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Running Head: Interactions in dryland systems

Shifting species interactions in terrestrial dryland ecosystems under altered water availability and climate change

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ABSTRACT

Species interactions play key roles in linking the responses of populations, communities, and ecosystems to environmental change. For instance, species interactions are an important determinant of the complexity of changes in trophic biomass with variation in resources. Water resources are a major driver of terrestrial ecology and climate change is expected to greatly alter the distribution of this critical resource. While previous studies have documented strong effects of global environmental change on species interactions in general, responses can vary from region to region. Dryland ecosystems occupy more than one-third of the Earth's land mass, are greatly affected by changes in water availability, and are predicted to be hotspots of climate change. Thus, it is imperative to understand the effects of environmental change on these globally significant ecosystems.

Here, we review studies of the responses of population-level plant-plant, plant-herbivore, and predator-prey interactions to changes in water availability in dryland environments in order to develop new hypotheses and predictions to guide future research. To help explain patterns of interaction outcomes, we developed a conceptual model that views interaction outcomes as shifting between (1) competition and facilitation (plant-plant), (2) herbivory, neutralism, or mutualism (plant-herbivore), or (3) neutralism and predation (predator-prey), as water availability crosses physiological, behavioural, or population-density thresholds. We link our conceptual model to hypothetical scenarios of current and future water availability to make testable predictions about the influence of changes in water availability on species interactions. We also examine potential implications of our conceptual model for the relative importance of top-down effects and the linearity of patterns of change in trophic biomass with changes in water availability. Finally, we highlight key research needs and some possible broader impacts of our findings. Overall, we hope to stimulate and guide future research that links changes in water availability to patterns of species interactions and the dynamics of populations and communities in dryland ecosystems.

Key words: climate change, precipitation, drought, moisture, water availability, species interactions, competition, mutualism, herbivory, predation, top-down, trophic biomass.

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I. INTRODUCTION

(1) Overview

One of the key challenges facing ecologists is to link ongoing global environmental changes to the interconnected responses of organisms, populations, communities, and ecosystems (Suding *et al*., 2008; Tylianakis *et al*., 2008; Yang & Rudolf, 2010). Many of these responses are directly predictable from altered environmental conditions. For example, increased precipitation may result in bottom-up effects on plant and rodent communities (Baez *et al*., 2006; Ernest, Brown & Parmenter, 2000), decreased winter precipitation can alter energy and nutrient flow through food webs (Warne, Pershall & Wolf, 2010), and higher temperatures may cause extreme mortality in small birds (McKechnie & Wolf, 2010). However, other responses may be less intuitive because they result from complex interactions among species (Brown *et al*., 2001; Ernest *et al*., 2000; Guo & Brown, 1996; Suttle, Thomsen & Power, 2007). For instance, population dynamics of some rodent communities in the Chihuahuan Desert were strongly correlated with the response of plant communities to precipitation changes, while others were not (Ernest *et al*., 2000). To better predict the ecological consequences of global environmental change, we require a greater understanding of how species interactions vary in rapidly shifting environments and how these changes influence responses at other levels of biological organization (Emmerson *et al*., 2005).

Interspecific interactions, including competition, facilitation, herbivory, mutualism, and predation (see Table 1 for definitions), are fundamental to the dynamics of populations, communities, and ecosystems (Fox, Fairbairn & Roff, 2001; Fretwell, 1987; Jones & Lawton, 1996; Paine, 1980) and are particularly sensitive to environmental change (Brooker, 2006). Interspecific interactions can be quantified by a large number of metrics (reviewed in Berlow *et al*., 2004). Some measures examine *per capita* effects of individuals of one species on individuals of another, whereas others examine the overall net effects of one population on another. Many experimental studies examine the outcome of interactions by looking for statistical effects of one population on another (Berlow *et al*., 2004). Herein, we refer to these population-level statistical methods of measuring species interactions as interaction outcomes (*sensu* Holland & DeAngelis, 2009; see Fig. 1, Table 1). Interaction outcomes measure the combined effects of one species on another and incorporate the effects of changes in density as well as direct and indirect *per capita* interactions. Here we focus on interaction outcomes in our conceptual model and discussion because of their common use in the literature, but we also include information on other measures of species interactions.

Species interactions are highly dynamic in space and time (Holland & DeAngelis, 2009; Paine, 1980; Ruesink, 1998). Changes in the strength and sign of interaction outcomes can arise from many mechanisms, including shifts in density or direct *per capita* interaction strengths of one or both of the species involved in the interaction. Theoretically, an interaction outcome of mutualism (+ +) can transition to commensalism (0 +) or parasitism (+ –) as one species reduces its supply of resources to another and/or the increased density of one species leads to its increased exploitation of the other species (Holland & DeAngelis, 2009). Alternatively, the interaction outcome of predation (+ –) may transition to commensalism (0 +) with weakened *per capita* interaction strengths and weakened consumer functional responses (Holland & DeAngelis, 2009). For instance, a major research effort has investigated how plant-plant interaction outcomes transition between facilitation and competition across gradients of physiological stress and water availability and many mechanistic hypotheses have been proposed to explain the generality of patterns of these interaction outcomes (Maestre *et al*., 2009).

Despite the fundamental importance of species interactions for the structure and dynamics of populations, communities, and ecosystems, we currently have little conceptual or empirical understanding of how global environmental change will impact species interactions and their consequences for communities and ecosystems. Tylianakis *et al*. (2008) recently reviewed the effects of global environmental changes on species interactions worldwide. In addition to climate, these included CO_2 enrichment, nitrogen deposition, biotic invasions, and land-use changes. They found strong effects of these environmental drivers on species interactions, but great variability in responses across different drivers of change and types of species interactions. This led them to call for a more extensive investigation of how biotic and abiotic context influences the effects of environmental change on species interactions.

While the arctic is widely thought to be a hotspot for climate-induced ecological change (see Shaver *et al*., 2000), dryland ecosystems are also predicted to be particularly sensitive to climate change (Diffenbaugh, Giorgi & Pal, 2008). Drylands are defined as regions that have an index of aridity (ratio of mean annual precipitation to mean annual potential evapotranspiration) below 0.65 (Middleton & Thomas, 1997). These ecosystems include key terrestrial biomes covering 41% of Earth's land surface and supporting over 38% of the total global human population of 6.5 billion (Reynolds *et al*., 2007), and are highly vulnerable to global change and desertification (Korner, 2000; Reynolds *et al*., 2007).

Here we introduce a conceptual model, informed by a broad review of the literature (Table 2), that examines how patterns of variable resources in dryland environments influence interaction outcomes whose magnitude and sign can change depending on changes in water availability over time (Fig. 2). We focus on changes in water availability, as water is the most important resource shaping the biology of dryland environments (Noy-Meir, 1973, 1974) and is highly sensitive to anthropogenic global environmental change (IPCC, 2007; Pearce, 2006). Water availability can be modified by inputs such as precipitation and irrigation, by losses such as evapotranspiration or infiltration, and by topography and the distribution of water bodies on the landscape (Belnap *et al*., 2005). After discussing our model, we highlight key limitations in our understanding of the linkages between changes in water availability and species interactions, suggesting needs for further study. We then discuss how our model could be used to predict potential consequences of changes in species interactions under hypothetical scenarios of current and future water availability.

(2) Species interactions in dryland ecosystems

Dryland ecosystems are often characterized by wide variation in precipitation inputs within years, between years, and across decades (Rodriguez-Iturbe *et al*., 1999). Some of these systems have strongly seasonal patterns of precipitation, with moderate levels of variability between years, whereas others are more stochastic. Variation may also follow decadal patterns. For example, the El Niño-Southern Oscillation (ENSO) is a cyclic phenomenon with a periodicity of approximately five years that is an important driver of patterns of precipitation in dry regions on both sides of the Pacific Ocean (Holmgren *et al*., 2001; Trenberth, 1997; Woodward, Lomas & Quaife, 2008). These changes in the timing and quantity of rainfall can modulate seed-bank dynamics (Gutierrez & Meserve, 2003), trigger increases or decreases in net primary production (Holmgren *et al*., 2006), influence population dynamics (Catenazzi & Donnelly, 2007; Lima, Stenseth & Jaksic, 2002*a*), modulate predator-prey dynamics (Letnic, Tamayo & Dickman, 2005; Lima *et al*., 2002*a*), and alter ecosystem subsidies (Polis *et al*., 1997).

Many long-lived plants and animals are adapted to, or tolerate, the somewhat predictable variability of ENSO cycles and other seasonal patterns (Chesson *et al*., 2004; Noy-Meir, 1973, 1974). For instance, resistant or dormant life stages often increase the survival of many dryland plants and animals during periods of drought (Chesson *et al*., 2004). However, in many cases, dryland organisms respond to changes in water availability through physiological or behavioural mechanisms, which can rapidly alter their interactions with other species (McCluney & Sabo, 2009; McDowell *et al*., 2008; Schowalter, Lightfoot & Whitford, 1999; Warne *et al*., 2010). These flexible organismal responses may be an effective means of dealing with unpredictable variation in water availability and extreme events (Stahlschmidt *et al*., 2011), and may be the only possible coping mechanisms when a tolerant life stage has not been reached during the sudden onset of a drought. Despite the ability of dryland organisms to tolerate resource variability, extreme events can still have large effects, altering population dynamics, resetting interactions among species, or altering the entire ecosystem (Breshears *et al*., 2005; McKechnie & Wolf, 2010). Thus, species interactions may be even more prone to rapid fluctuations in drylands than in other terrestrial ecosystems, and may commonly transition between multiple interaction outcomes.

