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

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

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5 19 ABSTRACT
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7 20 Species interactions play key roles in linking the responses of populations, communities,
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10 21 and ecosystems to environmental change. For instance, species interactions are an important
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12 22 determinant of the complexity of changes in trophic biomass with variation in resources. Water
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14 23 resources are a major driver of terrestrial ecology and climate change is expected to greatly alter
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16
17 24 the distribution of this critical resource. While previous studies have documented strong effects
18
19 25 of global environmental change on species interactions in general, responses can vary from
20
21 26 region to region. Dryland ecosystems occupy more than one-third of the Earth's land mass, are
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23
24 27 greatly affected by changes in water availability, and are predicted to be hotspots of climate
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26 28 change. Thus, it is imperative to understand the effects of environmental change on these
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28
29 29 globally significant ecosystems.

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31 30 Here, we review studies of the responses of population-level plant-plant, plant-herbivore,
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33 31 and predator-prey interactions to changes in water availability in dryland environments in order
34
35 32 to develop new hypotheses and predictions to guide future research. To help explain patterns of
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37 33 interaction outcomes, we developed a conceptual model that views interaction outcomes as
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39 34 shifting between (1) competition and facilitation (plant-plant), (2) herbivory, neutralism, or
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41 35 mutualism (plant-herbivore), or (3) neutralism and predation (predator-prey), as water
42
43 36 availability crosses physiological, behavioural, or population-density thresholds. We link our
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45 37 conceptual model to hypothetical scenarios of current and future water availability to make
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47 38 testable predictions about the influence of changes in water availability on species interactions.
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49 39 We also examine potential implications of our conceptual model for the relative importance of
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51 40 top-down effects and the linearity of patterns of change in trophic biomass with changes in water
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41 availability. Finally, we highlight key research needs and some possible broader impacts of our
 42 findings. Overall, we hope to stimulate and guide future research that links changes in water
 43 availability to patterns of species interactions and the dynamics of populations and communities
 44 in dryland ecosystems.

45

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

48

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70

71 I. INTRODUCTION

72 (1) Overview

73 One of the key challenges facing ecologists is to link ongoing global environmental
 74 changes to the interconnected responses of organisms, populations, communities, and
 75 ecosystems (Suding *et al.*, 2008; Tylianakis *et al.*, 2008; Yang & Rudolf, 2010). Many of these
 76 responses are directly predictable from altered environmental conditions. For example,
 77 increased precipitation may result in bottom-up effects on plant and rodent communities (Baez *et*
 78 *al.*, 2006; Ernest, Brown & Parmenter, 2000), decreased winter precipitation can alter energy and
 79 nutrient flow through food webs (Warne, Pershall & Wolf, 2010), and higher temperatures may
 80 cause extreme mortality in small birds (McKechnie & Wolf, 2010). However, other responses
 81 may be less intuitive because they result from complex interactions among species (Brown *et al.*,

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5 82 2001; Ernest *et al.*, 2000; Guo & Brown, 1996; Suttle, Thomsen & Power, 2007). For instance,
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7 83 population dynamics of some rodent communities in the Chihuahuan Desert were strongly
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10 84 correlated with the response of plant communities to precipitation changes, while others were not
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12 85 (Ernest *et al.*, 2000). To better predict the ecological consequences of global environmental
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14 86 change, we require a greater understanding of how species interactions vary in rapidly shifting
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17 87 environments and how these changes influence responses at other levels of biological
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19 88 organization (Emmerson *et al.*, 2005).

20
21 89 Interspecific interactions, including competition, facilitation, herbivory, mutualism, and
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23
24 90 predation (see Table 1 for definitions), are fundamental to the dynamics of populations,
25
26 91 communities, and ecosystems (Fox, Fairbairn & Roff, 2001; Fretwell, 1987; Jones & Lawton,
27
28 92 1996; Paine, 1980) and are particularly sensitive to environmental change (Brooker, 2006).
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30
31 93 Interspecific interactions can be quantified by a large number of metrics (reviewed in Berlow *et*
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33 94 *al.*, 2004). Some measures examine *per capita* effects of individuals of one species on
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35 95 individuals of another, whereas others examine the overall net effects of one population on
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38 96 another. Many experimental studies examine the outcome of interactions by looking for
39
40 97 statistical effects of one population on another (Berlow *et al.*, 2004). Herein, we refer to these
41
42 98 population-level statistical methods of measuring species interactions as interaction outcomes
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44
45 99 (*sensu* Holland & DeAngelis, 2009; see Fig. 1, Table 1). Interaction outcomes measure the
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47
48 100 combined effects of one species on another and incorporate the effects of changes in density as
49
50 101 well as direct and indirect *per capita* interactions. Here we focus on interaction outcomes in our
51
52 102 conceptual model and discussion because of their common use in the literature, but we also
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55 103 include information on other measures of species interactions.

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5 104 Species interactions are highly dynamic in space and time (Holland & DeAngelis, 2009;
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7 105 Paine, 1980; Ruesink, 1998). Changes in the strength and sign of interaction outcomes can arise
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9
10 106 from many mechanisms, including shifts in density or direct *per capita* interaction strengths of
11
12 107 one or both of the species involved in the interaction. Theoretically, an interaction outcome of
13
14 108 mutualism (+ +) can transition to commensalism (0 +) or parasitism (+ -) as one species reduces
15
16 109 its supply of resources to another and/or the increased density of one species leads to its
17
18 110 increased exploitation of the other species (Holland & DeAngelis, 2009). Alternatively, the
19
20 111 interaction outcome of predation (+ -) may transition to commensalism (0 +) with weakened *per*
21
22 112 *capita* interaction strengths and weakened consumer functional responses (Holland &
23
24 113 DeAngelis, 2009). For instance, a major research effort has investigated how plant-plant
25
26 114 interaction outcomes transition between facilitation and competition across gradients of
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28 115 physiological stress and water availability and many mechanistic hypotheses have been proposed
29
30 116 to explain the generality of patterns of these interaction outcomes (Maestre *et al.*, 2009).
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36 117 Despite the fundamental importance of species interactions for the structure and
37
38 118 dynamics of populations, communities, and ecosystems, we currently have little conceptual or
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40 119 empirical understanding of how global environmental change will impact species interactions
41
42 120 and their consequences for communities and ecosystems. Tylianakis *et al.* (2008) recently
43
44 121 reviewed the effects of global environmental changes on species interactions worldwide. In
45
46 122 addition to climate, these included CO₂ enrichment, nitrogen deposition, biotic invasions, and
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48 123 land-use changes. They found strong effects of these environmental drivers on species
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50 124 interactions, but great variability in responses across different drivers of change and types of
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5 125 species interactions. This led them to call for a more extensive investigation of how biotic and
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7 126 abiotic context influences the effects of environmental change on species interactions.
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10 127 While the arctic is widely thought to be a hotspot for climate-induced ecological change
11
12 128 (see Shaver *et al.*, 2000), dryland ecosystems are also predicted to be particularly sensitive to
13
14 129 climate change (Diffenbaugh, Giorgi & Pal, 2008). Drylands are defined as regions that have an
15
16 130 index of aridity (ratio of mean annual precipitation to mean annual potential evapotranspiration)
17
18 131 below 0.65 (Middleton & Thomas, 1997). These ecosystems include key terrestrial biomes
19
20 132 covering 41% of Earth's land surface and supporting over 38% of the total global human
21
22 133 population of 6.5 billion (Reynolds *et al.*, 2007), and are highly vulnerable to global change and
23
24 134 desertification (Korner, 2000; Reynolds *et al.*, 2007).
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29 135 Here we introduce a conceptual model, informed by a broad review of the literature
30
31 136 (Table 2), that examines how patterns of variable resources in dryland environments influence
32
33 137 interaction outcomes whose magnitude and sign can change depending on changes in water
34
35 138 availability over time (Fig. 2). We focus on changes in water availability, as water is the most
36
37 139 important resource shaping the biology of dryland environments (Noy-Meir, 1973, 1974) and is
38
39 140 highly sensitive to anthropogenic global environmental change (IPCC, 2007; Pearce, 2006).
40
41 141 Water availability can be modified by inputs such as precipitation and irrigation, by losses such
42
43 142 as evapotranspiration or infiltration, and by topography and the distribution of water bodies on
44
45 143 the landscape (Belnap *et al.*, 2005). After discussing our model, we highlight key limitations in
46
47 144 our understanding of the linkages between changes in water availability and species interactions,
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49 145 suggesting needs for further study. We then discuss how our model could be used to predict
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5 146 potential consequences of changes in species interactions under hypothetical scenarios of current
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7 147 and future water availability.
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9
10 148 **(2) Species interactions in dryland ecosystems**

11
12 149 Dryland ecosystems are often characterized by wide variation in precipitation inputs
13
14 150 within years, between years, and across decades (Rodriguez-Iturbe *et al.*, 1999). Some of these
15
16 151 systems have strongly seasonal patterns of precipitation, with moderate levels of variability
17
18 152 between years, whereas others are more stochastic. Variation may also follow decadal patterns.
19
20 153 For example, the El Niño-Southern Oscillation (ENSO) is a cyclic phenomenon with a
21
22 154 periodicity of approximately five years that is an important driver of patterns of precipitation in
23
24 155 dry regions on both sides of the Pacific Ocean (Holmgren *et al.*, 2001; Trenberth, 1997;
25
26 156 Woodward, Lomas & Quaipe, 2008). These changes in the timing and quantity of rainfall can
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28 157 modulate seed-bank dynamics (Gutierrez & Meserve, 2003), trigger increases or decreases in net
29
30 158 primary production (Holmgren *et al.*, 2006), influence population dynamics (Catenazzi &
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32 159 Donnelly, 2007; Lima, Stenseth & Jaksic, 2002a), modulate predator-prey dynamics (Letnic,
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34 160 Tamayo & Dickman, 2005; Lima *et al.*, 2002a), and alter ecosystem subsidies (Polis *et al.*,
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36 161 1997).
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42 162 Many long-lived plants and animals are adapted to, or tolerate, the somewhat predictable
43
44 163 variability of ENSO cycles and other seasonal patterns (Chesson *et al.*, 2004; Noy-Meir, 1973,
45
46 164 1974). For instance, resistant or dormant life stages often increase the survival of many dryland
47
48 165 plants and animals during periods of drought (Chesson *et al.*, 2004). However, in many cases,
49
50 166 dryland organisms respond to changes in water availability through physiological or behavioural
51
52
53 167 mechanisms, which can rapidly alter their interactions with other species (McCluney & Sabo,
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5 168 2009; McDowell *et al.*, 2008; Schowalter, Lightfoot & Whitford, 1999; Warne *et al.*, 2010).

