
EXPLORING NUTRIENT AVAILABILITY AND HERBIVOROUS INSECT POPULATION DYNAMICS ACROSS MULTIPLE SCALES

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ABSTRACT

1. Nutrient composition varies greatly across landscapes, which in turn influences the spatiotem-
2 poral variation and dynamics of populations. Yet few studies have investigated this pattern on
3 multiple scales.
4. We tested how nutrient limitation affects herbivore populations across spatial scales from indi-
5 vidual behavior to landscape level population dynamics using Australian plague locust, *Chor-*
6 *toicetes terminifera* (Walker), field populations and long-term survey data from across their
7 range.
8. At the individual level, juvenile locusts selected for a carbohydrate-biased intake target of 1
9 protein (p) 2 carbohydrate (c) and had the highest growth and shortest development time when
10 fed artificial diets with that same 1p:2c ratio over the duration of the 5th (final) juvenile instar.
11. At the field level, locusts kept in field cages with protein-biased plants redressed their nutritional
12 imbalance by selecting very carbohydrate-biased diets (up to a 1p:20c ratio) for more than a
13 week after being removed from the protein-biased environment. Once the deficiency was met,
14 locusts returned to the 1p:2c intake target.
15. Going up to the landscape level, outbreaks were negatively correlated with soil nitrogen and
16 showed a non-linear relationship with soil phosphorus peaking at approximately 4% soil phos-
17 phorus. We disentangled the relationship between mean annual precipitation and soil nitrogen
18 through leveraging both comprehensive locust surveys and remotely sensed soil and weather
19 data that spanned decades.
20. This paper is the first to integrate lab, field, and remote sensing approaches to demonstrate the
21 importance of nutrient balancing and acquisition across scales for herbivores. Specifically for
22 locusts, we show that low nitrogen environments promote outbreaks, likely by reducing plant
23 protein to carbohydrate ratios. Incorporating soil quality data into locust plague forecasting
24 models can help increase accuracy of predictions.

25 **Keywords** nitrogen • phosphorus • grasshoppers • population dynamics • non-linear modeling • nutrient limitation •
26 remote sensing

27 **1 INTRODUCTION**

28 Plant nutrients are usually more variable than animal body composition, which can make it challenging for herbivores
29 to acquire an optimal nutritional balance [Elser et al., 2000]. Nutrient balance affects individual performance [Batzli,
30 1986, Bernays et al., 1994] and, by extension, influences population dynamics [Elser et al., 2000]. One way many
31 primary consumers achieve an optimal blend of nutrients is through selecting different host plants or plant parts to
32 reach a specific amount and ratio, termed the intake target, IT [Simpson and Raubenheimer, 2012a]. For example,
33 giant pandas (*Ailuropoda melanoleuca*) synchronize their migration and reproduction cycles with seasonal nutrient
34 availability between different bamboo species [Nie et al., 2015]. While studies have investigated this trend between
35 available nutrients and animal populations, they usually happen at one scale and biological level. For example, much
36 grasshopper nutrition research has been done at the organismal or local population level using lab and/or field studies
37 [Behmer, 2009, Cease, 2024, Le Gall et al., 2019], with a few separate larger scale modeling endeavors [Welti et al.,

38 2020b, Zhou et al., 2019]. To our knowledge, no study has integrated individual herbivorous animal nutrition to
 39 continental level patterns in nutrient availability. Here we work across spatial scales, bridging field observations and
 40 cage manipulations with continental-scale insect pest outbreak modeling to see how the animal-nutrient relationship
 41 changes across multiple scales.

42 Food quality has long been considered an important predictor of animal population dynamics [Andersen et al., 2004,
 43 White, 1993]. Phosphorus and nitrogen commonly limit primary production in ecosystems, either separately or as co-
 44 limiting factors [Tyrrell, 1999, Vitousek et al., 2010], and are often investigated as limiting factors for higher trophic
 45 levels to determine the consequences to animal growth and reproduction [Andersen et al., 2004]. For example, blue-
 46 grass fields supplemented with high quality (e.g. increased nitrogen) food pellets increase vole (*Microtus ochrogaster*)
 47 densities compared to control fields by supporting higher adult survival, increased breeding, and growth rate [Cole and
 48 Batzli, 1978]. Less phosphorus in a dryland insect herbivore's (*Sabinia setosa*) host plant, velvet mesquite (*Prosopis*
 49 *velutina*), leads to individuals having decreased RNA content (slower growth) and lower abundance [Schade et al.,
 50 2003]. More broadly, nitrogen and phosphorus limitation has been shown in mammals [Randolph et al., 1995, White,
 51 1993], birds [Forero et al., 2002, Granbom and Smith, 2006], and insects [Floyd, 1996, Huberty and Denno, 2006,
 52 Marsh and Adams, 1995, Perkins et al., 2004] which is discussed further in White [2008] and Andersen et al. [2004].
 53 However, not all animal populations respond positively to increasing environmental nutrients. For example, studies
 54 from across the globe reveal that the abundances of many grasshopper species are positively [Joern et al., 2012, Ozment
 55 et al., 2021, Welti et al., 2020a,b, Zhu et al., 2020, 2019], or not related [Heidorn and Joern, 1987, Jonas and Joern,
 56 2008, Lenhart et al., 2015, Ozment et al., 2021] to plant nitrogen concentrations as reviewed in Cease [2024]. Can
 57 the relationship between herbivore abundance and environmental nutrients be explained by approaches that consider
 58 nutritional physiology at the organismal level, in addition to population and landscape ecology?

59 One excellent study system to understand the complex relationship of nutrient availability and population dynamics
 60 is a subset of grasshoppers called locusts [Cullen et al., 2017, Uvarov, 1977]. Locusts undergo massive population
 61 eruptions known as plagues that pose significant issues for global food security [Cease et al., 2015]. For example,
 62 the 2010-2011 Australian plague locust (*Chortoicetes terminifera*) plague could have caused AUD\$963 million in
 63 crop damage if not controlled [Millist and Ali, 2011]. In contrast to the nitrogen limitation paradigm (White 1993),
 64 locusts frequently show carbohydrate limitation. Many locust species, including *C. terminifera*, will select plants with
 65 a low protein:carbohydrate ratio and eat about double the amount of carbohydrate relative to protein when given a
 66 choice of artificial diets [Behmer, 2009, Brosemann et al., 2023, Lawton et al., 2021, Le Gall et al., 2019]. Their
 67 high energy, relative to protein, demand is heightened by their impressive long-distance migration. Marching bands
 68 of South American locusts (*Schistocerca cancellata*) eat predominantly from dishes containing carbohydrates and
 69 largely ignore dishes containing protein [Cease et al., 2023], and have the highest survival and lipid gain when eating
 70 carbohydrate-biased plants [Talal et al., 2020]. As adults, flight increases carbohydrate, but not protein, consumption
 71 in migratory locusts (*Locusta migratoria*) and locusts eating carbohydrate-biased diets fly for longer times [Talal et al.,
 72 2023]. At a local scale, high-use agricultural areas that decrease soil and plant nitrogen promote *Oedaleus* locust
 73 outbreaks in Senegal and China [Cease et al., 2012, Giese et al., 2013, Le Gall et al., 2019, Word et al., 2019]. Less is
 74 known about the relationship between plant phosphorus and locust populations, but grasshoppers and locusts can detect
 75 and regulate phosphorus during ingestion and post-ingestively to maintain homeostasis [Cease et al., 2016, Zhang
 76 et al., 2014]. Long-term laboratory rearing studies show negative effects of too little or excess dietary phosphorus,
 77 though short-term restrictions to low or high phosphorus diets appear to have no effects [Cease et al., 2016]. Field
 78 measurements of *Oedaleus asiaticus* in China show that locusts increase phosphorus excretion with increasing plant
 79 phosphorus content, suggesting that phosphorus may not be limiting in the Inner Mongolian Steppe for this species
 80 [Zhang et al., 2014]. Understanding the multi-scale flow of nitrogen and phosphorus from soils to continental scale
 81 population dynamics may reveal a connection between soil quality and locust plagues in Australia and further elucidate
 82 the pattern globally [Cease, 2024, Le Gall et al., 2019].

83 The arid interior of Australia is a highly variable environment [Morton et al., 2011] characterized by the Resource-
 84 Pulse Paradigm [Noy-Meir, 1974, Whitford, 2002]. Many Australian animal and plant populations irrupt following
 85 periods of favorable climatic conditions. For example, preceding vegetation growth is an important factor for *C. terminifera*
 86 population outbreaks [Lawton et al., 2022]. In addition to climatic variability, Australia is marked by poor
 87 natural soil fertility [Morton et al., 2011, Orians and Milewski, 2007]. Nutrients such as nitrogen and phosphorus are
 88 in short supply in unmodified soils. Subsequently, many native animals and plants are adapted to environments low
 89 in soil nutrients [Orians and Milewski, 2007]. Australia has several locust species, but the *C. terminifera* is the most
 90 widespread and economically damaging [Hunter et al., 2001]. As with many dryland animals, numerous studies have
 91 shown the relationship between climatic conditions and *C. terminifera* population outbreaks [Clark, 1974, Deveson
 92 and Walker, 2005, Farrow, 1982, Key, 1945], however few have investigated the relationship between soil and plant
 93 nutrients and this species' outbreaks.

94 In this study, we investigate the across scale relationship between soil and plant nutrients and animal populations using
 95 *C. terminifera*. We have three specific questions and subsequent predictions across scales:

- 96 1) What are the nutritional preferences of individuals from gregarious *C. terminifera* field populations? We
 97 expect individuals to be carbohydrate biased based on their active lifestyle, and to keep a constant intake
 98 target between populations.
- 99 2) What happens to *C. terminifera* when constrained to high nitrogen environments? We expect locusts to select
 100 particularly carbohydrate biased diets to redress a protein : carbohydrate imbalance in their local environment.
- 101 3) Can we use soil nutrients as a predictor of *C. terminifera* nymph outbreaks at the continental scale?

102 At larger scales, and accounting for climatic factors, we expect outbreaks to be associated with low nitrogen areas.
 103 Since terrestrial herbivores can require 5-50 times more nitrogen than phosphorus [Elser et al., 2000] and locusts
 104 likely have a higher capacity to post-ingestively regulate phosphorus in ranges found in nature [Cease et al., 2016,
 105 Zhang et al., 2014], we expect nitrogen to be a stronger predictor of populations at a continental scale as compared to
 106 phosphorus.

107 2 METHODS

108 Details regarding the scales of inference, the application of factors of interest, and the corresponding replicates can be
 109 found in Table 1. This table outlines the hierarchical structure of our experimental design across individual, population,
 110 and landscape levels.

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
individual	populations	150 locusts tested on varying macronutrient ratios with artificial diets.
individual	field cages	20 locusts in each cage
population	field cages	36 cages in each fertilization treatment
landscape	populations	67,144 1 km ² grids throughout Australia

Table 1: Replication statement for all scales of interest

111 2.1 Field site and animals

112 Lab-based and field cage experiments were conducted at the Trangie Agricultural Research Centre of the Department
 113 of Primary Industries in Trangie, New South Wales, Australia. We used field populations of the *C. terminifera*, which
 114 prefers open grassy areas and is a grass generalist [Key, 1945]. Solitarious populations of this locust species maintain
 115 their intake target closely regardless of spatiotemporal changes [Lawton et al., 2021]. We carried out these studies in
 116 November-December 2015, during the final nymphal and early adult stages of the spring *C. terminifera* generation.

117 2.2 Nutritional target and performance curve using synthetic diets

118 To control the nutrient availability within the experiments, we used isocaloric artificial diets made up of 42% macronutrients
 119 (differing ratios of protein and carbohydrates), 32% cellulose, and 4% of salt, sterols and vitamins. This
 120 artificial diet mixture has been used with this species [Clissold et al., 2014] and was developed by Simpson and Abis-
 121 gold [1985] from Dadd [1961]. We dried diets to a constant mass at 60°C before weighing the diets before and after
 122 all experiments.

123 We collected fourth and fifth instar nymphs from outbreeding populations on Nov. 12, 2015 from two locations: near
 124 Mendooran (31°40.791' S, 149°04.209' E) and Guntawang (32°23.988' S, 149°28.649' E), New South Wales. The
 125 Mendooran population was forming marching bands while the Guntawang population was at high density but was not
 126 actively marching during the collection period. Both populations were collected along dirt roads flanked by livestock
 127 grazing pastures containing a mix of grasses and forbs. We transported locusts back to the Trangie Agricultural
 128 Research Centre and kept them in large plastic bins with holes along with an assortment of grasses and forbs cut
 129 from the same field locusts were collected until experiments were started. For both experiments, locusts were housed
 130 individually in plastic cages (ca. 18 cm L x 12 cm W x 4 cm H) with small holes for ventilation. Each cage had two
 131 (nutritional target) or one (performance curve) artificial diets, a water tube capped with cotton, and a perch.

132 2.2.1 Nutrition target (choice diets)

133 We ran this experiment to determine the preferred dietary p:c ratio of *C. terminifera* field populations. We selected
 134 equal numbers of males and females from both Mendooran and Guntawang populations and individuals that had no
 135 visible wing bud separation to ensure they were early in the fifth instar. Locusts were heated with incandescent light
 136 bulbs on a 14:10 light:dark cycle. The average daytime and nighttime temperatures in the cages were 25.5°C and

137 23.4°C respectively, recorded from an iButton (Maxim). We randomly assigned 80 locusts (20 individuals per diet pair
 138 per population) to one of two treatment groups receiving pairs of either 7p:35c & 28p:14c or 7p:35c & 35p:7c (% p :
 139 % c by dry mass). We used two different pairs to ensure that the selected p:c ratio was not the result of eating randomly
 140 between the two dishes. We let locusts eat from the dishes for three days (Nov. 12-15, 2015) and calculated the mass
 141 of protein and carbohydrate each locust ate by subtracting the final dish weights from the initial dish weights.

142 **2.2.2 Performance curve (no-choice diets)**

143 We ran this experiment to determine the growth rate and development time to adulthood of *C. terminifera* juveniles
 144 in response to different dietary p:c ratios. We isolated fourth instar nymphs from the Mendooran population and
 145 housed them in individual cages. Each day, we retrieved individuals that had molted into the fifth (final) stadium to
 146 incorporate into the experiment. We added an assortment of grasses and forbs collected from grazing pastures in the
 147 Research Centre to the cage of fourth instars daily. On day one of the fifth instar, locusts were randomly assigned
 148 to one of four artificial diet treatment groups: (7p:35c, 14p:28c, 21p:21c, or 35p:7c), with 18 locusts per treatment
 149 (similar numbers of males and females for each group). Fifth instar locusts were started on diets between Nov. 15-19
 150 and we ended the experiment on Dec. 3, 2017. If locusts molted to adults before that point, we recorded the adult mass
 151 on the day they molted and ended that individual trial. We fed locusts their assigned diet ad lib such that there was
 152 always food available. We changed diets every three days until locusts molted to adults or until the experiment ended.
 153 Locusts were heated with incandescent light bulbs on a 14:10 Light:Dark cycle. The average daytime and nighttime
 154 temperatures in the cages were 26.2°C and 23.9°C, respectively, recorded from an iButton.

155 **2.3 Field cage experiments**

156 We ran this experiment to test the effects of different host plant nitrogen contents on locust nutrient balancing, growth,
 157 and survival. This experiment was conducted in a research field at the Trangie Research Centre that is used mainly for
 158 livestock grazing and had no history of fertilization. We marked nine 7 m x 7 m plots with 2 m alleyways between
 159 each plot. Each of the three nitrogen addition levels (0, 87.5, and 175 kg N/ha) was randomly assigned to three of the
 160 nine plots. We chose 175 kg N/ha as the upper range because this is similar to the fertilization rates of most crops. We
 161 added the fertilization treatment one time, on Nov. 2, 2015, in the form of urea, two weeks before a significant rainfall
 162 (ca. 60 mm). This treatment regime allowed us to see how increasing levels of nitrogen affected nutrient redressing
 163 and overall performance of locust populations through time.

164 We built 0.75 x 0.75 x 0.75 m cages with four steel fence posts and aluminum mesh. We secured the mesh to the
 165 ground by partially burying it and nailing thin slats of wood over the mesh edges. Before adding locusts to the cages,
 166 we removed any plant litter and arthropods (mostly spiders and locusts) so we could more easily count the locusts
 167 and limit predation. We added 20 4th instar locust nymphs to each field cage on the evening of November 13th and
 168 morning of November 14th. We randomly selected these nymphs from the Mendooran population we collected on
 169 November 12th (see synthetic diet methods section above). Each fertilized plot had four cages, for a total of 12 cages
 170 per fertilization level, and 36 cages and 720 locusts in total. We checked the cages every 4-5 days and removed any
 171 spiders.

172 We measured plant diversity and abundance in each locust cage and outside the cage within each fertilized plot. We
 173 also measured ground, litter, manure, and plant cover in each of the nine plots by randomly tossing three 0.25 x 0.25
 174 m quadrats within each of the nine plots. We took these ground cover and biodiversity measurements at the beginning
 175 and end of the experiment. We took plant leaf samples for nutrient analyses from each cage three times during the
 176 experiment on November 11th, November 25th, and December 1st, 2015. Plant species with resulting carbon, nitrogen,
 177 digestible carbohydrate and protein content as well as soil nitrogen (from 0-10 cm cores) can be seen in Supplementary
 178 Table 1. Plant species ground cover for each cage can be seen in Supplementary Table 2. The relationship between soil
 179 NO³ and NO⁴ within cage plots and cage plant carbohydrates and proteins are visualized in Supplementary Figure 1.

