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1 **RUNNING HEAD:** Water balance mediates top-down effects

2 **TITLE:** Animal water balance drives top-down effects in a riparian forest—implications
3 **for terrestrial trophic cascades**

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7
8 **Abstract**

9 Despite the clear importance of water balance to the evolution of terrestrial life, much
10 remains unknown about the effects of animal water balance on food webs. Based on recent
11 research suggesting animal water imbalance can increase trophic interaction strengths in cages,
12 we hypothesized that water availability could drive top-down effects in open environments,
13 influencing the occurrence of trophic cascades. We manipulated large spider abundance and
14 water availability in 20 × 20 m open-air plots in a streamside forest in Arizona, USA, and
15 measured changes in cricket and small spider abundance and leaf damage. As expected, large
16 spiders reduced both cricket abundance and herbivory under ambient, dry conditions, but not
17 where free water was added. When water was added (free or within moist leaves), cricket
18 abundance was unaffected by large spiders, but spiders still altered herbivory, suggesting
19 behavioural effects. Moreover, we found threshold-type increases in herbivory at moderately low
20 soil moisture (between 5.5% and 7% by volume), suggesting the possibility that water balance
21 may commonly influence top-down effects. Overall, our results point towards animal water

22 balance as an important driver of direct and indirect species interactions and food web dynamics
23 in terrestrial ecosystems.

24 **KEY WORDS:** Water web, food web, drought, precipitation, predation, herbivory

25

26 **Introduction**

27 The evolution of terrestrial life has been driven by the challenge of maintaining water
28 balance with scarce freshwater resources, but effects of animal water limitation on terrestrial
29 food webs have received little attention, in contrast to plant-mediated bottom-up effects [e.g. 1,
30 2-5]. This is a significant gap in our understanding of ecological dynamics, since over 40% of the
31 earth's land surface is classified as drylands [6] and precipitation limits diversity of plants and
32 animals at all but the highest latitudes globally, even outside of drylands [7]. Moreover, both
33 animal water demand and the availability of water are being altered by global changes in
34 temperature, precipitation, urbanization, and water infrastructure [8]. If water balance influences
35 food webs, it may also alter ecosystem form and function in ways that directly impact humans
36 (e.g. crop production in agroecosystems).

37 Water availability likely has both bottom-up and top-down effects on food webs [9], but
38 evidence for top-down effects comes mostly from observational research [5, 10-12], limited field
39 manipulations [13, 14], or cage experiments [15]. This evidence suggests that consumers may
40 meet water demands by consuming large amounts of moist food when environmental water
41 sources (e.g. saturated soil or open water) are unavailable [9, 10, 15]. In these situations,
42 terrestrial food webs can be viewed as water webs, with water driving trophic interactions [15].

43 Large scale, open-air manipulative experiments examining the direct importance of animal water
44 balance in structuring food webs are generally lacking [but see 16].

45 Systems with strong top-down effects can shift dramatically with relatively small changes
46 to the food web, leading to trophic cascades [17-19]. Trophic cascades, where predators affect
47 the abundance of primary producers by altering density or behaviour of intermediate trophic
48 levels [sensu 20, 21, 22], were once considered to be “all-wet,” occurring predominantly in
49 freshwater ecosystems [23-25]. However, recent research has demonstrated that terrestrial
50 trophic cascades are common and widespread, but often difficult to detect [17, 26, 27]. Trophic
51 cascades may be driven by direct reductions in density of herbivores by predators, or by predator
52 modifications of herbivore foraging behaviour (e.g. “fear”) [e.g. 28, 29-31]. Previous research
53 suggests that the magnitude of top-down effects may be influenced by consumer size and
54 metabolic rate, the existence of plant defences, the diversity of herbivores, the choice of plant
55 response metric, and environmental conditions like solar radiation, temperature, rainfall, or
56 disturbance [5, 26, 27, 32, 33]. Additionally, trait-mediated indirect interactions, like anti-
57 predator behaviour, often play a large role in driving these cascades [28, 29, 31, 34], with the
58 strength of these effects, relative to density-mediated indirect interactions (direct consumption),
59 likely driven by predator hunting modality (i.e. sit and wait) and habitat use relative to prey [29].

60 As yet, the importance of animal water balance in determining the strength of top-down
61 effects or the likelihood of trophic cascades, has received surprisingly little attention. Previous
62 work has shown that water balance can influence consumption of moist food for particular
63 consumers [9, 15]. We hypothesized that this alteration of consumption would lead to changes in
64 the strength of top-down effects in real food webs. We designed and executed a large and

65 intensive open-air manipulation of water resources (free water and water contained in moist
66 leaves) and the density of predators (large wolf spiders), measuring effects on lower trophic
67 levels, in a streamside forest in AZ, USA. Moreover, we simultaneously measured soil moisture
68 and temperature, in the hopes we could identify the range of environmental conditions under
69 which water balance might influence top-down effects.

70 We predicted that adding free water (direct water supply, available to all arthropods)
71 would lead to reductions in the strength of top-down effects of large spiders on crickets and
72 crickets on leaves (Figure 1, A1 vs A2). However, we expected an increase in the effect of large
73 spiders on small spiders based on the hypothesis that large spiders would switch from consuming
74 water-laden crickets to consuming high-nutrient small spiders as water became less limiting and
75 presumably nutrients became more limiting [*sensu* 35, 36].

76 When we added water contained in moist leaves (indirect water supply, not available to
77 spiders), we did not expect a change in the effect of spiders on crickets (Figure 1, A1 vs A3),
78 following results from a previous experiment [15]. However, we predicted that adding moist
79 leaves would lead to an increase in the abundance of crickets across spider treatments (through
80 cricket dispersal) and that greater abundance of crickets would lead to slight increases in the
81 effects of large spiders on small spiders, due to apparent competition [37]. Supplementing water
82 directly (free water) vs indirectly (via moist leaves) allowed us to better separate the effects of
83 spider water balance from effects of cricket dispersal or behaviour.

84 **Methods**

85 *Overview*

86 We examined changes in the abundance of crickets and spiders in twenty-four 20 × 20 m
87 open-air plots in two large (3-4 ha) floodplains along the semi-arid San Pedro River (Electronic
88 Supplementary Materials, Figure S1), during three experimental periods: 1) ambient, baseline
89 conditions for 16 days (t0, starting 7 May 2012), 2) water supplementation and spider removal
90 for 23 days from selected plots in a split-plot factorial design (t1, starting 23 May 2012), and 3)
91 only spider removal for 12 days, stopping water addition to simulate drying (t2, starting 15 June
92 2012; Electronic Supplementary Materials Text S1, Figure S2A, Figure 2). At the end of each
93 experimental period, we measured rates of herbivory in each plot. We focus on the rate of change
94 within plots across the first two experimental periods, using a Before-After-Control-Impact
95 (BACI) design, with results from the third period (simulated drying) shown and discussed mostly
96 within the supplementary materials. Comparing rates of change across treatments allows us to
97 control for initial differences among plots when examining treatment effects.

98 *Study Site*

99 Our study site was along a section of the San Pedro River, in SE Arizona, USA (a
100 biodiversity hotspot) with intermittent flow frequency (see Electronic Supplementary Materials,
101 Text S1 for more information). The river was flowing at the beginning of the measurement
102 period, but dried prior to initiation of experimental treatments (dried 19 May, Figure 2). This site
103 was the driest of the three floodplains included in a previous study of the effects of water
104 limitation on riparian animal populations [16], but has experienced greater flow permanence than
105 many other parts of this river [38]. In recent years, increasing withdrawals of groundwater from
106 the regional aquifer by rapidly growing cities, as well as local climate shifts, have resulted in
107 declining baseflows and increasing frequency of river drying in the dry season [39]. Monsoon

108 rains began during the last few days of experimental surveys, in the third experimental period (25
109 June, Figure 2), and major flood disturbance occurred shortly thereafter, which would have
110 prevented continuation of the experiment. Flooding during the monsoon season is likely to be
111 important in driving population dynamics for our focal species, but in this study, we focused on
112 the dry season to help us better understand how animal water balance influences food web
113 dynamics in general.

114 *Design*

115 After the initial pre-manipulative measurement period, we began reducing the abundance
116 of the top invertebrate predators, large wolf spiders (mostly *Hogna antelucana*, >1 cm head to
117 cephalothorax), via nightly removal by hand capture (Electronic Supplementary Materials, Text
118 S1). Removal occurred across plots (4 treatment plots plus 3 additional spider removal only
119 plots, Electronic Supplementary Materials, Figure S1) within three randomly selected sections of
120 the two experimental floodplains, leaving another three sections with ambient large spider
121 abundance. Floodplain sections were separated from one another by >60 m of floodplain forest
122 (Electronic Supplementary Materials, Figure S1). We manipulated large spider abundance but
123 not cricket abundance because we were primarily interested in the influence of water balance on
124 top-down effects from spiders to crickets to leaf consumption. Additionally, simultaneously
125 manipulating spider and cricket abundance would be untenable in large, open-air plots.

126 Using a split-plot design, we crossed the spider manipulations with alteration of water
127 availability, either directly as free water (R-Zilla Cricket Water Pillows—pouches filled with a
128 hydrated polymer that moistens a cotton mesh surface; Central Garden and Pet Company,
129 Walnut Creek, California, USA) or indirectly as “trophic water” contained within freshly picked

130 moist cottonwood (*Populus fremontii*) leaves (Electronic Supplementary Materials, Text S1).

131 Addition of moist leaves contributed only ~0.04%, on average, to the existing leaf litter of these

132 plots (approximately 0.0025 m³ of leaves were added to 6.4 m³ of existing litter), but added

133 leaves increased water availability 2.5x above the natural rate of addition of fresh green leaves

134 from the overlying canopy [10]. Water pillows were added to achieve the same rate of water

135 supplementation, 2.5x the natural flux in leaves. Because we contributed little to habitat structure

136 or food available to crickets (dry leaf litter), moist leaf addition primarily manipulated water

137 available to primary consumers (crickets), but not predators (spiders). This allowed us to better

138 separate the effects of spider water balance from effects on dispersal or behaviour of crickets.