6
7 169 These flexible organismal responses may be an effective means of dealing with unpredictable

8
9
10 170 variation in water availability and extreme events (Stahlschmidt *et al.*, 2011), and may be the

11
12 171 only possible coping mechanisms when a tolerant life stage has not been reached during the

13
14 172 sudden onset of a drought. Despite the ability of dryland organisms to tolerate resource

15
16 173 variability, extreme events can still have large effects, altering population dynamics, resetting

17
18 174 interactions among species, or altering the entire ecosystem (Breshears *et al.*, 2005; McKechnie

19
20 175 & Wolf, 2010). Thus, species interactions may be even more prone to rapid fluctuations in

21
22 176 drylands than in other terrestrial ecosystems, and may commonly transition between multiple

23
24 177 interaction outcomes.

25
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27
28 178 **(3) Climate change, water availability, and biological responses in dryland ecosystems**

29
30 179 Climate change will exert strong effects on water availability in dryland ecosystems by

31
32 180 altering global atmospheric circulation and resulting patterns of precipitation (IPCC, 2007;

33
34 181 Zhang *et al.*, 2007). More intense storms and droughts are expected, with increased variation in

35
36 182 ground-level water availability compared to current conditions (IPCC, 2007). Shifts in the

37
38 183 timing and quantity of rainfall are also expected, but whether there will be an increase or

39
40 184 decrease overall or within seasons varies geographically (IPCC, 2007). Although we generally

41
42 185 focus on the effects of changing water availability, temperature also influences water availability,

43
44 186 and thus it is important to note that altered rainfall and increasing temperature will interact to

45
46 187 affect dryland species. Increased temperatures associated with climate change will pose

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48 188 physiological water balance challenges to a wide suite of organisms as water losses increase (e.g.

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50 189 Wolf & Walsberg, 1996) and soil moisture and surface water declines with increased

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5 190 evapotranspiration. Increases in the frequency, intensity, and duration of heat waves are
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7 191 predicted (Meehl & Tebaldi, 2004), which may have great consequences for many animals
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9
10 192 (McKechnie & Wolf, 2010) and some plants (Smith, Diddenzopfy & Nobel, 1984) that are
11
12 193 already near their physiological heat and water balance limits. Increases in night-time minimum
13
14 194 temperatures (Karl, Knight & Plummer, 1995) may also create heat and water challenges for
15
16
17 195 nocturnal dryland animals, who may not be able to migrate or alter their behaviour in response to
18
19 196 climate changes (Tracy & Walsberg, 2002). These temperature changes will likely alter
20
21 197 interspecific and intraspecific behaviours and interactions. Thus, both temperature and
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23
24 198 precipitation are likely to alter the distribution, variability, and seasonality of water availability.
25
26 199 Almost every dryland region of the Earth has distinct rainfall patterns to which its organisms and
27
28 200 communities are phenologically adapted. Shifts in variation, timing, or magnitude of rainfall are
29
30 201 expected to have significant ecological impacts on these systems (e.g. Suttle *et al.*, 2007; Warne
31
32 202 *et al.*, 2010).

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37 38 204 **II. LINKING WATER AVAILABILITY TO SPECIES INTERACTIONS IN DRYLAND** 39 40 205 **ENVIRONMENTS**

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42 206 We propose a conceptual model (Fig. 2) to examine how variation in water availability
43
44 207 (e.g. precipitation, fog, soil moisture, surface water) varies across time and how this influences
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46 208 species interaction outcomes at the population level in drylands. These outcomes may change in
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48 209 magnitude and sign as they cross water availability thresholds. We develop our model by
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50 210 conducting a literature review and tabulating the observed responses of species interactions to
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52 211 changes in water availability. Our intention here is not to make definitive conclusions about
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5 212 general patterns of species interactions in all drylands globally, but rather to: (1) examine
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7 213 patterns reported in the literature, (2) review and develop hypotheses to explain these patterns,
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10 214 and (3) present example predictions arising from these hypotheses. In our review of plant-plant
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12 215 interactions, we include a large collection of studies, but do not attempt to include all studies on
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14 216 this topic, which have been recently reviewed elsewhere (Gómez-Aparicio, 2009; Maestre,
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16
17 217 Valladares & Reynolds, 2005). For plant-herbivore and predator-prey interactions, we include
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19 218 results of a thorough search, including all studies we could find, though few such studies occur.
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21 219 We examine the number of studies that suggest each type of change in interaction with altered
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24 220 water availability.

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26 221 Though very useful in many contexts, here we do not conduct formal effect-size meta-
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28 222 analysis for several reasons: (1) there were insufficient usable studies on plant-herbivore and
29
30 223 predator-prey interactions, (2) a recent meta-analysis has reviewed the outcome of plant-plant
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32 224 interactions at different stress levels (Maestre *et al.*, 2005), and (3) effect-size-based meta-
33
34 225 analysis is geared more towards making general conclusions about specific questions than
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36 226 hypothesis generation, and for the current state of our understanding of the topic of this review,
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38 227 hypothesis generation is what is needed. Thus, we tabulated responses of species interactions to
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40 228 changes in water availability and observed agreement or disagreement between studies, as well
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42 229 as our knowledge of particular aspects of these studies, to develop hypotheses or consider
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44 230 existing hypotheses to explain the observed patterns. Finally, we used these hypotheses to
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46 231 inform our conceptual model and make predictions for particular scenarios of initial and future
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48 232 conditions of water availability.
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5 233 Our model differs from past conceptual approaches, which have focused on (1) responses
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7 234 of biogeochemical processes or ecosystem properties, such as net primary productivity, to global
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9 235 change, rather than on species interactions (Field *et al.*, 2007; Shaver *et al.*, 2000), (2) individual
10
11 236 traits-based responses without addressing species interactions specifically (Suding *et al.*, 2008),
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14 237 and (3) examination of the effects of gradual but persistent global environmental change on
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17 238 individuals, communities, and ecosystems, without examining changes in environmental
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19 239 variability or in species interactions (Smith, Knapp & Collins, 2009). Although the previously
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21 240 examined topics are extremely important, species interactions remain a critical and understudied
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23
24 241 link between individual traits-based responses and community and ecosystem dynamics.
25
26 242 Moreover, generalized approaches often fall short of adequately describing ecological processes
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28
29 243 in dryland ecosystems (Collins *et al.*, 2008).

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31 244 Our model presents a dynamic worldview, showing species interactions as mutable,
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33 245 agreeing with recent theoretical and empirical insights (Navarrete & Berlow, 2006; Ruesink,
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35 246 1998; Sala & Graham, 2002). The model examines changes in the variability and timing of
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37
38 247 different levels of water availability, not just overall magnitudes, recognizing that the pattern of
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41 248 changes in resources may be just as important as changes in the mean resource level (e.g.
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43 249 Huxman *et al.*, 2004; Warne *et al.*, 2010). In the simplest case, our model presents linear
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45 250 thresholds of water availability at which species interactions change sign (e.g. ++ to +-).
46
47
48 251 However, these thresholds may be dynamic, changing with multiple environmental conditions
49
50 252 and physiological states. For example, the surface activity of Gila monsters (*Heloderma*
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52 253 *suspectum*) in the Sonoran Desert is promoted by increased hydration, with increased surface
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55 254 activity likely leading to stronger predation by the Gila monster (Davis & DeNardo, 2009).

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5 255 Since animal hydration is dependent on multiple environmental factors, not just water
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7 256 availability (e.g. temperature and humidity), nonlinear thresholds may exist across time,
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10 257 dependent on temperature and other factors. Thus, changes in environmental conditions or
11
12 258 functional traits could alter threshold height or shape (e.g. Fig. 2D). Additionally, changes in
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14 259 density of each species will influence the strength and sign of interaction outcomes (Chesson *et*
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16
17 260 *al.*, 2004; Holland & DeAngelis, 2009). Thus, we suggest that our conceptual model provides a
18
19 261 starting point for more quantitative approaches, which link multiple environmental factors and
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21 262 species traits to shifts in interspecific interactions.
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24 263 We divide the discussion of our model into three general categories: plant-plant, plant-
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26 264 herbivore, and predator-prey interaction outcomes (Figs. 1, 2). The plant-plant approach
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28 265 examines changes in the interplay between competition and facilitation interaction outcomes
29
30 266 along a water-stress gradient. The plant-herbivore approach examines shifts between
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32 267 mutualism/commensalism, herbivory, and neutral interactions, whereas the predator-prey
33
34 268 approach examines shifts between commensalism, predation, and neutral interactions with
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36 269 changes in water availability. We offer our model as a set of testable hypotheses rather than a
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38 270 consensus view of how species interactions will definitively change with water availability.
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43 271 **(1) Plant-plant interactions**

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45 272 Plant-plant interactions in dryland ecosystems can shift between facilitation and
46
47 273 competition with altered water availability (see Table 1 for definitions). For example, Maestre &
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49 274 Cortina (2004) compared the net effect of the tussock grass *Stipa tenacissima* on the
50
51 275 shrub *Pistacia lentiscus* at ten experimental sites across a gradient of rainfall in semi-arid
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53 276 Mediterranean steppes, using planted one-year-old seedlings. They found that competitive
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5 277 interactions dominated at both extremes of the gradient, whereas facilitation was found under
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7 278 intermediate conditions.