180 To test how the nitrogen fertilization treatments affected the nutritional status of the locusts, we collected 20 locusts
 181 from control and high N treatment cages (40 individuals in total) on November 23, 2015. We housed them in individual
 182 cages and gave them the choice of a low protein: carbohydrate diet and a high protein: carbohydrate diet. We changed
 183 their diets on days one, two, four, and six and ended the experiment at day nine. To ensure an adequate sample size,
 184 we included data from any individuals that died (approximately 60% mortality) before the experiment was completed
 185 and individuals which molted during the experiment. We calculated the mass of protein and carbohydrate locusts ate
 186 over each interval. This allowed us to see the nutritional redressing of individuals.

187 We collected all remaining field-cage locusts on Nov. 28, 2015 and recorded developmental stage and body mass.
 188 We calculated surviving proportion for each cage accounting for the locusts we removed for the nutritional status
 189 experiments as follows:

$$\text{survival proportion} = \frac{\text{number live locusts}}{\text{initial number added} - \text{number locusts removed for secondary experiment}}$$

190 We calculated the proportion molted to adult of the surviving locusts as:

$$\frac{\# \text{ adult locusts}}{\# \text{ live locusts}}$$

191 2.4 Correlating historical nymphal outbreaks with soil nitrogen and phosphorus

192 To understand the relationship between soil nutrients and locust outbreaks, we used the Australian Plague Locust
 193 Commission's (APLC) long-term locust survey dataset [Deveson and Hunter, 2002] and the Soil and Landscape Grid
 194 Australia-Wide 3D Soil Property Maps [Grundy et al., 2015].

195 2.4.1 Locust outbreak data

196 *Chortoicetes terminifera* data from 2000 - 2017 (~ 190,000 records) were used in this study. This database contains
 197 georeferenced points with a categorical ordinal variable 0-4 to represent approximate nymph densities. The value
 198 ranges for nymphs are: 0 = nil, 1 = < 5 m², 2 = 5-30 m², 3 = 31-80 m², and 4 = > 80 m². Population outbreaks are
 199 characterized by very high densities of gregarious nymphs (up to 1000 m²). We focused on nymphs as this life stage
 200 cannot fly and can be used to assess prior local habitat conditions. While the database extends into the 1980s, we only
 201 used data collected between 2000-2017 as this period overlapped with the soil grid data which was released in 2015.
 202 Since climatic conditions and migration patterns are drivers in outbreak occurrence [Lawton et al., 2022, Veran et al.,
 203 2015] they likely mask the relationship between static environmental variables like soil nutrients. To account for this
 204 variability, we spatially aggregated the survey dataset to a 1 km² grid as can be seen in Supplementary Figure 2. This
 205 allowed us to model how often locust outbreaks occur in grid cells rather than the actual outbreak. We used a 1 km²
 206 grid as this reflects the estimated maximum dispersal distance from hatching to 5th instar [Hunter et al., 2008]. We
 207 counted the number of outbreaks (APLC nymph density code 4), the number of nil records (APLC nymph density
 208 code 0), and total number of survey observations. This resulted in approximately 67,000 grid cells for the final dataset.
 209 Overall APLC survey point distribution can be seen in Figure 1 A.

210 2.4.2 Soil grid of Australia data

211 The soil and landscape grid of Australia is a modeled raster of 12 soil variables at a 90 m² resolution. These soil characteristics are available at multiple depths from surface to two meters below the surface. These depths and methodology
 212 are consistent with the specifications of the Global Soil Map project (<http://www.globalsoilmap.net>) [Grundy et al.,
 213 2015]. We extracted this data from Google Earth Engine [Gorelick et al., 2017]. In this data set both phosphorus
 214 and nitrogen units are the mass fraction of total nutrient in the soil by weight. We took the average of nitrogen and phosphorus
 215 and nitrogen of the top two depths (0 cm – 5 cm and 5 cm and 15 cm) as these are most relevant to nutrient content of
 216 grasses and forbs. Then, for each APLC survey grid we calculated the mean mass fraction of nitrogen and phosphorus
 217 in the soil to a 15 cm depth. Spatial distribution of soil nitrogen and phosphorus can be seen in Figure 1 B and Figure 1
 218 C respectively.

219 2.5 Statistics

220 All statistics were conducted with a generalized additive mixed modeling (GAMM) approach when possible. This
 221 allowed us to test for non-linear and linear trends in the dataset and specify the hierarchical nature of the data. All
 222 statistics were conducted in R and python. All scripts and packages used can be seen within the project code repository:
 223 [github repo](#)

225 2.5.1 Intake Targets

226 To determine intake targets, we constructed generalized additive model (GAM) (family: Multivariate Normal Distribution,
 227 Link: Identity) with the following variables when possible: diet pairing (factor), locust sex (factor), time period
 228 interval (integer), locust initial weight (numeric) following roughly the procedure found in Lawton et al. [2021]. We
 229 selected the inclusion of locust weight as either a non-linear or linear effect via Akaike information criterion (AIC),
 230 AIC adjusted for small sample size (AICc), and Bayesian information criterion (BIC). If weight was not an important
 231 variable, it was removed entirely from the model.

232 2.5.2 Field population

233 We calculated intake targets as discussed above. To see the impact of confined diet treatments, we constructed GAMs
 234 (family: gaussian, link: identity) with the following variables: treatment (factor), locust sex (factor), population
 235 (factor), and locust initial weight (numeric).

236 **2.5.3 Field Cage Experiments**

237 We assessed plant nutrients with a generalized additive mixed model (GAMM) (family: Multivariate Normal Distribution,
 238 link: identity) and included the following variables: plant carbohydrate (numeric, dependent), plant protein
 239 (numeric, dependent), treatment (factor, independent), cage (factor, random effect), plot (factor, random effect), and
 240 plant species (random effect). Redressing intake targets were conducted as discussed above (section 2.5.1). To see
 241 the difference between physiological performance and fertilizer treatments, we constructed GAMMs (family: Scaled
 242 T distribution, link: identity) for final locust mass. The independent variables in all models were treatment (factor),
 243 sex (factor), a two-dimensional smoother of available protein and carbohydrate, and cage number as a random effect.
 244 For both final adult proportion and survival proportion, we constructed a GAM (Family: gaussian, Link: identity)
 245 and included the following variables: treatment (factor) and a two-dimensional smoother of available protein and
 246 carbohydrate.

247 **2.5.4 Historical outbreaks and soil nutrient grid modeling**

248 To relate nymph survey grids to soil nitrogen and phosphorus, we constructed two GAMMs (family: tweedie, link:
 249 log) predicting the number of outbreaks (APLC Survey Category 4) and nil observations (category 0). Since soil
 250 nitrogen and mean annual precipitation are highly correlated with both variables decreasing going into the arid interior
 251 of Australia, we are unable to add precipitation directly to the model as it would bias the results. Instead, we built
 252 a comparison model with mean annual precipitation between 2000 and 2017 switched for soil nitrogen. To do this,
 253 we calculated the average precipitation between 2000 and 2017 for all survey grids using the European Centre for
 254 Medium-Range Weather Forecasts' ERA5 reanalysis dataset [Muñoz-Sabater et al., 2021]. This allowed us to visually
 255 compare the effect differences of soil nitrogen and mean annual precipitation on locust outbreaks. In other words, if
 256 soil nitrogen and mean annual precipitation were so tightly correlated that the effects are indistinguishable, the modeled
 257 results should look very similar. The soil models had the following independent variables: soil nitrogen, phosphorus,
 258 latitude / longitude, bioregion, and the number of observations within each grid. For the precipitation model, all
 259 variables were the same except mean annual precipitation replaced soil nitrogen and phosphorus. The inclusion of
 260 bioregions as a random effect allowed us to account for variation due to vegetation community and soil characteristics
 261 [Lawton et al., 2022]. The inclusion of latitude and longitude allowed us to account for spatial autocorrelation [Clayton
 262 et al., 1993]. Lastly, the inclusion of the total number of observations allowed us to account for sampling intensity
 263 biases.

264 **3 RESULTS**

265 **3.1 Field population**

266 **3.1.1 Choice experiment (nutritional target)**

267 *Chortoicetes terminifera* individuals from the two outbreeding populations regulated to a specific ratio of 1 protein : 2
 268 carbohydrate (Figure 2 A, Table 2). Model selection can be seen in Supplementary Table 3. Consumption in the two
 269 diet pairings did not differ, indicating non-random feeding (Supplementary Figure 3 A, Table 2). While the protein
 270 : carbohydrate ratio did not change, females consumed more food than males, likely due to being bigger overall
 271 (Supplementary Figure 3 B, Table 2).

macronutrient	variable	estimate	SE	p-value
carbohydrate	Intercept	0.026	0.002	0.000
	Mendooran	-0.001	0.002	0.483
	diet pair B	0.001	0.002	0.573
	male	-0.011	0.002	0.000
protein	Intercept	0.014	0.001	0.000
	Mendooran	-0.002	0.002	0.122
	diet pair B	0.002	0.002	0.293
	male	-0.006	0.002	0.000

Table 2: Generalized additive model results for macronutrient consumption (carbohydrate and protein) of two outbreeding populations of *C. terminifera* in Mendooran and Guntawang. Models were selected via AIC, AICc and BIC which can be seen in Supplementary Table 3. Family: multivariate gaussian distribution, link: identity, SE: standard error.

272 **3.1.2 No choice experiment (performance curves)**

273 *Chortoicetes terminifera* had higher specific mass growth rates and faster development times on the 1 protein : 2 car-
 274bohydrate (14 protein : 28 carbohydrate) diet as compared to the other diets (Figure 2 B & C, Table 3, Supplementary
 275 Table 4). Development time and specific growth rate did not differ between male and female locusts (Supplementary
 276 Figure 3 C & D, Table 3).

variable	Specific Growth Rate			Development Time		
	estimate	SE	p-value	estimate	SE	p-value
Intercept	0.061	0.004	0.000	15.780	1.555	0.000
21p:21c	-0.011	0.005	0.040	0.917	0.624	0.149
35p:7c	-0.010	0.006	0.091	1.709	0.665	0.013
7p:35c	-0.026	0.005	0.000	2.716	0.603	0.000
male	-0.003	0.004	0.398	-1.615	0.829	0.057
initial weight (g)				-21.048	10.407	0.049

Table 3: *Chortoicetes terminifera* physiological performance (specific growth rate and development time) when constrained to specific diets with varying protein and carbohydrate content. SE: standard error. Posthoc comparisons for both physiological performance metrics can be seen in Supplementary Table 4.

277 **3.2 Field Cage**

278 For the first 11 days of the 14 day field cage experiment, plant protein and carbohydrate contents remained consistently
 279 protein-biased for all treatments (Figure 3 A-C, Table 4), and only showed differences in protein content by the last
 280 sample period on December 1, which was after the end of the locust cage experiment. Accordingly, there was no
 281 effect of fertilizer on locust survival and adult proportion (Figure 3 D-F, Table 5). Locusts that were retrieved from
 282 field cages after nine days and were given a choice to regulate protein and carbohydrate intake showed a pattern
 283 consistent with rebalancing a shortage of carbohydrates (Figure 4, Table 6, Supplementary Figure 4). Irrespective of
 284 fertilizer treatment group, locusts initially selected very carbohydrate biased diets, but gradually, after 9 days, their
 285 trajectory returned close to the predicted intake target of 1p : 2c (Figure 4, Supplementary Figure 4).

macronutrient	variable	estimate	SE	statistic	p-value
carbohydrate	Intercept	0.127	0.007		0.000
	Medium	-0.020	0.007		0.005
	High	-0.011	0.007		0.121
	2015-11-25	-0.009	0.007		0.181
	2015-12-01	-0.012	0.006		0.033
	Medium:2015-11-25	0.019	0.010		0.063
	High:2015-11-25	0.004	0.010		0.656
	Medium:2015-12-01	0.019	0.008		0.017
	High:2015-12-01	0.010	0.008		0.222
	s(species)			67.305	0.000
protein	s(plot)			1.643	0.207
	s(cage)			3.442	0.130
	Intercept	0.209	0.017		0.000
	Medium	-0.001	0.014		0.928
	High	-0.034	0.014		0.014
	2015-11-25	0.026	0.010		0.014
	2015-12-01	-0.049	0.009		0.000

Medium:2015-11-25	-0.012	0.015	0.422
High:2015-11-25	-0.023	0.015	0.123
Medium:2015-12-01	0.008	0.013	0.516
High:2015-12-01	0.056	0.013	0.000
s(species)		307.929	0.000
s(plot)		214.489	0.000
s(cage)		89.944	0.000

Table 4: Generalized additive model results for plant macronutrient (carbohydrate and protein) differences between fertilization treatment. Family: multivariate gaussian distribution, link: identity, SE: standard error, s() denotes a smoothing parameter.

variable	estimate	SE	statistic	p-value
Intercept	0.326	0.007		0.000
male	-0.148	0.006		0.000
medium	0.015	0.010		0.117
high	-0.011	0.010		0.273
s(carb mg/mg, protein mg/mg)		0.002		0.416
s(cage number)		42.160		0.000

Table 5: Generalized additive model results for differences between final locust mass after the nitrogen fertilization experiment finished. Family: scaled T, link: identity, SE: standard error, and s() denotes a smoothing parameter.

macronutrient	variable	estimate	SE	statistic	p-value
carbohydrate	Intercept	0.013	0.004		0.001
	male	-0.011	0.004		0.009
	day 2	0.007	0.003		0.008
	day 3-4	0.016	0.003		0.000
	day 5-6	0.026	0.003		0.000
	day 7-9	0.035	0.003		0.000
	none	-0.006	0.004		0.136
	s(id)			484.706	0.000
	Intercept	0.002	0.001		0.119
	male	-0.004	0.001		0.009
protein	day 2	0.001	0.001		0.724
	day 3-4	0.003	0.001		0.023
	day 5-6	0.007	0.001		0.000
	day 7-9	0.013	0.001		0.000
	none	-0.001	0.001		0.475
	s(id)			110.728	0.381

Table 6: Generalized additive model results for nutrient imbalance dressing of field cage *C. terminifera* in the control and high fertilization treatments. Model also included interactive terms; however, none were significant and left out. SE: standard error and s() denotes a smoothing parameter.

286 **3.3 Locust outbreaks**

287 *Chortoicetes terminifera* outbreaks were negatively associated with soil nitrogen, which supports the hypothesis that
 288 nitrogen (in excess) acts as a limiting factor for population upsurges (Table 7, Figure 5 A). *C. terminiferas* had a
 289 nonlinear relationship with soil phosphorus with outbreaks occurring more often in areas with approximately 4% soil
 290 phosphorus and were strongly negatively associated with increasing phosphorus afterwards (Figure 5 B). For both
 291 nutrients, the absence models had a very weak relationship with soil nutrient in comparison to the outbreak models,
 292 demonstrating little model bias due to APLC survey protocol. There were significant nonlinear relationships between
 293 coordinates and the total number of observations in all models (Supplementary Figure 6; Supplementary Figure 7).
 294 The relationship between locust outbreaks and mean annual precipitation was very different from the relationship with
 295 soil nitrogen (Figure 5, Supplementary Figure 8). Soil nitrogen and phosphorus show weak positive correlations with
 296 woody vegetation cover, while mean annual precipitation exhibits high variation in its relationship with soil nitrogen
 297 and weak correlation with soil phosphorus (Supplementary Figure 5). Thus, the relationship between soil nitrogen and
 298 locust outbreaks cannot be fully explained by differences in woody vegetation.

variable	outbreak model			nil model		
	EDF	statistic	p-value	EDF	statistic	p-value
s(nitrogen)	6.273	25.620	0.000	6.426	35.340	0.000
s(phosphorus)	5.372	15.521	0.000	6.407	28.867	0.000
s(number of observations)	22.547	630.896	0.000	22.408	3,199.357	0.000
te(longitude,latitude)	56.140	1.148	0.012	131.476	3.302	0.000
s(ecoregion)	6.498	4.802	0.000	2.726	0.361	0.035

Table 7: Historical locust presence data modeling with soil nitrogen for outbreak, low presence, and no observation records with r-square and deviance explain reported. Family: tweedie, link: log, edf = estimated degrees freedom.

299 **4 DISCUSSION**

300 We show that herbivore diet preferences remain consistent between spatial levels, from individual foraging behavior
 301 and physiology to large scale population dynamics, with locust populations negatively related to environmental nitro-
 302 gen. Thus by going across scales, this study shows a consistent pattern of excess nitrogen limiting a pest herbivore and
 303 introduces a more nuanced view of phosphorus limitation on herbivore populations. Instead of the broad generaliza-
 304 tion that animals are always negatively or positively associated with certain nutrients, specific life history traits, such
 305 as energetically-costly migration, as well as organism-environment interactions should be considered. For forecast-
 306 ing pest populations dynamics, adding variables describing the nutritional quality of landscapes can inform seasonal
 307 scouting surveys. We hope that this study spurs future interest in multi-scale experiments and modeling of nutrient
 308 availability with animal population dynamics.

