Received: 21 February 2024 | Revised: 1 July 2024 | Accepted: 8 July 2024

DOI: 10.1111/ele.14488

PERSPECTIVE

ECOLOGY LETTERS WILEY

Unfolding the dynamics of ecosystems undergoing alternating wet-dry transitional states

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Abstract

A significant fraction of Earth's ecosystems undergoes periodic wet-dry alternating transitional states. These globally distributed water-driven transitional ecosystems, such as intermittent rivers and coastal shorelines, have traditionally been studied as two distinct entities, whereas they constitute a single, interconnected meta-ecosystem. This has resulted in a poor conceptual and empirical understanding of water-driven transitional ecosystems. Here, we develop a conceptual framework that places the temporal availability of water as the core driver of biodiversity and functional patterns of transitional ecosystems at the global scale. Biological covers (e.g., aquatic biofilms and biocrusts) serve as an excellent model system thriving in both aquatic and terrestrial states, where their succession underscores the intricate interplay between these two states. The duration, frequency, and rate of change of wet-dry cycles impose distinct plausible scenarios where different types of biological covers can occur depending on their desiccation/hydration resistance traits. This implies that the distinct eco-evolutionary potential of biological covers, represented by their trait profiles, would support different functions while maintaining similar multifunctionality levels. By embracing multiple alternating transitional states as interconnected entities, our approach can help to better understand and manage global change impacts on biodiversity and multifunctionality in water-driven transitional ecosystems, while providing new avenues for interdisciplinary studies.

KEYWORDS
alternating transitional states, biocrust, biofilm, biological covers, multifunctionality, succession, water availability

INTRODUCTION

Most ecosystems are either permanently covered by water (e.g., aquatic ecosystems such as oceans and permanent rivers) or usually dry (e.g., terrestrial ecosystems such as drylands and forests). However, an important part of Earth's ecosystems goes through recurrent wet-dry transitions (e.g., non-perennial rivers and lakes, and coastal shores, among others; Figure 1), which can lead to rapid ecosystem reconfiguration challenging the biota inhabiting these systems (Carpenter & Brock, 2006; Keith et al., 2022; Zhang et al., 2023). The strong temporal variability in these highly dynamic transitional ecosystems (named

For affiliations refer to page 11.

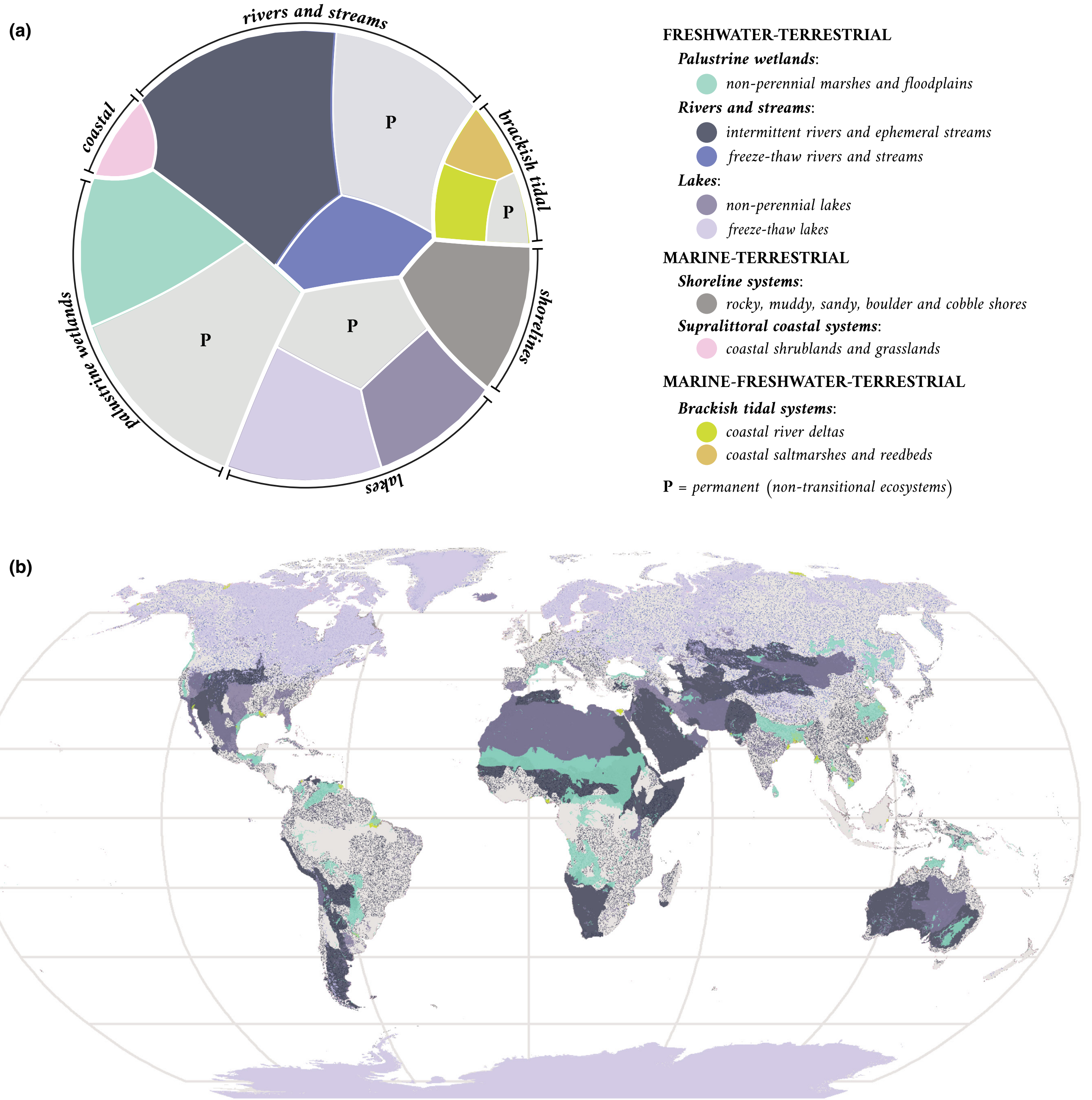


FIGURE 1 Natural water-driven transitional ecosystems occupy a significant proportion of the Earth's land surface and are globally distributed. (a) Fraction of land surface area occupied by the different water-driven transitional ecosystems, including six distinct biomes, further divided into nine ecosystem types (sensu Keith et al., 2020). The most widespread biomes are palustrine wetlands, rivers and streams, and lakes, which undergo transitions between freshwater and terrestrial states. The second most prevalent biomes consist of shorelines and supralittoral coastal systems, experiencing shifts between marine and terrestrial states. Lastly, brackish tidal systems, characterized by fluctuations among marine, freshwater, and terrestrial states, are the least widespread water-driven transitional ecosystems. (b) Water-driven transitional ecosystems exhibit a global distribution. They are present in small patches embedded in other ecosystem types or in large areas confined within specific regions. Adapted from Keith et al., 2020 and Keith et al., 2022. Note that artificial water-driven transitional ecosystems such as artificial shorelines, artificial wetlands, hydropeaking rivers, and rain puddles in urban ecosystems are not included, which can increase the overall surface of transitional ecosystems.