(3) Climate change, water availability, and biological responses in dryland ecosystems

Climate change will exert strong effects on water availability in dryland ecosystems by altering global atmospheric circulation and resulting patterns of precipitation (IPCC, 2007; Zhang *et al*., 2007). More intense storms and droughts are expected, with increased variation in ground-level water availability compared to current conditions (IPCC, 2007). Shifts in the timing and quantity of rainfall are also expected, but whether there will be an increase or decrease overall or within seasons varies geographically (IPCC, 2007). Although we generally focus on the effects of changing water availability, temperature also influences water availability, and thus it is important to note that altered rainfall and increasing temperature will interact to affect dryland species. Increased temperatures associated with climate change will pose physiological water balance challenges to a wide suite of organisms as water losses increase (e.g. Wolf & Walsberg, 1996) and soil moisture and surface water declines with increased evapotranspiration. Increases in the frequency, intensity, and duration of heat waves are predicted (Meehl & Tebaldi, 2004), which may have great consequences for many animals (McKechnie & Wolf, 2010) and some plants (Smith, Diddenzopfy & Nobel, 1984) that are already near their physiological heat and water balance limits. Increases in night-time minimum temperatures (Karl, Knight & Plummer, 1995) may also create heat and water challenges for nocturnal dryland animals, who may not be able to migrate or alter their behaviour in response to climate changes (Tracy & Walsberg, 2002). These temperature changes will likely alter interspecific and intraspecific behaviours and interactions. Thus, both temperature and precipitation are likely to alter the distribution, variability, and seasonality of water availability. Almost every dryland region of the Earth has distinct rainfall patterns to which its organisms and communities are phenologically adapted. Shifts in variation, timing, or magnitude of rainfall are expected to have significant ecological impacts on these systems (e.g. Suttle *et al*., 2007; Warne *et al*., 2010).

II. LINKING WATER AVAILABILITY TO SPECIES INTERACTIONS IN DRYLAND ENVIRONMENTS

We propose a conceptual model (Fig. 2) to examine how variation in water availability (e.g. precipitation, fog, soil moisture, surface water) varies across time and how this influences species interaction outcomes at the population level in drylands. These outcomes may change in magnitude and sign as they cross water availability thresholds. We develop our model by conducting a literature review and tabulating the observed responses of species interactions to changes in water availability. Our intention here is not to make definitive conclusions about general patterns of species interactions in all drylands globally, but rather to: (1) examine patterns reported in the literature, (2) review and develop hypotheses to explain these patterns, and (3) present example predictions arising from these hypotheses. In our review of plant-plant interactions, we include a large collection of studies, but do not attempt to include all studies on this topic, which have been recently reviewed elsewhere (Gómez-Aparicio, 2009; Maestre, Valladares & Reynolds, 2005). For plant-herbivore and predator-prey interactions, we include results of a thorough search, including all studies we could find, though few such studies occur. We examine the number of studies that suggest each type of change in interaction with altered water availability.

Though very useful in many contexts, here we do not conduct formal effect-size meta-analysis for several reasons: (1) there were insufficient usable studies on plant-herbivore and predator-prey interactions, (2) a recent meta-analysis has reviewed the outcome of plant-plant interactions at different stress levels (Maestre *et al*., 2005), and (3) effect-size-based meta-analysis is geared more towards making general conclusions about specific questions than hypothesis generation, and for the current state of our understanding of the topic of this review, hypothesis generation is what is needed. Thus, we tabulated responses of species interactions to changes in water availability and observed agreement or disagreement between studies, as well as our knowledge of particular aspects of these studies, to develop hypotheses or consider existing hypotheses to explain the observed patterns. Finally, we used these hypotheses to inform our conceptual model and make predictions for particular scenarios of initial and future conditions of water availability.

Our model differs from past conceptual approaches, which have focused on (1) responses of biogeochemical processes or ecosystem properties, such as net primary productivity, to global change, rather than on species interactions (Field *et al*., 2007; Shaver *et al*., 2000), (2) individual traits-based responses without addressing species interactions specifically (Suding *et al*., 2008), and (3) examination of the effects of gradual but persistent global environmental change on individuals, communities, and ecosystems, without examining changes in environmental variability or in species interactions (Smith, Knapp & Collins, 2009). Although the previously examined topics are extremely important, species interactions remain a critical and understudied link between individual traits-based responses and community and ecosystem dynamics. Moreover, generalized approaches often fall short of adequately describing ecological processes in dryland ecosystems (Collins *et al*., 2008).

Our model presents a dynamic worldview, showing species interactions as mutable, agreeing with recent theoretical and empirical insights (Navarrete & Berlow, 2006; Ruesink, 1998; Sala & Graham, 2002). The model examines changes in the variability and timing of different levels of water availability, not just overall magnitudes, recognizing that the pattern of changes in resources may be just as important as changes in the mean resource level (e.g. Huxman *et al*., 2004; Warne *et al*., 2010). In the simplest case, our model presents linear thresholds of water availability at which species interactions change sign (e.g. + + to + –). However, these thresholds may be dynamic, changing with multiple environmental conditions and physiological states. For example, the surface activity of Gila monsters (*Heloderma suspectum*) in the Sonoran Desert is promoted by increased hydration, with increased surface activity likely leading to stronger predation by the Gila monster (Davis & DeNardo, 2009).

Since animal hydration is dependent on multiple environmental factors, not just water availability (e.g. temperature and humidity), nonlinear thresholds may exist across time, dependent on temperature and other factors. Thus, changes in environmental conditions or functional traits could alter threshold height or shape (e.g. Fig. 2D). Additionally, changes in density of each species will influence the strength and sign of interaction outcomes (Chesson *et al*., 2004; Holland & DeAngelis, 2009). Thus, we suggest that our conceptual model provides a starting point for more quantitative approaches, which link multiple environmental factors and species traits to shifts in interspecific interactions.

We divide the discussion of our model into three general categories: plant-plant, plant-herbivore, and predator-prey interaction outcomes (Figs. 1, 2). The plant-plant approach examines changes in the interplay between competition and facilitation interaction outcomes along a water-stress gradient. The plant-herbivore approach examines shifts between mutualism/commensalism, herbivory, and neutral interactions, whereas the predator-prey approach examines shifts between commensalism, predation, and neutral interactions with changes in water availability. We offer our model as a set of testable hypotheses rather than a consensus view of how species interactions will definitively change with water availability.

(1) Plant-plant interactions

Plant-plant interactions in dryland ecosystems can shift between facilitation and competition with altered water availability (see Table 1 for definitions). For example, Maestre & Cortina (2004) compared the net effect of the tussock grass *Stipa tenacissima* on the shrub *Pistacia lentiscus* at ten experimental sites across a gradient of rainfall in semi-arid Mediterranean steppes, using planted one-year-old seedlings. They found that competitive interactions dominated at both extremes of the gradient, whereas facilitation was found under intermediate conditions.

Plant-plant interactions are mediated by multiple interacting factors, such as resource islands and neighbour-induced changes in microclimate and soil water availability. For instance, increases in soil moisture, reduced physiological stress provided by the shade of nurse plants, and enhanced soil fertility have been found to be primary mechanisms underlying positive effects of grasses and shrubs on shrub and tree seedling establishment in Mediterranean environments (e.g. Gómez-Aparicio, 2009; Maestre, Bautista & Cortina, 2003). At the population/community level, similar mechanisms are thought to underlie positive effects of nurse plants on the richness, abundance, and biomass of annual species (Pugnaire, Armas & Valladares, 2004). On the other hand, rainfall interception by shrub/tree canopies may reduce available soil moisture in areas where rain falls mostly in small events and thus competitive effects may dominate in these situations (Bellot *et al*., 2004).

Transitions from competition to facilitation along environmental gradients depend to a large degree on the characteristics of the species being studied (Choler, Michalet & Callaway, 2001; Maestre *et al*., 2009), the nature of the stress gradient involved (Kawai & Tokeshi, 2007; Maestre *et al*., 2009; Smit, Rietkerk & Wassen, 2009), and the performance measure (Maestre *et al*., 2005). Additionally, interactions may switch between competition and facilitation as plants transition to different life-history stages. For example, the giant saguaro in the Sonoran Desert (*Carnegiea gigantea*) requires a nurse plant (e.g. *Cercidium* sp.) for establishment, but then out-competes its nurse plant as it matures (McAuliffe, 1984). Depending on all of these factors, both facilitation and competition can be found across broad ranges of water availability, complicating the task of developing general models for the occurrence of competition and facilitation.