309 **4.1 Field populations**

310 Field populations of final instar *C. terminifera* behaviorally regulated to a 1 protein (p) : 2 carbohydrate (c) nutrient
 311 ratio, which supported the fastest nymphal growth and the lowest development time to adulthood (Figure 2 B & C),
 312 consistent with previous studies [Clissold et al., 2014, Lawton et al., 2021]. Locusts are highly mobile (*C. terminifera*
 313 can fly up to 500 km in a single night, [Deveson and Walker, 2005]) and the demand for energy via carbohydrates and
 314 lipids likely increases relative to protein demand during the later life stages of these animals.

315 Plant nutrient content in the nitrogen fertilization treatments was not significantly different until the last sample period,
 316 which likely explains the small effect on locust growth (Figure 3 A-C). Over the experimental period, protein content
 317 decreased in unfertilized treatments while both plant protein and carbohydrate remained constant in the fertilized
 318 treatments. If we prolonged the experiment, there might have been a noticeable difference in locust survivorship,
 319 weight gain, and adult proportion given the shift in nutrients among treatments (Figure 3 D-F).

320 Importantly, all field cage plants were protein biased (roughly 1p : 1c to 2p : 1c) as compared to the desired locust
 321 intake target of 1p : 2c. When locusts were subsampled from the field cages mid-experiment and given the opportunity
 322 to select carbohydrate or protein diets, they selected extremely carbohydrate-biased diets for more than a week. This
 323 behavior indicated that locusts in the small field cages were highly carbohydrate-limited, driving them to overeat
 324 carbohydrates to redress the imbalance. Interestingly, multiple studies have shown that the Australian nutritional
 325 landscape is often too protein-biased relative to what the *C. terminifera* prefers [Lawton et al., 2020, 2021]. Regardless,

326 populations are still persistent and outbreaks can occur at lower frequencies in these areas [Deveson, 2013, Key,
 327 1945]. How this species can achieve the optimal balance of nutrients within an unfavorable nutritional environment
 328 merits further investigation, but may include post-ingestive regulation and/or large-range foraging. Migratory locusts
 329 (*Locusta migratoria*) can choose microclimates that favor higher efficiency of carbohydrate or protein absorption
 330 depending on their host plant and nutritional status [Clissold et al., 2013]. For this study, we collected free-living
 331 locusts from the same region and a similar environment as where we built the field cages, yet those confined to field
 332 cages selected a 10x decrease in p:c (1p : 20c vs 1p : 2c). This result suggests that free-living locusts are able to persist
 333 in high protein regions by foraging over a larger range to seek out pockets of carbohydrate-rich plants and that the
 334 limited foraging range of the field cages precluded field-cage locusts from finding sufficient carbohydrates. Similarly,
 335 these results suggest that, while *C. terminifera* can persist in low numbers in nitrogen rich regions, those environments
 336 are unlikely to support extreme outbreaks due to a limitation of carbohydrate-rich resources. We tested this prediction
 337 using historical outbreak and large-scale soil nutrient modeling.

338 4.2 Historical outbreak modeling

339 This is the first time to our knowledge that terrestrial animal population dynamics have been modeled with nutrients at
 340 the continental level, allowing nutrient limitation to be tested at a scale not previously investigated. Locust outbreaks
 341 are associated with decreasing soil nitrogen (Figure 5 A), suggesting that nitrogen acts as a limiting factor not due
 342 to its deficit [White, 1993] but its excess. Plants growing in high nitrogen environments tend to have high p:c ratios,
 343 which force locusts to either undreat carbohydrates (limiting their energy to support growth and migration) or overeat
 344 protein (which can be toxic) to acquire sufficient carbohydrates [Behmer, 2009, Cease, 2024]. On the other end of the
 345 performance curve, *C. terminifera* do have a lower p:c range that limits performance, as shown using artificial diets
 346 (Figure 2 B-C). We also show that outbreaks are correlated with a low level of soil phosphorus, however, outbreaks
 347 peak at approximately 4%, suggesting that while locusts generally do well in low phosphorus environments, phospho-
 348 rus deficit can be limiting for locusts in extremely phosphorus poor soils (Figure 5 B). Because Australian soils are
 349 characteristically phosphorus poor [Donald, 1964], Australian animals like this locust are adapted to phosphorus poor
 350 environments and potentially having too much phosphorus is deleterious [Morton et al., 2011]. Locust populations
 351 may be more tightly correlated with soil nitrogen than phosphorus because terrestrial herbivores require 5-50 times
 352 more nitrogen than phosphorus [Elser et al., 2000], meaning they can more readily balance phosphorus by eating a few
 353 foods rich or poor in phosphorus but cannot as quickly regulate protein and carbohydrate energy because they make up
 354 the bulk of their required nutrients. Indeed, laboratory studies have revealed that short-term limitations in dietary phos-
 355 phorus have no apparent impact on grasshopper growth [Cease et al., 2016], suggesting that these mobile herbivores
 356 could seek out phosphorus-rich diets intermittently to overcome potential phosphorus limitation in field environments.
 357 However, in this study, we only tested this relationship with phosphorus at the continental level; further field and lab-
 358 oratory experiments are needed to explore this non-linear relationship between locust outbreaks and soil phosphorus.
 359 While we only looked at nitrogen and phosphorus, it is also important to note that animals require a suite of nutrients.
 360 Other nutrients such as potassium and sodium [Joern et al., 2012] warrant further investigation. Comparing locust
 361 outbreaks between continents would further show the relationship between nutrient availability and animal population
 362 dynamics. One excellent dataset for this would be SoilGrids (<https://www.isric.org/explore/soilgrids>) which provides
 363 soil nitrogen estimates globally at a 250-meter resolution.

364 Lastly, our results suggest that forecasting efforts for locusts should consider the inclusion of a nutritional landscape
 365 quality metric like soil nitrogen. Current forecasting models use climatic data (e.g. rainfall and soil moisture) or
 366 vegetation growth data (e.g. normalized difference vegetation index, NDVI) as the major predictors of outbreaks
 367 [Cressman, 2013]. While these climatic variables are clearly important, adding metrics to quantify the nutritional
 368 landscape can help increase forecasting model accuracy in environments with highly variable climates.

369 4.3 Locusts are more likely to be limited by high nitrogen environments than other grasshoppers

370 A five-decade review of grasshopper responses to plant nitrogen content showed that grasshoppers not classified as
 371 locusts have a variation of negative, neutral, and positive responses to increasing plant nitrogen [Cease, 2024]. Looking
 372 just at field surveys, there are more reports of a negative correlation between plant nitrogen and non-locust grasshopper
 373 abundance (17 reports) relative to neutral (6 reports) or positive (9 reports). This pattern corroborates long-term studies
 374 showing that dilution of plant nitrogen is correlated with declines of North American grasshopper populations [Welti
 375 et al., 2020b]. Of the studies that report positive correlations between individual grasshopper species abundance
 376 and plant nitrogen, most are from graminivorous (grass-feeding) species (11 reports), with 7 reports from mixed
 377 (grasses and forbs) or forb feeders [Cease, 2024]. This pattern supports the hypothesis that grass-feeders are more
 378 likely to be nitrogen-limited because grasses tend to have lower p:c ratios than forbs; although this trend was not
 379 significant and grass-feeders also regularly showed negative responses to high plant nitrogen. In contrast, there was
 380 a consistent negative effect of high plant nitrogen on locust species, regardless of whether they were graminivorous
 381 or mixed feeders. Because mass specific protein consumption is highly correlated with growth rate in both lab and
 382 field populations, but carbohydrate consumption is highly influenced by the environment [Talal et al., 2023], it is most

likely that locusts have similar protein requirements as other non-locust grasshopper species, but have much higher carbohydrate demands, potentially to support migration [Raubenheimer and Simpson, 1997, Talal et al., 2021, 2023]. Locusts are able to meet this increased demand for carbohydrate, while keeping protein consumption constant, by eating larger amounts of low p:c plants found in low nitrogen environments. In summary, these studies suggest that nymphal outbreaks of all locust species may be negatively correlated with soil nitrogen across continental scales, but that the correlation between plant nitrogen and non-locust grasshoppers may not be significant or consistent through space and time.

4.4 Comparing the relationship between plant macronutrients and herbivore abundance in other taxa

The effect of plant protein and carbohydrate on herbivore populations is predicted to depend on the herbivore's p:c intake target (IT) relative to its nutritional landscape (Le Gall et al., 2020). If there are sufficient plants on either side of the IT, herbivores can select from between them to achieve their IT. This complementary feeding has been recorded for field populations of blue sheep (*Pseudois nayaur*) in the Himalayan Mountains [Aryal et al., 2015], Black Howler Monkeys (*Alouatta pigra*) in Yucatán [Bridgeman, 2012], and other primates [Raubenheimer and Rothman, 2013]. There would be a predicted impact on populations if the nutritional landscape were to become more constricted or not overlap with the IT. For example, lab colonies of tobacco hornworms (*Manduca sexta* larvae) have an IT around 1:1 or sometimes slightly carbohydrate-biased [Wilson et al., 2019a] and their host plants tend to be carbohydrate-biased relative to their IT [Wilson et al., 2019b]. However, this does not seem to translate to population level effects, potentially due to secondary metabolites affecting growth more strongly than macronutrient balance and/or larvae may be able to compensate by overeating carbohydrates to acquire sufficient protein [Wilson et al., 2019a]. Overeating carbohydrates is not as detrimental as overeating protein, at least in the short term, and animals tend to be willing to overeat carbohydrates to a greater extent than protein [Cheng et al., 2008, Simpson and Raubenheimer, 2012b]. Therefore, herbivores facing a nutritional landscape with a p:c generally lower than their IT (i.e., carbohydrate excess) may not be as negatively impacted as herbivores facing one higher than their IT (i.e., protein excess). However, there are several examples of higher localized densities of herbivores in response to higher plant nitrogen and protein contents with thrips [Brown et al., 2002] and spruce budworm (*Choristoneura*) [De Grandpré et al., 2022] being two examples. These examples suggest that low p:c diets limit population growth of some herbivores, but more studies are needed to determine if this relationship is only localized or if it scales up. It may be that herbivore populations with lower numbers are not limited by a nutritional landscape at a large scale because they can differentially disperse locally among optimal patches, whereas herbivore populations with extreme numbers (i.e., eruptions) may be more limited by nutritionally unfavorable environments across scales.

There is evidence for phosphorus limitation in some species, but limited research showing a detrimental effect of excess phosphorus [Cease et al., 2016]. In aquatic insects such as *Daphnia* species, there is a strong positive association with phosphorus available and population dynamics Andersen et al. [2004]. However this trend is not seen in field cricket populations (*Gryllus veletis*) [Harrison et al., 2014] and other terrestrial insects. Loaiza et al. [2011] found no effect of phosphorus fertilization (but a positive effect of N fertilization) on Kansas tallgrass prairie grasshopper population distributions, whereas Joern et al. [2012] found consistent positive correlations between plant phosphorus and Nebraskan grassland grasshopper populations.

Making predictions about a population's nutritional demands can aid in making predictions about the relationship between nutritional landscapes and population dynamics. Across taxa, including fish, chickens, rats, cats, caribou, pigs, and dairy cattle, mass specific protein consumption is highly correlated with growth rate and decreases with age and body size [Talal et al., 2023]. In contrast, energy demand (carbohydrates and lipids) does not show a clear relationship with growth rate and instead is more affected by environment and activity [Talal et al., 2023]. Therefore, an animal's IT is predicted to be affected by the contrasting effects of growth (increases dietary p:c) and activity or stress (increases carbohydrate demand and therefore decreases dietary p:c), although other physiological and environmental factors affect p:c demand as well (see Table 1 in Cease [2024]). For example, monarch butterflies have been gradually increasing their already-high daily energy expenditure during migration due to warmer temperatures caused by climate change [Parlin et al., 2023]. Young and fast growing herbivores with low activity levels would be predicted to have a high p:c IT, whereas older juveniles and adults (slower mass specific growth) with high activity levels would be predicted to have a low p:c IT. Comparative studies with herbivores grouped functionally, such as other highly migratory animals (e.g. across insects, birds, mammals, and fish), or by growth rate or developmental stage, would likely provide interesting parallels that would assist in disentangling the complexities of plant macronutrient-herbivore relationships.

4.5 Synthesis and Application

Acquiring the right amount of nutrients is a critical component for animal growth, reproduction, and population dynamics [Doonan and Slade, 1995, Hansson, 1979, Keith, 1983]. However, in contrast to the conventional hypotheses that predict a broad positive linear relationship between herbivorous populations and nitrogen and phosphorus [Huberty and Denno, 2006, Mattson, 1980, White, 1978, 1993], the story is nuanced and probably most often non-linear.

439 For some species, especially those with high energy requirements, the relationship is the opposite (negatively associated
 440 with nitrogen) like many locust species and the effects can be seen at the continental scale. Land use and
 441 Land Cover Change (LULCC) impact on nutritional environments has important implications for animal population
 442 dynamics from conservation to pest management. While we did not make an explicit connection between LULCC and
 443 locust outbreaks in Australia, our results are consistent with previous research showing that LULCC that decreases
 444 soil quality and creates low nitrogen environments increases physiological performance and outbreaks of locusts (re-
 445 viewed in [Le Gall et al. \[2019\]](#)). Most importantly, we show that this relationship is consistent between scales from
 446 the individual locust to continental wide outbreaks. As such, proper management of soil nutrients can help keep locust
 447 populations from reaching outbreak sizes and should be considered across scales, from individual locust behavior to
 448 continental-wide plagues.

449 5 REFERENCES

- 450 Tom Andersen, James J. Elser, and Dag O. Hessen. Stoichiometry and population dynamics. *Ecology Letters*, 7
 451 (9):884–900, September 2004. ISSN 1461-023X, 1461-0248. doi: 10.1111/j.1461-0248.2004.00646.x. URL
<https://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2004.00646.x>.
- 452 Achyut Aryal, Sean C. P. Coogan, Weihong Ji, Jessica M. Rothman, and David Raubenheimer. Foods, macronutrients
 453 and fibre in the diet of blue sheep (*Psuedois nayaur*) in the Annapurna Conservation Area of Nepal. *Ecology
 454 and Evolution*, 5(18):4006–4017, September 2015. ISSN 2045-7758, 2045-7758. doi: 10.1002/ece3.1661. URL
<https://onlinelibrary.wiley.com/doi/10.1002/ece3.1661>.
- 455 George O. Batzli. Nutritional Ecology of the California Vole: Effects of Food Quality on Reproduction. *Ecology*, 67(2):
 456 406–412, April 1986. ISSN 0012-9658, 1939-9170. doi: 10.2307/1938583. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1938583>.
- 457 Spencer T. Behmer. Insect Herbivore Nutrient Regulation. *Annual Review of Entomology*, 54(1):165–187, January
 458 2009. ISSN 0066-4170, 1545-4487. doi: 10.1146/annurev.ento.54.110807.090537. URL <https://www.annualreviews.org/doi/10.1146/annurev.ento.54.110807.090537>.
- 459 E. A. Bernays, K. L. Bright, N. Gonzalez, and J. Angel. Dietary Mixing in a Generalist Herbivore: Tests of Two
 460 Hypotheses. *Ecology*, 75(7):1997–2006, October 1994. ISSN 00129658. doi: 10.2307/1941604. URL <http://doi.wiley.com/10.2307/1941604>.
- 461 LeAndra Luecke Bridgeman. The Feeding Ecology of YucatÁan Black Howler Monkeys (*Alouatta pigra*) in Man-
 462 grove Forest, Tabasco, Mexico. 2012. doi: 10.7936/K75T3HGP. URL <http://openscholarship.wustl.edu/etd/998>.
 Publisher: Washington University in St. Louis.
- 463 Jonah Brosemann, Rick Overton, Arianne J. Cease, Sydney Millerwise, and Marion Le Gall. Nutrient supply and
 464 accessibility in plants: effect of protein and carbohydrates on Australian plague locust (*Chortoicetes terminifera*)
 465 preference and performance. *Frontiers in Insect Science*, 3:1110518, July 2023. ISSN 2673-8600. doi: 10.3389/
 finsc.2023.1110518. URL <https://www.frontiersin.org/articles/10.3389/finsc.2023.1110518/full>.
- 466 Alison S. Scott Brown, Monique S. J. Simmonds, and Walter M. Blaney. Relationship between nutritional composition
 467 of plant species and infestation levels of thrips. *Journal of Chemical Ecology*, 28(12):2399–2409, 2002. ISSN
 468 00980331. doi: 10.1023/A:1021471732625. URL <http://link.springer.com/10.1023/A:1021471732625>.
- 469 Arianne J. Cease. How Nutrients Mediate the Impacts of Global Change on Locust Outbreaks. *Annual Review of
 470 Entomology*, 69(1):527–550, January 2024. ISSN 0066-4170, 1545-4487. doi: 10.1146/annurev-ento-120220-
 471 110415. URL <https://www.annualreviews.org/doi/10.1146/annurev-ento-120220-110415>.
- 472 Arianne J. Cease, James J. Elser, Colleen F. Ford, Shuguang Hao, Le Kang, and Jon F. Harrison. Heavy Livestock
 473 Grazing Promotes Locust Outbreaks by Lowering Plant Nitrogen Content. *Science*, 335(6067):467–469, January
 474 2012. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.1214433. URL <https://www.science.org/doi/10.1126/science.1214433>.
- 475 Arianne J. Cease, James J. Elser, Eli P. Fenichel, Joleen C. Hadrich, Jon F. Harrison, and Brian E. Robinson. Living
 476 With Locusts: Connecting Soil Nitrogen, Locust Outbreaks, Livelihoods, and Livestock Markets. *BioScience*, 65
 477 (6):551–558, June 2015. ISSN 1525-3244, 0006-3568. doi: 10.1093/biosci/biv048. URL <http://academic.oup.com/bioscience/article/65/6/551/303376/Living-With-Locusts-Connecting-Soil-Nitrogen>.
- 478 Arianne J. Cease, Michelle Fay, James J. Elser, and Jon F. Harrison. Dietary phosphate affects food selection, post-
 479 ingestive P fate, and performance of a polyphagous herbivore. *Journal of Experimental Biology*, page jeb.126847,
 480 January 2016. ISSN 1477-9145, 0022-0949. doi: 10.1242/jeb.126847. URL <https://journals.biologists.com/jeb/article/doi/10.1242/jeb.126847/262050/Dietary-phosphate-affects-food-selection-post>.

