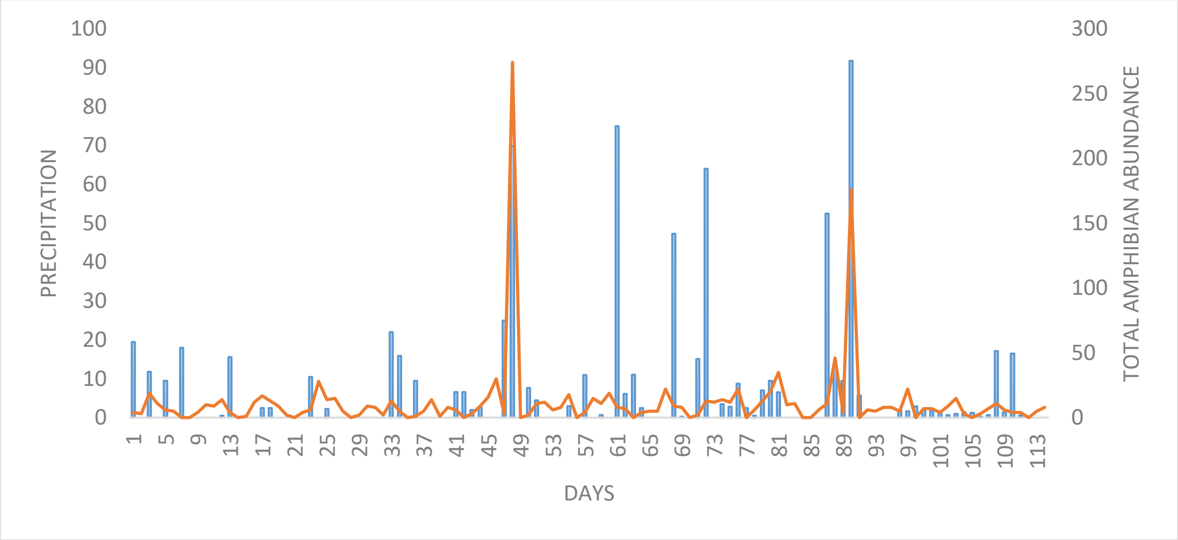

Figure 2. **Rainfall and amphibian abundance temporal patterns.** Comparison between overall amphibian species abundance of the study and rainfall patterns throughout the study period. The blue bars represent precipitation and orange line the abundance of amphibians.

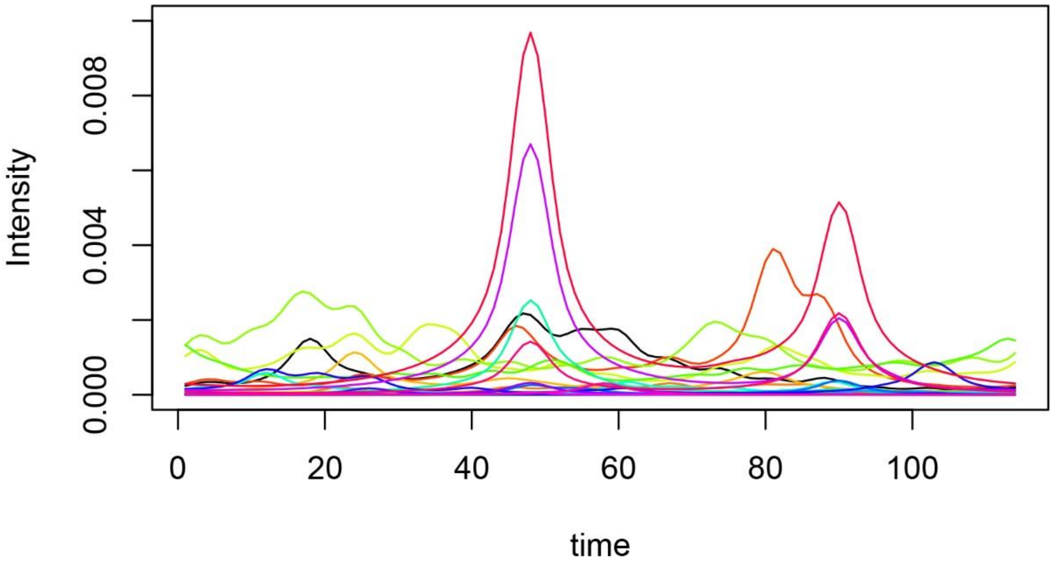

Figure 3. **Continuous abundance curve calculated from wavelet-transform analysis of the amphibian community of Nahá, Chiapas, Mexico**. Each line represents the temporal pattern of the abundance of a species, *S* = 25.

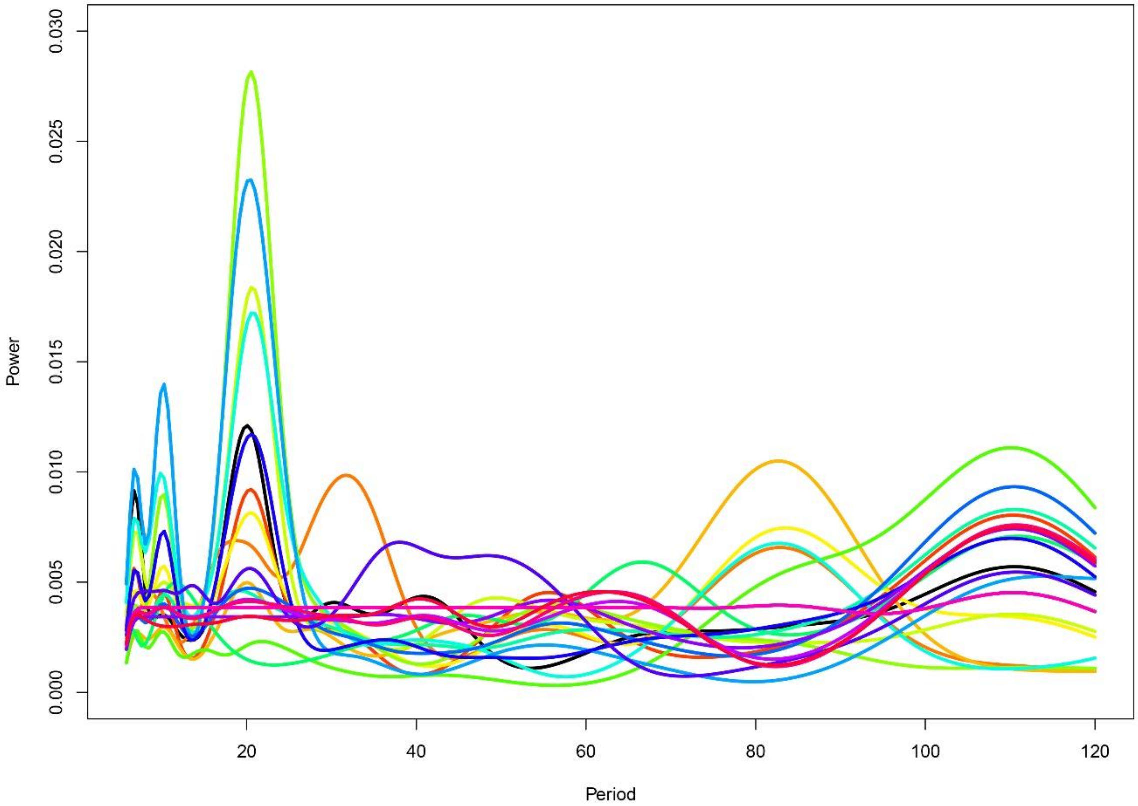

Figure 4. **Periodical patterns of the amphibian community of Nahá, Chiapas, Mexico**.

Each line represents the periodical pattern of a species, *S* = 25.

Table 2. Phenological (PD), periodical (PeD) and temporal β diversity of the overall amphibian community sampling.

