
EXPLORING NUTRIENT AVAILABILITY AND HERBIVOROUS INSECT POPULATION DYNAMICS ACROSS MULTIPLE SCALES

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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 selecting carbohydrate-heavy diets (up to a 1p:20c ratio) for over a week after removal from the protein-rich environment, returning 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, which can make it challenging for herbivores to acquire an optimal nutritional balance [Elser et al., 2000]. Nutrient balance affects individual performance [Batzli, 1986, Bernays et al., 1994] and, by extension, influences population dynamics [Elser et al., 2000]. One way many primary consumers achieve an optimal blend of nutrients is through selecting different host plants or plant parts to reach a specific amount and ratio, termed the intake target, IT [Simpson and Raubenheimer, 2012a]. For example, giant pandas (*Ailuropoda melanoleuca*) synchronize their migration and reproduction cycles with seasonal nutrient availability between different bamboo species [Nie et al., 2015]. 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 [Welti et al., 2020b, Zhou et al., 2019]. 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 [Andersen et al., 2004, White, 1993]. Phosphorus and nitrogen commonly limit primary production in ecosystems, either separately or as co-

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

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

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

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

- 91 1) What are the nutritional preferences of individuals from gregarious *C. terminifera* field populations? We
 92 expect individuals to be carbohydrate biased based on their active lifestyle, and to keep a constant intake
 93 target between populations.

- 94 2) What happens to *C. terminifera* when constrained to high nitrogen environments? We expect locusts to select
 95 particularly carbohydrate biased diets to redress a protein : carbohydrate imbalance in their local environment.
 96 3) Can we use soil nutrients as a predictor of *C. terminifera* nymph outbreaks at the continental scale?

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

102 2 METHODS

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

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

Table 1: Replication statement for all scales of interest

106 2.1 Field site and animals

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

112 2.2 Nutritional target and performance curve using synthetic diets

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

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

127 2.2.1 Nutrition target (choice diets)

128 We ran this experiment to determine the preferred dietary p:c ratio of *C. terminifera* field populations. We selected
 129 equal numbers of males and females from both Mendooran and Guntawang populations and individuals that had no
 130 visible wing bud separation to ensure they were early in the fifth instar. Locusts were heated with incandescent light
 131 bulbs on a 14:10 light:dark cycle. The average daytime and nighttime temperatures in the cages were 25.5°C and
 132 23.4°C respectively, recorded from an iButton (Maxim). We randomly assigned 80 locusts (20 individuals per diet pair
 133 per population) to one of two treatment groups receiving pairs of either 7p:35c & 28p:14c or 7p:35c & 35p:7c (% p :
 134 % c by dry mass). We used two different pairs to ensure that the selected p:c ratio was not the result of eating randomly
 135 between the two dishes. We let locusts eat from the dishes for three days (Nov. 12-15, 2015) and calculated the mass
 136 of protein and carbohydrate each locust ate by subtracting the final dish weights from the initial dish weights.

137 **2.2.2 Performance curve (no-choice diets)**

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

150 **2.3 Field cage experiments**

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

159 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
 160 ground by partially burying it and nailing thin slats of wood over the mesh edges. Before adding locusts to the cages,
 161 we removed any plant litter and arthropods (mostly spiders and locusts) so we could more easily count the locusts
 162 and limit predation. We added 20 4th instar locust nymphs to each field cage on the evening of November 13th and
 163 morning of November 14th. We randomly selected these nymphs from the Mendooran population we collected on
 164 November 12th (see synthetic diet methods section above). Each fertilized plot had four cages, for a total of 12 cages
 165 per fertilization level, and 36 cages and 720 locusts in total. We checked the cages every 4-5 days and removed any
 166 spiders.

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

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

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

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

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

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

186 **2.4 Correlating historical nymphal outbreaks with soil nitrogen and phosphorus**

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

190 **2.4.1 Locust outbreak data**

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

205 **2.4.2 Soil grid of Australia data**

206 The soil and landscape grid of Australia is a modeled raster of 12 soil variables at a 90 m² resolution. These soil charac-
 207 teristics are available at multiple depths from surface to two meters below the surface. These depths and methodology
 208 are consistent with the specifications of the Global Soil Map project (<http://www.globalsoilmap.net>) [Grundy et al.,
 209 2015]. We extracted this data from Google Earth Engine [Gorelick et al., 2017]. In this data set both phosphorus
 210 and nitrogen units are the mass fraction of total nutrient in the soil by weight. We took the average of nitrogen and
 211 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
 212 grasses and forbs. Then, for each APLC survey grid we calculated the mean mass fraction of nitrogen and phosphorus
 213 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
 214 C respectively.

215 **2.5 Statistics**

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

220 **2.5.1 Intake Targets**

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

227 **2.5.2 Field population**

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

231 **2.5.3 Field Cage Experiments**

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

240 and included the following variables: treatment (factor) and a two-dimensional smoother of available protein and
 241 carbohydrate.

242 **2.5.4 Historical outbreaks and soil nutrient grid modeling**

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

259 **3 RESULTS**

260 **3.1 Field population**

261 **3.1.1 Choice experiment (nutritional target)**

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

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

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

267 **3.1.2 No choice experiment (performance curves)**

268 *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 Table 4). Development time and specific growth rate did not differ between male and female locusts (Supplementary Figure 3 C & D, Table 3).

| Specific Growth Rate | Development Time |
|----------------------|------------------|
|----------------------|------------------|

| variable | 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.

272 3.2 Field Cage

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

| macronutrient | variable | estimate | SE | statistic | p-value |
|---------------|-------------------|----------|-------|-----------|---------|
| carbohydrate | Intercept | 0.127 | 0.007 | | 0.000 |
| | Medium | -0.020 | 0.007 | | 0.005 |
| | High | -0.011 | 0.007 | | 0.121 |
| | 2015-11-25 | -0.009 | 0.007 | | 0.181 |
| | 2015-12-01 | -0.012 | 0.006 | | 0.033 |
| | Medium:2015-11-25 | 0.019 | 0.010 | | 0.063 |
| | High:2015-11-25 | 0.004 | 0.010 | | 0.656 |
| | Medium:2015-12-01 | 0.019 | 0.008 | | 0.017 |
| | High:2015-12-01 | 0.010 | 0.008 | | 0.222 |
| | s(species) | | | 67.305 | 0.000 |
| protein | s(plot) | | | 1.643 | 0.207 |
| | s(cage) | | | 3.442 | 0.130 |
| | Intercept | 0.209 | 0.017 | | 0.000 |
| | Medium | -0.001 | 0.014 | | 0.928 |
| | High | -0.034 | 0.014 | | 0.014 |
| | 2015-11-25 | 0.026 | 0.010 | | 0.014 |
| | 2015-12-01 | -0.049 | 0.009 | | 0.000 |
| | Medium:2015-11-25 | -0.012 | 0.015 | | 0.422 |
| | High:2015-11-25 | -0.023 | 0.015 | | 0.123 |
| | Medium:2015-12-01 | 0.008 | 0.013 | | 0.516 |
| | High:2015-12-01 | 0.056 | 0.013 | | 0.000 |
| | s(species) | | | 307.929 | 0.000 |
| | s(plot) | | | 214.489 | 0.000 |

| | | |
|---------|--------|-------|
| s(cage) | 89.944 | 0.000 |
|---------|--------|-------|

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

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

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

| macronutrient | variable | estimate | SE | statistic | p-value |
|---------------|-----------|----------|-------|-----------|---------|
| carbohydrate | Intercept | 0.013 | 0.004 | | 0.001 |
| | male | -0.011 | 0.004 | | 0.009 |
| | day 2 | 0.007 | 0.003 | | 0.008 |
| | day 3-4 | 0.016 | 0.003 | | 0.000 |
| | day 5-6 | 0.026 | 0.003 | | 0.000 |
| | day 7-9 | 0.035 | 0.003 | | 0.000 |
| | none | -0.006 | 0.004 | | 0.136 |
| | s(id) | | | 484.706 | 0.000 |
| | | | | | |
| 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.