- 491 Arianne J. Cease, Eduardo V. Trumper, Héctor Medina, Fernando Copa Bazán, Jorge Frana, Jon Harrison, Nel-
 492 son Joaquin, Jennifer Learned, Mónica Roca, Julio E. Rojas, Stav Talal, and Rick P. Overson. Field bands
 493 of marching locust juveniles show carbohydrate, not protein, limitation. *Current Research in Insect Science*, 4:
 494 100069, 2023. ISSN 26665158. doi: 10.1016/j.cris.2023.100069. URL <https://linkinghub.elsevier.com/retrieve/pii/S2666515823000185>.
- 495 Ken Cheng, Stephen J. Simpson, and David Raubenheimer. A Geometry of Regulatory Scaling. *The American
 496 Naturalist*, 172(5):681–693, November 2008. ISSN 0003-0147, 1537-5323. doi: 10.1086/591686. URL <https://www.journals.uchicago.edu/doi/10.1086/591686>.
- 497 Dp Clark. The Influence of Rainfall on the Densities of Adult Chortoicetes Terminifera (Walker) in Central Western
 498 New South Wales, 1965-73. *Australian Journal of Zoology*, 22(3):365, 1974. ISSN 0004-959X. doi: 10.1071/
 499 ZO9740365. URL <http://www.publish.csiro.au/?paper=ZO9740365>.
- 500 D G Clayton, L Bernardinelli, and C Montomoli. Spatial Correlation in Ecological Analysis. *International Journal
 501 of Epidemiology*, 22(6):1193–1202, 1993. ISSN 0300-5771, 1464-3685. doi: 10.1093/ije/22.6.1193. URL <https://academic.oup.com/ije/article-lookup/doi/10.1093/ije/22.6.1193>.
- 502 Fiona J. Clissold, Nicole Coggan, and Stephen J. Simpson. Insect herbivores can choose microclimates to achieve
 503 nutritional homeostasis. *Journal of Experimental Biology*, page jeb.078782, January 2013. ISSN 1477-9145, 0022-
 504 0949. doi: 10.1242/jeb.078782. URL <https://journals.biologists.com/jeb/article/doi/10.1242/jeb.078782/258075/Insect-herbivores-can-choose-microclimates-to>.
- 505 Fiona J. Clissold, Helena Kertesz, Amelia M. Saul, Julia L. Sheehan, and Stephen J. Simpson. Regulation of water
 506 and macronutrients by the Australian plague locust, Chortoicetes terminifera. *Journal of Insect Physiology*, 69:35–
 507 40, October 2014. ISSN 00221910. doi: 10.1016/j.jinsphys.2014.06.011. URL <https://linkinghub.elsevier.com/retrieve/pii/S0022191014001267>.
- 508 F. R. Cole and G. O. Batzli. Influence of Supplemental Feeding on a Vole Population. *Journal of Mammalogy*, 59(4):
 509 809–819, November 1978. ISSN 1545-1542, 0022-2372. doi: 10.2307/1380145. URL <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1380145>.
- 510 Keith Cressman. Role of remote sensing in desert locust early warning. *Journal of Applied Remote Sensing*, 7(1):
 511 075098, May 2013. ISSN 1931-3195. doi: 10.1117/1.JRS.7.075098. URL <http://remotesensing.spiedigitallibrary.org/article.aspx?doi=10.1117/1.JRS.7.075098>.
- 512 Darren A. Cullen, Arianne J. Cease, Alexandre V. Latchininsky, Amir Ayali, Kevin Berry, Camille Buhl, Rien
 513 De Keyser, Bert Foquet, Joleen C. Hadrich, Tom Matheson, Swidbert R. Ott, Mario A. Poot-Pech, Brian E.
 514 Robinson, Jonathan M. Smith, Hojun Song, Gregory A. Sword, Jozef Vanden Broeck, Rik Verdonck, Heleen
 515 Verlinden, and Stephen M. Rogers. From Molecules to Management: Mechanisms and Consequences of
 516 Locust Phase Polyphenism. In *Advances in Insect Physiology*, volume 53, pages 167–285. Elsevier, 2017.
 517 ISBN 978-0-12-811833-7. doi: 10.1016/bs.aiip.2017.06.002. URL <https://linkinghub.elsevier.com/retrieve/pii/S0065280617300231>.
- 518 R.H. Dadd. The nutritional requirements of locustsIV. Requirements for vitamins of the B complex. *Journal of
 519 Insect Physiology*, 6(1):1–12, February 1961. ISSN 00221910. doi: 10.1016/0022-1910(61)90086-5. URL <https://linkinghub.elsevier.com/retrieve/pii/0022191061900865>.
- 520 Louis De Grandpré, Maryse Marchand, Daniel D. Kneeshaw, David Paré, Dominique Boucher, Stéphane Bourassa,
 521 David Gervais, Martin Simard, Jacob M. Griffin, and Deepa S. Pureswaran. Defoliation-induced changes in foliage
 522 quality may trigger broad-scale insect outbreaks. *Communications Biology*, 5(1):463, May 2022. ISSN 2399-3642.
 523 doi: 10.1038/s42003-022-03407-8. URL <https://www.nature.com/articles/s42003-022-03407-8>.
- 524 E. D. Deveson and P. W. Walker. Not a one-way trip: historical distribution data for Australian plague locusts support
 525 frequent seasonal exchange migrations. *Journal of Orthoptera Research*, 14(1):91–105, January 2005. ISSN 1082-
 526 6467, 1937-2426. doi: 10.1665/1082-6467(2005)14[91:NAOTHD]2.0.CO;2. URL <http://www.bioone.org/doi/abs/10.1665/1082-6467%282005%2914%5B91%3ANAOTHD%5D2.0.CO%3B2>.
- 527 Edward D. Deveson. Satellite normalized difference vegetation index data used in managing Australian plague locusts.
 528 *Journal of Applied Remote Sensing*, 7(1):075096, July 2013. ISSN 1931-3195. doi: 10.1117/1.JRS.7.075096. URL
 529 <http://remotesensing.spiedigitallibrary.org/article.aspx?doi=10.1117/1.JRS.7.075096>.
- 530 Ted Deveson and David Hunter. THE OPERATION OF A GISBASED DECISION SUPPORT SYSTEM FOR
 531 AUSTRALIAN LOCUST MANAGEMENT. *Insect Science*, 9(4):1–12, December 2002. ISSN 1672-9609,
 532 1744-7917. doi: 10.1111/j.1744-7917.2002.tb00167.x. URL <https://onlinelibrary.wiley.com/doi/10.1111/j.1744-7917.2002.tb00167.x>.
- 533 Colin Donald. Phosphorus in Australian agriculture. *Journal of the Australian Institute of Agricultural Science*, 30
 534 (75):195, 1964.

- 546 Terry J. Doonan and Norman A. Slade. Effects of Supplemental Food on Population Dynamics of Cotton Rats,
 547 *Sigmodon Hispidus*. *Ecology*, 76(3):814–826, April 1995. ISSN 0012-9658, 1939-9170. doi: 10.2307/1939347.
 548 URL <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1939347>.
- 549 James J. Elser, William F. Fagan, Robert F. Denno, Dean R. Dobberfuhl, Ayoola Folarin, Andrea Huberty, Sebastian
 550 Interlandi, Susan S. Kilham, Edward McCauley, Kimberly L. Schulz, Evan H. Siemann, and Robert W. Sterner.
 551 Nutritional constraints in terrestrial and freshwater food webs. *Nature*, 408(6812):578–580, November 2000. ISSN
 552 0028-0836, 1476-4687. doi: 10.1038/35046058. URL <https://www.nature.com/articles/35046058>.
- 553 Ra Farrow. Population Dynamics of the Australian Plague Locust, *Chortoicetes terminifera* (Walker) in Central
 554 Western New South Wales III. Analysis of Population Processes. *Australian Journal of Zoology*, 30(4):569, 1982.
 555 ISSN 0004-959X. doi: 10.1071/ZO9820569. URL <http://www.publish.csiro.au/?paper=ZO9820569>.
- 556 R. B. Floyd, editor. *Frontiers of population ecology*. CSIRO Pub, Collingwood, VIC, Australia, 1996. ISBN 978-0-
 557 643-05781-4.
- 558 M. G. Forero, J. L. Tella, K. A. Hobson, M. Bertellotti, and G. Blanco. Conspecific food competition explains
 559 variability in colony size: a test in Magellanic penguins. *Ecology*, 83(12):3466–3475, December 2002. ISSN 0012-
 560 9658. doi: 10.1890/0012-9658(2002)083[3466:CFCEVI]2.0.CO;2. URL [http://doi.wiley.com/10.1890/0012-9658\(2002\)083\[3466:CFCEVI\]2.0.CO;2](http://doi.wiley.com/10.1890/0012-9658(2002)083[3466:CFCEVI]2.0.CO;2).
- 561 M. Giese, H. Brueck, Y. Z. Gao, S. Lin, M. Steffens, I. Kögel-Knabner, T. Glindemann, A. Susenbeth, F. Taube,
 562 K. Butterbach-Bahl, X. H. Zheng, C. Hoffmann, Y. F. Bai, and X. G. Han. N balance and cycling of Inner Mongolia
 563 typical steppe: a comprehensive case study of grazing effects. *Ecological Monographs*, 83(2):195–219, May 2013.
 564 ISSN 0012-9615, 1557-7015. doi: 10.1890/12-0114.1. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/12-0114.1>.
- 565 Noel Gorelick, Matt Hancher, Mike Dixon, Simon Ilyushchenko, David Thau, and Rebecca Moore. Google Earth
 566 Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, 202:18–27, December 2017.
 567 ISSN 00344257. doi: 10.1016/j.rse.2017.06.031. URL <https://linkinghub.elsevier.com/retrieve/pii/S0034425717302900>.
- 568 Martin Granbom and Henrik G. Smith. Food Limitation During Breeding in a Heterogeneous Landscape. *The Auk*,
 569 123(1):97–107, January 2006. ISSN 1938-4254, 0004-8038. doi: 10.1093/auk/123.1.97. URL <https://academic.oup.com/auk/article/123/1/97/5562605>.
- 570 M. J. Grundy, R. A. Viscarra Rossel, R. D. Searle, P. L. Wilson, C. Chen, and L. J. Gregory. Soil and Landscape Grid
 571 of Australia. *Soil Research*, 53(8):835, 2015. ISSN 1838-675X. doi: 10.1071/SR15191. URL <http://www.publish.csiro.au/?paper=SR15191>.
- 572 Lennart Hansson. Food as a limiting factor for small rodent numbers: Tests of two hypotheses. *Oecologia*, 37(3):
 573 297–314, January 1979. ISSN 0029-8549, 1432-1939. doi: 10.1007/BF00347907. URL <http://link.springer.com/10.1007/BF00347907>.
- 574 Sarah J. Harrison, David Raubenheimer, Stephen J. Simpson, Jean-Guy J. Godin, and Susan M. Bertram. Towards
 575 a synthesis of frameworks in nutritional ecology: interacting effects of protein, carbohydrate and phosphorus on
 576 field cricket fitness. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792):20140539, 2014. doi:
 577 10.1098/rspb.2014.0539. URL <https://doi.org/10.1098/rspb.2014.0539>.
- 578 T. J. Heidorn and A. Joern. Feeding Preference and Spatial Distribution of Grasshoppers (Acrididae) in Response
 579 to Nitrogen Fertilization of *Calamovilfa longifolia*. *Functional Ecology*, 1(4):369, 1987. ISSN 02698463. doi:
 580 10.2307/2389793. URL <https://www.jstor.org/stable/2389793?origin=crossref>.
- 581 Andrea F. Huberty and Robert F. Denno. Consequences of nitrogen and phosphorus limitation for the performance of
 582 two planthoppers with divergent life-history strategies. *Oecologia*, 149(3):444–455, September 2006. ISSN 0029-
 583 8549, 1432-1939. doi: 10.1007/s00442-006-0462-8. URL <http://link.springer.com/10.1007/s00442-006-0462-8>.
- 584 D. M. Hunter, P. W. Walker, and R. J. Elder. Adaptations of locusts and grasshoppers to the low and variable
 585 rainfall of Australia. *Journal of Orthoptera Research*, 10(2):347–351, December 2001. ISSN 1082-6467, 1937-
 586 2426. doi: 10.1665/1082-6467(2001)010[0347:AOLAGT]2.0.CO;2. URL <http://www.bioone.org/doi/abs/10.1665/1082-6467%282001%29010%5B0347%3AAOLAGT%5D2.0.CO%3B2>.
- 587 D.M. Hunter, L. McCulloch, and P.A. Spurgin. Aerial detection of nymphal bands of the Australian plague
 588 locust (*Chortoicetes terminifera* (Walker)) (Orthoptera: Acrididae). *Crop Protection*, 27(1):118–123, January
 589 2008. ISSN 02612194. doi: 10.1016/j.cropro.2007.04.016. URL <https://linkinghub.elsevier.com/retrieve/pii/S0261219407001159>.
- 590 Anthony Joern, Tony Provin, and Spencer T. Behmer. Not just the usual suspects: Insect herbivore populations and
 591 communities are associated with multiple plant nutrients. *Ecology*, 93(5):1002–1015, May 2012. ISSN 0012-9658,
 592 1939-9170. doi: 10.1890/11-1142.1. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/11-1142.1>.

