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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
individual	cages	20 locusts in each cage
population	cages	36 cages in each fertilization treatment
Landscape	populations	67144 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<sub>3</sub> and NO<sub>4</sub> 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 (# adults/# 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 *C. terminifera* data from 2000 - 2017 (~ 190,000 records) were used in this study. This database contains georeferenced  
 197 points with a categorical ordinal variable 0-4 to represent approximate nymph densities. The value ranges for nymphs  
 198 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 characterized by very  
 199 high densities of gregarious nymphs (up to 1000 m<sup>2</sup>). We focused on nymphs as this life stage cannot fly and can be  
 200 used to assess prior local habitat conditions. While the database extends into the 1980s, we only used data collected  
 201 between 2000-2017 as this period overlapped with the soil grid data which was released in 2015. Since climatic  
 202 conditions and migration patterns are drivers in outbreak occurrence [Lawton et al., 2022, Veran et al., 2015] they  
 203 likely mask the relationship between static environmental variables like soil nutrients. To account for this variability,  
 204 we spatially aggregated the survey dataset to a 1 km<sup>2</sup> grid as can be seen in Supplementary Figure 2. This allowed us  
 205 to model how often locust outbreaks occur in grid cells rather than the actual outbreak. We used a 1 km<sup>2</sup> grid as this  
 206 reflects the estimated maximum dispersal distance from hatching to 5th instar [Hunter et al., 2008]. We counted the  
 207 number of outbreaks (APLC nymph density code 4), the number of nil records (APLC nymph density code 0), and  
 208 total number of survey observations. This resulted in approximately 67,000 grid cells for the final dataset. Overall  
 209 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 are consistent with the specifications of the Global Soil Map project (<http://www.globalsoilmap.net>) [Grundy et al., 2015]. We extracted this data from Google Earth Engine [Gorelick et al., 2017]. In this data set both phosphorus and nitrogen units are the mass fraction of total nutrient in the soil by weight. We took the average of nitrogen and phosphorus of the top two depths (0 cm – 5 cm and 5 cm and 15 cm) as these are most relevant to nutrient content of grasses and forbs. Then, for each APLC survey grid we calculated the mean mass fraction of nitrogen and phosphorus in the soil by weight to a 15 cm depth. Spatial distribution of soil nitrogen and phosphorus can be seen in Figure 1 B and Figure 1 C respectively.

## 220 **2.5 Statistics**

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

### 225 **2.5.1 Intake Targets**

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

236 **2.5.3 Field Cage**

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

246 **2.5.4 Historical outbreaks and soil nutrient grid modeling**

247 To relate nymph survey grids to soil nitrogen and phosphorus, we constructed two GAMMs (family: tweedie, link:  
 248 log) predicting the number of outbreaks (APLC Survey Category 4) and nil observations (category 0). Since both  
 249 soil nitrogen and mean annual precipitation are highly correlated (Pearson correlation = 0.93) with both variables  
 250 decreasing going into the arid interior of Australia, we are unable to add precipitation directly to the model as it  
 251 would bias the results. Instead, we built a comparison model with mean annual precipitation between 2000 and 2017  
 252 switched for soil nitrogen. To do this, we calculated the average precipitation between 2000 and 2017 for all survey  
 253 grids using the European Centre for Medium-Range Weather Forecasts' ERA5 reanalysis dataset [Muñoz-Sabater  
 254 et al., 2021]. This allowed us to visually compare the effect differences of soil nitrogen and mean annual precipitation  
 255 on locust outbreaks. In other words, if soil nitrogen and mean annual precipitation were so tightly correlated that  
 256 the effects are indistinguishable, the modeled results should look very similar. The soil models had the following  
 257 independent variables: soil nitrogen, phosphorus, latitude / longitude, bioregion, and the number of observations  
 258 within each grid. For the precipitation model, all variables were the same except mean annual precipitation replaced  
 259 soil nitrogen and phosphorus. The inclusion of bioregions as a random effect allowed us to account for variation due  
 260 to vegetation community and soil characteristics. The inclusion of latitude and longitude allowed us to account for  
 261 spatial autocorrelation [Clayton et al., 1993]. Lastly, the inclusion of the total number of observations allowed us to  
 262 account for sampling intensity biases.

263 **3 RESULTS**

264 **3.1 Field population**

265 **3.1.1 Choice experiment (nutritional target)**

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

271 **3.1.2 No choice experiment (performance curves)**

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

276 **3.2 Field Cage**

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

285 **3.3 Locust outbreaks**

286 *C. terminifera* outbreaks were negatively associated with soil nitrogen, which supports the hypothesis that nitrogen  
 287 (in excess) acts as a limiting factor for population upsurges (Table 7, Figure 5 A). *C. terminiferas* had a nonlinear  
 288 relationship with soil phosphorus with outbreaks occurring more often in areas with approximately 4% soil phosphorus

and were strongly negatively associated with increasing phosphorus afterwards (Figure 5 B). For both nutrients, the absence models had a very weak relationship with soil nutrient in comparison to the outbreak models, demonstrating little model bias due to APLC survey protocol. There were significant nonlinear relationships between coordinates and the total number of observations in all models (Supplementary Figure 6; Supplementary Figure 7). The relationship between locust outbreaks and mean annual precipitation was very different from the relationship with soil nitrogen (Figure 5, Supplementary Figure 8). Soil nitrogen and phosphorus show weak positive correlations with woody vegetation cover, while mean annual precipitation exhibits high variation in its relationship with soil nitrogen and weak correlation with soil phosphorus (Supplementary Figure 5). Thus, the relationship between soil nitrogen and locust outbreaks cannot be fully explained by differences in woody vegetation.

## 4 DISCUSSION

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

### 4.1 Field populations

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

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

Importantly, all field cage plants were protein biased (roughly 1p : 1c to 2p : 1c) as compared to the desired locust intake target of 1p : 2c. When locusts were subsampled from the field cages mid-experiment and given the opportunity to select carbohydrate or protein diets, they selected extremely carbohydrate-biased diets for more than a week. This behavior indicated that locusts in the small field cages were highly carbohydrate-limited, driving them to overeat carbohydrates to redress the imbalance. Interestingly, multiple studies have shown that the Australian nutritional landscape is often too protein-biased relative to what the *C. terminifera* prefers [Lawton et al., 2020, 2021]. Regardless, populations are still persistent and outbreaks can occur at lower frequencies in these areas [Deveson, 2013, Key, 1945]. How this species can achieve the optimal balance of nutrients within an unfavorable nutritional environment merits further investigation, but may include post-ingestive regulation and/or large-range foraging. Migratory locusts (*Locusta migratoria*) can choose microclimates that favor higher efficiency of carbohydrate or protein absorption depending on their host plant and nutritional status [Clissold et al., 2013]. For this study, we collected free-living locusts from the same region and a similar environment as where we built the field cages, yet those confined to field cages selected a 10x decrease in p:c (1p : 20c vs 1p : 2c). This result suggests that free-living locusts are able to persist in high protein regions by foraging over a larger range to seek out pockets of carbohydrate-rich plants and that the limited foraging range of the field cages precluded field-cage locusts from finding sufficient carbohydrates. Similarly, these results suggest that, while *C. terminifera* can persist in low numbers in nitrogen rich regions, those environments are unlikely to support extreme outbreaks due to a limitation of carbohydrate-rich resources. We tested this prediction using historical outbreak and large-scale soil nutrient modeling.