Amphibian community	PD			PeD				TBD		
q	0	1	2	0	1	2		0	1	2
	30.8	13.2	10.1	23.3	12.1	9.6	γ	25	12.06	9.61
	-	-	-	-	-	-	α	25	0.51	0.14
	-	-	-	-	-	-	β	1	23.49	65.57

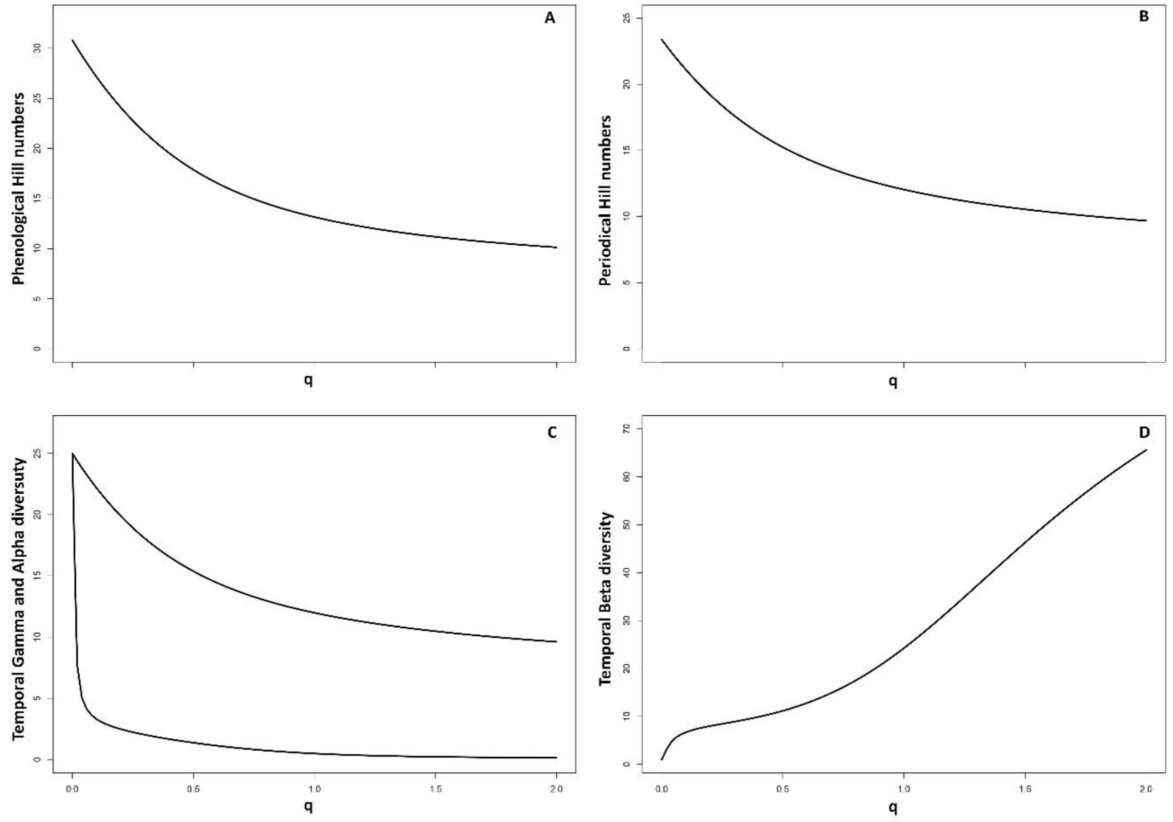

Figure 5. **Phenological, periodical and temporal Beta diversity Hill number profiles as functions of *q* (0≤q≤2) for the complete amphibian community of Nahá Chiapas, Mexico**. (A) Phenological Hill number diversity. (B) Periodical Hill number diversity. (C) Temporal α and γ diversity. (D) Temporal β diversity.

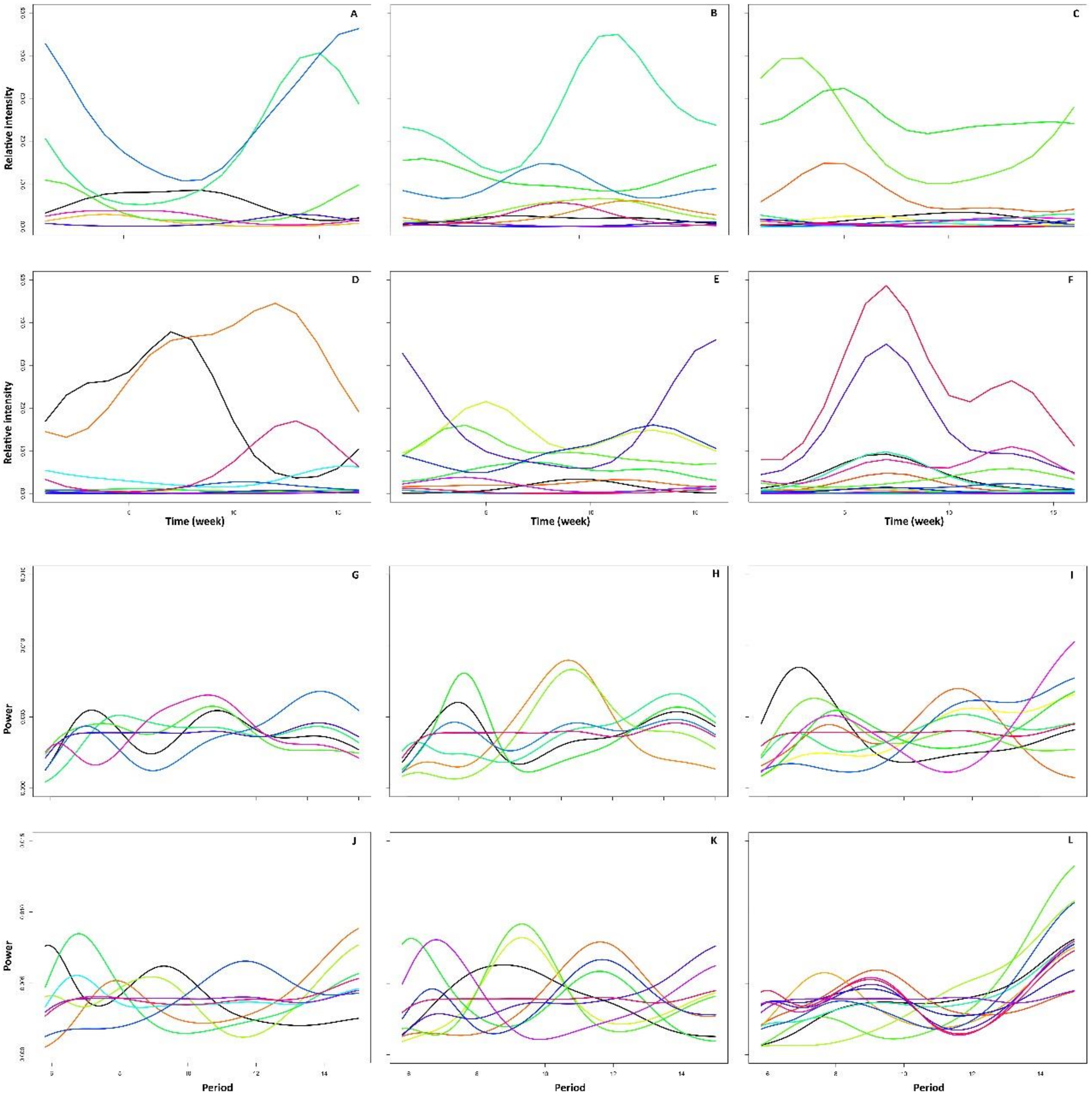

Figure 6. **Wavelet-transformed data for the temporal and periodical patterns of six amphibian communities in Nahá, Chiapas, Mexico**. Each curve represents one phenological or periodical curve. (A) Temporal patterns of site 1 (B) site 2, (C) site 3, (D) site 4, (E) site 5, (F) site 6. (G) Periodical patterns of site 1; (H) site 2; (I) site 3; (J) site 4; (K) site 5 and (L) site 6.

