

A Multiscale, Hierarchical Model of Pulse Dynamics in Arid-Land Ecosystems

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Abstract

Ecological processes in arid lands are often described by the pulse-reserve paradigm, in which rain events drive biological activity until moisture is depleted, leaving a reserve. This paradigm is frequently applied to processes stimulated by one or a few precipitation events within a growing season. Here we expand the original framework in time and space and include other pulses that interact with rainfall. This new hierarchical pulse-dynamics framework integrates space and time through pulse-driven exchanges, interactions, transitions, and transfers that occur across individual to multiple pulses extending from micro to watershed scales. Climate change will likely alter the size, frequency, and intensity of precipitation pulses in the future, and arid-land ecosystems are known to be highly sensitive to climate variability. Thus, a more comprehensive understanding of arid-land pulse dynamics is needed to determine how these ecosystems will respond to, and be shaped by, increased climate variability.

1. INTRODUCTION

Arid-land ecosystems are characterized by infrequent and variable precipitation, leading to a chronic shortage of soil moisture. Unlike mesic systems, in which protracted periods of moisture availability may be interrupted by short episodes of water stress, arid-land systems generally experience only brief periods or pulses of water sufficiency (Knapp et al. 2008). As a consequence, ecological processes in arid-land ecosystems are typically described in a “pulse dynamics” framework (Noy-Meir 1973), in which pulses of biological activity following wetting events punctuate periods of inactivity when soil water is scarce. Here, we review species and ecosystem responses to rain events and expand the traditional pulse-dynamics framework by integrating responses to and consequences of precipitation pulses at increasing spatial and temporal scales.

Our overarching goal in this review is to expand the spatial and temporal scales of the pulse-dynamics concept. To do so, we first review the historical development of pulse-dynamics theories. Then, we synthesize empirical studies into a four-tiered hierarchical framework that links biotic-abiotic exchanges with population dynamics and species interactions. We then discuss how species interactions can lead to ecosystem state transitions and how these state transitions promote landscape-scale resource transfers. In arid-land ecosystems, pulses of water directly and indirectly influence many ecosystem processes: For instance, they may serve as transport vectors, dissolve compounds and erode surfaces, alter redox conditions of soil microenvironments, and create disturbances. Furthermore, rain events may interact with larger-scale processes, such as shrub encroachment or wildfire, and thereby enhance connectivity among landscape components (e.g., upland areas and stream networks). We believe an expanded framework is needed to accurately reflect the full range of how pulsed processes operate within arid-land ecosystems. Although we acknowledge that rain does not drive all the important ecological processes in arid areas (Field et al. 2010), our review focuses on water because it is the resource that most frequently limits these processes in arid-land ecosystems.

Refining current understanding of pulse dynamics is particularly relevant to predicting how future changes in the amount, seasonality, and intensity of precipitation will affect arid-land ecosystems. In general, models of global climate change suggest that in the future wet areas will get wetter and dry areas will get drier (Stocker et al. 2013). Indeed, a global survey (Delgado-Baquerizo et al. 2013) of soil processes concluded that increasing aridity would decouple the carbon (C) and nitrogen (N) cycles and decrease C and N availability in arid-land soils. In the southwestern United States, for example, models predict increased mean annual winter and summer temperatures, a decrease in winter precipitation, and increasing variability in growing-season precipitation (Gutzler & Robbins 2011). Even with no net change in precipitation, the increase in regional temperatures (and attendant evapotranspiration) will lead to increased aridity. In addition, climate models indicate that in some regions precipitation seasonality may shift to later in the growing season (Cook & Seager 2013), which will have a disproportionate impact in areas currently dominated by summer or winter precipitation. Finally, models predict a greater frequency of extreme events, including longer, more severe droughts and an intensification of the hydrological cycle. A recent modeling study indicated that El Niño events, which currently affect weather patterns in arid lands of Australia, the Mediterranean region, and the US Southwest, are likely to become more frequent and intense (Cai et al. 2014). All these predictions translate into changes in the size, frequency, intensity, and timing of precipitation, the key elements driving pulsed resource dynamics.

2. HISTORY OF PULSE-DYNAMICS THEORY

The conceptual underpinnings of arid-land pulse dynamics started with two reviews on primary producers and consumers in arid-land environments (Noy-Meir 1973, 1974). Both reviews had

a strong energetics and systems-ecology focus, reflecting goals of the International Biological Program (IBP), which stimulated the development of this concept under the auspices of the desert biome. Noy-Meir (1973) argued that processes in arid lands, in contrast to mesic systems, were driven by water availability rather than by energy. Of note, Noy-Meir did not explicitly define a pulse event. Instead, he observed that in arid-land ecosystems, “there are only 10–50 rainy days a year, occurring in 3–15 rain events or clusters of rainy days, of which probably no more than 5–6 (sometimes only one) are sufficiently large to affect biotic parts of the system” (Noy-Meir 1973, p. 28). This mostly plant-centric view, developed somewhat from the perspective of the Negev Desert in Israel, underestimated the roles and responses of biological soil crusts (biocrusts) and other soil surface microbial communities that can react to even small wetting events. Thus, in this review, we provide an expanded discussion of pulse-driven microbial processes. Nevertheless, the number, timing, and size of precipitation events were considered to be, and remain, the key characteristics of rainfall patterns that drive pulse dynamics in arid-land systems.

Pulse-dynamics theories are distinct from the related pulse-reserve concept. The pulse-dynamics framework describes how biological processes track a moisture pulse without requiring the production of a reserve. In the pulse-reserve concept, rainfall exceeding some threshold initiates biological activities that result in a reserve, such as biomass or available N, which persists after moisture from the event is depleted. Although the pulse-reserve concept has been widely applied in arid-land ecology, surprisingly few studies demonstrate that pulses actually produce reserves. For example, N mineralization tracks moisture availability, but N uptake by microbes and plants may consume all available N released during a pulse, leaving no reserve (Dijkstra et al. 2012). Additionally, many processes, such as soil respiration, do not create reserves but instead deplete them (Sponseller 2007). The accumulation of net primary production (NPP) over the growing season, in contrast, clearly reflects a pulse-reserve process derived through C fixation and biomass production. To date, most empirical research has addressed pulse dynamics rather than the pulse-reserve concept, yet conceptual models are explicitly built around pulse reserves (Noy-Meir 1973, Reynolds et al. 2004, Collins et al. 2008). Therefore, the utility of the pulse-reserve concept relative to pulse dynamics remains unresolved for many arid-land processes.

Yang et al. (2008, p. 621) defined resource pulses as “episodes of increased resource availability in space and time that combine low frequency (rarity), large magnitude (intensity), and short duration (brevity).” Resource pulses are analogous to “hot moments,” defined as “short periods of time that exhibit disproportionately high reaction rates relative to longer intervening time periods” (McClain et al. 2003, p. 301). By generalizing from water pulses to pulses of resources, pulse dynamics can be applied to many different ecosystems (e.g., Nowlin et al. 2008) or interactions (e.g., Holt 2008). Resource pulses alter the physiological activities of individuals, population growth rates, species interactions, and ecosystem processes over the duration of the pulse. For example, the response of higher plants following rain has received extensive study (e.g., Huxman et al. 2004a, Ignace et al. 2009, Pockman & Small 2010), yet few consumer studies exist despite evidence of significant impacts of rainfall variability on heterotrophs in arid lands (e.g., Holt 2008, McCluney et al. 2012). Perhaps this differential impact reflects the fact that responses by primary producers to a single rain event can be directly and easily measured, whereas many consumers remain active during and between rain events, integrating multiple rain events over time—illustrating the need to expand the scales encompassed by the pulse-dynamics concept.