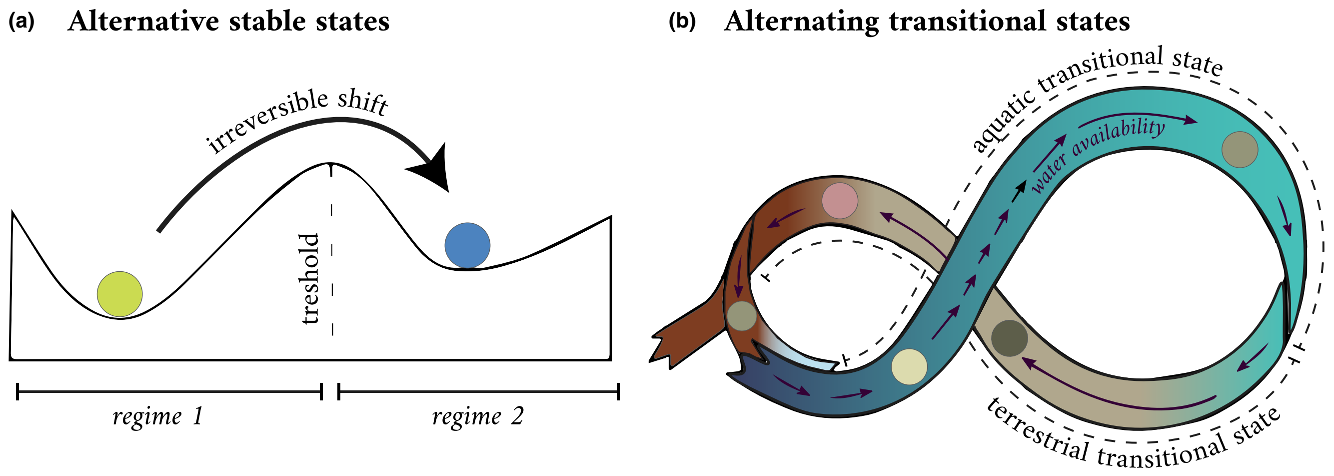
hereafter water-driven transitional ecosystems) has often led to approaches that consider the wet and dry phases of these ecosystems as two separate entities, whereas they represent interconnected facets of the same system. Thus, by embracing the inherent temporal dynamics of water-driven transitional ecosystems, we propose a conceptual framework that considers water availability as the main force driving biodiversity and ecosystem function across interconnected alternating transitional states at a global scale.

Strikingly, unlike ecosystems that undergo alternative stable states following disturbance (Beisner et al., 2003;

Lewontin, 1969), wet-dry or dry-wet transitions do not impose an irreversible shift on the ecosystem (Scheffer et al., 2001; Scheffer & Carpenter, 2003). In turn, these reversible shifts between alternating transitional states occur naturally and periodically (from minutes to years) in response to phases with contrasting water availability (Andersen et al., 2009; Fukami & Nakajima, 2011; Mushet et al., 2020; Figure 2). Consequently, water-driven transitional ecosystems fluctuate between alternating transitional states, which are non-stable and exhibit a tendency to revert back to the previous state after a certain period of time. The diverse nature of these transitional ecosystems is expressed through periodic shifts between marine and terrestrial states, freshwater and terrestrial states, or marine, freshwater, and terrestrial states (Keith et al., 2020; Figure 1). Anthropogenic activities may also alter their dynamics or generate new shifts in these ecosystems (e.g., artificial shorelines and wetlands, and rain puddles in urban ecosystems; Ellis et al., 2010; Keith et al., 2020). These wet-dry shifts determine alternating transitional states from aquatic to terrestrial and vice versa (Soininen et al., 2015; Messager et al., 2021; Figure 2) and create critical thresholds for biodiversity and functions which are not fully understood yet (Arias-Real et al., 2021; Zhang et al., 2023). We posit that water-driven shifts between alternating transitional states trigger the succession of biological communities and lead to cascading effects on ecosystem functions. In addition, we argue that these periodic changes represent interconnected phases within a single meta-ecosystem (Fanin et al., 2018; Scherer-Lorenzen et al., 2022).

Despite water-driven transitional ecosystems representing globally distributed biodiversity hotspots, we have largely ignored how water availability and timing govern species colonization and establishment, physiological activity, and survival across alternating transitional states. Thus, while some organisms may be active in both states, others may be uniquely active in one of them, or only survive as spores or seeds. Eco-physiological adaptations are therefore crucial to survive in aquatic and/or terrestrial states which alternate in terms of minutes, hours, days, or months, or which need to face the potential emergence of new habitats after resetting (e.g., massive floods or droughts).

Biological covers (Box 1) serve as a global model system for water-driven transitional ecosystems thriving in both aquatic and terrestrial states, where their succession underscores the intricate interplay between these wet-dry phases (Allen et al., 2012; Besemer, 2015; Reed et al., 2019; Weber et al., 2022). Species abundances within biological covers have a high dependence on fluctuating water availability regimes, making them useful systems for assessing biodiversity responses in water-driven transitional ecosystems (Figure 3). In addition, the species forming biological covers are small and have short lifespans, making them suitable for experimental studies. These characteristics allow them to serve as a tractable model system for testing specific hypotheses within the proposed framework. The insights gained from this model system can be transferred to other systems operating at larger spatial and temporal scales. Previous studies have been biased toward the aquatic state, leading to the notion that aquatic biofilms are the main communities able to inhabit water-driven transitional



(a) Alternative stable states

(b) Alternating transitional states

FIGURE 2 Transitional ecosystems periodically switch between different alternating transitional states in response to drivers such as water availability. (a) In non-transitional ecosystems, a disturbance exceeding a critical biotic or abiotic threshold triggers its reconfiguration in structure and function (Scheffer et al., 2001). Once this tipping point is reached, the ecosystem suffers an irreversible transition from one stable state to another that reconfigures the structure and function of the system (Scheffer & Carpenter, 2003). (b) In contrast, transitional ecosystems naturally and periodically alternate between different states, experiencing reversible ecosystem shifts (Fukami & Nakajima, 2011). In these ecosystems, states are non-stable and bounce back to the previous state after some time. Note that the length of aquatic and terrestrial states in the figure represents just one of the potential trajectories of wet-dry cycles. However, the length of the different transitional states may vary according to the duration, frequency, intensity, and rate of change of wet-dry cycles. Circles represent different biological communities.

