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# 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 <sup>2</sup> 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 NO<sup>3</sup> and NO<sup>4</sup> 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 m<sup>2</sup>, 2 = 5-30 m<sup>2</sup>, 3 = 31-80 m<sup>2</sup>, and 4 = > 80 m<sup>2</sup>. Population outbreaks are  
 199 characterized by very high densities of gregarious nymphs (up to 1000 m<sup>2</sup>). 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 km<sup>2</sup> 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 km<sup>2</sup>  
 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 m<sup>2</sup> 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.

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<sup>765</sup> **6 SUPPLEMENTARY**

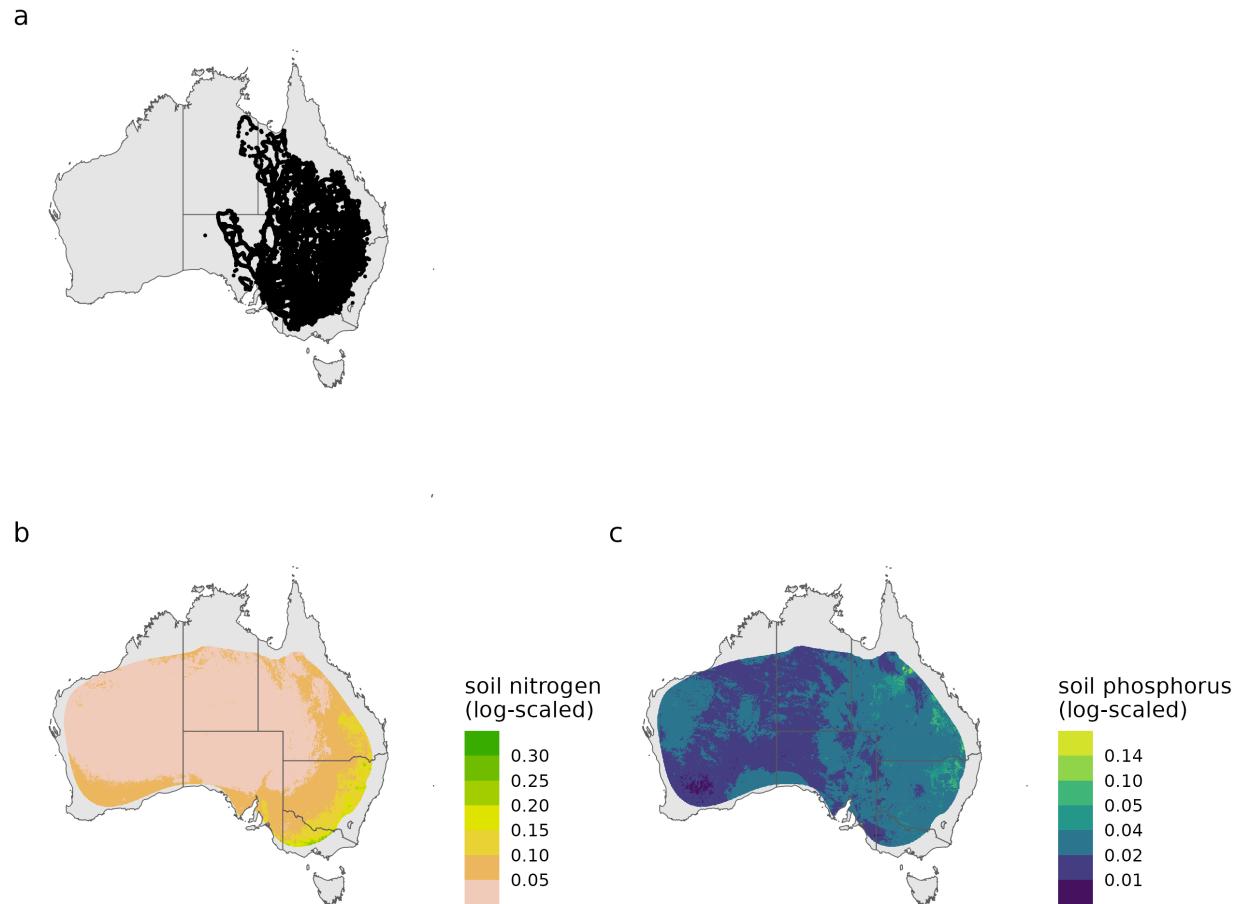
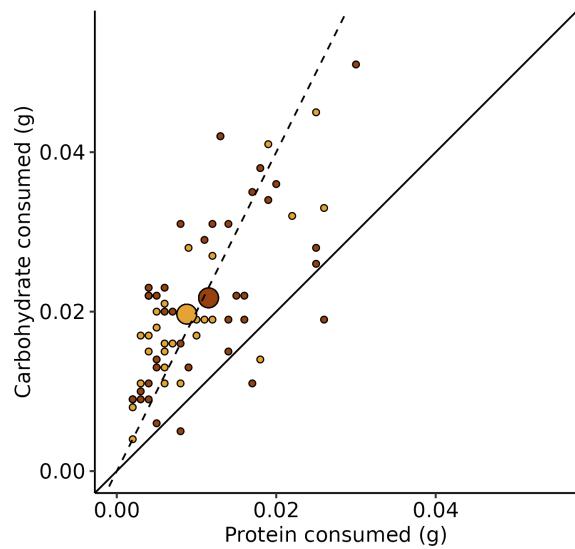


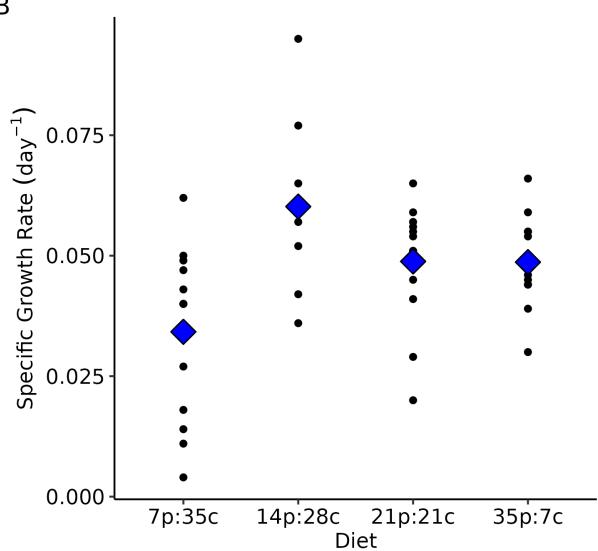
Figure 1: Locust survey data map and soil nutrients throughout the *C. terminifera* distribution. A: APLC survey dataset, B: mean proportion of nitrogen at 0-15 cm deep, C: mean proportion phosphorous at 0-15cm deep.