The original pulse-reserve model has only recently been embellished to incorporate a broader range of processes, time frames, functional-type responses, and interspecific interactions (Reynolds et al. 2004, Collins et al. 2008). Reynolds et al. (2004) added time lags (e.g., Huxman et al. 2004b), thresholds, and prior-state conditions to the pulse-reserve model to account for interactions among multiple precipitation events. These modifications recognized that pulses of precipitation might

increase existing soil water, such that a small rain that follows a larger event may yield large primary production responses. However, such responses are governed by plant functional traits, such as rooting depth, and antecedent conditions, allowing for variable production rates to occur in response to variation in rainfall amounts and intervals. The Reynolds et al. (2004) model was an important and insightful extension of the original pulse-reserve model, but it lacked explicit inclusion of microbial processes, soil nutrient pools (particularly soil N and C), and lateral transfer, all of which also regulate dynamics and interactions in arid-land ecosystems at multiple spatial scales (Austin et al. 2004, Belnap et al. 2005, Green et al. 2008).

Most recently, Collins et al. (2008) modified the Reynolds et al. (2004) model to reflect the key and potentially novel interactions and feedbacks between soil-moisture dynamics, microbial processes, soil nutrient pools, plant production, and consumers. Their modification, the threshold-delay nutrient dynamics (TDND) model, accommodated temporally variable linkages between microbial processes, soil nutrient availability, plant production, and consumer interactions, as well as potential temporal asynchrony between nutrient availability and uptake kinetics. For example, small rain events (<1 mm) or dew rarely initiate plant growth but can initiate N₂ and CO₂ fixation by biocrusts or microbial decomposition (e.g., N mineralization), increasing soil N during periods when plants remain inactive (Schwinning & Sala 2004, Pointing & Belnap 2012). Thus, one characteristic of pulse-driven ecosystems is that some (but certainly not all) key microbial processes may be temporarily decoupled from plant production during periods of light rains (Austin et al. 2004). Indeed, Sponseller (2007) suggested that over a 63-year period, only half of the storms in the Sonoran Desert were large enough to elicit plant responses. Larger events drive both microbial and plant processes simultaneously (Dijkstra et al. 2012). Nutrient availability and immobilization (e.g., decomposition, uptake, N mineralization) are then coupled in time. Because soil layers dry differentially (Huxman et al. 2004b), surface layers—where microbial abundance is high—dry rapidly and microbial processes cease while subsurface soil moisture—where microbes are less abundant—can continue to sustain plant production. But like previous pulse-reserve conceptual models, the TDND model was primarily conceived to address processes associated with individual pulse events at relatively small spatial scales.

3. HIERARCHICAL PULSE-DYNAMICS FRAMEWORK

As noted above, earlier pulse-reserve models were primarily constrained to single or clustered rain events, describing soil moisture variability within a growing season. Here we expand the original framework in time and space to include other events (fires, state changes) as they interact with rainfall over increasing scales (**Figure 1**). This multiscaled, hierarchical pulse-dynamics framework (HPDF) integrates space and time by concentrating on four pulse-related processes—exchanges, interactions, transitions, and transfers—that occur over a range from individual to multiple pulse events and extend from micro to watershed scales.

The lowest level of the HPDF focuses almost exclusively on event-scale pulse responses that have been widely studied because this level is most directly related to the original pulse-reserve model. From there we increase spatial and temporal scales by linking exchanges to population

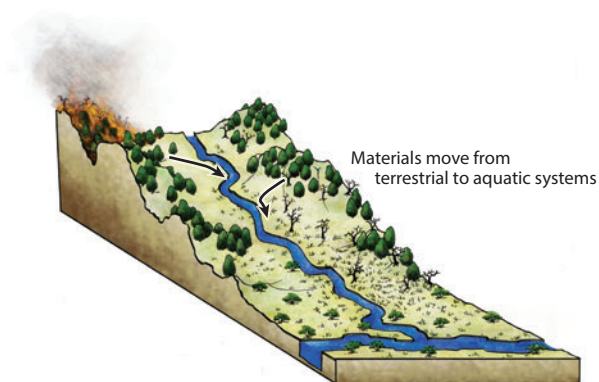
Figure 1

Components of the hierarchical pulse-dynamics framework (HPDF) focus on exchanges of nutrients and energy between organisms and the environment that occur in response to single or multiple water pulses within a growing season; interactions between species, within and among years; transitions within a landscape over years to decades; and rain-event-mediated transfers of materials among landscape units. Images drawn by Natalia Roberts.

PULSE-DRIVEN PROCESSES

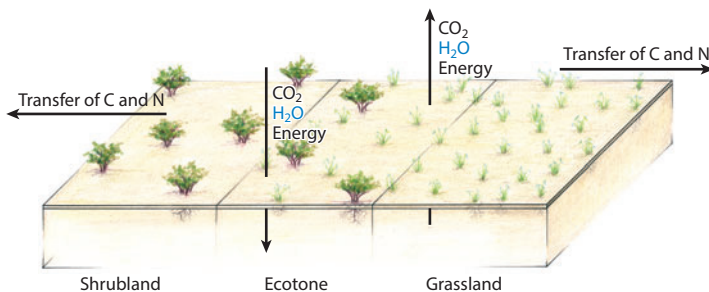
TIME AND SPATIAL SCALES

Transfers



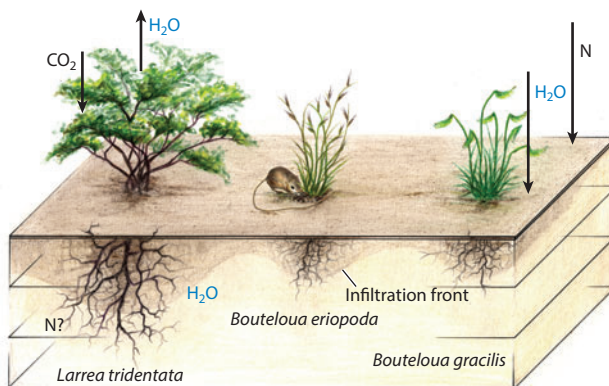
Century Landscape

Transitions



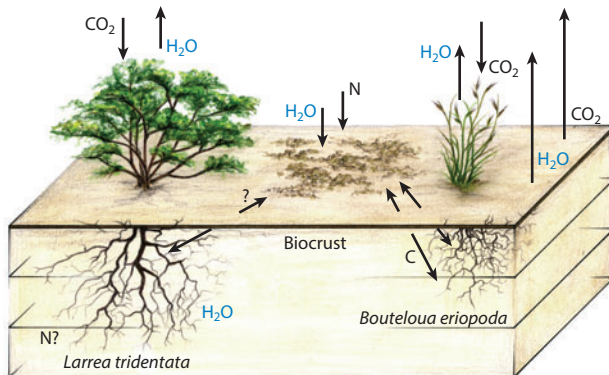
Decade Ecosystem

Interactions



Year Community

Exchanges



Season Population

Event Individual

dynamics and species interactions, and then to how interactions and population responses can lead to ecosystem transitions, such as shrub encroachment or tree mortality. The highest level of the HPDF addresses the large-scale consequences of these transitions primarily in response to high-intensity rain events. Although considerable research has occurred across these hierarchical levels, the majority of research thus far has dealt with highly localized responses to single rain events, almost all of it in southwestern US ecosystems. Moreover, no hierarchical frameworks exist that link pulse dynamics over a range of spatial and temporal scales. We hope that our expanded framework will stimulate research over the multiple scales at which pulse dynamics can operate and encourage others to explore the role of pulse dynamics in arid-land ecosystems globally.