139 To track changes in the density of crickets and spiders, we conducted nightly surveys

140 along transects. Each plot contained three parallel transects running the length of the plot (20 m)

141 and spaced 5 m apart, with each transect demarcated with twine. A pair of observers with

142 identical 200-lumen headlamps (Icon, Black Diamond) counted juvenile and adult crickets (*G.*

143 *alogus*) and small and large ground spiders (1 cm head to cephalothorax) within a 1 m band

144 along each transect (Electronic Supplementary Materials, Text S1). The location of initiation of

145 surveys rotated nightly and responses were averaged across a complete rotation of starting

146 locations (3 days) to reduce effects of temporal differences in activity.

147 On the final day of each experimental period, we measured herbivory (leaf damage) by

148 placing four freshly-picked cottonwood (*Populus fremontii*) leaves, attached to a wooden shim,

149 on the ground at the centre of each transect and recording the percent consumption of each leaf

150 in 10% categories the following day (Electronic Supplementary Materials, Text S1). During

151 surveys, every 1-2 nights, we measured soil moisture (readings from 3 locations within 1 m²)

152 near the centre of each floodplain section using a Delta-T soil moisture sensor (ML2X Theta
153 Probe with HH2 meter, Dynamax, Inc.). We also measured ground temperature using Hobo
154 micro-station data loggers equipped with smart sensors (Onset, Bourne, Massachusetts, USA)
155 housed in 15 x 21 x 19 cm white, plastic, ventilated, radiation shields, placed on the ground.

156 *Data Processing and Statistical Analysis*

157 Analyses of nightly surveys were conducted using likelihood ratio tests of linear mixed
158 models, with time, water addition, and spider removal as fixed factors, and floodplain section,
159 plot, and transect as nested random factors. Fixed factors were dropped, one at a time, from a full
160 model, testing for significant changes in likelihood [sensu 40]. If a significant interaction
161 between water addition and spider removal was detected, we tested our specific predictions using
162 post-hoc general linear hypothesis tests (Dunnett's), examining if large spiders had an effect on
163 crickets, small spiders, or leaves under different water addition treatments. All analyses were
164 conducted in R v. 3.0.2 [41], with nlme [42], lme4 [43], and multcomp [44] packages. We also
165 examined the relationship between rates of herbivory and soil moisture in the true control plots
166 (Electronic Supplementary Materials, Text S1, Figure S1) across the entire experiment using
167 glmm on individual leaves and breakpoint regression [via the 'segmented' package in R, 45] on
168 plot averages. See Electronic Supplementary Materials Text S1 for more details.

169 **Results**

170 *Environmental Conditions*

171 Two large rain events with an intervening dry, hot period characterized our 51-day study
172 (Figure 2A). Declining soil moisture and streamflow followed the initial, aseasonal rain event,
173 with complete river drying prior to initiation of experimental manipulations (day 13). Another

174 rain event near the end of the experiment (during the simulated drying period) raised soil

175 moisture and signalled the start of the monsoon season.

176 *Efficacy of spider removal*

177 We removed 2,691 large ground spiders (mostly *Hogna antelucana*) over 35 days (May
178 23rd – June 15th), significantly lowering the abundance of this top invertebrate predator (Figure
179 2B-D; Electronic Supplementary Materials, Table S1). Large spider abundance declined across
180 all plots—possibly reflecting natural seasonal variability unrelated to removal—but the rate of
181 decline was 14X greater in removal plots than the ambient plots (Figure 2C); this translated into
182 a mean of a 55% reduction in large spiders in the reduced spider plots during the
183 supplementation period (0.044 vs 0.020 spiders per m²). We found no significant effects of water
184 manipulation on large spider abundance (Table S1).

185 *Predator effects on primary consumers—crickets—with altered water resources*

186 Large spiders reduced the abundance of crickets (*Gryllus alogus*) under dry ambient
187 conditions, but not when either free water or moist leaves were experimentally added (i.e.,
188 significant water × spider interaction, Tables 1, S1; Figure 3). Cricket abundance increased in all
189 plots across the first two experimental periods, but spiders reduced the rate of increase by 37% in
190 dry ambient conditions (Figure 3); this translated into a mean of a 23% reduction in crickets in
191 ambient spider, dry control plots, during the supplementation period (1.48 vs 1.14 crickets per
192 m²). With cessation of water addition (simulated drying) in the third experimental period, cricket
193 abundance declined, especially in moist leaf addition plots, but this reduction did not appear to
194 be influenced by large spiders according to post-hoc tests (Figure S2; Table S2).

195 *Predator effects on intra-guild predators—small spiders—with altered water resources*

196 We found significant interactive effects of large spiders and water addition on the
197 abundance of small spiders, seemingly suggesting a positive effect of large spiders on small
198 spiders under dry conditions, but not with added water or moist leaves (Figures 1, 3; Table S1).
199 But, despite an overall significant water \times spider removal interaction, post-hoc comparisons did
200 not reveal significant differences (Table S2). Thus, water influenced the effect of the large focal
201 predators on smaller intra-guild predators, but the exact pattern and mechanism is unclear.
202 Cessation of water addition (simulated drying) coincided with increases in small spider
203 abundance, particularly in previously free-water supplemented plots, but effects did not vary
204 with large spider removal (Figure S2; Table S1&2). This pattern might be indicative of higher
205 survival or reproduction of spiders in previously water supplemented plots, but we did not test
206 this directly.

207 *Top-predator effects on herbivory with altered water resources*

208 Herbivory (leaf damage) increased between pre-treatment and supplementation periods as
209 soil moisture declined naturally (see Figure 2), but, the magnitude differed between water and
210 spider removal treatments (Figure 3; Tables S1, 1). Spiders depressed herbivory under dry
211 ambient conditions and where moist leaves were added, but slightly enhanced leaf consumption
212 with free water addition (Figure 3; Table 1). These effects were reversed on the final date of the
213 experiment, when soil moisture was again high due to rainfall, with leaf consumption near zero
214 in all plots (Figure S2; Table S1&2).

215 *Soil moisture and herbivory*

216 Across treatments, herbivory was most strongly and significantly correlated with soil
217 moisture (Table S1), with herbivory dropping sharply above 6.8% soil moisture (the maximum

218 value with > 50% consumption of leaves) or with consumption declining at 5.51% soil moisture
219 on average (breakpoint regression; Figure 4).

220 **Discussion**

221 Here we show that variation in water availability can modify the strength of top-down
222 effects (Figure 1B). Population-level effects of large spiders on crickets varied with water
223 availability, as predicted from previously observed shifts in per capita consumption in cages
224 [15]. Specifically, large spiders reduced cricket populations under dry ambient conditions, but
225 had no effect with water supplementation (Figure 1, B1 vs B2). This result followed expectations
226 from previous research in cages [15], and thus supports the hypothesis that short-term, small-
227 scale changes in per capita effects can roughly predict longer-term population-level dynamics
228 [19]. Similarly, as predicted, large spiders had positive effects on moist leaf material (reduced
229 herbivory) under dry conditions (Figure 1, B1), but in contrast to predictions (no effect), large
230 spiders increased herbivory where direct free water was added (reverse of a trophic cascade;
231 Figure 1, B2). Moreover, large spiders reduced herbivory with moist leaf addition, even though
232 the abundance of crickets was unaffected by large spiders (Figure 1, B3). Water also influenced
233 the effects of large spiders on small spiders, but the mechanism remains unclear, requiring
234 further exploration. Taken together, our results suggest that free water availability controlled the
235 size and direction of multi-level top-down effects in this system, but not always as predicted.

236 The increase in herbivory associated with spiders when free water was added (reverse
237 trophic cascade) was unexpected (expectation = no effect). Although we cannot directly test the
238 mechanism behind this observation, we hypothesize it may be due to large spiders deterring
239 crickets from accessing water pillows [video observation, J. Sblendorio and L. Ford II; sensu 46],

240 forcing crickets to rely more greatly on moist leaves to meet water demands [10]. Another
241 unexpected result was the lack of an effect of spiders on cricket abundance in moist leaf
242 additions. We hypothesize this could be due to high rates of recruitment of crickets to these plots
243 masking potential evidence of top-down effects (see rate of increase in crickets in moist leaf
244 plots in Figure 3) or perhaps could be associated with an increased water content of crickets in
245 those plots leading to lower per capita consumption by spiders.

246 Despite the lack of an effect of large spiders on cricket abundance with moist leaf
247 additions, large spiders still reduced herbivory in that treatment (see spider effect on moist leaves
248 in Figure 3 & Figure 1, B3). Although we cannot directly test a mechanism for this observation,
249 we hypothesize that this could be a consequence of a trait-mediated indirect interaction—“fear”
250 of predation by large spiders could have led to reductions in rates of leaf consumption, especially
251 when these leaves were more abundant [sensu 29, 46]. However, we admit there are other, more
252 complex possibilities. For instance, if spider consumption of crickets led to compensatory
253 dispersal of crickets into high spider plots at higher rates, new crickets could have changed
254 competitive interactions within these plots or showed other differences in behaviour that could
255 have reduced herbivory. But, overall, we believe it is most likely that trophic cascades in this
256 system are being driven by a combination of density-mediated indirect interactions
257 (consumption) and trait-mediated indirect interactions (behaviour), agreeing with expectations
258 from theory for a sit-and-pursue predator with prey confined to the same habitat as predators [see
259 29]. Moreover, although other possibilities exist, we hypothesize that the balance of trait-
260 mediated and density-mediated effects may depend on water availability—consumers may
261 perform a cost-benefit analysis: with limited water (free or in food), direct consumptive effects

262 may outweigh behavioural effects, whereas with greater water availability (free or in food)
263 behavioural effects may become more pronounced. We believe that water balance may play a
264 large role in driving the behaviour of terrestrial animals—dehydration can occur quickly and
265 may pose more certain risks than predation (perhaps epitomized by species interactions
266 surrounding watering holes in the African savanna [47]). But testing the hypotheses outlined
267 above requires additional experimentation.