3.3 Locust outbreaks

Chortoicetes terminifera outbreaks were negatively associated with soil nitrogen, which supports the hypothesis that nitrogen (in excess) acts as a limiting factor for population upsurges (Table 7, Figure 5 A). *C. terminiferas* had a nonlinear 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).

289 The relationship between locust outbreaks and mean annual precipitation was very different from the relationship with
 290 soil nitrogen (Figure 5, Supplementary Figure 8). Soil nitrogen and phosphorus show weak positive correlations with
 291 woody vegetation cover, while mean annual precipitation exhibits high variation in its relationship with soil nitrogen
 292 and weak correlation with soil phosphorus (Supplementary Figure 5). Thus, the relationship between soil nitrogen and
 293 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.

294 4 DISCUSSION

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

304 4.1 Field populations

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

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

315 Importantly, all field cage plants were protein biased (roughly 1p : 1c to 2p : 1c) as compared to the desired locust
 316 intake target of 1p : 2c. When locusts were subsampled from the field cages mid-experiment and given the opportunity
 317 to select carbohydrate or protein diets, they selected extremely carbohydrate-biased diets for more than a week. This
 318 behavior indicated that locusts in the small field cages were highly carbohydrate-limited, driving them to overeat
 319 carbohydrates to redress the imbalance. Interestingly, multiple studies have shown that the Australian nutritional
 320 landscape is often too protein-biased relative to what the *C. terminifera* prefers [Lawton et al., 2020, 2021]. Regardless,
 321 populations are still persistent and outbreaks can occur at lower frequencies in these areas [Deveson, 2013, Key,
 322 1945]. How this species can achieve the optimal balance of nutrients within an unfavorable nutritional environment
 323 merits further investigation, but may include post-ingestive regulation and/or large-range foraging. Migratory locusts
 324 (*Locusta migratoria*) can choose microclimates that favor higher efficiency of carbohydrate or protein absorption
 325 depending on their host plant and nutritional status [Clissold et al., 2013]. For this study, we collected free-living
 326 locusts from the same region and a similar environment as where we built the field cages, yet those confined to field
 327 cages selected a 10x decrease in p:c (1p : 20c vs 1p : 2c). This result suggests that free-living locusts are able to persist
 328 in high protein regions by foraging over a larger range to seek out pockets of carbohydrate-rich plants and that the

329 limited foraging range of the field cages precluded field-cage locusts from finding sufficient carbohydrates. Similarly,
 330 these results suggest that, while *C. terminifera* can persist in low numbers in nitrogen rich regions, those environments
 331 are unlikely to support extreme outbreaks due to a limitation of carbohydrate-rich resources. We tested this prediction
 332 using historical outbreak and large-scale soil nutrient modeling.

333 **4.2 Historical outbreak modeling**

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

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

364 **4.3 Locusts are more likely to be limited by high nitrogen environments than other grasshoppers**

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

385 **4.4 Comparing the relationship between plant macronutrients and herbivore abundance in other taxa**

386 The effect of plant protein and carbohydrate on herbivore populations is predicted to depend on the herbivore's p:c
 387 intake target (IT) relative to its nutritional landscape (Le Gall et al., 2020). If there are sufficient plants on either side
 388 of the IT, herbivores can select from between them to achieve their IT. This complementary feeding has been recorded
 389 for field populations of blue sheep (*Pseudois nayaur*) in the Himalayan Mountains [Aryal et al., 2015], Black Howler
 390 Monkeys (*Alouatta pigra*) in Yucatán [Bridgeman, 2012], and other primates [Raubenheimer and Rothman, 2013].
 391 There would be a predicted impact on populations if the nutritional landscape were to become more constricted or
 392 not overlap with the IT. For example, lab colonies of tobacco hornworms (*Manduca sexta* larvae) have an IT around
 393 1:1 or sometimes slightly carbohydrate-biased [Wilson et al., 2019a] and their host plants tend to be carbohydrate-
 394 biased relative to their IT [Wilson et al., 2019b]. However, this does not seem to translate to population level effects,
 395 potentially due to secondary metabolites affecting growth more strongly than macronutrient balance and/or larvae may
 396 be able to compensate by overeating carbohydrates to acquire sufficient protein [Wilson et al., 2019a]. Overeating
 397 carbohydrates is not as detrimental as overeating protein, at least in the short term, and animals tend to be willing
 398 to overeat carbohydrates to a greater extent than protein [Cheng et al., 2008, Simpson and Raubenheimer, 2012b].
 399 Therefore, herbivores facing a nutritional landscape with a p:c generally lower than their IT (i.e., carbohydrate excess)
 400 may not be as negatively impacted as herbivores facing one higher than their IT (i.e., protein excess). However,
 401 there are several examples of higher localized densities of herbivores in response to higher plant nitrogen and protein
 402 contents with thrips [Brown et al., 2002] and spruce budworm (*Choristoneura*) [De Grandpré et al., 2022] being two
 403 examples. These examples suggest that low p:c diets limit population growth of some herbivores, but more studies
 404 are needed to determine if this relationship is only localized or if it scales up. It may be that herbivore populations
 405 with lower numbers are not limited by a nutritional landscape at a large scale because they can differentially disperse
 406 locally among optimal patches, whereas herbivore populations with extreme numbers (i.e., irruptions) may be more
 407 limited by nutritionally unfavorable environments across scales.

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

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

429 **4.5 Synthesis and Application**

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

442 populations from reaching outbreak sizes and should be considered across scales, from individual locust behavior to
 443 continental-wide plagues.

