

Seasonality and predictability shape temporal species diversity

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Abstract. Temporal environmental fluctuations, such as seasonality, exert strong controls on biodiversity. While the effects of seasonality are well known, the predictability of fluctuations across years may influence seasonality in ways that are less well understood. The ability of a habitat to support unique, non-nested assemblages of species at different times of the year should depend on both seasonality (occurrence of events at specific periods of the year) and predictability (the reliability of event recurrence) of characteristic ecological conditions. Drawing on tools from wavelet analysis and information theory, we developed a framework for quantifying both seasonality and predictability of habitats, and applied this using global long-term rainfall data. Our analysis predicted that temporal beta diversity should be maximized in highly predictable and highly seasonal climates, and that low degrees of seasonality, predictability, or both would lower diversity in characteristic ways. Using stream invertebrate communities as a case study, we demonstrated that temporal species diversity, as exhibited by community turnover, was determined by a balance between temporal environmental variability (seasonality) and the reliability of this variability (predictability). Communities in highly seasonal mediterranean environments exhibited strong oscillations in community structure, with turnover from one unique community type to another across seasons, whereas communities in aseasonal New Zealand environments fluctuated randomly. Understanding the influence of seasonal and other temporal scales of environmental oscillations on diversity is not complete without a clear understanding of their predictability, and our framework provides tools for examining these trends at a variety of temporal scales, seasonal and beyond. Given the uncertainty of future climates, seasonality and predictability are critical considerations for both basic science and management of ecosystems (e.g., dam operations, bioassessment) spanning gradients of climatic variability.

Key words: climate; communities; desert annuals; migratory waterfowl; periodicity; seasons; stream invertebrates; temporal beta diversity; turnover; wavelets.

To everything there is a season (Ecclesiastes 3)

INTRODUCTION

Ecologists have long understood that environmental heterogeneity is intimately connected to species diversity. In theory, predictable oscillations in an environment should allow the coexistence of a great number species over a given timeframe, with each species experiencing optimum conditions at a different time and none

experiencing poor conditions for too long a time (Hutchinson 1961). Indeed, temporal periodicity in environmental conditions is a central component of ecosystems worldwide, and within-year seasonality is among the strongest and most well-known forms of such periodicity (Fig. 1). More recently, seasonality has been invoked to explain general phenomena such as life history adaptations (McNamara and Houston 2008), latitudinal diversity gradients (Hurlbert and Haskell 2003, Dalby et al. 2014), and community structure (Chesson 2000, Chase 2011), as well as specific phenomena such as migratory dynamics of birds (Somveille et al. 2015), estuarine fish diversity (Shimadzu et al. 2013), and stream invertebrate diversity (Bogan and Lytle 2007, Bonada

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FIG. 1. Examples of seasonal changes in two ecosystems: Sonoran Desert sand dunes at El Pinacate y Gran Desierto de Altar Biosphere Reserve (Sonora, Mexico) (A) before and (B) after winter rains and Chalone Creek at Pinnacles National Park (California, USA) during the (C) dry and (D) wet season.

and Resh 2013). However, efforts to generalize how both temporal variability in environmental conditions (seasonality) and the reliable recurrence of these different environments (predictability) determine species diversity within a single location require a common currency to measure predictability and seasonality.

Drawing on tools from modern wavelet analysis and information theory, as well as ecological theory, we provide a simple framework for understanding how the seasonality and predictability of an environment interact to shape temporal patterns of local diversity. We emphasize that, while seasonality is a well-known structuring force on biodiversity, our understanding of its regulatory influence on local communities is not complete without understanding its predictability. Following a discussion on the ways in which seasonality of environmental conditions can regulate diversity, we use this framework to generate predictions about within-latitude temporal diversity patterns, emphasizing the mechanisms that promote overall temporal diversity (i.e., temporal turnover), particularly for short-lived organisms. We then demonstrate the framework using stream community case studies from different regions at similar latitudes that span a seasonality–predictability gradient in rainfall

patterns (mediterranean-climate western United States, arid southwestern United States, maritime New Zealand). We focus on the types of systems and dynamics that this framework can directly address, but also demonstrate that the methods we outline allow the identification of various ecological trends across a variety of temporal scales. By providing a framework for quantitatively considering seasonality and predictability of environmental fluctuations, we hope to (1) spark renewed interest in the role of seasonality and (2) stimulate new research on the less well studied role of environmental predictability in governing diversity of natural systems. We believe that considering both concepts together can shed more light on temporal patterns of local diversity in a variety of systems allowing for better prediction and management of biodiversity under the ever-increasing threat of global change.

INCORPORATING SEASONALITY GIVES US A RICHER VIEW OF ECOSYSTEMS

Most environmental phenomena occur with seasonal oscillations, particularly temperature and precipitation, but even regular oscillations can vary in biologically important ways. For example, while the total annual

duration of daylight is invariant across the globe, the seasonal distribution of daylight varies dramatically with latitude. As a result of these differences in distribution, many ecosystems experience distinct seasonal conditions that can favor entirely different communities and food webs during parts of each year (McMeans et al. 2015) (Fig. 1). Seasonality tends to increase in importance with increasing distance from the equator. However, even tropical regions that are not subject to extreme temperature variations can experience seasonal fluctuations in key environmental characteristics, such as precipitation on land and upwelling in the ocean. These seasonal abiotic oscillations lead to seasonal pulses of resources, which in turn open up temporal niches for a wide variety of species to reside in local habitats.

Climatic variability is at the heart of the distribution of species globally and comprises many different components, including seasonality, harshness, predictability, and length of the favorable period for occupation (Jocque et al. 2010). Species life histories are finely tuned to capitalize on specialized temporal niches associated with this variability (Chesson 2000, Chase 2011; Fig. 2).

Consequently, temporal diversity can be promoted through a variety of channels, such as migration to exploit resources and escape competition (Somveille et al. 2015), highly synchronous seasonal reproduction, or seasonal fluctuations in abundance (Shimadzu et al. 2013; Fig. 2). In fact, oscillations in environmental conditions, such as seasonal shifts in productivity, can explain discrepancies in latitudinal diversity gradients (Hurlbert and Haskell 2003, Dalby et al. 2014). Nevertheless, this very seasonality can reduce diversity outside of tropical regions by acting as an environmental filter for organisms (Gouveia et al. 2013). Thus, while seasonality is clearly important, it appears to interact with other forces to produce observed patterns of biodiversity.

