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# EXPLORING NUTRIENT AVAILABILITY AND HERBIVOROUS INSECT POPULATION DYNAMICS ACROSS MULTIPLE SCALES

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A PREPRINT

2024-12-05

## ABSTRACT

Nutrient composition varies greatly across landscapes, influencing the spatiotemporal dynamics of populations. However, few studies have explored this pattern across multiple scales. We tested how nutrient limitation affects herbivore populations, from individual behavior to landscape-level dynamics, using the Australian plague locust, *Chortoicetes terminifera* (Walker). Our study combined field populations and long-term survey data across their range. At the individual level, juvenile locusts selected a carbohydrate-biased intake target of 1 protein (p) to 2 carbohydrate (c) and exhibited the highest growth rates and shortest development times when fed artificial diets matching this 1p:2c ratio during their final juvenile instar. In the field, locusts exposed to protein-biased plants corrected their nutritional imbalance by initially selecting carbohydrate-heavy diets (up to a 1p:20c ratio). Over a week after removal from the protein-rich environment, they returned to the 1p:2c intake target once the deficiency was balanced. At the landscape level, locust outbreaks were negatively correlated with soil nitrogen and exhibited a non-linear relationship with soil phosphorus, peaking at approximately 4% phosphorus content. By disentangling the interaction between mean annual precipitation and soil nitrogen, using comprehensive locust surveys and remotely sensed soil and weather data spanning decades, we show how environmental factors drive population dynamics. This study integrates lab, field, and remote sensing approaches, highlighting the importance of nutrient balancing across scales for herbivores. Specifically, we demonstrate that low-nitrogen environments promote locust outbreaks, likely by reducing plant protein-to-carbohydrate ratios. Incorporating soil quality data into locust plague forecasting models could significantly improve prediction accuracy.

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

## 1 INTRODUCTION

Plant nutrients are usually more variable than animal body composition both in their total amounts and ratios, which can make it challenging for herbivores to acquire an optimal nutritional balance. This topic has been well-explored using Ecological Stoichiometry, which looks at the relative amounts of elements moving through different ecological and biological levels and their consequences [Elser et al., 2000]. Nutrient balance affects individual performance [Batzli, 1986, Bernays et al., 1994] and—by extension through changes in growth, reproduction, and death rates—influences population dynamics [Elser et al., 2000]. While studies have investigated this trend between available nutrients and animal populations, they usually happen at one scale and biological level. For example, much grasshopper nutrition research has been done at the organismal or local population level using lab and/or field studies [Behmer, 2009, Cease, 2024, Le Gall et al., 2019], with a few separate larger scale modeling endeavors [Zhou et al., 2019, Welti et al. [2020b]]. To our knowledge, no study has integrated individual herbivorous animal nutrition to continental level patterns in nutrient availability. Here we work across spatial scales, bridging field observations and cage manipulations with continental-scale insect pest outbreak modeling to see how the animal-nutrient relationship changes across multiple scales.

Food quality has long been considered an important predictor of animal population dynamics [White, 1993, Andersen et al., 2004]. Primary production in terrestrial ecosystems is often limited by nitrogen (N) and phosphorus (P), either separately or as co-limiting factors [Tyrrell, 1999, Vitousek et al., 2010], and thus herbivores are often assumed to be

39 N- and/or P-limited as well. Furthermore, plants have higher carbon (C):N and C:P ratios than the consumers that eat  
 40 them and this mismatch in stoichiometry can make it challenging for primary consumers to meet their N and P needs  
 41 [Elser et al., 2000]. Most N in plants is found in amino acids or proteins, which are critical for animal growth and  
 42 enzymatic function. Phosphorus is necessary for RNA synthesis, energy storage and transfer via ATP, and numerous  
 43 other cellular processes. Limitations in one or both restrict herbivore growth and reproduction [Sterner and Elser,  
 44 2003]. For example, increased host plant C:P results in lower RNA content, slower growth, and reduced abundance  
 45 for the dryland insect herbivore *Sabinia setosa* [Schade et al., 2003]. Vole (*Microtus ochrogaster*) densities increase  
 46 in bluegrass fields supplemented with high quality (e.g. increased N) food pellets due to higher adult survival, and  
 47 increased breeding, and growth rates compared to control fields [Cole and Batzli, 1978]. More broadly, N- and P-  
 48 limitation has been shown in mammals [White, 1993, Randolph et al., 1995], birds [Forero et al., 2002, Granbom and  
 49 Smith, 2006], and insects [Floyd, 1996, Huberty and Denno, 2006, Marsh and Adams, 1995, Perkins et al., 2004]  
 50 which is discussed further in White [2008] and Andersen et al. [2004]. However, not all animal populations respond  
 51 positively to increasing N and P. For example, studies from across the globe reveal that the abundances of many  
 52 grasshopper species are positively [Joern et al., 2012, Zhu et al., 2019, Welti et al., 2020b,a, Zhu et al., 2020a, Ozment  
 53 et al., 2021], or not related [Heidorn and Joern, 1987, Jonas and Joern, 2008, Lenhart et al., 2015, Ozment et al., 2021]  
 54 to increasing plant N concentrations as reviewed in Cease [2024]. Grasshoppers restricted to low or high P diets have  
 55 decreased survival and body mass relative to grasshoppers fed their preferred diet of about 0.5% P Cease et al. [2016].  
 56 These different responses suggest that herbivores may not be broadly N and/or P limited and underscore that equating  
 57 plant N or P content to plant quality, as is commonly done in the ecological literature, may be misleading in the context  
 58 of herbivory.

59 Given the variation in responses, can the relationship between herbivore abundance and environmental nutrients be  
 60 explained by approaches that consider nutritional physiology at the organismal level, in addition to population and  
 61 landscape ecology? Unlike primary producers that can selectively uptake individual nutrients to meet their needs,  
 62 consumers must actively balance nutrients by eating from among foods packaged with different ratios [Raubenheimer  
 63 and Simpson, 1993], or via post-ingestive regulation [Zanotto et al., 1993]. The Geometric Framework for Nutrition  
 64 (GFN) is complementary to Ecological Stoichiometry and focuses on how consumers acquire specific blends of nutrients  
 65 and the consequences of eating imbalanced diets [Simpson and Raubenheimer, 2012]. If multiple food sources  
 66 are available, many herbivores actively select different host plants or plant parts to reach a specific amount and ratio  
 67 of nutrients that optimizes performance, termed the intake target, IT in the GFN [Simpson and Raubenheimer,  
 68 2012]. For example, giant pandas (*Ailuropoda melanoleuca*) synchronize their migration and reproduction cycles with  
 69 seasonal nutrient availability between different bamboo species [Nie et al., 2015]. The relationship between plant N  
 70 and herbivore performance is driven to a large extent by the herbivore's relative demands for protein and non-protein  
 71 energy (carbohydrates and lipids) [Behmer, 2009]. Protein demand can be well-predicted by growth rate, but energy  
 72 demand varies greatly across different environments and activity levels [Talal et al., 2024b]. Thus, smaller and fast-  
 73 growing animals are predicted to have high protein demands; and highly active animals are predicted to have high  
 74 energy demands. While protein limitation suppresses growth, overconsumption of protein has deleterious effects as  
 75 well, including well-described shortening of lifespans across many taxa [Le Couteur et al., 2015, Moatt et al., 2020].  
 76 Thus, if energy demands are particularly high, then consumers will require low protein, high energy diets so that they  
 77 can eat enough to acquire the energy they need without overeating protein [Raubenheimer and Simpson, 1999]. In  
 78 those cases, low N environments are predicted to be beneficial because they generally support growth of low protein,  
 79 high carbohydrate plants.

80 One excellent study system to explore the complex relationship of nutrient availability and population dynamics is  
 81 a subset of grasshoppers called locusts [Cullen et al., 2017, Uvarov, 1977]. Locusts undergo massive population  
 82 eruptions known as plagues that pose significant issues for global food security [Cease et al., 2015]. For example,  
 83 the 2010-2011 Australian plague locust (*Chortoicetes terminifera*) plague could have caused AUD\$963 million in  
 84 crop damage if not controlled [Millist and Ali, 2011]. In contrast to the nitrogen limitation paradigm (White 1993),  
 85 locusts frequently show carbohydrate limitation. Many locust species, including *C. terminifera*, will select plants with  
 86 a low protein:carbohydrate ratio and eat about double the amount of carbohydrate relative to protein when given a  
 87 choice of artificial diets [Behmer, 2009, Brosemann et al., 2023, Lawton et al., 2021, Le Gall et al., 2019]. Their  
 88 high energy, relative to protein, demand is heightened by their impressive long-distance migration. Marching bands  
 89 of South American locusts (*Schistocerca cancellata*) eat predominantly from dishes containing carbohydrates and  
 90 largely ignore dishes containing protein [Cease et al., 2023], and have the highest survival and lipid gain when eating  
 91 carbohydrate-biased plants [Talal et al., 2020]. As adults, flight increases carbohydrate, but not protein, consumption  
 92 in migratory locusts (*Locusta migratoria*) and locusts eating carbohydrate-biased diets fly for longer times [Talal  
 93 et al., 2023]. Locusts use lipids to fuel long distance flight, which they predominantly synthesize from carbohydrate  
 94 consumption. However, when given the choice, locusts balance lipid to carbohydrate intake to most efficiently grow  
 95 lipid stores from dietary lipids [Talal et al., 2024a]. At a local scale, high-use agricultural areas that decrease soil  
 96 and plant nitrogen promote *Oedaleus* locust outbreaks in Senegal and China [Cease et al., 2012, Giese et al., 2013,

97 Le Gall et al., 2019, Word et al., 2019]. Less is known about the relationship between plant phosphorus and locust  
 98 populations, but grasshoppers and locusts can detect and regulate phosphorus during ingestion and post-ingestively  
 99 to maintain homeostasis [Cease et al., 2016, Zhang et al., 2014]. Long-term laboratory rearing studies show negative  
 100 effects of too little or excess dietary phosphorus, though short-term restrictions to low or high phosphorus diets appear  
 101 to have no effects [Cease et al., 2016]. Field measurements of *Oedaleus asiaticus* in China show that locusts increase  
 102 phosphorus excretion with increasing plant phosphorus content, suggesting that phosphorus may not be limiting in  
 103 the Inner Mongolian Steppe for this species [Zhang et al., 2014]. Understanding the multi-scale flow of nitrogen and  
 104 phosphorus from soils to continental scale population dynamics may reveal a connection between soil quality and  
 105 locust plagues in Australia and further elucidate the pattern globally [Cease, 2024, Le Gall et al., 2019].