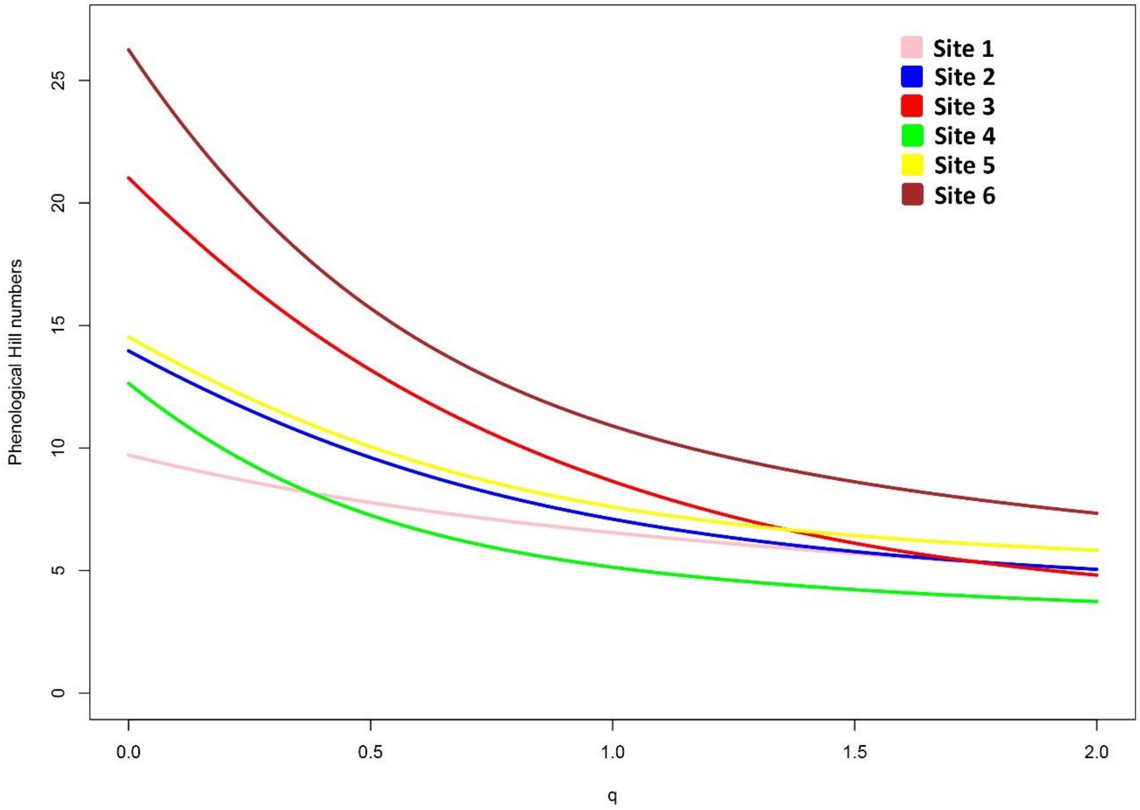

Figure 7. **Phenological Hill number profiles as functions of *q* (0≤q≤2) for six amphibian communities in Nahá, Chiapas, Mexico**. Each color corresponds to a single site.

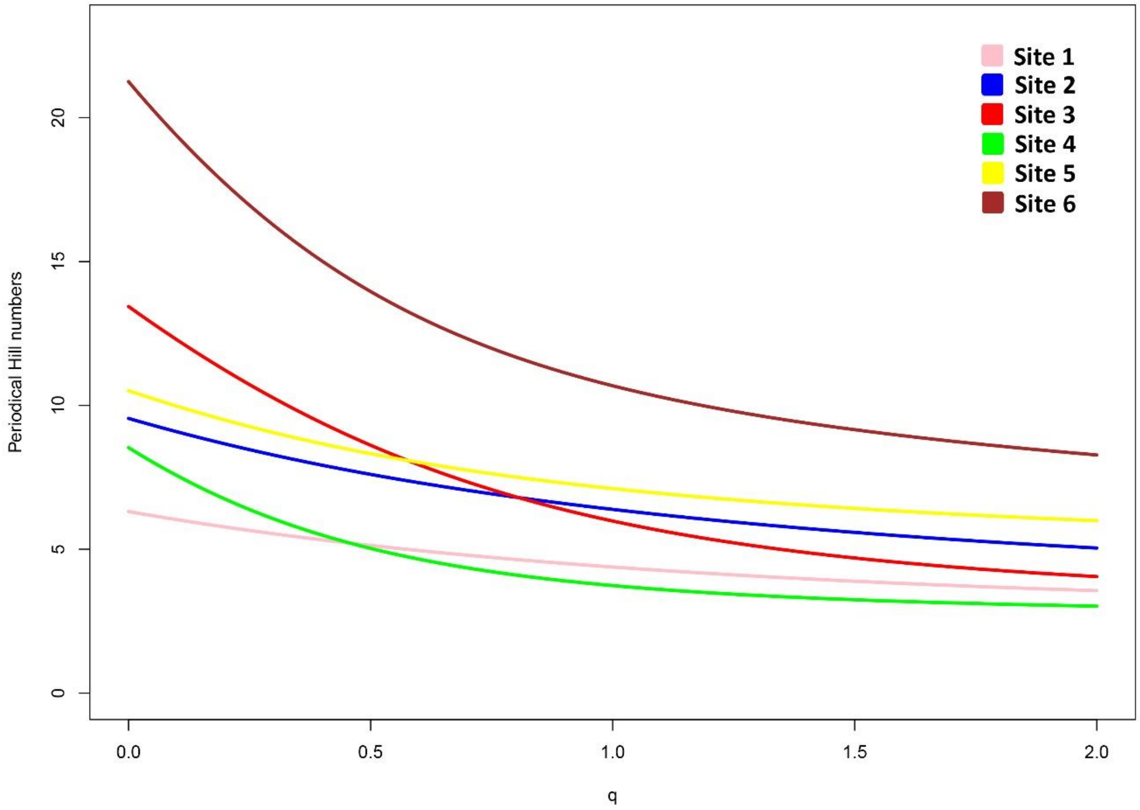

Figure 8. **Periodical Hill number profiles as functions of *q* (0≤q≤2) for six amphibian communities in Nahá, Chiapas, Mexico**. Each color corresponds to a single site.

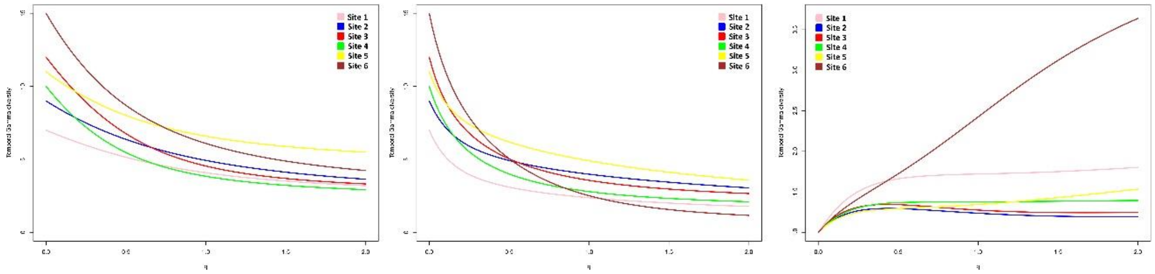

Figure 9. **Temporal γ, α and β Beta diversity profiles as functions of *q* (0≤q≤2) for six amphibian communities in Nahá, Chiapas, Mexico**. Each color corresponds to a single site.

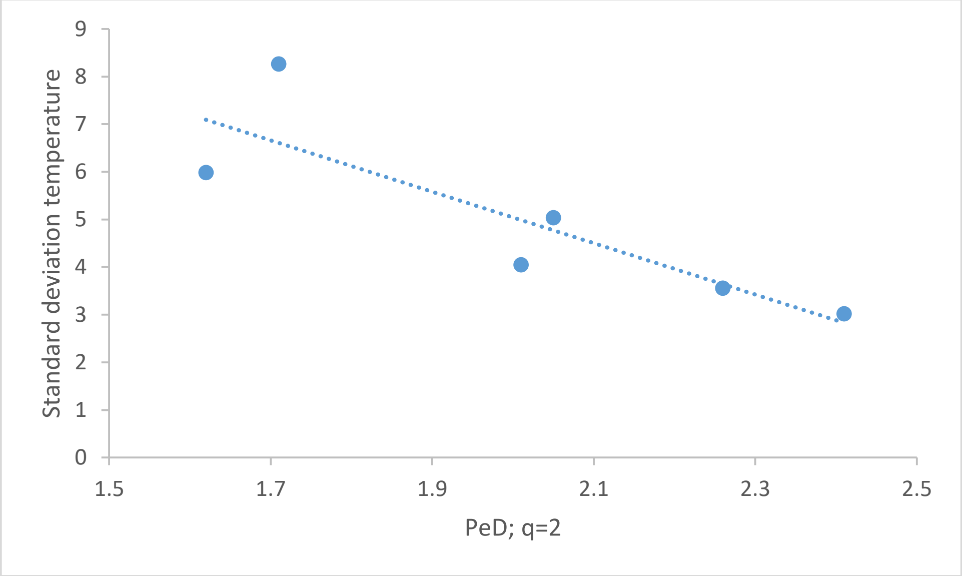

Figure 20. **Linear regression between the periodical diversity measure profile of order of q=2 and temperature standard deviation**.