BOX 1 Biological covers as a unifying term in water-driven transitional ecosystems

Biological covers are complex communities formed by algae, fungi, bacteria, cyanobacteria, protozoa, archaea, bryophytes, and/or lichens, which develop on the top layer of the substrates establishing a tight association with the surrounding inorganic and/or organic materials to form a cohesive structure. While a diverse array of organisms contributes to the composition and species diversity of the different types of biological covers, their unity stems from their cohesive physical structure. This arises as an emergent property from the intricate interplay between the organisms, the abiotic components of their immediate environment, and the dynamic interface between the two. The integration between organisms and the substrate is maintained due to the ability of the biological covers to bind substrate particles together through the production of extracellular polymeric substances. These substances create a matrix that embeds organisms and provides mechanical stability, binding soil particles and organic matter into cohesive layers (Chamizo et al., 2020; Flemming & Wingender, 2010). Additionally, the physical structure of the substrate itself – whether sediments, soils, leaf and wood litter, or rocks – provides a support for the organisms to grow upon and form structured glued aggregates.

By explicitly considering water-driven transitional ecosystems as integrated entities with different states governed by water availability, we contend that "biological covers" can serve as a unifying term for communities that share a common pool of taxa, albeit in varying proportions determined by water availability, and arranged into a coherent three-dimensional structure. This term spans a broad spectrum of biological structures, ranging from those closely associated with ecosystems having high water availability, such as aquatic biofilms, to those typically linked to ecosystems experiencing water scarcity, such as biocrust. It also includes cryptogamic covers that have a looser connection to the substrate and are prevalent outside drylands. The conventional approach of studying biofilms and biocrusts as separate entities, regardless of their common features (Battin et al., 2016; Besemer, 2015; Weber et al., 2022), may constrain our understanding of how the hydric fluctuations that characterize water-driven transitional ecosystems may shape biodiversity. In such cases, categorizing aquatic biofilms and biocrusts as distinct entities may underrepresent the eco-evolutionary potential of organisms to adapt to hydration and dehydration cycles. This includes lichens and bryophytes adapted to prolonged immersion, as well as cyanobacteria, algae, bacteria, and fungi capable to withstand desiccation, among others.

ecosystems (Box 1). However, during the terrestrial state, dry conditions may promote biocrusts rather than biofilms, opening a new avenue to address how water availability reconfigures the global distribution of biodiversity (Box 1). Therefore, the intrinsic dynamic of water-driven transitional ecosystems raises a fundamental question: Are aquatic biofilms and biocrusts in transitional ecosystems ecologically distinct communities or are they two expressions of the same community, solely differentiated by water availability? Considering similarities and shared features across aquatic biofilms and biocrusts, we argue that both could be seen as two expressions of equivalent communities, which vary notably in response to water availability (Box 1). First, biofilms and biocrusts share a pool of interacting taxa, with many species capable of transitioning from aquatic to terrestrial states and vice versa. Second, the consortia of organisms are in close contact within the same architectural structure, which is consistently supported by extracellular polymeric substances and/or the organic and inorganic substrates they inhabit. We then propose that fluctuating water availability in water-driven transitional

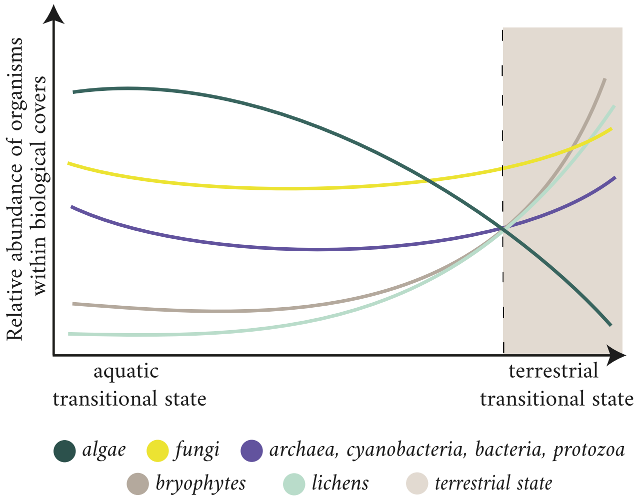


FIGURE 3 Wet-dry cycles shape the pattern of changes in the relative abundance of different organisms within biological covers over time in water-driven transitional ecosystems. Higher levels of water availability during the aquatic transitional state may favour biological covers with a higher presence of protozoa, cyanobacteria, bacteria, and algae that will be progressively colonized by lichens and bryophytes in the terrestrial transitional state (in light grey).

ecosystems may shape species abundance and composition within biological covers over time while preserving multiple ecosystem functions (Box 1). Global change is altering the distribution, extent, and timing of transitions in these ecosystems, thus providing a unique opportunity to understand how biodiversity may adapt to changing conditions and affect multiple ecosystem functions (multifunctionality).

We here propose an integrative conceptual framework to enhance our understanding of how water availability drives the dynamics of biodiversity and multifunctionality in transitional ecosystems and to boost new investigations in these fascinating ecosystems (Figure 4). This framework could improve our ability to identify the mechanisms driving these changes, and then predict the maintenance (or not)