The development of conceptual models aiming to predict how species interactions change along gradients of ecosystem productivity and resource availability has a long history in plant ecology (Bertness & Callaway, 1994; Goldberg & Novoplansky, 1997; Grime, 1973; Tilman, 1988). Among these models, the "stress gradient hypothesis" (SGH; Bertness & Callaway, 1994) has been one of the most influential. The SGH predicts that facilitation "*...should be particularly common in communities developing under high physical stress and in communities with high consumer pressure* (p.193)." By contrast, "*...where the physical environment is relatively benign and consumer pressure is less severe, positive interactions should be rare; as a result, competitive interactions should be the dominant structuring forces*" (Bertness & Callaway, 1994, p.193). Despite its popularity, support for the SGH is equivocal (e.g. Greenlee & Callaway, 1996; Maestre & Cortina, 2004; Tielborger & Kadmon, 2000) and the generality of the SGH is currently under vigorous debate (Lortie & Callaway, 2006; Maestre *et al*., 2005; Michalet, 2006); this has led to new conceptual models (Holmgren & Scheffer, 2010; Maestre *et al*., 2009; Malkinson & Tielbörger, 2010; Smit *et al*., 2009). The effects of the type of stress, the traits of the species involved, and herbivory on the SGH have all been explored (Maestre *et al*., 2009; Smit *et al*., 2009). However, refinements have focused on pair-wise species interactions, and thus have not modified the original SGH predictions at the population or community level.

In general, we hypothesize that positive plant-plant interactions should occur when soil water availability is increased by one plant above its own water needs, through mechanisms such as hydraulic redistribution and shading, providing supplementary resources to neighbours up to a point where water is no longer limiting (Maestre, Cortina & Bautista, 2004). Under conditions of high water stress, canopy interception and water uptake by a given plant may lead to a decrease in water availability under the plant compared to canopy interspaces, promoting competition over facilitation (e.g. Forseth, Wait & Casper, 2001; Knoop & Walker, 1985; Sala *et al*., 1989). Therefore, at high water stress levels, “nurse” plants may be unable to mitigate stressful conditions that decrease the survival and growth of their neighbours (Maestre *et al*., 2004; Michalet, 2006), leading to competitive interaction outcomes. On the other hand, at low levels of water stress (high water availability), other resources may limit plants (e.g. light) and these resources may promote competition. Following large pulses of moisture, limitation may occasionally be alleviated for short periods, resulting in temporary periods without interactions (Chesson *et al*., 2004; Goldberg & Novoplansky, 1997). Holmgren & Scheffer (2010) also argue that facilitative interactions should be more prevalent under intermediate stress conditions. When water availability is low, facilitative amelioration of stressful conditions by neighbours is insufficient to counter reductions in water availability. In addition, plants living under more benign conditions are usually more sensitive to water stress than those found under harsher conditions, so on average, plants living in areas with moderate water availability may depend more on facilitation than those living under conditions of low water availability (Holmgren & Scheffer, 2010). Once water stress is alleviated, however, competition may again become prevalent (see Callaway, 2007 for examples). Thus, we predict that facilitative interactions will be prevalent under moderate conditions, rather than monotonically increasing with abiotic stress (i.e. as water availability decreases), which is in contrast with predictions of the SGH.

In summary, we suggest that mechanisms producing variation in plant-plant species interactions as water availability changes reflect trade-offs between the relative increase or decrease in water stress caused by neighbours, combined with overall water limitation and variability in stress-tolerance traits. We predict two threshold lines in our conceptual model, with water availabilities above or below these lines promoting competition and between these lines fostering facilitation (Fig. 2), which is consistent with facilitation occurring at intermediate levels of abiotic stress (Fig. 2; Table 3; Maestre *et al*., 2009). We also show declines in the strength of competition under the lowest or highest water availabilities, where dormancy or temporary alleviation from abiotic limitation may reduce species interactions. We note that there may be some deviation from this general hypothesis in any particular study system due to context dependencies (e.g. Devitt & Smith, 2002; Hamerlynck *et al*., 2002). These context dependencies could be incorporated into the model by altering thresholds (Fig. 2D).

(2) Plant-herbivore interactions

Plant-herbivore interactions are highly responsive to water availability and thus are highly variable temporally. However, studies of water-induced changes in plant-herbivore interactions are less numerous than plant-plant interactions and theories dealing with these phenomena are lacking. Thus, to inform our model, we discuss each appropriate study in the hope of finding patterns that may suggest appropriate theories for water-based transitions in plant-herbivore interactions.

In many cases, plant-herbivore interaction outcomes switch from mutualistic to herbivorous, depending on water availability. For instance, Scogings & Mopipi (2008) documented a mutualistic interaction outcome between goats (*Capra hircus*) and *Acacia karroo* seedlings under high moisture conditions, where goats stimulated compensatory growth of seedlings (+ +), but herbivorous (+ –) interaction outcomes occurred under drier conditions. Similarly, white-throated wood rats (*Neotoma albigula*) act as dispersers of cacti during periods of normal precipitation when they graze cactus joints and fruit without negatively affecting the whole plant (+ +), but under drought conditions they graze the primary stems of cacti, which can impact plant viability and reproductive output in cacti such as saguaro (+ –) (*Carnegiea gigantea*) (B. Wolf, unpublished data). In this case, rodents disperse seeds under high-moisture conditions, but kill the cacti or reduce their long-term reproduction under low moisture availability. On the other hand, water additions sometimes have no effect. Holland (2002) irrigated senita cactus (*Pachycereus schottii*) and found positive effects of senita moths (*Upiga virescens*) on cactus reproduction, but no effect of water availability on moth pollination or larval fruit consumption. Also, Utrilla, Brizuela & Cibils (2006) found no net effect of a sheep (*Ovis aries*) population on vegetation populations, regardless of soil moisture.

In other situations, little possibility for mutualism exists, but shifts from neutral to herbivorous interaction outcomes may occur nonetheless. For example, along the San Pedro River in southeastern Arizona, field crickets (*Gryllus alogus*) appeared to switch between consuming detritus and moist vegetation (freshly picked leaves) when water was more or less available, respectively (McCluney & Sabo, 2009; Sabo *et al*., 2008). Alternatively, Vander Wall (1998) found higher seed predation by rodents under increased soil moisture in the Great Basin through an increased ability of the rodents to smell the moist seeds in underground caches. However, this represents a change in the magnitude of seed predation rather than a change in the sign of the interaction. Other studies have documented similar results, where increased water availability stimulates greater consumption of dry food, like seeds (Hochman & Kotler, 2006; Kotler, Dickman & Brown, 1998). In cases where water causes stimulation of additional herbivory, it is likely due to trade-offs between water and energy gains and losses associated with foraging, defecation, or non-consumptive resting. Without free-water (freely available water that is not contained within an organism) and with low plant water content, water losses associated with foraging activity or defecation may exceed water gains, causing negative water balance and dehydration. Under these conditions, organisms may reduce activity rates to conserve water (Davis & DeNardo, 2009). Increases in free-water availability from these low levels may allow for greater activity (Davis & DeNardo, 2009) and thus greater foraging for low-water-content plant materials and an increase in the strength of the interaction (the stimulation hypothesis, *sensu* McCluney & Sabo, 2009).

The examples above highlight how water availability can have major impacts on herbivore-plant interaction outcomes in dryland ecosystems (Table 2). Based on the literature, we hypothesize that trade-offs between water and energy requirements interact with water and energy availability to alter plant-herbivore interactions in dryland ecosystems. Specifically, we suggest that when water and energy resources are coupled (free water is unavailable) and water is limiting to herbivores, high consumption of moist plant material is necessary to maintain water balance. Under these conditions, the population-level interaction outcome may be strongly herbivorous (+ –) (the compensation hypothesis, McCluney & Sabo, 2009). However, when water availability is high, energy and water resources for herbivores are decoupled, and/or water is not limiting and energy requirements alone do not necessitate extremely high levels of consumption (the quenching hypothesis, McCluney & Sabo, 2009). Thus, because *per capita* herbivory is weak at high water availability relative to *per capita* effects of pollination, seed dispersal, or compensatory stimulation of growth, the result is that mutualistic or commensalistic population-level interaction outcomes are likely to occur. Yet, long-term increases in water availability may result in a positive reproductive response of herbivores, and high densities of herbivores may again lead to an herbivorous population-level interaction outcome. This scenario is more likely in drylands with strong seasonal precipitation patterns or in years with particularly high rainfall. Exceptionally strong herbivorous interaction outcomes could result from rapid declines in water availability after extended periods of low water stress. In this case, high densities of herbivores accumulated during low water stress would rapidly increase their rates of consumption during the onset of drought, strongly negatively affecting plants. This hypothesis has not yet been tested. At the lowest water availability, neutral interaction outcomes are likely to become more prominent as mobile herbivorous animals migrate or hide, or relatively immobile herbivores perish (Davis & DeNardo, 2009; "conservation hypothesis" proposed in McCluney & Sabo, 2009; McKechnie & Wolf, 2010).

As discussed above, increased consumption of dry food with increased water availability (Hochman & Kotler, 2006; Kotler *et al.*, 1998) likely lies at the transition between very low and moderate water availability. As water availability increases from these low levels, herbivorous animals may become more active and increase their foraging, particularly on dry foods ("stimulation hypothesis" proposed in McCluney & Sabo, 2009). Thus, our conceptual model is consistent with these hypotheses, with neutral interaction outcomes at very low water availability, strongly herbivorous interaction outcomes at moderate water availability, and mutualistic or commensalistic interaction outcomes at high water availability.