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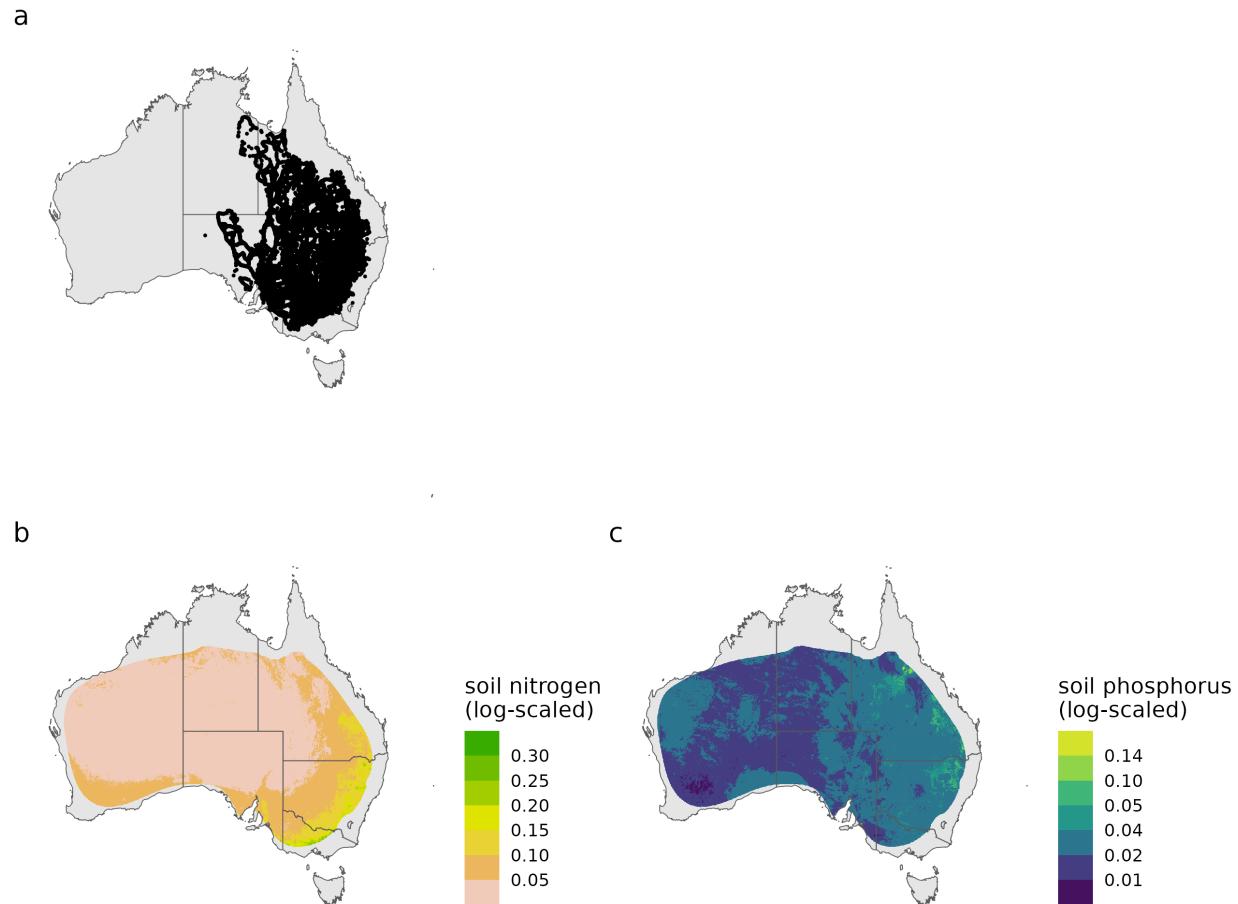
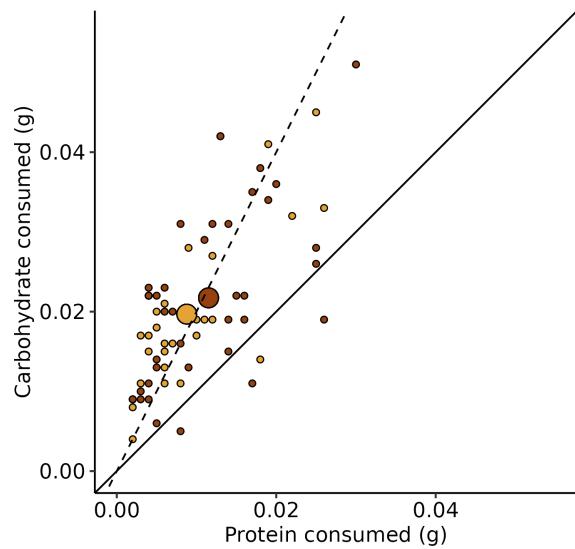


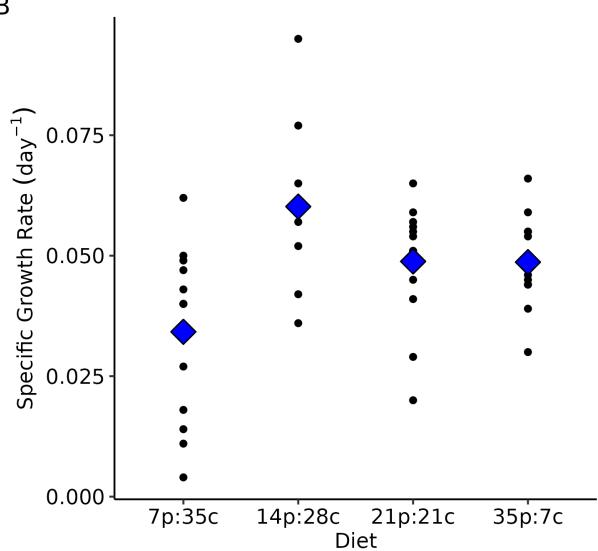
Figure 1: Locust survey data map and soil nutrients throughout the *C. terminifera* distribution. A: APLC survey dataset, B: mean proportion of nitrogen at 0-15 cm deep, C: mean proportion phosphorous at 0-15cm deep.

A

population Guntawang Mendooran



B



C

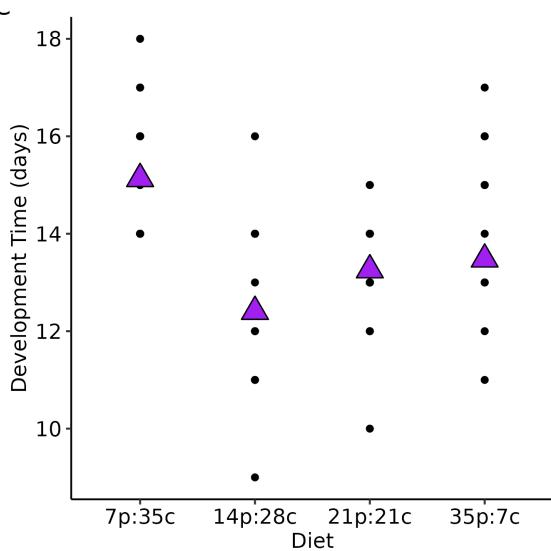


Figure 2: The nutritional preference (A) and physiological performance (B & C) of *C. terminifera* individuals that were collected from two marching bands of 5th instars. Raw data is shown as black dots with modeled estimated marginal means as large diamonds or triangles.