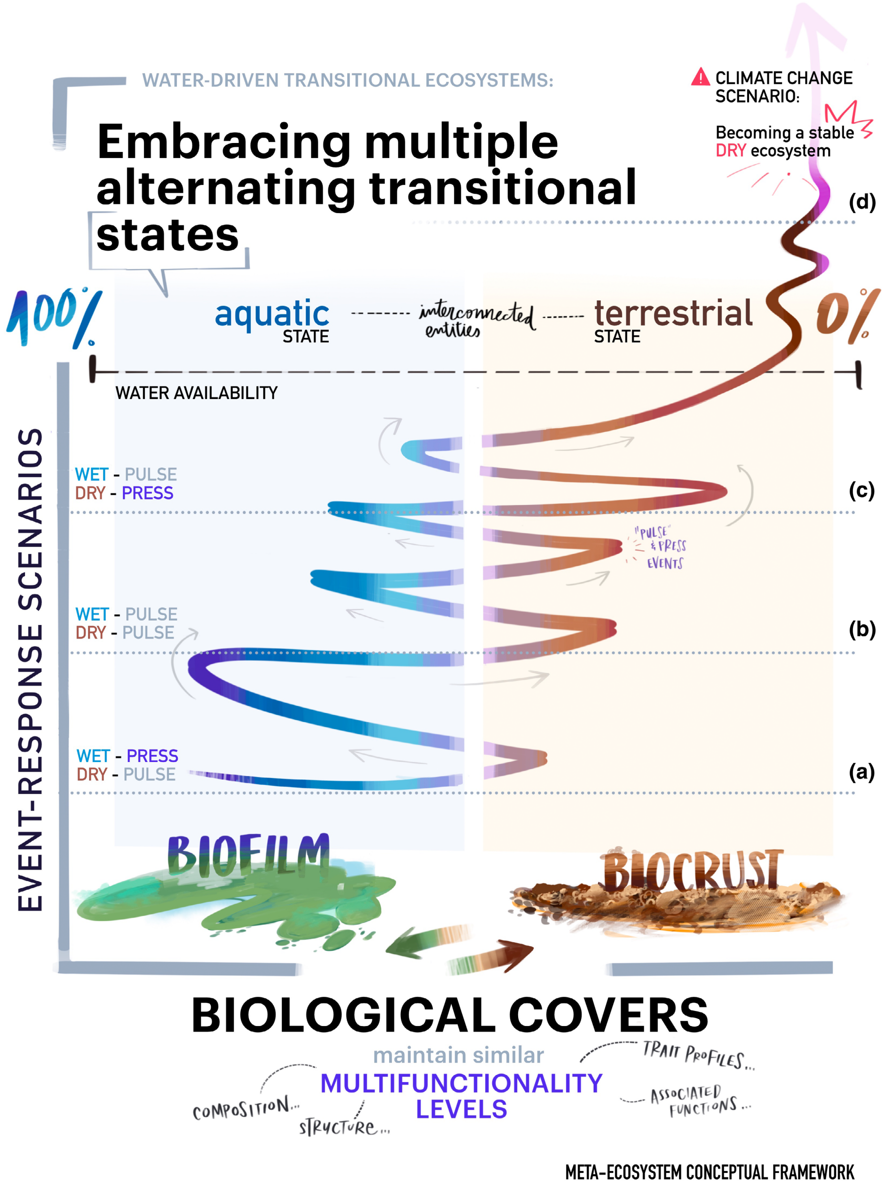


FIGURE 4 Conceptual diagram summarizing biodiversity and functioning in water-driven transitional ecosystems. Our framework embraces periodic transitions between aquatic and terrestrial transitional states within a single, interconnected meta-ecosystem. This goes beyond the current consideration of alternating transitional states as independent and disconnected entities, placing the temporal water availability as the core driver of biodiversity and functional patterns in water-driven transitional ecosystems. Under this integrative framework, biological covers (e.g., biofilms and biocrusts) comprise a common fraction of biodiversity for both transitional phases that undergo a successional dynamic in response to wet-dry transitions, determining biodiversity changes but maintaining ecosystem functioning. The succession of biological covers responds differently based on the duration, intensity, frequency, and rate of change of wet-dry events imposing three potential event-response scenarios: (a) Wet press-dry pulse, (b) wet pulse-dry pulse, and (c) wet pulse-dry press. Global change can alter the dynamics of wet-dry cycles causing strong changes in biological covers composition, structure, trait profiles, and associated functions. These impacts, especially considering the risk to become a stable dry ecosystem (d), pose threats to the contribution of water-driven transitional ecosystems to global biogeochemical cycles, climatic stability, and human welfare.

of ecological functions across alternating transitional states. Our framework integrates periodic transitions between aquatic and terrestrial transitional states within a single, interconnected meta-ecosystem. This goes beyond the current consideration of alternating transitional states as independent and disconnected entities. Under this integrative framework and considering that water availability triggers rapid and cyclic shifts between alternating transitional states, we expect that:

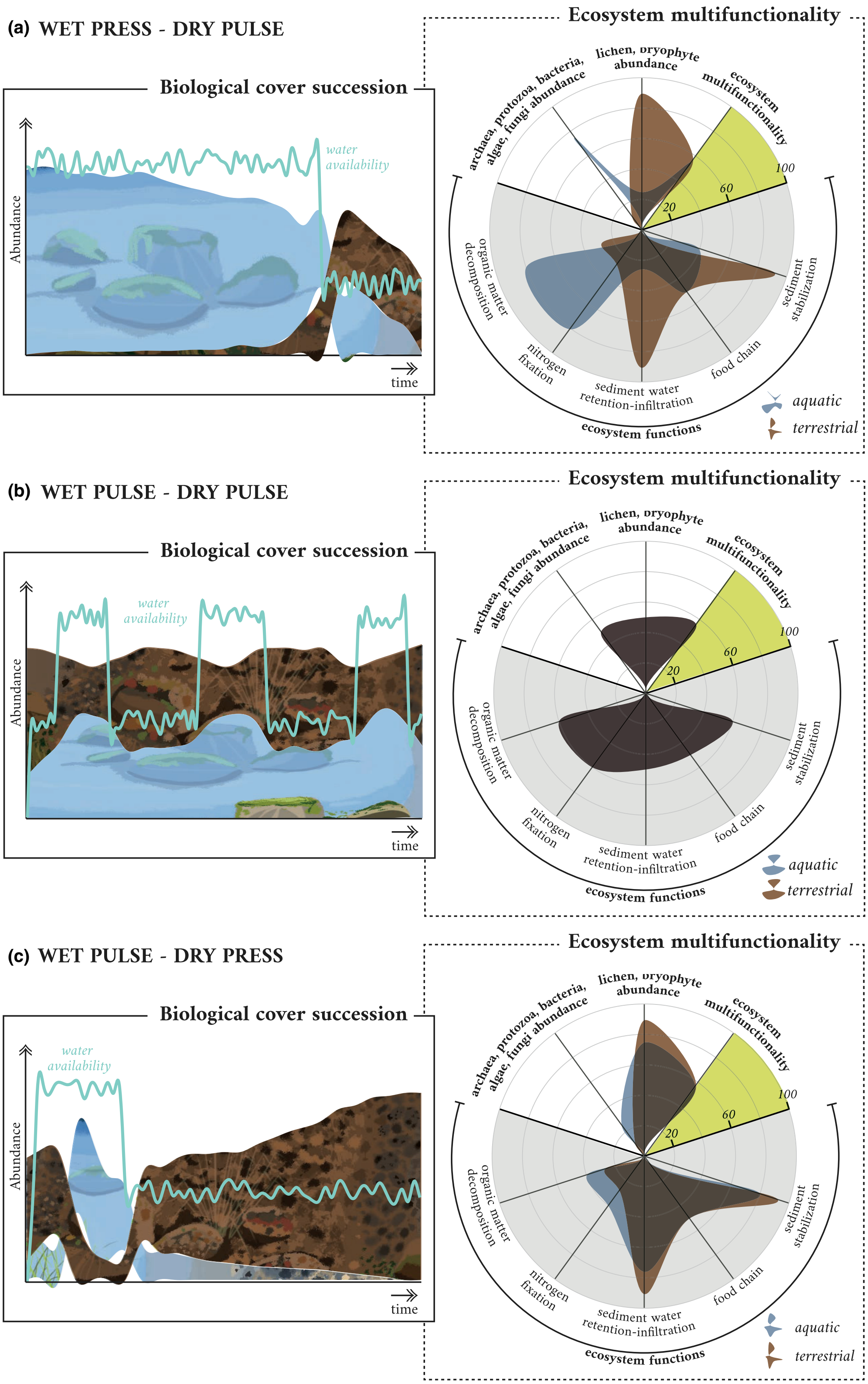
1. Biological covers may serve as a tractable global model system to unveil the response of biodiversity to fluctuating water regimes since, among others, they comprise a common fraction of biodiversity for both transitional phases, whether in active or dormant states. These communities undergo successional dynamics in response to wet-dry transitions, determining biodiversity changes but maintaining essential ecosystem functions. The functional turnover resulting from the replacement of taxa and their associated effect traits during succession may sustain multifunctionality through the functional complementarity and/or redundancy of taxa occurring at different states. Moreover, the succession of biological covers may respond differently based on the duration, intensity, frequency, and rate of change of wet-dry events.
2. Changes in wet-dry cycles linked to global change may alter the prevalence and global distribution of water-driven transitional ecosystems (e.g., drying lakes and rivers in response to droughts, new permanent freshwater habitats following massive floods). This poses the risk that specific transitional ecosystems could lose the alternation between wet and dry states, leading to stable dry or wet states.