3.1. Pulses and Exchanges

The first component of the HPDF addresses event-scale exchanges between soils and biocrusts, and soil microbes and plants, in response to a rainfall pulse (**Figure 1**). This section overlaps with the traditional pulse-reserve model presented in Noy-Meir (1973) but integrates microbial processes. Exchanges focus on the physiological mechanisms that underpin shifts in population dynamics and species interactions, which form the next tier of the hierarchy.

3.1.1. Biocrusts and wetting events. Biocrusts, a layer of photosynthetic and heterotrophic microorganisms concentrated at or a few millimeters below the soil surface, occur on up to 70% of arid-land soils (Pointing & Belnap 2012). Biocrusts fix both atmospheric C and N; they are an important N and C source to arid-land soils (Elbert et al. 2012). They are also an important source of fixed N at a global scale (Elbert et al. 2012). Because of their substantial cover, they also represent an interface of exchange between soil and atmosphere through which most pulse-driven inputs and losses to desert soils must pass (**Figure 2**; Belnap et al. 2003). Without moisture, biocrusts have no detectable activity; however, even extremely small events can activate them. The timing and amount of wetting events affect soil C cycles, as the photosynthetic components of biocrusts immediately begin respiring and fixing CO₂ at rates dependent on light, temperature, and the amount and duration of soil moisture (e.g., Lange 2003). During C fixation, biocrusts use soil CO₂, significantly raising the pH of their microenvironment (Garcia-Pichel & Belnap 1996), which affects the bioavailability of other elements in the soil (Gadd 1993). Dust, a critical nutrient source for many desert soils, is best retained when biocrusts are wet (Reynolds et al. 2001). Wetting also stimulates N₂ fixation, with rates again determined by temperature and soil moisture. Much of this newly fixed C and N (up to 50% and 88%, respectively) is secreted into surrounding soils within minutes to days of fixation, depending on precipitation characteristics (Belnap et al. 2003). When soils are wetted, microbial uptake of biocrust-released N is stimulated, increasing respired soil CO₂ and denitrification. Nitrogen losses are also influenced by soil porosity, stability, N content, moisture, temperature, and microbial populations, all of which are influenced by the presence of biocrusts (Barger et al. 2006).

Biocrusts also influence soil physical properties. They inhibit exchanges of gases in and out of the soil, especially when wetted, as component organisms swell with moisture. With each wetting event, biocrust organisms excrete polymers that increase soil aggregation; these, in turn, increase microbial activity, erosion resistance, and nutrient retention. Biocrusts can also magnify water harvested from wetting events by enhancing dew deposition and water capture, although work from Israel showed that higher amounts of biocrust exopolysaccharides can cause water runoff rather than water retention (Kidron & Büdel 2014). Where crusts enhance infiltration, more soil

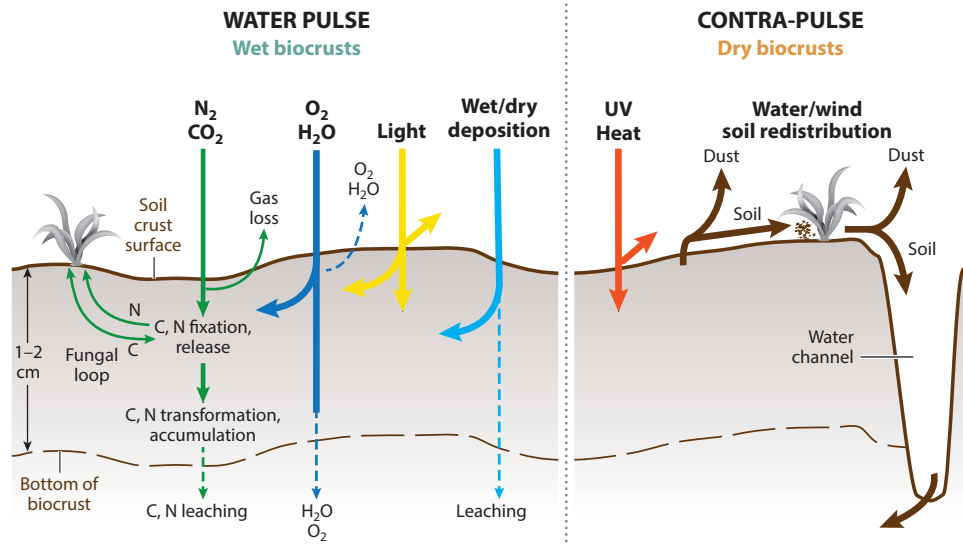


Figure 2

Diagram of the various types of materials and energy crossing the atmosphere–biocrust boundary. The left side of the diagram depicts processes that occur after a water pulse; the right side presents contra-pulse processes that occur when biocrusts and underlying soils are dry. In effect, the soil–atmosphere boundary is conceptually analogous to a cell membrane. Smaller molecules (H_2O , CO_2) diffuse through the biocrust boundary, whereas larger, more complex molecules or materials (e.g., complex carbohydrates) move via “active transport” by the vascular plants that extend above and below the soil surface and water as it carries materials (e.g., organic matter, dust, nutrients, seeds) into the soil. The size of the arrows indicates the relative amount of material/energy entering or leaving the soil, solid lines indicate processes with estimates of rates and flows, and dashed lines represent processes that have not been well quantified. The solid brown arrows represent materials (organic matter, nutrients, soil) lost from the soil surface through aeolian processes when dry or via runoff following rain events.

water means longer biological activity periods and greater NPP, which creates a positive feedback loop that further augments dew and precipitation harvesting (Barger et al. 2006).