(3) Predator-prey interactions

Predator-prey interactions differ from interactions involving plants because predators and prey are both behaviourally responsive (Ives & Dobson, 1987; Wolf & Mangel, 2007). Prey manage risk of predation and predators manage the fear experienced by their prey, with predators and prey interacting *via* foraging games (Hugie & Dill, 1994; Kotler *et al*., 2002). For example, gerbils (*Gerbillus andersoni allenbyi*) in the Negev Desert manage predation risk from barn owls (*Tyto alba*) by altering foraging time allocation, apprehension, and vigilance (Dall, Kotler & Bouskila, 2001). Microhabitat, moonlight, and the presence of predators modulate this risk (Kotler, Brown & Bouskila, 2001; Kotler, Brown & Mitchell, 1993). How gerbils and their predators interact in these systems is influenced by their energetic state (Berger-Tal & Kotler, 2010). While most of the previous research on foraging games has focused on energetic state, water requirements are a fundamental constraint for dryland organisms and water balance often drives their behaviours, including those behaviours that determine predator-prey interactions (Golightly & Ohmart, 1984; McCluney & Sabo, 2009; Valeix *et al*., 2008). Thus, many foraging behaviours are likely to revolve around water limitation in dryland systems. For instance, several different African herbivores altered their drinking behaviour in response to changes in predation risk and water availability (Valeix *et al*., 2008). In that system, increased predation risk was associated with a decrease in drinking time or the probability of drinking, while decreased availability of water holes was correlated with increased drinking time or the probability of drinking.

Few studies have directly investigated the effects of water availability on predator-prey interactions. However, we note that Golightly & Ohmart (1984) indicated that in order for kit foxes (*Vulpesm acrotis*) and coyotes (*Canis latrans*) in Arizona to meet water demands in the absence of free water, they needed to consume more rodents than that required to meet energy demands, regardless of seasonality. Similarly, McCluney & Sabo (2009) found that short-term *per capita* interactions between field crickets (*G. alogus*) and wolf spiders (*Hogna antelucana*) along a semi-arid floodplain in Arizona changed from strongly predatory to essentially neutral as water availability increased. Loveridge *et al*. (2006) also showed an increase in the kill rate of young elephants (*Loxodonta africana*) by lions (*Panthera leo*) during low rainfall in an African savanna, which may have been due to separation of young calves from water-stressed herds. Gotelli (1993) implied the occurrence of a decreasing effect of ant lions (*Myrmeleon* spp.) in Oklahoma on a variety of prey where precipitation was highest. Precipitation negatively affected ant lions by promoting a physical soil crust, which prevented ant lion larvae from digging below ground. Ant lions also seemed to reduce the abundance of other ground-dwelling arthropods. Thus, ant lions and other arthropods no longer interacted under increased precipitation, shifting the interaction from predatory to neutral with increased precipitation. The first two examples of changes in the interaction with altered water resources are likely mediated by the consumers need for the water contained within prey, but for the last two examples, the mechanism is different, though the pattern is the same.

Spiller & Schoener (2008) proposed a unimodal relationship between the amount of precipitation and predator-prey interaction outcomes between lizards and spiders on islands in the Bahamas. We believe this pattern also applies to dryland systems driven by the costs and benefits of predation under varying water availability (McCluney & Sabo, 2009). In agreement with Spiller & Schoener (2008) and our previous discussion of plant-herbivore relationships, at very low water availability predators may avoid water losses associated with increased hunting activities and instead seek refuge and conserve water (*sensu* Davis & DeNardo, 2009; "conservation hypothesis" proposed in McCluney & Sabo, 2009) or may perish, leading to reduced or neutral population-level interaction outcomes. Intermediate water availability may strongly affect animal behaviour because prey become both water and energy sources, and thus interspecific interactions may intensify (Golightly & Ohmart, 1984; McCluney & Sabo, 2009). At higher water availability, water and energy sources may be decoupled, and other factors may limit animals more than water. Under these conditions, behaviours may switch to non-predatory endeavours, promoting more commensal interactions (e.g. McCluney & Sabo, 2009). In agreement with Spiller & Schoener (2008), as well as with the stress gradient theory proposed by Menge & Sutherland (1987), the highest water levels may be associated with severe disturbance in some habitats (e.g. desert washes), which may have greater impacts on higher trophic levels, causing migration or mortality and decreased interactions with lower trophic levels. Most evidence in drylands favours this unimodal relationship between water availability and predator-prey interactions (Golightly & Ohmart, 1984; Gotelli, 1993; Loveridge *et al*., 2006; McCluney & Sabo, 2009; Valeix *et al*., 2008; Tables 2 & 3), thus our conceptual model reflects this approach (Fig. 2).

III. IMPACTS OF CLIMATE CHANGE ON THE BALANCE OF SPECIES INTERACTIONS IN DRYLAND ECOSYSTEMS

We have presented a basic conceptual model of how population-level interaction outcomes in drylands may shift with altered water availability. This model is based on a review of published studies (Table 2) and an examination of potential trade-offs between water requirements, demands for other resources, and the relative availability of water and other resources (Fig. 2). The hypotheses and predictions associated with this model are in agreement with general patterns in the literature, though particular exceptions occur. We use this model and hypothetical scenarios of current and future water availability to illustrate how the model can lead to testable predictions for shifts in species interactions under environmental change. We caution that predictions may vary depending on the initial and future water conditions of a particular region and the predictions made here are for example purposes only.

To make predictions about how changes in water availability influence interaction outcomes, we first assume scenarios of current water availability. For simplicity, we assume initial conditions of intermediate water availability with moderate variation across time (Fig. 2). This scenario is likely to be representative of many dryland ecosystems, particularly those with strong seasonality, but it does not represent all drylands. Our example scenarios illustrate the types of changes in interactions that might be expected in certain dryland systems. Scenarios can be useful in conveying information about plausible outcomes under a given set of assumptions about present and future conditions, but should not be viewed as representing the only possible outcomes (Carpenter, 2005). For future conditions, we examine three separate scenarios, relative to current conditions (Fig. 2): (1) increased variation in water availability, but the same mean, (2) increased variation and increased mean, and (3) increased variation and decreased mean. These scenarios agree with climate projections of greater variation in precipitation and soil moisture, as well as the potential for increases or decreases in mean precipitation from one region to another (IPCC, 2007).

(1) Plant-plant predictions

We make two predictions: (*a*) increased variation in water availability leads to greater instances of population-level competitive interaction outcomes, but also greater variability in these interactions, and (*b*) increases or decreases in mean water availability leads to increases in competitive interaction outcomes. Our scenario of current water availability assumes that moderate conditions predominate in a relative sense, which promotes facilitative interactions more than competition (Maestre *et al*., 2009). Thus increases in variability of soil moisture would be expected to lead to both (*a*) greater instances of neighbour plants lowering—rather than increasing—water availability and thus promoting competition (Bellot *et al*., 2004), and (*b*) complete alleviation of water stress, promoting competition for other resources, such as light (Espigares, López-Pintor & Rey Benayas, 2004). However, increasing variability will mean that these competitive interactions will be short-lived and vary significantly from year to year (Chesson *et al*., 2004). In a recent review, Knapp *et al*. (2008) discussed some of the ecological consequences that a more variable climate would have for both mesic and xeric ecosystems. They predicted that altered precipitation regimes would have an overall positive effect on the water balance of deep-rooted xeric plants that experience less seasonal water stress because larger rainfall events recharge deeper soil layers, thereby increasing the amount of time when soil water content is above stress thresholds (Heisler-White *et al*., 2009). Such an effect might be expected to increase the frequency of facilitative plant-plant interactions in dryland ecosystems. However, this assumes a scenario of initial water availability lower than our current scenario used for example purposes. We also point out that with increased variation in precipitation, any increase in facilitation from more intense rain pulses may be negated by more intense and longer droughts, exacerbated by temperature-induced increases in evapotranspiration, which might be expected to increase the frequency of competitive interactions (Maestre *et al*., 2003). In highly variable dryland systems, increased variability might have little effect on the balance of interactions, except to reduce the occurrence of interactions altogether. However, substantial effects on particular populations or communities are likely, even if the balance of these interactions is not altered.

Changes in mean water availability in our qualitative scenario analysis may greatly alter the balance of plant-plant species interactions in dry environments, with increases or decreases promoting competition. Additionally, we note that many dryland regions are expected to experience a substantial change in summer precipitation. As some plants rely heavily on summer precipitation, whereas some do not utilize it, large changes in the seasonality of precipitation will differentially favour some plant species over others (Schwinning *et al*., 2002; Schwinning & Ehleringer, 2001). We note that changes in the strength of competitive or facilitative interactions may vary greatly with small changes in water availability, even when the signs of the interactions do not.