Overall, we argue that embracing the whole wet-dry cycle is essential to understand, manage and protect the biodiversity and functioning of water-driven transitional ecosystems on a global scale. This knowledge is today more important than ever as the number of ecosystems facing wet-dry or dry-wet transitions is increasing globally in response to climate change (Messager et al., 2021).

CONCEPTUAL EVENT-RESPONSE SCENARIOS TO STUDY WATER-DRIVEN TRANSITIONAL ECOSYSTEMS AS A WHOLE

The inherent temporal dynamics of water-driven transitional ecosystems respond to different wet-dry events, which can be categorized as pulse and press events (Jentsch & White, 2019; Ryo et al., 2019). The duration of water availability or scarcity determines the distinction between "pulse" and "press" events. "Pulse" events are characterized by a peak of water availability or scarcity, while "press" events are sustained over time (Jentsch & White, 2019). Both types of wet-dry events may affect the response of biological communities, which in turn shapes the succession of biological covers and their contribution to ecosystem functioning (Figures 3 and 5). Specifically, the lifespan of species within the community (or at least the fraction of the community of interest) could potentially unveil the ecologically relevant temporal scale required for defining pulse and press events. For instance, if an event falls within the lifespan of the species, it could be defined as a pulse event; however, if it exceeds their lifespan, it could be considered a press event. Thus, pulse events would ensure evolutionary pressure to maintain traits capable of existing in both aquatic and terrestrial phases. Conversely, if only press events occur, there would be evolutionary pressure leading to the maintenance of traits specific to only one phase. Besides, the emerging event-response relationships based on the duration, frequency, and rate of change of pulse and press events, result in alternative outcomes setting the arena for biological covers to express their eco-evolutionary potential. Here, we define three potential event-response scenarios to capture the wet-dry fluctuations, including events of varying duration and intensity. These scenarios represent the most likely combinations of pulse and press events characteristic of water-driven transitional ecosystems where biological covers can thrive. The response of biological covers under these scenarios considers the complete range of environmental conditions where the species conforming distinct biological covers could potentially thrive in the absence of biotic interactions (i.e., their fundamental niche; Hutchinson, 1957). Thus, to address the

FIGURE 5 Three distinct event-response scenarios arise from the intrinsic temporal dynamic of water-driven transitional ecosystems. For each scenario, varying pulse and press events (light blue line) modulate the composition of biological covers considering the physiological thresholds of the organisms involved. The composition of biological covers in different successional stages may maintain multifunctionality through a diverse set of ecosystem functions in aquatic and terrestrial alternating transitional states. Each panel depicts the relative contribution of each biological cover to ecosystem multifunctionality across three event-response scenarios: Wet press-dry pulse (a), wet pulse-dry pulse (b), and wet pulse-dry press (c). These relative contributions are calculated considering the main, minor, and shared functions performed by each type of organisms within each biological cover (i.e., assigned values of 1, 0.2, and 0.5, respectively). By taking into account the abundance of each organism within a given transitional state, an abundance-weighted relative contribution is calculated for each function (light grey). Ultimately, ecosystem multifunctionality (yellow) is quantified as the sum of all relative contributions, benchmarked against the maximum potential multifunctionality scenario where all ecosystem functions are maximized (Manning et al., 2018).



response of biological covers under fluctuating regimes of water availability we rely on the species' physiological capabilities and requirements for resources, without considering the influence of other factors. Overall, these potential scenarios exemplify the wet-dry dynamics within which lies the realm of alternating transitional states for biological covers across biomes from daily to annual cycles.

A Long and sustained aquatic transitional state followed by a short terrestrial state (i.e., *wet press-dry pulse*; Figure 5a). This is common in palustrine wetlands (e.g., non-perennial marshes and floodplains) and may favour the prevalence of biological covers dominated by protozoa, cyanobacteria, bacteria, and algae. The physical forces exerted by water flow create optimal environmental conditions for their establishment, growth, and dispersal by coupling water availability with physiological activity pulses (Besemer et al., 2007). Under these conditions, certain lichen-dominated biological covers may be favoured over rocks (Coste et al., 2016). For example, lichens of the genus *Verrucaria* are adapted to prolonged immersion from 8 to 10 months throughout the year (Hawksworth, 2000) and are able to resist these conditions. Following the sustained aquatic transitional state, the subsequent dry pulse may facilitate the colonization and establishment of terrestrial drying-tolerant lichens and bryophytes (Baldauf et al., 2021). Dry pulses can reduce the abundance of water-adapted biological covers, with potential negative impacts on their biodiversity and associated functions. However, this decline follows a steady pattern, related to their ability to withstand and recover from drying, the occurrence of flash storms, and the potential use of microhabitat wet refugia (Lan et al., 2021; Selwood & Zimmer, 2020).