3.1.2. Other microbial processes. In addition to biocrusts on the soil surface, microbial communities in the upper profile of soils, in the rhizosphere, and living within plants (mycorrhizae, endophytes) mediate nutrient exchanges between the soil and atmosphere. Even small rains that infiltrate only 1–2 cm of soil can stimulate a variety of soil microbial processes, including N mineralization, decomposition, and respiration (e.g., Austin et al. 2004, Huxman et al. 2004b). Respiration of labile C compounds occurs rapidly following both large and small rainfall pulses (e.g., Cable et al. 2008, Munson et al. 2010). Respiration following rain results from rapid microbial growth, mineralization of soil organic C and dead microbial biomass, breakdown of plant root exudates, and abiotic processes (e.g., carbonate dissolution). Most respired C, however, is derived from organic rather than abiotic sources and likely reflects rapid microbial metabolism that occurs within minutes to hours of a rain event (Freier & Schimel 2003, Breecker et al. 2012). This microbial processing of C compounds results in a pulse of soil respiration (Vargas et al. 2012). Initial respiration pulses vary in magnitude, however, and are not consistent either within or across sites (Jenerette et al. 2008, Williams et al. 2009), suggesting that a complex combination of biotic and abiotic mechanisms triggers these pulses (Fan et al. 2012). For example, soil respiration over

a three-month period in Chihuahuan Desert grassland was higher when pulses were large (three 20-mm rain events) than with the same amount of rain delivered in smaller events (twelve 5-mm events) (Vargas et al. 2012). Diverse variables, including soil surface characteristics, temperature, antecedent moisture, and CaCO_3 content, all likely modulate how soil respiration responds to the timing and size of rain events.

Soil microorganisms in lowland elements of desert landscapes, such as riparian zones, playas, and ephemeral channels, also respond to pulses from rainfall. Responses may be similar to the responses in xeric uplands or more muted, similar to mesic landscapes, depending upon flow permanence, season, and antecedent conditions (Belnap et al. 2005). For example, during the dry season, experimental pulses simulating 1-cm rainfall or 20-cm overland flow increased fluxes of CO_2 and nitrous oxide (N_2O), nitric oxide (NO), and methane (CH_4) fluxes from floodplain soils by factors of 3, 13, 50, and 30, respectively. However, when soils were wetter during the monsoon season, similar experimental pulses resulted in very slight increases (N_2O , CH_4) or even decreases (CO_2) (Harms & Grimm 2012). Floodplains occupy a small proportion of arid landscapes but retain received water (and material) for longer periods of time, extending the time frame over which processes occur. As a consequence, pulsed responses in floodplain areas may be less intense following subsequent rains compared with those in dryer upland areas. As in uplands, their responses to precipitation are partly conditioned on the hydration role of water, but they also may be responding to the release of previously unavailable resources or changes in redox conditions (Belnap et al. 2005, Harms & Grimm 2012).

Decomposition reflects microbially mediated exchanges in soils during and after rains. Extracellular enzymes secreted primarily by microbes break down complex organic compounds, enabling nutrient acquisition from multiple sources and pathways (Sinsabaugh et al. 2002). Enzymes require soil moisture to function; during dry intervals they may degrade, reducing the response potential of subsequent water pulses (Austin et al. 2004). Alternatively, stabilized enzymes, such as phenol oxidase and peroxidase, can act as reserves that initiate rapid microbial response to moisture (Stursova & Sinsabaugh 2008). Ladwig and colleagues (L.M. Ladwig, R.L. Sinsabaugh, S.L. Collins, and M.L. Thomey, in review) measured enzyme activities before and immediately after experimental rain events in Chihuahuan Desert grassland. They found that activities of alkaline phosphatase, β -glucosidase, leucine aminopeptidase, and phenol oxidase nearly doubled within hours after a 30-mm rain event early in the monsoon season. Enzyme levels a month later were comparable with levels before the first rain event 30 days earlier. Thus, enzymatic activities over the growing season reflect the rapid production of extracellular enzymes immediately following rains and the subsequent breakdown of extracellular enzymes during and between rain events. These results support a pulse-dynamics but not pulse-reserve process for extracellular enzyme production in these desert grassland soils.

3.1.3. Vascular plants. Vascular plants also respond rapidly to precipitation pulses, resulting in short-term exchanges of C via photosynthesis and respiration. Although most events in arid ecosystems are too small to elicit plant responses (Lauenroth & Bradford 2012), 5-mm events resulted in net C uptake in the dominant perennial grass of the shortgrass steppe, *Bouteloua gracilis* (Sala & Lauenroth 1982), and the dominant Chihuahuan Desert grassland species, *Bouteloua eriopoda* (Thomey et al. 2011). Potts et al. (2006) found that semiarid grasslands varied in C assimilation following a 39-mm rain event, as amounts were influenced by species composition, soil type, and antecedent precipitation.

Carbon assimilation during the growing season generally results in net biomass accumulation. Results from field precipitation manipulations directly support the pulse-reserve concept for vascular plant productivity. For example, aboveground NPP was higher in shortgrass steppe

(Heisler-White et al. 2008) and desert grassland (Thomey et al. 2011) when exposed to the same amount of precipitation that was delivered in only a few large rain events as compared with more frequent, smaller events. Yet, despite these short-term gains in production, net ecosystem C exchange in some arid ecosystems may be balanced over annual or multiyear time frames, as reserves gained in one year are ultimately decomposed or respired during subsequent years (Anderson-Teixeira et al. 2011).

3.1.4. Fungal loop. The fungal loop hypothesis proposes that networks of thermal- and drought-tolerant fungi store C and transform and translocate nutrients between soils and plants (**Figure 2**). Several studies have shown fungi to be important players in N transformations in desert soils and likely responsible for much of the denitrification observed in arid-land soils (McLain & Martens 2006, Marusenko et al. 2013). Fungi have also been implicated in moving C and nutrients between biocrust and plants when wetted. In a Chihuahuan Desert grassland, Green et al. (2008) experimentally demonstrated that $^{15}\text{N-NO}_3$ applied to surface soils moved rapidly—within 24–48 h—between root-free, fungal-dominated cyanobacteria biocrusts (where N_2 fixation naturally occurs) and perennial grasses up to 1 m away. Also, ^{13}C -labeled organic C applied to leaf surfaces moved from the plant into biocrusts. Similar N transfers from root-free, fungal-dominated, biocrust soils to nearby plants has also been observed in Utah with lichen biocrusts (J. Belnap, unpublished data) and China with moss biocrusts (W. Zhuang, Y. Zhang & M. Downing, unpublished data). Because of the speed of the transfer and the lack of root involvement, these exchanges most likely occurred via fungal hyphae. Despite this intriguing evidence, more work is needed to demonstrate the validity of the fungal loop hypothesis. The fungal loop may be an important stabilizing force under the variable precipitation regimes that characterize arid-land ecosystems and implies an entirely new mechanism for nutrient transfer and uptake by desert plants—bidirectional movement between plants and soils via dark septate endophytes (DSE)—unlike that documented for any other ecosystem.

In summary, considerable research demonstrates that several exchanges in arid-land ecosystems exhibit pulse dynamics in response to rain events. These processes include C and N uptake and loss, N mineralization, and decomposition. Soil respiration is also closely tied to soil moisture and substrate availability, both of which vary in response to the size, frequency, and duration of rain events. Because of shifts in the rates of exchanges, rains can alter the abundance of microbial and plant populations, as well as the strength and direction of plant–microbe, plant–plant, and plant–consumer interactions, connecting the physiological exchanges to their population- and community-level consequences (McCluney et al. 2012).

3.2. Pulses and Interactions

The second level of the HPDF focuses on how individual or multiple resource pulses affect species interactions, along with population and community dynamics, at seasonal to interannual timescales within a given community type, such as desert grassland (**Figures 1 and 2**). These interactions can then drive vegetation pattern and ecological state transitions.