Several studies have suggested mechanisms by which temporal fluctuations affect pairwise or community-wide species interactions, and thus patterns of biodiversity. Although limited resources and interspecific competition can lead to the exclusion of species (Connell 1978), seasonal variation in environmental conditions can facilitate the persistence of similar species (Tilman and Pacala 1993). Such seasonal variation (temporal environmental

	Examples Aquatic insects in temporary streams	Seasonal factor Stream flow	Mechanism/process Dormant egg and larval stages to survive dry seasons, reactivate during wet seasons; terrestrial insects occupy streambeds during dry season.	Citations Canada, Spain, USA (1,2,3)
	Annual plants in deserts	Precipitation	Rapid development and growth with seeds that lay dormant until following wet season; some species grow during winter- spring rains, others during summer rains.	USA (4,5,6)
	Fish in floodplains	River flooding	Disperse into floodplains when rivers top their banks, consume abundant resources in floodplains, return to primary river channels as flow recedes.	Australia, Bangladesh, USA (7,8,9)
	Waterbirds in lakes and wetlands	Vegetation growth	Migratory waterfowl occupy productive mid-latitude lakes and wetlands when vegetative growth is highest (summer), then migrate to other habitats during unproductive winter season.	Global (10)
	Plants and crustaceans in vernal pools	Hydroperiod	Crustaceans (e.g., fairy shrimp) active during wet season, enter dormant stage when pools dry; plants grow during drying phase, dormant seeds persist through wet phase.	Australia, Chile, USA (11, 12, 13)

FIG. 2. Examples of taxa with life cycles that are synchronized to take advantage of predictable, seasonal changes in environmental conditions. Citations: 1, Hynes (1976); 2, Jacobi and Cary (1996); 3, López-Rodríguez et al. (2009); 4, Mulroy and Rundel (1977); 5, Guo and Brown (1997); 6, Mathias and Chesson (2013); 7, Craig et al. (2004); 8, Jeffres et al. (2008); 9, Arthington and Balcombe (2011); 10, Dalby et al. (2014); 11, Keeley and Zedler (1998); 12, Collinge and Ray (2009); 13, Kneitel (2014).

variation) operates in a conceptually similar way to physical heterogeneity (spatial environmental variation) through preventing competitive exclusion and creating niches for species in different seasons. For instance, the storage effect allows multiple species to occupy similar habitats through populations “storing” the gains made in good years to buffer against losses in bad years (Chesson 2000). Thus, theory suggests that, at least in principle, organisms can capitalize on seasonal dynamics in ways that enhance the overall diversity of a single habitat.

LIFE-HISTORY EVOLUTION IN SEASONAL ENVIRONMENTS

The life histories of organisms are intimately connected to seasonality. Fundamental vital rates such as growth, mortality, and reproduction seldom remain static over time, but vary in response to environmental conditions that change seasonally. Thus, many important life-history decisions are likely governed by seasonality, including age and size at maturity, timing of migration or breeding, and allocation to growth vs. reproduction (McNamara and Houston 2008). Life-history models that explicitly incorporate seasonality predict that when disturbances such as floods, droughts, or fires recur with sufficient seasonality, selection will favor strategies that produce synchrony with this disturbance regime (Cohen 1966, Rowe et al. 1994, Lytle 2001). Seasonality can thus be viewed as an adaptive force that entrains the life histories of organisms into specific temporal strategies. From a community perspective, this should have a direct effect on the composition of the local species pool. In environments with strong, recurrent seasonality, species should possess specific adaptations or abilities for coping with seasonal environments (due to selection for seasonal life histories) and community composition should differ from one part of the season to another (due to life-history trade-offs that favor specialization on a particular season). The latter prediction is directly testable by examining patterns of community structure across seasons, and is the focus of this study.

Life history evolution is not confined to annual time scales, however. Processes operating at other temporal frequencies, such as diel fluctuations in light levels, monthly changes in ocean tidal cycles, and supra-annual changes in oceanic and atmospheric conditions can all potentially drive the evolution of life histories. The relevant factor is the temporal scale of the environmental phenomenon with respect to the lifespan of the organisms. For example, models examining the timing of maturation in seasonal environments predict a strong evolutionary response when the lifespan of the organism corresponds roughly to the frequency of environmental fluctuations (Iwasa and Levin 1995, Lytle 2001). On the other hand, organisms with too-short or too-long lifespans may fail to evolve synchronous life history strategies, even though this may reduce fitness and even result in ecological exclusion from the system (Lytle and Poff 2004). For these reasons, we need analytical methods that visualize

ecological processes across a range of time scales in order to identify the most important frequencies, with respect to the organisms of interest.

SEASONALITY AND PREDICTABILITY DEFINED

Seasonality can be defined in many ways, depending on the application. The astronomical definition of the four seasons relates to the timing of the summer and winter solstices and vernal and autumnal equinoxes, which differs slightly from the meteorological definition based on calendar dates (Timm et al. 2008). From an economic perspective, Hylleberg (1992:4) defined seasonality as “the systematic, although not necessarily regular, intra-year movement caused by the changes of the weather, the calendar, and timing of decisions, directly or indirectly through the production and consumption decisions made by the agents of the economy.” We used a definition of seasonality of environmental phenomena based on Lieth (1974:5): “Seasonality is the occurrence of certain obvious biotic and abiotic events or groups of events within a definite limited period or periods of the astronomic (solar, calendar) year.” Essentially, this represents the degree to which within-year conditions are distinct. Thus, a mediterranean-zone climate creates a highly seasonal environment because summer conditions are dry and warm while winter conditions are cool and wet. Colwell (1974) used information theory to formalize this notion: Colwell’s M , or “contingency,” measures the degree to which biological events such as flowering, or physical events such as monthly rainfall totals, are tied to specific times of the year (Box 1). Colwell’s M is useful as a measure of seasonality, in that high values indicate strong differences across seasons.

While environments can be seasonal, however, they are not necessarily predictable (and vice versa). Predictability can be variously defined depending on the phenomenon of interest and has been the topic of much discussion (Resh et al. 1988, Poff 1992, Lytle and Poff 2004). For our purposes, we define predictability as the regularity of recurrence of the within cycle (e.g., annual) distribution of events across multiple cycles. For instance, if the annual distribution of rainfall recurs each year, regardless of what that annual distribution is, it is considered predictable. Thus, in the case of our mediterranean-zone example, the dry season is highly predictable if it recurs reliably during the same summer months from year to year. By contrast, some temperate oceanic regions (e.g., New Zealand, as demonstrated in the following case study) can experience wet months nearly any time of the year, varying from year to year, so predictability is low. In many biologically important cases, events recur on an annual time scale, but this need not be the case: phenomena such as lunar tidal cycles, El Niño – Southern Oscillation, and the Pacific Decadal Oscillation all recur at non-annual time scale, and thus have a characteristic and measurable predictability associated with them. Wavelet analysis (Box 1) can be employed to quantify the

Box 1. A framework for measuring seasonality and predictability

Wavelets

Spectral analysis partitions the variability within a time series into different components characterized by different frequencies. The contribution of each frequency (period) to the variability (power) within a time series can be revealed by plotting the power spectrum (power as a function of frequency). This power spectrum then enables examination of key temporal scales of variability within the time series.

Some have recommended the use of the Fourier transform to decompose variation in ecological or environmental phenomena, such as streamflow (Sabo and Post 2008). However, wavelets have the advantage over Fourier transforms in their scale independence and ability to examine multiple scales simultaneously (Torrence and Compo 1998). Rather than simply detecting the dominant frequencies averaged over an entire time series, wavelets can preserve the location of an event in space or time, enabling tracking of periodic phenomena over the time series. Essentially, wavelet transforms decompose a time series into three-dimensional space: time, scale/frequency, and power, where power represents the magnitude of variance at a given wavelet scale and time. Thus, they can help to reveal more subtle structures that would otherwise be missed in multi-scaled, non-stationary, time series data (Smith et al. 1998).