- 601 Jayne L. Jonas and Anthony Joern. Hostplant quality alters grass/forb consumption by a mixedfeeding insect herbivore,
 602 *Melanoplus bivittatus* (Orthoptera: Acrididae). *Ecological Entomology*, 33(4):546–554, August 2008. ISSN 0307-
 603 6946, 1365-2311. doi: 10.1111/j.1365-2311.2008.01004.x. URL <https://resjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2311.2008.01004.x>.
- 605 Lloyd B. Keith. Role of Food in Hare Population Cycles. *Oikos*, 40(3):385, May 1983. ISSN 00301299. doi:
 606 10.2307/3544311. URL <https://www.jstor.org/stable/3544311?origin=crossref>.
- 607 K.H.L. Key. The general ecological characteristics of the outbreak areas and outbreak years of the Australian plague
 608 locust (Chortoicetes terminifera Walk.). 1945. doi: 10.25919/RTPX-F935. URL <https://publications.csiro.au/publications/publication/PIprocite:8058408f-539f-4540-b888-0ddale0c113d>. Publisher: Melbourne, Vic., Council
 610 for Scientific and Industrial Research.
- 611 Douglas Lawton, Cathy Waters, Marion Le Gall, and Arianne Cease. Woody vegetation remnants within pastures
 612 influence locust distribution: Testing bottom-up and top-down control. *Agriculture, Ecosystems & Environment*,
 613 296:106931, July 2020. ISSN 01678809. doi: 10.1016/j.agee.2020.106931. URL <https://linkinghub.elsevier.com/retrieve/pii/S016788092030116X>.
- 615 Douglas Lawton, Marion Le Gall, Cathy Waters, and Arianne J. Cease. Mismatched diets: defining the nutritional
 616 landscape of grasshopper communities in a variable environment. *Ecosphere*, 12(3):e03409, March 2021. ISSN
 617 2150-8925, 2150-8925. doi: 10.1002/ecs2.3409. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.3409>.
- 619 Douglas Lawton, Peter Scarth, Edward Deveson, Cyril Piou, Allan Spessa, Cathy Waters, and Arianne J. Cease. Seeing
 620 the locust in the swarm: accounting for spatiotemporal hierarchy improves ecological models of insect populations.
 621 *Ecography*, 2022(2):ecog.05763, February 2022. ISSN 0906-7590, 1600-0587. doi: 10.1111/ecog.05763. URL
 622 <https://nsojournals.onlinelibrary.wiley.com/doi/10.1111/ecog.05763>.
- 623 Marion Le Gall, Rick Overson, and Arianne Cease. A Global Review on Locusts (Orthoptera: Acrididae) and Their
 624 Interactions With Livestock Grazing Practices. *Frontiers in Ecology and Evolution*, 7:263, July 2019. ISSN 2296-
 625 701X. doi: 10.3389/fevo.2019.00263. URL <https://www.frontiersin.org/article/10.3389/fevo.2019.00263/full>.
- 626 Paul A. Lenhart, Micky D. Eubanks, and Spencer T. Behmer. Water stress in grasslands: dynamic responses of plants
 627 and insect herbivores. *Oikos*, 124(3):381–390, March 2015. ISSN 0030-1299, 1600-0706. doi: 10.1111/oik.01370.
 628 URL <https://onlinelibrary.wiley.com/doi/10.1111/oik.01370>.
- 629 Viviana Loaiza, Jayne L. Jonas, and Anthony Joern. Grasshoppers (orthoptera: Acrididae) select vegetation patches
 630 in local-scale responses to foliar nitrogen but not phosphorus in native grassland: Grasshopper distribution and
 631 food quality. *Insect Science*, 18(5):533–540, 10 2011. doi: 10.1111/j.1744-7917.2010.01376.x. URL <https://onlinelibrary.wiley.com/doi/10.1111/j.1744-7917.2010.01376.x>.
- 633 Nr Marsh and Ma Adams. Decline of Eucalyptus tereticornis Near Bairnsdale, Victoria: Insect Herbivory and Nitrogen
 634 Fractions in Sap and Foliage. *Australian Journal of Botany*, 43(1):39, 1995. ISSN 0067-1924. doi: 10.1071/
 635 BT9950039. URL <http://www.publish.csiro.au/?paper=BT9950039>.
- 636 William J. Mattson. Herbivory in Relation to Plant Nitrogen Content. *Annual Review of Ecology and Systematics*,
 637 11(1):119–161, November 1980. ISSN 0066-4162. doi: 10.1146/annurev.es.11.110180.001003. URL <https://www.annualreviews.org/doi/10.1146/annurev.es.11.110180.001003>.
- 639 Nicola Millist and Abdalla Ali. Benefitcost analysis of Australian plague locust control operations for 201011,
 640 2011. URL <https://www.agriculture.gov.au/sites/default/files/sitecollectiondocuments/animal-plant/aplc/research-papers/locust-control-11.pdf>.
- 642 S.R. Morton, D.M. Stafford Smith, C.R. Dickman, D.L. Dunkerley, M.H. Friedel, R.R.J. McAllister, J.R.W. Reid, D.A.
 643 Roshier, M.A. Smith, F.J. Walsh, G.M. Wardle, I.W. Watson, and M. Westoby. A fresh framework for the ecology
 644 of arid Australia. *Journal of Arid Environments*, 75(4):313–329, April 2011. ISSN 01401963. doi: 10.1016/j.jaridenv.2010.11.001. URL <https://linkinghub.elsevier.com/retrieve/pii/S0140196310003010>.
- 646 Joaquín Muñoz-Sabater, Emanuel Dutra, Anna Agustí-Panareda, Clément Albergel, Gabriele Arduini, Gianpaolo
 647 Balsamo, Souhail Boussetta, Margarita Choulga, Shaun Harrigan, Hans Hersbach, Brecht Martens, Diego G.
 648 Miralles, María Piles, Nemesio J. Rodríguez-Fernández, Ervin Zsoter, Carlo Buontempo, and Jean-Noël Thé-
 649 paut. ERA5-Land: a state-of-the-art global reanalysis dataset for land applications. *Earth System Science
 650 Data*, 13(9):4349–4383, September 2021. ISSN 1866-3516. doi: 10.5194/essd-13-4349-2021. URL <https://essd.copernicus.org/articles/13/4349/2021/>.
- 652 Yonggang Nie, Zejun Zhang, David Raubenheimer, James J. Elser, Wei Wei, and Fuwen Wei. Obligate herbivory
 653 in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry.
 654 *Functional Ecology*, 29(1):26–34, January 2015. ISSN 0269-8463, 1365-2435. doi: 10.1111/1365-2435.12302.
 655 URL <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.12302>.

- 656 Immanuel Noy-Meir. Desert Ecosystems: Higher Trophic Levels. *Annual Review of Ecology and Systematics*, 5(1):
 657 195–214, November 1974. ISSN 0066-4162. doi: 10.1146/annurev.es.05.110174.001211. URL <https://www.annualreviews.org/doi/10.1146/annurev.es.05.110174.001211>.
- 659 Gordon H. Orians and Antoni V. Milewski. Ecology of Australia: the effects of nutrientpoor soils and intense fires. *Biological Reviews*, 82(3):393–423, August 2007. ISSN 1464-7931, 1469-185X. doi: 10.1111/j.1469-185X.2007.00017.x. URL <https://onlinelibrary.wiley.com/doi/10.1111/j.1469-185X.2007.00017.x>.
- 662 Katerina A. Ozment, Ellen A. R. Welti, Monica Shaffer, and Michael Kaspari. Tracking nutrients in space and time: *Ecology and Evolution*, 11(10):5413–5423, May 2021. ISSN 2045-7758, 2045-7758. doi: 10.1002/ece3.7435. URL <https://onlinelibrary.wiley.com/doi/10.1002/ece3.7435>.
- 666 Adam F. Parlin, Mitchell J. Kendzel, Orley R. Taylor, Theresa M. Culley, Stephen F. Matter, and Patrick A. Guerra. The cost of movement: assessing energy expenditure in a long-distant ectothermic migrant under climate change. *Journal of Experimental Biology*, 226(21):jeb245296, November 2023. ISSN 0022-0949, 1477-9145. doi: 10.1242/jeb.245296. URL <https://journals.biologists.com/jeb/article/226/21/jeb245296/334654/The-cost-of-movement-assessing-energy-expenditure>.
- 671 Marc C. Perkins, H. Arthur Woods, Jon F. Harrison, and James J. Elser. Dietary phosphorus affects the growth of larval *Manduca sexta*. *Archives of Insect Biochemistry and Physiology*, 55(3):153–168, March 2004. ISSN 0739-4462, 1520-6327. doi: 10.1002/arch.10133. URL <https://onlinelibrary.wiley.com/doi/10.1002/arch.10133>.
- 674 J. C. Randolph, G. N. Cameron, and P. A. McClure. Nutritional Requirements for Reproduction in the Hispid Cotton Rat, *Sigmodon hispidus*. *Journal of Mammalogy*, 76(4):1113–1126, December 1995. ISSN 1545-1542, 0022-2372. doi: 10.2307/1382603. URL <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1382603>.
- 677 D. Raubenheimer and S. J. Simpson. Integrative models of nutrient balancing: application to insects and vertebrates. *Nutrition Research Reviews*, 10(1):151–179, January 1997. ISSN 0954-4224, 1475-2700. doi: 10.1079/NRR19970009. URL https://www.cambridge.org/core/product/identifier/S0954422497000103/type/journal_article.
- 681 David Raubenheimer and Jessica M. Rothman. Nutritional Ecology of Entomophagy in Humans and Other Primates. *Annual Review of Entomology*, 58(1):141–160, January 2013. ISSN 0066-4170, 1545-4487. doi: 10.1146/annurev-ento-120710-100713. URL <https://www.annualreviews.org/doi/10.1146/annurev-ento-120710-100713>.
- 684 John D. Schade, Marcia Kyle, S. E. Hobbie, W. F. Fagan, and J. J. Elser. Stoichiometric tracking of soil nutrients by a desert insect herbivore. *Ecology Letters*, 6(2):96–101, February 2003. ISSN 1461-023X, 1461-0248. doi: 10.1046/j.1461-0248.2003.00409.x. URL <https://onlinelibrary.wiley.com/doi/10.1046/j.1461-0248.2003.00409.x>.
- 687 S. J. Simpson and J. D. Abisgold. Compensation by locusts for changes in dietary nutrients: behavioural mechanisms. *Physiological Entomology*, 10(4):443–452, December 1985. ISSN 0307-6962, 1365-3032. doi: 10.1111/j.1365-3032.1985.tb00066.x. URL <https://resjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-3032.1985.tb00066.x>.
- 690 Stephen J Simpson and David Raubenheimer. *The nature of nutrition: a unifying framework from animal adaptation to human obesity*. Princeton university press, 2012a.
- 692 Stephen J. Simpson and David Raubenheimer. *The Nature of Nutrition: A Unifying Framework from Animal Adaptation to Human Obesity*. Princeton University Press, 1 edition, July 2012b. ISBN 978-0-691-14565-5 978-1-4008-4280-3. doi: 10.23943/princeton/9780691145655.001.0001. URL <https://academic.oup.com/princeton-scholarship-online/book/23993>.
- 696 Stav Talal, Arianne J. Cease, Jacob P. Youngblood, Ruth Farington, Eduardo V. Trumper, Hector E. Medina, Julio E. Rojas, A. Fernando Copa, and Jon F. Harrison. Plant carbohydrate content limits performance and lipid accumulation of an outbreaking herbivore. *Proceedings of the Royal Society B: Biological Sciences*, 287(1940):20202500, December 2020. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2020.2500. URL <https://royalsocietypublishing.org/doi/10.1098/rspb.2020.2500>.
- 701 Stav Talal, Arianne Cease, Ruth Farington, Hector E. Medina, Julio Rojas, and Jon Harrison. High carbohydrate diet ingestion increases post-meal lipid synthesis and drives respiratory exchange ratios above 1. *Journal of Experimental Biology*, 224(4):jeb240010, February 2021. ISSN 0022-0949, 1477-9145. doi: 10.1242/jeb.240010. URL <https://journals.biologists.com/jeb/article/224/4/jeb240010/237230/High-carbohydrate-diet-ingestion-increases-post>.
- 705 Stav Talal, Jon F. Harrison, Ruth Farington, Jacob P. Youngblood, Hector E. Medina, Rick Overton, and Arianne J. Cease. Body mass and growth rates predict protein intake across animals, June 2023. URL <http://biorxiv.org/lookup/doi/10.1101/2023.06.20.545784>.
- 708 Toby Tyrrell. The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature*, 400(6744): 525–531, August 1999. ISSN 0028-0836, 1476-4687. doi: 10.1038/22941. URL <https://www.nature.com/articles/22941>.

- 711 Boris Petrovi Uvarov. *Grasshoppers and locusts. 2: Behaviour, ecology, biogeography population dynamics*. Univ.
712 Press, Cambridge, 1977. ISBN 978-0-85135-072-1.
- 713 Sophie Veran, Stephen J. Simpson, Gregory A. Sword, Edward Deveson, Sylvain Piry, James E. Hines, and Karine
714 Berthier. Modeling spatiotemporal dynamics of outbreaking species: influence of environment and migration in
715 a locust. *Ecology*, 96(3):737–748, March 2015. ISSN 0012-9658, 1939-9170. doi: 10.1890/14-0183.1. URL
716 <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/14-0183.1>.
- 717 Peter M. Vitousek, Stephen Porder, Benjamin Z. Houlton, and Oliver A. Chadwick. Terrestrial phosphorus limitation:
718 mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications*, 20(1):5–15, January
719 2010. ISSN 1051-0761, 1939-5582. doi: 10.1890/08-0127.1. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/08-0127.1>.
- 721 Ellen A. R. Welti, Rebecca M. Prather, Nathan J. Sanders, Kirsten M. De Beurs, and Michael Kaspari. Bottomup when
722 it is not topdown: Predators and plants control biomass of grassland arthropods. *Journal of Animal Ecology*, 89(5):
723 1286–1294, May 2020a. ISSN 0021-8790, 1365-2656. doi: 10.1111/1365-2656.13191. URL <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.13191>.
- 725 Ellen A. R. Welti, Karl A. Roeder, Kirsten M. De Beurs, Anthony Joern, and Michael Kaspari. Nutrient dilution
726 and climate cycles underlie declines in a dominant insect herbivore. *Proceedings of the National Academy of
727 Sciences*, 117(13):7271–7275, March 2020b. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1920012117. URL
728 <https://pnas.org/doi/full/10.1073/pnas.1920012117>.
- 729 T. C. R. White. The importance of a relative shortage of food in animal ecology. *Oecologia*, 33(1):71–86, 1978. ISSN
730 0029-8549, 1432-1939. doi: 10.1007/BF00376997. URL <http://link.springer.com/10.1007/BF00376997>.
- 731 T. C. R. White. The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews*,
732 83(3):227–248, August 2008. ISSN 1464-7931, 1469-185X. doi: 10.1111/j.1469-185X.2008.00041.x. URL
733 <https://onlinelibrary.wiley.com/doi/10.1111/j.1469-185X.2008.00041.x>.
- 734 Thomas C. R. White. *The Inadequate Environment*. Springer Berlin Heidelberg, Berlin, Heidelberg, 1993. ISBN 978-
735 3-642-78301-2 978-3-642-78299-2. doi: 10.1007/978-3-642-78299-2. URL <http://link.springer.com/10.1007/978-3-642-78299-2>.
- 737 W. G. Whitford. *Ecology of desert systems*. Academic Press, San Diego, 2002. ISBN 978-0-12-747261-4.
- 738 J. Keaton Wilson, L. Ruiz, and G. Davidowitz. Dietary Protein and Carbohydrates Affect Immune Function and
739 Performance in a Specialist Herbivore Insect (*Manduca sexta*). *Physiological and Biochemical Zoology*, 92(1):
740 58–70, January 2019a. ISSN 1522-2152, 1537-5293. doi: 10.1086/701196. URL <https://www.journals.uchicago.edu/doi/10.1086/701196>.
- 742 Jerome Keaton Wilson, Laura Ruiz, Jesse Duarte, and Goggy Davidowitz. The nutritional landscape of host plants
743 for a specialist insect herbivore. *Ecology and Evolution*, 9(23):13104–13113, December 2019b. ISSN 2045-7758,
744 2045-7758. doi: 10.1002/ece3.5730. URL <https://onlinelibrary.wiley.com/doi/10.1002/ece3.5730>.
- 745 Mira L. Word, Sharon J. Hall, Brian E. Robinson, Balanding Manneh, Alioune Beye, and Arianne J. Cease. Soil-
746 targeted interventions could alleviate locust and grasshopper pest pressure in West Africa. *Science of The Total
747 Environment*, 663:632–643, May 2019. ISSN 00489697. doi: 10.1016/j.scitotenv.2019.01.313. URL <https://linkinghub.elsevier.com/retrieve/pii/S0048969719303560>.
- 749 Zijia Zhang, James J. Elser, Arianne J. Cease, Ximei Zhang, Qiang Yu, Xingguo Han, and Guangming Zhang.
750 Grasshoppers Regulate N:P Stoichiometric Homeostasis by Changing Phosphorus Contents in Their Frass. *PLoS
751 ONE*, 9(8):e103697, August 2014. ISSN 1932-6203. doi: 10.1371/journal.pone.0103697. URL <https://dx.plos.org/10.1371/journal.pone.0103697>.
- 753 Xiaolong Zhou, Xudong Liu, Pengfei Zhang, Zhi Guo, and Guozhen Du. Increased community compositional dissimililarity
754 alleviates species loss following nutrient enrichment at large spatial scales. *Journal of Plant Ecology*, 12(2):
755 376–386, March 2019. ISSN 1752-993X. doi: 10.1093/jpe/rty035. URL <https://academic.oup.com/jpe/article/12/2/376/5096732>.
- 757 Hui Zhu, Venuste Nkurunziza, Jingting Wang, Qinfeng Guo, Hang Ruan, and Deli Wang. Effects of large herbivore
758 grazing on grasshopper behaviour and abundance in a meadow steppe. *Ecological Entomology*, 45(6):1357–1366,
759 December 2020. ISSN 0307-6946, 1365-2311. doi: 10.1111/een.12919. URL <https://resjournals.onlinelibrary.wiley.com/doi/10.1111/een.12919>.
- 761 Yu Zhu, Zhiwei Zhong, Jordi F. Pagès, Deborah Finke, Deli Wang, Quanhui Ma, Nazim Hassan, Hui Zhu, and Ling
762 Wang. Negative effects of vertebrate on invertebrate herbivores mediated by enhanced plant nitrogen content. *Journal of Ecology*,
763 107(2):901–912, March 2019. ISSN 0022-0477, 1365-2745. doi: 10.1111/1365-2745.13100. URL
764 <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.13100>.