Table 3. Phenological (PD), periodical (PeD) and temporal β diversity (DBT) values of the six amphibian communities.

N	DP			DPe			DBT		
q	0	1	2	0	1	2	0	1	2

Site 1	7	9.71	6.58	5.04	6.31	4.4	3.56	γ	7	4.11	3.19
								α	7	2.39	1.77
								β	1	1.71	1.8
Site 2	9	13.96	7.16	5.05	9.54	6.42	5.04	γ	9	4.97	3.64
								α	9	4.01	3.04
								β	1	1.23	1.19
Site 3	12	21.02	8.77	4.81	13.43	6.05	4.05	γ	12	4.59	3.31
								α	12	3.59	2.66
								β	1	1.27	1.24
Site 4	10	12.64	5.18	3.73	8.53	3.76	3.02	γ	10	3.88	2.92
								α	10	2.82	2.09
								β	1	1.37	1.39
Site 5	11	14.52	7.66	5.82	10.51	7.14	5.99	γ	11	6.62	5.49
								α	11	4.94	3.58
								β	1	1.34	1.53
Site 6	15	26.25	11.02	7.33	21.25	10.76	8.27	γ	15	6.15	4.23
								α	15	2.57	1.16
								β	1	2.39	3.63

Table 4. Environmental characteristics of the six sampled sites. Mean temperature (MT), higher temperature (HT), lower temperature (LT), mean relative humidity (MRH), temperature standard deviation (SDT) and relative humidity standard deviation.

Site	MT	HT	LT	MRH	SDT	SDRH
1	20.98	28.59	14.52	97.00	2.26	6.06
2	20.79	27.43	15.10	93.55	2.05	7.26
3	20.63	28.81	14.84	98.14	2.01	4.63
4	21.08	30.31	14.76	95.41	2.41	7.98
5	20.98	26.18	15.67	97.25	1.62	9.38
6	21.01	26.96	15.41	84.00	1.71	9.04

Discussion

We sampled the amphibian communities of six sites in the Lacandon rainforest of southeastern Mexico during the rainy season. We showed that patterns of phenology, periodicity, and temporal beta diversity of the amphibian communities varied among these six sites. Changes in q profiles across all sites were not uniform. Lastly, we show that mean temperature was negatively correlated with temporal beta diversity.

We detected a total of 25 amphibian species across the six sites, which is considerably higher than other studies that have sampled larger areas for longer periods (Kirlin et al. 2006; Wanger et al. 2010; Ochoa-Ochoa and Whittaker 2014); however, higher amphibian richness has also been observed in studies with different levels of sampling effort (Heinermann et al. 2015; Dubos et al. 2020; Sun et al. 2021). Our study site is situated in a natural protected area (38 km^2) in a transitional region between tropical and temperate forests, and biodiversity is likely elevated in this region because of the diversity of habitats occurring in a small region, embedded in a matrix of deforested landscapes. Over the six sampled sites we registered more than the 22 species reported in the management plan of the area, but less than 30 reported in other spatial-temporal study (Ochoa-Ochoa and Whittaker 2014). Probably the sampling effort and method influenced these differences, since we used permanent plots and the aforementioned study used transects, which encourages to consider a greater number of microhabitats and spatial variation. We found that sites varied in the total number of species; we recorded between 7 and 15 species per site. Variation in species richness occurs frequently over small spatial scales in heterogeneous environments in tropical areas in several taxa including amphibians. The variation in species richness among sites was expected because we selected sites with different habitat types to ensure that as much of the overall diversity of the region as possible was sampled. The number of species in each site is closely related to habitat type and variation in environmental conditions, especially water availability (CITA). Sites with higher water availability such as streams or ephemeral ponds had greater numbers of amphibian species, confirming that this environmental trait is closely related to amphibian richness and abundance (Qian et al. 2007; Soares and Brito

2007; da Silva et al. 2012). However, our sampling was restricted to the rainy season; thus, our findings would only apply for a small part of the year when rainfall is high (Ochoa-Ochoa and Whittaker 2014; Ochoa-Ochoa et al. 2014; Heinermann et al. 2015). The low species richness at site 1 probably stems from the fact that this plot comprises secondary forest and was burned 10 years ago. This is consistent with previous studies suggesting that amphibian diversity is lower in secondary forest compared with primary forest (Thomson and Reuters 2003; Wanger et al. 2010).

The temporal and periodical patterns of the amphibian community are diverse. Some species are highly abundant at certain times of the season and other are evenly abundant over longer periods of time. There is also variation in the temporal overlap of species over time. This likely stems from differences in micro environmental preferences of the species (Guayasamin and Chris Funk 2009; Sun et al. 2021); alternatively, biotic interactions among species could explain this pattern (Prates et al. 2019).

The periodical data show that species vary in their periodical patterns, which is related to variation in the frequency of detection of each species across the sampling period. Our data show clearly that periodical patterns provide distinct information compared with temporal patterns. That is, species with similar periodical curves are not necessarily active at the same times. In other words, two species could have annual periodic patterns and belong to the same period group, but one species appears at the beginning of the rainy season and the other at the end of the rainy season, thus the concurrence of both species aren’t overlapping. Furthermore, overlap in the temporal patterns of species does not necessarily indicate that the period over which they are active is the same.

Consistent with other studies employing Hill number-based measures of spatial perspective, there was a decrease in phenological and periodical Hill number diversity as q increased (Chao et al. 2014; Chiu and Chao 2014; Chao and Chiu 2016). Noteworthily, when q =0 for PD, the value of PD was higher than *S*, which indicates a diverse number of ways by which the activity of species can be partitioned over temporal scales during the rainy season. This occurs in the same way in the measure that we based our framework, this is because the formula considers the sum of the distances of paired species (Chao and Chiu 2016). When q = 2 (i.e., when more weight is given to abundance), there are approximately 10 dominant phenological curves, being the ways that amphibians partition the temporal axis over the rainy season. When q = 0 for PeD, the values were slightly lower than *S*, and each species exhibits their own periodical pattern, aside from two species that share the same periodical patterns.. In general, this indicates that amphibians exhibit particular responses to several environmental cues, especially due to differences in their variation in reproductive modes, which permits more niche partitioning (Crump 2015).

Temporal βdiversity is a measure based on the coefficient between temporal γdiversity and temporal αdiversity. When q = 0 for temporal γand αdiversity, the total number of species encountered throughout the sampling period is accounted for. The same value of γ and α isbecause wavelet analysis takes into account a non-zero value of occurrence of species along time, thus considers a low probability to encounter any species at any time. When abundance is taken into account for temporal γ, there are approximately 10 dominant species across the sampling period. However, values of temporal αdiversity were lower than 1. Given that temporal αdiversity is the mean number of species at each sampling point, this means that less than one species is expected to be detected during each visit to the study sites. The diferences between γand αdiversity q profiles values results in high temporal βdiversity values with high temporal heterogeneity in the amphibian community. Given that these are novel measures; we are unable to compare the results of our study with data from the literature. We speculate that the levels of temporal, periodical, and temporal beta diversity at our study sites are lower compared with other tropical sites but potentially higher than other temperate sites.

Overall, there was extensive variation among sites in phenological and periodical patterns. The q profiles revealed that there are differences in phenological and periodical Hill number diversity values. This allows us to resolve differences in temporal and periodical diversity among sites. Likewise, the rate at which diversity values changed with increasing q varied among sites. This indicates that regardless of the total number of species that was detected at each site, the ways in which the species partition their activities (i.e., PD) over time and the periodicity at which they carry out their activities vary among sites. Our data also indicate that the evenness of the species among sites varied. For example, in site 1, the relative abundances of all species encountered was relatively similar; by contrast, in site 6, the relative abundances of species varied extensively.