### 4.2 Historical outbreak modeling

This is the first time to our knowledge that terrestrial animal population dynamics have been modeled with nutrients at the continental level, allowing nutrient limitation to be tested at a scale not previously investigated. Locust outbreaks are associated with decreasing soil nitrogen (Figure 5 A), suggesting that nitrogen acts as a limiting factor not due to its deficit [White, 1993] but its excess. Plants growing in high nitrogen environments tend to have high p:c ratios, which force locusts to either undereat carbohydrates (limiting their energy to support growth and migration) or overeat

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

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

#### 368 **4.3 Locusts are more likely to be limited by high nitrogen environments than other grasshoppers**

369 A five-decade review of grasshopper responses to plant nitrogen content showed that grasshoppers not classified as loc-  
 370 custs have a variation of negative, neutral, and positive responses to increasing plant nitrogen [Cease, 2024]. Looking  
 371 just at field surveys, there are more reports of a negative correlation between plant nitrogen and non-locust grasshopper  
 372 abundance (17 reports) relative to neutral (6 reports) or positive (9 reports). This pattern corroborates long-term studies  
 373 showing that dilution of plant nitrogen is correlated with declines of North American grasshopper populations [Welti  
 374 et al., 2020b]. Of the studies that report correlations between individual grasshopper species abundance and plant nitro-  
 375 gen, most are from graminivorous (grass-feeding) species (11 reports), with 7 reports from mixed (grasses and forbs)  
 376 or forb feeders [Cease, 2024]. The abundance of non-locust graminivorous species tended to be more positively corre-  
 377 lated with plant nitrogen, which would support the hypothesis that grass-feeders are more likely to be nitrogen-limited  
 378 because grasses tend to have lower p:c ratios than forbs; although this trend was not significant and grass-feeders  
 379 also regularly showed negative responses to high plant nitrogen. In contrast, there was a consistent negative effect  
 380 of high plant nitrogen on locust species, regardless of whether they were graminivorous or mixed feeders. Because  
 381 mass specific protein consumption is highly correlated with growth rate in both lab and field populations, but carbo-  
 382 hydride consumption is highly influenced by the environment [Talal et al., 2023], it is most likely that locusts have  
 383 similar protein requirements as other non-locust grasshopper species, but have much higher carbohydrate demands,  
 384 potentially to support migration [Raubenheimer and Simpson, 1997, Talal et al., 2021, 2023]. Locusts are able to meet  
 385 this increased demand for carbohydrate, while keeping protein consumption constant, by eating larger amounts of low  
 386 p:c plants found in low nitrogen environments. In summary, these studies suggest that nymphal outbreaks of all locust  
 387 species may be negatively correlated with soil nitrogen across continental scales, but that the correlation between plant  
 388 nitrogen and non-locust grasshoppers may not be significant or consistent through space and time.

#### 389 **4.4 Comparing the relationship between plant macronutrients and herbivore abundance in other taxa**

390 The effect of plant protein and carbohydrate on herbivore populations is predicted to depend on the herbivore's p:c  
 391 intake target (IT) relative to its nutritional landscape (Le Gall et al., 2020). If there are sufficient plants on either side  
 392 of the IT, herbivores can select from between them to achieve their IT. This complementary feeding has been recorded  
 393 for field populations of blue sheep (*Pseudois nayaur*) in the Himalayan Mountains [Aryal et al., 2015], Black Howler  
 394 Monkeys (*Alouatta pigra*) in Yucatán [Bridgeman, 2012], and other primates [Raubenheimer and Rothman, 2013].  
 395 There would be a predicted impact on populations if the nutritional landscape were to become more constricted or  
 396 not overlap with the IT. For example, lab colonies of tobacco hornworms (*Manduca sexta* larvae) have an IT around  
 397 1:1 or sometimes slightly carbohydrate-biased [Wilson et al., 2019a] and their host plants tend to be carbohydrate-  
 398 biased relative to their IT [Wilson et al., 2019b]. However, this does not seem to translate to population level effects,  
 399 potentially due to secondary metabolites affecting growth more strongly than macronutrient balance and/or larvae may

400 be able to compensate by overeating carbohydrates to acquire sufficient protein [Wilson et al., 2019a]. Overeating  
 401 carbohydrates is not as detrimental as overeating protein, at least in the short term, and animals tend to be willing  
 402 to overeat carbohydrates to a greater extent than protein [Cheng et al., 2008, Simpson and Raubenheimer, 2012b].  
 403 Therefore, herbivores facing a nutritional landscape with a p:c generally lower than their IT (i.e., carbohydrate excess)  
 404 may not be as negatively impacted as herbivores facing one higher than their IT (i.e., protein excess). However,  
 405 there are several examples of higher localized densities of herbivores in response to higher plant nitrogen and protein  
 406 contents with thrips [Brown et al., 2002] and spruce budworm (*Choristoneura*) [De Grandpré et al., 2022] being two  
 407 examples. These examples suggest that low p:c diets limit population growth of some herbivores, but more studies  
 408 are needed to determine if this relationship is only localized or if it scales up. It may be that herbivore populations  
 409 with lower numbers are not limited by a nutritional landscape at a large scale because they can differentially disperse  
 410 locally among optimal patches, whereas herbivore populations with extreme numbers (i.e., irruptions) may be more  
 411 limited by nutritionally unfavorable environments across scales.

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

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

#### 433 4.5 Synthesis and Application

434 Acquiring the right amount of nutrients is a critical component for animal growth, reproduction, and population dy-  
 435 namics [Doonan and Slade, 1995, Hansson, 1979, Keith, 1983]. However, in contrast to the conventional hypotheses  
 436 that predict a broad positive linear relationship between herbivorous populations and nitrogen and phosphorus [Hu-  
 437 berty and Denno, 2006, Mattson, 1980, White, 1978, 1993], the story is nuanced and probably most often non-linear.  
 438 For some species, especially those with high energy requirements, the relationship is the opposite (negatively associ-  
 439 ated with nitrogen) like many locust species and the effects can be seen at the continental scale. Land use and Land  
 440 Cover Change (LULCC) impact on nutritional environments has important implications for animal population dynam-  
 441 ics from conservation to pest management. While we did not make an explicit connection between LULCC and locust  
 442 outbreaks in Australia, our results are consistent with previous research showing that LULCC that decreases soil qual-  
 443 ity and creates low nitrogen environments increases physiological performance and outbreaks of locusts (reviewed in  
 444 Le Gall et al. [2019]). Most importantly, we show that this relationship is consistent between scales from the individual  
 445 locust to continental wide outbreaks. As such, proper management of soil nutrients can help keep locust populations  
 446 from reaching outbreak sizes and should be considered across scales, from individual locust behavior to continental  
 447 wide plagues.