268 Levels of leaf damage were highly correlated with soil moisture (more strongly than
269 water addition treatments) with a non-linear, threshold-type transition from almost full
270 consumption to almost zero consumption between 5.5% (breakpoint regression) and 6.8%
271 volumetric soil moisture (maximum soil moisture with > 50% leaf consumption). This level
272 likely represents the point at which crickets switch from obtaining water from moist leaf material
273 to obtaining water from environmental sources. We believe this transition point could vary
274 considerably among taxa and ecosystems, due to differences in physiological traits (e.g.
275 cutaneous water loss), drivers of water loss (e.g. temperature, humidity), and availability and
276 quality of trophic water sources (e.g. chemically defended leaves). However, to provide some
277 guidance as to the potential frequency of water-mediated top-down effects, we examined
278 volumetric soil moisture measurements across the US using the COSMOS Soil Moisture
279 Network database [48] and found that soil moistures below 6.81% can be found in 49% of the 65
280 US measurement locations, over the seven year period from 2008-2014—even mesic locations in
281 the southeastern US and in northern Wisconsin and Michigan showed values below this
282 threshold, but the greatest frequency was within the US sunbelt (Electronic Supplementary
283 Materials, Figure S5). These results correspond well to previous suggestions that patterns of

284 animal species richness are at least partially limited by water at all but the highest latitudes
285 [energy only at $> 50^\circ$; 7]. If the effects of soil moisture on arthropod foraging behaviour and
286 population dynamics found here can be generalized beyond our study (note: our research site was
287 far from the driest in the database, Figure S5, Table S3), our results suggest that a broad range of
288 terrestrial food webs could be influenced by changes in water availability. The relative
289 importance of changes in water availability on animal-mediated top-down effects (isolated here)
290 compared to plant-mediated bottom-up effects (circumvented here) remains to be investigated.
291 But our research is directly relevant to situations where plant and animal water availability are
292 decoupled (e.g. trees that use groundwater when surface soils are dry; mobile animals that can
293 access sparse surface water in dry landscapes). Moreover, animals living in mesic environments
294 may be even more sensitive to short-term dry, hot periods (due to fewer adaptations to these
295 conditions), with water-mediated top-down effects possibly manifesting at higher soil moistures.
296 Thus, the potential for effects of water balance on animal foraging behaviour and food web
297 dynamics should be considered when investigating terrestrial food web ecology in many biomes.
298 Moreover, water-mediated trophic interactions could underlie food web responses to changes in
299 spatial and temporal patterns of water availability expected with global climate change,
300 groundwater pumping, and human infrastructure.

301

302 **DATA ACCESSABILITY:** Data is available in the Electronic Supplementary Material.

303 **COMPETING INTERESTS:** We have no competing interests.

304 **AUTHOR CONTRIBUTIONS:** KM designed, conducted, and analyzed the study and wrote
305 the manuscript. JS provided advice on the design and analysis of the study and edited the
306 manuscript.

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315

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434

435 **Figure and Table Captions**

436 Figure 1. Comparison of predicted and observed effects of large (>1 cm) ground spiders, under
437 three water treatments, on a desert riparian food web. The water drop symbol indicates the
438 experimental supplementation of free water (via water pillows) and the leaf symbol indicates
439 fluxes of water in moist leaf material (natural and experimental). Water was supplemented 2.5X
440 the ambient rate of water flux (via natural greenfall). The width of arrows represents the
441 qualitative size of fluxes of water (grey arrows) or the strength of top-down effects (black
442 arrows). Mathematical symbols indicate direction of effects, while numbers are parameter
443 estimates of the rate of change (see Table 1). Under dry ambient conditions (left) and with added
444 moist leaves (right), we expected large spiders to have strong negative effects on cricket
445 abundance and positive effects on leaf abundance, but we expected these effects to disappear
446 with free water (middle). Additionally, we expected large spiders to switch between consumption
447 of crickets (without water) and small spiders (with water). Observed patterns matched the
448 expectation that free water would greatly influence top-down effects. But water addition was
449 insufficient to “quench” cricket leaf consumption (*sensu* McCluney and Sabo 2009), large
450 spiders did not reduce cricket abundance with moist leaf additions, and the effects of large

451 spiders on herbivory where water was added were likely behavioural, since there were no effects
452 of large spiders on cricket abundance in those treatments. Effects of large spiders on small
453 spiders also did not match expectations, with large spiders positively affecting small spiders
454 under dry ambient conditions, but having no effects in other treatments.

455

456 Figure 2. Changes in soil moisture (A), air temperature (A), and spider abundance (B-D) over the
457 duration of the experiment. Error bars are standard error of the mean. C and D represent
458 estimates of the rate of change in large spider abundance per unit time, between each of the
459 experimental periods, from model parameter estimates, which controls for plot differences.
460 Spider removal significantly reduced the abundance of large spiders by the end of the
461 supplementation period (Table S1).

462

463 Figure 3. Effects of large spiders on crickets, small spiders, and leaves, reported as the rate of
464 change from the initial, pre-manipulation period to the end of the spider removal, water addition
465 period. Plots are divided into ambient water plots ("Control," "C," black symbols), free water
466 supplemented plots ("Water," "W," blue symbols), and moist leaf supplemented plots ("Moist
467 Leaves," "ML," green symbols). "A" and "R" on the X-axes refer to ambient and reduced
468 densities of large spiders. Error bars are standard error of the mean. Effect sizes are estimates of
469 the rate of change in each response per unit time (3-day survey blocks for crickets and spiders,
470 experimental periods for leaves), based on model parameter estimates, which controls for plot
471 differences. Large spiders had a significant negative effect on crickets in control plots and
472 positive effect on moist leaves in all treatments (but note the effect is opposite for free water)

473 according to post-hoc Dunnet tests (Table 1). The response of moist leaf material is displayed as
474 the amount remaining so that it is more easily comparable to other graphs, but this means that it
475 displays the inverse of consumption (noted by the arrow on the right hand side). Post-hoc tests
476 for small spiders do not show significant differences (Table S2), despite an overall significant
477 time \times water \times spider removal interaction (Table S1). Results for the post water addition,
478 “simulated drying” period (see Figure 2) are reported in the Electronic Supplementary Materials.
479 See Figures S2-4 for plots of full time series.

480

481 Figure 4. Soil moisture vs herbivory in each true control plot. Scatterplot of the mean
482 consumption of leaves per plot, per measurement date, showing maximum soil moisture with
483 $>50\%$ consumption (6.8% by volume) and average point of decline in consumption (5.51%)
484 from breakpoint (piecewise) regression (solid line).

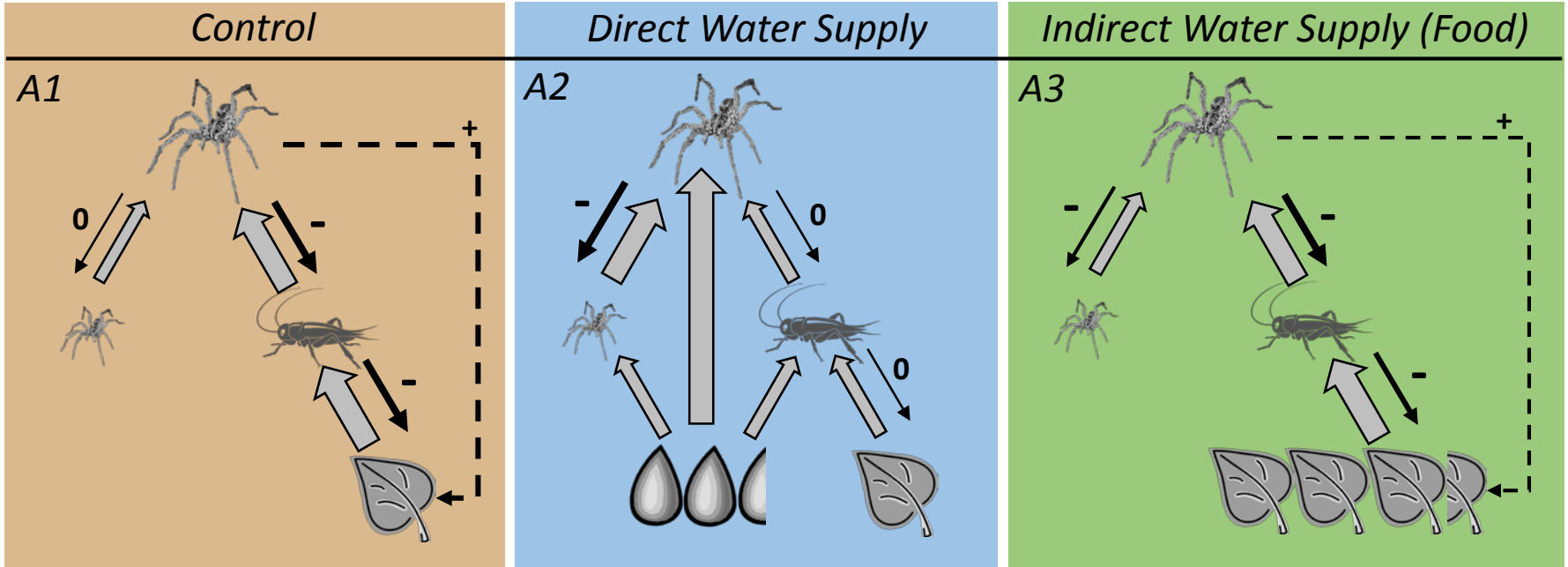
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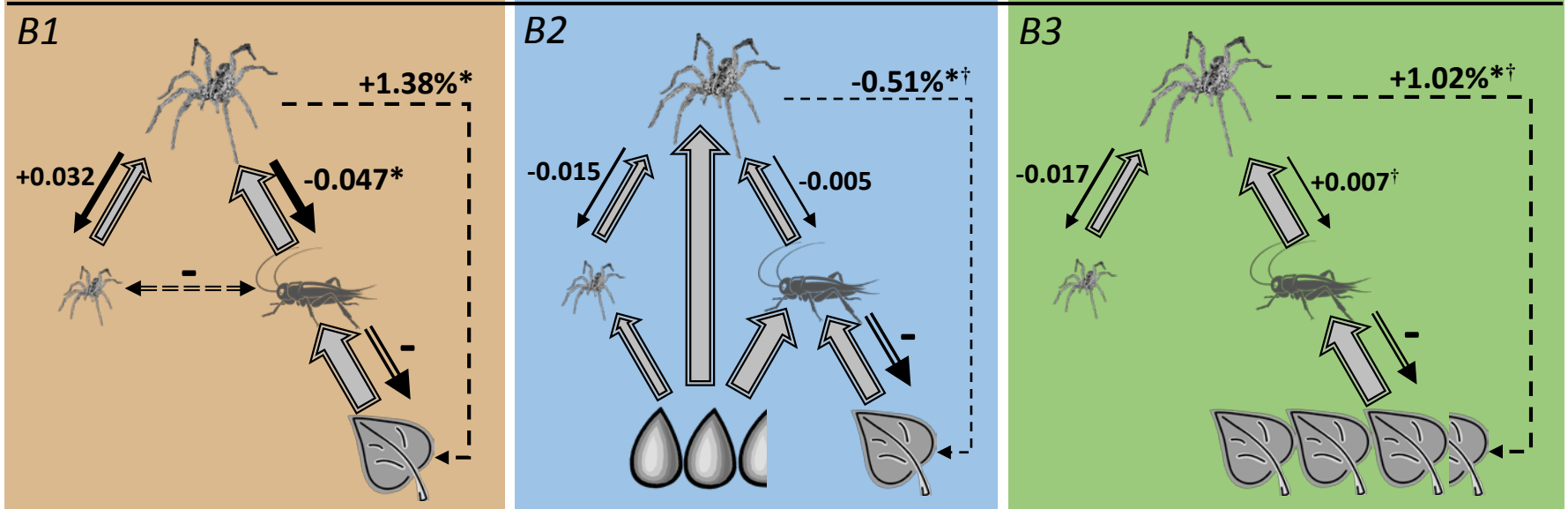
487 Table 1. Post-hoc general linear hypothesis tests (Dunnet’s) for the effects of spiders on crickets
488 or leaf material, within each water treatment, following finding of a significant interaction
489 between spider treatments and water supplementation treatments in the full model (during the
490 first two periods, pre-experiment and supplementation).