106 The arid interior of Australia is a highly variable environment [Morton et al., 2011] characterized by the Resource-  
 107 Pulse Paradigm, where episodic resource boosts drive ecological dynamics and population responses [Noy-Meir, 1974,  
 108 Whitford, 2002]. Many Australian animal and plant populations irrupt following periods of favorable climatic con-  
 109 ditions. Preceding vegetation growth is a key factor influencing *C. terminifera* population outbreaks [Lawton et al.,  
 110 2022]. While climatic variability plays a significant role, another critical factor in Australia is its naturally poor soil  
 111 fertility, with essential nutrients like nitrogen and phosphorus often in short supply in unmodified soils [Morton et al.,  
 112 2011, Orians and Milewski, 2007]. This nutrient scarcity has shaped the adaptation of many native plants and animals  
 113 to thrive in low-nutrient environments [Orians and Milewski, 2007]]. Among Australia's locust species, *C. terminifera*  
 114 is the most widespread and economically damaging [Hunter et al., 2001]. Although numerous studies have linked  
 115 climatic conditions to *C. terminifera* population outbreaks [Clark, 1974, Deveson and Walker, 2005, Farrow, 1982,  
 116 Key, 1945], the role of soil and plant nutrients in driving these outbreaks remains underexplored.

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

- 119 1. What are the nutritional preferences and performance curves of individuals from gregarious *C. terminifera*  
 120 field populations? We expect individuals to select and perform best on carbohydrate-biased diets based on  
 121 their active lifestyle, and to keep a constant intake target between populations.
- 122 2. How does *C. terminifera* respond behaviorally when constrained to high-nitrogen environments? To redress  
 123 a nutritional imbalance of a high p:c diet, locusts will seek out and eat carbohydrate-rich diets if such foods  
 124 become available.
- 125 3. Can we use soil nutrients as a predictor of *C. terminifera* nymph outbreaks at the continental scale, accounting  
 126 for climatic factors? We expect outbreaks to be negatively correlation with soil nitrogen at this level because  
 127 low nitrogen environments generally promote growth of low p:c vegetation. Given locusts' capacity to post-  
 128 ingestively regulate phosphorus within natural ranges [Cease et al., 2016, Zhang et al., 2014], we predict  
 129 nitrogen to be a stronger predictor of population dynamics at the continental scale.

## 130 2 METHODS

131 Details regarding the scales of inference, the application of factors of interest, and the corresponding replicates can be  
 132 found in Table 1. This table outlines the hierarchical structure of our experimental design across individual, population,  
 133 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

### 134 2.1 Field site and animals (Questions 1 and 2)

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

141 **2.2 Nutritional target and performance curve using synthetic diets (Question 1)**

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

146 We collected fourth and fifth instar nymphs from outbreaking populations on Nov. 12, 2015 from two locations: near  
 147 Mendooran (31°40.791' S, 149°04.209' E) and Guntawang (32°23.988' S, 149°28.649' E), New South Wales. The  
 148 Mendooran population was forming marching bands while the Guntawang population was at high density but was not  
 149 actively marching during the collection period. Both populations were collected along dirt roads flanked by livestock  
 150 grazing pastures containing a mix of grasses and forbs. We transported locusts back to the Trangie Agricultural  
 151 Research Centre and kept them in large plastic bins with holes along with an assortment of grasses and forbs cut  
 152 from the same field locusts were collected until experiments were started. For both experiments, locusts were housed  
 153 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  
 154 (nutritional target) or one (performance curve) artificial diets, a water tube capped with cotton, and a perch.

155 **2.2.1 Nutrition target (choice diets)**

156 We ran this experiment to determine the preferred dietary p:c ratio of *C. terminifera* field populations. We selected  
 157 equal numbers of males and females from both Mendooran and Guntawang populations and individuals that had no  
 158 visible wing bud separation to ensure they were early in the fifth instar. Locusts were heated with incandescent light  
 159 bulbs on a 14:10 light:dark cycle. The average daytime and nighttime temperatures in the cages were 25.5°C and  
 160 23.4°C respectively, recorded from an iButton (Maxim). We randomly assigned 80 locusts (20 individuals per diet pair  
 161 per population) to one of two treatment groups receiving pairs of either 7p:35c & 28p:14c or 7p:35c & 35p:7c (% p :  
 162 % c by dry mass). We used two different pairs to ensure that the selected p:c ratio was not the result of eating randomly  
 163 between the two dishes. We let locusts eat from the dishes for three days (Nov. 12-15, 2015) and calculated the mass  
 164 of protein and carbohydrate each locust ate by subtracting the final dish weights from the initial dish weights.

165 **2.2.2 Performance curve (no-choice diets)**

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

178 **2.3 Field cage experiments (Question 2)**

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

187 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  
 188 ground by partially burying it and nailing thin slats of wood over the mesh edges. We removed any plant litter and  
 189 arthropods (mostly spiders and locusts) so we could more easily count the locusts and limit predation. This removal  
 190 may have also affected factors such as light availability for plants and soil temperature, which could have influenced  
 191 plant growth and other ecological dynamics. We added 20 4th instar locust nymphs to each field cage on the evening of  
 192 November 13th and morning of November 14th. We randomly selected these nymphs from the Mendooran population  
 193 we collected on November 12th (see synthetic diet methods section above). Each fertilized plot had four cages, for a  
 194 total of 12 cages per fertilization level, and 36 cages and 720 locusts in total. We checked the cages every 4-5 days  
 195 and removed any spiders.

196 We measured plant diversity and abundance in each locust cage and outside the cage within each fertilized plot. We  
 197 also measured ground, litter, manure, and plant cover in each of the nine plots by randomly tossing three 0.25 x 0.25  
 198 m quadrats within each of the nine plots. We took these ground cover and biodiversity measurements at the beginning  
 199 and end of the experiment. We took plant leaf samples for nutrient analyses from each cage three times during the  
 200 experiment on November 11th, November 25th, and December 1st, 2015. Plant species with resulting carbon, nitrogen,  
 201 digestible carbohydrate and protein content as well as soil nitrogen (from 0-10 cm cores) can be seen in Supplementary  
 202 Table 1. Plant species ground cover for each cage can be seen in Supplementary Table 2. The relationship between soil  
 203 NO<sup>3</sup> and NO<sup>4</sup> within cage plots and cage plant carbohydrates and proteins are visualized in Supplementary Figure 1.  
 204 To test how the nitrogen fertilization treatments affected the nutritional status of the locusts, we collected 20 locusts  
 205 from control and high N treatment cages (40 individuals in total) on November 23, 2015. We housed them in individual  
 206 cages and gave them the choice of a low protein: carbohydrate diet and a high protein: carbohydrate diet. We changed  
 207 their diets on days one, two, four, and six and ended the experiment at day nine. To ensure an adequate sample size,  
 208 we included data from any individuals that died (approximately 60% mortality) before the experiment was completed  
 209 and individuals which molted during the experiment. We calculated the mass of protein and carbohydrate locusts ate  
 210 over each interval. This allowed us to see the nutritional redressing of individuals.  
 211 We collected all remaining field-cage locusts on Nov. 28, 2015 and recorded developmental stage and body mass.  
 212 We calculated surviving proportion for each cage accounting for the locusts we removed for the nutritional status  
 213 experiments as follows:

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

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

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

## 215 **2.4 Correlating historical nymphal outbreaks with soil nitrogen and phosphorus (Questions 3)**

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

### 219 **2.4.1 Locust outbreak data**

220 *Chortoicetes terminifera* data from 2000 - 2017 (~ 190,000 records) were used in this study. This database contains  
 221 georeferenced points with a categorical ordinal variable 0-4 to represent approximate nymph densities. The value  
 222 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  
 223 characterized by very high densities of gregarious nymphs (up to 1000 m<sup>2</sup>). We focused on nymphs as this life stage  
 224 cannot fly and can be used to assess prior local habitat conditions. While the database extends into the 1980s, we only  
 225 used data collected between 2000-2017 as this period overlapped with the soil grid data which was released in 2015  
 226 to account for any potential shifts in soil nutrient composition. Since climatic conditions and migration patterns are  
 227 drivers in outbreak occurrence [Lawton et al., 2022, Veran et al., 2015] they likely mask the relationship between static  
 228 environmental variables like soil nutrients. To account for this variability, we spatially aggregated the survey dataset  
 229 to a 1 km<sup>2</sup> grid as can be seen in Supplementary Figure 2. This allowed us to model how often locust outbreaks occur  
 230 in grid cells rather than the actual outbreak. We used a 1 km<sup>2</sup> grid as this reflects the estimated maximum dispersal  
 231 distance from hatching to 5th instar [Hunter et al., 2008]. Since it is often difficult to accurately assess categories  
 232 2-3 given the small differences in densities, We counted the number of outbreaks (APLC nymph density code 4),  
 233 the number of nil records (APLC nymph density code 0), and total number of survey observations. This resulted in  
 234 approximately 67,000 grid cells for the final dataset. Overall APLC survey point distribution can be seen in Figure 1  
 235 A.

### 236 **2.4.2 Soil grid of Australia data**

237 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 charac-  
 238 teristics are available at multiple depths from surface to two meters below the surface. These depths and methodology  
 239 are consistent with the specifications of the Global Soil Map project (<http://www.globalsoilmap.net>) [Grundy et al.,  
 240 2015]. We extracted this data from Google Earth Engine [Gorelick et al., 2017]. In this data set both phosphorus  
 241 and nitrogen units are the mass fraction of total nutrient in the soil by weight. We took the average of nitrogen and  
 242 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  
 243 grasses and forbs. Then, for each APLC survey grid we calculated the mean mass fraction of nitrogen and phosphorus

244 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  
 245 C respectively.

## 246 2.5 Statistics

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

### 251 2.5.1 Intake Targets (Question 1 and 2)

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

### 258 2.5.2 Field population (Question 1)

259 We calculated intake targets as discussed above. To see the impact of confined diet treatments on both specific growth  
 260 rate and development time, we constructed two linear models (family: gaussian, link: identity) with the following  
 261 variables: treatment (factor), locust sex (factor), population (factor), and locust initial weight (numeric).