3.2.1. Fungi–plant interactions. Considerable evidence suggests that fungi dominate many arid-land ecosystem processes and mediate exchanges of materials between soils, plants, biocrusts, and the atmosphere during rains (McLain & Martens 2006, Marusenko et al. 2013). Thus, fungi are likely to be important players regulating population and community dynamics in the context of the HPDF (**Figures 1 and 2**). Mycorrhizae and the relatively unknown dark septate endophytes (DSE) colonize most desert plants and may buffer them against abiotic stresses, such as heat,

drought, and nutrient stress (Ghimire et al. 2011, Loro et al. 2012). Indeed, a recent meta-analysis (Kivlin et al. 2013) showed that DSEs protect plants, particularly desert grasses, against drought better than other fungal groups (Mandyam & Jumpponen 2005, Sánchez Márquez et al. 2012). Although detailed work suggests that fungal-mediated resource exchanges occur between plants and biocrusts (the fungal loop), these short-term exchanges have yet to be connected to the dynamics of plant or microbe populations. Recent conceptual advances may facilitate the integration of exchanges and interaction outcomes by explicitly incorporating resources into species interaction models (e.g., Jones et al. 2012). Experimental manipulations of fungal symbiosis in field settings can help resolve how the outcomes of plant–fungal interactions are affected by the size, frequency, and intensity of rain events. For example, the abundance of DSE in Chihuahuan Desert grassland increased in rhizosphere soils in response to increased rainfall (Herrera et al. 2011).

3.2.2. Vascular plant–plant interactions. Several comparative studies have been conducted on how plant–water relations and C assimilation modulate the competitive dynamics between grasses and shrubs in response to the size and frequency of rain events (Schwinning et al. 2003, Li et al. 2013). Many such analyses address the two-layer hypothesis of niche partitioning of soil resources (Walter 1971), which states that grasses use water and nutrients from the upper 30 cm of soil, whereas woody species also avoid competition with grasses by foraging in deeper soil layers. Infiltration to shallow and deep soils is a direct function of the size of a rain event, or series of rain events. Although Ward et al. (2013) found general support for the two-layer hypothesis, Schwinning et al. (2003) reported that two native grass species in Utah outcompeted two native shrub species for soil water regardless of event size and season. Similarly, Pockman & Small (2010) found that the photosynthetic rate of the C₄ desert grass *B. eriopoda* was more than double that of the C₃ shrub *Larrea tridentata* following a 15-mm rain event, probably because most *L. tridentata* roots occurred below the depth of infiltration. In contrast, Throop et al. (2012) found that photosynthetic rates of the woody shrub *Prosopis glandulosa* consistently outperformed *B. eriopoda* across a range of soil-moisture conditions. Such species-level differences in the responses of short-term exchanges to pulse events may ultimately drive the outcomes of species interactions and state transitions.

Shifts in plant–plant interactions under changing and more variable precipitation regimes can lead directly to changes in species composition and potentially facilitate shrub encroachment (Báez et al. 2013). Projecting how pulse regimes will shift the outcomes of plant–plant interactions may benefit from knowledge of plant exchanges. Species-specific responses in leaf-level photosynthesis to pulses and different rooting depths (two-layer hypothesis) are well documented but may not necessarily predict competitive outcomes nor explain patterns of dominance or changes in species composition. For example, Thomey et al. (2014) showed that the photosynthetic response of *B. gracilis* to water pulses outperformed that of *B. eriopoda*, despite the fact that abundance of *B. eriopoda* is increasing faster than *B. gracilis* across a desert–grassland ecotone (Collins & Xia 2015). Mechanistic models that directly incorporate resource exchanges into competition coefficients could be developed to mechanistically link these two levels of the HPDF. Ultimately, altered plant–plant interactions during rainfall pulses may resolve, in part, the much-studied grassland-to-shrubland ecosystem transition (see Section 3.3).

A good illustration of how species-specific differences in exchanges can result in altered community dynamics comes from abrupt tree die-offs in semiarid woodlands of the western United States (Van Mantgem et al. 2009). Many arid-land tree species use different strategies to deal with precipitation variability and extended droughts (McDowell et al. 2008), leading to differential mortality as a function of within- and between-season rainfall patterns (Plaut et al. 2013). Drought responses by trees and the mechanisms of drought-induced mortality result from two

primary exchange-based mechanisms: C starvation, which is caused by prolonged stomatal closure, leading to respiration rates exceeding assimilation (McDowell et al. 2008), or hydraulic failure, a complete loss of water transport from soil to leaves (Martinez-Vilalta et al. 2002). Species-specific patterns of stomatal regulation of water loss during drought comprise a continuum between these two distinct strategies, and these strategies affect abundance and survival among competing tree species. Isohydic species maintain relatively constant leaf water potential as soil water fluctuates during and between rain events. As soil water potential declines to some threshold, stomata of isohydric species remain closed for the duration of the drought (e.g., Adams et al. 2009). At the other extreme, anisohydric species maintain gas exchange as soil water potential declines between rains by allowing leaf water potential to decrease well below values observed at higher soil moisture. Prolonged periods of stomatal closure in isohydric species may increase their susceptibility to C starvation, whereas the low water potentials that occur in anisohydric species might predispose them to hydraulic failure. These differing strategies can result in differential mortality rates and large-scale shifts in species composition during extended droughts (Breshears et al. 2005). Recent evidence also suggests that some tree species may exhibit acclimation to precipitation anomalies (prolonged drought or increased precipitation), and this acclimation alters the ability of individuals to use subsequent precipitation pulses (Plaut et al. 2013).

3.2.3. Consumer–plant interactions. McCluney et al. (2012) recently reviewed the impacts of changes in water availability (both amount and variability) on plant–consumer interactions. They hypothesized that plant–consumer interactions would shift from neutral to herbivorous to commensalism under increasing water availability. For example, at very low water availability plant–consumer interactions are likely minimal because high physiological stress reduces the abundances of both plants and consumers. As moisture availability increases, herbivory becomes the dominant interaction because consumers, such as crickets (McCluney & Sabo 2009) or desert granivores (Kotler et al. 1998), get their moisture from living plant tissue. Under high water availability, resources are more abundant and distributed, and the per capita impact of herbivory becomes more diffuse. McCluney et al. (2012) also hypothesized that high water availability over time could lead to increases in consumer populations, which would then feed back to increase herbivory. Such population increases have been documented in Sonoran and Chihuahuan Desert rodent communities during El Niño years (Jaksic et al. 1997). Overall, McCluney et al. (2012) found surprisingly few studies addressing how changes in water availability would alter plant–consumer interactions in arid-land ecosystems.

The temporal dynamics of arid-land consumer populations are directly related to water pulses and seasonal plant production. Ratadas, or rodent outbreaks, driven by El Niño, are excellent examples of transient consumer dynamics in response to increased seasonal precipitation (Jaksic & Lima 2003). As noted earlier, the life spans of many consumers integrate multiple rain events. Although Noy-Meir (1974, pp. 197–98) recognized that “. . . desert animals have pulses of activity and production coinciding with (or slightly lagging) periods of favorable conditions (rain, green vegetation), and pass unfavorable periods in an inactive and resistant ‘reserve’ form,” he focused more on describing physiological and behavioral strategies for dealing with heat and unpredictable rainfall rather than on the pulse dynamics of plant–consumer interactions.