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764 **6 SUPPLEMENTARY**

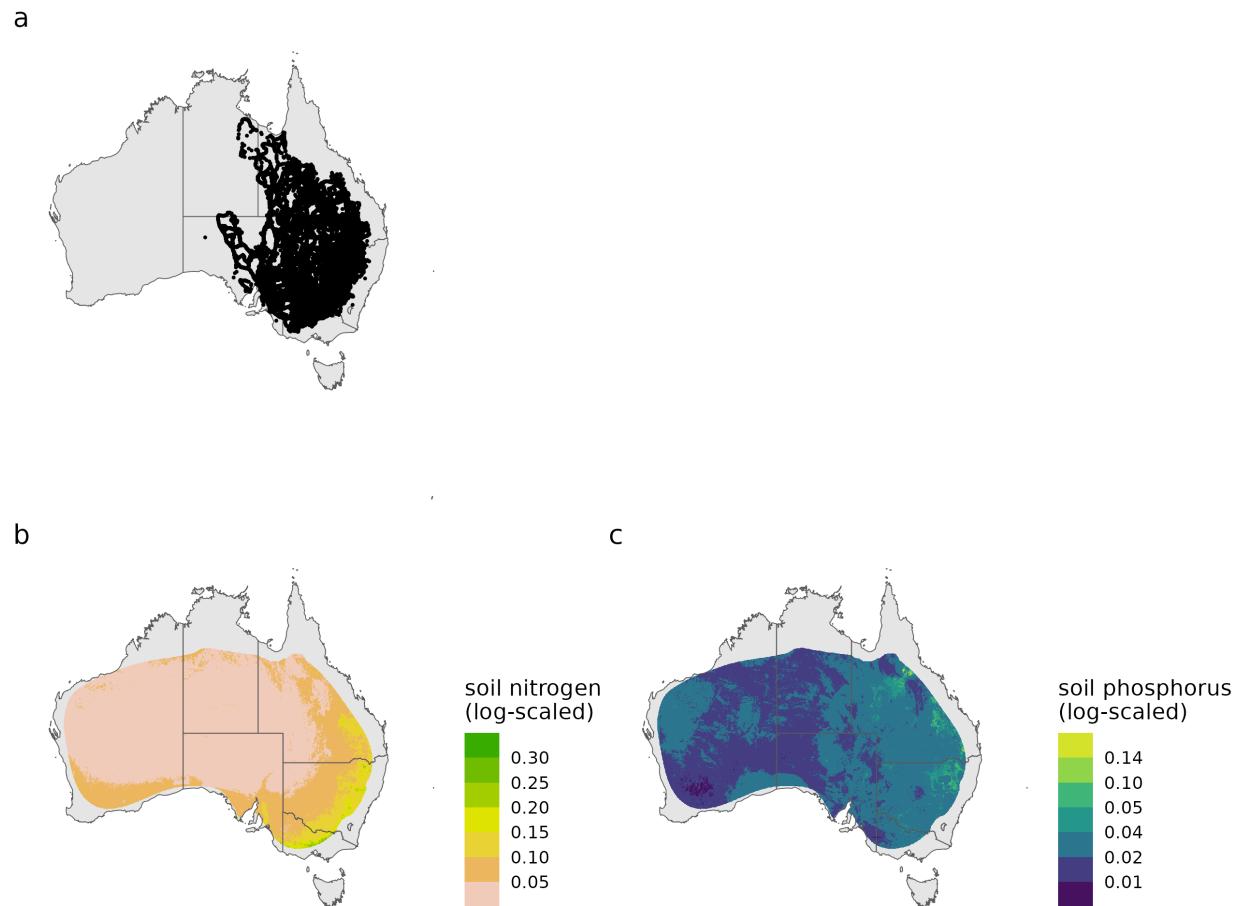
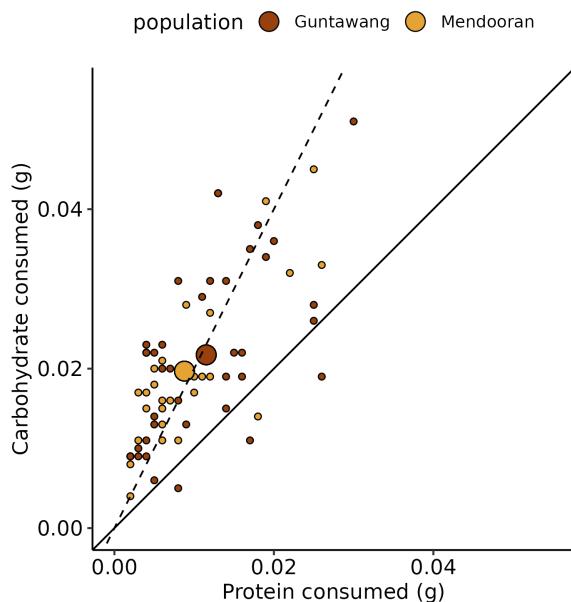


Figure 1: Locust survey data map and soil nutrients throughout the *C. terminifera* distribution. A: APLC survey dataset, B: mean proportion phosphorous at 0-15cm deep, C: mean proportion of nitrogen at 0-15 cm deep.

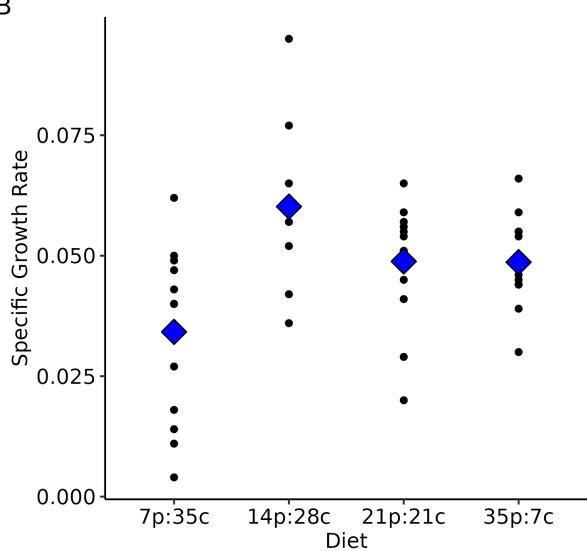
macronutrient	variable	estimate	SE	p-value
carbohydrate	Intercept	0.026	0.002	0.000
	Mendooran	-0.001	0.002	0.483
	diet pair B	0.001	0.002	0.573
	male	-0.011	0.002	0.000
protein	Intercept	0.014	0.001	0.000
	Mendooran	-0.002	0.002	0.122
	diet pair B	0.002	0.002	0.293
	male	-0.006	0.002	0.000

Table 2: Generalized additive model results for macronutrient consumption (carbohydrate and protein) of two out-breaking 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.

A



B



C

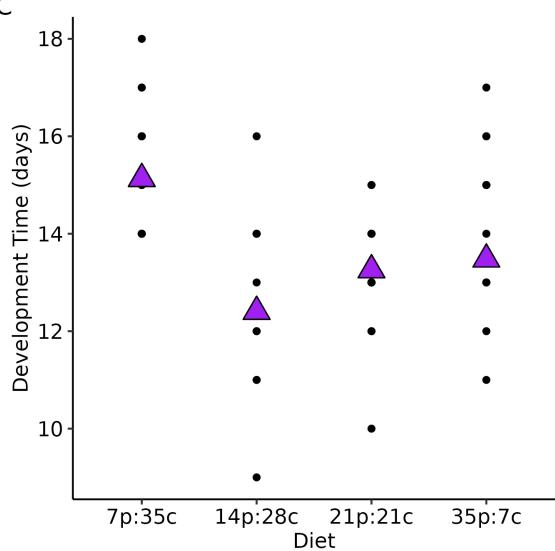


Figure 2: The nutritional preference (A) and physiological performance (B & C) of *C. terminifera* individuals that were collected from two marching bands of 5th instars. Raw data is shown as black dots with modeled estimated marginal means as large diamonds or triangles.

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: *C. 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.