(2) Plant-herbivore predictions

We predict that: (*a*) increased variation in water availability will increase the frequency of mutualistic, commensal, or neutral plant-herbivore interaction outcomes, and (*b*) increases in mean water availability will promote plant-herbivore mutualisms or commensal interaction outcomes, whereas decreases will promote strong herbivory or neutral interactions depending on the degree of reduction. Our scenario of current water availability assumes intermediate availability and moderate variation, leading to a predominance of herbivorous interaction outcomes. Thus, increases in the variability of water availability would be expected to lead to both (*a*) greater instances of neutral effects due to reduced foraging activity and due to reduced densities of herbivores at low water availability and (*b*) higher instances of mutualistic or commensal interaction outcomes due to reduced herbivory relative to pollination and other positive interactions because of a decoupling of water and energy/nutrient requirements at high water availability. However, increases in variation of water availability may also occasionally produce some strongly herbivorous interactions when herbivores are still actively foraging, but free water is scarce (e.g. McCluney & Sabo, 2009; Fig. 2). Major increases in the variability of water would also increase the occurrence of temporary water pulses that could promote a predominance of behavioural adjustments in herbivory, without time for reproductive effects. Increases in mean water availability may be expected to greatly increase mutualisms or commensal interaction outcomes, whereas decreases may promote neutral interaction outcomes, but also may lead to occasional strong herbivorous interactions, depending on the degree of change in water availability. We note that the neutral interaction outcomes result when herbivores are no longer active in these ecosystems, so declines in water availability that do not reach this threshold should increase herbivory.

(3) Predator-prey predictions

We predict that (*a*) increased variation in water availability will increase the frequency of neutral or commensal predator-prey interactions, and (*b*) increased mean water availability will lead to greater commensal interactions, whereas decreased mean water availability will lead to either increases in the strength of predatory interaction outcomes or to neutral interaction outcomes, depending on the degree of change. Our scenario of current water availability assumes intermediate water levels and moderate variation, leading to predominantly predatory interaction outcomes. Thus, increases in the variation of water availability are expected to increase (*a*) instances of neutral effects due to reduced activity and reduced densities of predators at low water availability and (*b*) instances of commensal interaction outcomes due to reduced predation when water becomes less limiting (due to decoupling of water and energy/nutrient sources) at high water availability. Increases in the variation in water availability may also lead to temporary periods of stronger predation when predation increases with lowered water availability before a threshold is reached where predators switch to water conservation behaviour and are no longer active components of these ecosystems (e.g. McCluney & Sabo, 2009). As with herbivores, a major increase in variability could be expected to lead to a predominance of short-term behavioural changes in predation rather than changes in reproduction. Increases in water availability are likely to lead to increased commensalistic population-level interaction outcomes, whereas reduced water availability is likely to lead to either increases in the strength of predatory interaction outcomes or to neutral net effects, dependent on the degree of reduction in water availability.

(4) Community response predictions

We predict that (*a*) increased variation of water resources will lead to either greater bottom-up effects and linearity of changes in patterns of trophic biomass, or highly unpredictable non-linear dynamics of trophic biomass, depending on degree and pattern of the increase in variability, and (*b*) increases in mean water availability will promote linear, bottom-up propagation of effects, while decreases will promote top-down non-linear dynamics of trophic biomass until decreases create depauperate communities with few interacting species. Trying to connect changes in interactions across multiple trophic levels in any particular food web is difficult. However, we cautiously suggest that it is possible to connect changes in the balance of plant-plant interaction outcomes to plant-herbivore interaction outcomes and to predator-prey interaction outcomes under our scenarios of current and future water availability.

Several theories can lend insight as to how communities may change in response to alterations in species interactions related to altered water availability. For instance, the idea first postulated by Hairston, Smith & Slobodkin (1960) and later developed into the exploitation ecosystems hypothesis (Oksanen *et al*., 1981) holds that bottom-up control of ecosystems results in linear accumulation of biomass across trophic levels with increased resource availability, whereas top-down control results in non-linear patterns. Numerous studies have now documented support for this hypothesis across a range of terrestrial ecosystems (Elmhagen *et al*., 2010; Mäntylä, Klemola & Laaksonen, 2010; Oksanen & Oksanen, 2000; Terborgh *et al*., 2006, 2001). For instance, in a meta-analysis, Mäntylä *et al*. (2010) found strong support for top-down effects of birds on the abundance of insects, prevalence of leaf damage, and amount of plant biomass across studies and ecosystems. Top-down control seems particularly important in less productive systems (Oksanen & Oksanen, 2000), including drylands. Stronger predator-prey and plant-herbivore species interactions represent greater top-down effects with greater effects on biomass of lower trophic levels (e.g. Chase, 2003) and this should lead to non-linear changes in biomass. Agreeing with this hypothesis, other theories and evidence also suggest that particularly strong species interactions in communities promote rapid non-linear shifts in biomass in various trophic levels in response to environmental change (i.e. the keystone species concept) (Bascompte, 2009; Brown & Heske, 1990; May, 1973; McCann, Hastings & Huxel, 1998). These theories suggest that understanding patterns and strengths of species interactions may be important to projection of the effects of global environmental change on communities and ecosystems.

Moderate increases in mean water availability from the levels in our initial scenarios could promote plant-plant competition, plant-herbivore mutualism or commensalism, and reduced predator-prey interactions (increased commensalism). Plant-plant competition would likely be relatively weak because water would no longer be limiting and this is typically the most important resource for dryland plants (Noy-Meir, 1973). Combining weak plant-plant competition with weak or positive plant-herbivore and predator-prey interactions would lead to an expectation of bottom-up effects and relatively linear, predictable patterns of changes in trophic biomass in these wetter communities.

Decreases in water availability from our initial scenario would be expected to promote competitive plant-plant interaction outcomes, strongly herbivorous plant-herbivore interactions, and strong predator-prey interactions, up until active predators, herbivores, and plants are progressively lost from the system. Thus, such a shift could promote stronger top-down effects and greater non-linearity and unpredictability of the responses of trophic biomass. We note that extreme decreases in water availability may result in communities dominated by bottom-up effects and linear, predictable patterns, but only because these communities will contain few species that seldom interact.

Under increased climate variability, with little change in mean values, the balance of interactions would be unlikely to be greatly affected. However, based on our conceptual model, an increase in the variability of moisture should lead to more frequent crossing of climate thresholds, and thus an increase in the variability of types of interaction outcomes for any pair of organisms (Fig. 2A). Predicting the effects of increased variability in interactions on trophic biomass and species coexistence is complicated. On the one hand, dynamic context-dependent species interactions may improve the stability and coexistence of ecological communities (Chesson *et al*., 2004; Navarrete & Berlow, 2006) and this dynamism would be expected to increase with increased variation in water resources. On the other hand, large increases in variability of water availability could be expected to lead to instances of populations of herbivores or predators with suddenly high rates of herbivory or predation that could promote highly non-linear dynamics in the short-term (Holmgren *et al*., 2001; Letnic & Dickman, 2006; Lima, Stenseth & Jaksic, 2002*b*; Smith *et al*., 2009). This might be particularly true if high variability leads to a predominance of short pulses of resources that do not allow for large reproductive or growth responses of plant communities, but do promote rapid changes in herbivory and predatory behaviour. Thus, the magnitude of changes in variability may influence the effects of these changes on patterns of trophic biomass in ecological communities.

Taken together, our predictions suggest that increases in the mean water availability or small increases in variability from our initial scenario should lead to more bottom-up, linear, and predictable dynamics of trophic biomass, but that decreases in water availability and large increases in variation may lead to top-down, non-linear, and unpredictable effects on trophic biomass. This idea seems to be supported by at least one study showing that bottom-up responses of plant and rodent communities to precipitation in the Chihuahuan Desert were common, but strong exceptions were occasionally observed that were difficult to explain (Ernest *et al*., 2000). Similar observations have been made in other systems as well (Holmgren *et al*., 2001; Lima *et al*., 2002*b*). However, we note that our predictions are dependent on the scenarios chosen for initial and future water availability conditions and studies examining particular regions are likely to vary. For example, in regions that already experience great variability, further increases in variability could be expected to decrease linearity or predictability and decrease total biomass or diversity.

IV. RESEARCH NEEDS

(1) Plant-plant

Substantial research has investigated how variation in moisture availability influences plant-plant interactions, but key questions remain unresolved. For instance, understanding what situations promote competition or facilitation at low water levels is an important direction for future research (see Brooker *et al*., 2008 for a recent review). Future studies on this topic should explicitly consider the stress tolerance and competitive ability of the interacting species, which can heavily influence the outcome of the interaction (Maestre *et al*., 2009). In this regard, recent research has shown that facilitation occurs only if surrounding vegetation is able to alleviate the abiotic factors by which a focal species has deviated from its physiological optima in the field (Gross *et al*., 2010). As such, the intensity of biotic interactions is likely to be linked with species traits, as they reflect particular tolerances. A more thorough knowledge of these linkages could substantially improve our ability to predict how the outcome of plant-plant interactions changes along water availability gradients (Maestre *et al*., 2009).

Given the strong seasonality within most dryland ecosystems, research is needed to determine how interactions during one season affect interspecific outcomes over time. In the

Southwestern U.S., for example, high moisture availability from winter and spring precipitation may increase primary production of spring annuals (e.g. Muldavin *et al*., 2008), which in turn may reduce soil resource availability during subsequent summer rains. For example, Hall *et al.* (2011) found that soil N mineralization rates decreased from spring to autumn in the northern Sonoran Desert and this could result in increasing competitive interactions among species as resource availability decreases during the later growing season (e.g. Harris & Facelli, 2003).