### 262 2.5.3 Field Cage Experiments (Question 2)

263 We assessed plant nutrients with a generalized additive mixed model (GAMM) (family: Multivariate Normal Distribu-  
 264 tion, link: identity) and included the following variables: plant carbohydrate (numeric, dependent), plant protein  
 265 (numeric, dependent), treatment (factor, independent), cage (factor, random effect), plot (factor, random effect), and  
 266 plant species (random effect). Redressing intake targets were conducted as discussed above (section 2.5.1). To see  
 267 the difference between physiological performance and fertilizer treatments, we constructed GAMMs (family: Scaled  
 268 T distribution, link: identity) for final locust mass. The independent variables in all models were treatment (factor),  
 269 sex (factor), a two-dimensional smoother of available protein and carbohydrate, and cage number as a random effect.  
 270 For both final adult proportion and survival proportion, we constructed a GAM (Family: gaussian, Link: identity)  
 271 and included the following variables: treatment (factor) and a two-dimensional smoother of available protein and  
 272 carbohydrate.

### 273 2.5.4 Historical outbreaks and soil nutrient grid modeling (Question 3)

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

## 290 3 RESULTS

### 291 3.1 Field population (Question 1)

#### 292 3.1.1 Choice experiment (nutritional target)

293 *Chortoicetes terminifera* individuals from the two outbreaking populations regulated to a specific ratio of 1 protein  
 294 : 2 carbohydrate (Figure 2 A, Table 2). Model selection can be seen in Supplementary Table 3. Consumption in  
 295 the two diet pairings did not differ, indicating that instead of consuming between the diets randomly (which would be  
 296 expected if nutrients had no impact on diet consumption) locusts were actively balancing their protein and carbohydrate

297 consumption (Supplementary Figure 3 A, Table 2). While the protein : carbohydrate ratio did not change, females  
 298 consumed more food than males, likely due to being bigger overall (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 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. Diet pair A and B had the following protein to carbohydrate ratios: 7p:35c & 28p:14c and 7p:35c & 35p:7c respectively. Family: multivariate gaussian distribution, link: identity, SE: standard error.

### 299 3.1.2 No choice experiment (performance curves)

300 *Chortoicetes terminifera* had higher specific mass growth rates and faster development times on the 1 protein : 2 carbohydrate (14 protein : 28 carbohydrate) diet as compared to the other diets (Figure 2 B & C, Table 3, Supplementary  
 301 Table 4). Development time and specific growth rate did not differ between male and female locusts (Supplementary  
 302 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.

### 304 3.2 Field Cage (Question 2)

305 For the first 11 days of the 14 day field cage experiment, plant protein and carbohydrate contents remained consistently  
 306 protein-biased for all treatments (Figure 3 A-C, Table 4), and only showed differences in protein content by the last  
 307 sample period on December 1, which was after the end of the locust cage experiment. Accordingly, there was no  
 308 effect of fertilizer on locust survival and adult proportion (Figure 3 D-F, Table 5). Locusts that were retrieved from  
 309 field cages after nine days and were given a choice to regulate protein and carbohydrate intake showed a pattern  
 310 consistent with rebalancing a shortage of carbohydrates (Figure 4, Table 6, Supplementary Figure 4). Irrespective of  
 311 fertilizer treatment group, locusts initially selected very carbohydrate biased diets, but gradually, after 9 days, their  
 312 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
	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
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.

### 313 3.3 Locust outbreaks (Question 3)

314 *Chortoicetes terminifera* outbreaks were negatively associated with soil nitrogen, which supports the hypothesis that  
 315 nitrogen (in excess) acts as a limiting factor for population upsurges (Table 7, Figure 5 A). *C. terminifera*s had a  
 316 nonlinear relationship with soil phosphorus with outbreaks occurring more often in areas with approximately 4% soil  
 317 phosphorus and were strongly negatively associated with increasing phosphorus afterwards (Figure 5 B). For both  
 318 nutrients, the absence models had a very weak relationship with soil nutrient in comparison to the outbreak models,  
 319 demonstrating little model bias due to APLC survey protocol. There were significant nonlinear relationships between  
 320 coordinates and the total number of observations in all models (Supplementary Figure 6; Supplementary Figure 7).  
 321 The relationship between locust outbreaks and mean annual precipitation was very different from the relationship with  
 322 soil nitrogen ( Figure 5, Supplementary Figure 8). Soil nitrogen and phosphorus show weak positive correlations with  
 323 woody vegetation cover, while mean annual precipitation exhibits high variation in its relationship with soil nitrogen  
 324 and weak correlation with soil phosphorus (Supplementary Figure 5). Thus, the relationship between soil nitrogen and  
 325 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.

## 326 4 DISCUSSION

327 We show that herbivore diet preferences remain consistent between spatial levels, from individual foraging behavior  
 328 and physiology to large scale population dynamics, with locust populations negatively related to environmental nitro-  
 329 gen. Thus by going across scales, this study shows a consistent pattern of excess nitrogen limiting a pest herbivore  
 330 and introduces a more nuanced view of phosphorus limitation on herbivore populations. Instead of the broad gener-  
 331 alization 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. While this study advances our understanding of nutrient limitation across scales, future work should aim to explicitly assess phosphorus nutrient imbalances at finer scales. This could help elucidate whether phosphorus mismatches at smaller scales influence broader patterns of herbivore population dynamics. Investigating multi-scale nutrient interactions, including a wider array of nutrients such as potassium and sodium, could also provide a more comprehensive framework for modeling herbivore responses to environmental heterogeneity. For forecasting pest populations dynamics, 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.

#### 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 less 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 protein (which can be toxic) to acquire sufficient carbohydrates [Behmer, 2009, Cease, 2024]. On the other end of the performance curve, *C. terminifera* do have a lower p:c range that limits performance, as shown using artificial diets (Figure 2 B-C). We also show that outbreaks are correlated with a low level of soil phosphorus, however, outbreaks peak at approximately 4%, suggesting that while locusts generally do well in low phosphorus environments, phosphorus deficit can be limiting for locusts in extremely phosphorus poor soils (Figure 5 B). Because Australian soils are characteristically phosphorus poor [Donald, 1964], Australian animals like this locust are adapted to phosphorus poor environments and potentially having too much phosphorus is deleterious [Morton et al., 2011]. Locust populations may be more tightly correlated with soil nitrogen than phosphorus because terrestrial herbivores require 5-50 times more nitrogen than phosphorus [Elser et al., 2000], meaning they can more readily balance phosphorus by eating a few foods rich or poor in phosphorus but cannot as quickly regulate protein and carbohydrate energy because they make up the bulk of their required nutrients. Indeed, laboratory studies have revealed that short-term limitations in dietary phosphorus have no apparent impact on grasshopper growth [Cease et al., 2016], suggesting that these mobile herbivores could seek out phosphorus-rich diets intermittently to overcome potential phosphorus limitation in field environments. However, in this study, we only tested this relationship with phosphorus at the continental level; further field and lab-

388 oratory experiments are needed to explore this non-linear relationship between locust outbreaks and soil phosphorus.  
 389 While we only looked at nitrogen and phosphorus, it is also important to note that animals require a suite of nutrients.  
 390 Other nutrients such as potassium and sodium [Joern et al., 2012] warrant further investigation. Comparing locust  
 391 outbreaks between continents would further show the relationship between nutrient availability and animal population  
 392 dynamics. One excellent dataset for this would be SoilGrids (<https://www.isric.org/explore/soilgrids>) which provides  
 393 soil nitrogen estimates globally at a 250-meter resolution.

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

#### 399 **4.3 Locusts are more likely to be limited by high nitrogen environments than other grasshoppers**

400 A five-decade review of grasshopper responses to plant nitrogen content showed that grasshoppers not classified as  
 401 locusts have a variation of negative, neutral, and positive responses to increasing plant nitrogen [Cease, 2024]. Looking  
 402 just at field surveys, there are more reports of a negative correlation between plant nitrogen and non-locust grasshopper  
 403 abundance (17 reports) relative to neutral (6 reports) or positive (9 reports). This pattern corroborates long-term studies  
 404 showing that dilution of plant nitrogen is correlated with declines of North American grasshopper populations [Welti  
 405 et al., 2020b]. Of the studies that report positive correlations between individual grasshopper species abundance  
 406 and plant nitrogen, most are from graminivorous (grass-feeding) species (11 reports), with 7 reports from mixed  
 407 (grasses and forbs) or forb feeders [Cease, 2024]. This pattern supports the hypothesis that grass-feeders are more  
 408 likely to be nitrogen-limited because grasses tend to have lower p:c ratios than forbs; although this trend was not  
 409 significant and grass-feeders also regularly showed negative responses to high plant nitrogen. In contrast, there was  
 410 a consistent negative effect of high plant nitrogen on locust species, regardless of whether they were graminivorous  
 411 or mixed feeders. Because mass specific protein consumption is highly correlated with growth rate in both lab and  
 412 field populations, but carbohydrate consumption is highly influenced by the environment [Talal et al., 2023], it is most  
 413 likely that locusts have similar protein requirements as other non-locust grasshopper species, but have much higher  
 414 carbohydrate demands, potentially to support migration [Raubenheimer and Simpson, 1997, Talal et al., 2021, 2023].  
 415 Locusts are able to meet this increased demand for carbohydrate, while keeping protein consumption constant, by  
 416 eating larger amounts of low p:c plants found in low nitrogen environments. In summary, these studies suggest that  
 417 nymphal outbreaks of all locust species may be negatively correlated with soil nitrogen across continental scales, but  
 418 that the correlation between plant nitrogen and non-locust grasshoppers may not be significant or consistent through  
 419 space and time.