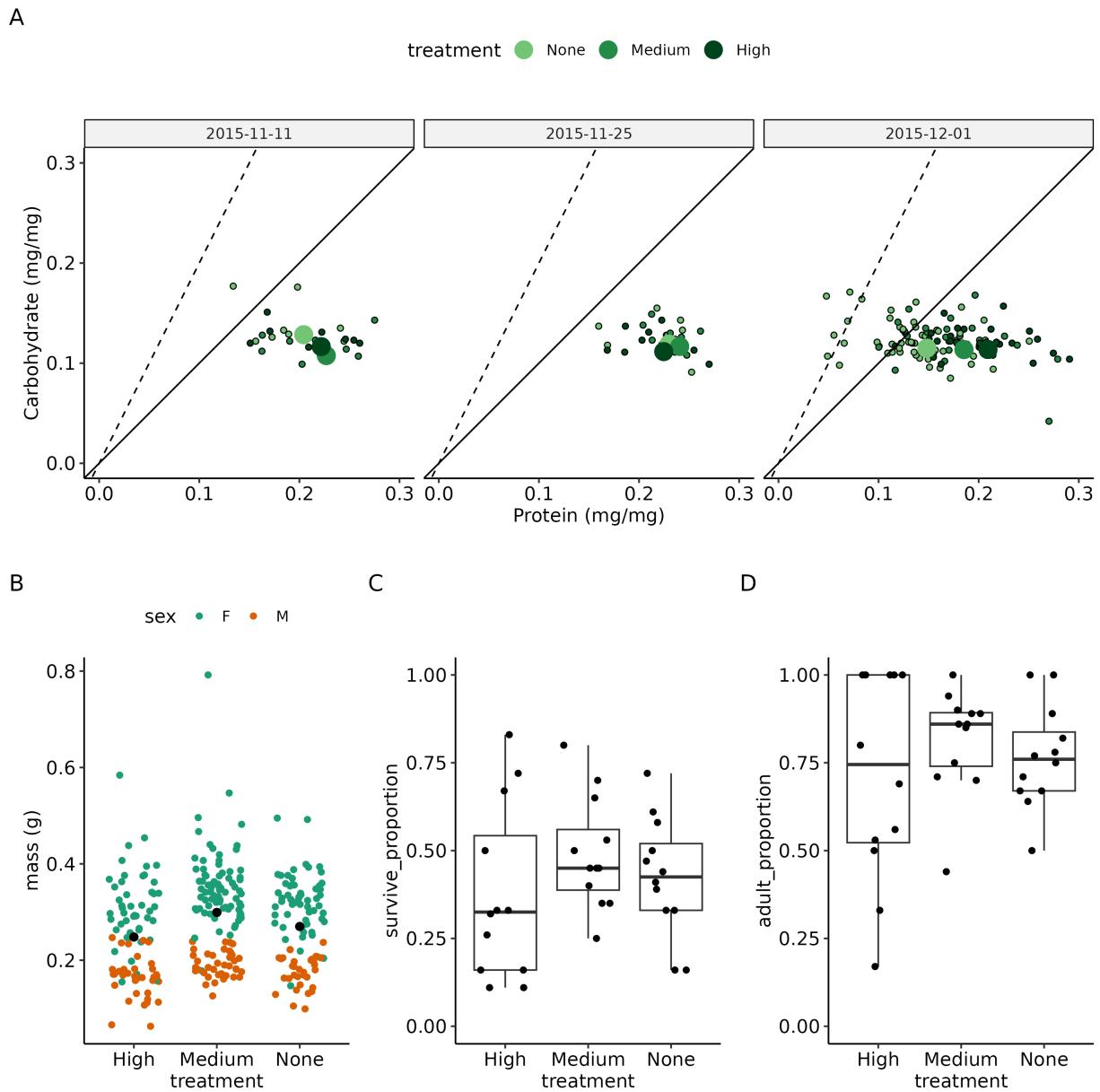


Figure 3: Nitrogen addition field cage experiments with plant nutrient change through time (A-C) and grasshopper performance metrics (D-F) are shown. Dashed line represents a 1p : 2c ratio, the solid line represents a 1p : 1c ratio. Black dots in B represent means.

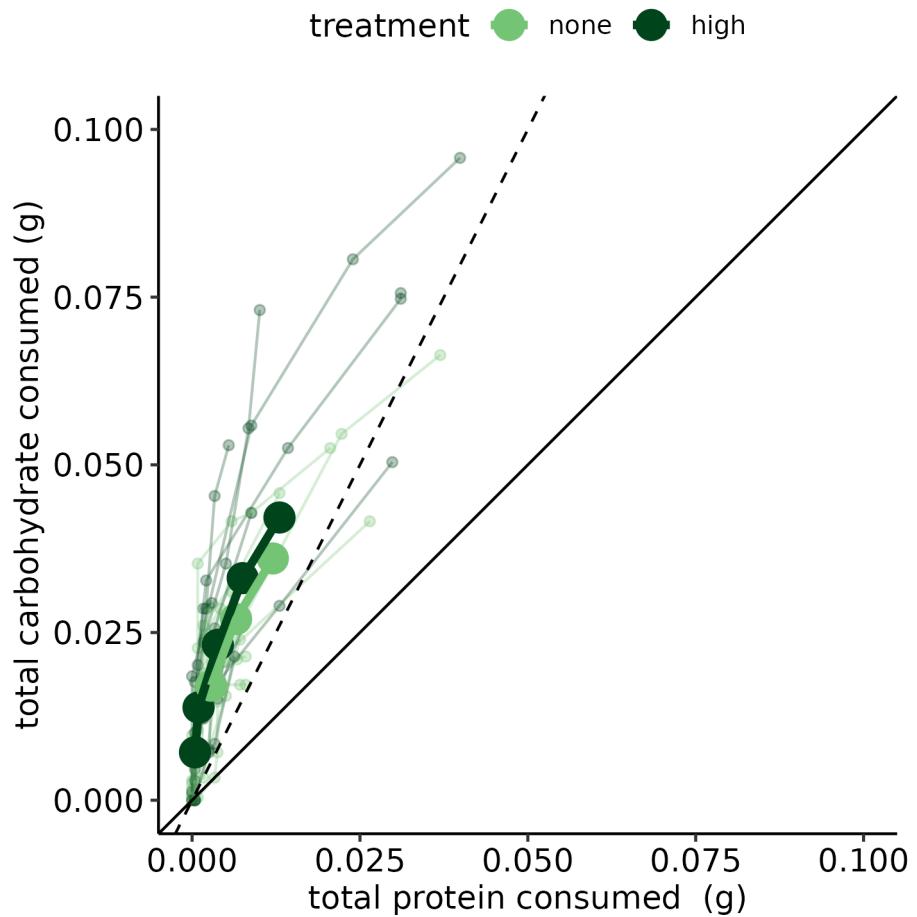


Figure 4: Nutrient imbalance redressing with artificial diet mixing of *C. terminifera* individuals taken from fertilized treatment cages. Colors represent treatment. Smaller lines represent raw individual locust intake targets with large lines and points representing estimated marginal means. Individual time step targets can be seen in 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
	s(plot)			1.643	0.207
	s(cage)			3.442	0.130
protein	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
protein	Intercept	0.002	0.001		0.119
	male	-0.004	0.001		0.009
	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.