(2) Animal

While animal physiologists have a history of examining the importance of water as a resource (e.g. Davis & Denardo, 2006; Golightly & Ohmart, 1984; Hadley, 1994; Noy-Meir, 1974), animal ecologists have only recently focused on how water availability affects animal community structure and species interactions (e.g. McCluney & Sabo, 2009; Spiller & Schoener, 2008; Wolf & Martinez del Rio, 2003). As such, general theories of the influence of water on plant-herbivore and predator-prey interactions are in their infancy. There is a great need for more research, explicitly testing the recent theories suggested by others (e.g. McCluney & Sabo, 2009; Spiller & Schoener, 2008) and expanded here. These efforts will be aided if new studies better document the extent of water limitation and clearly measure and distinguish *per capita* and net population-level interactions using a measure that is comparable across studies (Berlow *et al*., 2004). Methods of standardization in reporting the extent of water availability are also greatly needed. We propose that soil water potential, gravimetric hydration state, and fluid osmolality are comparable across studies and thus these measures should be more widely reported. These are better measures than simply recording precipitation, since total precipitation is not necessarily the best determinant of organismal water availability.

V. EXTENSIONS AND CONSEQUENCES

Our model and predictions suggest that rapid global change in water resources will have significant consequences for species interactions in dryland ecosystems. As variation in water availability increases, so should variability of biotic interactions, assuming that extremes of water availability are not already dominating. In some cases, changes in the sign or strength of interaction outcomes may promote large mismatches in the population sizes of interacting species and in their effects on each other (Holmgren *et al*., 2001; Lima *et al*., 2002*b*; Smith *et al*., 2009). Periods of low water stress may promote increased reproduction of herbivores (especially) and predators (somewhat), leading to increased population densities. For instance, a temporary increase in water availability can increase vascular plant productivity and herbivore numbers in the Atacama Desert and Central Australia (Holmgren *et al*., 2006; Jaksic, 2001; Letnic *et al*., 2005), leading to rodent outbreaks (Lima *et al*., 2002*b*). Numbers of vertebrate predators have also been shown to increase, although there is a delayed response (Holmgren *et al*., 2001; Letnic *et al*., 2005; Lima *et al*., 2002*a*). A sudden decrease in water availability would be expected to cause increases in *per capita* herbivory and predation with high densities of individuals, which could lead to rapid and unpredictable changes in population abundances, including population crashes (Holmgren *et al*., 2001; Lima *et al*., 2002*b*). Thus, consequences of increases in the variability of water resources and extreme events may be exacerbated by fluctuations in species interactions, leading to population outbreaks and die-offs.

Alternatively, some of the moisture variability inherent in dryland ecosystems, when combined with variable species life history and drought-tolerant life stages, is essential to maintaining coexistence and diversity (Chesson *et al*., 2004) and this variability may also increase species coexistence by limiting the effects of strong species interactions (Navarrete & Berlow, 2006), which can destabilize communities (May, 1973; McCann *et al*., 1998). Despite the increases in coexistence and diversity conveyed by some moisture variability, as discussed above, we could also expect to see greater incidences of occasional outbreaks and die-offs in these systems, especially with large increases in water resource variability.

We note that at the lowest water availabilities another threshold may exist, where species interactions are near zero due to the inactivity or extirpation of one or more of the interacting species. While dryland species are often adapted to climate variability, there may be levels of aridity for which species cannot survive. For instance, the hyper-arid Atacama Desert in Chile supports relatively little life over much of its range (Barros *et al*., 2008; Navarro-Gonzalez *et al*., 2003). A similar threshold is likely to exist at the highest level of moisture, where catastrophic flood disturbance may reduce interactions (e.g. Spiller & Schoener, 2008). Reduction in the strength of population-level interaction outcomes caused by climate extremes would result from large negative effects of these events on populations and communities, primarily through mortality or dispersal (Gutschick & BassiriRad, 2003; McKechnie & Wolf, 2010; Thibault & Brown, 2008). Additionally, there is a growing consensus that the magnitude and frequency of extreme climate events will exceed past natural variability, invalidating the concept of "stationarity" (i.e. the future will be similar to the past) for ecology or management (Jentsch, Kreyling & Beierkuhnlein, 2007; Milly *et al*., 2008). Very high variability in water availability may prevent populations growing in response to precipitation pulses from reaching resistant or tolerant life stages and reduce the diversity-maintaining storage effect (Chesson *et al*., 2004).

Thus, extreme climate events may have particularly strong consequences for populations, communities, and ecosystems that may be beyond our ability to predict based on current observations.

There is considerable evidence that alterations in water supply can have ecosystem-level effects that are mediated by species interactions. Several recent studies suggest that the response of animal interactions to changes in precipitation can have ecosystem consequences, without specifically measuring the interaction. Warne *et al*. (2010) showed that in the Chihuahuan Desert, winter droughts can decrease forage quality by reducing C_3 plants and that this affects the entire food web, which they predict would reduce nutrient cycling and reduce secondary production. In central Kentucky, Lensing & Wise (2006) found that precipitation changes affected interactions between spiders and decomposers, which altered rates of organic matter decomposition. When a moist site experienced decreased rainfall, spiders sped decomposition, while at higher rainfall, spiders had little effect, or possibly a slight negative effect on decomposition. They suggested changes in decomposition with altered moisture resulted from altered spider-collembola-fungus interaction outcomes. Other studies have documented similar patterns, suggesting that species interactions modify the ecosystem response to changes in water availability (Brown *et al*., 2001; Ernest *et al*., 2000; Guo & Brown, 1996; Owen-Smith & Mills, 2006).

VI. CONCLUSIONS

(1) We summarize existing studies to show that variation in water availability in response to a changing climate will have strong effects on species interactions.

(2) While these interactions may be complex, nonlinear, and context dependent, recent evidence suggests that the balance of interactions may be important in determining the linearity of bottom-up responses of communities to moisture and in modulating community patterns and ecosystem processes.

(3) Following from hypothetical water availability scenarios and ecological theory, we illustrate how our model can be used to make predictions for responses of species interactions and patterns of trophic biomass to changes in water availability. We suggest that, for drylands with intermediate water availability and moderate variability, increases in mean water availability or small increases in variation could encourage linear, bottom-up accumulation of trophic biomass, but declines in mean water availability or large increases in variability may lead to nonlinear top-down responses.

(4) Our conceptual model is designed to guide future research efforts to link alteration of water availability regimes in dryland systems to changes in biotic interactions that will ultimately have strong effects on populations, communities, and ecosystems.

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Table 1. Definitions of interaction outcome terms used herein.

Interaction term	**Sign**	**Definition**
Plant-plant		
Competition	- -	The populations of two species of plants suppress each other
Facilitation	+ + or + 0	The population of one species of plant benefits the other or they mutually benefit each other
Plant-herbivore		
Herbivory	- +	A population of a plant is negatively affected by an herbivore population, but the plant population positively affects the herbivore population
Commensalism	0 +	A population of a plant is unaffected by an herbivore population, but the plant population positively affects the herbivore population
Mutualism	+ +	Populations of a plant and an herbivore benefit one another
Predator-prey		
Predation	+ -	A population of a predator is positively affected by a prey population, but the predator population negatively affects the prey population
Commensalism	+ 0	A population of a predator is positively affected by a prey population, but the predator population does not affect the prey population
All groups		
Neutral	0 0	Neither population influences the other

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Table 2. Studies showing clear responses of species interactions to changes in water availability. For plant-plant interactions, this list is not exhaustive, but for plant-herbivore and predator-prey interactions, this list contains all papers we could find that measure the response of species interactions to changes in water availability. For definitions of interaction terms, see Table 1.

Type of change in water	Interacting species (sp. 1 – sp. 2)	Interaction at low moisture[1]	Interaction at high moisture[1]	Measure	Climate / location[2]	Reference
			Plant-plant interactions			
Xeric *vs* mesic sites and wet and dry years	Bunchgrasses – *Lesquerella carinata*	Facilitation (0 +)	Competition (- -)	Spatial associations and seedling survival	Xeric/western Montana	Greenlee & Callaway (1996)
Natural precipitation gradient	*Stipa tenacissima – Lepidium subulatum*	Facilitation (0 +)	Facilitation (0 +)	Spatial associations	Semi-arid/ central Spain	Soliveres *et al*. (2010)
Temporal variation in climate (precipitation)	*Stipa tenacissima – Lepidium subulatum*	Facilitation (0 +)	Competition (- -)	Seedling/sapling growth	Semi-arid/ central Spain	Soliveres *et al*. (2010)
Temporal variation in climate (precipitation)	*Koeleria castellana – Helianthemum squamatum*	Neutral (0 0)	Facilitation (0 +)	Spatial associations	Semi-arid/ central Spain	de la Cruz *et al*. (2008)
Temporal variation in climate (precipitation)	*Thymus lacaitae – Helianthemum squamatum*	Neutral (0 0)	Facilitation (0 +)	Spatial associations	Semi-arid/ central Spain	de la Cruz *et al*. (2008)