B Repeated alternating cycles of wet and dry pulses (i.e., *wet pulse-dry pulse*, Figure 5b). This is common on the shorelines, where it exists the potential to host a wide range of biological covers. Sediments may maintain a certain level of humidity during dry pulses, which aligns with the hydration-dehydration cycles required for the physiological activation of lichens and bryophytes (Cernava et al., 2019). The maintenance of a certain level of humidity also enables biological covers dominated by archaea, protozoa, cyanobacteria, bacteria, algae, and fungi to resist and reactivate rapidly when the wet pulse returns (Jansson & Hofmockel, 2020; Malard & Guisan, 2023). Furthermore, extracellular polymeric substances may play a key role to cope with hydration-dehydration cycles in shoreline mats.

C Short aquatic transitional state followed by a prolonged terrestrial one (i.e., *wet pulse-dry press*, Figure 5c). This is commonly found in ephemeral streams and may favour the prevalence of biological covers dominated by lichens and bryophytes. Organisms better adapted to aquatic conditions may initially survive the dry event due to their desiccation-resistance traits (Arias-Real et al., 2023). Prolonged drying may modify the bacterial communities, favouring more drying-tolerant species and increasing the abundance of gram-positive bacteria (commonly found in soils), while decreasing gram-negative bacteria (Gionchetta et al., 2020, 2024). Even some organisms which are adapted to long-term dehydration may help further colonizers; this is the case for the aquatic cyanobacterium *Tychonema* which provides a hospitable fresh sediment for secondary colonizers (Elliott et al., 2019). Generally, though, prolonged drying can exceed the physiological thresholds of most aquatic and drying-tolerant organisms, which ultimately results in the replacement of communities. Additionally, when the wet pulse reaches a high magnitude (e.g., extreme flood event), the sediment undergoes an abrupt reconfiguration that can influence the communities of the following dry state (Death et al., 2015; Wohl, 2021). As such, during the subsequent dry press, this newly formed soil may represent a system reset where community assembly will be governed by the colonization of lichens and bryophytes from adjacent areas (Weber et al., 2016).

LIFE IN WATER-DRIVEN TRANSITIONAL ECOSYSTEMS: HOW ALTERNATING TRANSITIONAL STATES COULD SHAPE BIODIVERSITY AND MULTIFUNCTIONALITY. BIOLOGICAL COVERS AS A MODEL SYSTEM

Water-driven transitional ecosystems are biodiversity hotspots and vital hubs of ecological activity and biogeochemical cycles, serving as evolutionary and ecological refuges (Allen et al., 2012; Araújo, 2002). Biological covers, also known as biocrusts in terrestrial ecosystems and biofilms in aquatic environments, are one of the most ubiquitous communities rapidly adapting to changing and harsh abiotic conditions (Eldridge et al., 2023). They are fundamental for supporting substrate stability and water regulation, global biogeochemical cycles, plant growth, and microbiome regulation, among others (Battin et al., 2016; Eldridge et al., 2023).

The organisms making up the biological covers show adaptations (i.e., response traits) that enable them to withstand recurring and predictable disturbances (de los Ríos et al., 2003; Concostrina-Zubiri et al., 2022; Malik & Bouskill, 2022). Different bundles of desiccation/hydration-resistance traits provide them with a unique ability to overcome wet-dry transitions (Allison, 2023; Jansson & Hofmockel, 2020; Román et al., 2021). This biota also possesses a range of effect traits that provide contrasting relative contributions to ecosystem functions (Battin, 2003; Besemer, 2015; Battin et al., 2016; Rodríguez-Caballero et al., 2018; Figure 5). For example, in a scenario marked by a prolonged aquatic state followed by a brief terrestrial state, ecosystem multifunctionality will be sustained through a greater contribution of organic matter decomposition and nitrogen fixation during the aquatic phase, while sediment water retention, infiltration, and stabilization will be enhanced during the terrestrial phase (Figure 5a). The replacement of taxa and their associated effect traits during succession may result in a functional turnover (Figures 3 and 5). The high functional complementarity between replaced and emerging/establishing communities makes possible the maintenance of ecosystem multifunctionality throughout transitional states (Barry et al., 2019). Furthermore, multifunctionality is supported by the functional redundancy of taxa occurring in the different states (Concostrina-Zubiri et al., 2021; Delgado-Baquerizo et al., 2016; Maestre et al., 2013). Considering alternating transitional states as interconnected entities, biological covers exemplify that water-driven transitional ecosystems can potentially maintain a relatively stable level of multifunctionality within and across different event-response scenarios by favouring specific ecosystem functions in each successional stage.

While the multifunctionality of the system may remain stable in aquatic and terrestrial alternating states (Figure 5), the drastic shifts in physicochemical conditions may determine metabolic changes of the biological cover, affecting carbon cycles (Granados et al., 2020; Timoner et al., 2012). Water-driven transitional ecosystems may act as net carbon emitters as they do not have mechanisms to retain carbon (e.g., humic substances in soils and wood) by their transitional nature (Gómez-Gener et al., 2020; Keller et al., 2020; Raymond et al., 2013). However, the net balance of greenhouse gases in these ecosystems would depend on factors such as the duration of each transitional state, the organic matter availability in the system and the velocity at which successional and physiological responses track abiotic changes (Keller et al., 2020; Ma et al., 2023). Depending on the dominant biological activity (photosynthesis vs. respiration), biological covers may potentially impact the global estimations of greenhouse gas emissions and dynamics. Specifically, transitions to dry conditions and rewetting can exacerbate greenhouse gas emissions through a disruption of natural wet-dry dynamics, generating new hotspots of greenhouse gas emissions (Pilla et al., 2022; Weber et al., 2015). Therefore, a better understanding of the conditions and mechanisms through which water-driven transitional ecosystems boost greenhouse gas emissions in response to global change is needed to safeguard biogeochemical and climatic stability (Van Stan et al., 2023).

WATER-DRIVEN TRANSITIONAL ECOSYSTEMS UNDER GLOBAL CHANGE

In a world where the duration and intensity of wet-dry cycles are expected to change rapidly, water-driven transitional ecosystems will face significant threats (Maestre et al., 2013; Reed et al., 2012; Rodriguez-Caballero et al., 2018). Water availability is globally shifting due to changing rainfall, rising temperature, extreme weather events, water withdrawal, flow regulation (e.g., dams), and land use changes (Sabater et al., 2023; Scherer-Lorenzen et al., 2022).