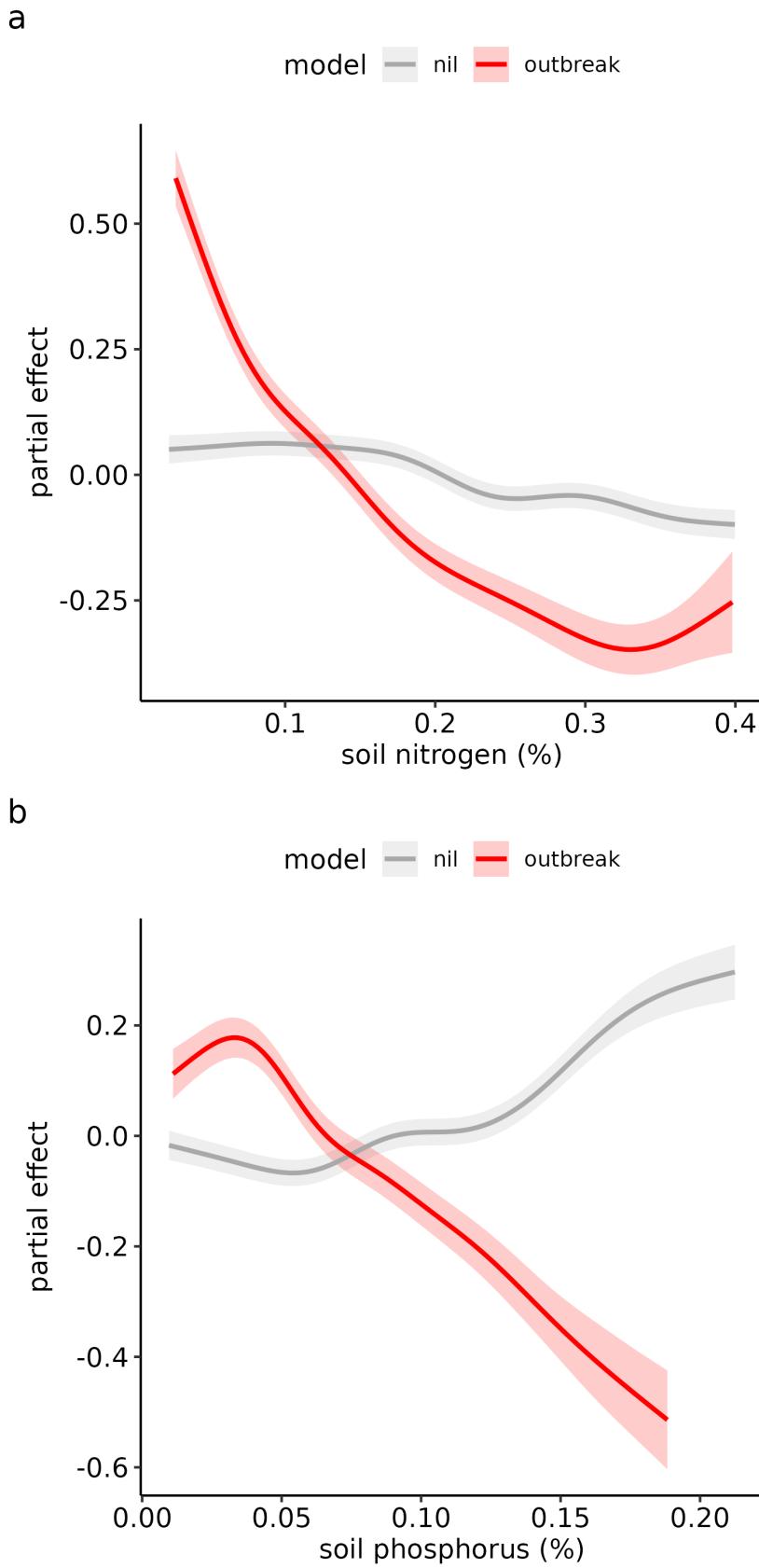
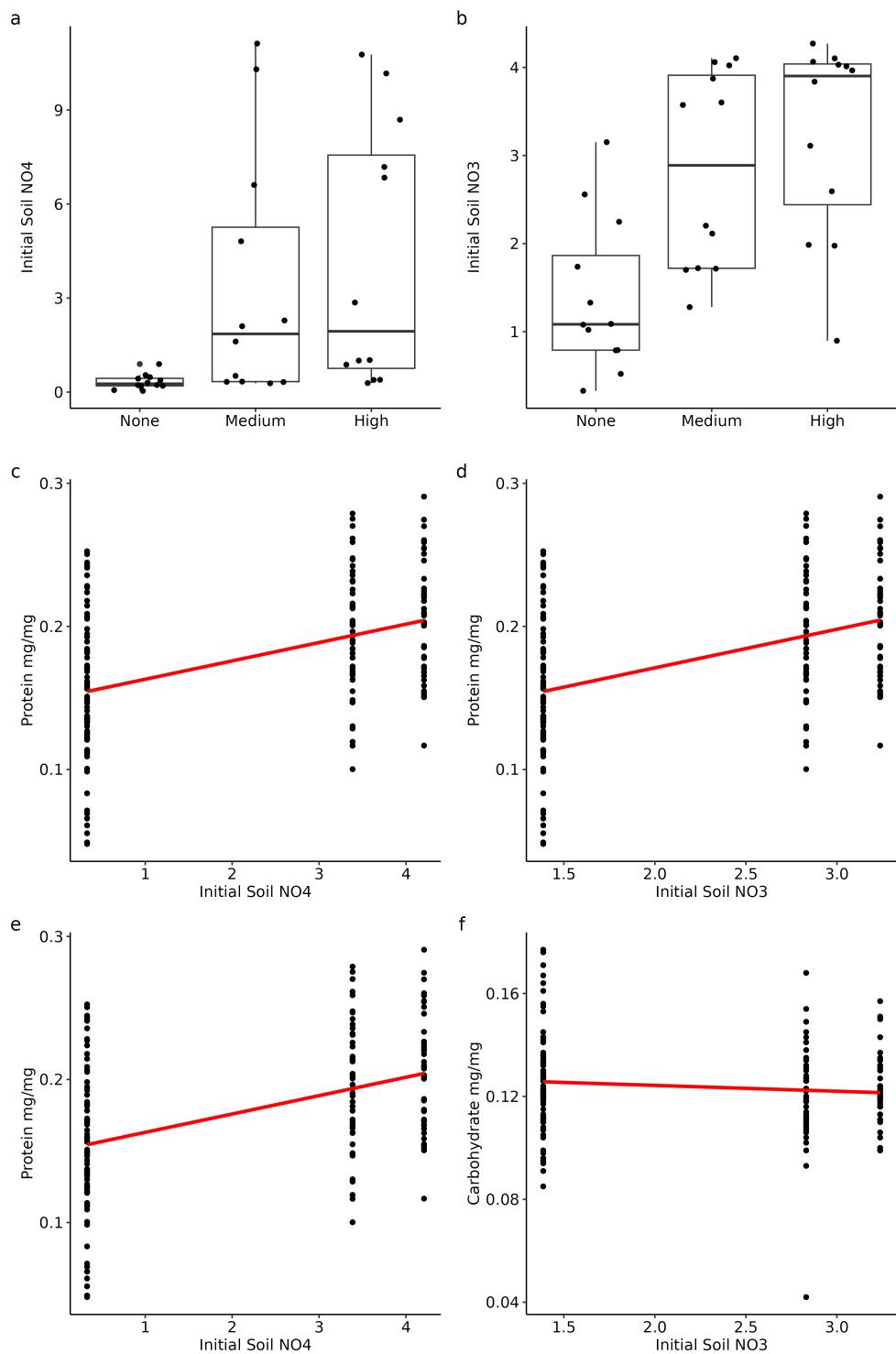


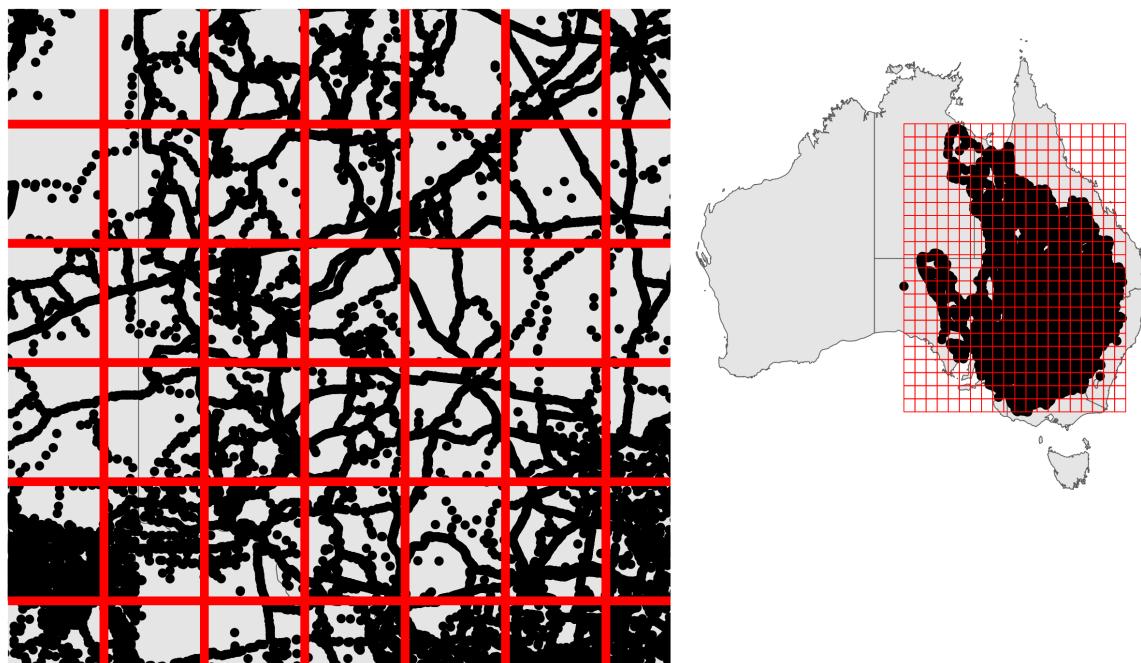
Figure 5: Relationship between outbreaks and nil observations for both soil nitrogen (A) and phosphorus (B). Partial effect is the modeled predictions after accounting for bioregion and spatial autocorrelation.