A

population Guntawang Mendooran



B



C

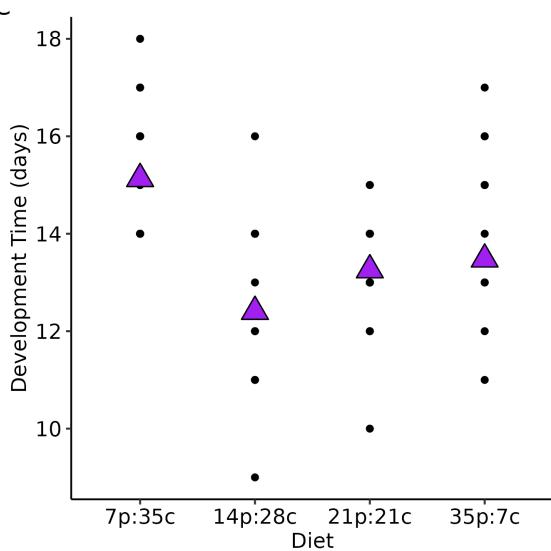


Figure 2: The nutritional preference (A) and physiological performance (B & C) of *C. terminifera* individuals that were collected from two marching bands of 5th instars. Raw data is shown as black dots with modeled estimated marginal means as large diamonds or triangles.

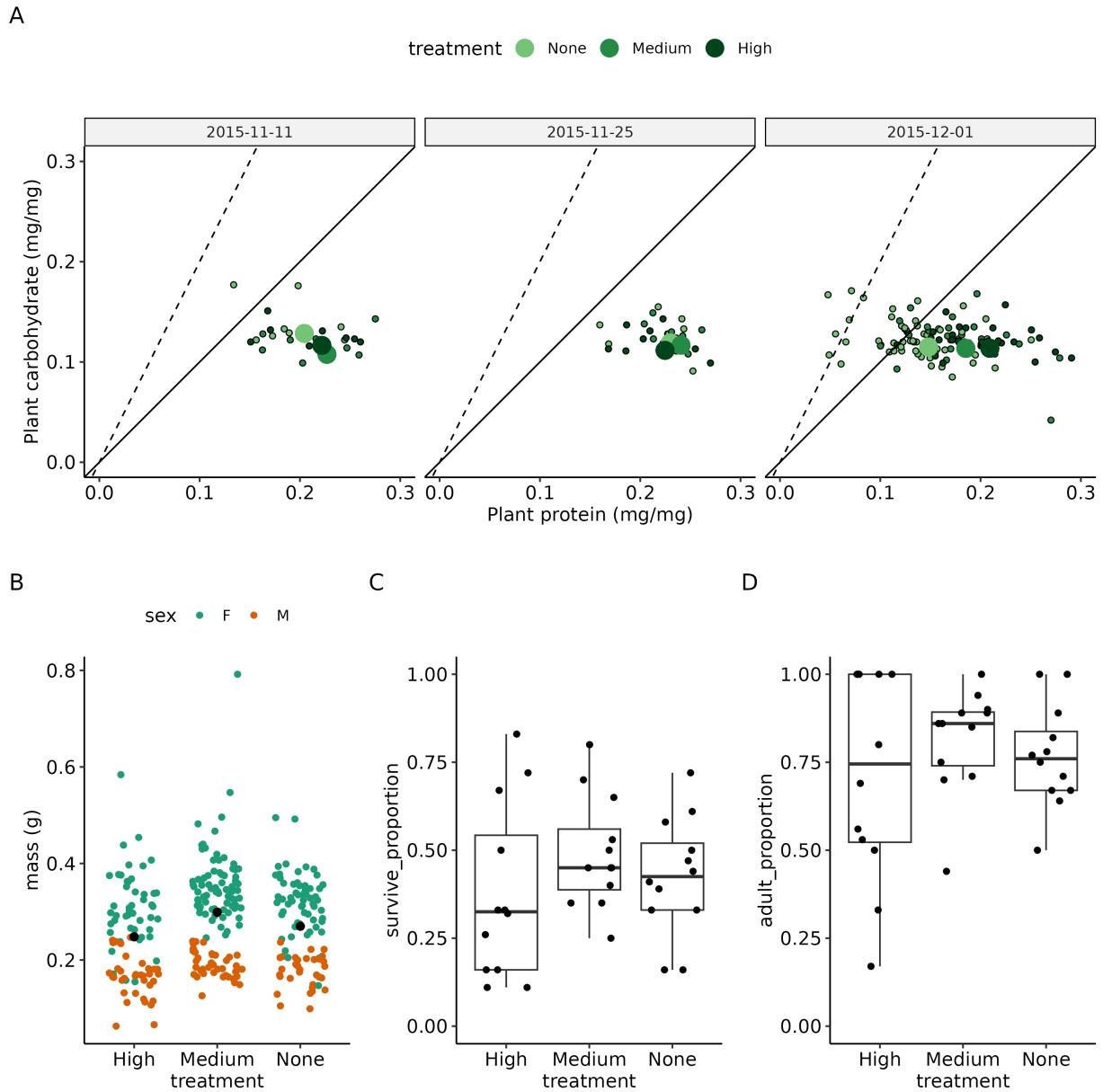


Figure 3: Nitrogen addition field cage experiments with plant nutrient change through time (A) and grasshopper performance metrics (B-C) are shown. Dashed line represents a 1p : 2c ratio, the solid line represents a 1p : 1c ratio. Black dots in B represent overall means whereas boxplots represent the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