Temporal βdiversity measures provided distinct insights into the temporal properties of the amphibian community. The total number of species encountered per site ranged from 7 to 15 when $q = 0$. However, when more weight is given to the abundance of species, approximately 2 to 5 species are dominant. This indicates that the amphibian communities in Nahá were generally dominated by 2 to 5 species, and the rest of the species can be considered rare; however, the dominant species were not the same among sites, giving us insights that the temporal niche of species is a plastic trait, and could change throughout space. For example, the most common species encountered at each site was as follows*: Craugastor loki* (Site 1), *Craugastor laticeps* (Site 2 & 3), *Agalychnis moreletii* (Site 4), *Ptychohyla hypomykter* (Site 5), and *Tlalocohyla picta* (Site 6).

This could be explained by the fact that each species has specific requirements and habitat is likely facilitating the environmental cues for some species.

Particularrly, αdiversity refers to the mean effective number of species encountered at single sampling time points. When q = 0, temporal alpha diversity behaves similarly to temporal gamma diversity (7 to 15 species).. However, when more weight is given to the abundance of species, approximately 1 to 4 species are dominant. This indicates that the mean number of amphibians observed per site ranges from 1 to 4. This matches with our experience in the field, since the number of species observed where around this values. Therefore, α diversity has an important component in the monitoring experimental design. If the distance of the α diversity values between q = 0 and q = 2 is large, it is likely that monitoring programs may be designed with higher or equal time resolution, and vice versa. Likewise, periodic diversity may also need to be considered for this point.

Temporal beta diversity refers to the effective number of unique communities across the sampling period. Given that beta diversity is calculated based on the relationship between the mean number of species that are observed per sampling period (temporal alpha diversity) relative to temporal gamma diversity, temporal beta diversity indicates the number of effective unique communities. All of the study sites had approximately one unique community regardless of the value of q. The exception was Site 6, which had approximately four unique communities when q = 2. This indicates that the amphibian community at Site 6 is the least homogeneous among all sites and across the entire sampling period. This was not expected because the proximity to the town, however there is a geographical barrier (hill about 50 m of height) that separates both sites preventing disturbance, in other studies it has been observed that geographical barriers help to conserve sites (xxx). Likewise, site 6 has the particularity of being a temporary pool next to a mature forest, generating a large number of microhabitats during the rainy season, as some studies report (XXX). Finally, because the dominant species is not always the same and there is a high spatial variation, andspecies show variation in their temporal niche, results suggests that same species responds differentially to environmental heterogeneity and also to the possible interactions with other members of the community.

The level of variation in the environmental variables among our study sites was low (Table 4), which was expected given the proximity of each of our sites. The unique non-random relationship between the environmental variables and temporal diversity measures, was between the standard deviation of temperature and periodical diversity in order of $q = 2$. We found that these two variables were negatively correlated. This suggests that periodical patterns of amphibian community decrease when variation in temperature is high. In other words, the periodicity of the activities of species is reduced when temperatures are more variable. This result has important conservation implications. The average temperature of the planet is steadily increasing, and deforestation is known to increase temperature variation in ecosystems due to a lack of vegetation that can serve as a buffer against temperature fluctuations. Our findings suggest that continued global change will alter the activity patterns of amphibian species and thus the periodical patterns of amphibian communities. This also indicates that monitoring programs need to consider temperature variation to ensure that amphibian communities are completely sampled as mean global temperature increases.

The main aim of our study was to explore the patterns of the rainy seasonof diversity of several amphibian communities. Future studies are needed to determine whether other environmental variables (e.g. leaf litter availability, predator presence, vertical and horizontal vegetation structure) that were not measured in our study could potentially explain patterns of temporal diversity observed among communities.

Conclusions

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Table S1. **AIC values of tested models.**

PD; q = 0		
Model	AICc	Δ AICc
1.gamlog	44.77	0
1.gam	44.77	0
1.gaus	45.65	0.88
1.gauslog	45.65	0.88
MRH.gauslog	51.35	6.58
MRH.gam	51.57	6.8
SDT.gamlog	51.69	6.92

PD; q = 1		
Model	AICc	Δ AICc
1.gam	31.89	0
1.gamlog	31.89	0
1.gaus	32.27	0.38
1.gauslog	32.27	0.38
SDT.gamlog	36.07	4.18
SDT.gam	36.78	4.9
SDT.gaus	37.33	5.45

MRH.gaus	51.9	7.13
MRH.gamlog	51.92	7.14
SDT.gam	51.99	7.22
LT.gamlog	53.07	8.29
SDT.gaus	53.1	8.33
SDT.gauslog	53.31	8.54
LT.gam	53.34	8.57
HT.gamlog	54.04	9.27
HT.gam	54.08	9.31
LT.gaus	54.29	9.52
MT.gam	54.39	9.62
MT.gamlog	54.41	9.64
LT.gauslog	54.48	9.7
SDRH.gam	54.67	9.9
SDRH.gamlog	54.69	9.92
HT.gaus	55.03	10.26
HT.gauslog	55.06	10.29
MT.gauslog	55.26	10.49
MT.gaus	55.29	10.51
SDRH.gauslog	55.55	10.77
SDRH.gaus	55.56	10.79

SDT.gauslog	37.81	5.92
MRH.gauslog	38.18	6.29
MRH.gaus	38.62	6.73
MRH.gam	38.74	6.85
HT.gamlog	38.89	7
MRH.gamlog	39.03	7.14
HT.gam	39.22	7.33
HT.gaus	39.77	7.88
LT.gamlog	39.86	7.97
LT.gam	39.98	8.09
HT.gauslog	39.98	8.1
LT.gaus	40.37	8.49
LT.gauslog	40.48	8.6
MT.gamlog	41.51	9.62
MT.gam	41.52	9.63
SDRH.gam	41.77	9.88
SDRH.gamlog	41.78	9.89
MT.gaus	41.9	10.01
MT.gauslog	41.91	10.02
SDRH.gauslog	42.14	10.25
SDRH.gaus	42.15	10.27

PD; q = 2		
Model	AICc	Δ AICc
1.gamlog	25.77	0
1.gam	25.77	0
1.gaus	26.14	0.37
1.gauslog	26.14	0.37
SDT.gamlog	28.16	2.39
HT.gamlog	28.49	2.72
SDT.gam	28.52	2.75
HT.gam	29.11	3.34
SDT.gaus	29.29	3.52
SDT.gauslog	29.48	3.71
HT.gaus	30.18	4.41
HT.gauslog	30.52	4.75
MRH.gauslog	30.93	5.17
MRH.gaus	31.32	5.55
MRH.gam	31.61	5.84
MRH.gamlog	31.86	6.1

PeD; q = 0		
Model	AICc	Δ AICc
1.gam	42.37	0
1.gamlog	42.37	0
1.gaus	43.9	1.53
1.gauslog	43.9	1.53
MRH.gauslog	46.49	4.12
MRH.gam	47.14	4.77
MRH.gaus	47.66	5.28
MRH.gamlog	47.76	5.38
SDT.gamlog	48.3	5.93
SDT.gam	48.64	6.26
LT.gamlog	49.61	7.23
LT.gam	50.12	7.75
SDT.gaus	50.82	8.45
SDT.gauslog	51.03	8.66
HT.gamlog	51.05	8.68
HT.gam	51.11	8.74

LT.gam	32.13	6.36
LT.gamlog	32.15	6.38
LT.gauslog	32.54	6.77
LT.gaus	32.55	6.78
SDRH.gam	34.11	8.35
SDRH.gamlog	34.24	8.47
SDRH.gauslog	34.46	8.69
SDRH.gaus	34.6	8.83
MT.gamlog	35.67	9.9
MT.gam	35.68	9.91
MT.gaus	36.06	10.29
MT.gauslog	36.06	10.29

SDRH.gam	51.7	9.33
SDRH.gamlog	51.81	9.44
LT.gaus	51.93	9.56
LT.gauslog	52.22	9.85
MT.gam	52.35	9.97
MT.gamlog	52.35	9.98
HT.gaus	52.86	10.49
HT.gauslog	52.91	10.53
SDRH.gauslog	53.22	10.84
SDRH.gaus	53.34	10.97
MT.gauslog	53.87	11.5
MT.gaus	53.87	11.5