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

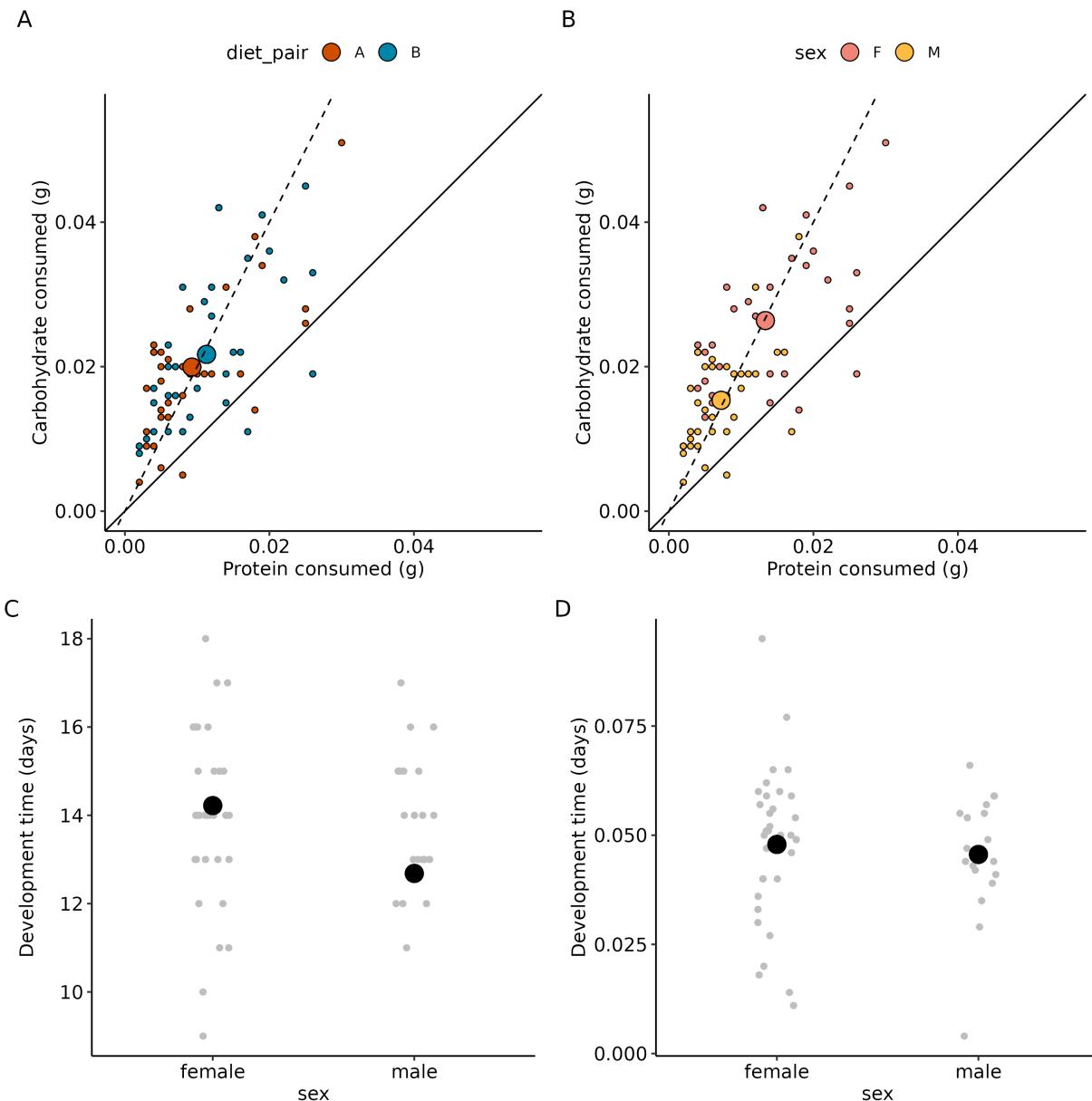
Table 7: Historical locust presence data modeling with soil nitrogen for outbreak, low presence, and no observation records with r-square and deviance explain reported. Family: tweedie, link: log, edf = estimated degrees freedom.



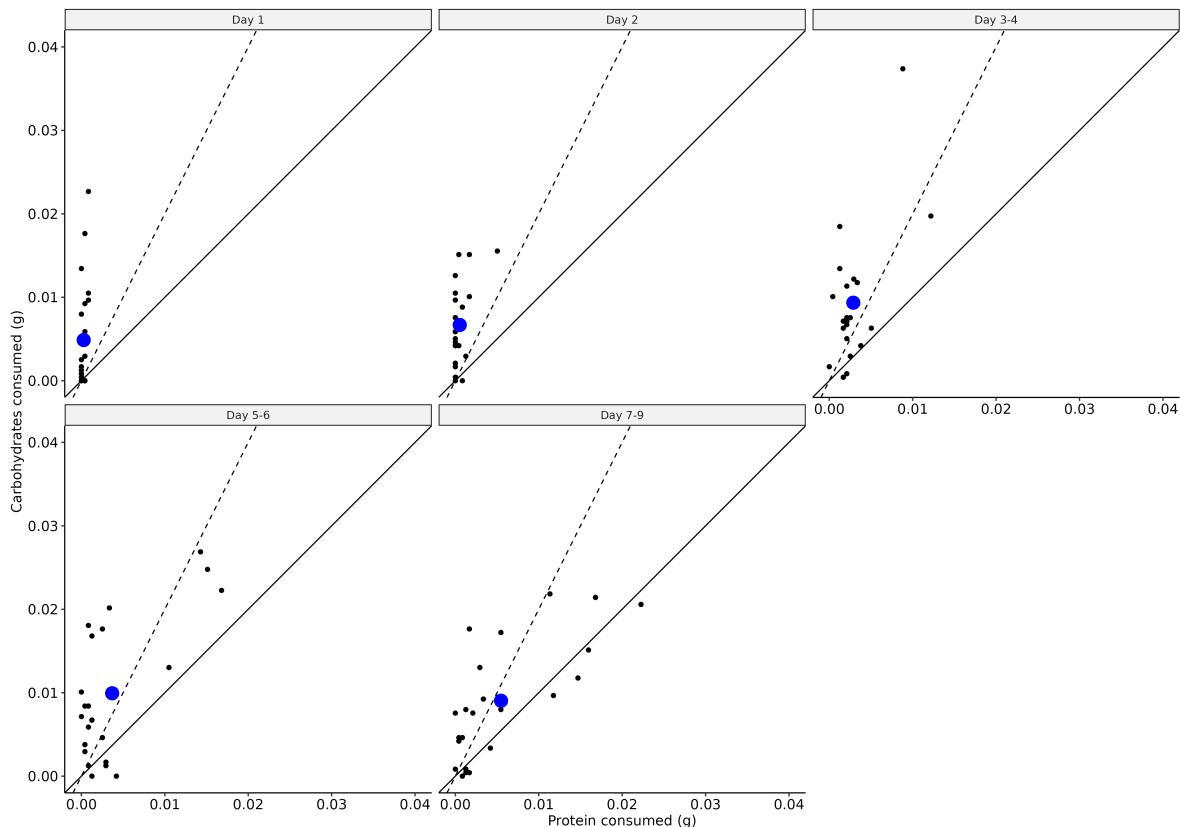
Supplementary Figure 1: Field cage soil nitrogen content by treatment (A & B) and regressed with plant carbohydrates and protein (C-F).