9
10 279 Plant-plant interactions are mediated by multiple interacting factors, such as resource
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12 280 islands and neighbour-induced changes in microclimate and soil water availability. For instance,
13
14 281 increases in soil moisture, reduced physiological stress provided by the shade of nurse plants,
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16 282 and enhanced soil fertility have been found to be primary mechanisms underlying positive
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18 283 effects of grasses and shrubs on shrub and tree seedling establishment in Mediterranean
19
20 284 environments (e.g. Gómez-Aparicio, 2009; Maestre, Bautista & Cortina, 2003). At the
21
22 285 population/community level, similar mechanisms are thought to underlie positive effects of nurse
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24 286 plants on the richness, abundance, and biomass of annual species (Pugnaire, Armas &
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26 287 Valladares, 2004). On the other hand, rainfall interception by shrub/tree canopies may reduce
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28 288 available soil moisture in areas where rain falls mostly in small events and thus competitive
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30 289 effects may dominate in these situations (Bellot *et al.*, 2004).

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35 290 Transitions from competition to facilitation along environmental gradients depend to a
36
37 291 large degree on the characteristics of the species being studied (Choler, Michalet & Callaway,
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39 292 2001; Maestre *et al.*, 2009), the nature of the stress gradient involved (Kawai & Tokeshi, 2007;
40
41 293 Maestre *et al.*, 2009; Smit, Rietkerk & Wassen, 2009), and the performance measure (Maestre *et*
42
43 294 *al.*, 2005). Additionally, interactions may switch between competition and facilitation as plants
44
45 295 transition to different life-history stages. For example, the giant saguaro in the Sonoran Desert
46
47 296 (*Carnegiea gigantea*) requires a nurse plant (e.g. *Cercidium* sp.) for establishment, but then out-
48
49 297 competes its nurse plant as it matures (McAuliffe, 1984). Depending on all of these factors, both
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5 298 facilitation and competition can be found across broad ranges of water availability, complicating
6
7 299 the task of developing general models for the occurrence of competition and facilitation.
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9
10 300 The development of conceptual models aiming to predict how species interactions change
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12 301 along gradients of ecosystem productivity and resource availability has a long history in plant
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14 302 ecology (Bertness & Callaway, 1994; Goldberg & Novoplansky, 1997; Grime, 1973; Tilman,
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16
17 303 1988). Among these models, the “stress gradient hypothesis” (SGH; Bertness & Callaway,
18
19 304 1994) has been one of the most influential. The SGH predicts that facilitation “...*should be*
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21 305 *particularly common in communities developing under high physical stress and in communities*
22
23 306 *with high consumer pressure* (p.193).” By contrast, “...*where the physical environment is*
24
25 307 *relatively benign and consumer pressure is less severe, positive interactions should be rare; as a*
26
27 308 *result, competitive interactions should be the dominant structuring forces*” (Bertness &
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29 309 Callaway, 1994, p.193). Despite its popularity, support for the SGH is equivocal (e.g. Greenlee
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31 310 & Callaway, 1996; Maestre & Cortina, 2004; Tielborger & Kadmon, 2000) and the generality of
32
33 311 the SGH is currently under vigorous debate (Lortie & Callaway, 2006; Maestre *et al.*, 2005;
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35 312 Michalet, 2006); this has led to new conceptual models (Holmgren & Scheffer, 2010; Maestre *et*
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37 313 *al.*, 2009; Malkinson & Tielbörger, 2010; Smit *et al.*, 2009). The effects of the type of stress, the
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39 314 traits of the species involved, and herbivory on the SGH have all been explored (Maestre *et al.*,
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41 315 2009; Smit *et al.*, 2009). However, refinements have focused on pair-wise species interactions,
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43 316 and thus have not modified the original SGH predictions at the population or community level.
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49 317 In general, we hypothesize that positive plant-plant interactions should occur when soil
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51 318 water availability is increased by one plant above its own water needs, through mechanisms such
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53 319 as hydraulic redistribution and shading, providing supplementary resources to neighbours up to a
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Running Head: Interactions in dryland systems

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5 320 point where water is no longer limiting (Maestre, Cortina & Bautista, 2004). Under conditions
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7 321 of high water stress, canopy interception and water uptake by a given plant may lead to a
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9 322 decrease in water availability under the plant compared to canopy interspaces, promoting
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11 323 competition over facilitation (e.g. Forseth, Wait & Casper, 2001; Knoop & Walker, 1985; Sala *et*
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13 324 *al.*, 1989). Therefore, at high water stress levels, “nurse” plants may be unable to mitigate
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15 325 stressful conditions that decrease the survival and growth of their neighbours (Maestre *et al.*,
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17 326 2004; Michalet, 2006), leading to competitive interaction outcomes. On the other hand, at low
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19 327 levels of water stress (high water availability), other resources may limit plants (e.g. light) and
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21 328 these resources may promote competition. Following large pulses of moisture, limitation may
22
23 329 occasionally be alleviated for short periods, resulting in temporary periods without interactions
24
25 330 (Chesson *et al.*, 2004; Goldberg & Novoplansky, 1997). Holmgren & Scheffer (2010) also argue
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27 331 that facilitative interactions should be more prevalent under intermediate stress conditions.
28
29 332 When water availability is low, facilitative amelioration of stressful conditions by neighbours is
30
31 333 insufficient to counter reductions in water availability. In addition, plants living under more
32
33 334 benign conditions are usually more sensitive to water stress than those found under harsher
34
35 335 conditions, so on average, plants living in areas with moderate water availability may depend
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37 336 more on facilitation than those living under conditions of low water availability (Holmgren &
38
39 337 Scheffer, 2010). Once water stress is alleviated, however, competition may again become
40
41 338 prevalent (see Callaway, 2007 for examples). Thus, we predict that facilitative interactions will
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43 339 be prevalent under moderate conditions, rather than monotonically increasing with abiotic stress
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45 340 (i.e. as water availability decreases), which is in contrast with predictions of the SGH.
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5 341 In summary, we suggest that mechanisms producing variation in plant-plant species
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7 342 interactions as water availability changes reflect trade-offs between the relative increase or
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10 343 decrease in water stress caused by neighbours, combined with overall water limitation and
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12 344 variability in stress-tolerance traits. We predict two threshold lines in our conceptual model,
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14 345 with water availabilities above or below these lines promoting competition and between these
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17 346 lines fostering facilitation (Fig. 2), which is consistent with facilitation occurring at intermediate
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19 347 levels of abiotic stress (Fig. 2; Table 3; Maestre *et al.*, 2009). We also show declines in the
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21 348 strength of competition under the lowest or highest water availabilities, where dormancy or
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24 349 temporary alleviation from abiotic limitation may reduce species interactions. We note that there
25
26 350 may be some deviation from this general hypothesis in any particular study system due to
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28 351 context dependencies (e.g. Devitt & Smith, 2002; Hamerlynck *et al.*, 2002). These context
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31 352 dependencies could be incorporated into the model by altering thresholds (Fig. 2D).

33 353 **(2) Plant-herbivore interactions**

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35 354 Plant-herbivore interactions are highly responsive to water availability and thus are
36
37 355 highly variable temporally. However, studies of water-induced changes in plant-herbivore
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39 356 interactions are less numerous than plant-plant interactions and theories dealing with these
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42 357 phenomena are lacking. Thus, to inform our model, we discuss each appropriate study in the
43
44 358 hope of finding patterns that may suggest appropriate theories for water-based transitions in
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46
47 359 plant-herbivore interactions.

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49
50 360 In many cases, plant-herbivore interaction outcomes switch from mutualistic to
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52 361 herbivorous, depending on water availability. For instance, Scogings & Mopipi (2008)
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54 362 documented a mutualistic interaction outcome between goats (*Capra hircus*) and *Acacia karroo*

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5 363 seedlings under high moisture conditions, where goats stimulated compensatory growth of
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7 364 seedlings (+ +), but herbivorous (+ -) interaction outcomes occurred under drier conditions.
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10 365 Similarly, white-throated wood rats (*Neotoma albigula*) act as dispersers of cacti during periods
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12 366 of normal precipitation when they graze cactus joints and fruit without negatively affecting the
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14 367 whole plant (+ +), but under drought conditions they graze the primary stems of cacti, which can
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16 368 impact plant viability and reproductive output in cacti such as saguaro (+ -) (*Carnegiea*
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18 369 *gigantea*) (B. Wolf, unpublished data). In this case, rodents disperse seeds under high-moisture
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20 370 conditions, but kill the cacti or reduce their long-term reproduction under low moisture
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22 371 availability. On the other hand, water additions sometimes have no effect. Holland (2002)
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24 372 irrigated senita cactus (*Pachycereus schottii*) and found positive effects of senita moths (*Upiga*
25
26 373 *virescens*) on cactus reproduction, but no effect of water availability on moth pollination or
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28 374 larval fruit consumption. Also, Utrilla, Brizuela & Cibils (2006) found no net effect of a sheep
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30 375 (*Ovis aries*) population on vegetation populations, regardless of soil moisture.
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36 376 In other situations, little possibility for mutualism exists, but shifts from neutral to
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38 377 herbivorous interaction outcomes may occur nonetheless. For example, along the San Pedro
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40 378 River in southeastern Arizona, field crickets (*Gryllus alogus*) appeared to switch between
41
42 379 consuming detritus and moist vegetation (freshly picked leaves) when water was more or less
43
44 380 available, respectively (McCluney & Sabo, 2009; Sabo *et al.*, 2008). Alternatively, Vander Wall
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46 381 (1998) found higher seed predation by rodents under increased soil moisture in the Great Basin
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48 382 through an increased ability of the rodents to smell the moist seeds in underground caches.
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50 383 However, this represents a change in the magnitude of seed predation rather than a change in the
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52 384 sign of the interaction. Other studies have documented similar results, where increased water
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Running Head: Interactions in dryland systems

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5 385 availability stimulates greater consumption of dry food, like seeds (Hochman & Kotler, 2006;
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7 386 Kotler, Dickman & Brown, 1998). In cases where water causes stimulation of additional
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10 387 herbivory, it is likely due to trade-offs between water and energy gains and losses associated
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12 388 with foraging, defecation, or non-consumptive resting. Without free-water (freely available
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14 389 water that is not contained within an organism) and with low plant water content, water losses
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17 390 associated with foraging activity or defecation may exceed water gains, causing negative water
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19 391 balance and dehydration. Under these conditions, organisms may reduce activity rates to
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21 392 conserve water (Davis & DeNardo, 2009). Increases in free-water availability from these low
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24 393 levels may allow for greater activity (Davis & DeNardo, 2009) and thus greater foraging for low-
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26 394 water-content plant materials and an increase in the strength of the interaction (the stimulation
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28 395 hypothesis, *sensu* McCluney & Sabo, 2009).