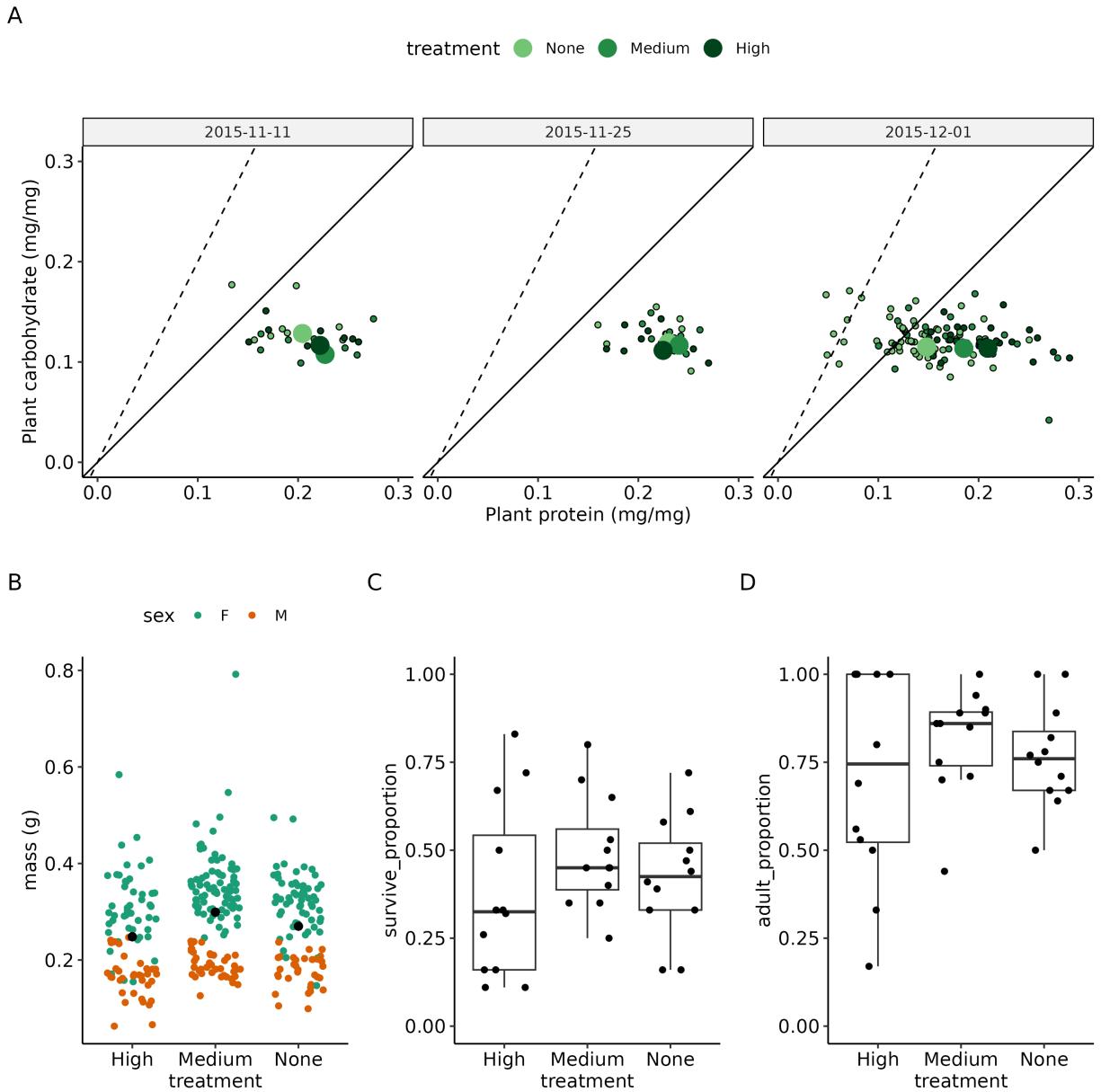


Figure 3: Nitrogen addition field cage experiments with plant nutrient change through time (A) and grasshopper performance metrics (B-C) are shown. Dashed line represents a 1p : 2c ratio, the solid line represents a 1p : 1c ratio. Black dots in B represent overall means whereas boxplots represent the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

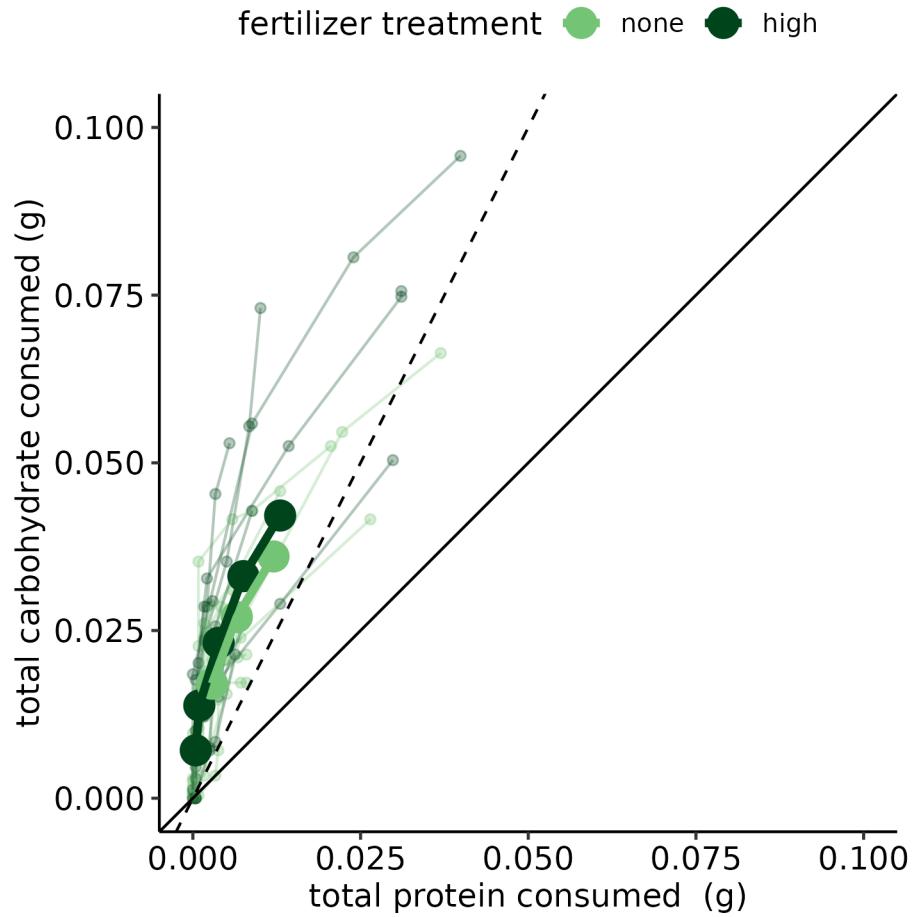
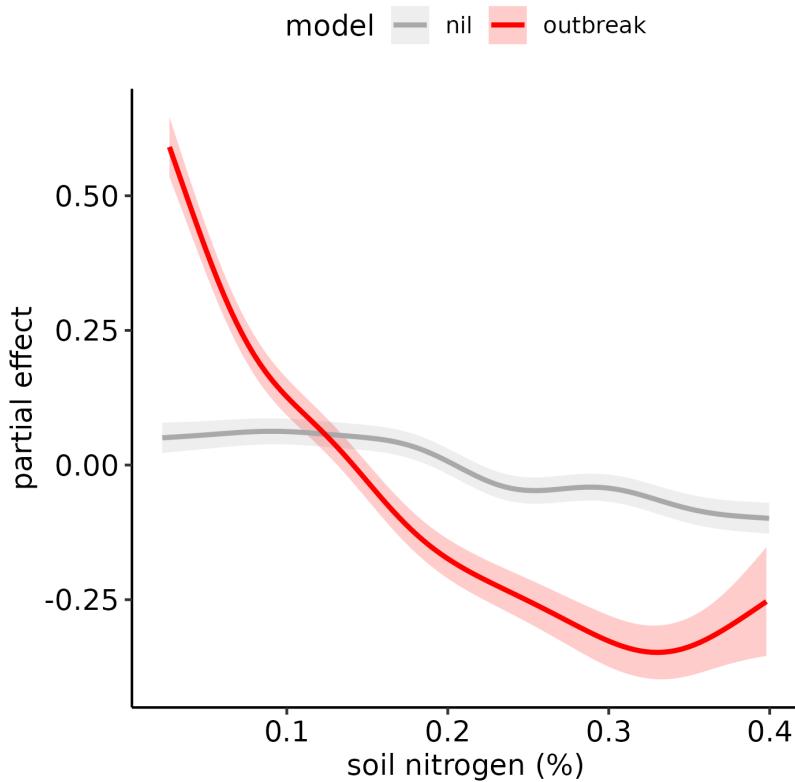