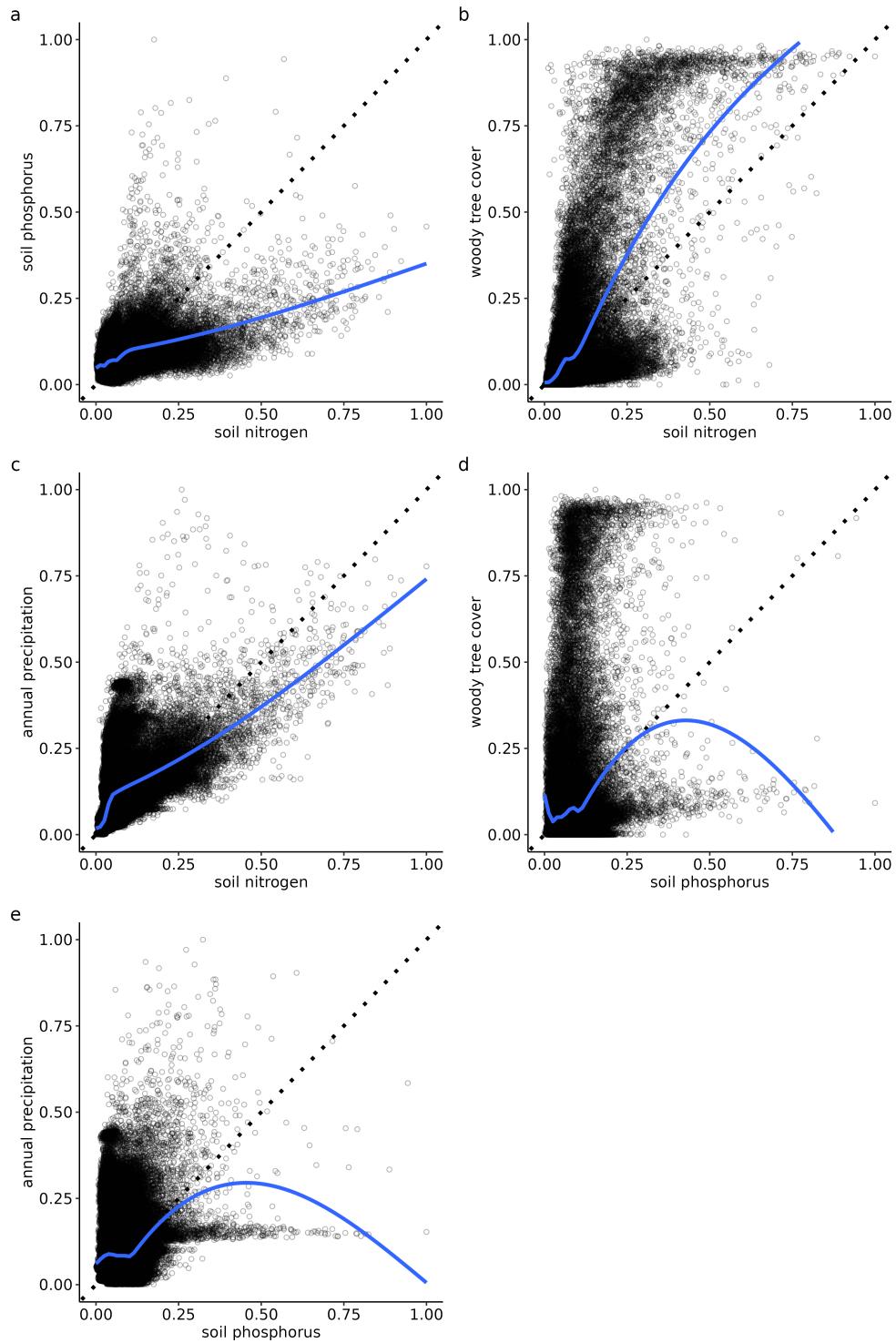
Supplementary Figure 2: Map showing how we summarized point observation data to a fishnet grid throughout eastern Australia. Entire extent can be seen in the inlet map. We summed the number of 4 (outbreak) observations, nil observations (0), and the total observations. Grid not at a 1 km<sup>2</sup> scale in this figure for demonstration purposes as the cells would be too small to see.



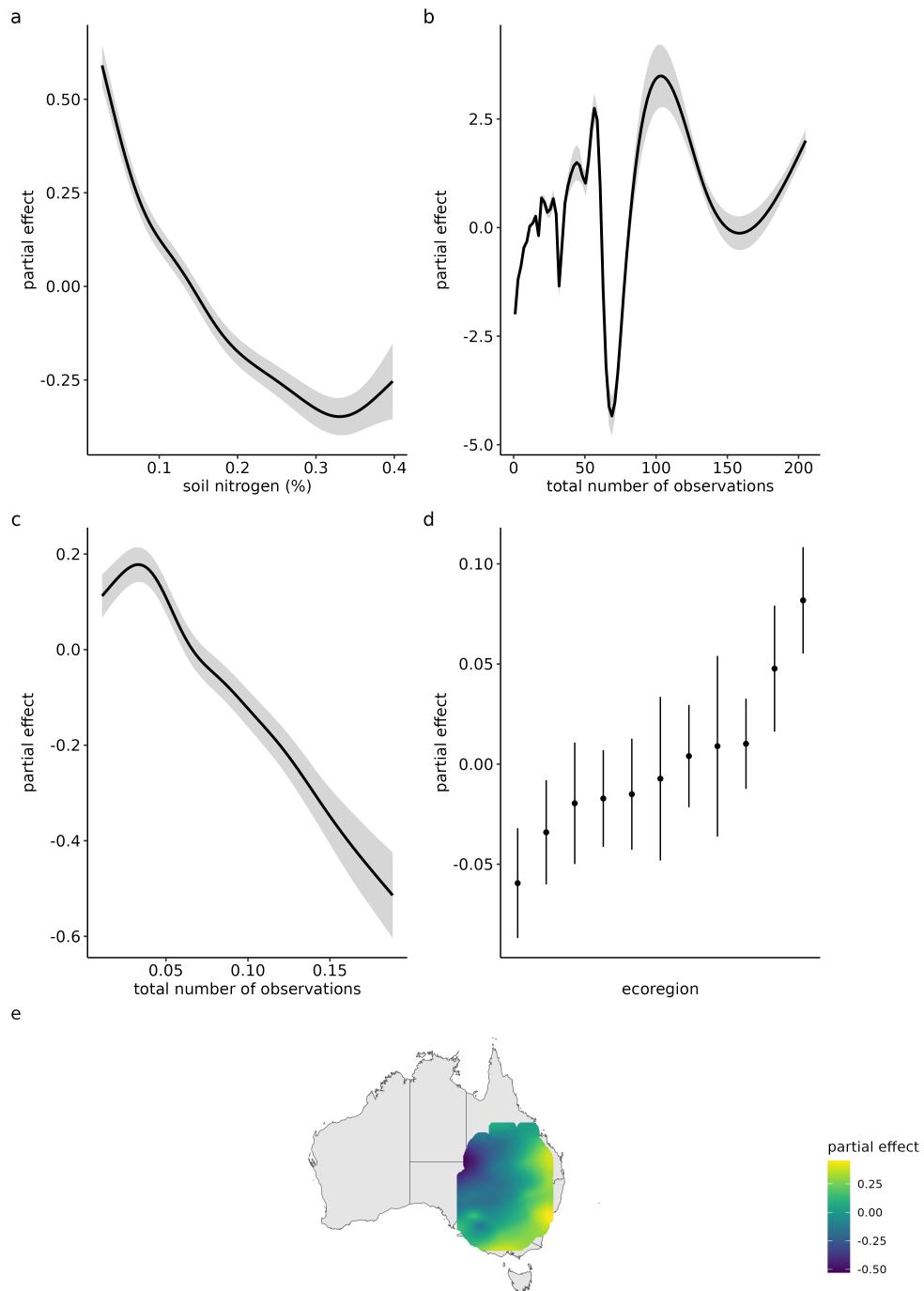
Supplementary Figure 3: Nutrient consumption for outbreaking field populations of *C. terminifera* by diet pair (A) and sex (B) and development time (C) specific growth rate (D) by sex. The P:C ratio did not differ between diet pairing and sex. Females consumed more diet (but kept the same ratio) than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