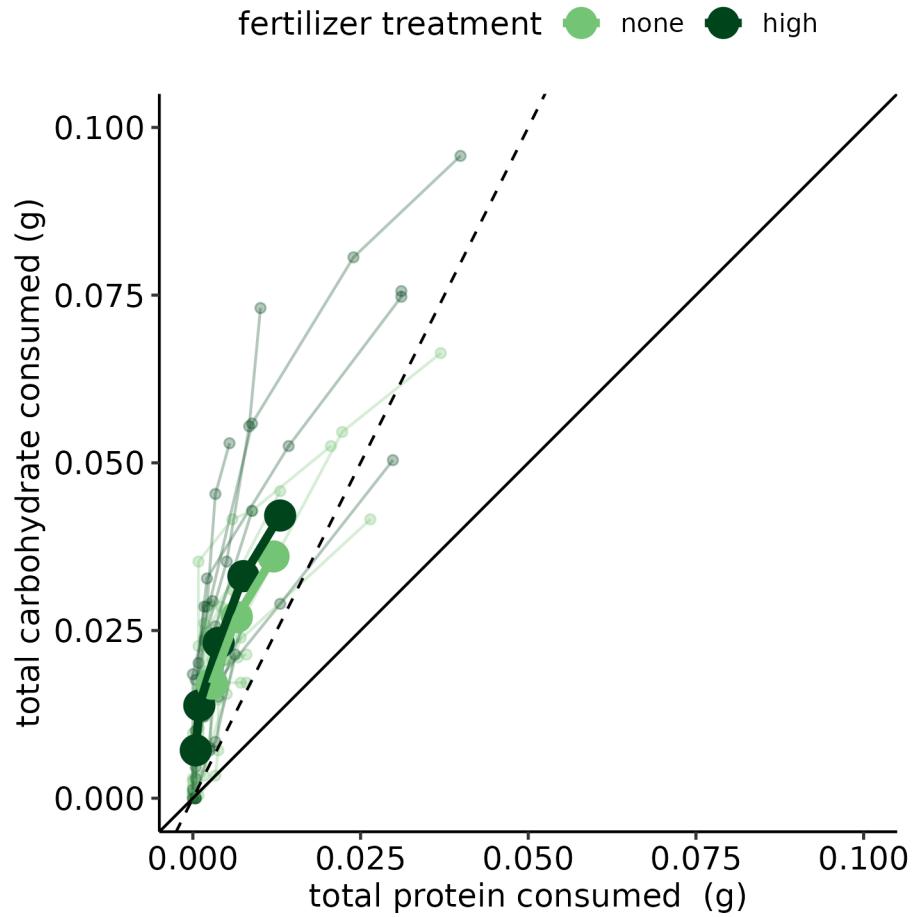
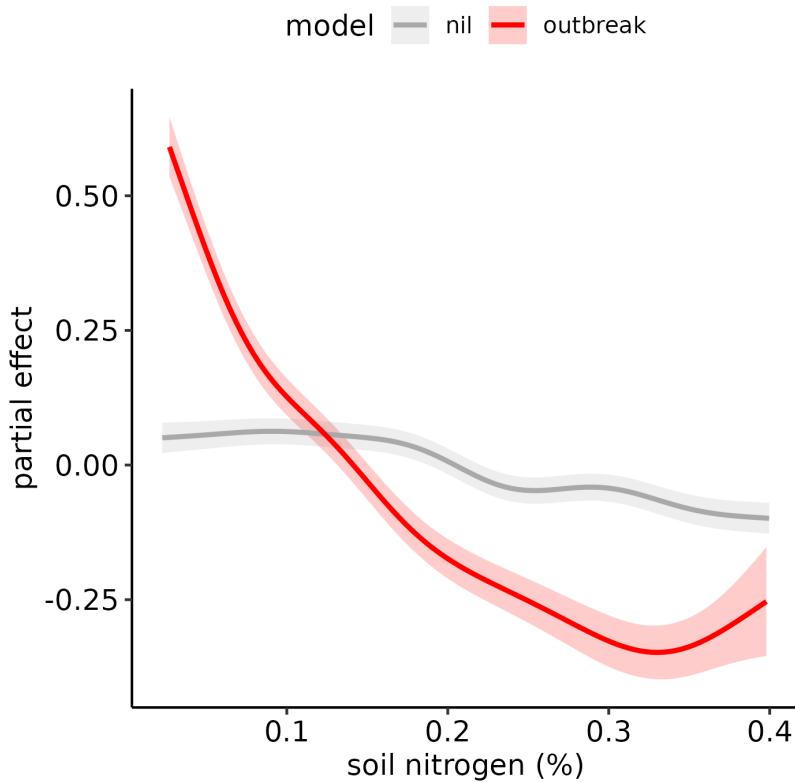


Figure 4: Nutrient imbalance redressing with artificial diet mixing of *C. terminifera* individuals taken from fertilized treatment cages. Colors represent fertilizer treatment. Smaller lines represent raw individual locust intake targets; large lines and points represent estimated marginal means. Points 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