#### 420 **4.4 Comparing the relationship between plant macronutrients and herbivore abundance in other taxa**

421 The effect of plant protein and carbohydrate on herbivore populations is predicted to depend on the herbivore's p:c  
 422 intake target (IT) relative to its nutritional landscape (Le Gall et al., 2020). If there are sufficient plants on either side  
 423 of the IT, herbivores can select from between them to achieve their IT. This complementary feeding has been recorded  
 424 for field populations of blue sheep (*Pseudois nayaur*) in the Himalayan Mountains [Aryal et al., 2015], Black Howler  
 425 Monkeys (*Alouatta pigra*) in Yucatán [Bridgeman, 2012], and other primates [Raubenheimer and Rothman, 2013].  
 426 There would be a predicted impact on populations if the nutritional landscape were to become more constricted or  
 427 not overlap with the IT. For example, lab colonies of tobacco hornworms (*Manduca sexta* larvae) have an IT around  
 428 1:1 or sometimes slightly carbohydrate-biased [Wilson et al., 2019a] and their host plants tend to be carbohydrate-  
 429 biased relative to their IT [Wilson et al., 2019b]. However, this does not seem to translate to population level effects,  
 430 potentially due to secondary metabolites affecting growth more strongly than macronutrient balance and/or larvae may  
 431 be able to compensate by overeating carbohydrates to acquire sufficient protein [Wilson et al., 2019a]. Overeating  
 432 carbohydrates is not as detrimental as overeating protein, at least in the short term, and animals tend to be willing  
 433 to overeat carbohydrates to a greater extent than protein [Cheng et al., 2008, Simpson and Raubenheimer, 2012].  
 434 Therefore, herbivores facing a nutritional landscape with a p:c generally lower than their IT (i.e., carbohydrate excess)  
 435 may not be as negatively impacted as herbivores facing one higher than their IT (i.e., protein excess). However,  
 436 there are several examples of higher localized densities of herbivores in response to higher plant nitrogen and protein  
 437 contents with thrips [Brown et al., 2002] and spruce budworm (*Choristoneura*) [De Grandpré et al., 2022] being two  
 438 examples. These examples suggest that low p:c diets limit population growth of some herbivores, but more studies  
 439 are needed to determine if this relationship is only localized or if it scales up. It may be that herbivore populations  
 440 with lower numbers are not limited by a nutritional landscape at a large scale because they can differentially disperse  
 441 locally among optimal patches, whereas herbivore populations with extreme numbers (i.e., irruptions) may be more  
 442 limited by nutritionally unfavorable environments across scales.

443 Herbivore responses to nutrient variation often exhibit species-specific patterns, even among closely related species  
 444 within the same feeding guild. For instance, generalist grasshoppers (*Melanoplus* spp.) coexist by occupying dis-  
 445 tinct nutritional niches, varying their protein-to-carbohydrate intake ratios despite consuming overlapping host plants  
 446 [Behmer and Joern, 2008]. Similarly, *Euchorthippus cheui* and *E. unicolor* display opposing preferences for nitrogen-  
 447 enriched versus nitrogen-depleted host plants, leading to divergent population responses to fertilization and grazing  
 448 pressure [Zhu et al., 2020b, 2023]. These examples highlight how phenological or physiological differences shape  
 449 responses to shared nutritional landscapes. Building on these findings, we hypothesize that related locust species,  
 450 including *Chortoicetes terminifera*, may also exhibit distinct nutrient preferences, potentially driven by local adapta-  
 451 tions to environmental conditions. Investigating these differences could provide insights into how nutrient availability  
 452 influences herbivore population dynamics across ecological scales.

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

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

#### 474 4.5 Synthesis and Application

475 Acquiring the right amount of nutrients is a critical component for animal growth, reproduction, and population dy-  
 476 namics [Doonan and Slade, 1995, Hansson, 1979, Keith, 1983]. However, in contrast to the conventional hypotheses  
 477 that predict a broad positive linear relationship between herbivorous populations and nitrogen and phosphorus [Hu-  
 478 berthy and Denno, 2006, Mattson, 1980, White, 1978, 1993], the story is nuanced and probably most often non-linear.  
 479 For some species, especially those with high energy requirements, the relationship is the opposite (negatively asso-  
 480 ciated with nitrogen) like many locust species and the effects can be seen at the continental scale. Land use and  
 481 Land Cover Change (LULCC) impact on nutritional environments has important implications for animal population  
 482 dynamics from conservation to pest management. While we did not make an explicit connection between LULCC and  
 483 locust outbreaks in Australia, our results are consistent with previous research showing that LULCC that decreases  
 484 soil quality and creates low nitrogen environments increases physiological performance and outbreaks of locusts (re-  
 485 viewed in Le Gall et al. [2019]). Most importantly, we show that this relationship is consistent between scales from  
 486 the individual locust to continental wide outbreaks. As such, proper management of soil nutrients can help keep locust  
 487 populations from reaching outbreak sizes and should be considered across scales, from individual locust behavior to  
 488 continental-wide plagues.

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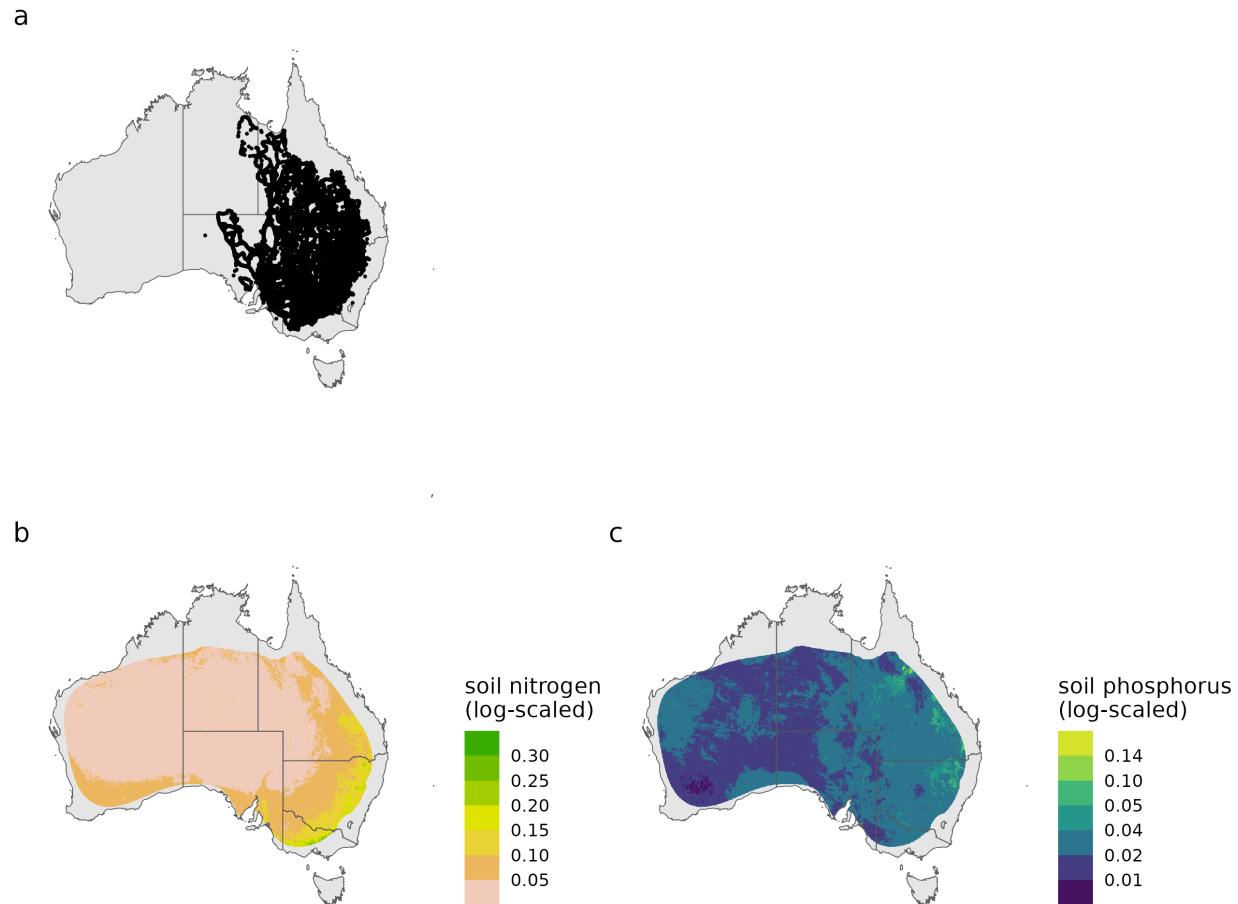
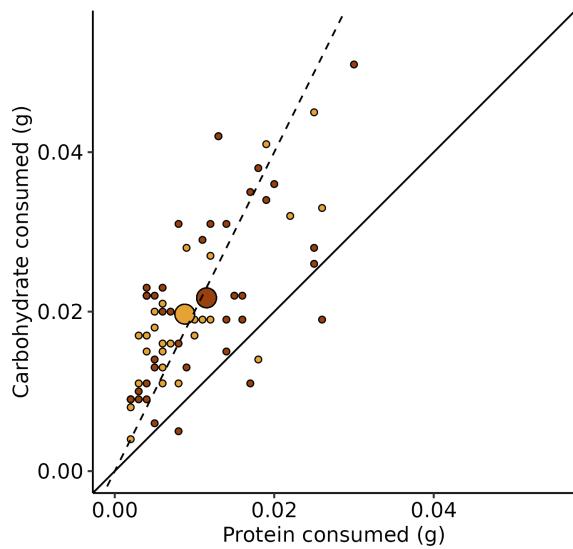


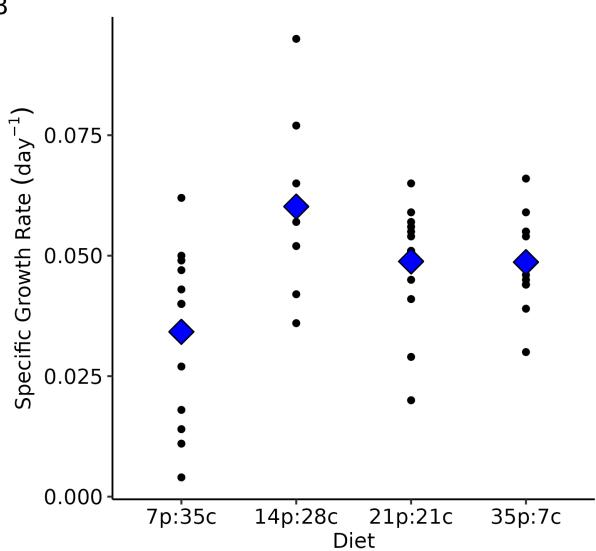
Figure 1: Locust survey data map and soil nutrients throughout the *C. terminifera* distribution. A: APLC survey dataset, B: mean proportion of nitrogen at 0-15 cm deep, C: mean proportion phosphorous at 0-15cm deep.