Figure 4: Nutrient imbalance redressing with artificial diet mixing of *C. terminifera* individuals taken from fertilized treatment cages. Colors represent fertilizer treatment. Smaller lines represent raw individual locust intake targets; large lines and points represent estimated marginal means. Points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

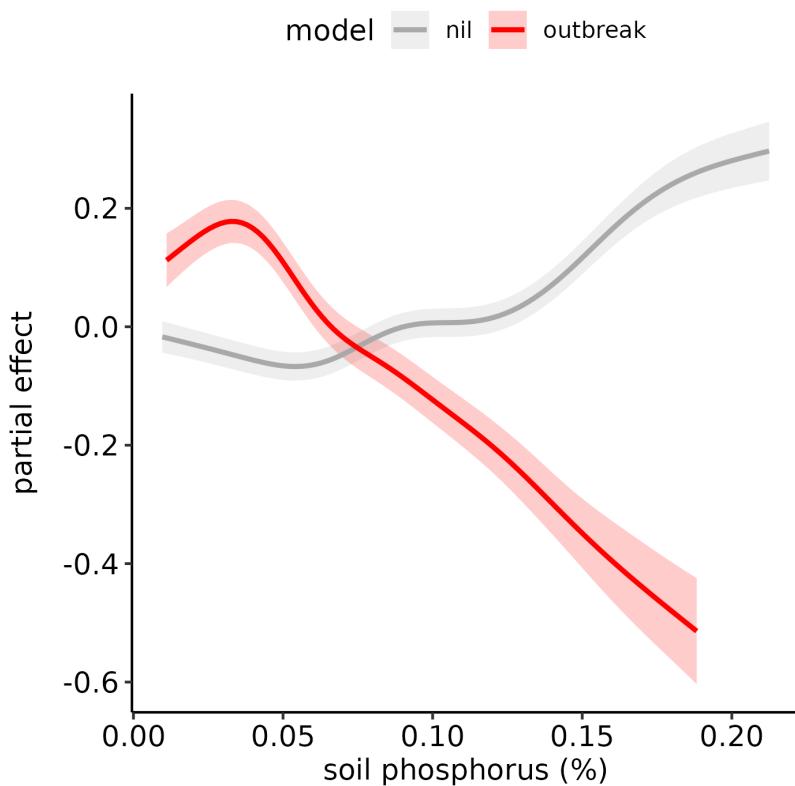
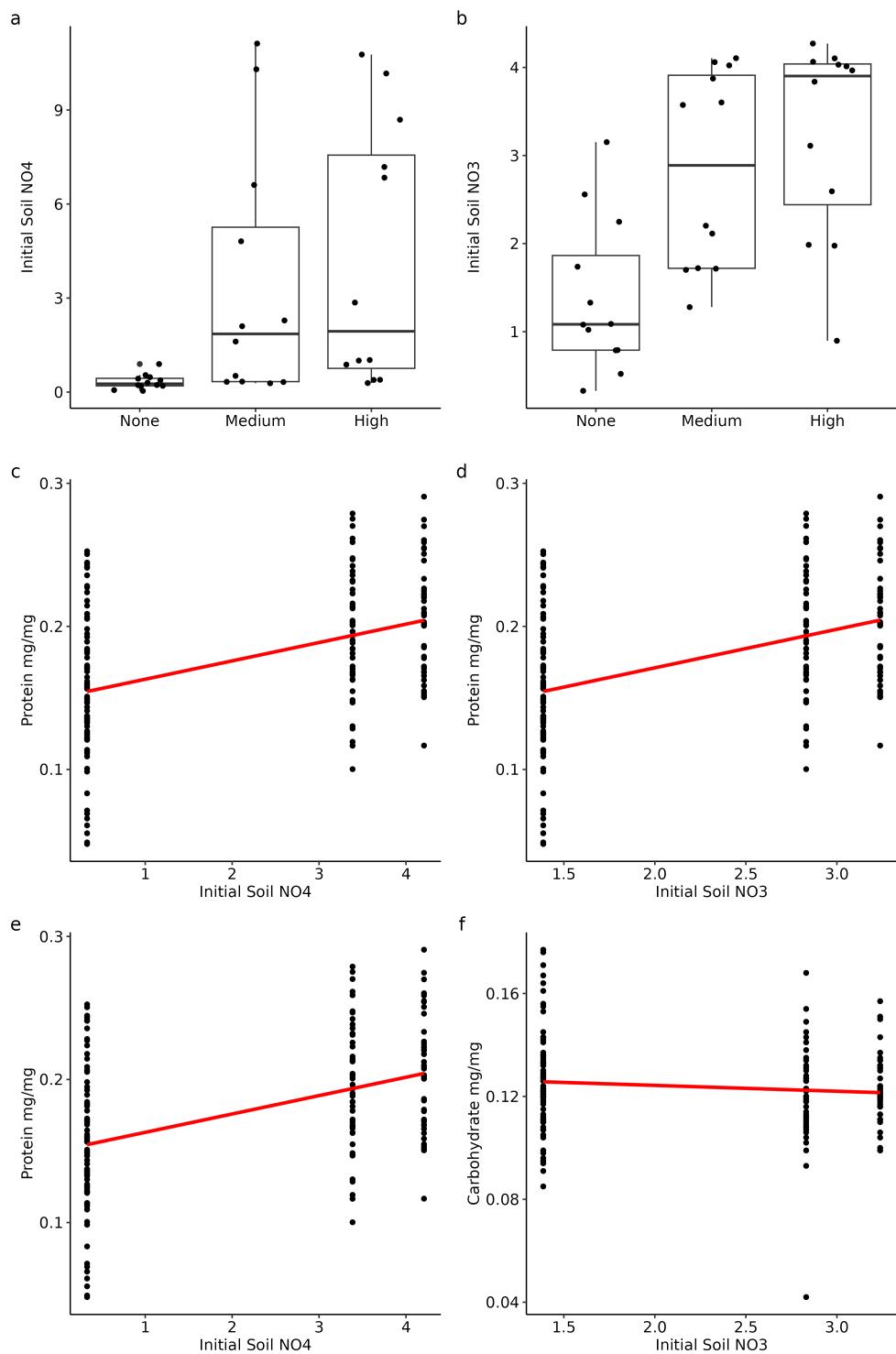
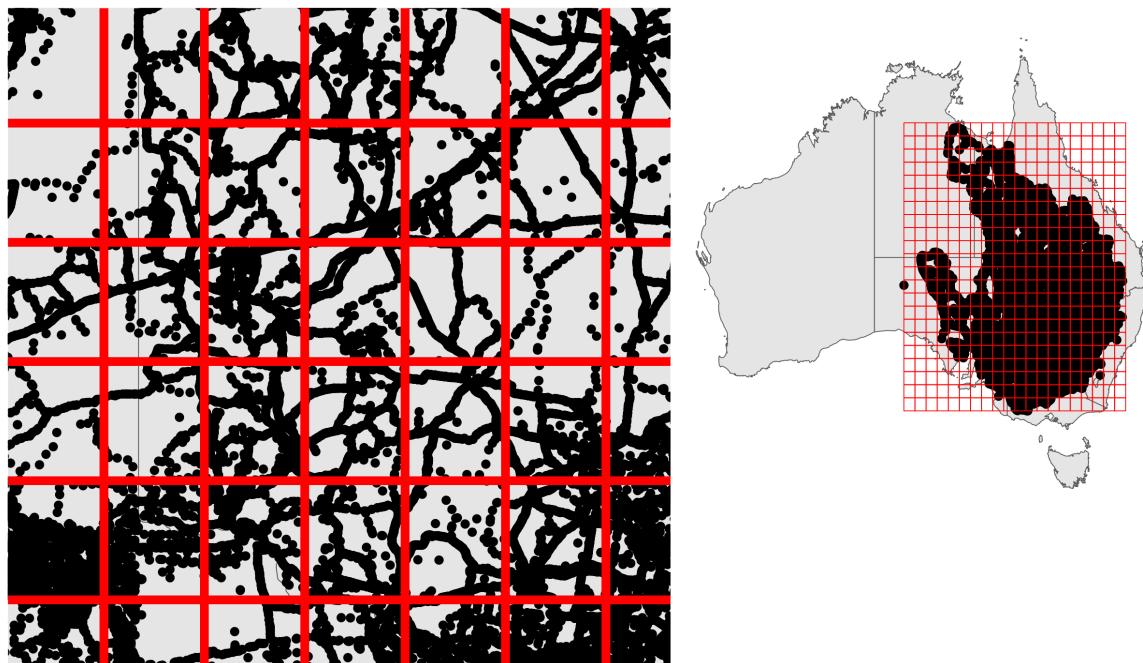