Using both Ricker discrete population models and predator–prey models, Holt (2008) showed that resource pulses (e.g., mast seed production) could result in transient dynamics of rapidly increasing then decreasing consumer populations. The shape and duration of this response were a function of the interplay between bottom-up and top-down controls on consumer populations. Examples of this effect include stimulation of soil biota in wet periods resulting in high rates of decomposition and nutrient transformations (Ward 2009). In other cases arid-land consumers

may rapidly but indirectly respond to resource pulses. For example, the population size of the moth *Vanessa cardui* can erupt in response to changes in the resource base for larva, in this case the desert annual *Cryptantha crassisejala*. Larvae of *V. cardui* were rarely ($<3 \text{ m}^{-2}$) observed in years when abundance of *C. crassisejala* averaged $1.5 \text{ plants m}^{-2}$, but increased to 34 m^{-2} when abundance of *C. crassisejala* reached $35\text{--}50 \text{ plants m}^{-2}$ during years with high winter precipitation (Cates 1980).

Temporal expansion of traditional pulse-dynamics frameworks allows integration of multiple events, revealing how seasonal variability in resource exchanges scales up to affect consumer population dynamics. In the southwestern United States, winter and spring rains produce a pulse of nutritious C_3 biomass, which provides the bulk of energy to the food web. Summer rains, in contrast, produce greater relative biomass composed primarily of less-nutritious C_4 grasses. Variation among primary consumers in dietary strategies predicts consumer responses to these seasonal pulse dynamics. For example, of 30 grasshopper species surveyed in the northern Chihuahuan Desert, 10 species appeared to specialize on a high-quality C_3 diet, 2–3 species were generalists and tracked bulk resource abundance, and more than 14 species relied on lower-quality C_4 resources (Engel et al. 2009). In the small mammal community composed of granivorous, folivorous, and omnivorous rodents, approximately 70–90% of the incorporated C was derived from the higher-quality C_3 resources. During dry years when C_3 production failed, omnivores used up to 80% C_4 resources, and granivores relied on seed-cache reserves.

Consumer-resource interactions can vary dramatically over seasonal time frames. Higher trophic level consumers can exhibit large shifts in C sources when seasonal precipitation fails (Engel et al. 2009). Interannual precipitation variability produces periods when few high-quality C_3 resources are available to consumers (e.g., some lizards and small mammals), and fallback reserves may provide a marginal or inadequate resource base to drive consumer populations. For example, Warne et al. (2010) reported that after a failure of winter rains and C_3 production, small mammals and lizards relied on C_4 resources carried over from the previous year's production, demonstrating the importance of prior year production and degree of diet flexibility needed to sustain higher trophic levels. These large shifts in resource use were seen throughout the food web and demonstrated a strong reliance by consumers on less-preferred resource reserves of low nutritional quality. How community structure and abundance would change as winter rains that drive C_3 production continue to decrease is uncertain. Resource reserves of the more persistent C_4 production may offer a buffer to some consumer populations, but decreases in resource quality and abundance must drive consumer biomass and diversity downward, resulting in significant changes in community structure and ecosystem function.

3.3. Pulses and Transitions

At larger spatial scales and over longer (decadal) time periods, transitions and ecotone shifts may occur as species interactions respond to changes in precipitation amount, intermittency, and seasonality (Figure 1). These transitions are often abrupt and irreversible, suggesting that the underlying dynamics are bistable and the observed transitions represent a shift between alternative stable states (D'Odorico et al. 2012). Some ecosystem states have low resilience to changes in environmental conditions or disturbance, which can drive them across a critical threshold into a "new" alternative state. The system may then remain locked in this new state even after the external drivers (e.g., drought, disturbance) return to their initial conditions. The emergence of alternative stable states is typically associated with positive feedbacks that act between ecosystems and environmental drivers at multiple scales (Peters et al. 2004). Although the conceptual underpinnings of state transitions are built primarily on mathematical models, empirical studies have

demonstrated the occurrence of state transitions in freshwater lakes (Carpenter et al. 2011) and grass-shrub transitions in arid and semiarid ecosystems (Bestelmeyer et al. 2012, D’Odorico et al. 2012). In fact, state transition models have replaced more traditional range management concepts that were historically based on succession and “climax” conditions, and these concepts are now widely applied in rangeland management (Briske et al. 2005).

Linking back to plant–microbe interactions, the extent to which biocrusts/belowground microbial assemblages and plant–soil interactions promote or inhibit grass-to-shrub transitions is poorly understood. Increased frequency of small precipitation events can initiate a transition from moss-dominated biocrusts to cyanobacteria-dominated biocrusts (Reed et al. 2012). Soil mosses select against germination of large seeds, whereas cyanobacteria allow for almost all seed sizes to germinate (Boeken & Shachak 1994). Regarding plant–soil interactions, there is growing evidence that certain fungal species, particularly DSE in arid-land systems, span continents and occur in diverse plant hosts (Khidir et al. 2010, Knapp et al. 2012). Thus, these microbial species comprise a generally reliable assemblage in arid-land soils that might facilitate or inhibit shrub establishment. In that regard, mycorrhizal fungi enhance dominance of perennial C₄ grasses, and thus the stability of mesic grassland vegetation (Hartnett & Wilson 1999, Van der Putten et al. 2013). In this case, when fungi were eliminated in native grassland through soil fumigation, the abundance of C₄ grasses declined, vegetation cover decreased, and production and diversity of C₃ species increased (Hartnett & Wilson 1999).

Bistability results from the interaction between abiotic environmental variability and various positive and negative biotic feedbacks, particularly facilitation. Scanlon et al. (2007) found that bistable patch structure (vegetation patches in a matrix of unvegetated soil) in the southern Kalahari arose through the interactive effects of spatially variable water availability and local-scale facilitation. Moreover, vegetation patch structure can be altered by environmental variability as well as land-use practices, such as grazing. In Mediterranean ecosystems in Spain, Greece, and Morocco, Kefi et al. (2007) found that grazing pressure altered patch structure, leading to desertification. Desertification can be avoided by reducing grazing pressure before crossing a critical transition threshold reflected in the distribution of vegetation patch sizes in the landscape. Other landscape-scale factors can also push systems into alternative stable states, including fire, cropping, and energy development as well as the interaction of these drivers with climatic regimes.

As noted previously, semiarid landscapes with sufficient annual precipitation often consist of two alternative stable states: grassland and woodland or shrubland. Transitions from grassland to shrubland can result from a combination of many factors, including changes in amount and variability of precipitation (Fernandez-Illescas & Rodriguez-Iturbe 2004). An increase in the inter-annual variability of precipitation or changes in its intermittency can lead to bistable soil moisture dynamics (D’Odorico et al. 2000). In this case, a series of dry years may promote shrub dominance over grasses, whereas a series of wet years may favor grasses over shrubs (Peters et al. 2014), both of which could drive transitions between grass and shrub dominance. Currently, woody vegetation is expanding into grasslands in Africa, Australia, South America, and North America in response to multiple factors, including changing patterns of precipitation (Van Auken 2000, Eldridge et al. 2011).