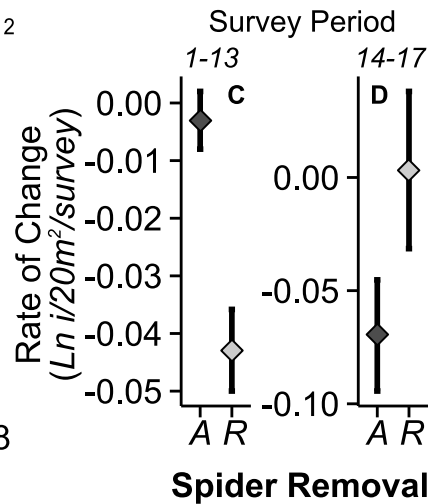
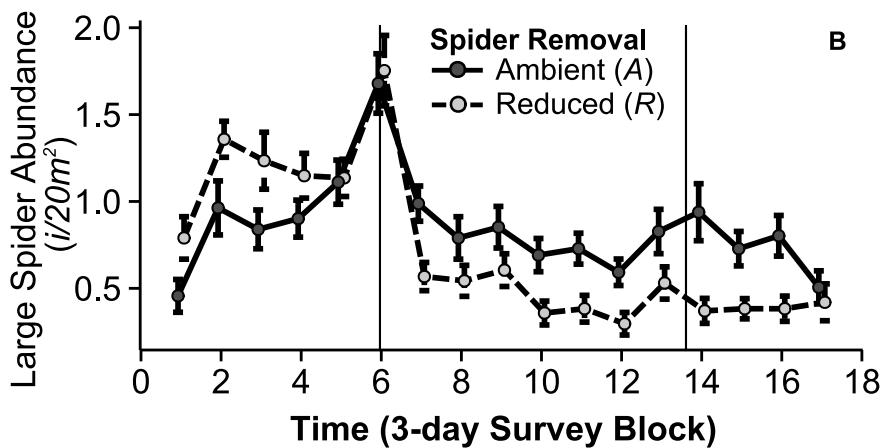
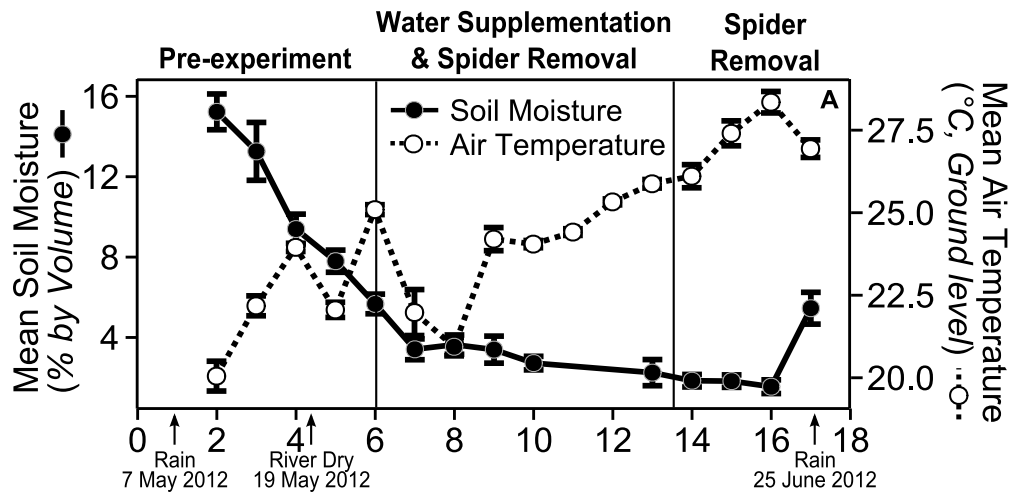
Water flux Indirect effect † = Possible behavioral effect (fear)
 Direct effect Unmeasured effect * = Statistically significant effect

A. Predicted

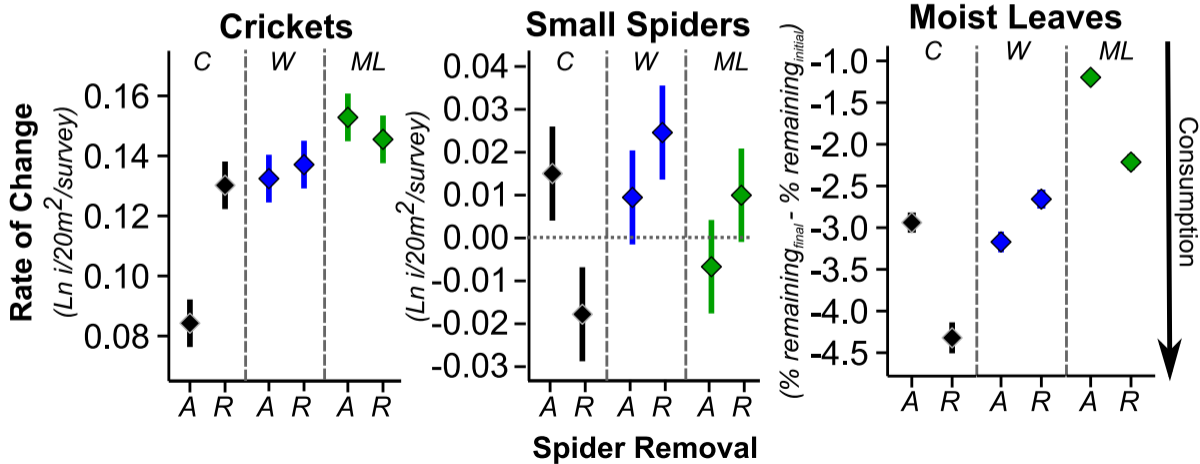


B. Observed





Spider Removal	Water Addition
A = Ambient	◆ Control (C)
R = Reduced	◆ Water (W)
	◆ Moist Leaves (ML)