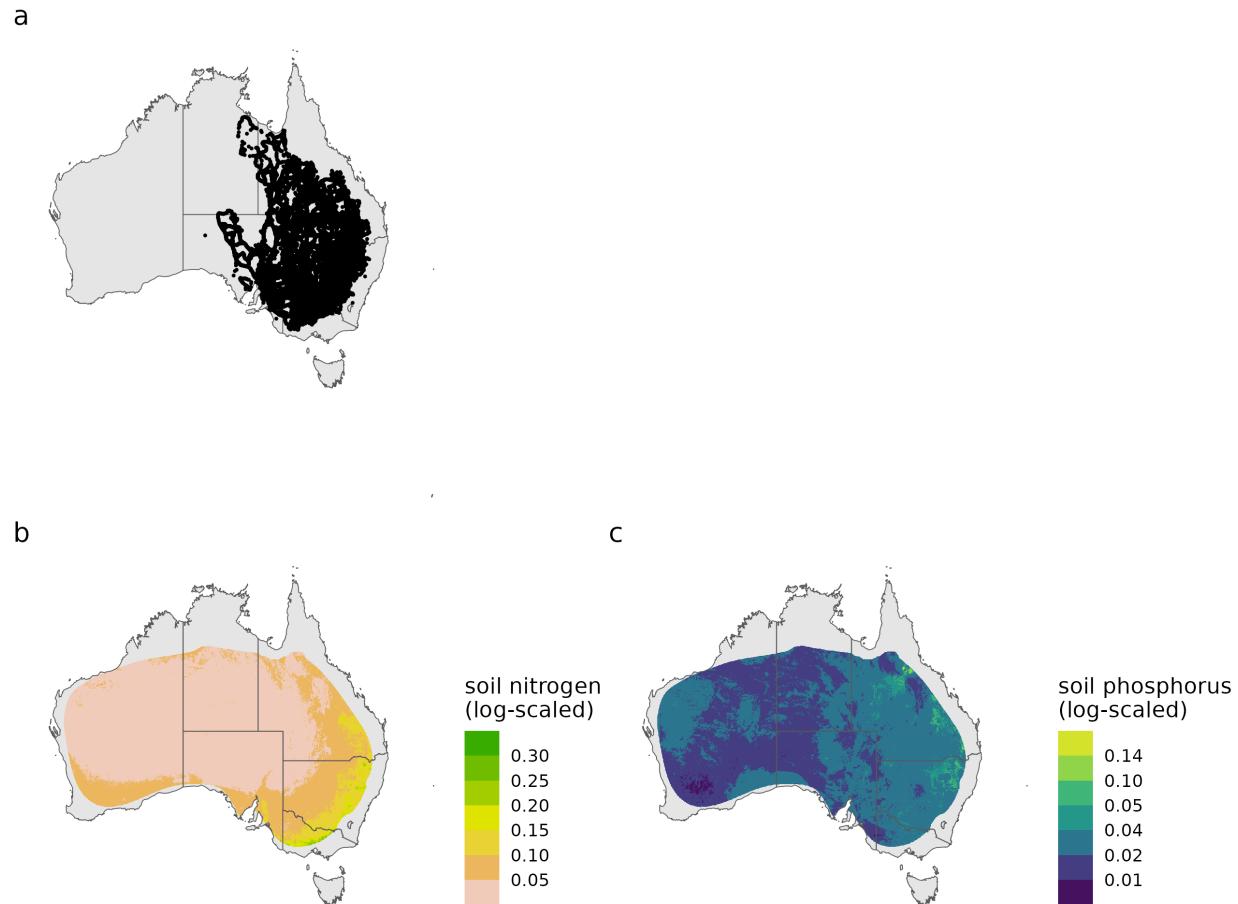
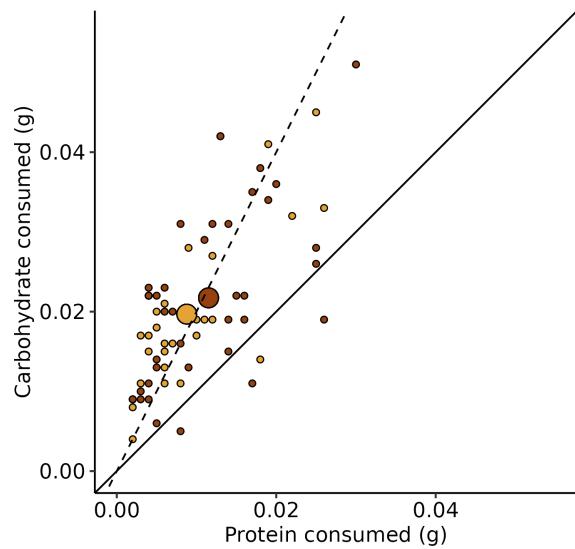


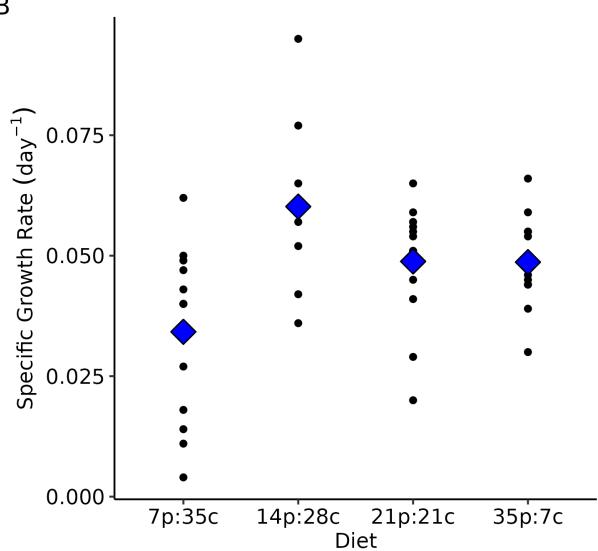
Figure 1: Locust survey data map and soil nutrients throughout the *C. terminifera* distribution. A: APLC survey dataset, B: mean proportion of nitrogen at 0-15 cm deep, C: mean proportion phosphorous at 0-15cm deep.

A

population Guntawang Mendooran



B



C

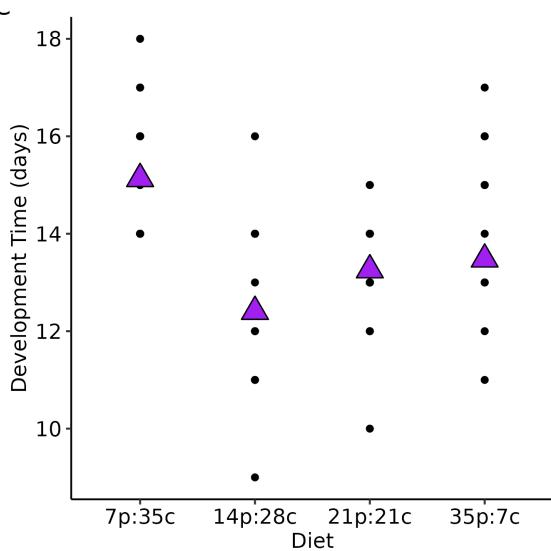


Figure 2: The nutritional preference (A) and physiological performance (B & C) of *C. terminifera* individuals that were collected from two marching bands of 5th instars. Raw data is shown as black dots with modeled estimated marginal means as large diamonds or triangles.

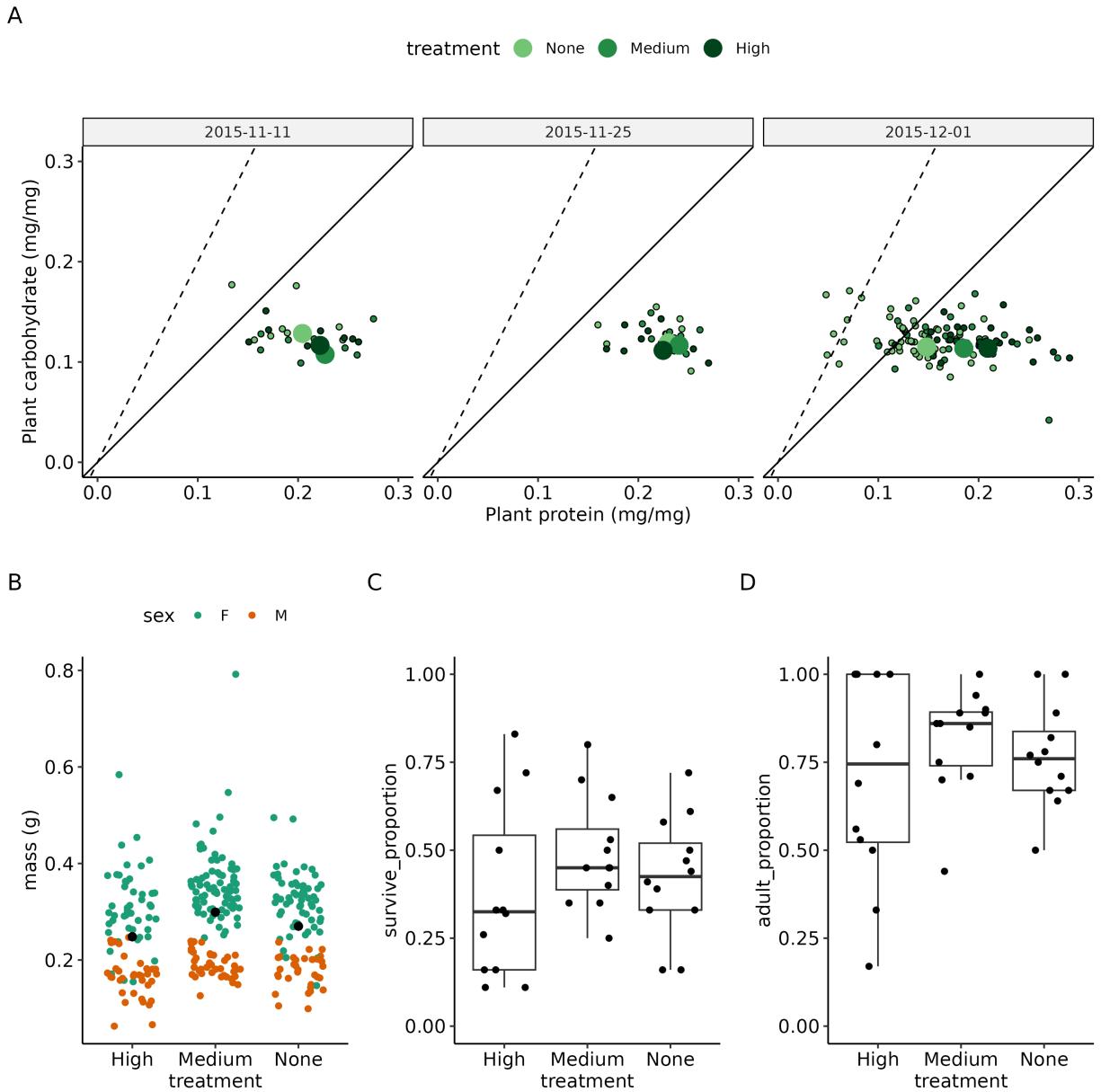


Figure 3: Nitrogen addition field cage experiments with plant nutrient change through time (A) and grasshopper performance metrics (B-C) are shown. Dashed line represents a 1p : 2c ratio, the solid line represents a 1p : 1c ratio. Black dots in B represent overall means whereas boxplots represent the lower, median, and upper quartiles.

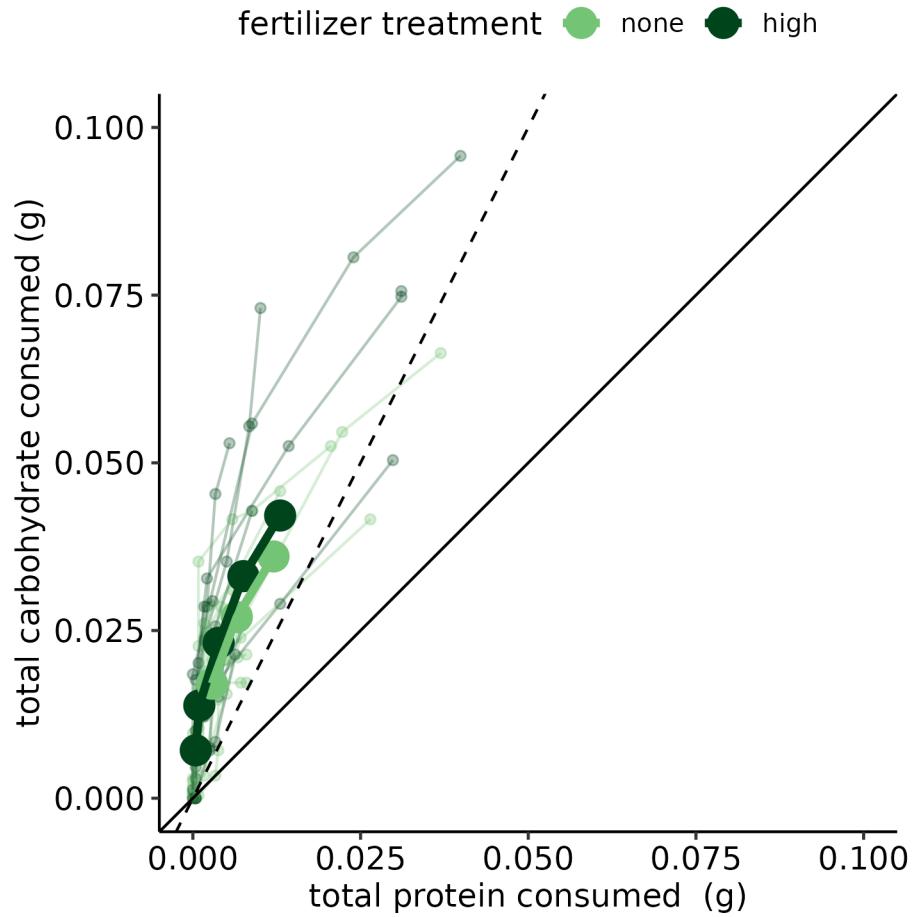
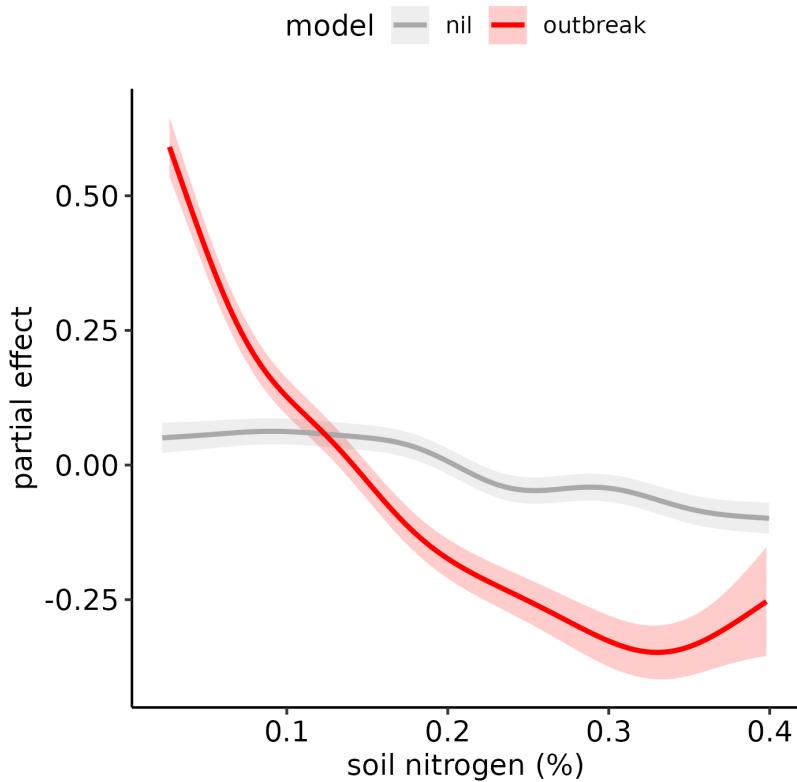


Figure 4: Nutrient imbalance redressing with artificial diet mixing of *C. terminifera* individuals taken from fertilized treatment cages. Colors represent fertilizer treatment. Smaller lines represent raw individual locust intake targets; large lines and points represent estimated marginal means. Points along each line represent sampling times on days 1, 2, 4, 6, and 9. Individual time step targets can be seen in Supplementary Figure 4.