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31 396 The examples above highlight how water availability can have major impacts on
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33 397 herbivore-plant interaction outcomes in dryland ecosystems (Table 2). Based on the literature,
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35
36 398 we hypothesize that trade-offs between water and energy requirements interact with water and
37
38 399 energy availability to alter plant-herbivore interactions in dryland ecosystems. Specifically, we
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40 400 suggest that when water and energy resources are coupled (free water is unavailable) and water
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43 401 is limiting to herbivores, high consumption of moist plant material is necessary to maintain water
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45 402 balance. Under these conditions, the population-level interaction outcome may be strongly
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47 403 herbivorous (+ -) (the compensation hypothesis, McCluney & Sabo, 2009). However, when
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50 404 water availability is high, energy and water resources for herbivores are decoupled, and/or water
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52 405 is not limiting and energy requirements alone do not necessitate extremely high levels of
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55 406 consumption (the quenching hypothesis, McCluney & Sabo, 2009). Thus, because *per capita*

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5 407 herbivory is weak at high water availability relative to *per capita* effects of pollination, seed
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7 408 dispersal, or compensatory stimulation of growth, the result is that mutualistic or commensalistic
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9 409 population-level interaction outcomes are likely to occur. Yet, long-term increases in water
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11 410 availability may result in a positive reproductive response of herbivores, and high densities of
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13 411 herbivores may again lead to an herbivorous population-level interaction outcome. This scenario
14
15 412 is more likely in drylands with strong seasonal precipitation patterns or in years with particularly
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17 413 high rainfall. Exceptionally strong herbivorous interaction outcomes could result from rapid
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19 414 declines in water availability after extended periods of low water stress. In this case, high
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21 415 densities of herbivores accumulated during low water stress would rapidly increase their rates of
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23 416 consumption during the onset of drought, strongly negatively affecting plants. This hypothesis
24
25 417 has not yet been tested. At the lowest water availability, neutral interaction outcomes are likely
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27 418 to become more prominent as mobile herbivorous animals migrate or hide, or relatively
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29 419 immobile herbivores perish (Davis & DeNardo, 2009; “conservation hypothesis” proposed in
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31 420 McCluney & Sabo, 2009; McKechnie & Wolf, 2010).

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38 421 As discussed above, increased consumption of dry food with increased water availability
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40 422 (Hochman & Kotler, 2006; Kotler *et al.*, 1998) likely lies at the transition between very low and
41
42 423 moderate water availability. As water availability increases from these low levels, herbivorous
43
44 424 animals may become more active and increase their foraging, particularly on dry foods
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46 425 (“stimulation hypothesis” proposed in McCluney & Sabo, 2009). Thus, our conceptual model is
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48 426 consistent with these hypotheses, with neutral interaction outcomes at very low water
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50 427 availability, strongly herbivorous interaction outcomes at moderate water availability, and
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52 428 mutualistic or commensalistic interaction outcomes at high water availability.
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Running Head: Interactions in dryland systems

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5 429 **(3) Predator-prey interactions**
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7 430 Predator-prey interactions differ from interactions involving plants because predators
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9 431 and prey are both behaviourally responsive (Ives & Dobson, 1987; Wolf & Mangel, 2007). Prey
10
11 432 manage risk of predation and predators manage the fear experienced by their prey, with predators
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13 433 and prey interacting *via* foraging games (Hugie & Dill, 1994; Kotler *et al.*, 2002). For example,
14
15 434 gerbils (*Gerbillus andersoni allenbyi*) in the Negev Desert manage predation risk from barn owls
16
17 435 (*Tyto alba*) by altering foraging time allocation, apprehension, and vigilance (Dall, Kotler &
18
19 436 Bouskila, 2001). Microhabitat, moonlight, and the presence of predators modulate this risk
20
21 437 (Kotler, Brown & Bouskila, 2001; Kotler, Brown & Mitchell, 1993). How gerbils and their
22
23 438 predators interact in these systems is influenced by their energetic state (Berger-Tal & Kotler,
24
25 439 2010). While most of the previous research on foraging games has focused on energetic state,
26
27 440 water requirements are a fundamental constraint for dryland organisms and water balance often
28
29 441 drives their behaviours, including those behaviours that determine predator-prey interactions
30
31 442 (Golightly & Ohmart, 1984; McCluney & Sabo, 2009; Valeix *et al.*, 2008). Thus, many foraging
32
33 443 behaviours are likely to revolve around water limitation in dryland systems. For instance,
34
35 444 several different African herbivores altered their drinking behaviour in response to changes in
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37 445 predation risk and water availability (Valeix *et al.*, 2008). In that system, increased predation
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39 446 risk was associated with a decrease in drinking time or the probability of drinking, while
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41 447 decreased availability of water holes was correlated with increased drinking time or the
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43 448 probability of drinking.
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52 449 Few studies have directly investigated the effects of water availability on predator-prey
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54 450 interactions. However, we note that Golightly & Ohmart (1984) indicated that in order for kit
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5 451 foxes (*Vulpes m acrotis*) and coyotes (*Canis latrans*) in Arizona to meet water demands in the
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7 452 absence of free water, they needed to consume more rodents than that required to meet energy
8
9
10 453 demands, regardless of seasonality. Similarly, McCluney & Sabo (2009) found that short-term
11
12 454 *per capita* interactions between field crickets (*G. alogus*) and wolf spiders (*Hogna antelucana*)
13
14 455 along a semi-arid floodplain in Arizona changed from strongly predatory to essentially neutral as
15
16
17 456 water availability increased. Loveridge *et al.* (2006) also showed an increase in the kill rate of
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19 457 young elephants (*Loxodonta africana*) by lions (*Panthera leo*) during low rainfall in an African
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21 458 savanna, which may have been due to separation of young calves from water-stressed herds.
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23
24 459 Gotelli (1993) implied the occurrence of a decreasing effect of ant lions (*Myrmeleon* spp.) in
25
26 460 Oklahoma on a variety of prey where precipitation was highest. Precipitation negatively affected
27
28 461 ant lions by promoting a physical soil crust, which prevented ant lion larvae from digging below
29
30 462 ground. Ant lions also seemed to reduce the abundance of other ground-dwelling arthropods.
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32
33 463 Thus, ant lions and other arthropods no longer interacted under increased precipitation, shifting
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35 464 the interaction from predatory to neutral with increased precipitation. The first two examples of
36
37 465 changes in the interaction with altered water resources are likely mediated by the consumers
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39 466 need for the water contained within prey, but for the last two examples, the mechanism is
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41 467 different, though the pattern is the same.
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45 468 Spiller & Schoener (2008) proposed a unimodal relationship between the amount of
46
47 469 precipitation and predator-prey interaction outcomes between lizards and spiders on islands in
48
49 470 the Bahamas. We believe this pattern also applies to dryland systems driven by the costs and
50
51 471 benefits of predation under varying water availability (McCluney & Sabo, 2009). In agreement
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53 472 with Spiller & Schoener (2008) and our previous discussion of plant-herbivore relationships, at
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5 473 very low water availability predators may avoid water losses associated with increased hunting
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7 474 activities and instead seek refuge and conserve water (*sensu* Davis & DeNardo, 2009;
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9
10 475 "conservation hypothesis" proposed in McCluney & Sabo, 2009) or may perish, leading to
11
12 476 reduced or neutral population-level interaction outcomes. Intermediate water availability may
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14 477 strongly affect animal behaviour because prey become both water and energy sources, and thus
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17 478 interspecific interactions may intensify (Golightly & Ohmart, 1984; McCluney & Sabo, 2009).
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19 479 At higher water availability, water and energy sources may be decoupled, and other factors may
20
21 480 limit animals more than water. Under these conditions, behaviours may switch to non-predatory
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23
24 481 endeavours, promoting more commensal interactions (e.g. McCluney & Sabo, 2009). In
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26 482 agreement with Spiller & Schoener (2008), as well as with the stress gradient theory proposed by
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28
29 483 Menge & Sutherland (1987), the highest water levels may be associated with severe disturbance
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31 484 in some habitats (e.g. desert washes), which may have greater impacts on higher trophic levels,
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33 485 causing migration or mortality and decreased interactions with lower trophic levels. Most
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36 486 evidence in drylands favours this unimodal relationship between water availability and predator-
37
38 487 prey interactions (Golightly & Ohmart, 1984; Gotelli, 1993; Loveridge *et al.*, 2006; McCluney &
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40 488 Sabo, 2009; Valeix *et al.*, 2008; Tables 2 & 3), thus our conceptual model reflects this approach
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43 489 (Fig. 2).
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52 491 **III. IMPACTS OF CLIMATE CHANGE ON THE BALANCE OF SPECIES**

53 492 **INTERACTIONS IN DRYLAND ECOSYSTEMS**

54 493 We have presented a basic conceptual model of how population-level interaction
55 494 outcomes in drylands may shift with altered water availability. This model is based on a review

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5 495 of published studies (Table 2) and an examination of potential trade-offs between water
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7 496 requirements, demands for other resources, and the relative availability of water and other
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10 497 resources (Fig. 2). The hypotheses and predictions associated with this model are in agreement
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12 498 with general patterns in the literature, though particular exceptions occur. We use this model and
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14 499 hypothetical scenarios of current and future water availability to illustrate how the model can
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16 500 lead to testable predictions for shifts in species interactions under environmental change. We
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18 501 caution that predictions may vary depending on the initial and future water conditions of a
19
20
21 502 particular region and the predictions made here are for example purposes only.
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24 503 To make predictions about how changes in water availability influence interaction
25
26 504 outcomes, we first assume scenarios of current water availability. For simplicity, we assume
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28 505 initial conditions of intermediate water availability with moderate variation across time (Fig. 2).
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30 506 This scenario is likely to be representative of many dryland ecosystems, particularly those with
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32 507 strong seasonality, but it does not represent all drylands. Our example scenarios illustrate the
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34 508 types of changes in interactions that might be expected in certain dryland systems. Scenarios can
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36 509 be useful in conveying information about plausible outcomes under a given set of assumptions
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38 510 about present and future conditions, but should not be viewed as representing the only possible
39
40 511 outcomes (Carpenter, 2005). For future conditions, we examine three separate scenarios, relative
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42 512 to current conditions (Fig. 2): (1) increased variation in water availability, but the same mean, (2)
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44 513 increased variation and increased mean, and (3) increased variation and decreased mean. These
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46 514 scenarios agree with climate projections of greater variation in precipitation and soil moisture, as
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48 515 well as the potential for increases or decreases in mean precipitation from one region to another
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51 516 (IPCC, 2007).