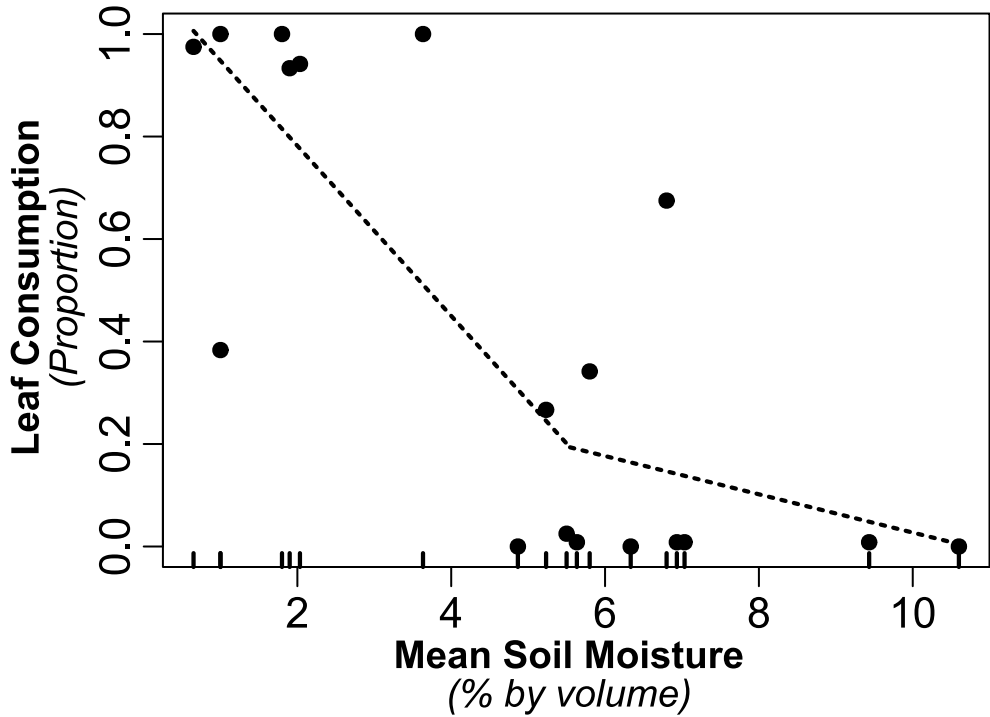


Table 1

Water Treatment	Estimated effect of spider removal	SE	z-value	p-value
	<u>Cricket Abundance</u> (change per unit time, ln i/20m ²)			
<i>Control</i>	0.046	0.011	4.10	<0.000
<i>Water</i>	0.005	0.011	0.42	0.967
<i>Moist Leaves</i>	-0.007	0.011	-0.65	0.886
	<u>Leaf Consumption</u> (change per unit time, %)			
<i>Control</i>	-1.382	0.205	-6.74	<0.000
<i>Water</i>	0.513	0.148	3.47	0.002
<i>Moist Leaves</i>	-1.016	0.079	-12.88	<0.000

Media summary

Despite the clear importance of water balance to the evolution of terrestrial life, much is unknown about the effects of animal water balance on food webs. Here we show that the amount of water available to predators (spiders) can change the effects of these predators on prey (crickets) and vegetation (moist leaves). Moreover, water balance appears to drive the consumption of moist food under soil moisture conditions that are currently common across the US and may become increasingly common with climate change. Thus, rainfall and drought may influence how predators control prey and rates of herbivory.

Electronic Supplementary Material

Text S1. Detailed Methods

Study Site and Species Descriptions

The experiment was conducted in a pair of large adjoining floodplain forests along the San Pedro River, in southeastern AZ, USA. Each floodplain was 3-4 ha in size and was dominated by an overstory of Fremont cottonwood (*Populus fremontii*) and Goodings willow (*Salix goodingii*), with an understory of tamarisk (*Tamarix* spp.), seepwillow (*Bacharis* spp.), and mesquite (*Prosopis velutina*). In riparian forests along the San Pedro, moist green cottonwood leaves fall to the forest floor (“greenfall”) daily, providing a flux of groundwater to aboveground consumers (Sabo et al. 2008). Dry leaf litter, mostly from cottonwoods, dominated the ground cover, but bunch grasses, primarily Johnson (*Sorghum halepense*) and Sacaton (*Sporobolus wrightii*) were present in abundance at some locations. In general these grasses were dormant and dry during the study. Uplands, not directly involved in this study, were characterized by plants of the Chihuahuan desert, including creosote (*Larrea tridentata*) and yucca (*Yucca* spp.). Previous work has demonstrated that riparian habitat along the San Pedro is, in general, cooler and more humid than desert uplands in this semi-arid region (Sabo et al. 2008).

Damp-loving field crickets (*Gryllus alogus*) were the numerically dominant low-level omnivorous consumer in these riparian forests, while the wolf spider *Hogna antelucana* was the largest, most abundant invertebrate predator. *G. alogus* is endemic to the southwestern US, but *H. antelucana* has a widespread distribution across the US (Shorthouse 2009). In several previous studies as well as this one, *G. alogus* has been observed consuming dry leaf litter, seeds, moist green leaves, and dead or immobilized conspecifics, while *H. antelucana* has most commonly been observed preying on *G. alogus*, but is a generalist sit-and-pursue predator (K. McCluney, pers. obs.). Other, less numerous, but fairly common invertebrates in this food web include roaches (Order Blattodea), camel crickets (Family Rhabdophoridae), ground beetles (Tenebrionidae: *Eleodes*), and a variety of smaller spider species (e.g., *Pardosa* spp.). Additionally, tree and ground lizards, medium sized mammalian carnivores or omnivores, and insectivorous birds likely prey on ground-dwelling arthropods in this system (Soykan and Sabo 2009, K. McCluney, pers. obs.).

The San Pedro River is one of the last free-flowing (undammed) rivers in the American west and has a high diversity of birds (100 breeding species, 250 migratory), mammals (80 species), and reptiles (65 species) (Stromberg and Tellmann 2009). Along the 140 km of this south to north flowing dryland river, sections can be found that flow perennially, intermittently, or ephemerally (Turner and Richter 2011). The hydrology and ecology of the San Pedro are driven by distinct seasonality, with a hot, dry early summer (May-June) and a wet monsoon (July-September) season. Most of the yearly precipitation falls in the monsoon season, resulting in large floods that can create major disturbance events in the river and the floodplain.

Design

Previous pilot work suggested that dispersal of spiders over short distances was significant (observations of marked individuals traveling >30 m in less than a week). Therefore, complete randomization of spider and water treatments would have produced unintentional adjacent removal or spillover of spiders, diluting the effect of the removal treatment—a central goal of the experiment. To maximize treatment success, we set up our plots with restricted randomization in a classic split-plot design (Figure 2), in which spider removal plots were randomly assigned to three blocks within six regions of the floodplain, separated by >60 m from ambient spider block. Water treatments (free and trophic) and controls were randomly assigned to plots within each of these regions.

Large spider removal was conducted nightly, directly following completion of surveys in each plot. Large spiders (>1 cm head to cephalothorax) were removed from each spider removal plot by two individuals searching for 6 mins (8 mins on the first night) with the same headlamps as those used for surveys. Spiders were also removed from 3 “ghost” plots in each spider removal section, immediately adjacent to experimental plots, but no further activities were conducted in these plots (Figure S1). These plots were used solely to increase our removal rate of spiders in the reduction regions of the floodplain.

Water treatments were applied to a column of 3 plots that bordered each other on a side (Figure S1), with either free water or trophic water added to the plots on each end (randomly assigned), with the middle plot left as a control (“middle control”). Additionally, we created another control plot, spaced at least 20 m from the other plots (“true control”). Middle control plots were excluded from analyses and discussion within this manuscript, since their purpose was to examine arthropod movement rather than understand how water influenced trophic cascades.

During the supplementation period, water pillows or freshly picked cottonwood leaves were added daily as resource “patches.” Each “patch” was added to each plot in a random location by creating a “pace-sized” grid for each plot and using a random number generator, with replacement, to determine the location of each resource patch in terms of number of paces in each direction. Thus resource patches were randomly distributed in each plot with some locations having up to two (maximum observed in our random draws) resource patches clumped together, but with most locations having only one resource patch or none. This design also ensured that the number of resources on or off a transect varied randomly. Each plot received 25 resource patches.

Water pillows contain approximately 30 mL of water and can stay wet for extended periods of time. Each plot received 750 mL of additional water per day, a rate equivalent to 2.5x the rate of water flux naturally occurring in greenfall (Sabo et al. 2008). Water pillows are made commercially for the pet industry, specifically for house crickets and hermit crabs, but we have successfully used this product in the lab and field for a variety of arthropods (McCluney and Sabo 2009). In all, we added 150 water pillows per day across all plots (4.5 L of water), or 3,450 (103.5 L of water) over the course of the experiment.

Moist green leaves were picked from the same location each day, from trees at a similarly sized floodplain upstream of the study site. To equal an equivalent volume of water as provided in the water pillows, each moist leaf patch consisted of 19 cottonwood leaves placed in a mesh bag with 2.5 cm openings. This equaled 475 leaves per plot, per day, 2,850 leaves across all plots each day, and 65,550 across the addition period. In both cases, water was supplemented at 2.5 times the ambient rate of cottonwood greenfall water flux (Sabo et al. 2008). However, crickets

may compete for access to water pillows and defend them against conspecifics (unpublished data). Thus, the relative delivery of water to crickets may have differed between these treatments, since there was substantially greater surface area of bags of moist leaves than of water pillows and we commonly observed >10 crickets on a single bag of leaves, but rarely this many on a water pillow, and usually less than 5 at a time (unpublished data).

Surveys

To reduce the perception of observer effects as treatment effects, the same pair of observers would conduct surveys for 10 days at a time, with transitions to a new pair of observers timed to avoid experimental transition periods. The location of initiation of surveys rotated nightly and responses were averaged across a complete rotation of starting locations (3 days) to reduce effects of temporal differences in activity.

Data Processing and Statistical Analysis

In statistical analyses, responses were typically expressed as the natural log of 3-day means of the count data, to reduce effects of a different starting location on each of those nights and to meet model assumptions (normality). We tested if temporal autocorrelation was important by comparing models that assumed compound symmetry or autoregressive variance-covariance structures and picked the best model, based on AIC, for subsequent analysis. Analyses of leaf damage were conducted similarly, but due to the non-normal, proportion-based measurements, we compared generalized linear mixed effects models with a binomial link function.

To properly compare experimental periods, we divided the analyses, first comparing changes between the initial pre-treatment period and the supplementation and spider removal period. Then we separately examined the post-supplementation (but still spider removal) simulated drought period.

Comparison of Soil Moisture-Herbivory Relationships With US Soil Moisture Patterns

We compared the relationship between soil moisture and herbivory found in our study with measurements from the COSMOS soil moisture sensor network (Zreda et al.) from 2008-2014 to predict the potential frequency of animal water stress across the US. Specifically, we divided the number of observations of soil moisture below the threshold value for water limitation (from experimental measurements) by the total number of observations, for each site. We excluded measurements below 35 cm soil depth and from November through March each year, focusing on ground arthropod available soil moisture during the growing season. We also excluded a limited number of values lower than 0% or higher than 100% to remove erroneous measurements.