Since the biodiversity and multifunctionality of water-driven transitional ecosystems depend on the duration, frequency, intensity, and rate of change of wet-dry events, global change can alter the normal sequence between alternating transitional states and their timing (Arias-Real et al., 2021; Ryo et al., 2019). In areas that have become more humid due to increased ice melting, snowmelt, precipitation, floods and peak flows, water-driven transitional ecosystems will experience longer aquatic periods, therefore negatively impacting bryophytes and lichens (e.g., *wet pulse*-*dry press* ➔ *wet pulse*-*dry pulse* ➔ *wet press*-*dry pulse*; Figure 5). However, under the drying trend affecting several world's regions, the consequences of prolonged drying may lead to a higher prevalence of water-driven transitional ecosystems experiencing short aquatic transitional states followed by a prolonged terrestrial one (e.g., *wet press*-*dry pulse* ➔ *wet pulse*-*dry pulse* ➔ *wet pulse*-*dry press*; Figure 6). In extreme cases, a long-term sustained terrestrial transitional state (i.e., *dry press*) may trigger a reconfiguration in the structure and function of water-driven transitional ecosystems, resulting in an irreversible transition to a dry stable state (Figure 6). In this dry, stable state, biocrusts will dominate due to their adaptations to cope with water deficits (e.g., dormancy and mitigation of oxidative stress through amphiphilic molecules; Green et al., 2011). In addition, individuals can aggregate and develop a layered structure from recurring biocrust burial by fresh sediments and later recolonization on top (Weber et al., 2022). Exceptionally, in the most severe cases of extreme wet events (e.g., floods), massive sediment and rock transport may drive the ecosystem rejuvenation in terms of nutrient and energy fluxes (Barnes et al., 2018). This may enable the formation of young soils (e.g., fluvisols), thereby reinitiating the biological cover succession, given the new free-up space for colonization (Peltzer et al. 2010). Conversely, less intense wet events can be beneficial to maintain established biocrust communities, as increased moisture will support their biological activity pulses.

NOVELTIES AND FUTURE DIRECTIONS

Our proposed integrative conceptual framework helps to enhance our understanding of water-driven transitional ecosystems, offering four main benefits. First, our proposed wet-dry scenarios may aid to gain a deeper understanding of the community assembly rules across contrasting water availability dynamics, which can also help to anticipate global change impacts

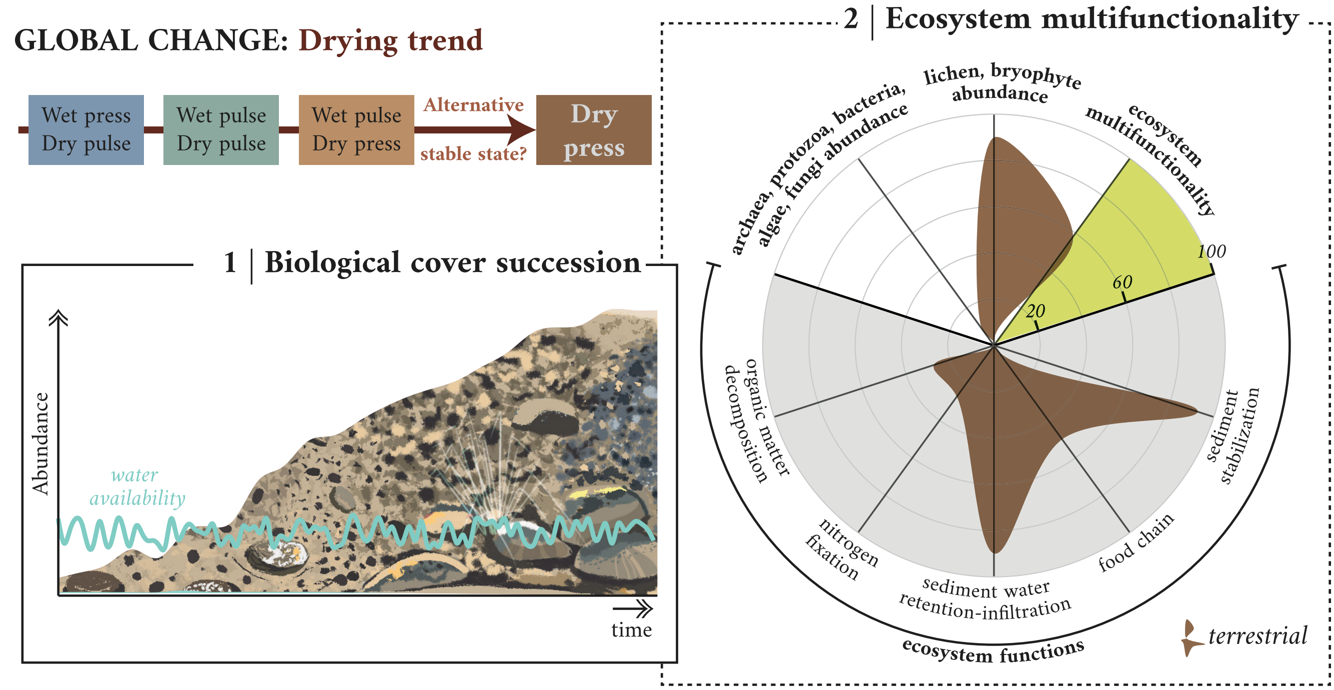


FIGURE 6 Biological cover abundance and multifunctionality in water-driven transitional ecosystems under global change. In response to the drying trend affecting several world's regions, water-driven transitional ecosystems could suffer a reconfiguration in their structure and functioning, resulting in a dry stable state.

on biodiversity. For example, by identifying functional trait combinations that are favoured by each wet-dry scenario, we can better assess the sensitivity of biological cover organisms to alterations in water availability dynamics. Second, by considering the broad spectrum of biological covers occurring in varying wet-dry scenarios, our framework may contribute to a more accurate quantification of the biogeochemical consequences of altering water availability dynamics. For example, determining how carbon and nutrient dynamics are influenced by contrasting wet-dry scenarios can help to improve the estimations of global biogeochemical cycles. Third, this framework could improve our ability to identify the mechanisms and predict the maintenance of multiple functions across alternating transitional states in these ecosystems. For example, by considering the biological covers occurring in both dry and wet states, we can better understand which biodiversity effects drive ecosystem functioning levels and trade-offs under different water availability dynamics. Ultimately, we can uncover the emergent properties dictating the transition between community stages, including the rate of functional recovery and the extent of influence of one stage's composition on the next. This provides a novel perspective on transitional ecosystems, enabling the identification of emergent properties that remain elusive when dry and wet states are examined in isolation.