PeD; q = 1

Model	AICc	Δ AICc
1.gamlog	33.89	0
1.gam	33.89	0
SDT.gamlog	34.21	0.32
1.gaus	34.81	0.93
1.gauslog	34.81	0.93
SDT.gam	35.7	1.82
HT.gamlog	37.66	3.77
SDT.gaus	37.68	3.8
MRH.gauslog	37.87	3.99
LT.gamlog	38.16	4.28
SDT.gauslog	38.31	4.42
HT.gam	38.36	4.47
MRH.gaus	38.57	4.69
LT.gam	38.96	5.07
MRH.gam	39	5.12
MRH.gamlog	39.36	5.48
LT.gaus	40.1	6.21
HT.gaus	40.21	6.33
HT.gauslog	40.52	6.64
LT.gauslog	40.63	6.74
SDRH.gam	42.09	8.21
SDRH.gamlog	42.33	8.44
SDRH.gauslog	42.97	9.09
SDRH.gaus	43.25	9.37
MT.gamlog	43.89	10

PeD; q = 2

Model	AICc	Δ AICc
SDT.gamlog	30.46	0
1.gamlog	30.82	0.36
1.gam	30.82	0.36
SDT.gam	31.4	0.94
1.gaus	31.81	1.35
1.gauslog	31.81	1.35
HT.gamlog	32.45	1.99
HT.gam	33.09	2.63
LT.gamlog	33.34	2.88
SDT.gaus	33.9	3.44
SDT.gauslog	34.16	3.7
LT.gam	34.19	3.73
MRH.gauslog	35.21	4.75
LT.gaus	35.59	5.13
MRH.gaus	35.71	5.25
HT.gaus	35.76	5.3
HT.gauslog	35.92	5.46
MRH.gam	35.95	5.49
LT.gauslog	36.15	5.69
MRH.gamlog	36.2	5.74
SDRH.gam	37.38	6.92
SDRH.gamlog	37.79	7.33
SDRH.gauslog	38.49	8.03
SDRH.gaus	38.96	8.5
MT.gamlog	40.68	10.22

MT.gam	43.89	10
MT.gaus	44.81	10.93
MT.gauslog	44.81	10.93

MT.gam	40.69	10.23
MT.gaus	41.69	11.23
MT.gauslog	41.71	11.25

TBD; q = 1		
Model	AICc	Δ AICc
1.gam	12.95	0
1.gamlog	12.95	0
1.gaus	14.21	1.26
1.gauslog	14.21	1.26
MRH.gam	15.66	2.71
MRH.gauslog	15.91	2.96
MRH.gamlog	16.22	3.27
MRH.gaus	16.75	3.8
MT.gamlog	21.16	8.22
MT.gam	21.21	8.26
SDRH.gam	21.9	8.95
SDRH.gamlog	21.91	8.97
SDT.gam	22.19	9.24
SDT.gamlog	22.21	9.26
HT.gamlog	22.42	9.47
HT.gam	22.44	9.49
LT.gam	22.69	9.74
LT.gamlog	22.69	9.74
MT.gaus	22.88	9.93
MT.gauslog	22.91	9.96
SDRH.gauslog	23.34	10.39
SDRH.gaus	23.36	10.41
SDT.gauslog	23.56	10.61
SDT.gaus	23.57	10.63
HT.gaus	23.79	10.84
HT.gauslog	23.8	10.86
LT.gauslog	23.98	11.03
LT.gaus	23.98	11.04

TBD; q = 2		
Model	AICc	Δ AICc
1.gam	20.42	0
1.gamlog	20.42	0
MRH.gam	20.49	0.07
MRH.gauslog	20.96	0.54
MRH.gamlog	21.74	1.32
1.gaus	22.99	2.57
1.gauslog	22.99	2.57
MRH.gaus	23.29	2.87
SDRH.gam	28.2	7.77
SDRH.gamlog	28.32	7.9
MT.gamlog	28.44	8.02
SDT.gam	28.5	8.08
MT.gam	28.54	8.12
SDT.gamlog	28.6	8.18
HT.gamlog	29.17	8.74
HT.gam	29.22	8.8
LT.gamlog	29.35	8.92
LT.gam	29.35	8.93
SDRH.gauslog	31.45	11.03
SDRH.gaus	31.56	11.14
SDT.gauslog	31.58	11.16
SDT.gaus	31.65	11.23
MT.gaus	31.85	11.43
MT.gauslog	31.9	11.48
HT.gaus	32.17	11.75
HT.gauslog	32.2	11.78
LT.gaus	32.21	11.79
LT.gauslog	32.22	11.8

Table S2. Phenological diversity of most frequent species along sites.

Species	# Sites Detected	q = 0	q = 1	q = 2
Bolitoglossa rufescens	6	6.89	4.70	3.93
Craguastor chac	5	6.19	3.97	3.34
Craugastor laticeps	5	6.76	4.74	3.73
Craugastor loki	6	6.21	5.5	5.07
Gastrophryne elegans	5	7.26	5.28	4.45
Smilisca baudini	5	15.28	11.73	11.36

CAPÍTULO VI

DISCUSIÓN GENERAL Y CONCLUSIONES

Discusión

Un aspecto fundamental para el entendimiento de las comunidades bióticas es el estudio del eje temporal (Magurran et al. 2019). Las medidas de diversidad temporal existentes no integran de una forma adecuada los patrones temporales de las comunidades ya que por un lado pasan por alto algunos supuestos de las series de tiempo y son medidas poco comparables entre estudios (Engen et al. 2011; Baselga 2012; Legendre and Gauthier 2014b). Por esta razón, este trabajo se centró principalmente en el desarrollo de las medidas de diversidad fenológica, periódica y beta temporal que se basan en los análisis de series de tiempo y la teoría de los Números de Hill. Esta perspectiva provee formas de medir la diversidad temporal de forma eficiente, facilita la interpretación y permite su comparación, esto se ha observado en otras medidas construidas bajo el mismo marco teórico (Chao and Chiu 2016; Chao et al. 2019a, b; Ohlmann et al. 2019). Cada una de las medidas resume aspectos clave de los cambios temporales de las comunidades. La diversidad fenológica se refiere al número efectivo de las diferentes formas en la que las especies presentan sus patrones de actividad o estadios a lo largo del ciclo de vida (Sánchez-Ochoa et al. 2022). La diversidad periódica se refiere al número efectivo de patrones cíclicos que las especies presentan en una comunidad. Y la diversidad beta temporal resume la cantidad de comunidades únicas, es decir, el número efectivo de comunidades con diferente composición de especies a lo largo tiempo. Finalmente, la aplicación de las tres medidas de diversidad temporal fue hecha y analizada con datos de una comunidad de anfibios en la selva Lacandona, en Chiapas.

El paso inicial en el desarrollo de las tres medidas fue la trasformación de las series de tiempo para tener un modelo continuo de los patrones temporales de las especies, ya que la misma toma de datos de las series de tiempo, genera vacíos de información, formando variables discretas (Mondal and Percival 2010). Así, el cálculo de un modelo continuo nos ayuda a desarrollar las medidas de diversidad fenológica y diversidad beta temporal. Por otro lado, los análisis de series de tiempo también pueden calcular los patrones periódicos de las especies, lo que hace viable el cálculo de la diversidad periódica que también se propone en la tesis (Dale and Mah 1998; Cho and Chon 2006; Tonkin et al. 2017a). Para dichas trasformaciones y cálculos periódicos se decidió usar la transformada de wavelet ya que se ha probado como eficiente en diversos estudios ecológicos, particularmente en aspectos relacionados con la dinámica de poblaciones, transmisión de enfermedades, migración de organismos y cambios en el metabolismo (Schmidt and Skidmore 2004; Allen et al. 2006; González-Nuevo et al. 2006; Keitt 2008; Benítez et al. 2010; Tonkin et al. 2017b; Anneville et al. 2018; Roberts and Mannion 2019). Desde un punto de vista matemático, el análisis wavelet resulta ser mejor que la transformada de Fourier y la función empírica ortogonal, ya que éstas dos últimas son más robustas para datos lineales, estacionarios y con una única señal dominante (Sifuzzaman et al. 2009). El análisis wavelet considera las frecuencias de cada intervalo de tiempo a lo largo de toda la serie de tiempo en diferentes escalas temporales, y no solo en una como ocurre con Fourier (Torrence and Compo 1998; Cho and Chon 2006; Sifuzzaman et al. 2009). Estos aspectos ofrecen un cálculo más preciso en variables que suelen ser fluctuantes y muy dinámicas, como lo son los cambios temporales de variables biológicas (Dale and Mah 1998; Cho and Chon 2006).