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Figure S1. A) Site map with water treatments denoted by colors and spider treatments denoted by the presence of a line through the plot. Ambient plots between water addition plots (“middle control”) were excluded from analysis and discussion in this paper, with comparisons only made with adjacent ambient plots separated by >20 m (“true control”). Additional spiders were removed from “ghost” plots, but responses were not measured. See methods and Appendix B for more thorough description. B) Field crickets (*Gryllus alogus*) drinking water from the surface of a water pillow. C) The wolf spider *Hogna antelucana* hunting the field cricket *Gryllus alogus* on added leaves (by JL Sabo).

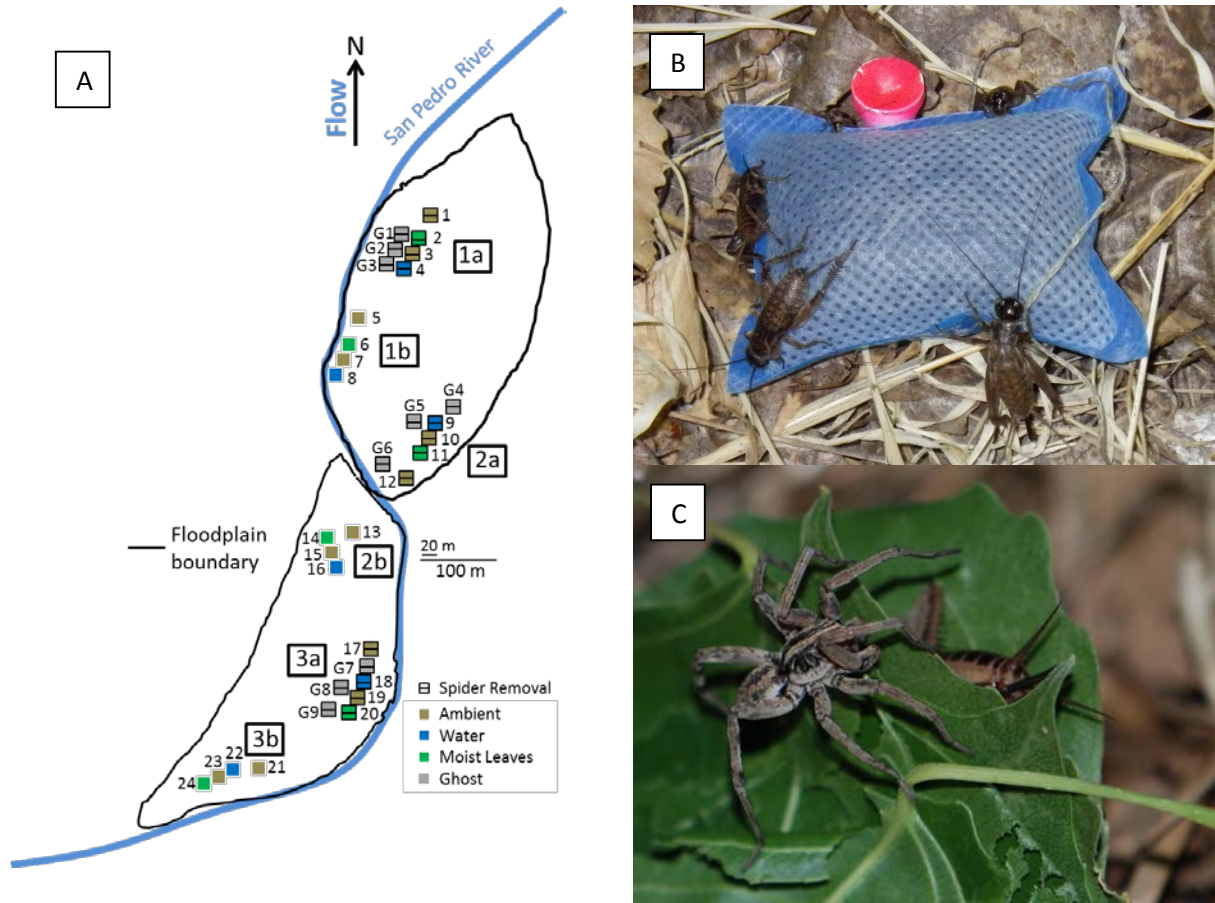


Figure S2. Changes in cricket abundance associated with large spider removal for each water treatment. Plots are divided into ambient water plots (“Control,” white background, top row), free water supplemented plots (“Water,” blue background, middle row), and moist leaf supplemented plots (“Moist Leaves,” green background, bottom row). A and R on the X-axes refer to ambient and reduced densities of large spiders. Error bars are standard error of the mean. D-I represent estimates of the rate of change in cricket abundance per unit time, between each of the experimental periods, based on model parameter estimates, which controls for plot differences. Spider removal significantly increased the abundance of crickets in ambient dry conditions only (Table 1).

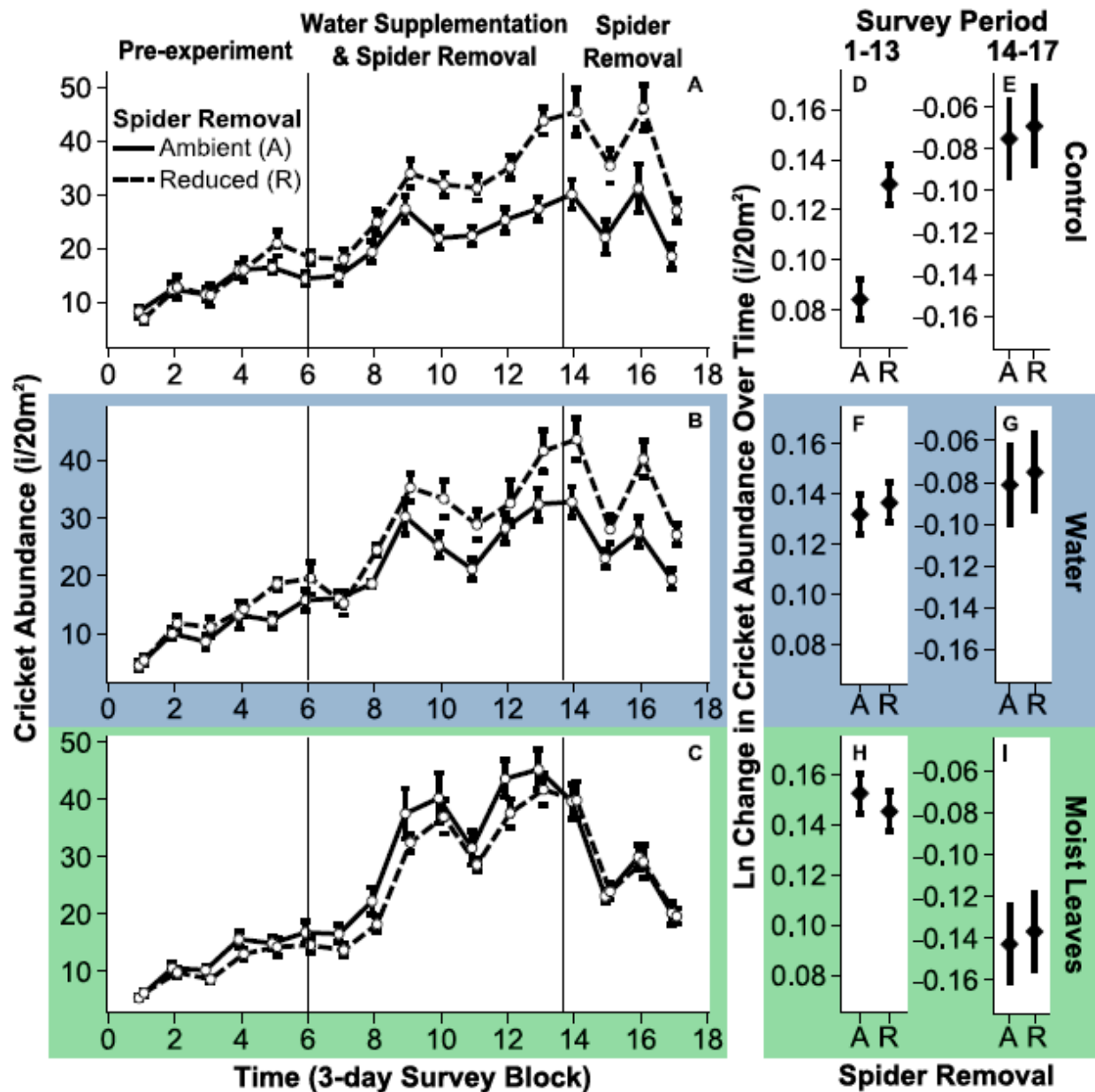


Figure S3. Changes in small spider abundance associated with large spider removal for each water treatment (A-C). Plots are divided into ambient water plots (“Control,” white background, top row), free water supplemented plots (“Water,” blue background, middle row), and moist leaf supplemented plots (“Moist Leaves,” green background, bottom row). A and R on the X-axes refer to ambient and reduced densities of large spiders. Error bars are standard error of the mean. D-I represent estimates of the rate of change in small spider abundance per unit time, between each of the experimental periods, based on model parameter estimates.