Transitions can also occur due to changes in the intermittency and magnitude of water pulses as they affect the strength of some important positive soil moisture–vegetation feedbacks. These feedbacks play a crucial role in determining the stability and bistability of arid-land ecosystems (Klausmeier 1999). For instance, soils under plant canopies accumulate nutrients and are often wetter than in adjacent intercanopy areas owing to shading and greater soil infiltration capacity (D’Odorico et al. 2012, Field et al. 2012). Therefore, subcanopy areas offer preferential sites that facilitate seedling establishment, a nurse-plant effect resulting in a positive feedback that may

explain ecosystem bistability (Rietkerk & Van de Koppel 1997). The switch from infrequent/high-magnitude to more frequent/low-magnitude rain pulses could increase canopy-interception losses and offset the positive effect of shading and enhanced infiltration on the soil water balance under plant canopies (Eldridge et al. 2011). Likewise, changes in the intermittency of precipitation are expected to affect the intensity and direction of hydraulic redistribution (the nocturnal transport of water through the root system) and consequently alter the strength of the associated positive and negative feedbacks to deep-rooted vegetation.

Clearly, we know a lot about the consequences of state change in arid-land ecosystems and less about the drivers of state change and bistability. A combination of drivers likely is needed to push the system from one state to another, and these drivers may be both natural and anthropogenic. For example, C₄ grasslands expanded globally during the late Miocene, presumably as a consequence of warmer, drier conditions, increased fire frequency, and low atmospheric CO₂ concentration (Edwards et al. 2010). Now, during the Anthropocene, we are seeing a global reversal of this trend. Woody plant encroachment into grasslands is increasing on many continents (Bond 2008, Higgins & Scheiter 2012) in response to changes in climate, land use, fire frequency, drought, and elevated atmospheric CO₂ concentration. Although the combination of drivers of woody plant encroachment varies regionally, it is essential to determine how the outcome of this important and pervasive global transformation will alter the services provided to the ~2 billion people currently living in arid-land regions (Reynolds et al. 2007, Maestre et al. 2012).

3.4. Pulses and Transfers

This level of the HPDF focuses primarily on the consequences of state transitions and their interactions with rainfall pulses at large spatial scales. Widespread tree die-off and shrub encroachment have many ecological consequences. Conifer die-off affects C, water, and energy balance; biocrusts and associated processes; and plant-microbe interactions (Breshears et al. 2005, Van Mantgem et al. 2009). Shrub encroachment, however, may lead to either no change or a net increase in C storage (Kurc & Small 2007, Anderson-Teixeira et al. 2011), changes in plant species diversity (Eldridge et al. 2011), increased surface runoff and nutrient losses (Turnbull et al. 2010; **Figure 2**), and altered surface energy balance, which creates a positive feedback loop that can sustain and promote further shrub encroachment (D'Odorico et al. 2010).

Infrequent but extreme events that may occur at decadal to centennial intervals (e.g., fires, floods, insect outbreaks, drought cycles, wet periods, or extreme climatic events) affect the degree to which landscape components are connected through the transfer of water, organic matter, sediment, seeds, and nutrients (Benavides-Solorio & MacDonald 2001, Belnap et al. 2005) (**Figures 1 and 2**). These landscape-scale connections occur in arid systems globally because of high heterogeneity in geomorphic units that vary in soil properties, parent material, landscape position, vegetation type, and previous management practices (Monger & Bestelmeyer 2006), with consequences for grassland resistance to shrub encroachment (Rachal et al. 2012). Transport vectors that influence connectivity among landscape units include water, wind, and animals. These vectors are governed by broad-scale climate (wind, water) or socio-economic drivers (domestic grazers) interacting with landscape heterogeneity in vegetation and physical properties to influence the magnitude and direction of transfers among landscape units (Okin et al. 2006).

Precipitation pulses move resources to neighboring landscape units, as described by the trigger-transfer-pulse-reserve framework (Ludwig et al. 2005). This framework links events that initiate spatial transfer of materials and patch (reserve) processes to pulsed responses, such as plant growth. For example, resources moved from upslope locations can result in increases of water, organic matter, and nutrients in downslope landscape units (Michaelides et al. 2012) or in recipient aquatic

systems (Shakesby & Doerr 2006; **Figure 2**). In many cases, large precipitation events can transfer up to four times the annual inputs of these soil nutrients from their upland origin to downslope recipient systems (Turnbull et al. 2010). Reduced soil stability associated with disturbed biocrusts allows wind to move sediments and deposit them locally under adjacent plant canopies, increasing decomposition, nutrient availability, and resource heterogeneity and thus influencing microbial and vegetation dynamics (Field et al. 2010). In other cases, wind transfers sediment and deposits it hundreds of kilometers downwind, increasing snow-pack melt rates and reducing water amounts entering large river systems by an average of 5% annually (Painter et al. 2010; **Figure 2**). The amount of resources transferred during a storm often greatly exceeds in situ resource availability in recipient systems. Nevertheless, the relative importance of redistributed resources from neighboring units varies with the size, frequency, and intensity of storms that ultimately move materials from one landscape unit to another.

Water plays multiple roles in transfer events, often interacting with vegetation structure: as a vector, a limiting resource, a solvent, and a disturbance agent (Belnap et al. 2005, Harms & Grimm 2012). It is important to note that rainfall-initiated runoff may be the only time when uplands are connected to some downstream components of landscapes; these connections are highly episodic. Transfers of water and materials among landscape units may produce localized areas nested in the landscape in which rates of elemental cycling and other ecosystem processes are greatly elevated for variable periods of time (McClain et al. 2003). These localized areas, called biogeochemical hot spots, often occur at terrestrial–aquatic interfaces in arid ecosystems as substrates, and reactants from upland donor systems, such as organic matter, or reactive N, are moved by surface flow following rain events into riparian and aquatic systems where soil moisture is more persistent. The mechanisms producing these responses are mediated by water and can include the in situ dissolution of previously unavailable materials (e.g., organic C, N, or P) that may be required for a microbial reaction or plant uptake or the transport of those materials into the recipient system. For example, Harms et al. (2009) showed that floodplain soil denitrification rates were an order of magnitude higher in a perennial reach of the San Pedro River compared with an intermittent reach, even though both sites exhibited order-of-magnitude increases in denitrification rates in response to rainfall and runoff inputs of water during the monsoon season. Some evidence suggests that riparian floodplains retain nutrients in seasonally inundated soils during dry periods, which are released when wetted (Harms & Grimm 2012); this would be the rare case of a reserve, although it operates in reverse (the previously stored materials are released with the pulse).

As a disturbance agent, the erosive force of water reshapes landscape geomorphic surfaces, redistributes sediments, and scours and kills riparian and aquatic biota. Stream networks in arid lands often are extensive, even if they are seldom wet such that drainage density (stream channels/area) tends to be high in arid landscapes (Leopold et al. 1964). Moving along stream networks, from upland hillslopes to ephemeral channels to perennial streams and rivers, as the duration of water availability increases, the proportion of area represented by each landscape element decreases (Belnap et al. 2005). Those landscape components with a short duration of water availability exhibit more pulse-driven dynamics compared with more mesic, modulated dynamics in areas where water is continually available (i.e., perennial rivers), although these generalizations are modified by interannual and seasonal variability in precipitation (Harms & Grimm 2012). In support of this generality, seasonal soil respiration was ten times higher in riparian areas compared with uplands, where respiration pulses were C limited and typically lasted for only 24 h even though soil moisture was still available (Sponseller & Fisher 2008). Overall, these space–time interactions extend the pulse-dynamics idea in which arid lands “hug” the space and time axes as they are characterized not by long-duration activity over broad spatial scales but rather by short bursts of activity over large spatial extents (upland areas) and longer-duration responses in very localized areas (i.e., riparian

zones). In other words, pulse dynamics apply more to uplands, which constitute the vast majority of the areal extent in a watershed, whereas more continuous high-reaction rates occur in the very localized, spatially restricted regions of perennial streams and rivers (the “hot spots” of arid lands).