A

population Guntawang Mendooran



B



C

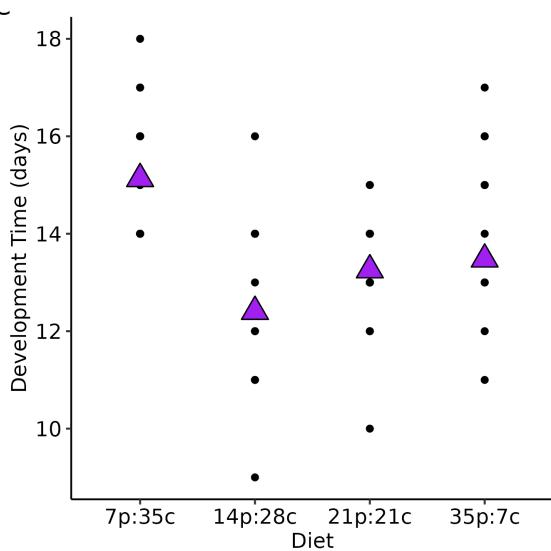


Figure 2: The nutritional preference (A) and physiological performance (B & C) of *C. terminifera* individuals that were collected from two marching bands of 5th instars. Raw data is shown as black dots with modeled estimated marginal means as large diamonds or triangles.

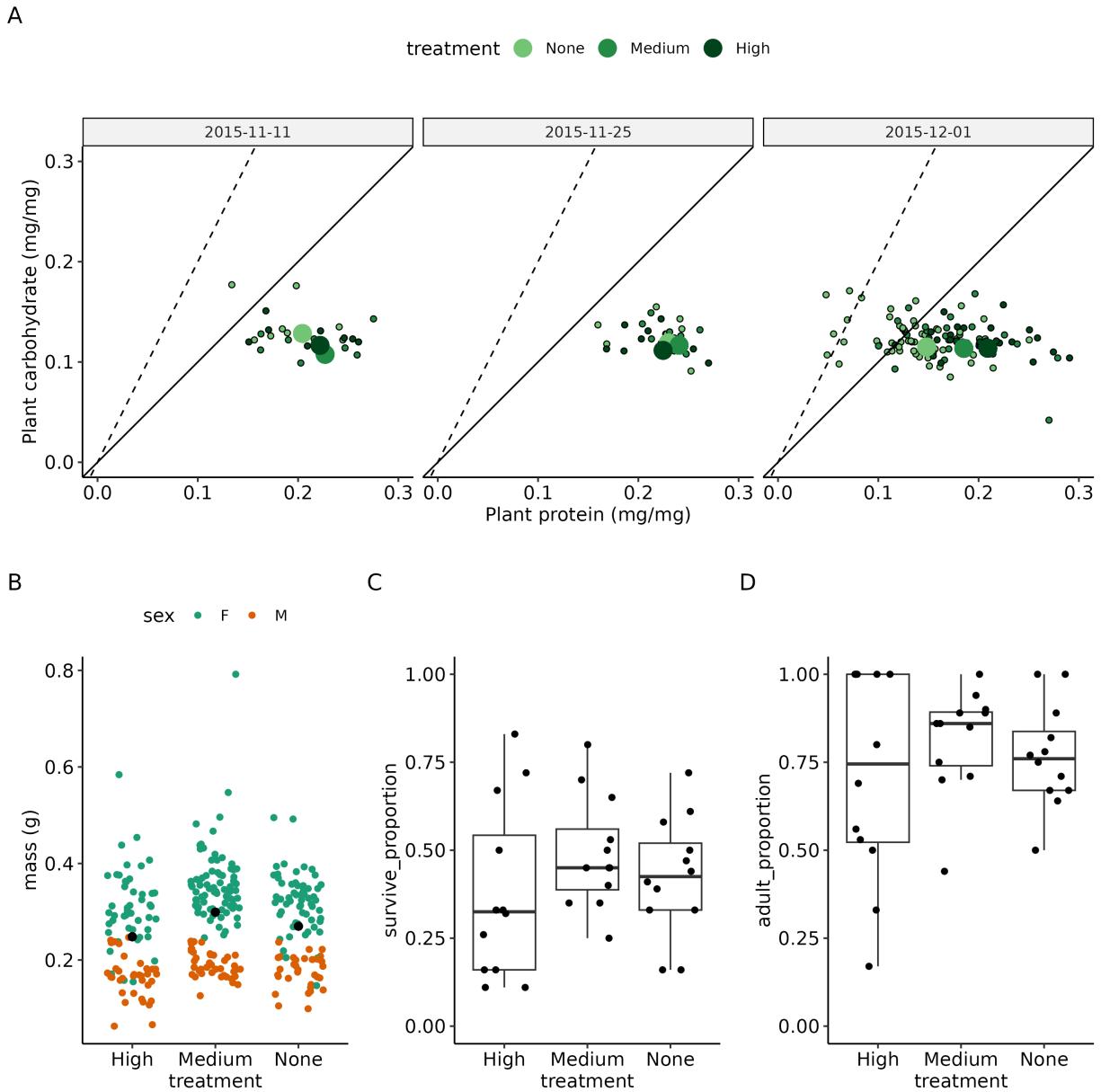


Figure 3: Nitrogen addition field cage experiments with plant nutrient change through time (A) and grasshopper performance metrics (B-C) are shown. Dashed line represents a 1p : 2c ratio, the solid line represents a 1p : 1c ratio. Black dots in B represent overall means whereas boxplots represent the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

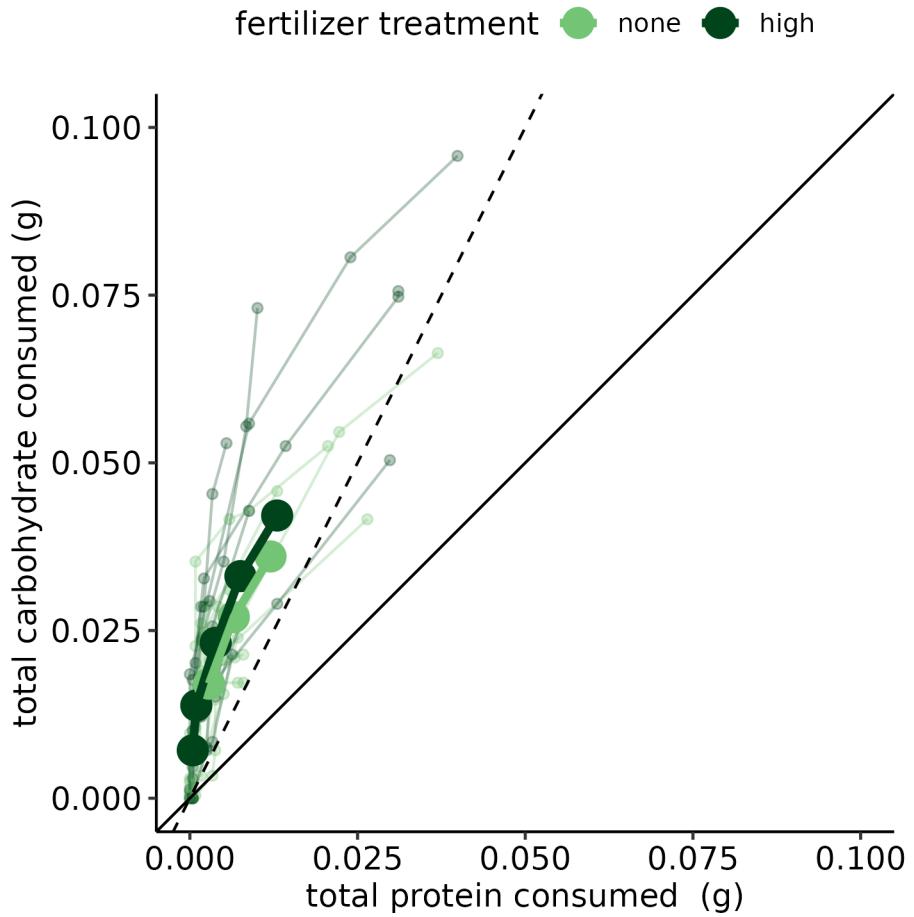
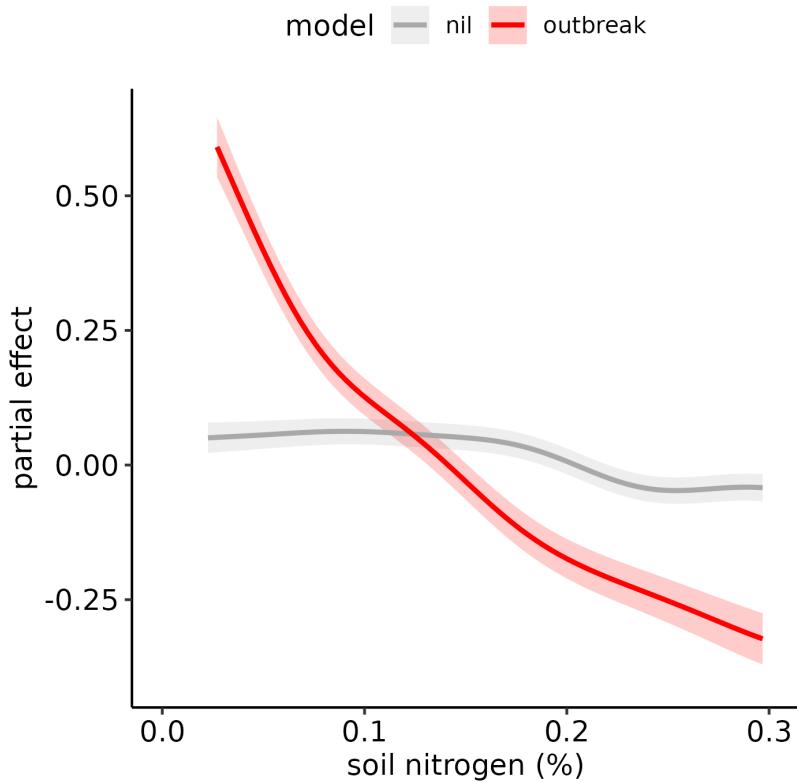


Figure 4: Nutrient imbalance redressing with artificial diet mixing of *C. terminifera* individuals taken from fertilized treatment cages. Colors represent fertilizer treatment. Smaller lines represent raw individual locust intake targets; large lines and points represent estimated marginal means. Points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