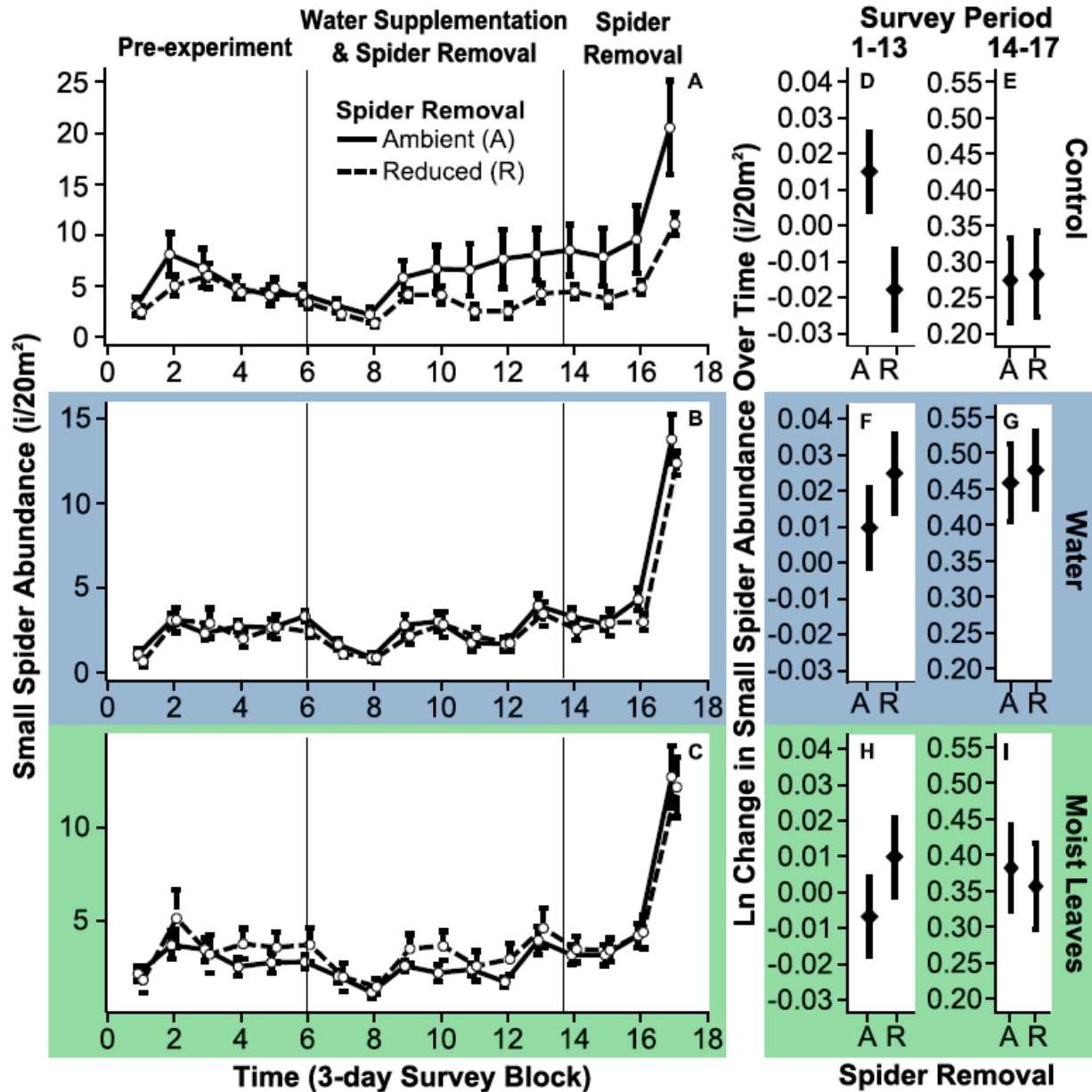


Figure S4. Changes in leaf consumption associated with large spider removal for each water treatment (A-C). Plots are divided into ambient water plots (“Control,” white background, top row), free water supplemented plots (“Water,” blue background, middle row), and moist leaf supplemented plots (“Moist Leaves,” green background, bottom row). A and R on the X-axes refer to ambient and reduced densities of large spiders. Error bars are standard error of the mean. D-I represent estimates of the rate of change of leaf material per unit time, between each of the experimental periods, based on model parameter estimates, which controls for plot differences. Spider removal led to small decreases in leaf material in dry control (D) and moist leaf addition (H) treatments, but slight increases in water addition plots (F) (change from experimental period 0 to 1, Table 2). Changes from experimental period 1 to 2 (E, G, I) are just reversals of previous patterns as water limitation was alleviated by rainfall (see Figure 2A).

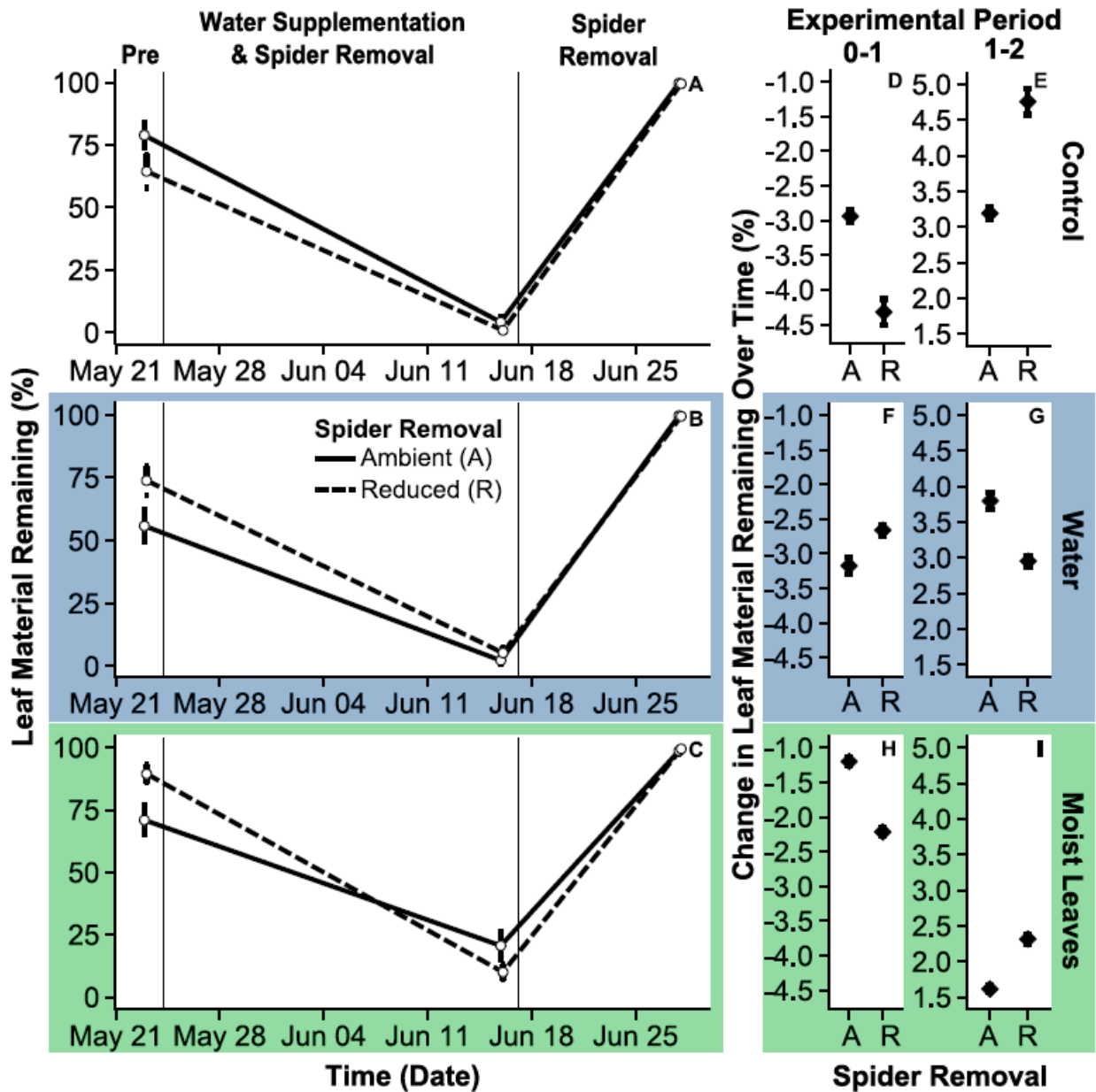


Figure S5. Expected distribution and frequency of water-limited trophic interactions during the growing season (April-October), based on extrapolation from experimental measurements to observations in the COSMOS soil moisture network. Coloration represents the frequency of observations shallower than 35 cm that fall below the maximum cutoff for water-limited herbivory observed in experimental work (6.8% volumetric soil moisture). 49% of all stations in the US and 63% of all stations in the sunbelt (below dashed line) have experienced soil moistures that could promote water limited trophic interactions.

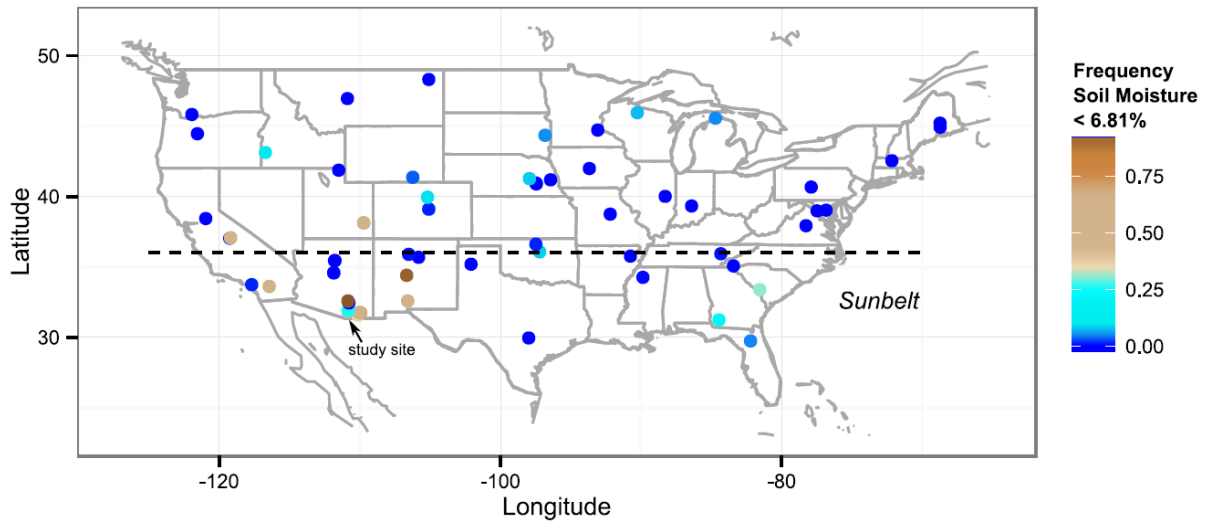


Figure S6. Expected average distribution and frequency of water-limited trophic interactions during the growing season (April-October), based on extrapolation from experimental measurements to observations in the COSMOS soil moisture network. Coloration represents the frequency of observations shallower than 35 cm that fall below the breakpoint regression suggested average cutoff for water-limited herbivory observed in experimental work (5.51%). 40% of all stations in the US and 56% of all stations in the sunbelt (below dashed line) have experienced soil moistures that should promote water limited trophic interactions.