Temporal variation in climate (precipitation)	*Herniaria fruticosa – Helianthemum squamatum*	Facilitation (0 +)	Neutral (0 0)	Spatial associations	Semi-arid/ central Spain	de la Cruz *et al*. (2008)
Temporal variation in climate (precipitation)	*Teucrium pumilum – Helianthemum squamatum*	Facilitation (0 +)	Facilitation (0 +)	Spatial associations	Semi-arid/ central Spain	de la Cruz *et al*. (2008)
Mesic *vs* xeric habitats	*Mimosa luisana – Neobuxbaumia tetetzo*	Competition (- -)	Competition (- -)	Seedling survival	Semi-arid/ Mexico	Valiente-Banuet & Ezcurra (1991)
Natural precipitation gradient	Perennial plants – perennial plants (community-level study)	Competition (- -)	Facilitation (+ +)	Co-occurrence analyses	Semi-arid/ central - SE Spain	Maestre *et al*. (2010)
Temporal variation in climate (precipitation)	*Mimosa luisana – Agave macrocarpa*	Facilitation (0 +)	Neutral (0 0)	Seedling survival	Semi-arid/ Mexico	Arizaga & Ezcurra (2002)
Watering treatments	Grasses – *Prosopis glandulosa*	Competition (- -)	Competition (- -)	Seedling survival	Semi-arid/ Texas	Brown & Archer (1999)
Watering treatments	*Austrocedrus chilensis* seedlings – shrubs	Competition (- -)	Facilitation (+ +)	Number of juveniles, *Austricedrus* recruitment	Semi-arid to sub-humid/ northern Patagonia Argentina	Kitzberger *et al*. (2000)

Watering treatments	*Cercocarpus* seedlings – *Artemisia* shrubs	Competition (- -)	Competition (- -)	Seedling survival	Wet winter, dry summer/ NE Utah	Ibanez & Schupp (2001)
Seasonal precipitation	*Cryptantha flava* – *Artemisia* and *Chrysothamnus* shrubs	Competition (- -)	Facilitation (+ 0)	Total number of rosettes, number of flowering stalks	Arid/ NE Utah	Peek & Forseth (2003)
Wet *vs* dry year	*Retama sphaerocarpa* shrubs – herbal species	Facilitation (0 +)	Competition (- -)	Species composition of soil seed bank, seed density	Semi-arid/ SE Spain	Pugnaire & Lazaro (2000)
Productivity gradient	*Retama sphaerocarpa* shrub – herbal species	Facilitation (0 +)	Neutral (0 0)	Plant dry mass	Semi-arid/ SE Spain	Pugnaire & Luque (2001)
Mesic *vs* xeric habitats	*Olneya tesota* – herb	Facilitation (0 +)	Competition (- -)	Plant richness and abundance	Arid/ Sonoran Desert	Tewksbury & Lloyd (2001)
Temporal variation in climate (precipitation)	Juvenile *Pinus edulis* – *Fallugia paradoxa*	Facilitation (+ 0)	Competition (- -)	Height and mortality of juvenile *P. edulis*	Semi-arid/ southwestern US woodland	Sthultz *et al*. (2007)
Watering experiment	*Larrea tridentate* – *Opuntia rastrera*	Neutral (0 0)	Competition (- -)	Plant and soil water potential	Semi-arid/ Chihuahuan Desert	Briones *et al*. (1998)
Natural precipitation gradient	Juvenile *Stipa tenacissima* – shrub *Cistus clusii*	Neutral (0 0)	Facilitation (+ 0)	Basal diameter, height, number of tillers, and dry mass	Semi-arid/ SE Spain	Armas & Pugnaire (2005)

Temporal variation in climate (precipitation)	*Aspidosperma quebracho-blanco* – nurse plants	Competition (- -)	Facilitation (+ 0)	Seedling survival	Arid/ central Argentina	Barchuk *et al.* (2005)
Precipitation events, soil water content	*Ambrosia dumosa* shrubs – annuals		Facilitation (0 +)	Shoot elongation, biomass, seeds per spikelet, seeds per head	Arid/ Mojave Desert	Holzapfel & Mahall (1999)
Temporal variation in climate (precipitation)	Shrub – annuals	Competition (- -) or neutral (0 0)	Neutral (0 0) or facilitation (0 +)	Fitness parameters: density, no. of seeds/plant	Arid/ Negev Desert	Tielborger & Kadmon (2000)
Natural precipitation gradient	*Stipa tenacissima – Pistacia lentiscus* seedlings	Competition (- -)	Competition (- -)	Seedling survival	Semi-arid steppe/ SE Spain	Maestre & Cortina (2004)
Rainfall	*Larrea divaricata* – desert shrubs	Competition (- -)		Plant density	Arid/ Sonoran and Mojave deserts	King & Woodell (1973)
Natural variation in precipitation - measured water potential	*Ambrosia – Larrea*	Competition (- -)		Plant density	Arid/ Mojave Desert	Fonteyn & Mahall (1978)
No manipulation or measurement of water	*Carnegiea gigantean – Cercidium microphyllum* nurse plant	Facilitation (+ 0)	Competition (- -)	Stem die back, nurse plant mortality – trunk diameter	Arid/ Sonoran Desert	McAuliffe (1984)
Plant-herbivore						

Irrigation	*Acacia karroo* seedlings – simulated goat browsing	Herbivory (- +)	Mutualism (+ +)	Seedling growth	Semi-arid/ South Africa	Scogings & Mopipi (2008)
Precipitation	Saguaro cacti – wood rats	Herbivory (- +)	Mutualism (+ +)		Arid/ Sonoran Desert	B. Wolf (unpublished data)
Irrigation	Senita cacti – senita moths	Mutualism (+ +)	Mutualism (+ +)	Flower, fruit, and seed production	Arid/ Sonoran Desert	Holland (2002)
Soil moisture	Vegetation – sheep	Commensal (0 +)	Commensal (0 +)	Vegetation biomass	Semi-arid/ Patagonia Argentina	Utrilla *et al.* (2006)
Distance from river	Moist cottonwood and willow leaves – consumers	“Herbivory” (- +)	Neutral (0 0)	Net consumption	Semi-arid/ SE Arizona river	Sabo *et al.* (2008)
Moisture addition and precipitation	Moist cottonwood leaves – field crickets	“Herbivory” (- +)	Neutral (0 0)	*Per capita* consumption	Semi-arid/ SE Arizona river	McCluney & Sabo (2009)
Observed and altered soil moisture	Seeds – rodents	Weak herbivory (- +)	Strong herbivory (- +)	Seeds caches taken / caches available	Semi-arid/ Nevada pine forest	Vander Wall (1998)
Water bowls added	Seeds – ravens	Weak herbivory (- +)	Strong herbivory (- +)	Giving-up density	Arid/ Simpson Desert	Kotler *et al.* (1998)
Water bowls added	Seeds – rodents	Herbivory (- +)	Herbivory (- +)	Giving-up density	Arid/ Simpson Desert	Kotler *et al.* (1998)
Water bowls added	Nubian ibex – alfalfa pellets	Weak herbivory (- +)	Strong herbivory (- +)	Giving-up density	Arid/ Negev Desert	Hochman & Kotler (2006)
Regulated *vs* unregulated river	Cottonwood saplings – voles	Herbivory (- +)	Neutral (0 0)	Sapling survival	Semi-arid/ Colorado and Utah rivers	Andersen & Cooper (2000)

Predator-prey						
Moisture addition	Field crickets – wolf spiders	Predatory (- +)	Neutral (0 0)	Dynamic index of *per capita* effects	Semi-arid/ SE Arizona river	McCluney & Sabo (2009)
Rainfall	Elephants – lions	Strong predation (- +)	Weak predation (- +)	Kill rate	Semi-arid/ Zimbabwe	Loveridge *et al.* (2006)
Natural variability	Spiders – lizards	Pattern of weak predation, strong predation, weak predation with increasing precipitation		Pop effect size: ln (no predator / predator)	Bahamian Islands	Spiller & Schoener (2008)

[1] The symbols for the effect are noted in the order of the list of species 1 and 2. See Table 1 for definitions.

[2] Generally, climate and location are listed as reported by the authors.

Table 3. Common interaction outcomes at each level of water availability. This summary is based on the papers listed in Table 2 and others discussed in the text. For definitions of interaction terms, see Table 1. The term "strong" indicates that the strength of the interaction is high.