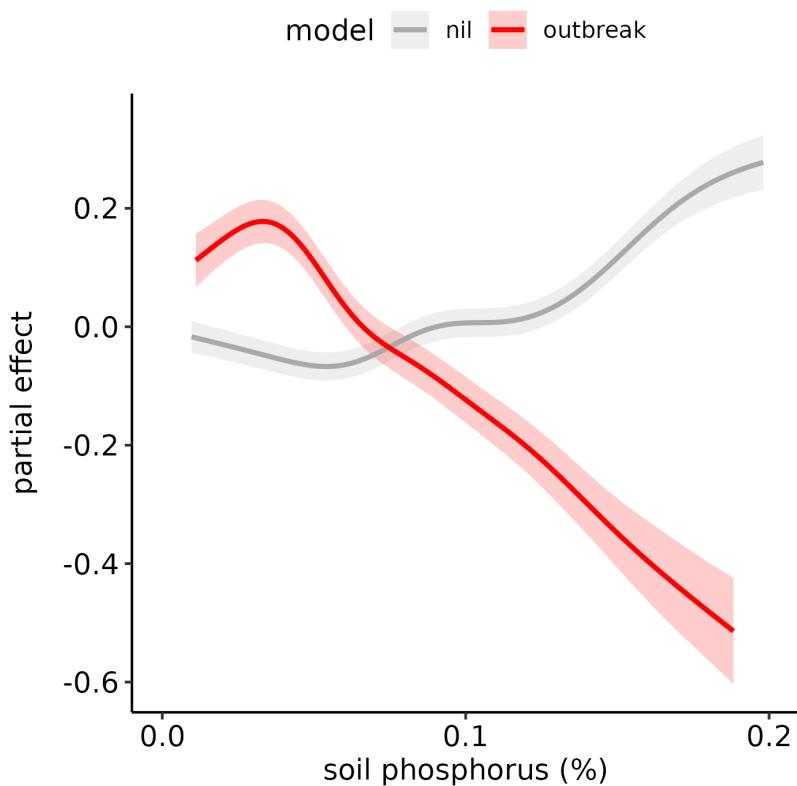
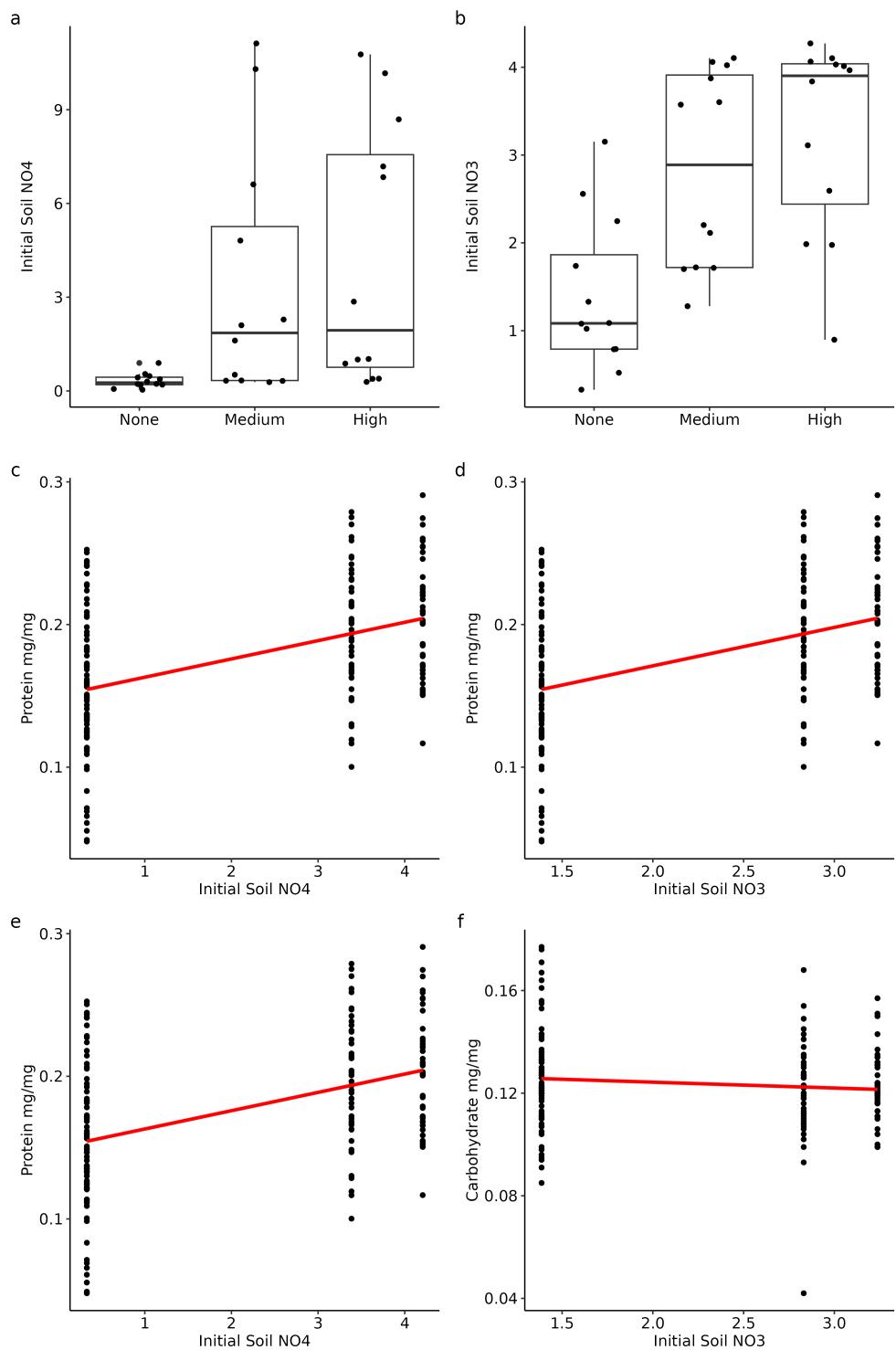
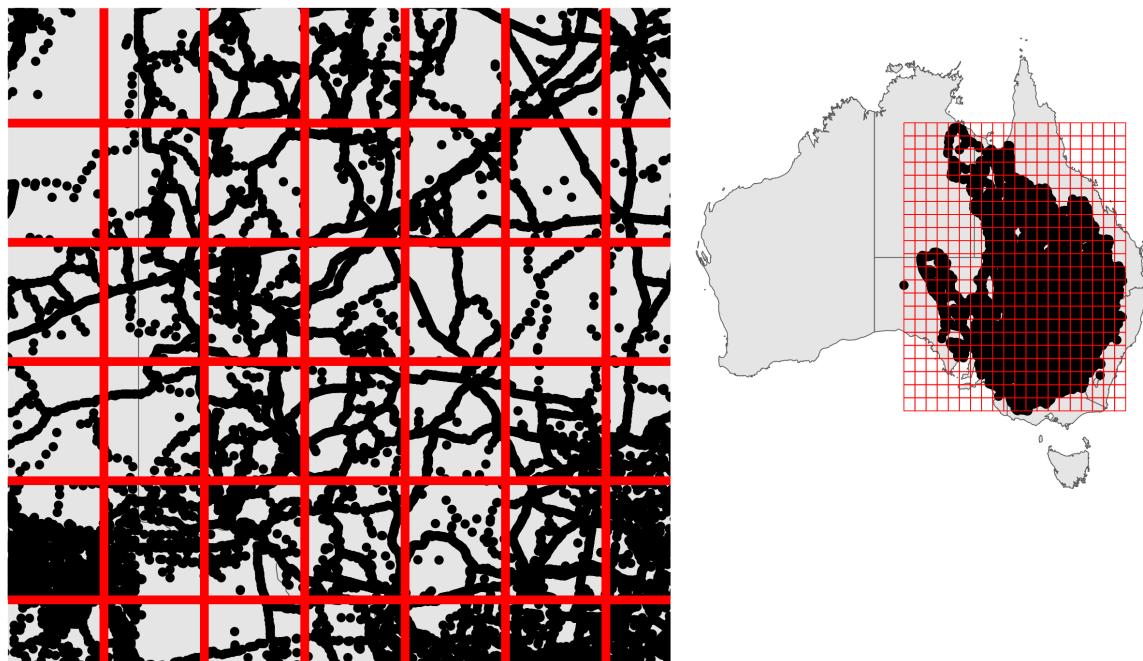