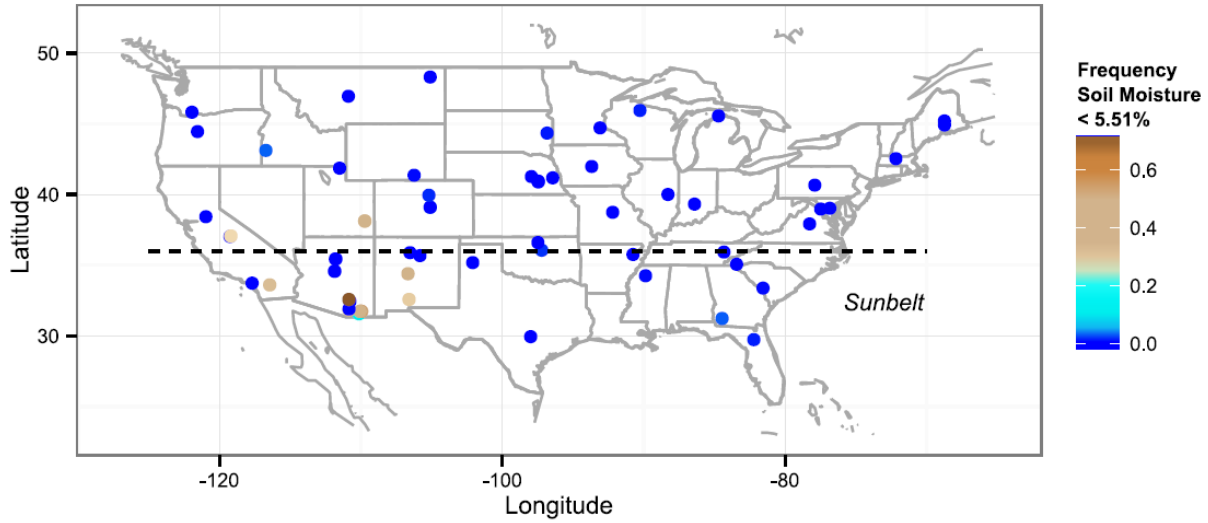


Table S1. Effects of treatments (or soil moisture) on measured response variables, shown as the effect of removing each term from the full model (likelihood ratio tests).

Model component removed	df	Δ AIC	LRT (χ^2)	p-value
<u>Pre-experiment and Supplementation</u>				
<u>Large Spiders</u>				
-Time * water * spider removal	2	-3.28	0.72	0.697
-Time * water	2	-3.92	0.07	0.965
-Time * spider removal	1	27.58	29.58	<0.000
-Water * spider removal	2	-2.81	1.19	0.552
-Water	2	-0.95	3.05	0.218
<u>Crickets</u>				
-Time * water * spider removal	2	8.05	12.05	0.002
<u>Small Spiders</u>				
-Time * water * spider removal	2	2.47	6.47	0.039
<u>Herbivory (Leaf Material Remaining)</u>				
-Time * water * spider removal	2	99.9	103.9	<0.000
<u>Post-supplementation</u>				
<u>Large Spiders</u>				
-Time * water * spider removal	2	-3.80	0.20	0.904
-Time * water	2	-2.20	1.80	0.407
-Time * spider removal	1	2.50	4.50	0.034
-Water * spider removal	2	-3.53	0.46	0.793
-Water	2	-1.10	2.90	0.235
<u>Crickets</u>				
-Time * water * spider removal	2	-0.88	3.11	0.211
-Time * water	2	6.27	10.27	0.006
-Time * spider removal	1	-1.89	0.11	0.745
-Water * spider removal	2	4.45	8.45	0.015
<u>Small Spiders</u>				
-Time * water * spider removal	2	-3.72	0.28	0.869
-Time * water	2	2.27	6.28	0.043
-Time * spider removal	1	-1.98	0.02	0.890
-Water * spider removal	2	-2.45	1.55	0.460
-Spider removal	1	-1.29	0.71	0.398
<u>Herbivory (Leaf Material Remaining)</u>				
-Time * water * spider removal	2	131.80	135.78	<0.000
<u>Leaf Consumption in True Control Plots Across Experiment</u>				
-Soil Moisture	1	6520.0	6522	<0.000

Table S3. The frequency with which soil moistures from the COSMOS soil moisture network fell below the maximum (6.8%) or breakpoint regression suggested average (5.51%) cutoff for water-limited herbivory from experiments.

Site	Latitude	Longitude	freq.6.8	freq.5.51	nobs
Austin Cary	29.738	-82.219	0.048	0.006	6989
Freeman Ranch	29.949	-97.997	0.000	0.000	12447
JERC	31.236	-84.462	0.231	0.026	8572
San Pedro 2	31.562	-110.140	0.336	0.138	12295
Kendall	31.737	-109.942	0.512	0.326	15536
Rancho No Tengo	31.744	-110.022	0.775	0.655	3817
Lucky Hills	31.744	-110.052	0.582	0.404	5134
Santa Rita Mesquite	31.820	-110.840	0.598	0.427	3141
Santa Rita Creosote	31.909	-110.839	0.256	0.000	5455
Mount Lemmon	32.442	-110.782	0.000	0.000	3521
Biosphere 2	32.580	-110.851	0.936	0.717	11857
Jornada Mixed Shrubland	32.580	-106.600	0.430	0.285	3098
Savannah River	33.383	-81.566	0.306	0.002	3010
Desert Chaparral UCI	33.609	-116.451	0.580	0.311	8446
Coastal Sage UCI	33.734	-117.696	0.010	0.000	17805
Goodwin Creek	34.255	-89.874	0.002	0.001	10648
Sevilleta New Grass	34.400	-106.674	0.918	0.359	184
Hauser Farm South	34.577	-111.859	0.000	0.000	3487
Hauser Farm North	34.580	-111.863	0.000	0.000	3510
Coweeta	35.066	-83.437	0.000	0.000	6616
Bushland	35.188	-102.096	0.000	0.000	11977
Flag Ponderosa Pine	35.439	-111.804	0.000	0.000	12490
Flag Wildfire	35.446	-111.772	0.000	0.000	12499
Santa Fe Watershed-SF1	35.679	-105.827	0.000	0.000	4941
Jonesboro	35.760	-90.762	0.000	0.000	2416
VCNP CZO	35.890	-106.533	0.004	0.000	13914
Chestnut Ridge NOAA	35.931	-84.332	0.003	0.001	11688
SMAP-OK	36.064	-97.217	0.074	0.013	20276
ARM-1	36.605	-97.488	0.009	0.000	20251
Soaproot	37.031	-119.256	0.000	0.000	16055
P301	37.068	-119.194	0.487	0.264	16091
UVA	37.923	-78.274	0.000	0.000	7997
Tower Ruin	38.117	-109.718	0.377	0.284	7905
Lower Salt Creek	38.129	-109.735	0.490	0.424	7971
Tonzi Ranch	38.432	-120.966	0.000	0.000	16173
Mozark	38.744	-92.200	0.000	0.000	12956
Sterling	38.974	-77.485	0.000	0.000	6928
Beltsville	39.030	-76.846	0.000	0.000	12080
Manitou Forest Ground	39.101	-105.103	0.171	0.027	14530

Manitou Forest Tower	39.101	-105.102	0.009	0.000	19796
Morgan Monroe	39.323	-86.413	0.000	0.000	11567
Marshall Colorado	39.950	-105.196	0.087	0.010	18796
Bondville	40.006	-88.290	0.000	0.000	16755
Shale Hills	40.665	-77.907	0.000	0.000	11718
York Rainfed	40.890	-97.459	0.000	0.000	1315
York Irrigated Soybean	40.934	-97.459	0.000	0.000	1316
York Irrigated Maize	40.948	-97.487	0.000	0.000	1693
Neb Field 3	41.180	-96.441	0.000	0.000	17016
CC Pasture	41.269	-97.947	0.073	0.000	1003
GLEES	41.364	-106.239	0.034	0.001	13581
Daniel Forest	41.865	-111.509	0.000	0.000	10290
Iowa Validation Site	41.983	-93.684	0.000	0.000	18218
Harvard Forest	42.538	-72.172	0.000	0.000	15644
Reynolds Creek	43.121	-116.723	0.163	0.027	9450
Brookings	44.345	-96.836	0.052	0.005	9299
Metolius	44.452	-121.557	0.000	0.000	15977
Rosemount	44.714	-93.090	0.000	0.000	13660
Caribou Bog	44.917	-68.736	0.000	0.000	2104
Howland	45.204	-68.740	0.000	0.000	13139
UMBS	45.560	-84.714	0.051	0.000	12048
Wind River	45.821	-121.952	0.000	0.000	15314
Park Falls	45.946	-90.272	0.068	0.006	15165
Tenderfoot Creek	46.951	-110.887	0.000	0.000	11651
Fort Peck	48.308	-105.102	0.000	0.000	13503
Saskatoon	52.133	-106.617	0.000	0.000	2017