Depending on the data and objectives, there are a variety of wavelet functions that can be used, including Morlet, Mexican hat, and Paul. The Morlet wavelet is well suited for hydrological time-series data, being a nonorthogonal, complex wavelet transform (Torrence and Compo 1998). Nonorthogonal wavelets tend to be more robust to noise and to variations in data length than other decompositions (Cazelles et al. 2008). Moreover, “complex” wavelets are better at capturing oscillatory behavior than “real” wavelets, which are better used for isolating individual peaks or discontinuities (Torrence and Compo 1998). The significance of wavelet power spectra can be tested against background (noise) spectra. In this case, we used the default white noise spectrum (constant variance across all scales). Using this approach allows direct comparison between time series, as after detrending the time series, it is standardized to obtain a measure of wavelet power relative to unit-variance white noise. When the wavelet power exceeds the background, it is deemed significant (here at 95% confidence level; Torrence and Compo 1998).

Colwell's indices

Colwell (1974) devised three interrelated metrics based on information theory to quantify the general characteristics of periodic phenomena: predictability (P), constancy (C), and contingency (M). P represents the relative certainty of knowing a state at a given time, and is the sum of constancy and contingency. C represents the degree to which a state stays the same throughout all seasons. M describes how closely different states correspond to different time periods within a year. Thus, M contains information about the degree of seasonality experienced by an environment. As P is the converse of uncertainty, it stands to reason that its calculation is based on the mathematics of information theory (Colwell 1974). P is maximized when the environmental phenomenon is constant throughout the year, if the seasonal fluctuation is consistent across all years, or a combination of both. It is important to note that Colwell's P is a fundamentally different metric from our wavelet-derived estimate of predictability. When analyzing annual data, Colwell's P is linked to within-season dynamics, while our wavelet-derived measure can be applied at any temporal scale.

Combined

In our framework, we combine the simplicity of Colwell's information-theoretic metrics and the power and graphical quality of wavelets to define seasonality and predictability, respectively. We opted to combine these two approaches as Colwell's metrics are inherently linked (i.e., predictability is the sum of contingency and consistency). Specifically, our measure of seasonality is M/P , which is Colwell's measure of contingency standardized by Colwell's within-season predictability. This measures the degree to which the environment varies during the course of a single year. Our measure of predictability uses the proportion of wavelet power that is significant at the 12-month interval across the entire time series. That said, we could have also compared the standardized wavelet power at the 12-month interval to achieve a similar result (as per Fig. 4D). Furthermore, the chosen period of interest can be adapted to any given recurrence interval and wavelets can be employed as an exploratory tool to identify dominant frequencies in the data. This flexible measure of predictability allows us to examine the importance of phenomena that recur at intervals less than or greater than the typical annual cycle.

predictability of periodic phenomena such as rainy and dry seasons (Daubechies 1990, Torrence and Compo 1998). A benefit of wavelet analysis is that it allows us to quantify the strength of predictability at any time scale. Although we are often interested in phenomena that

recur on an annual basis, we can also explore data for patterns that recur at other time scales.

Wavelet analysis has been used for a variety of applications in ecology and other fields (Daubechies 1990, Cazelles et al. 2008), such as comparing compensatory

dynamics vs. synchrony in response to disturbance (Keitt 2008); tracking glacial flow influences in streams (Cauvy-Fraunié et al. 2015); and tracking cycles of measles outbreaks (Grenfell et al. 2001). For instance, Winder and Cloern (2010) were able to identify dominant time periods in phytoplankton cycles and found considerable variability across different aquatic ecosystems. Wavelet analysis has proven useful in precisely locating and quantifying multi-scaled phenomena, both periodic and stochastic, in time-series data (e.g., rainfall, river flows, temperature) that may fluctuate daily, seasonally, or annually (Steel and Lange 2007). In this study, we use wavelet analysis because it is a flexible tool particularly useful for trend detection at multiple time scales, whether sub- or super-annual, quantification of effect size across time scales, and data visualization (Box 1).

MECHANISTIC WAYS THAT SEASONALITY AND PREDICTABILITY REGULATE DIVERSITY: A CONCEPTUAL FRAMEWORK

Large differences in within-year conditions (seasonality) coupled with the reliable recurrence of seasonal events (predictability) should produce different responses of diversity depending on whether single-time-point diversity or temporal diversity is considered (Fig. 3). Seasonal exclusion of certain species may lower the richness of a site at any given time, but different species may occupy the same site in different seasons, thus increasing the overall diversity of a given site when the seasonal cycle is predictable (Bogan and Lytle 2007, Bonada et al. 2007). In contrast, unpredictable seasonal events could be detrimental, leading to a lack of ability of organisms to synchronize their life cycles with the seasonal phenomena (Lytle and Poff 2004, Wernberg et al. 2013) and a decrease in temporal diversity.

Alternatively, low seasonality should lead to low turnover of species within the annual cycle. Coupled with predictable climate, as is found in many tropical regions,

local diversity can be high at any given point in time. Indeed, realized niches are smaller than fundamental niches in predictable systems, whereas fundamental and realized niches will be closer in unpredictable systems (Fjeldså and Lovett 1997, Santos and Almeida-Cortez 2009). One of the prevailing mechanisms behind the latitudinal diversity gradient reflects this differentiation, where species in the tropics have more specialized niches, and thus tighter species packing through greater environmental stability (Hutchinson 1959, MacArthur 1972). For these ideas to play out on a global scale, however, a dispersal–specialization trade-off is required (Jocque et al. 2010).

Under this framework, predictably seasonal environmental conditions promote the greatest temporal diversity through more specialists occupying available temporal niches and, in turn, greater temporal turnover in composition (Fig. 3). At the other end of the spectrum, unpredictable aseasonal systems generate the lowest temporal diversity, harboring broad generalists with little seasonal turnover.

CASE STUDY: RIVER COMMUNITY STRUCTURE ACROSS MAJOR BIOMES

Streams and rivers are highly dynamic systems, strongly driven by disturbances such as floods and droughts (Resh et al. 1988, Lake 2000, Death 2008). The flow regime is a central force characterizing river systems (Poff et al. 1997, Lytle and Poff 2004, Bunn et al. 2006), with organisms having evolved a variety of behaviors and life-history traits to thrive under these highly fluctuating conditions (Lytle 2001, Lytle and Poff 2004, Lytle et al. 2008). Recent studies of stream communities have identified high degrees of temporal beta diversity, with unique invertebrate communities present within a single location during rainy vs. dry seasons (e.g., Bêche et al. 2006, Bogan and Lytle 2007). In a study across multiple aquatic ecosystems, Korhonen et al. (2010) found greater turnover within years compared to between years, indicating a greater role of seasonal turnover vs. annual turnover. Seasonal stream communities can be taxonomically distinct, and are often characterized by species that differ greatly in thermal tolerance, mode of respiration, trophic position, and other ecological traits (Bêche et al. 2006, Bonada and Resh 2013). The high predictability of dry and wet seasons has been proposed as one of the main reasons for the high aquatic diversity observed in mediterranean climate areas (Bonada and Resh 2013). Additionally, the unreliable recurrence of a season can lead to the elimination of sensitive taxa from communities (e.g., Bogan and Lytle 2011). By contrast, Tonkin et al. (2016) found little evidence of seasonal turnover in Afrotropical streams, which can have clear differences in precipitation between seasons (high seasonality), but relatively low coherence in among-year patterns (low predictability). Thus, the interplay between seasonality and predictability appears to play an important role in determining local diversity in many river and stream ecosystems.