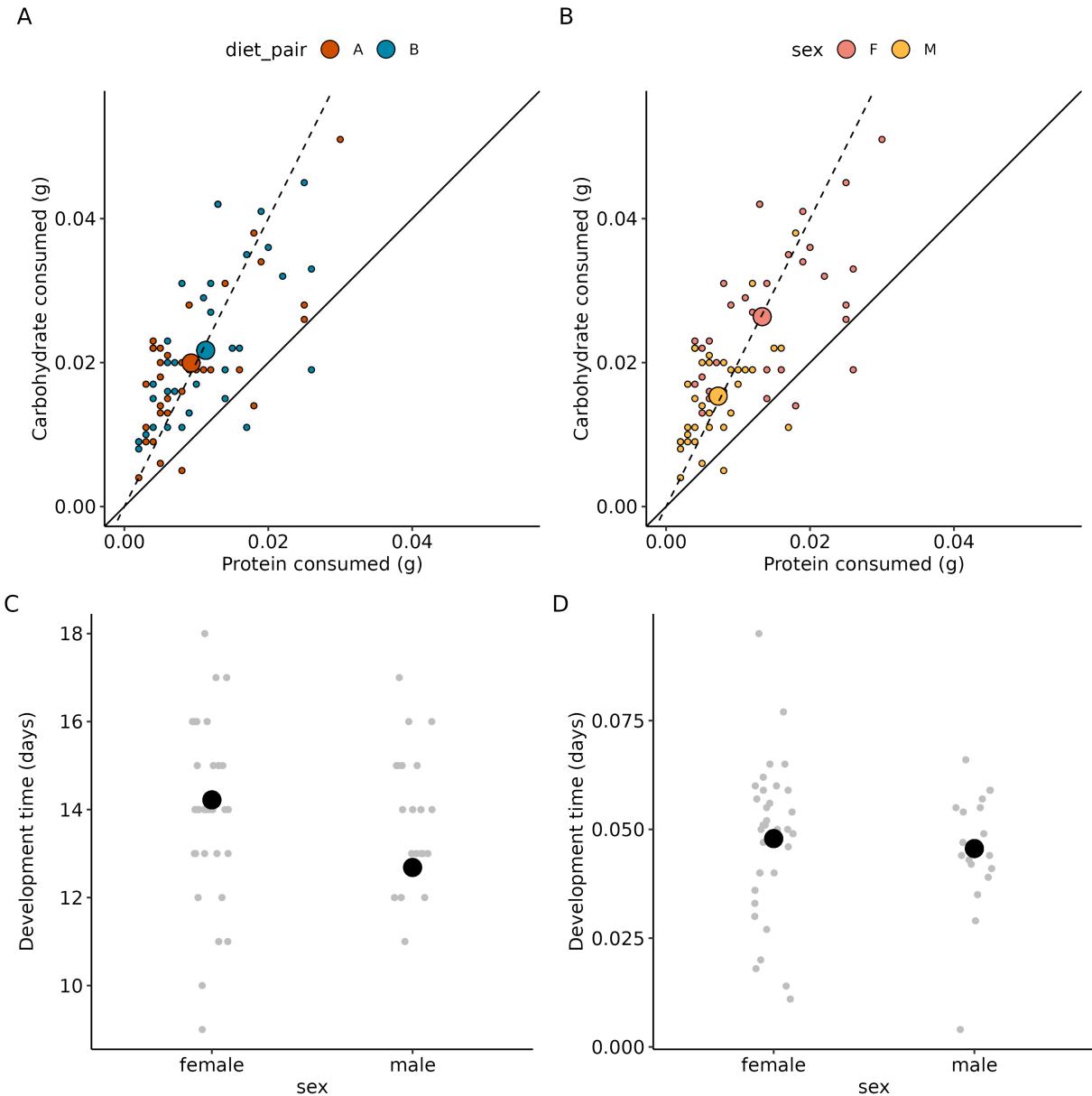
Figure 5: Relationship between outbreaks and nil observations for both soil nitrogen (A) and phosphorus (B). Partial effect is the modeled predictions after accounting for bioregion and spatial autocorrelation.



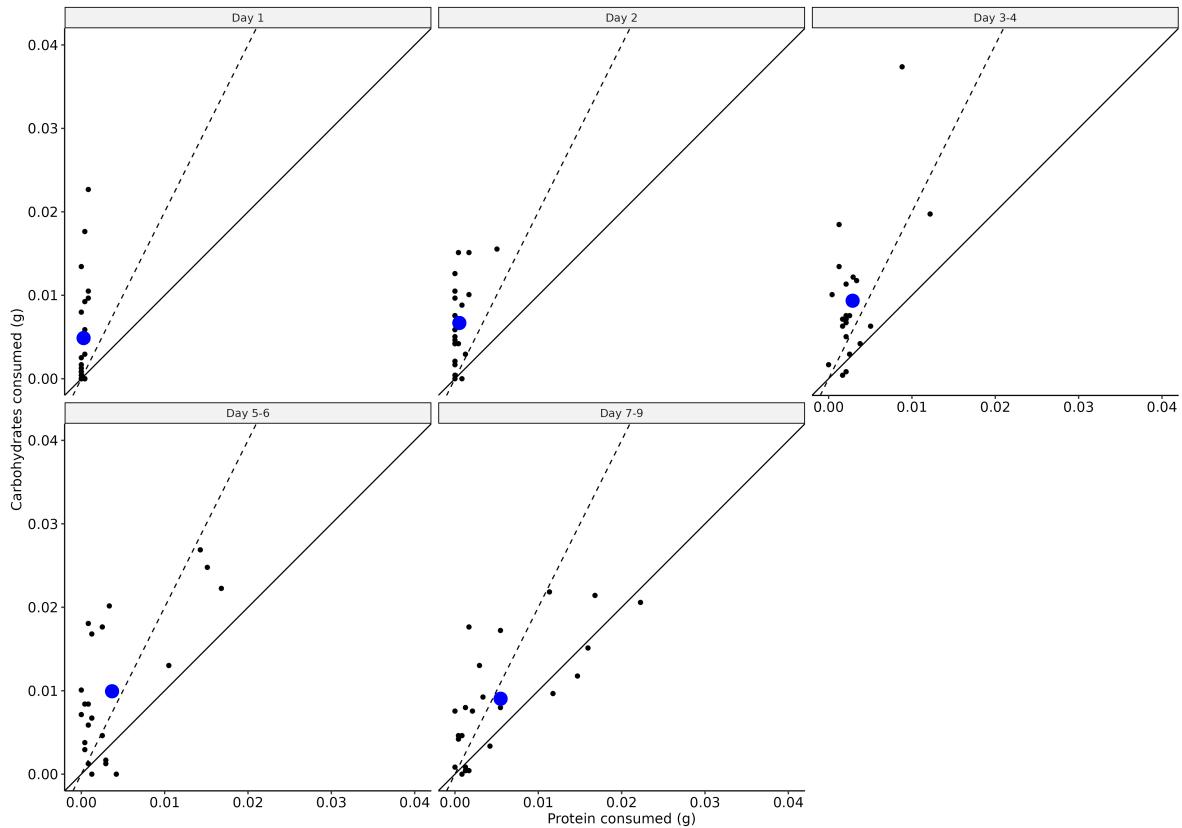
Supplementary Figure 1: Field cage soil nitrogen content by treatment (A & B) and regressed with plant carbohydrates and protein (C-F).



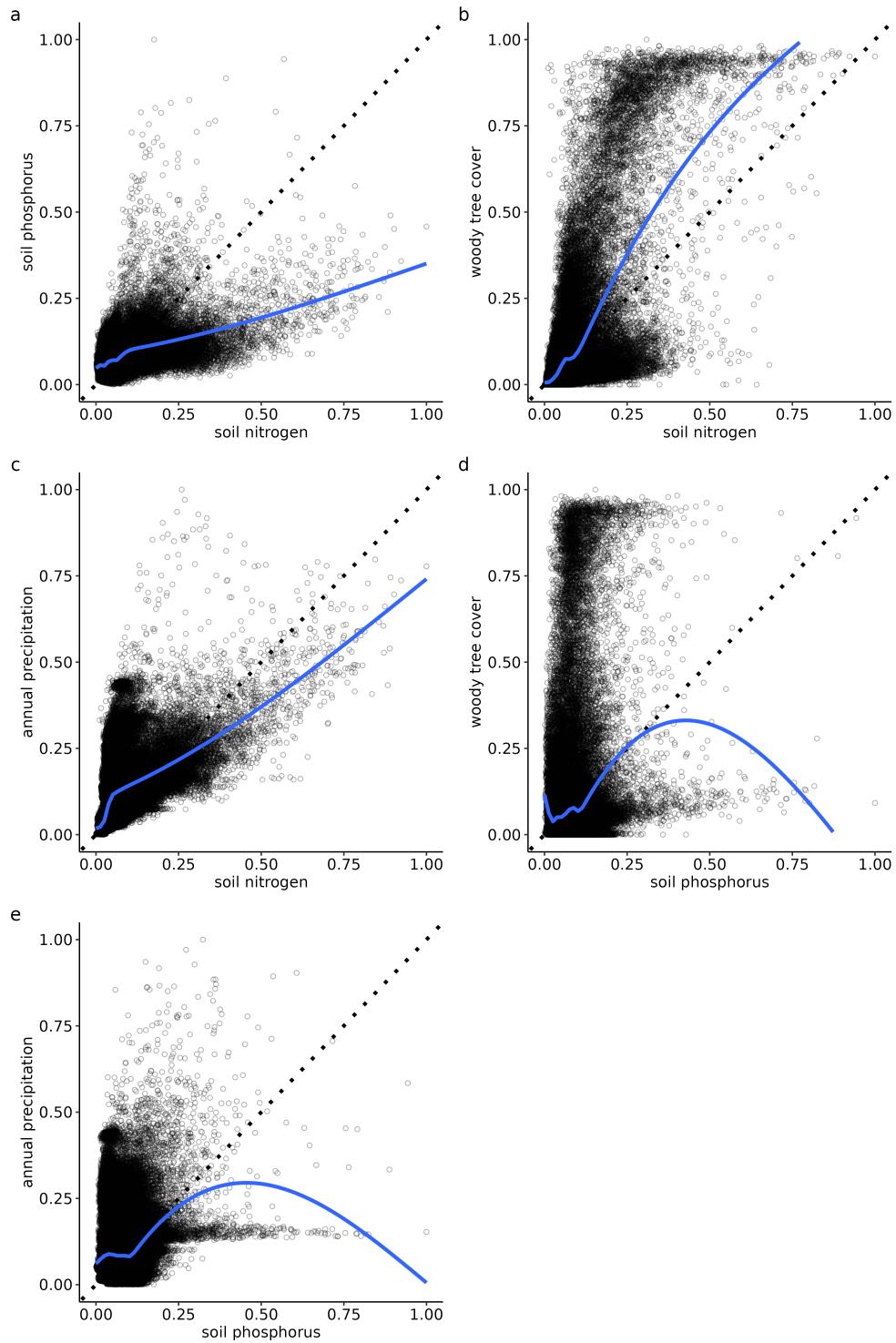
Supplementary Figure 2: Map illustrating the summarization of point observation data into a fishnet grid across eastern Australia. The full extent is shown in the inset map. We summed the number of outbreak, nil, and total observations. The grid in this figure is not at a  $1 \text{ km}^2$  scale for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