State transitions influence, and even enhance, the rate of material transfers in arid landscapes. Shrub encroachment can dramatically reduce total vegetation cover in some cases by at least 50%, leading to significantly higher losses of organic matter and nutrients relative to grassland during rain events (Turnbull et al. 2010) or sediment movement during dry periods (Field et al. 2010; **Figure 2**). At regional scales, mega-droughts, insect infestations, wildfires, and extreme climatic events—and their interactions—can potentially lead to large-scale mortality of dominant species (Breshears et al. 2005, Van Mantgem et al. 2009). Widespread mortality and other disturbances can double the amount of runoff following large rain events, resulting in high rates of nutrient transfers in piñon-juniper woodlands (Wilcox et al. 2003). Record-breaking wildfires have burned hundreds of thousands of hectares in the western United States in the past decade (Westerling et al. 2006), resulting in widespread loss of vegetative dominants, altered ecosystem-atmosphere coupling, and movement of sediment, C, and nutrients from donor to recipient systems by large rain events. Indeed, sediment transfers from uplands to recipient aquatic ecosystems can increase threefold (Shakesby & Doerr 2006, Badia & Marti 2008), and transfers of nutrients, dissolved organic carbon, and trace elements may increase more than twofold following fires (Smith et al. 2011). Recently, extensive transfers of nutrients and organic matter into aquatic ecosystems following the 63,500-ha Las Conchas fire in New Mexico were triggered by heavy rains associated with the start of the summer monsoon immediately following the fire. These nutrient pulses created high sediment loads and historically low dissolved oxygen levels for >24 h that were propagated more than 50 km downstream from the burned area, resulting in fish kills and threats to the water supply for the Albuquerque metro area (C. Dahm, R. Candelaria-Ley, C. Reale, J. Real & D. Van Horn, unpublished data).

4. THE FUTURE OF PULSE DYNAMICS IN ARID-LAND ECOSYSTEMS

Arid-land ecosystems already experience high interannual variability in climate, and this variability is likely to increase in the future. Above-average precipitation in these regions is often a function of the occurrence of a small number of large rain events (Petrie et al. 2014). In contrast, dry years are typically characterized by a regime that includes mostly small- to medium-sized rain events and few or no large events. As dry regions get drier under climate change, decreasing mean annual precipitation might mean more small rains and fewer large events in any given year. An increase in frequency of small precipitation events can prevent biocrust organisms from maintaining a positive C balance (Reed et al. 2012). Moreover, under similar rainfall regimes, higher temperatures will reduce soil moisture; thus microbes will be less active, further lowering nutrient availability in what are already highly oligotrophic soils (Delgado-Baquerizo et al. 2013). Lower moisture and higher temperatures will also increase the potential for C starvation and hydraulic failure in semiarid forests. Higher temperatures and extended heat waves will challenge the physiological tolerances of many arid-land consumers (Tyllianakis et al. 2008, McKechnie & Wolf 2010, Walther 2010). Losses of these biological functions may lead to higher erosion associated with extreme precipitation. Furthermore, much of what we know about pulse dynamics comes primarily from the southwestern United States, even though arid and semiarid ecosystems comprise >40% of terrestrial environments. Thus, far more work is needed to determine how these globally extensive ecosystems will respond to future changes in precipitation regimes.

In summary, arid-land ecosystems have been viewed through the traditional lens of rainfall pulses and the pulse-reserve concept for decades. Overall, we find very little observation or

experimental evidence for pulses leading to reserves except in a few obvious but nevertheless important instances, such as NPP. And yet, the pulse-reserve concept is the leading framework for describing processes in arid-land ecosystems. Pulse dynamics, by contrast, are well researched and documented, especially at the event scale, and such dynamics may characterize processes in a variety of ecosystems in addition to arid-land environments. Here we have expanded the pulse-dynamics concept into a more broadly based, hierarchical, multiscaled framework by illustrating how rainfall pulses drive biotic-abiotic exchanges, influence species interactions, and potentially drive state transitions. The HPDF explicitly incorporates short-term, local-scale processes tied to single rainfall events and links these to species interactions. Species interactions and environmental context form the core of pulse-driven regional-scale state transitions, and these state transitions then alter the rate and magnitude of transfers of materials between landscape units in drylands. Moreover, rainfall pulses interact with other environmental presses and pulses, and these interactions operate over multiple spatial and temporal scales. Clearly, one of the key remaining challenges is to better understand how processes within the nested hierarchical components of arid-land ecosystems—and their interactions—lend stability to these climatically sensitive ecosystems. Much exciting research remains to be done to support, challenge, or refute the primary role of pulse dynamics as drivers of arid-land ecosystem processes.

SUMMARY POINTS

1. Arid-land ecosystems are characterized by highly variable precipitation regimes, high temperatures, and frequent shortages of water, and global climate change models predict that many arid regions will get warmer and drier in the future.
2. Many important ecological processes in arid lands are driven by the size, frequency, and intensity of precipitation pulses, all of which will likely change under climate change.
3. The widely referenced pulse-reserve paradigm describes arid-land ecosystem responses to precipitation pulses, but there is surprisingly little evidence that pulses result in reserves except in a few important instances.
4. The pulse-reserve paradigm is essentially an event-scale framework, but precipitation pulses operate at multiple spatial and temporal scales.
5. The hierarchical pulse-dynamics framework expands the spatial and temporal scales of the pulse-dynamics paradigm by conceptually linking individual responses to precipitation pulses with species interactions, ecological state transitions, and transfers of materials among landscape components.

FUTURE ISSUES

1. What components of arid-land ecosystems follow the pulse-reserve paradigm rather than simply pulse dynamics?
2. Do reserves from pulses promote ecosystem stability?
3. Are processes in arid ecosystems asynchronous during a pulse event, and if so, how will climate change affect this asynchrony?

4. Do plant–biocrust/microbe interactions promote resistance to altered precipitation patterns and drought, and how will such interactions be altered by more extreme climatic events?
5. Can we quantitatively link the somewhat overlapping hierarchical levels described in the hierarchical pulse-dynamics framework?
6. What are the key drivers of ecosystem state changes in arid lands, and what mitigating forces can we use to prevent or promote them?
7. How will the changing dynamics of arid-land ecosystems affect connected systems, such as streams, rivers, playas, and groundwater, especially given likely changes in the frequency and magnitude of connections between these landscape components?
8. What are the limitations of pulse-dynamics frameworks, and are these frameworks broadly relevant to systems that are less water limited than arid-land ecosystems?

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