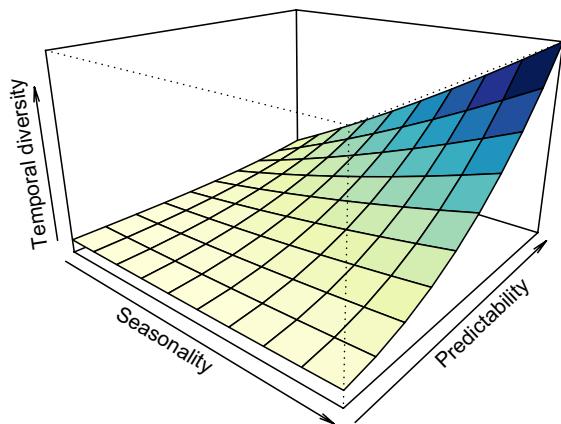


FIG. 3. Hypothetical predictions of the relationship between seasonality, predictability, and temporal diversity.

We identified three geographic regions with varying levels of seasonality and predictability to demonstrate this concept, and generate predictions about the patterns and mechanisms promoting temporal diversity at these locations. For our biotic data, we focused on stream invertebrate communities (organisms with a near-annual life cycle, given our temporal focus is seasonality), sourcing published data meeting our criteria of: two seasons sampled per year (wet-dry/summer-winter) across a minimum of two years per location, a minimum of 25 total replicates, and benthic sampling using a standardized stream-type specific method across all samples. These regions consisted of (1) the central California mediterranean climate zone (Resh et al. 2005), which experiences highly seasonal and predictable rainfall patterns (N samples: 35); (2) the Sonoran Desert in Arizona (Bogan and Lytle 2007), which exhibits strongly seasonal, but less predictable, rainfall patterns (N samples: 27); and (3) central North Island New Zealand (Tonkin and Death 2012), which experiences highly unpredictable climate with potential for significant rainfall events in all four seasons (N samples: 32).

Climatic conditions

We characterized seasonality using Colwell's (1974) contingency metric (M). To standardize the role of seasonality in relation to overall predictability, we divided M by overall predictability (the sum of M and constancy [C]; see Box 1; i.e., how much seasonality contributes to predictability). We then used wavelet analysis to independently characterize the predictability of this seasonal pattern, by identifying dominant temporal cycles (12 months, 6 months, etc.) in the long-term data sets (Box 1). Based on our definition of predictability as the regularity of recurrence of the annual distribution of events, we quantified predictability as the proportion of time-steps over the full time series with significant power at the 12-month frequency (i.e., annually). This metric is independent of the within-year distribution of seasonal events, but simply measures the degree to which a given distribution recurs from year to year. Put simply, this measures how consistent the annual repeatability of rainfall patterns is.

To calculate Colwell's indices, we used the R package "hydrostats" (Bond 2015). While this package is intended for use with river flow data, the method is applicable to any seasonal phenomenon. We used the default "transform" method for defining break points when binning data (a required step in Colwell's method; Colwell 1974). This first applies a $\log_{10}(x + 1)$ transformation, before splitting the data into the ten equal size bins. To perform the wavelet analysis, we used the R package "WaveletComp" (Roesch and Schmidbauer 2014). To conduct our wavelet analysis, we employed the Morlet wavelet as our "mother wavelet," which represents a sine wave modulated by a Gaussian function (Torrence and Compo 1998).

The monthly rainfall data demonstrate the transition from strongly seasonal-predictable patterns for California to highly unpredictable for New Zealand (Fig. 4A, B). A clear annual cycle is evident in the wavelet plots for California, with continuous strong power at the 12-month frequency (Fig. 4C), while the signal is less clear in Arizona, with evidence of a secondary peak at the 6-month frequency. This results from the biseasonal rainfall pattern (winter frontal storms and summer monsoons) in this zone. However, as the power spectrum indicates, the predictability of rainfall in Arizona is much lower than in California (Fig. 4C). New Zealand exhibits no clear seasonality in rainfall patterns (Fig. 4C). These patterns are illustrated clearly in the average wavelet power across the full 30-year period, with California exhibiting the strongest peak at 12 months, Arizona at 6 months, and New Zealand at 3 months (Fig. 4D). While average wavelet power (Fig. 4D) does not encapsulate the full utility of wavelets (trends over the 30-year period are not captured), our metric of predictability quantifies how often there is a strong 12-month signal across the full time series, and this metric tracked the trend found for the average power (Fig. 4D, E, Box 1). Moreover, the graphical power of wavelets allows for detection of clear trends, if present, in the power spectrum across the given time period (Fig. 4C). California and Arizona recorded similar values of Colwell's contingency metric, indicating similar levels of seasonality, while New Zealand exhibited much lower seasonality (Fig. 4E).

To place our three study regions in the context of other regions globally, but within a similar distance from the equator, we compared several other regions in a similar latitudinal zone (both Northern and Southern Hemispheres; Fig. 4E). We did this to minimize the role of various factors such as productivity, seasonal harshness, and history of glaciation in our comparison, while allowing a consideration of a wide variety of climatic conditions, which would be difficult to find when limited to higher or lower latitudes. While this framework could be applied at any latitude, climatic conditions tend to become less predictable and harsher with shorter favorable periods as latitude increases (Stevens 1989). We added additional sites in the arid zone of the southwestern United States to determine the ability of these metrics to separate regions in close proximity with subtle variation in weather patterns. Globally, Donnybrook in Western Australia emerged as the most predictably seasonal environment, representative of its strongly mediterranean climate, followed by Springerville in eastern Arizona and Carriel Sur Airport in Chile (also mediterranean). By contrast, Hilo, Hawaii, and Dublin, Ireland were the least predictably seasonal of these zones, similar to New Zealand's pattern. This approach clearly distinguished between different climatic zones of locations within relatively close proximity, such as Chile and Argentina or Western Australia and Melbourne (Fig. 4E). This is particularly apparent when considering different locations within Arizona, including Springerville in the east