a



b

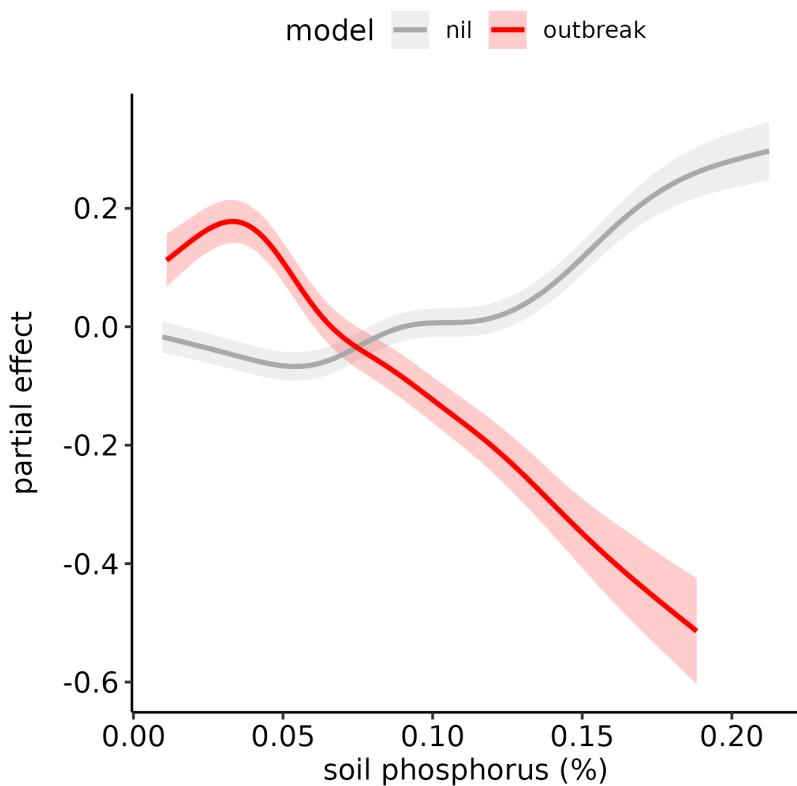
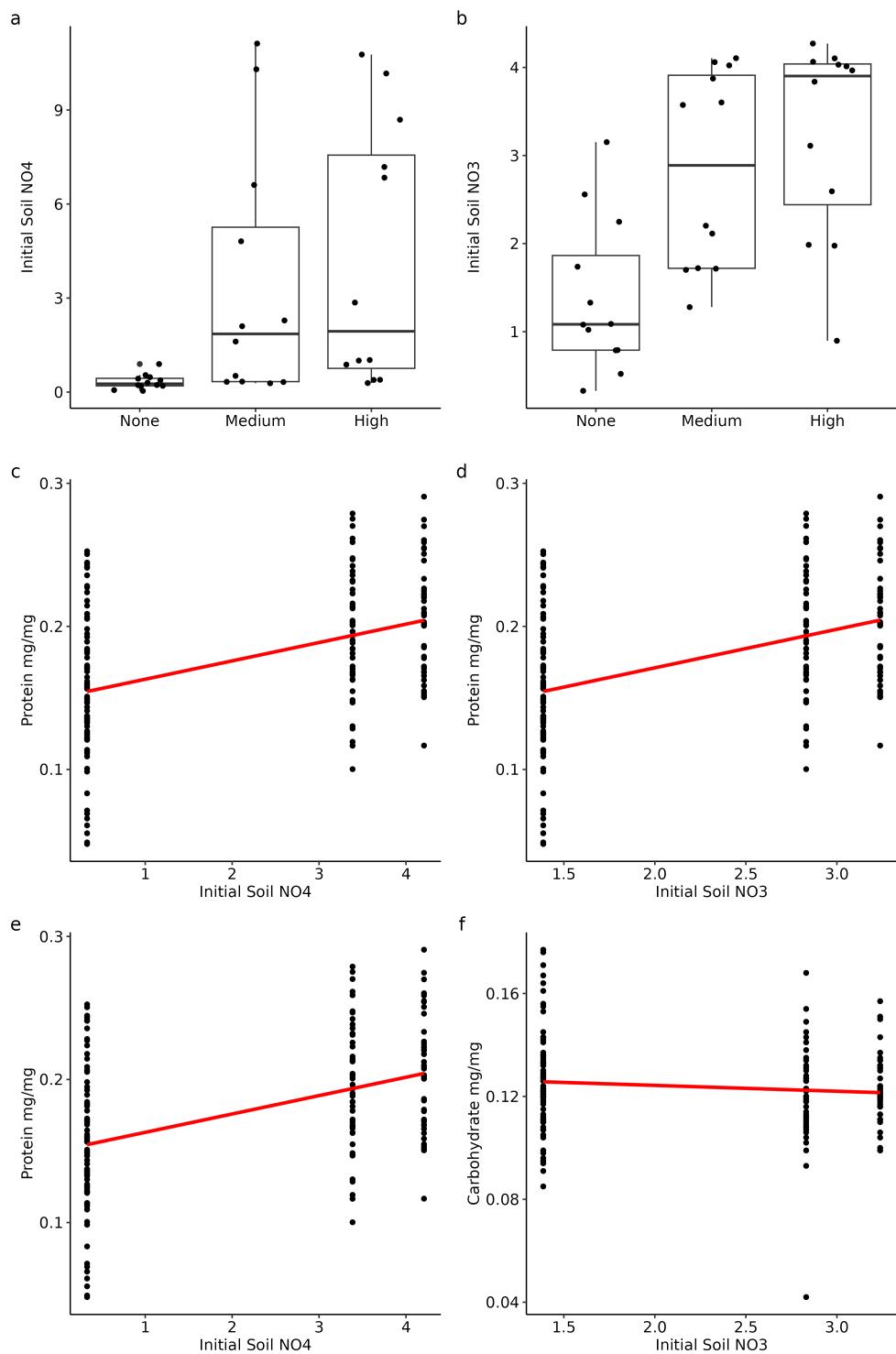
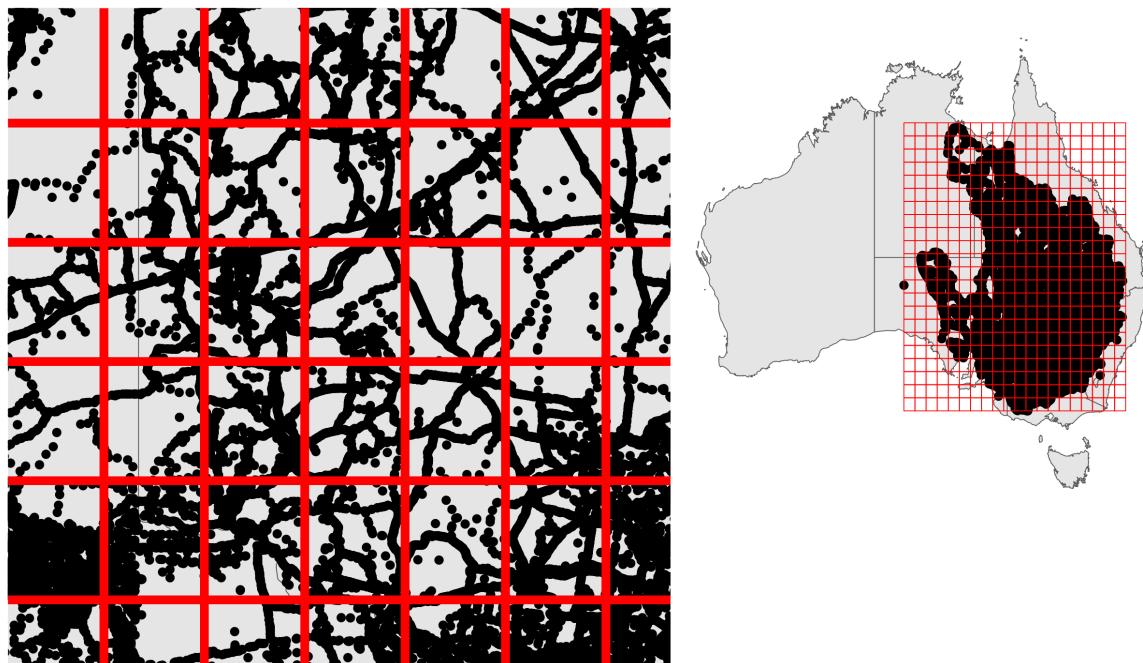


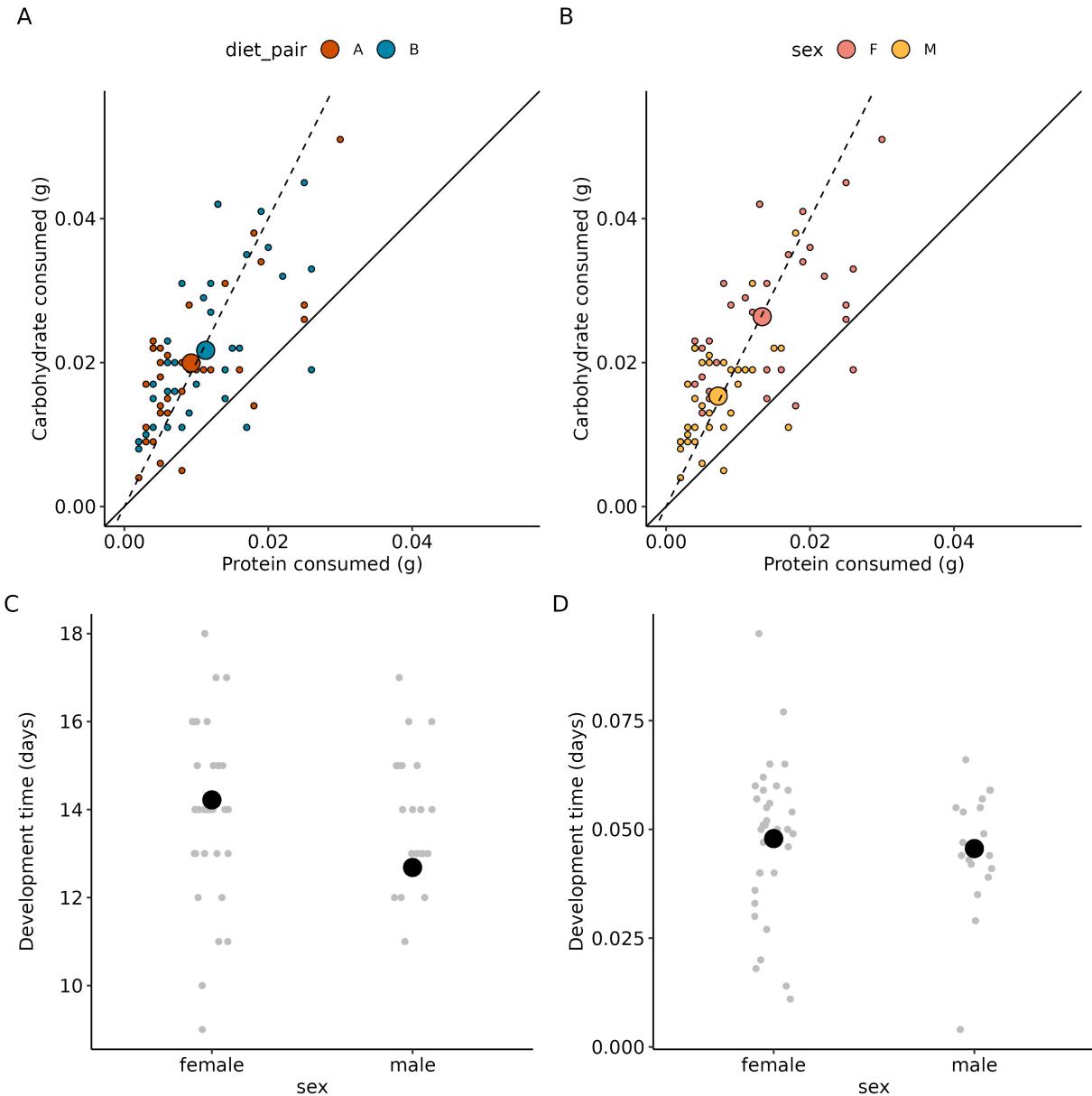
Figure 5: Relationship between outbreaks and nil observations for both soil nitrogen (A) and phosphorus (B). Partial effect is the modeled predictions after accounting for bioregion and spatial autocorrelation.



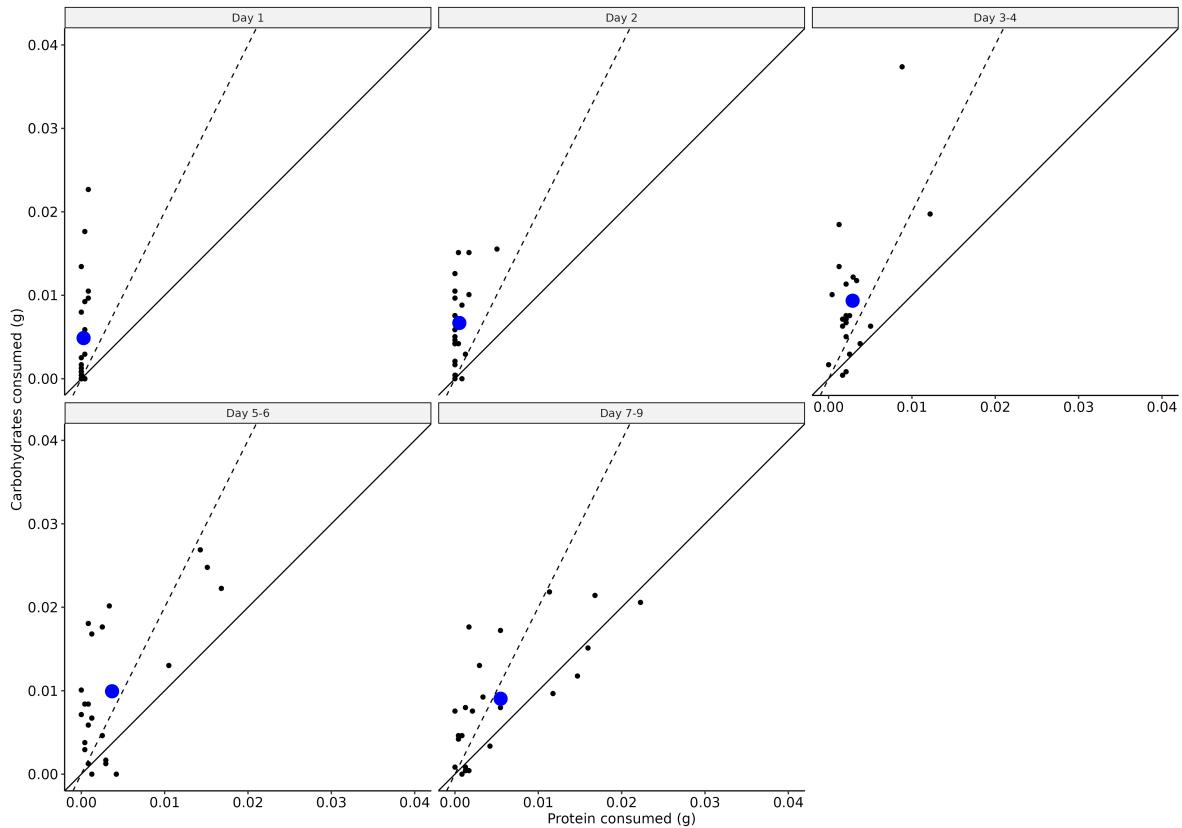
Supplementary Figure 1: Field cage soil nitrogen content by treatment (A & B) and regressed with plant carbohydrates and protein (C-F).



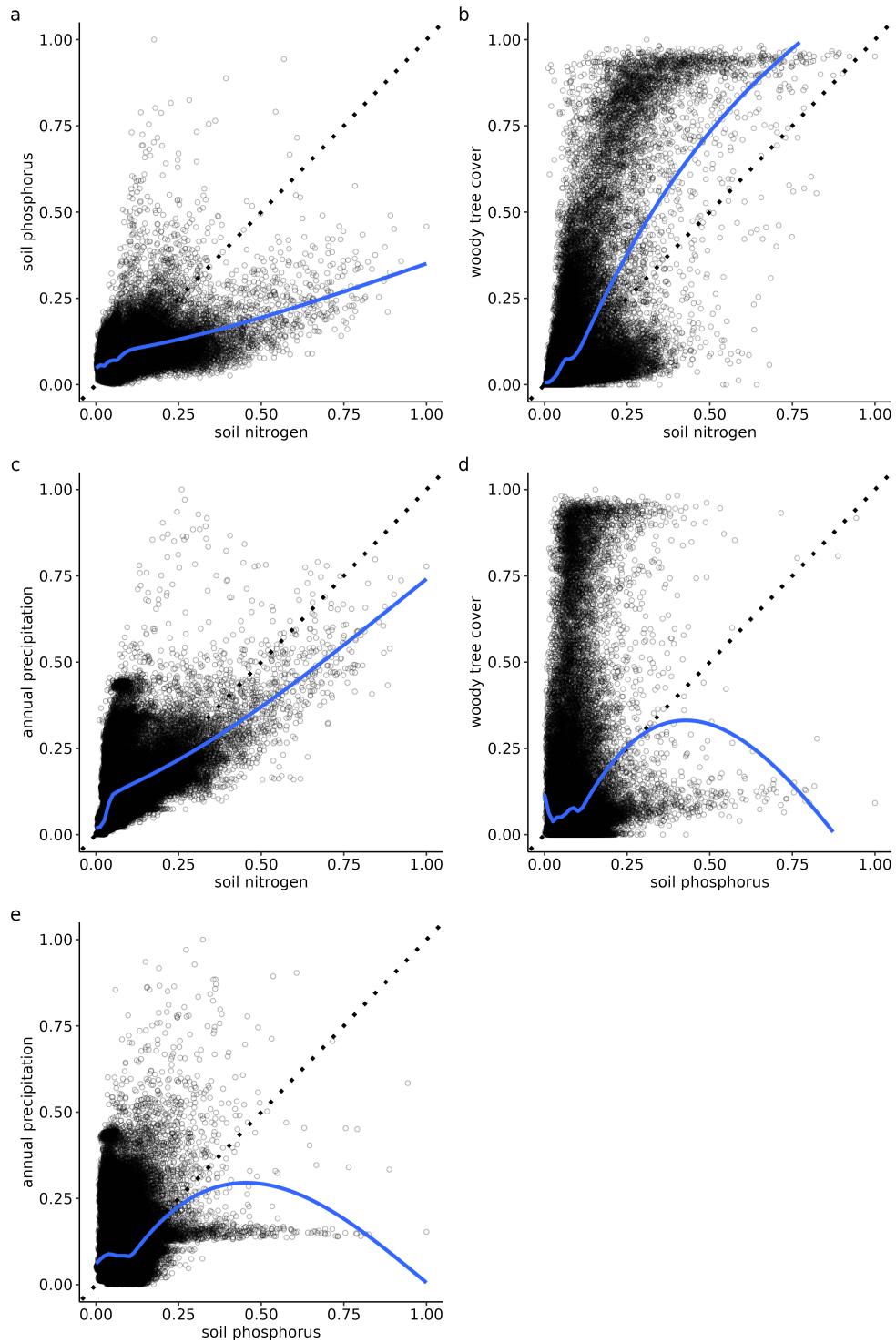
Supplementary Figure 2: Map illustrating the summarization of point observation data into a fishnet grid across eastern Australia. The full extent is shown in the inset map. We summed the number of outbreak, nil, and total observations. The grid in this figure is not at a 1 km^2 scale for demonstration purposes, as the cells would be too small to see.