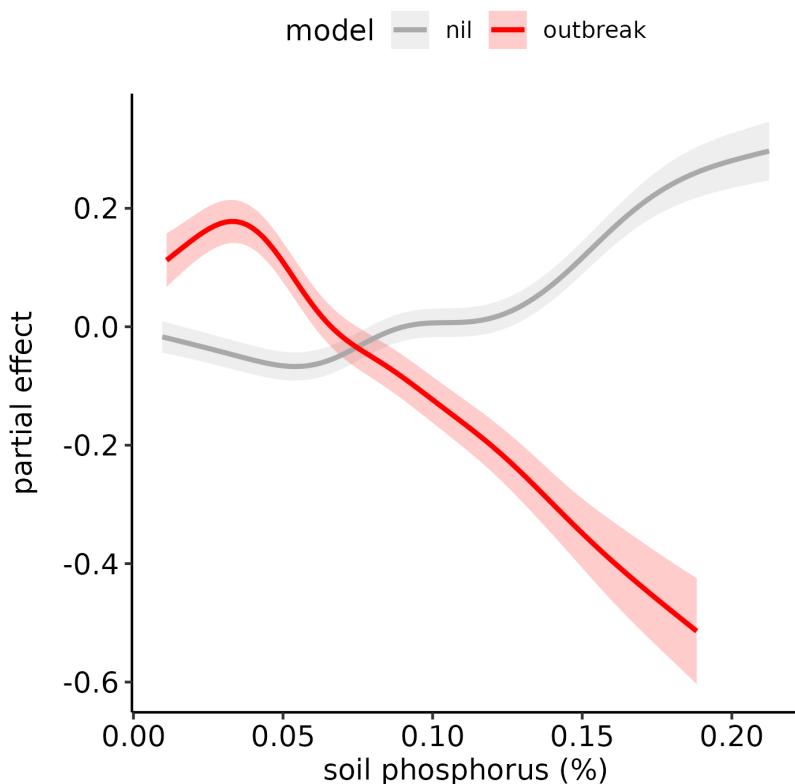
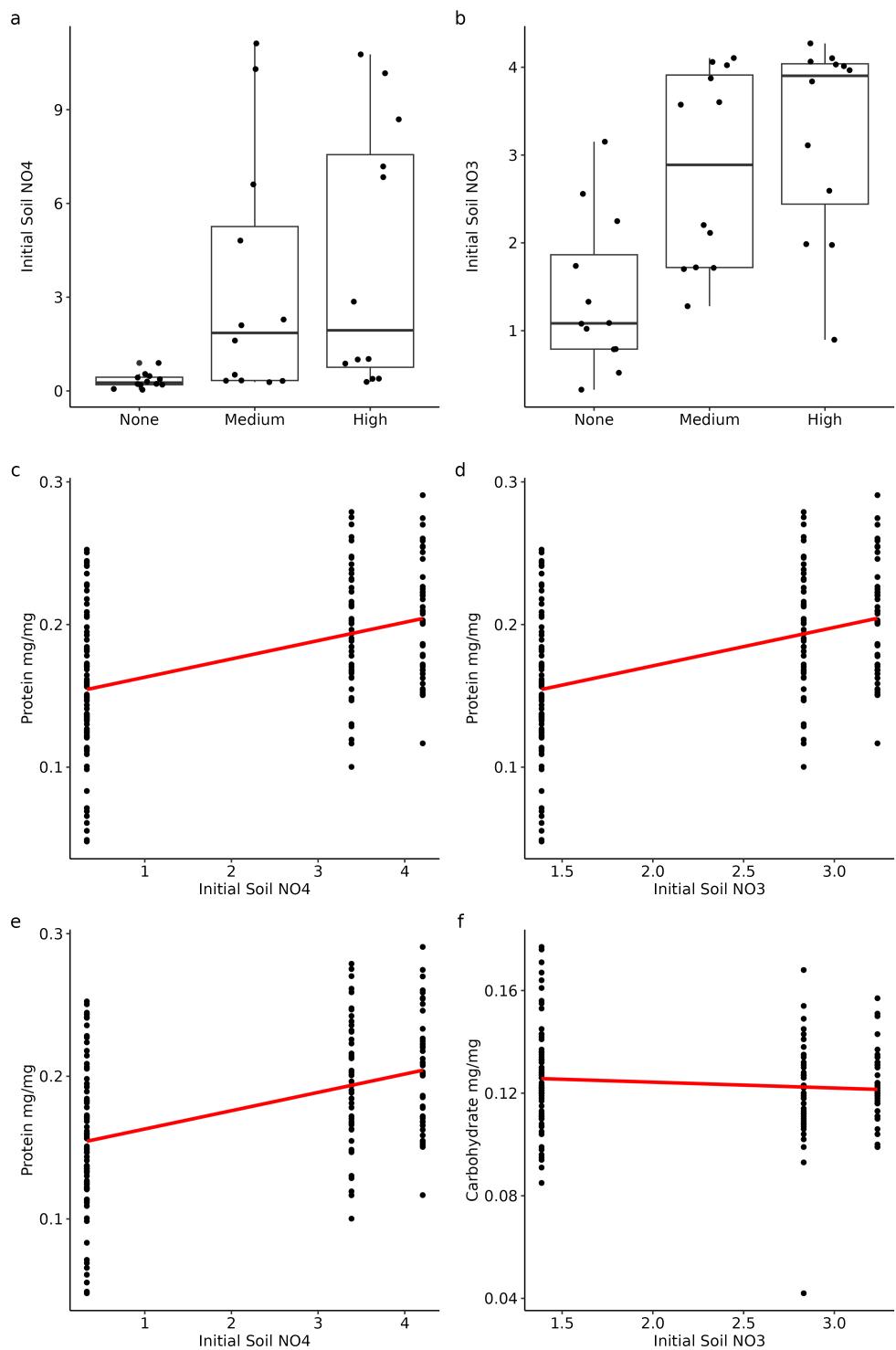
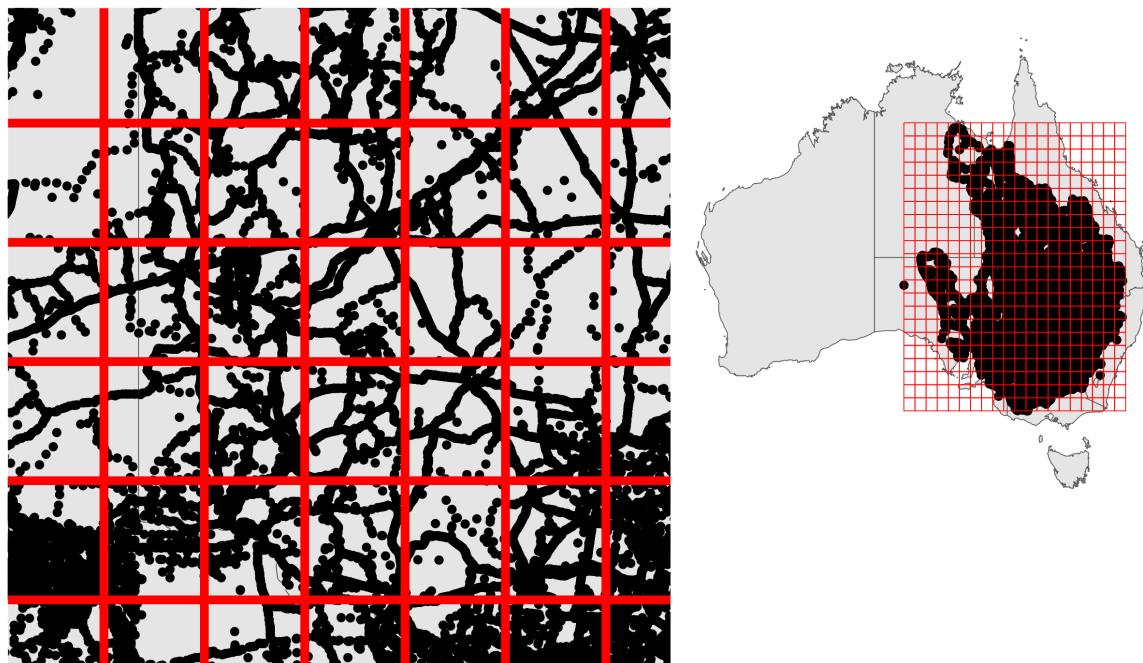