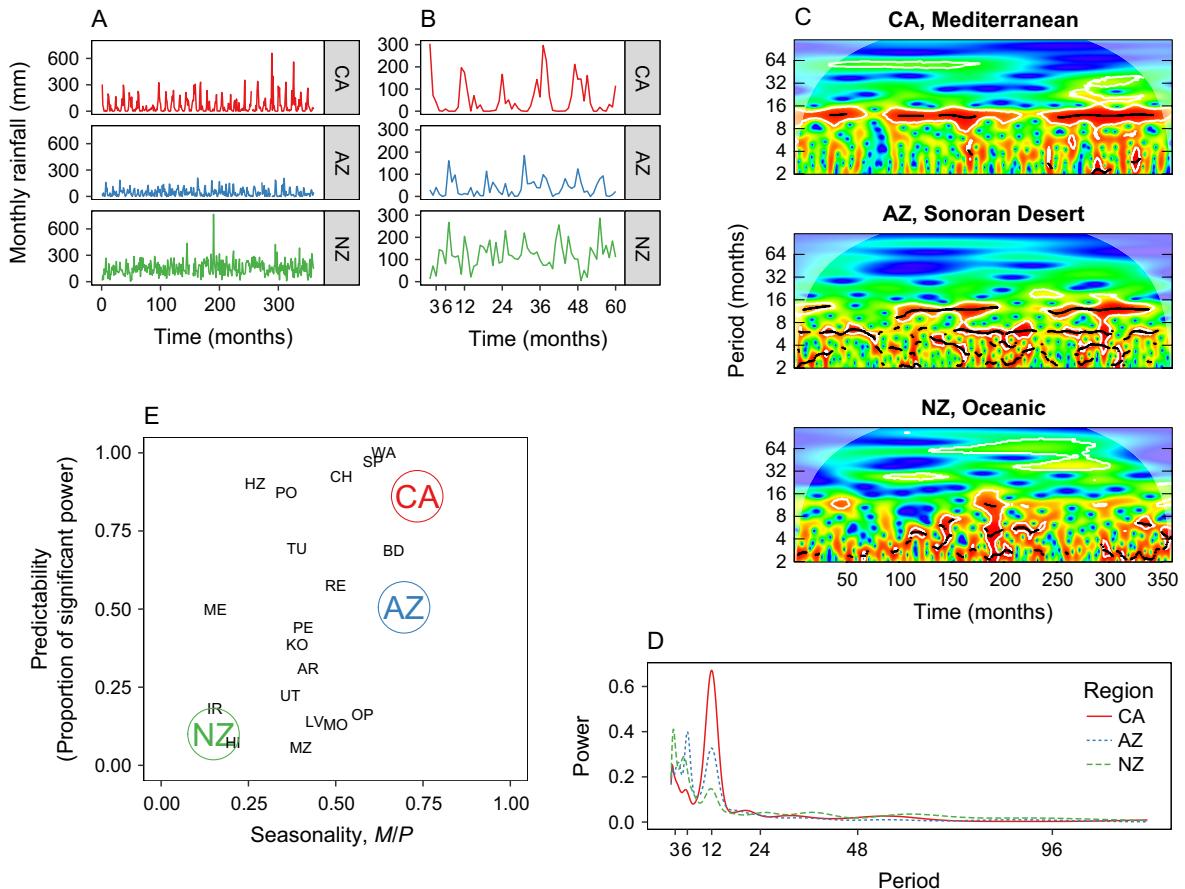


FIG. 4. Seasonality and predictability of 30-yr monthly rainfall data for multiple regions. (A) Time series of monthly rainfall over a 30-yr period for the three selected regions, and (B) over the first 5 yr. (C) Wavelet power spectrum of the three regions using the full rainfall time series. Red represents greater wavelet power and blue low. Note the area in the upper corners of each plot, which is outside the “cone of influence,” where predictive ability is weaker due to zero padding at the ends of the time series (Torrence and Compo 1998). (D) Average wavelet power across the full spectrum of periods. Different time series are directly comparable as the wavelet power is relative to unit-variance white noise. (E) Biplot of seasonality vs. predictability. Seasonality is measured as Colwell’s *M/P* (contingency/predictability). Predictability is measured as the proportion of significant wavelet power at the 12-month time period. Regions are CA, California mediterranean, USA; AZ, Sonoran desert, Arizona, USA; NZ, central North Island, New Zealand; AR, Argentina; PO, Portugal; WA, Western Australia; ME, Melbourne, Australia; HZ, Hangzhou, China; CH, Chile; TU, Turkey; HI, Hilo, Hawaii, USA; KO, Kona, Hawaii, USA; IR, Dublin, Ireland; OP, Organ Pipe Cactus National Monument, Arizona, USA; MO, Mojave Desert, California, USA; UT, Canyonlands, Utah, USA; RE, Reno, Nevada, USA; LV, Las Vegas, Nevada, USA; MZ, Montezuma, Arizona, USA; SP, Springerville, Arizona, USA; BD, Bisbee-Douglas Airport, Arizona, USA; PE, Petrified Forest National Park, Arizona, USA.

(predictable-seasonal), Organ Pipe Cactus National Monument in the southwest (unpredictable, moderately seasonal), Bisbee-Douglas Airport in the southeast (seasonal-predictable), Montezuma in the center (low-moderate seasonality, unpredictable), and Petrified Forest National Park in the northeast (moderate seasonality and predictability).

Diversity patterns

We examined differences in temporal beta diversity among regions, rather than total annual species richness, because it allows a standardized comparison between regions with different species pools and potential levels of gamma diversity (i.e., New Zealand is a small isolated

land mass compared to continental USA). Under this framework, predictably seasonal environmental conditions (like those observed in California) promote the highest levels of temporal diversity (Fig. 5A). In these cases, temporal beta diversity (temporal changes in composition) is generated through replacements of species between seasons (turnover; distinct communities in time), rather than through losses and gains of species between seasons (nestedness; one season’s assemblage is a nested subset of the other) (Bonada and Resh 2013). We expect this because the two seasons do not necessarily reflect high and low quality conditions, but distinct habitats with specialist niches. At the other end of the spectrum, aseasonal and unpredictable systems (e.g., New Zealand) generate the lowest temporal diversity, harboring