Para el análisis wavelet se necesitan especificar dos parámetros: la función escalar y el límite de atenuación ($\boldsymbol{\tau}$). La función escalar es un parámetro que está relacionado con la naturaleza de los datos de la serie de tiempo y modifica los valores finales de los datos transformados (Cho and Chon 2006; González-Nuevo et al. 2006; Cazelles et al. 2008). Las funciones escalares son diversas por sí mismas y cada una es recomendable para cierto tipo de datos (Cazelles et al. 2008). En las medidas propuestas en la tesis se recomendó el uso de la función escalar Morlet debido a que es una función viable sobre variables con poca predictibilidad y su capacidad de responder a una resolución de altas frecuencias (Cazelles et al. 2008). Otras funciones escalares como Daubechies funcionan mejor en secuencias que tienen comportamientos fractales (Akansu et al. 1993; Singh et al. 2011) y “Mexican Hat” es mejor en series de tiempo con señales fuertes de inicio con reducciones graduales (e. g. temblores o tsunamis) (Zhou and Adeli 2003). A pesar de que se conocen de algunas funciones escalares los mejores usos, es necesario analizar de una forma objetiva las variables biológicas, pero sale de los objetivos de la tesis.

El parámetro $\boldsymbol{\tau}$ refleja la tasa de ocurrencia o desaparición de los atributos de las especies en el tiempo. Aunque es un parámetro que no suele modificarse en los análisis wavelet, tiene una importancia biológica muy grande. En la naturaleza, los procesos biológicos ocurren de una manera gradual y continua bajo diferentes escalas y nunca abrupta. Como ya se ha dicho, los registros y el propio muestreo por sí mismo genera variables discretas, sin embargo, cada proceso biológico ocurre de forma diferente entre especies. Por ejemplo, la floración de diferentes individuos dentro de una población de cactus puede presentarse en una sola noche (Petit 2001), mientras que, en otras especies de árboles tropicales, los procesos de floración pueden durar algunas semanas (Newstrom et al. 1994; Brown and Hopkins 1996). De esta manera, independientemente de la comunidad, ambos procesos ocurren de manera continua, pero son dependientes de la escala temporal. Por lo tanto, cada proceso biológico debería estar ajustado por sus características intrínsecas de la especie, acotado a los datos obtenidos. Es así que el parámetro $\boldsymbol{\tau}$ toma mucha importancia biológica ya que va a afectar directamente la concurrencia de los procesos biológicos que se estén midiendo o evaluando, afectando los valores de las tres medidas propuestas. Es relevante mencionar que, dentro de las tres medidas propuestas, la única en la que se modificaron los valores de $\boldsymbol{\tau}$ fue en la medida de diversidad β temporal, sin embargo, en todas es objeto de discusión y generación de nuevo conocimiento, ya que en ningún análisis wavelet se toma en cuenta y se usa un valor predeterminado (2).

El parámetro τ en la medida de diversidad β temporal está modificado para que ajuste las curvas temporales a la tasa de cambio en las abundancias o intensidades de cada una de las especies a lo largo de todo el muestreo. De esta manera, le da más peso a las curvas modeladas cuando tenemos una resolución baja en el muestreo y le asigna valores más cercanos a lo observado cuando la resolución de muestreo es alta. De esta manera se podría dejar la subjetividad del valor que el análisis tiene por defecto ($\boldsymbol{\tau}$ = 2). Asi mismo, esta idea sugiere que sería bueno integrar la probabilidad de detección de las especies dentro de la comunidad a cualquier medida de diversidad, incluyendo la espacial, siendo un parámetro que ajustaría los valores en función de las frecuencias de detección en el estudio. Los cambios en los valores de $\boldsymbol{\tau}$ modifican los valores de las tres medidas, pero no los patrones en los resultados. $\boldsymbol{\tau}$ resultó ser un parámetro que debe revisarse y evaluarse a fondo en otro trabajo, para afinar los valores resultantes de cada medida; sin embargo, este aspecto salía del objetivo de cada uno de los capítulos.

Las medidas de diversidad fenológica (Capítulo 2) y periódica (Capítulo 3) están construidas a partir de la teoría de los números de Hill basados en medidas de distancia. El índice de Morisita-Horn fue una aproximación adecuada para medir las distancias del área de sobrelapamiento entre pares de especies de los modelos de curvas temporales y curvas periódicas, así como fue usado en otro estudio (Luna-Nieves et al. 2022). Además del índice de Morisita-Horn hay otras formas de medir el área de sobrelapamiento bajo dos curvas, uno es el índice de sobrelapamiento de Jaccard (Smith et al. 1996; Yue and Clayton 2005) y otro el coeficiente de sobrelapamiento de Szymkiewicz-Simpson (Ramos-Guajardo et al. 2020). Estos dos índices no fueron considerados ya que no consideran al mismo tiempo el área de sobrelapamiento dentro y fuera. Por un lado, el índice de Jaccard ignora por completo el área donde no están sobrelapadas ambas áreas. Por otro, el coeficiente de Szymkiewics-Simpson considera el área de sobrelapamiento más el área de la curva de menor tamaño, por lo tanto, ninguna de estas dos medidas es considerada para los análisis. La principal razón de esta decisión es que la presencia o ausencia del sobrelapamiento en las especies es un reflejo de diversos procesos biológicos temporales. Esto puede asociarse principalmente al nicho temporal de los organismos, dando información parcial sobre la existencia y magnitud de las posibles interacciones entre ellos como la competencia, mutualismo y facilitación (Kochmer and Handel 1986; Murdoch et al. 2002; Donohue 2005; José and Zavala 2010; Hodgson et al. 2011; Bergamo et al. 2018; Lane et al. 2018).

Las tres medidas propuestas son aplicaciones de marcos teóricos ya desarrollados donde usan el principio de los números de Hill. Siendo más pragmáticos, tanto la diversidad fenológica (capítulo 2) como la diversidad periódica (capítulo 3) tienen la misma base matemática (Chao et al. 2014a; Chiu and Chao 2014); sin embargo, en la primera se utilizan las series de tiempo transformadas y en la segunda las curvas periódicas. Para la diversidad beta temporal (capítulo 3) se usó la aproximación de descomposición de beta de números de Hill que propone Chao (Chao and Chiu 2016). La principal ventaja de las tres medidas propuestas es que, al estar basadas en los números de Hill, los valores resultantes son más fáciles de interpretar y lo más importante es que resultan ser una manera viable para comparar la diversidad temporal entre estudios. De igual manera, nuestras medidas mantienen los patrones de diversidad en los órdenes de q como el resto de medidas bajo el marco teórico de los números de Hill (Jost 2006a).

Desde un punto de vista ecológico y siendo más específicos sobre cada medida cada una tiene su propia interpretación. En cuanto a la diversidad fenológica (capítulo 2) los valores se interpretan como el "número de formas fenológicas diferentes de la comunidad" (Sánchez-ochoa et al. 2022). Por otro lado, la diversidad periódica (capítulo 3) se interpreta como el "número de patrones periódicos diferentes de la comunidad". Finalmente, con la diversidad β temporal, al ser una medida compuesta por dos valores, se conceptualizan la diversidad γ temporal y α temporal. La diversidad γ temporal está definida como el "número efectivo de especies a lo largo de todo el periodo de estudio en un sitio determinado", la diversidad α temporal se define como el "número efectivo promedio de especies por unidad de tiempo" y la diversidad β temporal se define como el "número de comunidades únicas a lo largo del tiempo", las definiciones están basadas en cada uno de los marcos teóricos en los que están fundamentados.