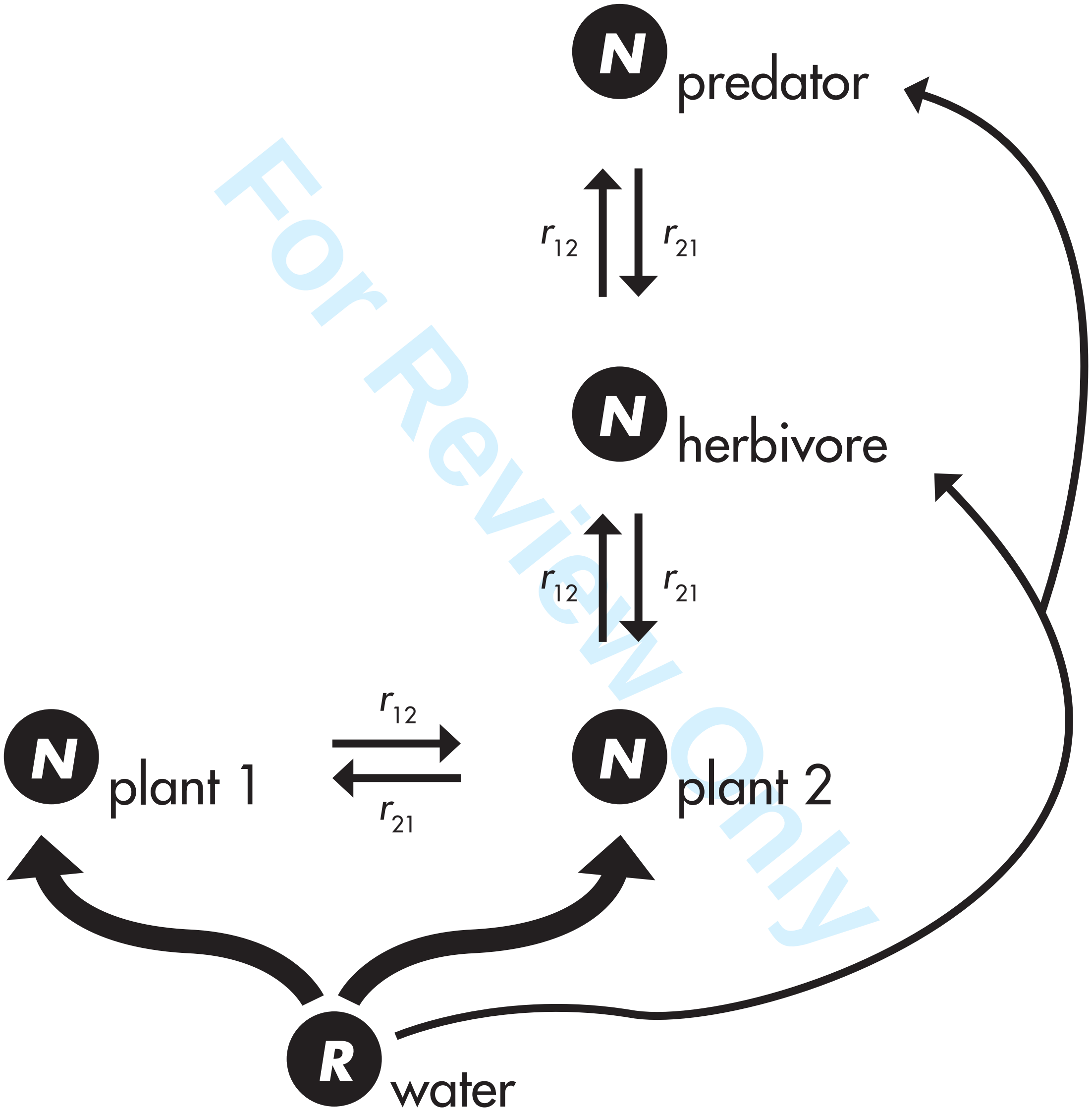
	Common interaction outcome at each water availability				
Interacting groups	Very low (severe drought)	Low	Medium	High	Very high
Plant-plant	neutral	competition	facilitation	competition	neutral
Plant-herbivore	neutral	strong herbivory	herbivory	commensalism or mutualism	neutral
Predator-prey	neutral	strong predation	predation	commensalism	neutral

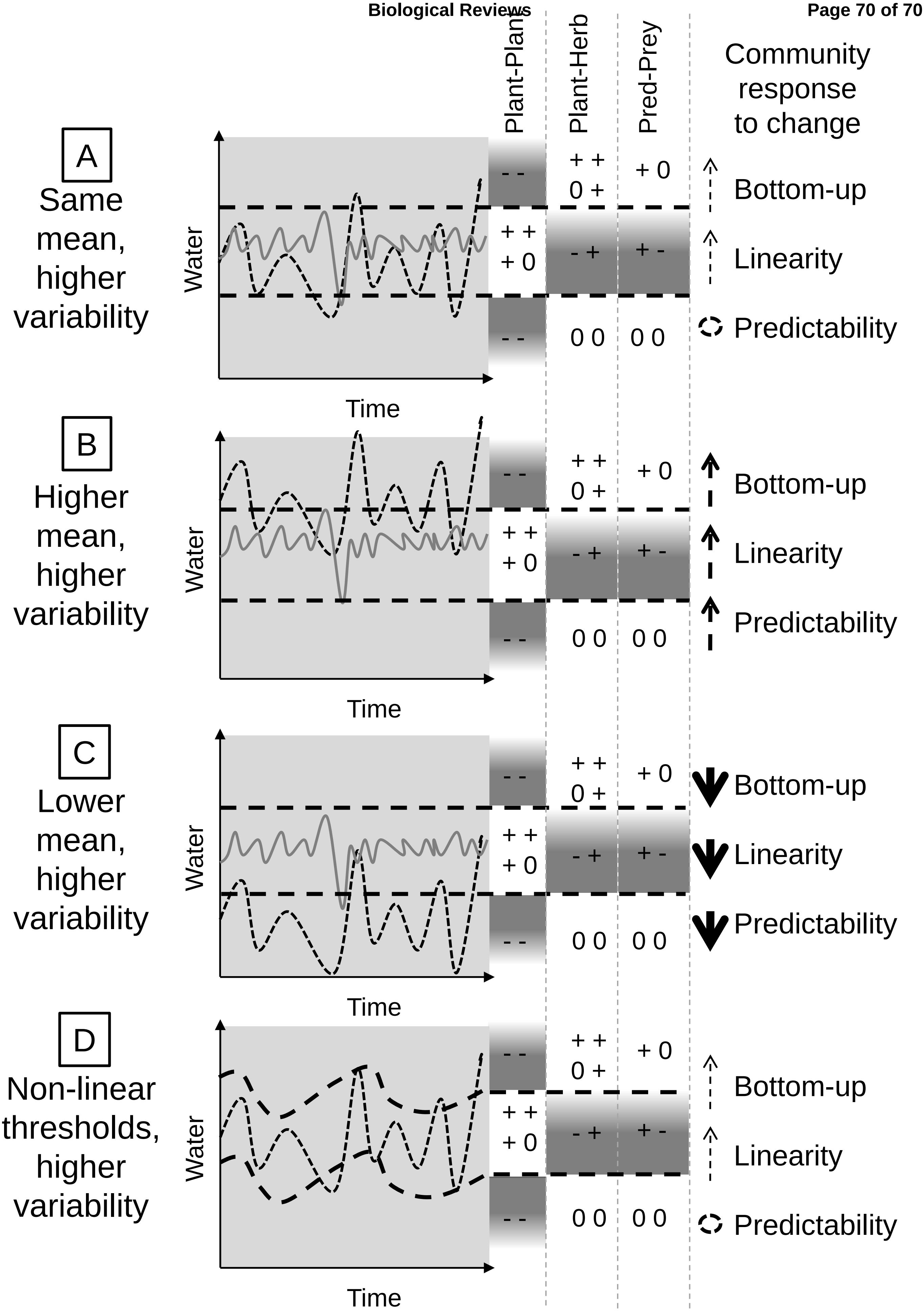
FIGURE LEGENDS

Fig. 1. Conceptual diagram of interactions between selected functional types examined herein. *R* refers to the supply rate of a resource (water), *N* are the densities of each species, and *r* are the interaction outcomes (partial correlation coefficients) between two species. Interaction outcomes can change in sign and magnitude and are a function of several factors, including direct and indirect *per capita* effects and densities (*N*). Water supply rates influence interaction outcomes and species densities through bottom-up effects on productivity and by modulating *per capita* interactions directly.

Fig. 2. Conceptual model illustrating possible organismal interactions under scenarios of current and future water availability. Solid grey lines indicate hypothetical current conditions, which we assume are intermediate levels of water availability and moderate variation. Dashed black lines indicate scenarios of possible future water availability conditions with each scenario occurring in a separate graph: (A) equal mean/higher variation, (B) higher mean/higher variation, (C) lower mean/higher variation, and (D) shifting climate thresholds. Long-dashed black lines indicate water thresholds for sign changes in interaction outcomes. Interactions of a given type occur in the space between any two-climate thresholds and this type is labeled on the right-hand side of each graph (see Table 1 for definitions of these symbols) for each of the three categories of interactions we consider. The grey highlighting behind the category designations indicate a change in the strength of interactions, with stronger interactions occurring at darker grey levels

of water availability. We note that for all graphs, at very low or very high water levels, neutral interactions (0 0) are expected, because severe droughts or flooding disturbance are expected to reduce the densities of species low enough to prevent interactions from occurring. At far right, we indicate predictions for how the community will respond to each scenario of water availability. “Bottom-up” refers to the degree to which bottom-up or top-down forces influence the community, “linearity” indicates the degree to which patterns of trophic biomass will respond linearly to changes in water availability, and “predictability” suggests the change in the predictability of responses of trophic biomass to changes in water availability. D shows a future climate scenario with increased variation in water resources and an intermediate mean, but in this case, the thresholds for changes in interaction outcomes are not constant, but instead vary across time. These thresholds are likely to be based on a variety of other variables that change across time (e.g. temperature). See Table 2 for a list of the studies used in generating this model.


N
predator
r_{12}
r_{21}
N
herbivore
r_{12}
r_{21}
N
plant 1
r_{12}
r_{21}
N
plant 2
R
water


Plant-Plant
Plant-Herb
Pred-Prey
Community response to change
A
Same mean, higher variability
Water
Time
- -
+ +
0 +
+ 0
+ +
+ 0
- +
+ -
- -
0 0
0 0
Bottom-up
Linearity
Predictability
B
Higher mean, higher variability
Water
Time
- -
+ +
0 +
+ 0
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Predictability
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Lower mean, higher variability
Water
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Bottom-up
Linearity
Predictability
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Non-linear thresholds, higher variability
Water
Time
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