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5 517 **(1) Plant-plant predictions**
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7 518 We make two predictions: (a) increased variation in water availability leads to greater
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9 519 instances of population-level competitive interaction outcomes, but also greater variability in
10
11 520 these interactions, and (b) increases or decreases in mean water availability leads to increases in
12
13 521 competitive interaction outcomes. Our scenario of current water availability assumes that
14
15 522 moderate conditions predominate in a relative sense, which promotes facilitative interactions
16
17 523 more than competition (Maestre *et al.*, 2009). Thus increases in variability of soil moisture
18
19 524 would be expected to lead to both (a) greater instances of neighbour plants lowering—rather than
20
21 525 increasing—water availability and thus promoting competition (Bellot *et al.*, 2004), and (b)
22
23 526 complete alleviation of water stress, promoting competition for other resources, such as light
24
25 527 (Espigares, López-Pintor & Rey Benayas, 2004). However, increasing variability will mean that
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27 528 these competitive interactions will be short-lived and vary significantly from year to year
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29 529 (Chesson *et al.*, 2004). In a recent review, Knapp *et al.* (2008) discussed some of the ecological
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31 530 consequences that a more variable climate would have for both mesic and xeric ecosystems.
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33 531 They predicted that altered precipitation regimes would have an overall positive effect on the
34
35 532 water balance of deep-rooted xeric plants that experience less seasonal water stress because
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37 533 larger rainfall events recharge deeper soil layers, thereby increasing the amount of time when
38
39 534 soil water content is above stress thresholds (Heisler-White *et al.*, 2009). Such an effect might
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41 535 be expected to increase the frequency of facilitative plant-plant interactions in dryland
42
43 536 ecosystems. However, this assumes a scenario of initial water availability lower than our current
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45 537 scenario used for example purposes. We also point out that with increased variation in
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47 538 precipitation, any increase in facilitation from more intense rain pulses may be negated by more
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Running Head: Interactions in dryland systems

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5 539 intense and longer droughts, exacerbated by temperature-induced increases in
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7 540 evapotranspiration, which might be expected to increase the frequency of competitive
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9 541 interactions (Maestre *et al.*, 2003). In highly variable dryland systems, increased variability
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11 542 might have little effect on the balance of interactions, except to reduce the occurrence of
12
13 543 interactions altogether. However, substantial effects on particular populations or communities
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15 544 are likely, even if the balance of these interactions is not altered.
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19 545 Changes in mean water availability in our qualitative scenario analysis may greatly alter
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21 546 the balance of plant-plant species interactions in dry environments, with increases or decreases
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23 547 promoting competition. Additionally, we note that many dryland regions are expected to
24
25 548 experience a substantial change in summer precipitation. As some plants rely heavily on summer
26
27 549 precipitation, whereas some do not utilize it, large changes in the seasonality of precipitation will
28
29 550 differentially favour some plant species over others (Schwinning *et al.*, 2002; Schwinning &
30
31 551 Ehleringer, 2001). We note that changes in the strength of competitive or facilitative interactions
32
33 552 may vary greatly with small changes in water availability, even when the signs of the interactions
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35 553 do not.
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40 554 **(2) Plant-herbivore predictions**

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42 555 We predict that: (a) increased variation in water availability will increase the frequency
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44 556 of mutualistic, commensal, or neutral plant-herbivore interaction outcomes, and (b) increases in
45
46 557 mean water availability will promote plant-herbivore mutualisms or commensal interaction
47
48 558 outcomes, whereas decreases will promote strong herbivory or neutral interactions depending on
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50 559 the degree of reduction. Our scenario of current water availability assumes intermediate
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52 560 availability and moderate variation, leading to a predominance of herbivorous interaction
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5 561 outcomes. Thus, increases in the variability of water availability would be expected to lead to
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7 562 both (a) greater instances of neutral effects due to reduced foraging activity and due to reduced
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10 563 densities of herbivores at low water availability and (b) higher instances of mutualistic or
11
12 564 commensal interaction outcomes due to reduced herbivory relative to pollination and other
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14 565 positive interactions because of a decoupling of water and energy/nutrient requirements at high
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17 566 water availability. However, increases in variation of water availability may also occasionally
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19 567 produce some strongly herbivorous interactions when herbivores are still actively foraging, but
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22 568 free water is scarce (e.g. McCluney & Sabo, 2009; Fig. 2). Major increases in the variability of
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24 569 water would also increase the occurrence of temporary water pulses that could promote a
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26 570 predominance of behavioural adjustments in herbivory, without time for reproductive effects.
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29 571 Increases in mean water availability may be expected to greatly increase mutualisms or
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31 572 commensal interaction outcomes, whereas decreases may promote neutral interaction outcomes,
32
33 573 but also may lead to occasional strong herbivorous interactions, depending on the degree of
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35
36 574 change in water availability. We note that the neutral interaction outcomes result when
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38 575 herbivores are no longer active in these ecosystems, so declines in water availability that do not
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40 576 reach this threshold should increase herbivory.

41 42 43 577 **(3) Predator-prey predictions**

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45 578 We predict that (a) increased variation in water availability will increase the frequency of
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47 579 neutral or commensal predator-prey interactions, and (b) increased mean water availability will
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50 580 lead to greater commensal interactions, whereas decreased mean water availability will lead to
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52 581 either increases in the strength of predatory interaction outcomes or to neutral interaction
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55 582 outcomes, depending on the degree of change. Our scenario of current water availability assumes

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5 583 intermediate water levels and moderate variation, leading to predominantly predatory interaction
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7 584 outcomes. Thus, increases in the variation of water availability are expected to increase (a)
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10 585 instances of neutral effects due to reduced activity and reduced densities of predators at low
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12 586 water availability and (b) instances of commensal interaction outcomes due to reduced predation
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14 587 when water becomes less limiting (due to decoupling of water and energy/nutrient sources) at
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17 588 high water availability. Increases in the variation in water availability may also lead to
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19 589 temporary periods of stronger predation when predation increases with lowered water
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21 590 availability before a threshold is reached where predators switch to water conservation behaviour
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24 591 and are no longer active components of these ecosystems (e.g. McCluney & Sabo, 2009). As
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26 592 with herbivores, a major increase in variability could be expected to lead to a predominance of
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28 593 short-term behavioural changes in predation rather than changes in reproduction. Increases in
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31 594 water availability are likely to lead to increased commensalistic population-level interaction
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33 595 outcomes, whereas reduced water availability is likely to lead to either increases in the strength
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35 596 of predatory interaction outcomes or to neutral net effects, dependent on the degree of reduction
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37
38 597 in water availability.

40 598 **(4) Community response predictions**

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43 599 We predict that (a) increased variation of water resources will lead to either greater
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45 600 bottom-up effects and linearity of changes in patterns of trophic biomass, or highly unpredictable
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47 601 non-linear dynamics of trophic biomass, depending on degree and pattern of the increase in
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49
50 602 variability, and (b) increases in mean water availability will promote linear, bottom-up
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52 603 propagation of effects, while decreases will promote top-down non-linear dynamics of trophic
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55 604 biomass until decreases create depauperate communities with few interacting species. Trying to

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5 605 connect changes in interactions across multiple trophic levels in any particular food web is
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7 606 difficult. However, we cautiously suggest that it is possible to connect changes in the balance of
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10 607 plant-plant interaction outcomes to plant-herbivore interaction outcomes and to predator-prey
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12 608 interaction outcomes under our scenarios of current and future water availability.
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14 609 Several theories can lend insight as to how communities may change in response to
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17 610 alterations in species interactions related to altered water availability. For instance, the idea first
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19 611 postulated by Hairston, Smith & Slobodkin (1960) and later developed into the exploitation
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21 612 ecosystems hypothesis (Oksanen *et al.*, 1981) holds that bottom-up control of ecosystems results
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23 613 in linear accumulation of biomass across trophic levels with increased resource availability,
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25 614 whereas top-down control results in non-linear patterns. Numerous studies have now
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27
28 615 documented support for this hypothesis across a range of terrestrial ecosystems (Elmhagen *et al.*,
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30 616 2010; Mäntylä, Klemola & Laaksonen, 2010; Oksanen & Oksanen, 2000; Terborgh *et al.*, 2006,
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32 617 2001). For instance, in a meta-analysis, Mäntylä *et al.* (2010) found strong support for top-down
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34 618 effects of birds on the abundance of insects, prevalence of leaf damage, and amount of plant
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36 619 biomass across studies and ecosystems. Top-down control seems particularly important in less
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38 620 productive systems (Oksanen & Oksanen, 2000), including drylands. Stronger predator-prey and
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40 621 plant-herbivore species interactions represent greater top-down effects with greater effects on
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42 622 biomass of lower trophic levels (e.g. Chase, 2003) and this should lead to non-linear changes in
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44 623 biomass. Agreeing with this hypothesis, other theories and evidence also suggest that
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46 624 particularly strong species interactions in communities promote rapid non-linear shifts in
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48 625 biomass in various trophic levels in response to environmental change (i.e. the keystone species
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50 626 concept) (Bascompte, 2009; Brown & Heske, 1990; May, 1973; McCann, Hastings & Huxel,
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5 627 1998). These theories suggest that understanding patterns and strengths of species interactions
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7 628 may be important to projection of the effects of global environmental change on communities
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10 629 and ecosystems.

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12 630 Moderate increases in mean water availability from the levels in our initial scenarios
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14 631 could promote plant-plant competition, plant-herbivore mutualism or commensalism, and
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17 632 reduced predator-prey interactions (increased commensalism). Plant-plant competition would
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19 633 likely be relatively weak because water would no longer be limiting and this is typically the most
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21 634 important resource for dryland plants (Noy-Meir, 1973). Combining weak plant-plant
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24 635 competition with weak or positive plant-herbivore and predator-prey interactions would lead to
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26 636 an expectation of bottom-up effects and relatively linear, predictable patterns of changes in
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28
29 637 trophic biomass in these wetter communities.