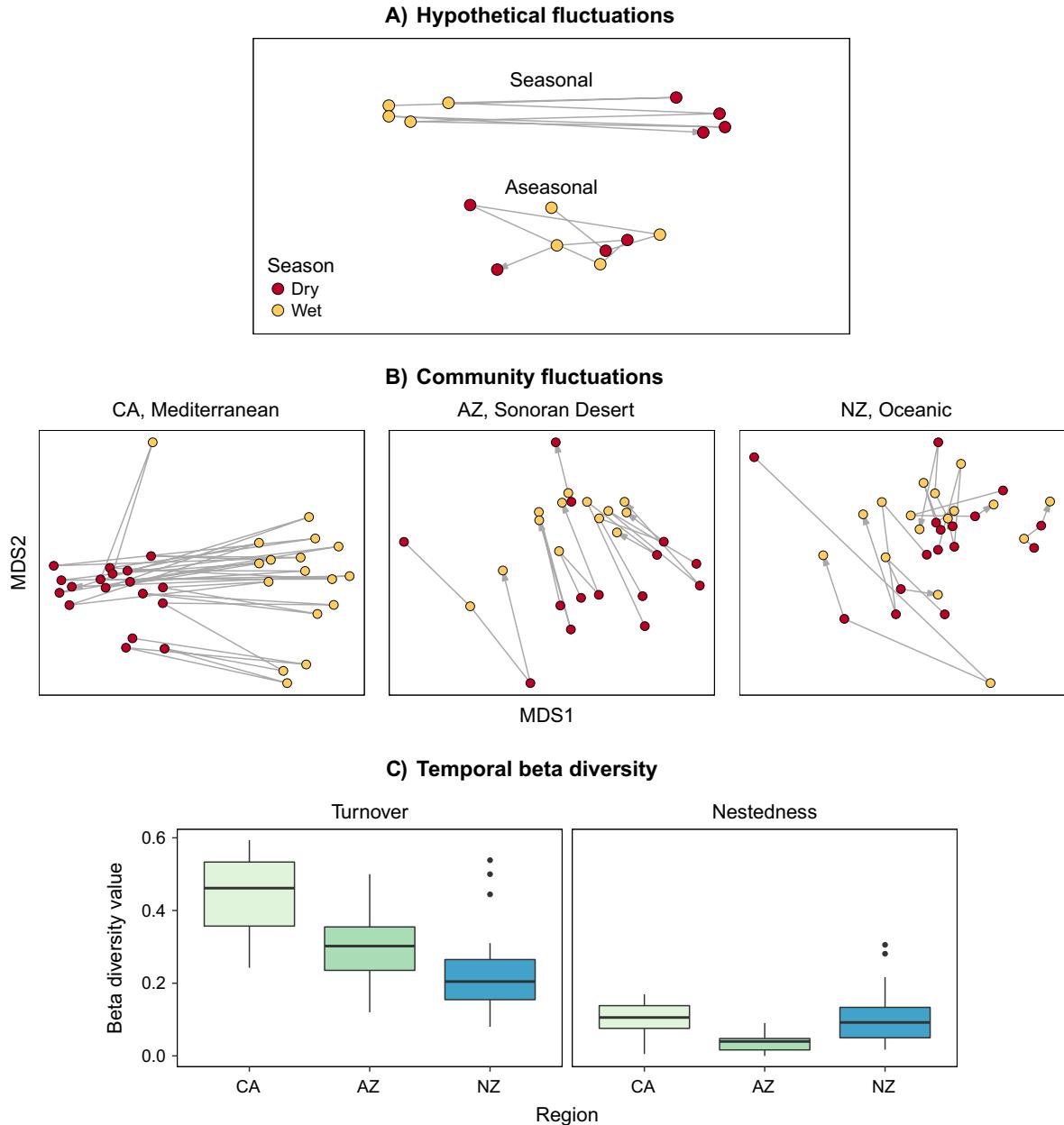


FIG. 5. Diversity response to seasonality. (A) Hypothetical community response (based on ordination) to wet-dry season fluctuations. (B) Ordinations of stream invertebrate communities in the three case study regions (California, Arizona, New Zealand) demonstrating the fluctuations in community structure between two seasons. (C) Within-year temporal beta diversity, based on Baselga’s beta diversity partitioning framework. Turnover (β_{sim}): pure turnover component of Sorensen dissimilarity (variability produced by the replacement of species between seasons). Nestedness (β_{nes}): pure nestedness component of Sorensen dissimilarity (variability produced through assemblages in one season being a subset of those in the other season). Box plots display the median, interquartile range (IQR), the furthest point within $1.5 \times$ IQR (whiskers), and outliers (points).

communities that show little seasonal turnover (Fig. 5A). In summary, turnover will be maximized under highly predictable seasonal conditions, while nestedness may dominate in unpredictable aseasonal environments.

We compared invertebrate data sets from our three regions using two approaches. First, we examined community fluctuation patterns at each site, using

nonmetric multidimensional scaling ordinations (nMDS; Bray-Curtis distance on abundance data) in the *R* package *vegan* (Oksanen et al. 2013). Second, we examined the mean intra-annual (summer vs. winter) temporal beta diversity for each site, separated into its turnover and nestedness components. These metrics, averaged across all years and all sites, indicate how much temporal beta diversity is due to

replacements rather than losses of species between seasons. We used the statistical framework developed by (Baselga 2010) in the betapart package (Baselga and Orme 2012) that allows the differentiation of overall beta diversity into nestedness (β_{nes} ; nestedness component of Sorensen dissimilarity) and turnover (β_{sim} ; turnover component of Sorensen dissimilarity) components.

Ordinations of communities in each zone matched our hypotheses that more predictable, seasonal environments would lead to greater and more predictable community fluctuations between seasons, despite differences in replication schemes (Fig. 5A, B). California invertebrate communities exhibited much clearer seasonal fluctuations than New Zealand (Fig. 5B). Moreover, these results were reflected in the mean temporal beta diversity within each year (Fig. 5C). Specifically, the turnover component of beta diversity clearly declined from California to New Zealand. The oscillations of Arizona stream communities fell in between the highly predictable Californian streams and those of the more unpredictable New Zealand streams. This is indicative of the strong seasonal fluctuations that occur in these desert streams, and the fact that this periodicity is less predictable than the mediterranean climate of California.

New Zealand rivers tend to be short, swift, steep, and flood prone due to the unpredictable climate (Winterbourn et al. 1981). Coupled with this is a lack of seasonal organic matter input, due to the largely evergreen nature of the New Zealand flora (Winterbourn et al. 1981). As a result, New Zealand has evolved a unique, largely generalist stream invertebrate fauna, adapted to persist in highly dynamic streams without strong seasonal synchrony. Seasonal differences may exist at some level, such as food web attributes (Thompson and Townsend 1999), but these differences may be more subtle than full community turnover.

In contrast, mediterranean climate streams, such as those in California, have seasonally predictable flows that vary greatly in magnitude (Bonada and Resh 2013), and in turn a highly endemic aquatic fauna with some particular biological traits adapted to seasonal flooding and drying periods (Ball et al. 2013). During the dry summer months, streams are dominated by OCH taxa (Odonata, Coleoptera, and Hemiptera), which specialize on low-flow, warm water conditions (Bonada et al. 2006). During the wet winter months, rheophilic EPT taxa (Ephemeroptera, Plecoptera, and Trichoptera) predominate, taking advantage of colder, fast-flowing conditions. Although both the OCH and EPT faunas can co-occur year-round, the favorable season for growth is offset greatly according to season. Thus, two distinct community types are able to utilize a single habitat during different times of the year.

Desert streams such as those in Arizona, USA, are subject to considerable variation in flow (Sabo and Post 2008), often characterized by intense flash floods (Grimm and Fisher 1989). In general, frontal winter storms result in several months of flow and cold water conditions, but the hot summer dry season causes flow

to diminish or cease and harsh water quality conditions to arise (Bogan and Lytle 2007). Additionally, late summer brings monsoonal rainfall to Arizona, causing brief, but destructive, high-flow periods in streams (Lytle 2000). However, these seasonal patterns can be dampened or enhanced by longer term climate trends (Bogan et al. 2013). As a result, stream invertebrate taxa in the region have a wide variety of adaptations to flow variability, including seasonal flow variability and stochastic flood events (Gray and Fisher 1981, Lytle 2000, Bogan et al. 2013). Nonetheless, some desert streams do exhibit temporal segregation of OCH and EPT taxa as with mediterranean streams, albeit to a lesser extent (Bogan and Lytle 2007).