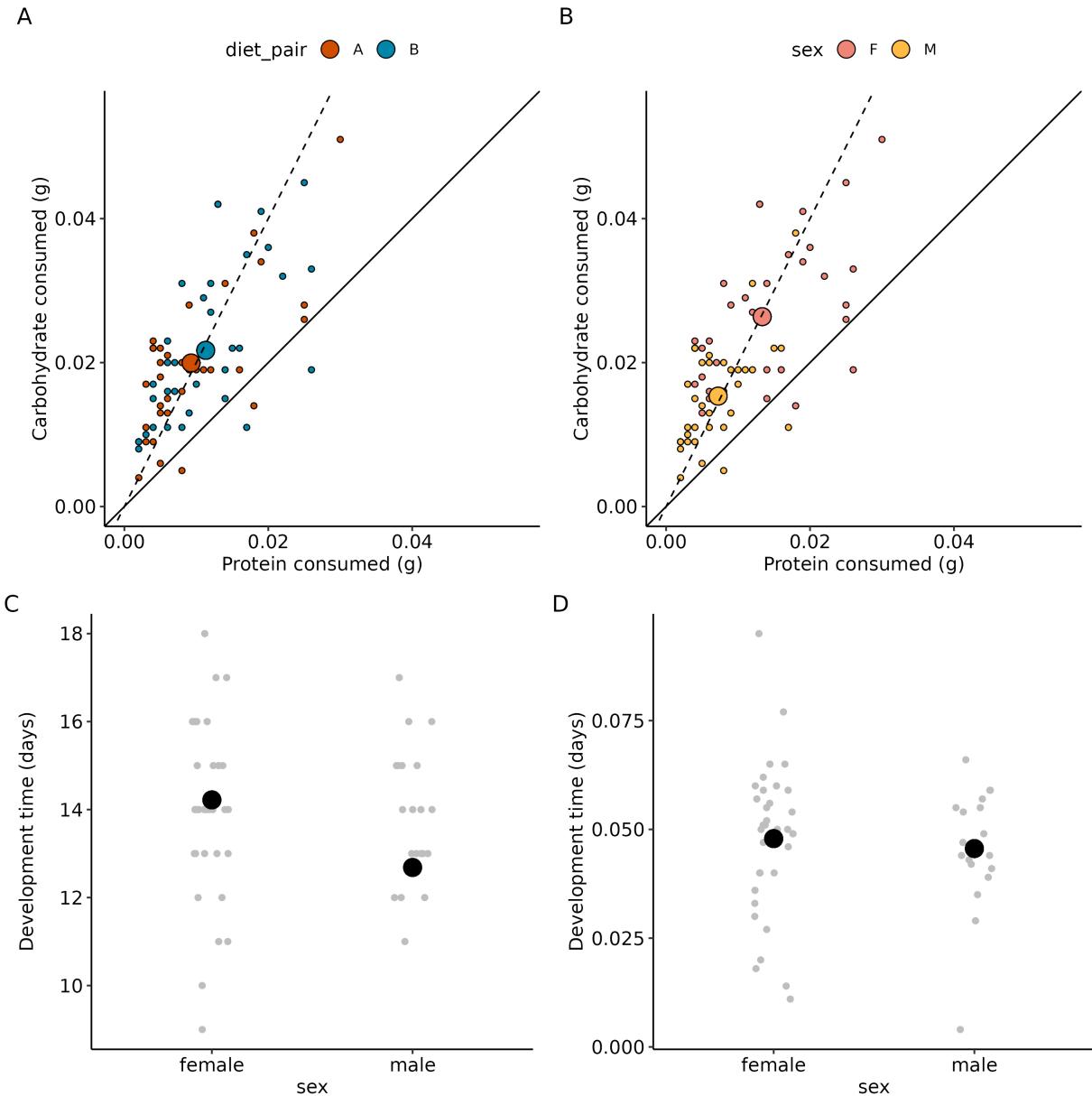
Figure 5: Relationship between outbreaks and nil observations for both soil nitrogen (A) and phosphorus (B). Partial effect is the modeled predictions after accounting for bioregion and spatial autocorrelation.