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31 638 Decreases in water availability from our initial scenario would be expected to promote
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33 639 competitive plant-plant interaction outcomes, strongly herbivorous plant-herbivore interactions,
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36 640 and strong predator-prey interactions, up until active predators, herbivores, and plants are
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38 641 progressively lost from the system. Thus, such a shift could promote stronger top-down effects
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40 642 and greater non-linearity and unpredictability of the responses of trophic biomass. We note that
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43 643 extreme decreases in water availability may result in communities dominated by bottom-up
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45 644 effects and linear, predictable patterns, but only because these communities will contain few
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47 645 species that seldom interact.

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50 646 Under increased climate variability, with little change in mean values, the balance of
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52 647 interactions would be unlikely to be greatly affected. However, based on our conceptual model,
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55 648 an increase in the variability of moisture should lead to more frequent crossing of climate

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5 649 thresholds, and thus an increase in the variability of types of interaction outcomes for any pair of
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7 650 organisms (Fig. 2A). Predicting the effects of increased variability in interactions on trophic
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10 651 biomass and species coexistence is complicated. On the one hand, dynamic context-dependent
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12 652 species interactions may improve the stability and coexistence of ecological communities
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14 653 (Chesson *et al.*, 2004; Navarrete & Berlow, 2006) and this dynamism would be expected to
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16 654 increase with increased variation in water resources. On the other hand, large increases in
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18 655 variability of water availability could be expected to lead to instances of populations of
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21 656 herbivores or predators with suddenly high rates of herbivory or predation that could promote
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24 657 highly non-linear dynamics in the short-term (Holmgren *et al.*, 2001; Letnic & Dickman, 2006;
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26 658 Lima, Stenseth & Jaksic, 2002b; Smith *et al.*, 2009). This might be particularly true if high
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28 659 variability leads to a predominance of short pulses of resources that do not allow for large
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31 660 reproductive or growth responses of plant communities, but do promote rapid changes in
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34 661 herbivory and predatory behaviour. Thus, the magnitude of changes in variability may influence
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36 662 the effects of these changes on patterns of trophic biomass in ecological communities.

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38 663 Taken together, our predictions suggest that increases in the mean water availability or
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40 664 small increases in variability from our initial scenario should lead to more bottom-up, linear, and
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43 665 predictable dynamics of trophic biomass, but that decreases in water availability and large
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45 666 increases in variation may lead to top-down, non-linear, and unpredictable effects on trophic
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48 667 biomass. This idea seems to be supported by at least one study showing that bottom-up
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50 668 responses of plant and rodent communities to precipitation in the Chihuahuan Desert were
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52 669 common, but strong exceptions were occasionally observed that were difficult to explain (Ernest
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55 670 *et al.*, 2000). Similar observations have been made in other systems as well (Holmgren *et al.*,

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5 671 2001; Lima *et al.*, 2002*b*). However, we note that our predictions are dependent on the scenarios
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7 672 chosen for initial and future water availability conditions and studies examining particular
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9 673 regions are likely to vary. For example, in regions that already experience great variability,
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11 674 further increases in variability could be expected to decrease linearity or predictability and
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13 675 decrease total biomass or diversity.
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18 19 677 **IV. RESEARCH NEEDS**

20 21 678 **(1) Plant-plant**

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24 679 Substantial research has investigated how variation in moisture availability influences
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26 680 plant-plant interactions, but key questions remain unresolved. For instance, understanding what
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28 681 situations promote competition or facilitation at low water levels is an important direction for
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30 682 future research (see Brooker *et al.*, 2008 for a recent review). Future studies on this topic should
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32 683 explicitly consider the stress tolerance and competitive ability of the interacting species, which
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34 684 can heavily influence the outcome of the interaction (Maestre *et al.*, 2009). In this regard, recent
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36 685 research has shown that facilitation occurs only if surrounding vegetation is able to alleviate the
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38 686 abiotic factors by which a focal species has deviated from its physiological optima in the field
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40 687 (Gross *et al.*, 2010). As such, the intensity of biotic interactions is likely to be linked with species
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42 688 traits, as they reflect particular tolerances. A more thorough knowledge of these linkages could
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44 689 substantially improve our ability to predict how the outcome of plant-plant interactions changes
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46 690 along water availability gradients (Maestre *et al.*, 2009).
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52 691 Given the strong seasonality within most dryland ecosystems, research is needed to
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54 692 determine how interactions during one season affect interspecific outcomes over time. In the
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5 693 Southwestern U.S., for example, high moisture availability from winter and spring precipitation
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7 694 may increase primary production of spring annuals (e.g. Muldavin *et al.*, 2008), which in turn
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9 695 may reduce soil resource availability during subsequent summer rains. For example, Hall *et al.*
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11 696 (2011) found that soil N mineralization rates decreased from spring to autumn in the northern
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13 697 Sonoran Desert and this could result in increasing competitive interactions among species as
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15 698 resource availability decreases during the later growing season (e.g. Harris & Facelli, 2003).

19 699 **(2) Animal**

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21 700 While animal physiologists have a history of examining the importance of water as a
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23 701 resource (e.g. Davis & Denardo, 2006; Golightly & Ohmart, 1984; Hadley, 1994; Noy-Meir,
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25 702 1974), animal ecologists have only recently focused on how water availability affects animal
26
27 703 community structure and species interactions (e.g. McCluney & Sabo, 2009; Spiller & Schoener,
28
29 704 2008; Wolf & Martinez del Rio, 2003). As such, general theories of the influence of water on
30
31 705 plant-herbivore and predator-prey interactions are in their infancy. There is a great need for
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33 706 more research, explicitly testing the recent theories suggested by others (e.g. McCluney & Sabo,
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35 707 2009; Spiller & Schoener, 2008) and expanded here. These efforts will be aided if new studies
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37 708 better document the extent of water limitation and clearly measure and distinguish *per capita* and
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39 709 net population-level interactions using a measure that is comparable across studies (Berlow *et*
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41 710 *al.*, 2004). Methods of standardization in reporting the extent of water availability are also
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43 711 greatly needed. We propose that soil water potential, gravimetric hydration state, and fluid
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45 712 osmolality are comparable across studies and thus these measures should be more widely
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47 713 reported. These are better measures than simply recording precipitation, since total precipitation
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49 714 is not necessarily the best determinant of organismal water availability.

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7 716 **V. EXTENSIONS AND CONSEQUENCES**
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10 717 Our model and predictions suggest that rapid global change in water resources will have
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12 718 significant consequences for species interactions in dryland ecosystems. As variation in water
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14 719 availability increases, so should variability of biotic interactions, assuming that extremes of
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16 720 water availability are not already dominating. In some cases, changes in the sign or strength of
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18 721 interaction outcomes may promote large mismatches in the population sizes of interacting
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20 722 species and in their effects on each other (Holmgren *et al.*, 2001; Lima *et al.*, 2002*b*; Smith *et al.*,
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22 723 2009). Periods of low water stress may promote increased reproduction of herbivores
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24 724 (especially) and predators (somewhat), leading to increased population densities. For instance, a
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26 725 temporary increase in water availability can increase vascular plant productivity and herbivore
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28 726 numbers in the Atacama Desert and Central Australia (Holmgren *et al.*, 2006; Jaksic, 2001;
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30 727 Letnic *et al.*, 2005), leading to rodent outbreaks (Lima *et al.*, 2002*b*). Numbers of vertebrate
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32 728 predators have also been shown to increase, although there is a delayed response (Holmgren *et*
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34 729 *al.*, 2001; Letnic *et al.*, 2005; Lima *et al.*, 2002*a*). A sudden decrease in water availability would
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36 730 be expected to cause increases in *per capita* herbivory and predation with high densities of
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38 731 individuals, which could lead to rapid and unpredictable changes in population abundances,
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40 732 including population crashes (Holmgren *et al.*, 2001; Lima *et al.*, 2002*b*). Thus, consequences of
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42 733 increases in the variability of water resources and extreme events may be exacerbated by
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44 734 fluctuations in species interactions, leading to population outbreaks and die-offs.
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52 735 Alternatively, some of the moisture variability inherent in dryland ecosystems, when
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54 736 combined with variable species life history and drought-tolerant life stages, is essential to
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5 737 maintaining coexistence and diversity (Chesson *et al.*, 2004) and this variability may also
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7 738 increase species coexistence by limiting the effects of strong species interactions (Navarrete &
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9 739 Berlow, 2006), which can destabilize communities (May, 1973; McCann *et al.*, 1998). Despite
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11 740 the increases in coexistence and diversity conveyed by some moisture variability, as discussed
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13
14 741 above, we could also expect to see greater incidences of occasional outbreaks and die-offs in
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16 742 these systems, especially with large increases in water resource variability.

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19 743 We note that at the lowest water availabilities another threshold may exist, where species
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21 744 interactions are near zero due to the inactivity or extirpation of one or more of the interacting
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23 745 species. While dryland species are often adapted to climate variability, there may be levels of
24
25 746 aridity for which species cannot survive. For instance, the hyper-arid Atacama Desert in Chile
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27 747 supports relatively little life over much of its range (Barros *et al.*, 2008; Navarro-Gonzalez *et al.*,
28
29 748 2003). A similar threshold is likely to exist at the highest level of moisture, where catastrophic
30
31 749 flood disturbance may reduce interactions (e.g. Spiller & Schoener, 2008). Reduction in the
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33 750 strength of population-level interaction outcomes caused by climate extremes would result from
34
35 751 large negative effects of these events on populations and communities, primarily through
36
37 752 mortality or dispersal (Gutschick & BassiriRad, 2003; McKechnie & Wolf, 2010; Thibault &
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39 753 Brown, 2008). Additionally, there is a growing consensus that the magnitude and frequency of
40
41 754 extreme climate events will exceed past natural variability, invalidating the concept of
42
43 755 “stationarity” (i.e. the future will be similar to the past) for ecology or management (Jentsch,
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45 756 Kreyling & Beierkuhnlein, 2007; Milly *et al.*, 2008). Very high variability in water availability
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47 757 may prevent populations growing in response to precipitation pulses from reaching resistant or
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49 758 tolerant life stages and reduce the diversity-maintaining storage effect (Chesson *et al.*, 2004).