Using the proposed framework, several factors still need explicit consideration. To effectively assess how biological covers respond to fluctuating wet-dry cycles in water-driven transitional ecosystems, it might be necessary to account for the biotic interactions, dispersal capacities, and the time required for a species to express its eco-evolutionary potential, so it may adapt to a rapid ecosystem reconfiguration. The physical template should also be accurately characterized. The dynamics of water availability should be determined by considering factors such as precipitation properties, topography and substrate characteristics, since these affect infiltration, surface and subsurface runoff, run-on, percolation, and evaporation (Dahlin et al., 2021). Furthermore, the biological and physical legacies from previous alternating states should be considered, since might affect the spatial and temporal turnover of organisms. That is, the composition of biological covers in one alternating state can be influenced by the performance of the biological cover in the previous state, as well as by changes in the substrate they inhabit.

We contend that the theoretical event-response scenarios proposed here remain plausible considering the fundamental niche of the species conforming distinct biological covers. However, the actual range of environmental conditions, as well as the constraints imposed by interspecific interactions, should be reconsidered when implementing this framework in specific study cases. A significant step toward a more predictive framework for water-driven transitional ecosystems, concerning biodiversity and functioning, would involve filling the current data gap related to the spatial and temporal dynamics of these ecosystems as a whole. This includes understanding the dynamics of the biological covers they host and their contribution to the ecosystem functioning during both wet and dry phases. To this end, it becomes necessary combining long-term observational monitoring with experimental studies, which consider the intra-annual water availability across spatial scales. Moreover, experimental studies should delve into the functional response of distinct biological covers under different water availability scenarios. This may be useful to comprehend which taxa can survive under different water regimes and which ones remain active. Promising tools to unveil these responses are state-of-the-art metagenomics and metatranscriptomics approaches.

Overall, our proposed framework can help us better study two important research questions about water-driven transitional ecosystems. This framework overcomes the limitations of the traditional view, which treats transitional states as separate entities.

1. How global change in wet-dry cycles alter global fluxes of energy and matter? Wet-dry transitions influence abiotic conditions and biodiversity, thereby impacting biogeochemical cycles and greenhouse gas emissions. Understanding the range of wet-dry conditions that maintain ecosystem functioning within safe boundaries is key to promote sustainability. Scaling up these results can help to anticipate consequences for biogeochemical cycles by understanding which functions can be favoured following alterations of wet-dry conditions (e.g., aridification can favour respiration over production, despite multifunctionality is maintained);
2. What is the role of meta-community and eco-evolutionary dynamics in transitional ecosystems? Evaluating the interplay between habitat filtering, biotic interactions and organism dispersal is key to predict biodiversity changes over transitional states. Biological cover response will depend not only on wet-dry transitions but also on potential competition/facilitation mechanisms that mediate the spatial organization and interaction of co-occurring organisms. This succession will also depend on the ability of organisms to colonize and establish in new areas due to their dispersal abilities and the speed of their morpho-physiological adaptation to cope with rapid environmental change.

CONCLUDING REMARKS

We here propose a conceptual framework that places the temporal water availability as the core driver of biodiversity and functional patterns of transitional ecosystems at the global scale (Figure 4). The duration, frequency, intensity, and rate of change of wet-dry cycles impose distinct plausible scenarios where the organisms of the different types of biological covers can withstand and eventually overcome non-favourable hydric conditions through their desiccation/hydration-resistance traits. This implies that the eco-evolutionary potential of the different biological covers, represented by their trait profiles, would support different functions over wet-dry transitions while maintaining similar multifunctionality levels (Barry et al., 2019; Cadotte et al., 2013; Manning et al., 2018; van der Plas, 2019). We also expose that global change can alter the dynamics of dry-wet cycles causing substantial changes in biological covers composition, structure, trait profiles, and associated functions. These impacts, especially considering the risk to become a stable dry ecosystem, may pose threats to the contribution of water-driven transitional ecosystems to global biogeochemical cycles, climatic stability, and human welfare, calling for a more intense investigation of these ecosystems. Overall, we provide a framework dealing with the uncertainty of life under wet-dry transitions and their effects on ecosystem multifunctionality. It is our hope that embracing wet-dry transitions will foster a new field of novel interdisciplinary research considering alternating transitional states as interconnected entities.

AUTHOR CONTRIBUTIONS

Rebeca Arias-Real and Pilar Hurtado formed the original concept and wrote the first draft of the manuscript. All authors further developed ideas, added sections, and extensively revised the paper.

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ACKNOWLEDGEMENTS

We gratefully acknowledge Greta C. Vega for assistance with Figure 1b and Christopher J. Ellis for valuable comments on the manuscript. P.H. and R.A-R. acknowledge funding by the Iberian Society of Ecology (SIBECOL) through a Grant for Early Career Researchers 2022. R.A-R. held a post-doctoral grant “Juan de la Cierva”

JDC2022-048728-I from the Spanish Ministry of Universities and the Next Generation EU. P.H. held a post-doctoral grant "Margarita Salas" from the Spanish Ministry of Universities and the Next Generation EU Recovery. M.D-B. acknowledges support from TED2021-130908B-C41/AEI/10.13039/501100011033/ Unión Europea Next Generation EU/PRTR and from the Spanish Ministry of Science and Innovation for the I+D+i project PID2020-115813RA-I00 funded by MCIN/AEI/10.13039/501100011033. S.S.A. acknowledges the support from the Spanish Ministry of Science and Innovation through the project PID2020-115708RB-C22 and the EU project DRYVER (H2020-grant agreement 869226-2). C.G-C. was supported by a Junior Leader Fellowship contract (LCF/BQ/PR22/11920005) funded by "la Caixa" Foundation (ID 100010434). Y.C. acknowledges support from TED2021-132332B-C21 funded by MCIN/AEI/10.13039/501100011033 and the European Unión "Next Generation EU"/PRTR. N.G.M. acknowledges support from the Spanish Ministry of Science and Innovation through projects PID2019-106840GA-C22 and PID2022-140985NB-C22. R.A-R. and A.d.R. acknowledge support from the Spanish Ministry of Science and Innovation through the project PID2019-105469RB-C22. A.R. acknowledges support from the Spanish Ministry of Science and Innovation through the project PID2021-123735OB-C21/MCIN/ AEI/ 10.13039/501100011033/FEDER, UE.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/ele.14488.

DATA AVAILABILITY STATEMENT

No data were used in this article.

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How to cite this article: Arias-Real, R., Delgado-Baquerizo, M., Sabater, S., Gutiérrez-Cánovas, C., Valencia, E., Aragón, G. et al. (2024) Unfolding the dynamics of ecosystems undergoing alternating wet-dry transitional states. *Ecology Letters*, 27, e14488. Available from: https://doi.org/10.1111/ele.14488