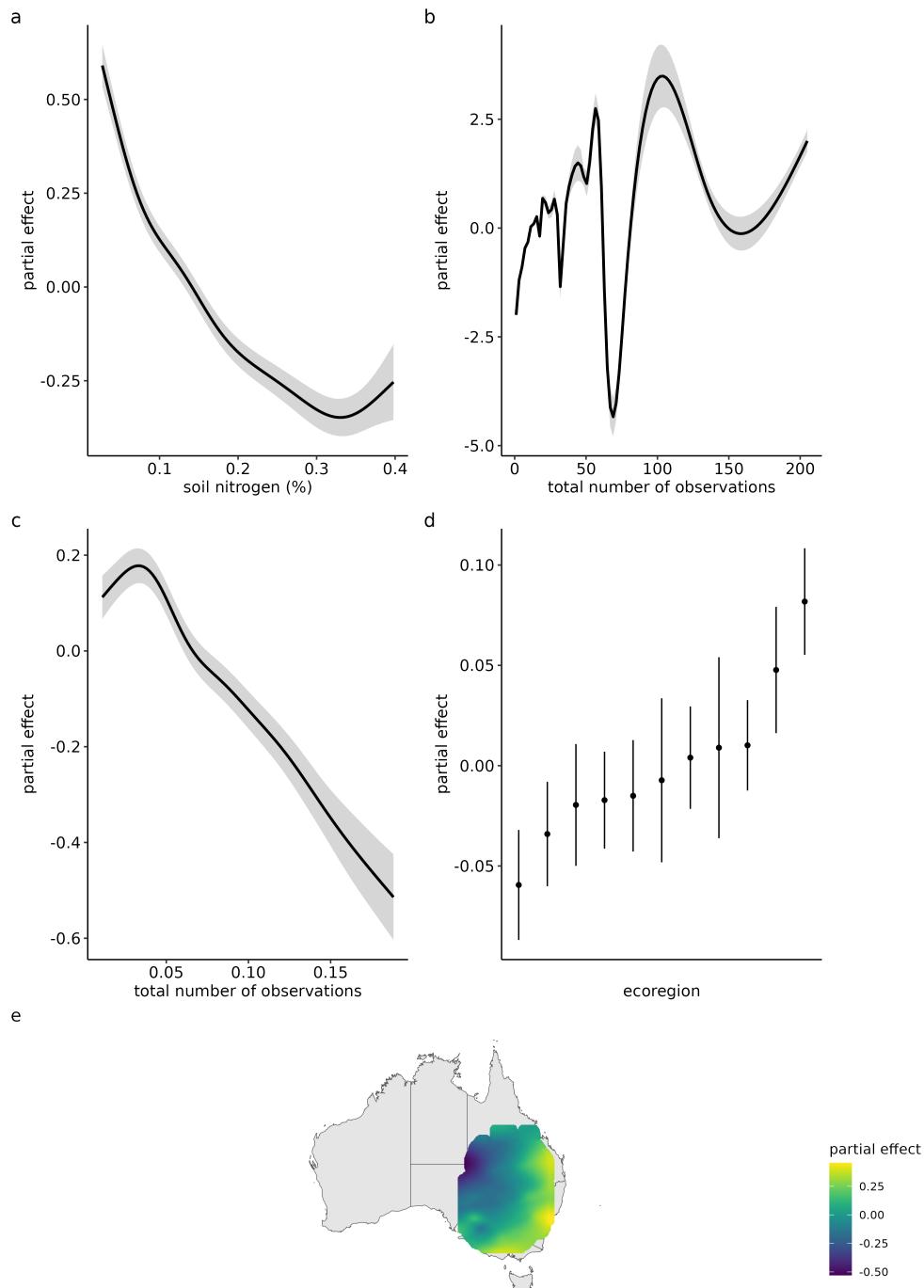
Supplementary Figure 3: Nutrient consumption for outbreaking field populations of *C. terminifera* by diet pair (A) and sex (B) and development time (C) specific growth rate (D) by sex. The P:C ratio did not differ between diet pairing and sex. Females consumed more diet (but kept the same ratio) than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



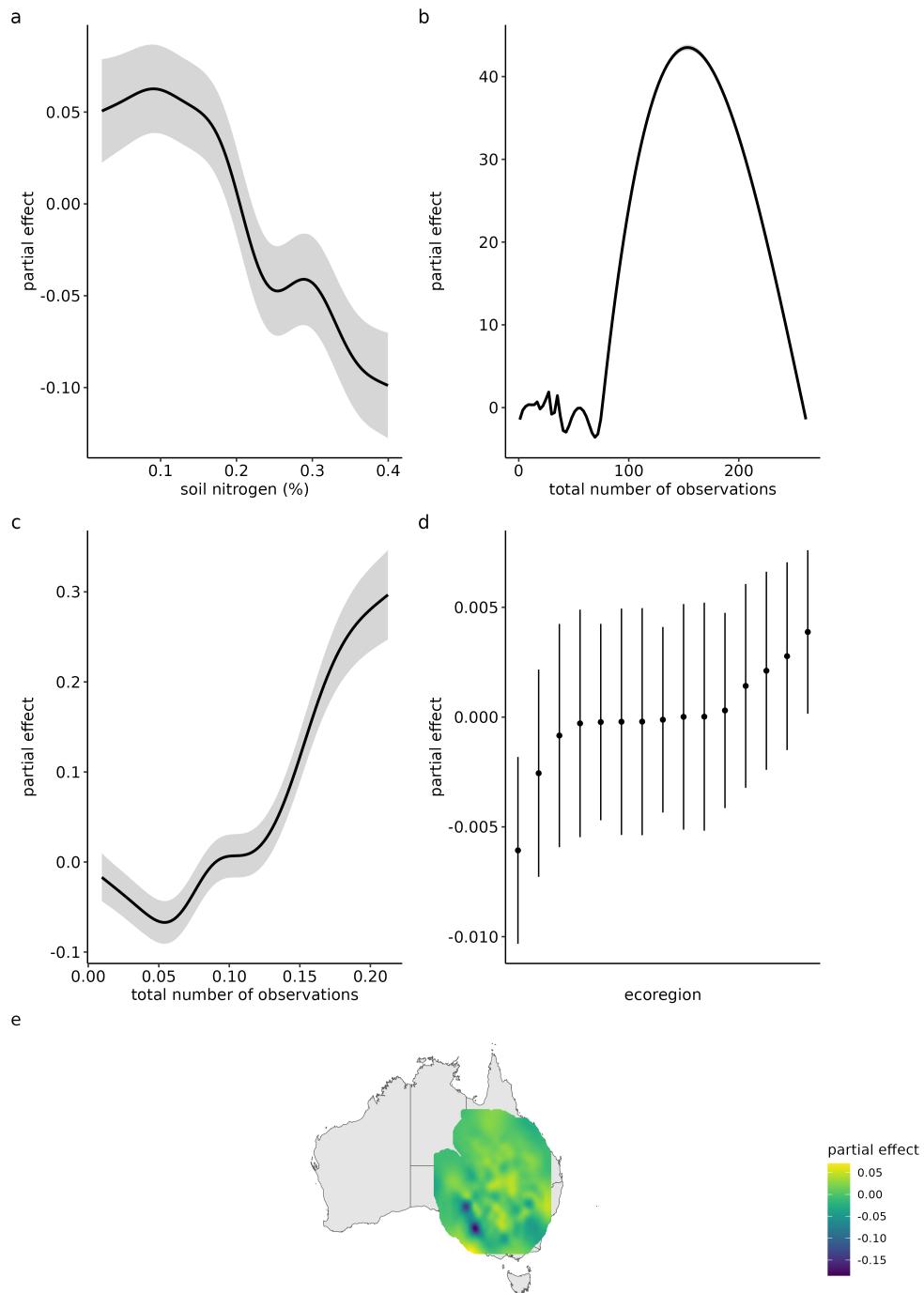
Supplementary Figure 4: Individual time step intake targets for grasshoppers kept in both high nitrogen fertilization and control cages. Blue dots represent estimated marginal means from the model while blacks dots represent raw individual intake targets.



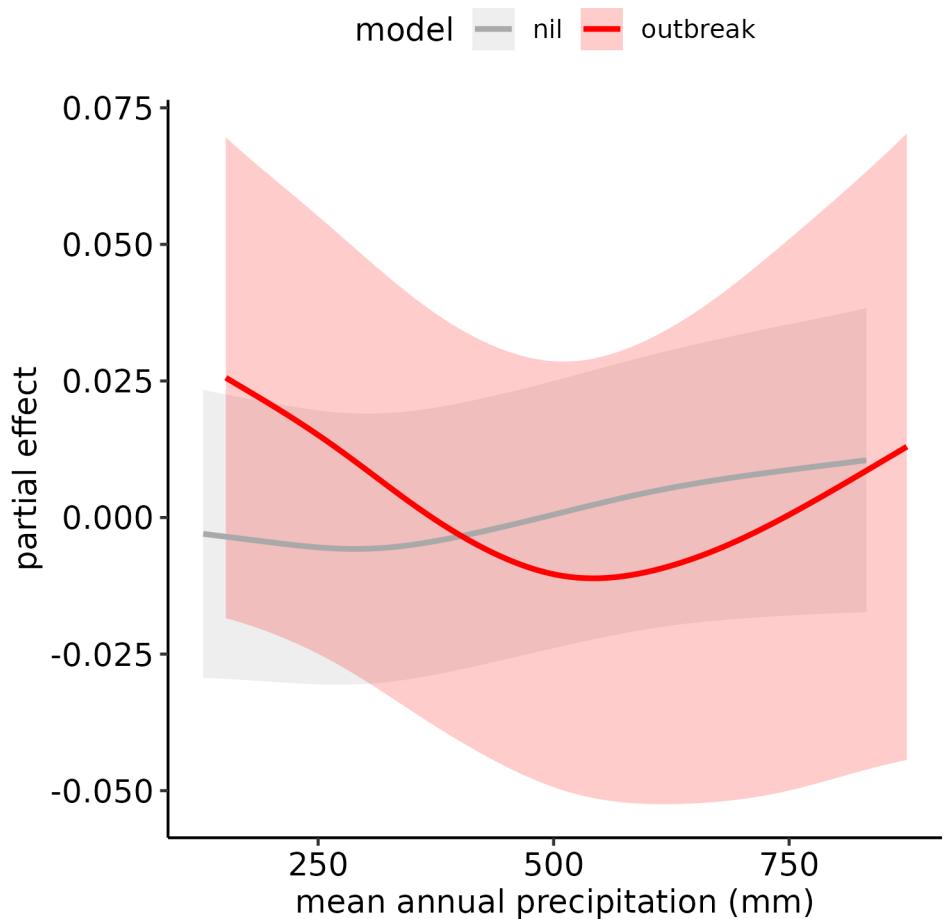
Supplementary Figure 5: Environmental variable correlations between mean annual precipitation, soil nitrogen, soil phosphorus, and woody vegetation pixel coverage. Mean annual precipitation was sourced from WorldClim V1 Bio-clim, soil nitrogen and phosphorus was sourced from Soil and Landscape Grid of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