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5 759 Thus, extreme climate events may have particularly strong consequences for populations,
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7 760 communities, and ecosystems that may be beyond our ability to predict based on current
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10 761 observations.

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12 762 There is considerable evidence that alterations in water supply can have ecosystem-level
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14 763 effects that are mediated by species interactions. Several recent studies suggest that the response
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17 764 of animal interactions to changes in precipitation can have ecosystem consequences, without
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19 765 specifically measuring the interaction. Warne *et al.* (2010) showed that in the Chihuahuan
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21 766 Desert, winter droughts can decrease forage quality by reducing C₃ plants and that this affects the
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23 767 entire food web, which they predict would reduce nutrient cycling and reduce secondary
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26 768 production. In central Kentucky, Lensing & Wise (2006) found that precipitation changes
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28 769 affected interactions between spiders and decomposers, which altered rates of organic matter
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31 770 decomposition. When a moist site experienced decreased rainfall, spiders sped decomposition,
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33 771 while at higher rainfall, spiders had little effect, or possibly a slight negative effect on
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36 772 decomposition. They suggested changes in decomposition with altered moisture resulted from
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38 773 altered spider-collembola-fungus interaction outcomes. Other studies have documented similar
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40 774 patterns, suggesting that species interactions modify the ecosystem response to changes in water
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43 775 availability (Brown *et al.*, 2001; Ernest *et al.*, 2000; Guo & Brown, 1996; Owen-Smith & Mills,
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45 776 2006).

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48 49 778 **VI. CONCLUSIONS**

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52 779 (1) We summarize existing studies to show that variation in water availability in response to a
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55 780 changing climate will have strong effects on species interactions.

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5 781 (2) While these interactions may be complex, nonlinear, and context dependent, recent evidence
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7 782 suggests that the balance of interactions may be important in determining the linearity of bottom-
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10 783 up responses of communities to moisture and in modulating community patterns and ecosystem
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12 784 processes.

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14 785 (3) Following from hypothetical water availability scenarios and ecological theory, we illustrate
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16
17 786 how our model can be used to make predictions for responses of species interactions and patterns
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19 787 of trophic biomass to changes in water availability. We suggest that, for drylands with
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21 788 intermediate water availability and moderate variability, increases in mean water availability or
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23 789 small increases in variation could encourage linear, bottom-up accumulation of trophic biomass,
24
25 790 but declines in mean water availability or large increases in variability may lead to nonlinear top-
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27
28 791 down responses.

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31 792 (4) Our conceptual model is designed to guide future research efforts to link alteration of water
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33 793 availability regimes in dryland systems to changes in biotic interactions that will ultimately have
34
35 794 strong effects on populations, communities, and ecosystems.
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42
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Table 1. Definitions of interaction outcome terms used herein.

Interaction term	Sign	Definition
<u>Plant-plant</u>		
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
<u>Plant-herbivore</u>		
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
<u>Predator-prey</u>		
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
<u>All groups</u>		
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
<i>Plant-plant interactions</i>						
Xeric vs mesic sites and wet and dry years	Bunchgrasses – <i>Lesquerella carinata</i>	Facilitation (0 +)	Competition (- -)	Spatial associations and seedling survival	Xeric/western Montana	Greenlee & Callaway (1996)
Natural precipitation gradient	<i>Stipa tenacissima</i> – <i>Lepidium subulatum</i>	Facilitation (0 +)	Facilitation (0 +)	Spatial associations	Semi-arid/central Spain	Soliveres <i>et al.</i> (2010)
Temporal variation in climate (precipitation)	<i>Stipa tenacissima</i> – <i>Lepidium subulatum</i>	Facilitation (0 +)	Competition (- -)	Seedling/sapling growth	Semi-arid/central Spain	Soliveres <i>et al.</i> (2010)
Temporal variation in climate (precipitation)	<i>Koeleria castellana</i> – <i>Helianthemum squamatum</i>	Neutral (0 0)	Facilitation (0 +)	Spatial associations	Semi-arid/central Spain	de la Cruz <i>et al.</i> (2008)
Temporal variation in climate (precipitation)	<i>Thymus lacaitae</i> – <i>Helianthemum squamatum</i>	Neutral (0 0)	Facilitation (0 +)	Spatial associations	Semi-arid/central Spain	de la Cruz <i>et al.</i> (2008)

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5	Temporal						
6	variation in	<i>Herniaria fruticosa</i> –					
7	climate	<i>Helianthemum</i>	Facilitation (0 +)	Neutral (0 0)	Spatial	Semi-arid/	de la Cruz <i>et</i>
8	(precipitation)	<i>squamatum</i>			associations	central Spain	<i>al.</i> (2008)
9							
10							
11	Temporal						
12	variation in	<i>Teucrium pumilum</i> –					
13	climate	<i>Helianthemum</i>	Facilitation (0 +)	Facilitation (0 +)	Spatial	Semi-arid/	de la Cruz <i>et</i>
14	(precipitation)	<i>squamatum</i>			associations	central Spain	<i>al.</i> (2008)
15							
16							
17							
18	Mesic vs xeric	<i>Mimosa luisana</i> –					Valiente-
19	habitats	<i>Neobuxbaumia tetetzo</i>	Competition (- -)	Competition (- -)	Seedling survival	Semi-arid/	Banuet &
20						Mexico	Ezcurra
21							(1991)
22	Natural	Perennial plants –					
23	precipitation	perennial plants	Competition (- -)	Facilitation (+ +)	Co-occurrence	Semi-arid/	Maestre <i>et</i>
24	gradient	(community-level			analyses	central - SE	<i>al.</i> (2010)
25		study)				Spain	
26							
27	Temporal						
28	variation in	<i>Mimosa luisana</i> –					Arizaga &
29	climate	<i>Agave macrocarpa</i>	Facilitation (0 +)	Neutral (0 0)	Seedling survival	Semi-arid/	Ezcurra
30	(precipitation)					Mexico	(2002)
31							
32							
33	Watering	Grasses – <i>Prosopis</i>					Brown &
34	treatments	<i>glandulosa</i>	Competition (- -)	Competition (- -)	Seedling survival	Semi-arid/	Archer
35						Texas	(1999)
36							
37	Watering	<i>Austrocedrus</i>				Semi-arid to	
38	treatments	<i>chilensis</i> seedlings –	Competition (- -)	Facilitation (+ +)	Number of	sub-humid/	Kitzberger <i>et</i>
39		shrubs			juveniles,	northern	<i>al.</i> (2000)
40					<i>Austricedrus</i>	Patagonia	
41					recruitment	Argentina	

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

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5	Temporal	<i>Aspidosperma</i>					
6	variation in	<i>quebracho-blanco</i> –	Competition (- -)	Facilitation (+ 0)	Seedling survival	Arid/ central	Barchuk <i>et</i>
7	climate	nurse plants				Argentina	<i>al.</i> (2005)
8	(precipitation)						
9							
10	Precipitation	<i>Ambrosia dumosa</i>			Shoot elongation,		
11	events, soil	shrubs – annuals		Facilitation (0 +)	biomass, seeds	Arid/ Mojave	Holzapfel &
12	water content				per spikelet, seeds	Desert	Mahall
13					per head		(1999)
14					Fitness		
15	Temporal	Shrub – annuals	Competition (- -)	Neutral (0 0)	parameters:	Arid/ Negev	Tielborger &
16	variation in		or	or	density, no. of	Desert	Kadmon
17	climate		neutral (0 0)	facilitation (0 +)	seeds/plant		(2000)
18	(precipitation)						
19	Natural	<i>Stipa tenacissima</i> –				Semi-arid	Maestre &
20	precipitation	<i>Pistacia lentiscus</i>	Competition (- -)	Competition (- -)	Seedling survival	steppe/ SE	Cortina
21	gradient	seedlings				Spain	(2004)
22							
23	Rainfall	<i>Larrea divaricata</i> –	Competition (- -)		Plant density	Arid/ Sonoran	King &
24		desert shrubs				and Mojave	Woodell
25						deserts	(1973)
26							
27	Natural						
28	variation in	<i>Ambrosia</i> – <i>Larrea</i>	Competition (- -)		Plant density	Arid/ Mojave	Fonteyn &
29	precipitation -					Desert	Mahall
30	measured water						(1978)
31	potential						
32	No	<i>Carnegiea gigantean</i>			Stem die back,		
33	manipulation or	– <i>Cercidium</i>			nurse plant	Arid/ Sonoran	McAuliffe
34	measurement of	<i>microphyllum</i> nurse	Facilitation (+ 0)	Competition (- -)	mortality – trunk	Desert	(1984)
35	water	plant			diameter		
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Plant-herbivore

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Irrigation	<i>Acacia karroo</i> 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 <i>et al.</i> (2006)
Distance from river	Moist cottonwood and willow leaves – consumers	“Herbivory” (- +)	Neutral (0 0)	Net consumption	Semi-arid/ SE Arizona river	Sabo <i>et al.</i> (2008)
Moisture addition and precipitation	Moist cottonwood leaves – field crickets	“Herbivory” (- +)	Neutral (0 0)	<i>Per capita</i> 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 <i>et al.</i> (1998)
Water bowls added	Seeds – rodents	Herbivory (- +)	Herbivory (- +)	Giving-up density	Arid/ Simpson Desert	Kotler <i>et al.</i> (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)

Running Head: Interactions in dryland systems

<i>Predator-prey</i>						
Moisture addition	Field crickets – wolf spiders	Predatory (- +)	Neutral (0 0)	Dynamic index of <i>per capita</i> effects	Semi-arid/ SE Arizona river	McCluney & Sabo (2009)
Rainfall	Elephants – lions	Strong predation (- +)	Weak predation (- +)	Kill rate	Semi-arid/ Zimbabwe	Loveridge <i>et al.</i> (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)

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1240 ¹The symbols for the effect are noted in the order of the list of species 1 and 2. See Table 1 for definitions.

1241 ²Generally, climate and location are listed as reported by the authors.

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Running Head: Interactions in dryland systems

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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

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Running Head: Interactions in dryland systems

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.