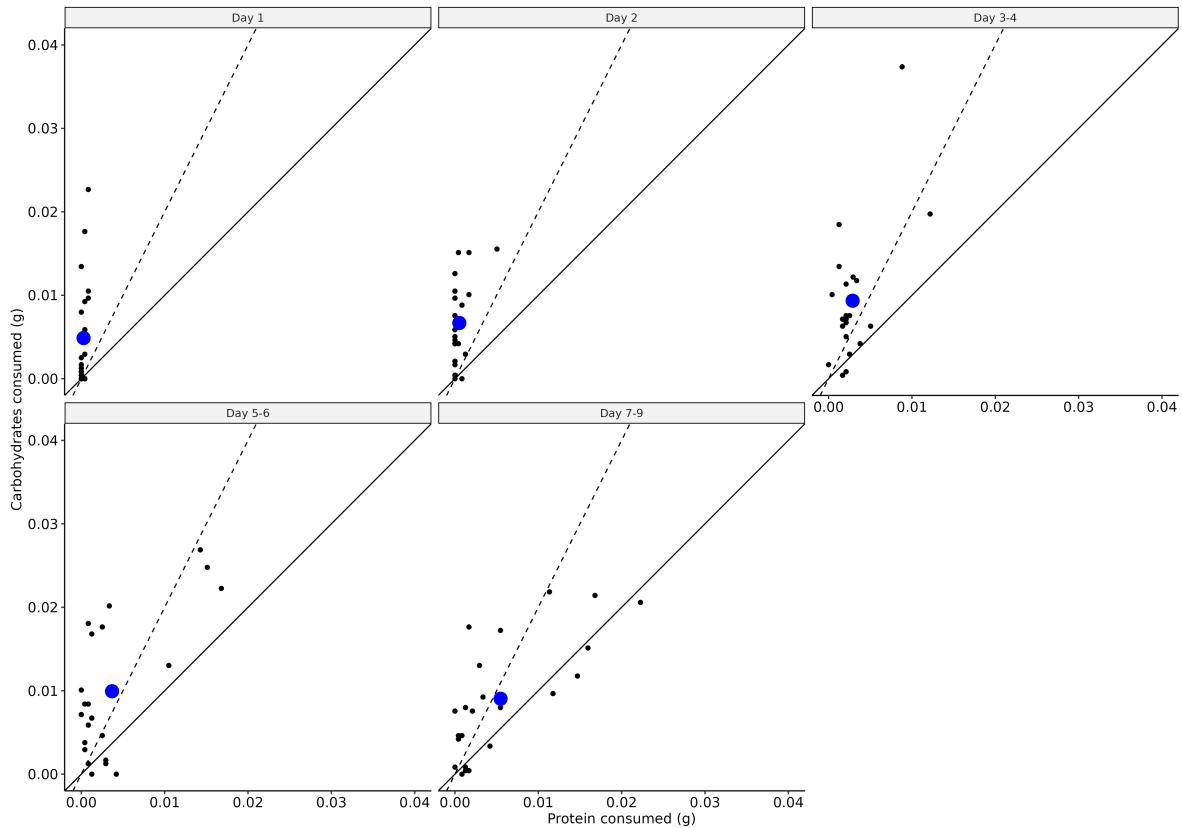
Supplementary Figure 1: Field cage soil nitrogen content by treatment (A & B) and regressed with plant carbohydrates and protein (C-F).



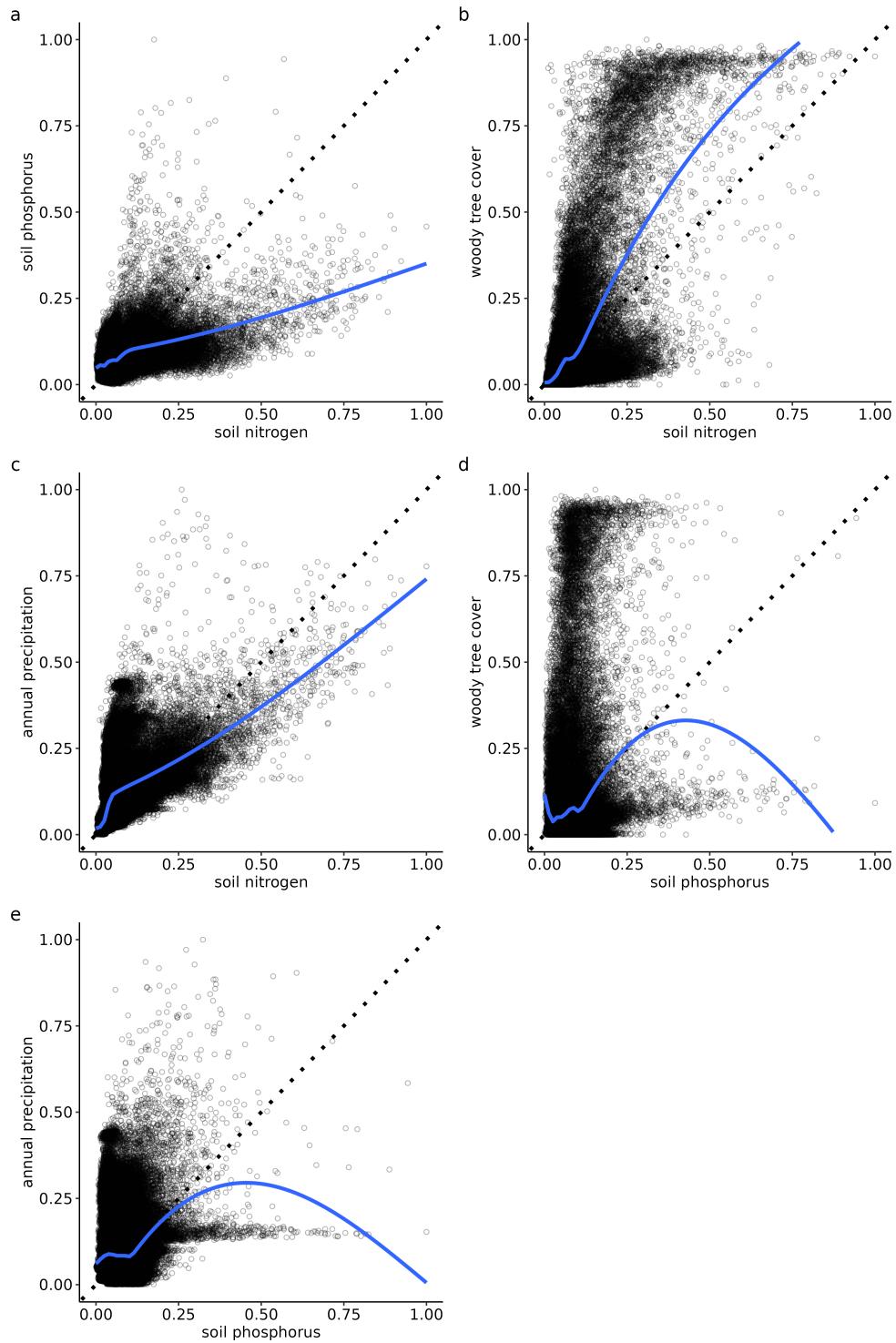
Supplementary Figure 2: Map illustrating the summarization of point observation data into a fishnet grid across eastern Australia. The full extent is shown in the inset map. We summed the number of outbreak, nil, and total observations. The grid in this figure is not at a  $1 \text{ km}^2$  scale for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