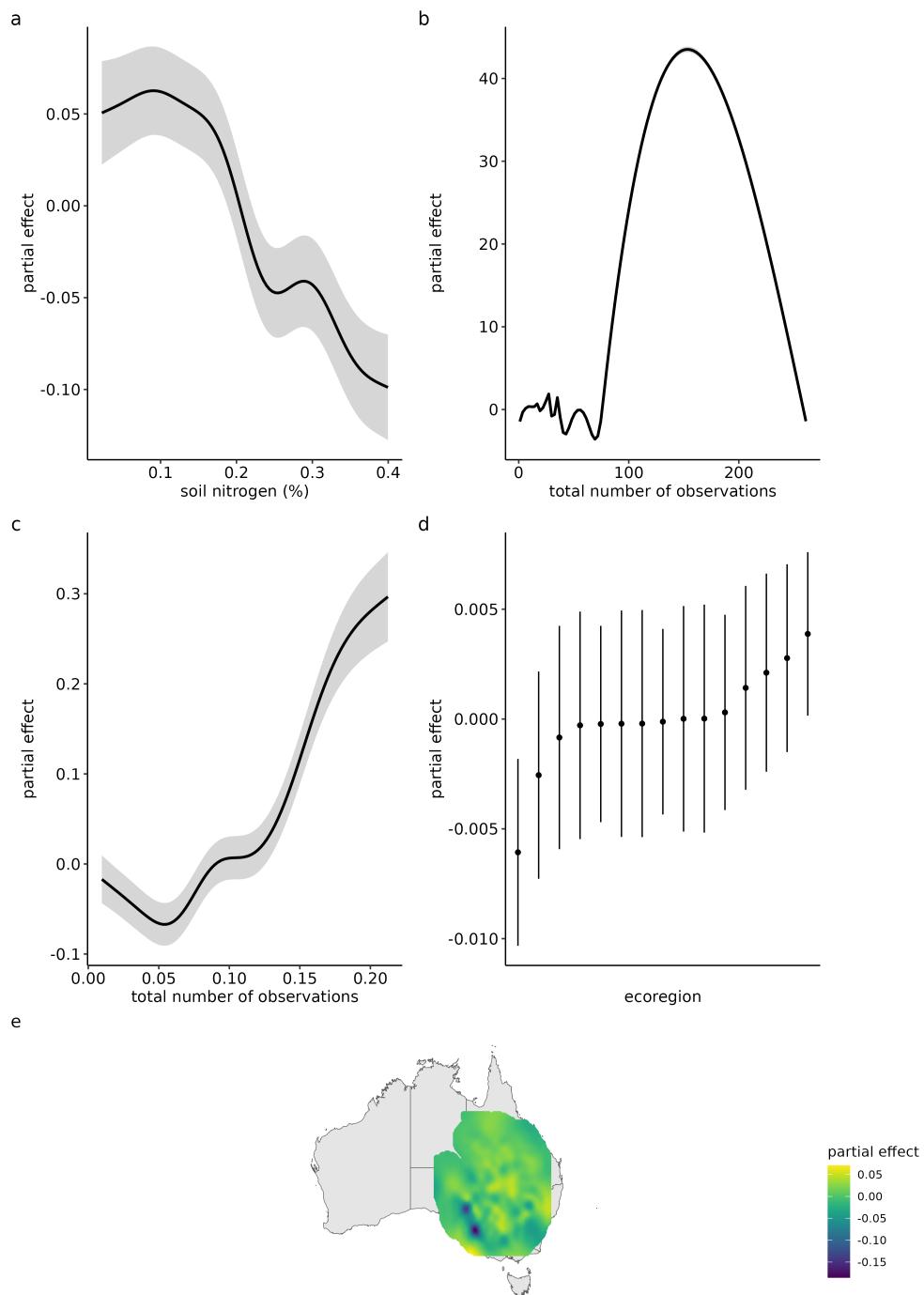
Supplementary Figure 4: Individual time step intake targets for grasshoppers kept in both high nitrogen fertilization and control cages. Blue dots represent estimated marginal means from the model while blacks dots represent raw individual intake targets.



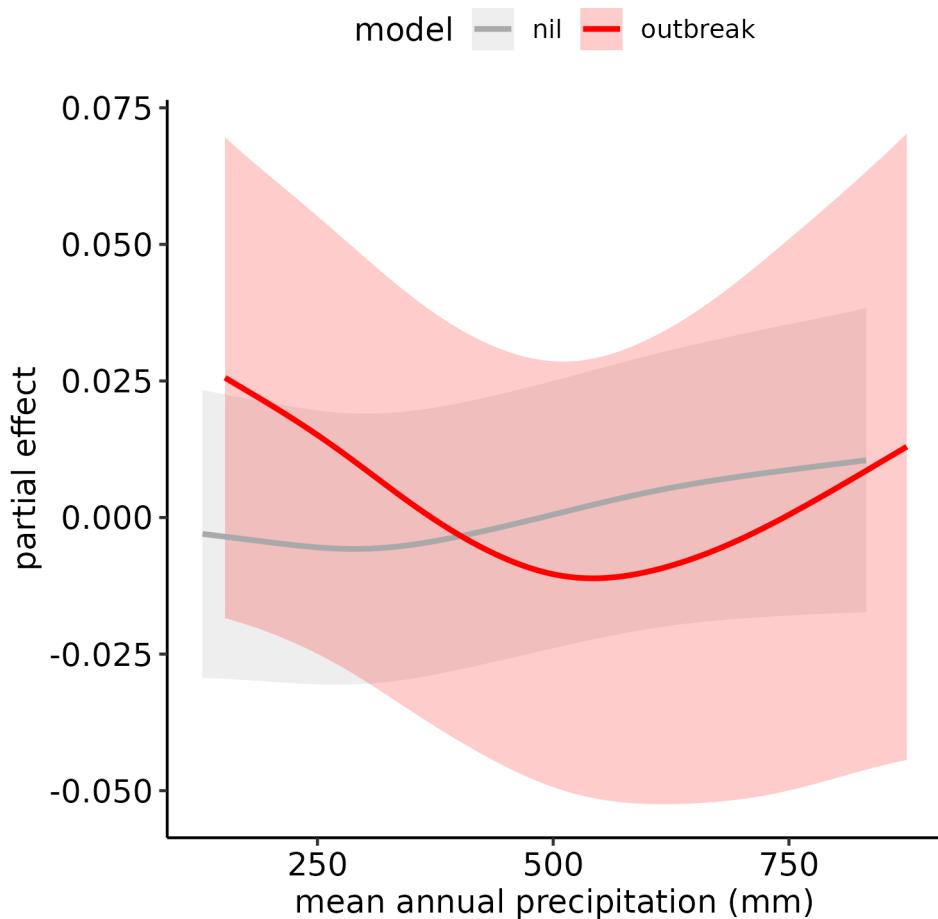
Supplementary Figure 5: Environmental variable correlations between mean annual precipitation, soil nitrogen, soil phosphorus, and woody vegetation pixel coverage. Mean annual precipitation was sourced from WorldClim V1 Bio-clim, soil nitrogen and phosphorus was sourced from Soil and Landscape Grid of 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	Plant N	Plant Protein	Plant Carbohydrate	Soil NO3	Soil NO4
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>Plasplodium 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		
	<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		
Medium	<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		
	<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		
None	<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, Prot = protein, Carb = Carbohydrates.

plant	None	Medium	High
plant cover	35.48	35.24	27.38
<i>Urochloa panicoides</i>	13.33	15.00	47.50
<i>Enteropogon acicularis</i>	60.12	65.48	67.38
<i>Austrodanthonia caespitosa</i>	15.36	18.33	15.24
<i>Cyperus rotundus</i>	19.33	17.29	15.00
<i>stipa species</i>	0.00	5.00	0.00

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