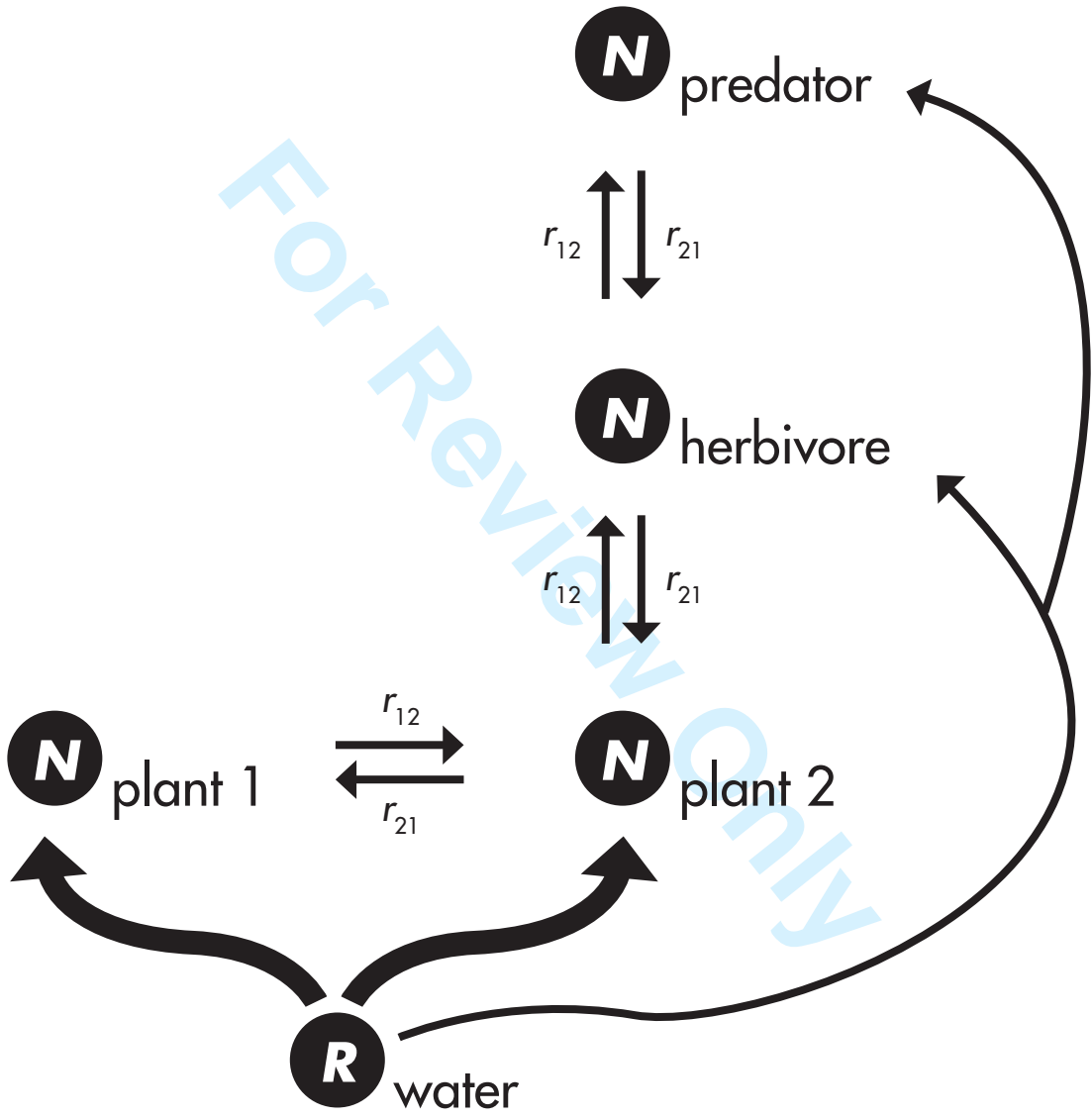
Fig. 2. Conceptual model illustrating possible organismal interactions under scenarios of current and future water availability. Solid grey lines indicate hypothetical current conditions, which we assume are intermediate levels of water availability and moderate variation. Dashed black lines indicate 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

Running Head: Interactions in dryland systems

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5 1268 of water availability. We note that for all graphs, at very low or very high water levels, neutral
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7 1269 interactions (0 0) are expected, because severe droughts or flooding disturbance are expected to
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10 1270 reduce the densities of species low enough to prevent interactions from occurring. At far right,
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12 1271 we indicate predictions for how the community will respond to each scenario of water
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14 1272 availability. “Bottom-up” refers to the degree to which bottom-up or top-down forces influence
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17 1273 the community, “linearity” indicates the degree to which patterns of trophic biomass will respond
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19 1274 linearly to changes in water availability, and “predictability” suggests the change in the
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21 1275 predictability of responses of trophic biomass to changes in water availability. D shows a future
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24 1276 climate scenario with increased variation in water resources and an intermediate mean, but in this
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26 1277 case, the thresholds for changes in interaction outcomes are not constant, but instead vary across
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29 1278 time. These thresholds are likely to be based on a variety of other variables that change across
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31 1279 time (e.g. temperature). See Table 2 for a list of the studies used in generating this model.
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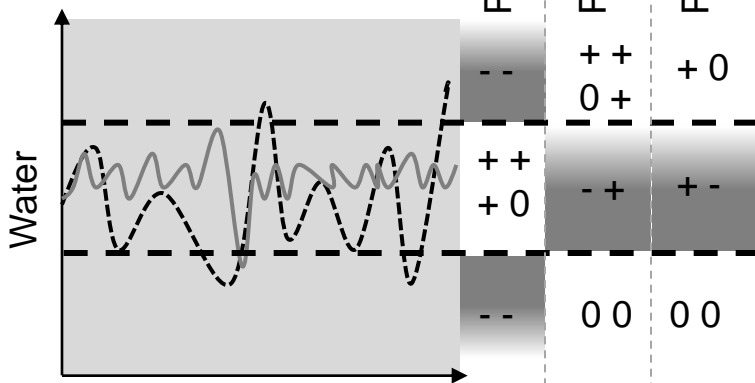
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A
Same mean,
higher
variability



	Plant-Plant	Plant-Herb	Pred-Prey
Top	--	++	+0
Middle	++	0+	+-
Bottom	--	00	00

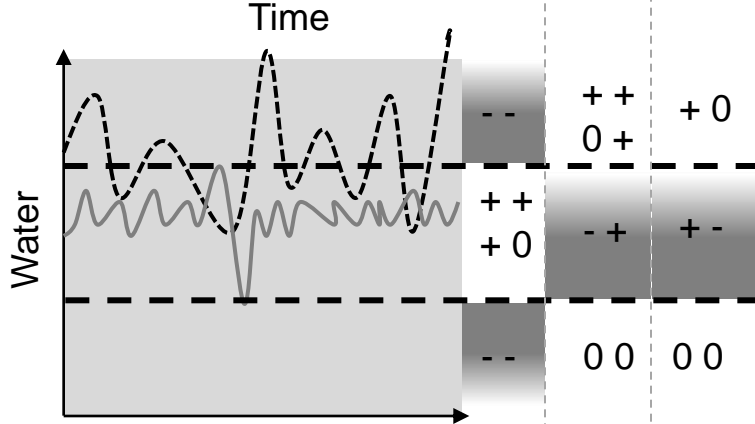
Community response to change

↑ Bottom-up

↑ Linearity

↻ Predictability

B
Higher mean,
higher
variability



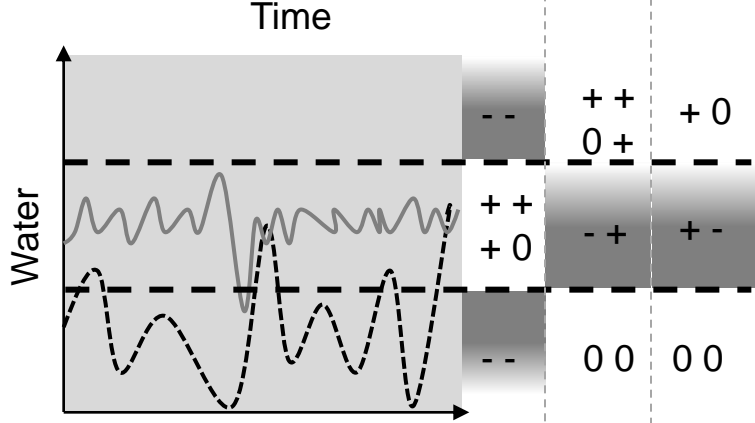
	Plant-Plant	Plant-Herb	Pred-Prey
Top	--	++	+0
Middle	++	0+	+-
Bottom	--	00	00

↑ Bottom-up

↑ Linearity

↑ Predictability

C
Lower mean,
higher
variability



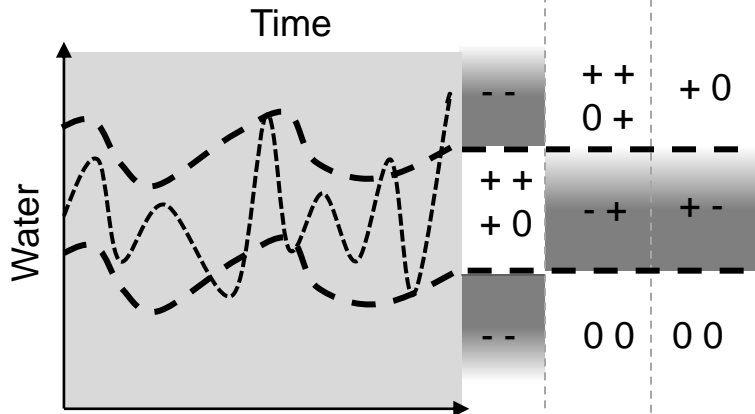
	Plant-Plant	Plant-Herb	Pred-Prey
Top	--	++	+0
Middle	++	0+	+-
Bottom	--	00	00

↓ Bottom-up

↓ Linearity

↓ Predictability

D
Non-linear
thresholds,
higher
variability



	Plant-Plant	Plant-Herb	Pred-Prey
Top	--	++	+0
Middle	++	0+	+-
Bottom	--	00	00

↑ Bottom-up

↑ Linearity

↻ Predictability