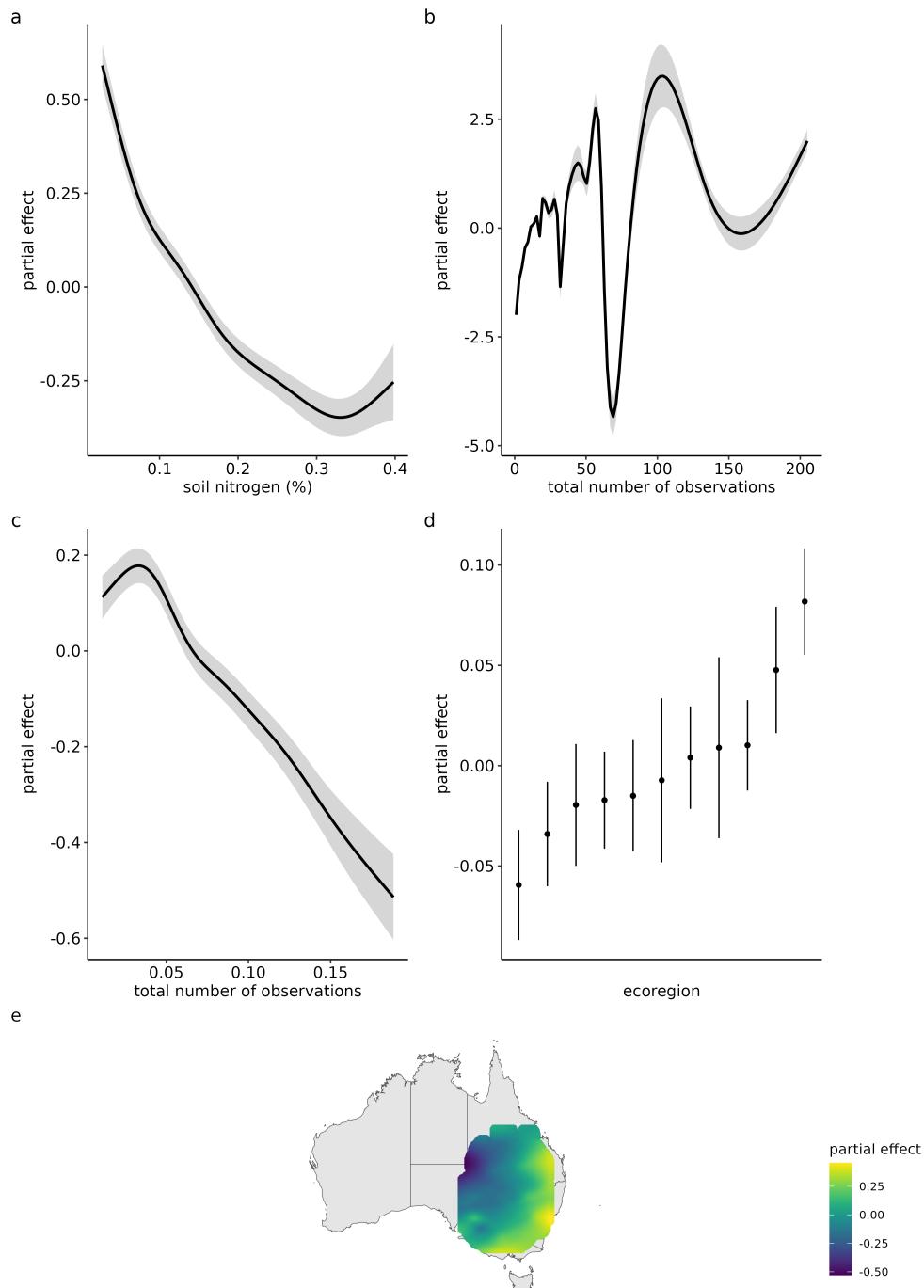
Supplementary Figure 3: Nutrient consumption for outbreaking field populations of *C. terminifera* by diet pair (A) and sex (B) and development time (C) specific growth rate (D) by sex. The P:C ratio did not differ between diet pairing and sex. Females consumed more diet (but kept the same ratio) than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