Nestedness vs. turnover.—In line with our expectation, turnover, rather than nestedness, was the dominant mechanism promoting temporal beta diversity in our study streams. That is, community changes between seasons were driven by species replacements, rather than losses and gains. This pattern was consistent between the three regions, indicating that regardless of the level of overall temporal beta diversity, the underlying mechanism promoting differences between seasons remained the same. Rather than the two seasons representing low vs. high quality conditions, where nestedness would be expected, they represent two distinct temporal niches. In contrast, nestedness could be the dominant pattern when some seasons are much harsher than others, such as in polar regions. In fact, evidence suggests decreasing speed of intra-annual turnover with increasing latitude for aquatic organisms (Korhonen et al. 2010). Thus, an interesting testable hypothesis is whether intra-annual nestedness replaces intra-annual turnover when moving from mid to high latitudes.

GENERALIZING THE APPROACH

Here, we have shown that climate seasonality and predictability are clearly related to diversity patterns. We have specifically focused on stream communities in our case study for several reasons. Streams are dynamic systems strongly influenced by abiotic conditions, and thus diversity patterns might be expected to track these characteristic changes in habitat type. Also, a large proportion of stream invertebrates complete their life cycle within a single year, which leads to measurable differences in species abundances within the time frame of a single year. It therefore stands to reason that seasonal precipitation and temperature regimes play a key role in regulating temporal community dynamics in these systems as we have demonstrated.

In the following sections, we discuss other cases and systems where this framework applies to community dynamics and consider the limitations of our approach. We also explore how the framework may be applied to different time scales, from daily through to multi-year cycles. For example, seasonality, no matter how strong or

predictable, will not lead to complete compositional turnover of communities with life cycles spanning more than one year. However, seasonality controls other aspects of population dynamics, encapsulated in the study of phenology.

Aridland annual plants

A short life cycle is a key criterion for intra-annual temporal diversity turnover to be apparent (the focus of our case study). Aridland annual plants (Figs. 1A, B, and 2), which also fit this criterion, are particularly dependent on within-year variability in rainfall. These communities are typically divided into summer and winter assemblages, which persist spatially but have little temporal overlap because their active growth and reproductive stages occur during different seasons (Mulroy and Rundel 1977, Guo and Brown 1997). This clear temporal segregation of summer and winter assemblages, through the partitioning of a key limiting resource (water), maintains and promotes high temporal beta diversity. One of the key aspects behind segregation of these communities is the fact that these plants harbor no reserve capability other than in their seeds, which are dependent on water for reactivation (Noy-Meir 1973).

The predictability of precipitation has a key role in regulating diversity of these plant communities. This is particularly apparent for summer annuals, exemplified by an increase in diversity moving south in the southwestern United States, which corresponds with an increase in the amount and predictability of rainfall (Mulroy and Rundel 1977). Compared to the highly diverse Sonoran Desert annual plant communities, the Mojave Desert mainly supports species with specific adaptations to survive long periods of dry conditions (e.g., seed dormancy; Mulroy and Rundel 1977). Our metrics disentangled some of this variation in predictability, but the pattern was more complex than a north-south increase in predictability, as we also observed differences along a roughly west-east gradient (Fig. 4E).

Wavelets identified a secondary six-month peak in rainfall in our Sonoran Desert case study. In a recent study examining a desert annual plant community, Mathias and Chesson (2013) demonstrated that while a single seasonal pulse of rainfall assisted with the persistence of plants via the storage effect, a second pulse made this process evolutionarily stable. With very simple differences in their growth responses following rain pulses, persistence collapsed over evolutionary time when based on a single pulse of rainfall. However, with two seasonal rainfall pulses, the tendency toward ecological specialization increased (Mathias and Chesson 2013). This, in turn, led to stable coexistence with respect to evolutionary processes. While we do not specifically examine these mechanisms, we note that our framework can be applied to understand the abiotic constraints on, and mechanisms promoting, other key ecological mechanisms for the maintenance of biodiversity.

Migratory waterfowl

Seasonality plays a key role in promoting temporal diversity of birds in many areas. While birds generally follow the typical latitudinal gradient in species richness, a secondary peak is evident at around 45° N (e.g., Jetz et al. 2012), particularly for waterfowl (Dalby et al. 2014). This secondary peak appears to be driven by an exploitation of a seasonally available niche, reflecting seasonal variation in plant productivity (Dalby et al. 2014), demonstrated by the large proportion of migratory waterfowl species at these mid-latitudes (Fig. 2). Early studies made such predictions of high migratory percentages where seasonal differences in productivity are greatest (MacArthur 1959, Herrera 1978). It is therefore not surprising that stationary measures of climate can be poor predictors of species richness for waterfowl (Dalby et al. 2014) and other birds (Hurlbert and Haskell 2003, Hawkins 2004). For instance, Hurlbert and Haskell (2003) demonstrated that birds track seasonally shifting plant productivity regardless of season, and increasing amplitude of the seasonal variability may increase numbers of migrants. These two cases (migratory waterfowl and aridland annual plants) highlight that different mechanisms can be employed to exploit seasonal variation in environmental conditions and, in turn, promote temporal beta diversity.

Beyond seasonality

Temporal fluctuations occur at a variety of ecologically relevant time scales ranging from daily to decadal. These include diurnal temperature cycles, short return-time fire dynamics, multi-year climatic cycles such as the El Niño Southern Oscillation, and long-term glacial advances and retreats. One such example is the fire dynamics of chaparral plant communities. Chaparral systems in southern California can burn as frequently as every 2–10 years (Hanes 1971). They support numerous species dependent on fire, including some whose seeds can germinate only when chemically stimulated by smoke (Barro and Conard 1991, Bond and Keeley 2005). A few species of perennial shrubs dominate pre-fire communities, but numerous other species thrive in post-fire years, including a guild of specialized fire-annuals only found in the first post-fire year and a guild of fire-perennials that dominate two to four years after fire (Keeley et al. 1981). Because the pre-fire dominant shrubs also regenerate within a few years, plant species richness peaks one year after fire and then gradually decreases until the next fire (Barro and Conard 1991). Thus, short-return-time fires should increase the temporal diversity of plants in California chaparral communities. This kind of system is clearly appropriate for wavelet analysis, and previous studies have examined fire return interval in this context (e.g., Brown et al. 2005). What remains a potentially novel area of research, however, is the role of seasonality in conjunction with a fire regime of a given

predictability. For example, do highly seasonal environments, such as the California chaparral ecosystem, support greater diversity than habitats with similar fire predictability but less seasonality? This is a testable hypothesis that arises directly from the predictability–seasonality framework described above.

What these examples highlight is the importance of synchrony between environmental fluctuations and the life histories of organisms or the ecological phenomenon of interest. Of course, lifespan complications can be overcome when migration becomes a primary determinant of seasonal variability in diversity, as we have touched on for waterfowl biogeography. Despite our focus on seasonal dynamics, these examples highlight that our framework can extend beyond seasonality and apply to an array of time scales, phenomena, ecological dynamics and organisms. Wavelets are a flexible tool for this task, suited to identifying dominant frequencies, whether sub- or super-annual, the predictability of these frequencies, and non-stationary trends over time.