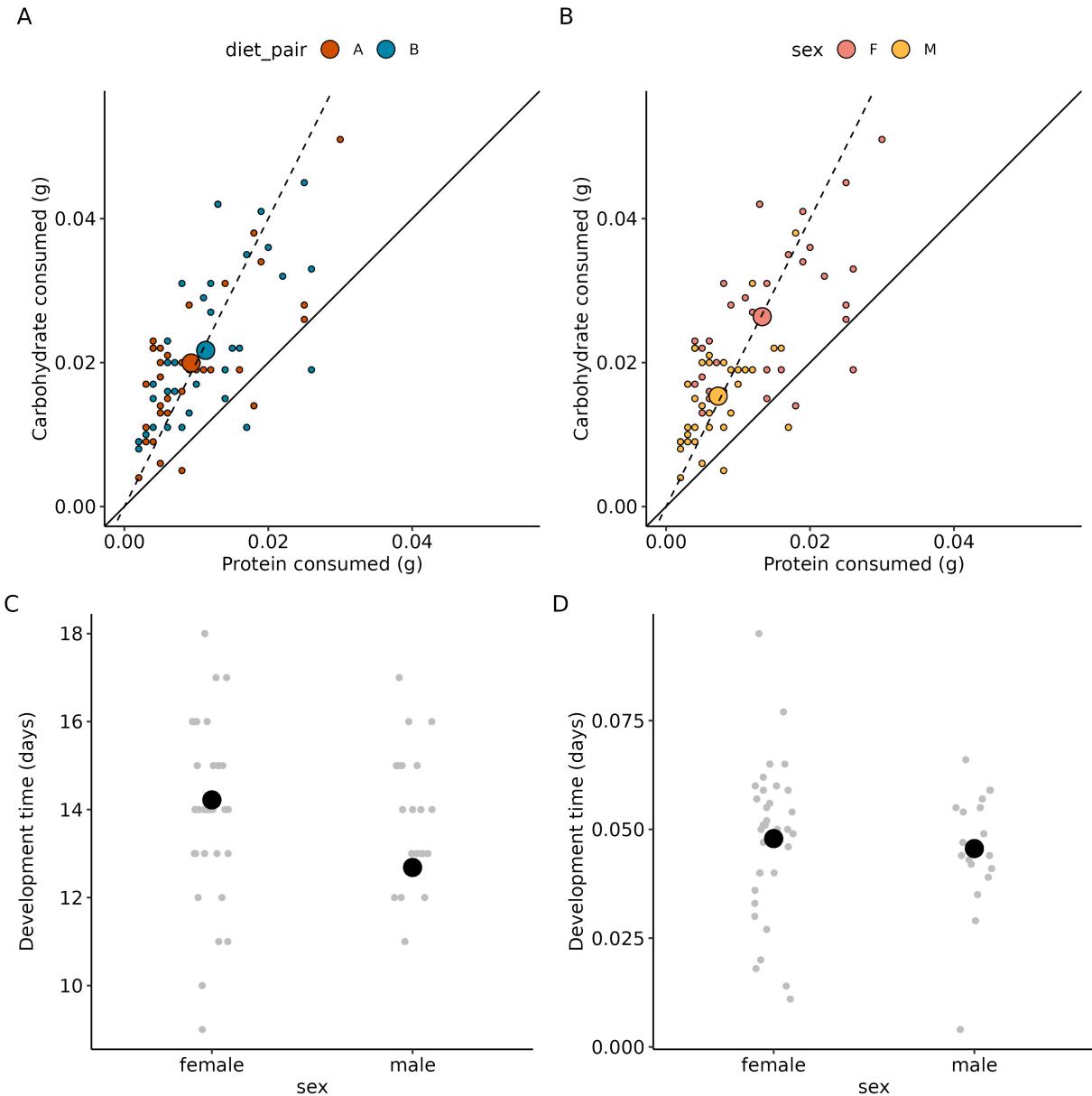
Figure 5: Relationship between outbreaks and nil observations for both soil nitrogen (A) and phosphorus (B). Partial effect is the modeled predictions after accounting for bioregion and spatial autocorrelation.