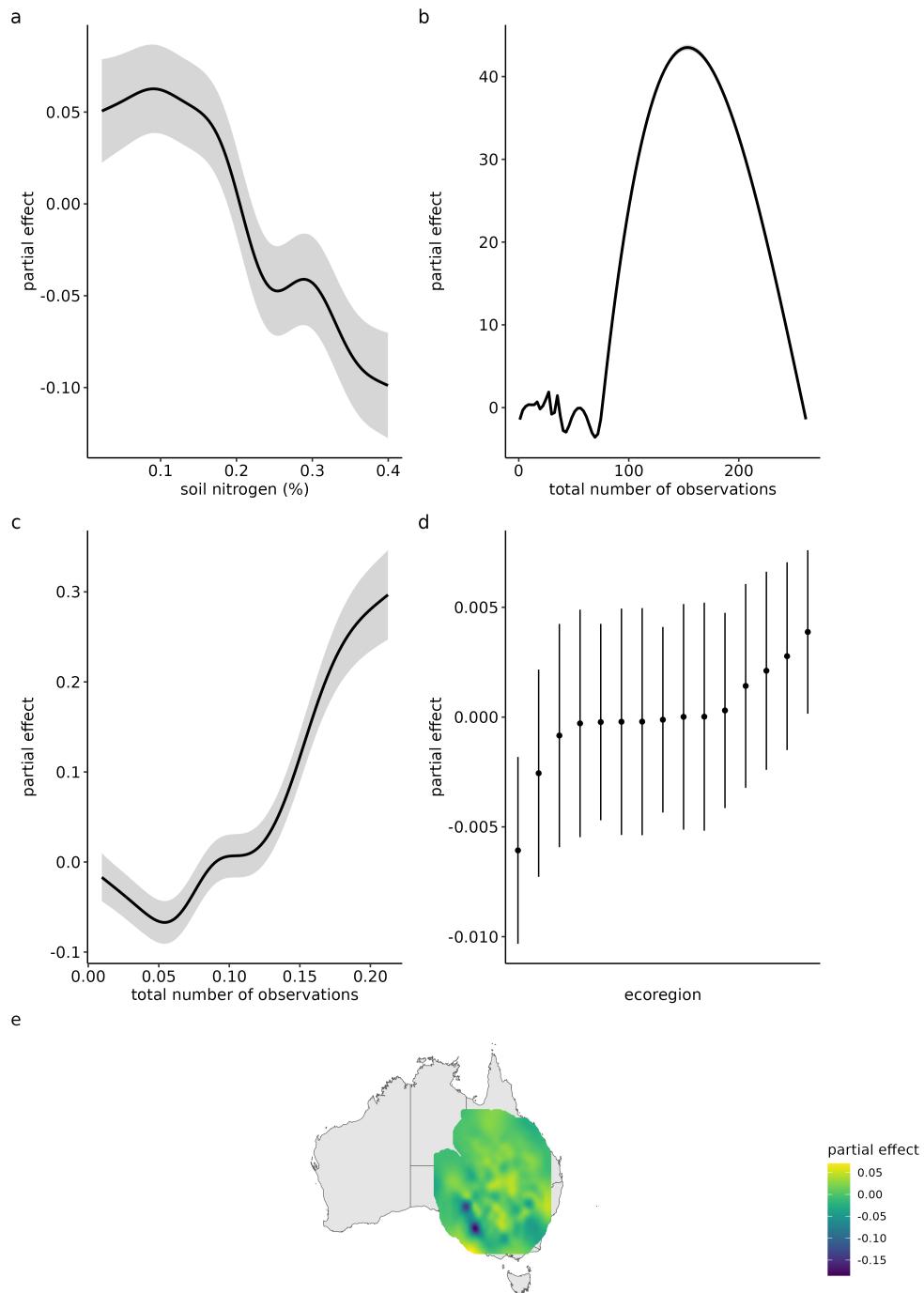
Supplementary Figure 4: Individual time step intake targets for grasshoppers kept in both high nitrogen fertilization and control cages. Blue dots represent estimated marginal means from the model while blacks dots represent raw individual intake targets.



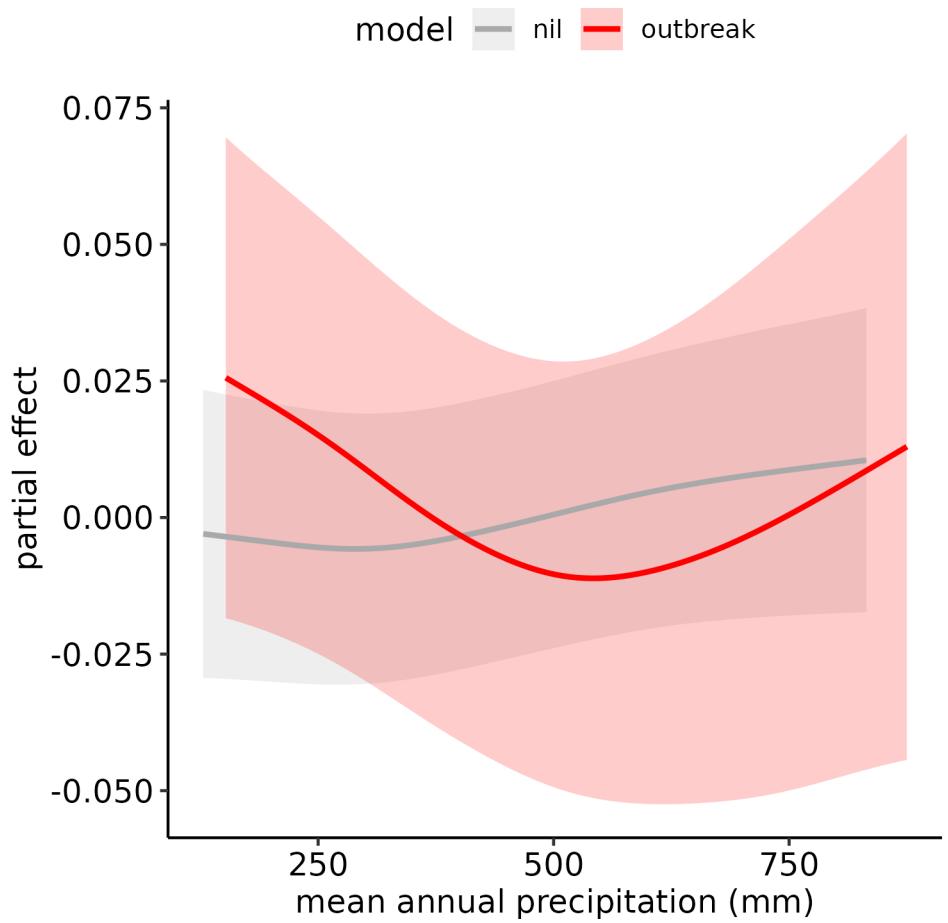
Supplementary Figure 5: Environmental variable correlations between mean annual precipitation, soil nitrogen, soil phosphorus, and woody vegetation pixel coverage. Mean annual precipitation was sourced from WorldClim V1 Bio-clim, soil nitrogen and phosphorus was sourced from Soil and Landscape Grid of 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