En cualquier caso, cuando los valores de $q = 0$, las medidas representan únicamente la riqueza de especies evaluadas; sin embargo, hay ocasiones que los valores de la diversidad fenológica y periódica pueden llegar a ser un poco más altos que el número de curvas fenológicas o periódicas analizadas (S). Esto se debe a que, al ser medidas basadas en distancias entre pares de especies, por lo tanto la cantidad de comparaciones es mayor que la riqueza específica, biológicamente esto indica que el atributocomunitario temporalpueden ocurrir de diferentes formas por especie; sin embargo, esto no cambia la interpretación ni su comparabilidad. Desde un punto de vista ecológico, cuando hay especies con curvas temporales o periódicas similares, pertenecerían al mismo grupo fenológico o periódico y, por el contrario, cuando dos especies tienen bajo sobrelapamiento en las curvas, pertenecerían a un grupo fenológico o periódico distinto. Cuando los valores de $q > 0$, las medidas tendrían un mayor peso a la abundancia o intensidad en el proceso biológico medido. De esta manera, especies con curvas fenológicas o periódicas poco comunes no serán tomadas en cuenta y al final los valores de diversidad fenológica o periódica serán el número de curvas más abundantes. Así, a pesar del parámetro *q*, valores elevados en la diversidad fenológica y periódica representan un mayor arreglo heterogéneo y menor sobrelapamiento entre los nichos temporales de las especies (Percival and Walden 2000).

En cuanto a la diversidad β temporal, los valores de γ- y α- son consistentes con los patrones en órdenes de *q* de las medidas de diversidad espacial y las otras dos medidas propuestas (Ricotta 2018; Chao et al. 2019b); sin embargo, los valores de β temporal no muestran los mismos patrones. Esto se debe principalmente a la diferencia en la tasa de cambio de la diversidad γ- y α-, siendo la diversidad α- (número efectivo promedio de especies que se hay por unidad de tiempo) la que determinaría los patrones de unicidad de las comunidades (diversidad β- temporal); sin embargo, es importante mencionar que probablemente al usar otra perspectiva diferente al cociente de γ- y α-, se observen diferentes patrones (Anderson et al. 2011; Baselga 2012; Legendre and Gauthier 2014a). Por otro lado, la diversidad α- temporal tiene una relación estrecha con la detectabilidad ya que, al ser el promedio de especies por unidad de tiempo, se está considerando indirectamente la probabilidad de encuentro de un número de especies en un momento y sitio particular. Sin embargo, puede ser importante considerarlo desde inicio en el cálculo de la transformación de las series de tiempo ya que se ha visto que algún valor de la detectabilidad de las especies es importante integrarlo a los estudios de diversidad (Wintle et al. 2005; Tanadini and Schmidt 2011; Banks-Leite et al. 2014; Veech et al. 2016).

Las simulaciones que se hicieron representan diferentes escenarios que buscan mostrar la variación de los valores en cada una de las medidas. Los resultados muestran que las diferencias en las abundancias, áreas de sobrelapamiento, variación en el número de especies y la equitatividad modifican los distintos valores de diversidad. De esta manera las medidas de diversidad son sensibles a diversos atributos comunitarios y a la variación de parámetro *q* como ocurren en otras medidas basados en los números de Hill (Jost 2006b; Chao et al. 2014a). Específicamente, los valores más altos de diversidad, en cualquiera de los tres casos, corresponden a los sitios que presentan una alta equitatividad, así como se ha mostrado en diversos estudios. Asi mismo, las simulaciones con valores más bajos de diversidad corresponden con aquellas que tienen menor variación en los atributos o con menor número de especies puestas a prueba. Estos aspectos son consistentes con el marco teórico de la diversidad en que los valores más altos están asociados a alta equitatividad y un número elevado de especies (Hill 1973; Ricotta 2018; Chao and Ricotta 2019).

Por otro lado, al probar las simulaciones se pudieron observar algunas limitaciones en la base teórica en la que nos basamos para las medidas de diversidad fenológica y periódica (Chao et al. 2014a, 2019a). De manera particular, al ser medidas de distancia entre especies pareadas, tanto las medidas de diversidad funcional y filogenética que Chao propone, así como las nuestras, propicia que haya sobreestimaciones en algunos casos. Por un lado, hay sobreestimaciones y valores más altos que la riqueza específica cuando *q*=0; sin embargo, esto no cambia los patrones ni la interpretación y comparabilidad. Por otro lado, cuando los patrones en el atributo de todas las especies son iguales o muy similares, los valores de diversidad se sobreestiman de igual forma, si bien resulta ser un problema, es difícil que estas situaciones ocurran en la naturaleza, esto no se discute en las propuestas de Chao, ya que sus medidas se aplicaron directo en datos de campo y no se hicieron simulaciones como en las medidas de esta tesis. A pesar de estos inconvenientes, el marco teórico de nuestras tres medidas provee medidas adecuadas para medir diversos atributos comunitarios (fenología, periodicidad y heterogeneidad en las comunidades). Algo importante que mencionar es que las tres medidas están construidas a partir del procesamiento de los datos por el análisis de series de tiempo considerando la intensidad o abundancia de los procesos biológicos. Esto hace que nuestra medida no sea aplicable a los datos de presencia/ausencia y sería necesario modificar algunos aspectos del marco teórico para adaptarlo a la naturaleza de los datos binarios.

Finalmente, las tres medidas fueron puestas a prueba con datos de campo incluyendo nuestro caso de estudio de una comunidad de anfibios de Nahá, Chiapas. Las tres medidas evaluaron satisfactoriamente todos los datos de campo (Heinermann et al. 2015) y los patrones de diversidad en ordenes de *q* se comportaron de manera similar a las medidas existentes basadas en los números de Hill (Chao et al. 2014b; Ohlmann et al. 2019; Thorn et al. 2020). Particularmente en el estudio de caso se logró mostrar la utilidad de las medidas de diversidad fenológica, periódica y β temporal a lo largo de los seis sitios que se consideraron en el muestro. Los valores de diversidad fenológica, periódica y β temporal mostraron variación a lo largo de todos los sitios, ya que los patrones temporales por especie son distintos entre sí y son diferentes entre los sitios. Esto se ha observado en otros estudios sobre la riqueza específica, siendo las variaciones micro ambientales las que determinan la variación espacial de la diversidad de anfibios, y probablemente ocurra lo mismo con el eje temporal; sin embargo, se necesitan más datos para hacer esta afirmación (Werner et al. 2007; Heinermann et al. 2015; Dubos et al. 2020; Atkinson et al. 2021).

Los métodos propuestos incorporan el análisis de series tiempo y el marco teórico de los números de Hill, siendo consistentes con otras medidas de diversidad de atributos comunitarios (Chao et al. 2014a; Chiu and Chao 2014; Chao and Chiu 2016). Asi mismo, se mostró que pueden ser usadas con diferentes taxones y esfuerzo de muestreo; sin embargo, se necesitan más estudios para poder entender los patrones temporales de la diversidad. Por otro lado, también se demostró en el último capítulo de la tesis que las medidas de diversidad temporal pueden ser usadas como variable de respuesta a diversas variables ambientales, así como sucede con otras medidas de diversidad. Particularmente, en el estudio de caso se realizaron correlaciones de una sola variable, pero pueden ser usadas para contestar preguntas más complejas que consideren la diversidad de patrones temporales o la heterogeneidad de las comunidades en el tiempo. Por lo tanto, la aplicación de estas medidas es muy amplia, convirtiéndolas en medidas que contribuyen a muchas áreas del conocimiento de la ecología.

Conclusiones

Las medidas de diversidad fenológica, periódica y β temporal, producen valores de fácil interpretación y comparabilidad para evaluar de diferentes atributos temporales. Asi mismo, las medidas propuestas mantienen las propiedades de otros marcos teóricos de diversidad con el enfoque de los números de Hill. Tanto la diversidad fenológica, periódica y β temporal pueden ser aplicados a grupo taxonómico y en diversas resoluciones de esfuerzo de muestro. Finalmente, las tres medidas no son excluyentes entre sí y pueden ser usadas de forma complementaria entre sí o con otras medidas que responden a atributos comunitarios particulares como la filogenia o atributos funcionales. Asi mismo, cualquier valor de diversidad temporal, ya sea la diversidad fenológica, periódica y β temporal, pueden ser la variable de respuesta de diversas preguntas, así como se mostró en el último capítulo. De esta manera, el marco teórico desarrollado en esta tesis tiene implicaciones importantes en el diseño de monitoreo y conservación de las especies y comunidades, gracias a tener un mayor entendimiento de los patrones temporales para su manejo, conservación o restauración.

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