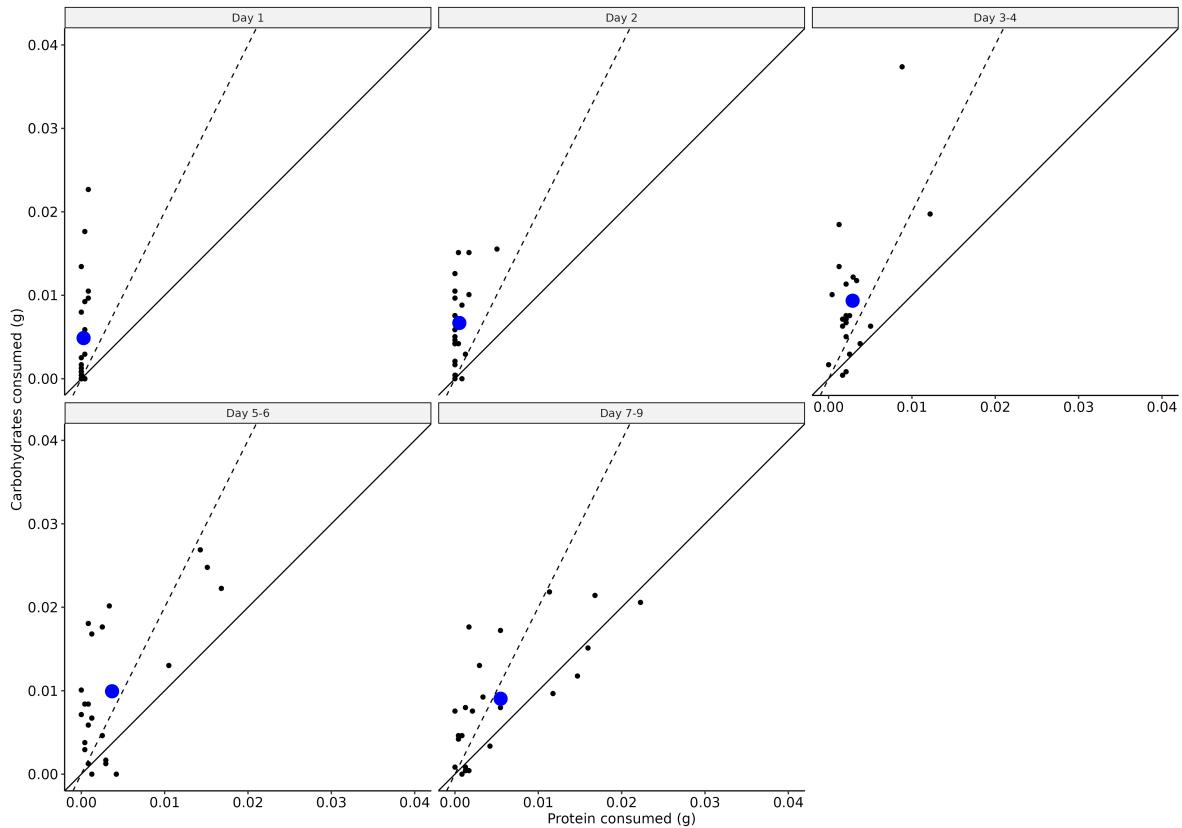
Supplementary Figure 1: Field cage soil nitrogen content by treatment (A & B) and regressed with plant carbohydrates and protein (C-F).



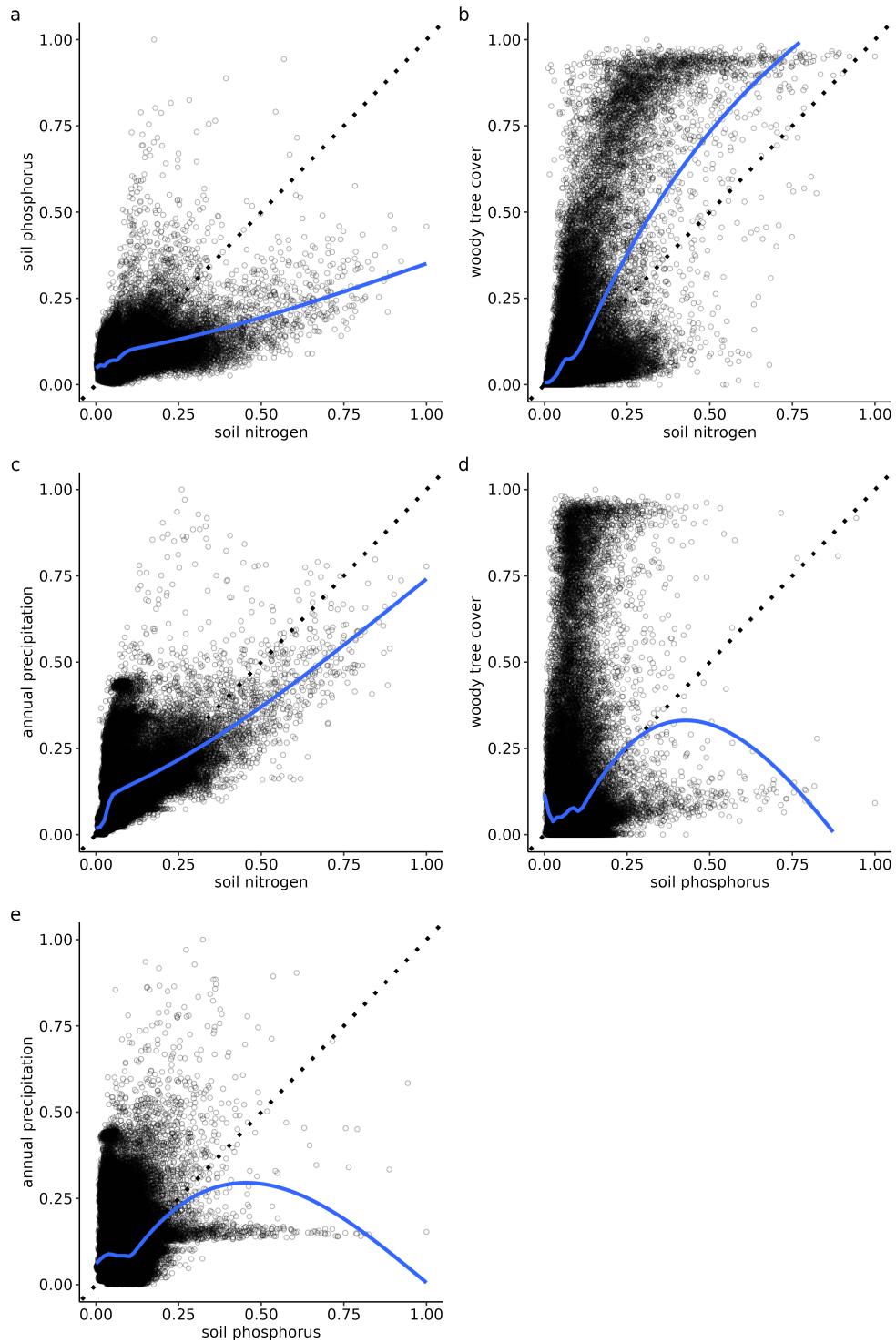
Supplementary Figure 2: Map illustrating the summarization of point observation data into a fishnet grid across eastern Australia. The full extent is shown in the inset map. We summed the number of outbreak, nil, and total observations. The grid in this figure is not at a 1 km^2 scale for demonstration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