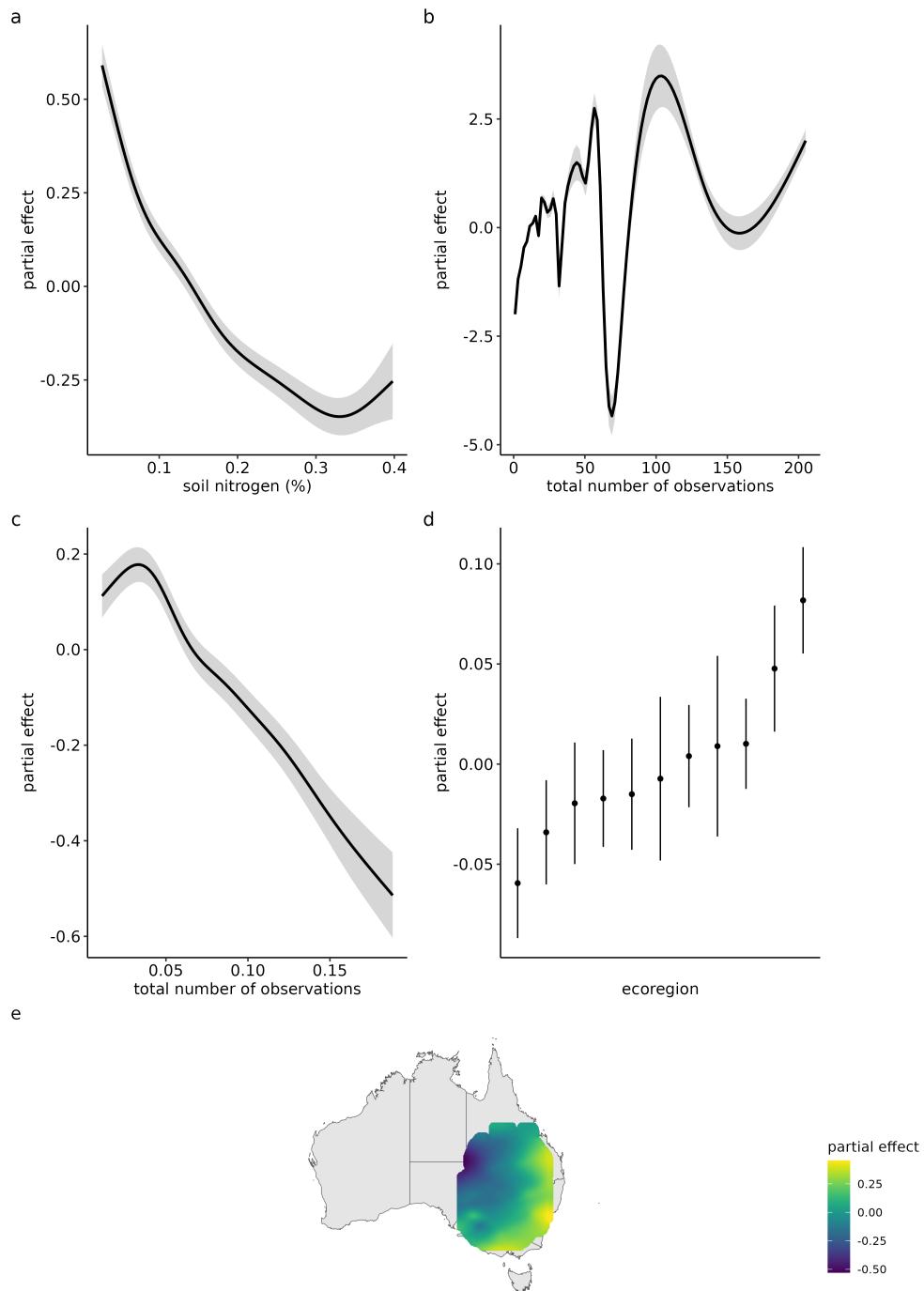
Supplementary Figure 3: Nutrient consumption for outbreaking field populations of *C. terminifera* by diet pair (A) and sex (B) and development time (C) specific growth rate (D) by sex. The P:C ratio did not differ between diet pairing and sex. Females consumed more diet (but kept the same ratio) than males. Big circles represent estimated marginal means from the model while little circles represent raw data.



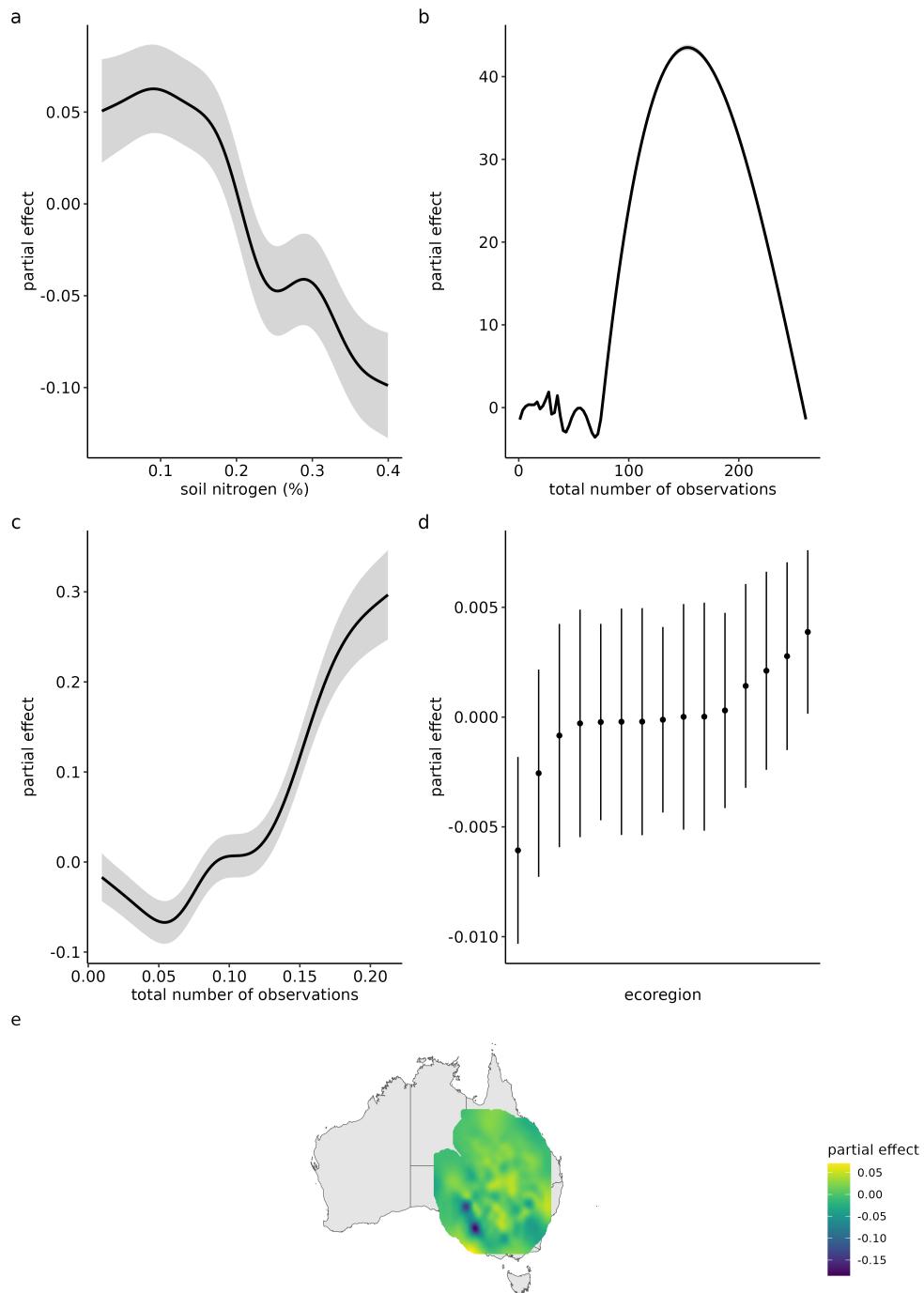
Supplementary Figure 4: Individual time step intake targets for grasshoppers kept in both high nitrogen fertilization and control cages. Blue dots represent estimated marginal means from the model while blacks dots represent raw individual intake targets.



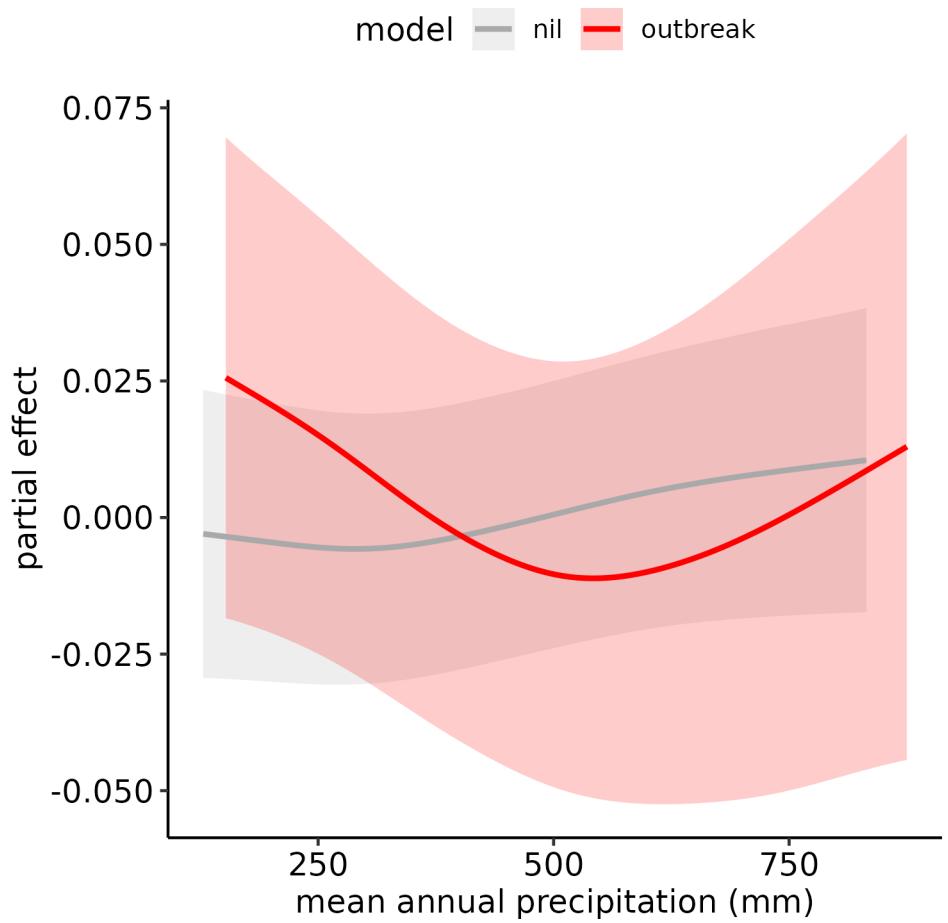
Supplementary Figure 5: Environmental variable correlations between mean annual precipitation, soil nitrogen, soil phosphorus, and woody vegetation pixel coverage. Mean annual precipitation was sourced from WorldClim V1 Bio-clim, soil nitrogen and phosphorus was sourced from Soil and Landscape Grid of Australia, and woody vegetation pixel coverage was sourced from Global Forest Cover Change dataset. We averaged woody coverage for each pixel between the years 2000 and 2017. For all rasters, we randomly sampled 100,000 georeferenced points and extracted values. All values have been scaled and min-max normalized (to fall within 0-1) for visual clarity otherwise, unit scales would mask relationships. Dashed line represents a 1:1 slope and the blue line is a cubic spline with 10 knots.



Supplementary Figure 6: Historical outbreaks record survey data modeling with soil nitrogen and phosphorus.



Supplementary Figure 7: Historical nil record survey data modeling with soil nitrogen and phosphorus.



Supplementary Figure 8: The relationship between locust outbreaks and nil observations and mean annual precipitation. This is included as a visual comparison for the soil nitrogen relationship seen in Figure 5

treatment	species	date	Plant C mg/mg	Plant N	Plant P mg/mg	Plant Carb mg/mg	Soil NO3 mg/L	Soil NO4 mg/L
High	<i>Digitaria spp.</i>	2015-12-01	0.419	0.027	0.182	0.108	3.238	4.207
	<i>Enteropogon spp.</i>	2015-11-11	0.425	0.030	0.199	0.128		
	<i>Enteropogon spp.</i>	2015-11-25	0.414	0.028	0.180	0.120		
	<i>Enteropogon spp.</i>	2015-12-01	0.414	0.024	0.163	0.125		
	<i>Cyperus spp.</i>	2015-11-11	0.423	0.030	0.228	0.125		
	<i>Cyperus spp.</i>	2015-11-25	0.415	0.032	0.220	0.131		
	<i>Cyperus spp.</i>	2015-12-01	0.417	0.027	0.227	0.126		
	<i>Plaspladium spp.</i>	2015-12-01	0.400	0.029	0.233	0.120		
	<i>Rytidosperma spp.</i>	2015-11-11	0.424	0.023	0.206	0.125		
	<i>Rytidosperma spp.</i>	2015-11-25	0.422	0.029	0.243	0.112		
	<i>Rytidosperma spp.</i>	2015-12-01	0.419	0.025	0.217	0.117		
Medium	<i>Enteropogon spp.</i>	2015-11-11	0.431	0.042	0.209	0.126	2.831	3.385
	<i>Enteropogon spp.</i>	2015-11-25	0.417	0.026	0.210	0.137		
	<i>Enteropogon spp.</i>	2015-12-01	0.415	0.022	0.146	0.124		
	<i>Cyperus spp.</i>	2015-11-11	0.424	0.038	0.213	0.119		
	<i>Cyperus spp.</i>	2015-11-25	0.420	0.029	0.239	0.127		
	<i>Cyperus spp.</i>	2015-12-01	0.418	0.022	0.188	0.135		
	<i>Plasplodium spp.</i>	2015-12-01	0.414	0.020	0.243	0.094		
	<i>Rytidosperma spp.</i>	2015-11-11	0.422	0.037	0.227	0.106		
	<i>Rytidosperma spp.</i>	2015-11-25	0.420	0.028	0.242	0.115		
	<i>Rytidosperma spp.</i>	2015-12-01	0.422	0.021	0.181	0.116		
None	<i>Enteropogon spp.</i>	2015-11-11	0.432	0.031	0.164	0.145	1.387	0.331
	<i>Enteropogon spp.</i>	2015-11-25	0.414	0.021	0.194	0.115		
	<i>Enteropogon spp.</i>	2015-12-01	0.405	0.023	0.114	0.130		
	<i>Cyperus spp.</i>	2015-11-11	0.425	0.032	0.228	0.144		
	<i>Cyperus spp.</i>	2015-11-25	0.417	0.027	0.232	0.137		
	<i>Cyperus spp.</i>	2015-12-01	0.408	0.026	0.154	0.126		
	<i>Plasplodium spp.</i>	2015-12-01	0.399	0.028	0.183	0.095		
	<i>Austrostipa spp.</i>	2015-12-01	0.416	0.013	0.150	0.104		
	<i>Rytidosperma spp.</i>	2015-11-11	0.420	0.026	0.190	0.124		
	<i>Rytidosperma spp.</i>	2015-11-25	0.417	0.027	0.232	0.133		
	<i>Rytidosperma spp.</i>	2015-12-01	0.418	0.022	0.142	0.121		
	unknown	2015-12-01	0.413	0.031	0.168	0.101		

Supplementary Table 1: Field plot nutrient content for plant species collected from within the treatment plots but outside of the locust cages for three time points during the experiment. Soil nitrogen is also shown per each treatment. Trt = Treatment, C = carbon, N = Nitrogen, P = protein, Carb = Carbohydrates.

plant	None	Medium	High
plant cover	35.5%	35.2%	27.4%
<i>Urochloa panicoides</i>	13.3%	15.0%	47.5%
<i>Enteropogon acicularis</i>	60.1%	65.5%	67.4%
<i>Austrodanthonia caespitosa</i>	15.4%	18.3%	15.2%
<i>Cyperus rotundus</i>	19.3%	17.3%	15.0%
<i>stipa species</i>	0.0%	5.0%	0.0%

Supplementary Table 2: Averaged plant ground cover (%) across all cages per treatment. Ground cover was estimated on November 11th, 2015.

model	deltaBIC	deltaAIC	deltaAICc
macronutrient ~ population + diet_pair + sex + s(initial_mass_g, k=30)	0.01	0.00	0.01
macronutrient ~ population + diet_pair + sex + initial_mass_g	7.28	2.81	4.80
macronutrient ~ population + diet_pair + sex	0.00	0.00	0.00
macronutrient ~ 1	2.56	15.96	12.28

Supplementary Table 3: Model selection criteria via Akaike information criterion (AIC), AIC corrected for small sample size (AICc), and bayesian information criterion. Model formula with the dependent variable on the left side and independent variables on the right side of the equation. For all criteria, the lower the number, more negative in this case, the better fit model.

comparisons	Development Time			Specific Growth Rate		
	estimate	SE	adjusted p-value	estimate	SE	adjusted p-value
14p:28c - 21p:21c	-0.917	0.624	0.465	0.011	0.005	0.164
14p:28c - 35p:7c	-1.709	0.664	0.062	0.010	0.006	0.322
14p:28c - 7p:35c	-2.716	0.603	0.000	0.026	0.005	0.000
21p:21c - 35p:7c	-0.792	0.609	0.567	-0.001	0.005	0.997
21p:21c - 7p:35c	-1.799	0.571	0.014	0.015	0.005	0.020
35p:7c - 7p:35c	-1.007	0.619	0.374	0.016	0.005	0.029

Supplementary Table 4: Posthoc comparisons for diet treatments for *C. terminifera* individual specific growth rate and development time. SE = standard error