Extending across latitudinal gradients

While we focus on precipitation specifically for our case study, one could argue that temperature becomes the more important seasonality mechanism as one moves away from the tropics (Addo-Bediako et al. 2000, Smol et al. 2005). However, our framework can be applied to any fluctuating environmental factor. Likewise, there are many other contingencies that could interrupt the observed patterns as more cases are considered over wider geographic extents. Among others, these may include island size and distance from mainland (theory of island biogeography; MacArthur and Wilson 1967); latitude (energy, climatic stability, historical factors such as glaciation history); anthropogenic influences such as land use change; and neutral processes (Hubbell 2001). All of these factors influence regional diversity and thus limit temporal diversity patterns at local scales. Furthermore, the relative response of communities to seasonal abiotic fluctuations will depend on the level of compensatory dynamics occurring. If populations within a community are not synchronized, being stabilized by compensatory dynamics, community oscillations may be dampened in response to abiotic fluctuations (Micheli et al. 1999, Downing et al. 2008). Below we highlight two key contingencies applicable to this framework.

As we have framed it, our approach is more relevant to mid-latitude zones, hence the geographic focus of our case study. Because they have fewer available temporal niches, high-latitude sites may not show high temporal beta diversity despite strong seasonality and predictability. In other words, one-half of the seasonal cycle is usually unsuitable for the reproductive phase of taxa that might otherwise take advantage of it (e.g., plants; Qian and Ricklefs 2007). Indeed, low temporal turnover rates were observed in algae and invertebrate communities of Arctic lakes that remained cold over the last century,

while lakes that exhibited warming trends had higher turnover rates (Smol et al. 2005). Alternatively, Jocque et al. (2010) argue that a dispersal–specialization trade-off may be at the heart of the latitudinal diversity gradient. Given the harsher conditions at high latitudes, selection favors species with strong dispersal abilities compared to highly specialized and narrow niches. This together with past events such as glaciations has resulted in a lower regional diversity in these zones (Gaston 2000), which limits the potential response of species to seasonality. Under this scenario, the seasonality–predictability framework would tend to underestimate overall diversity as well as seasonal turnover.

Utility and application

Anthropogenic stressors are altering the natural periodicity of abiotic and biotic events. Dams are a prime example of anthropogenic stressors that severely alter seasonality of flow in river systems. Jardine et al. (2015) demonstrated the fundamental role that flow rhythmicity has on governing riverine diversity. They showed that more rhythmic rivers support more diverse fish assemblages, more stable bird populations and greater riparian forest production. Dams can alter the timing of natural flow events through holding back water for storage during high flows and releasing at a steady rate throughout the year, removing seasonality completely. At finer scales, hydropeaking produces much finer-scale unnaturally variable fluctuations on the daily scale, which can have major negative effects on riverine biota (Kennedy et al. 2016). While older dams are increasingly being decommissioned in the developed world, the scale of new dam projects worldwide is immense, both in developed and developing countries (Zarfl et al. 2014). The development of environmental flow regimes, which is also expanding rapidly (Tonkin et al. 2014), is ameliorating the effects of dam development and operation in places. However, it is extremely difficult and costly to replicate the full gamut of seasonal conditions needed to satisfy the complex life histories of all riverine species.

A striking example of a disruption to natural periodicity is human modification of natural light cycles (Gaston et al. 2014). Organisms and ecosystems are fundamentally organized by daily and seasonal light–dark cycles. Day length, for example, is a key indicator of seasonal changes and therefore phenological events such as reproduction and migration. Because selection favors life history strategies in synchrony with the environment (Cohen 1966, Rowe et al. 1994, Lytle 2001), altered light–dark cycles are disrupting these seasonal phenologies in a vast array of terrestrial and aquatic organisms (Gaston et al. 2014).

Climate change is affecting the timing, predictability and magnitude of seasonal events (Gaston et al. 2009, Both et al. 2010). Given the narrow temporal niche of many species, climate change is poised to have a major impact on diversity, regardless of the system of

consideration. It is inevitable that seasonal periodicities will be altered in future climatic conditions, but responses of biodiversity to these alterations may not track climate change directly (Gaston et al. 2009). These mismatches may reflect complex underlying associations, such as those between the timing of food requirements and food availability for avian long-distance migrants (Both et al. 2010). Increasing seasonality may in fact be problematic in some instances through resource bottlenecks associated with increased dry season severity (Williams and Middleton 2008). Evidence from marine (Wernberg et al. 2013) and freshwater (Bogan and Lytle 2011) systems shows that climate change can push communities in novel trajectories that may not be recoverable to their previous state. In a particularly vivid example of alteration to a key seasonal phenomenon, Clark et al. (2013) demonstrated how climate-induced tipping points are problematic in polar ecosystems through an interaction between sunlight seasonality and the timing of ice loss. They showed that nonlinear changes in annual light levels, through earlier break-up of sea ice, can induce tipping points in shallow seabed zones, leading to a transition from heterotrophic to autotrophic states. Understanding linkages between seasonality, predictability and diversity will help to anticipate the changes that novel climate regimes will have on present-day diversity.

Finally, the reliability of bioassessment in seasonal environments will be hampered without a clear understanding of temporal dynamics. It is critical to understand how many temporal sub-communities co-occur within a particular site as different seasons may indicate contrasting and potentially misleading ecological status (Linke et al. 1999). For example, sampling during a single season in some mediterranean streams could lead to a considerable underestimate of overall diversity, since many taxa would only be present at low numbers or in difficult-to-detect life stages, such as early instars and diapausing eggs, or at refuge locations (Bonada and Resh 2013). Understanding the seasonality and predictability of a particular ecosystem is therefore critical to adequately assessing its representative biodiversity. Managers should strive to sample representative seasons that capture the majority of within-year variability in communities and also incorporate reference conditions specific to each season (i.e., spatiotemporally distinct reference conditions).

CONCLUSIONS

We have demonstrated that understanding the influence of seasonal and non-seasonal environmental oscillations on diversity is not complete without a clear understanding of the predictability of these events. It is critical to understand these temporal dynamics to understand effects of global change. Much of the biotic processes in the natural world (i.e., life-cycle timing) are tied to these abiotic fluctuations. Given the impacts that anthropogenic influences are having and continue to

have on the natural seasonal cycle, it is imperative that we strive to understand the influence of seasonal cycles on the diversity of these systems.

Our framework and demonstrated case-study results have implications for both the basic science and management of ecosystems that span gradients of predictability and seasonality. First, the importance of understanding seasonality and predictability for examining local diversity and the associated importance of appropriate timing of sampling. Second, quantitative metrics from wavelet analysis and information theory are valuable tools for examining temporal periodicity in abiotic and biotic dynamics at different scales and may aid the detection of climate change trends that could eventually cause changes in community structure. Third, while predictable, highly seasonal environments may contain the greatest amount of overall diversity, some of these species may be at risk from even small changes to predictability or seasonality.

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