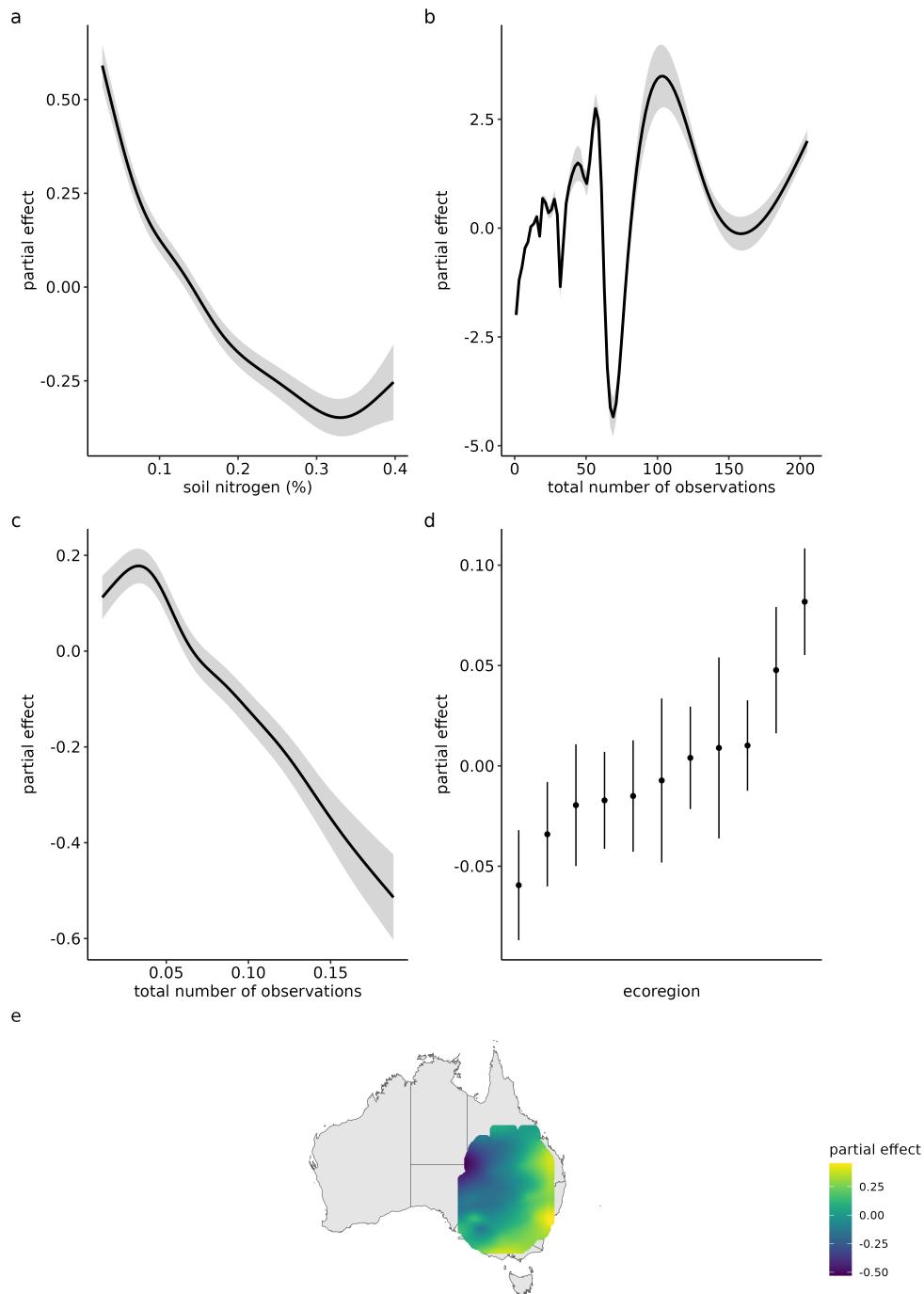
Supplementary Figure 3: Nutrient consumption for outbreaking field populations of *C. terminifera* by diet pair (A) and sex (B) and development time (C) specific growth rate (D) by sex. The P:C ratio did not differ between diet pairing and sex. Females consumed more diet (but kept the same ratio) than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



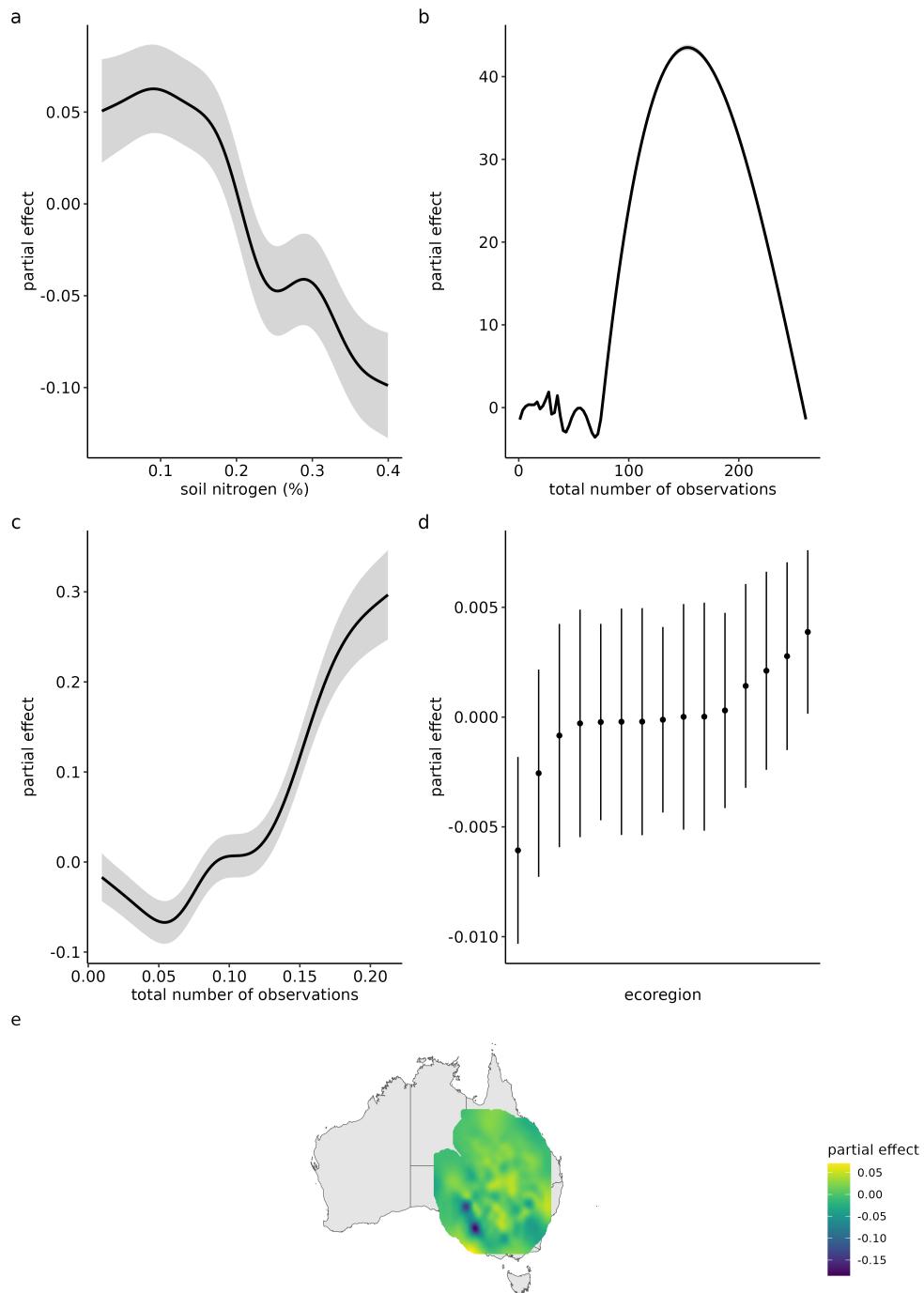
Supplementary Figure 4: Individual time step intake targets for grasshoppers kept in both high nitrogen fertilization and control cages. Blue dots represent estimated marginal means from the model while blacks dots represent raw individual intake targets.



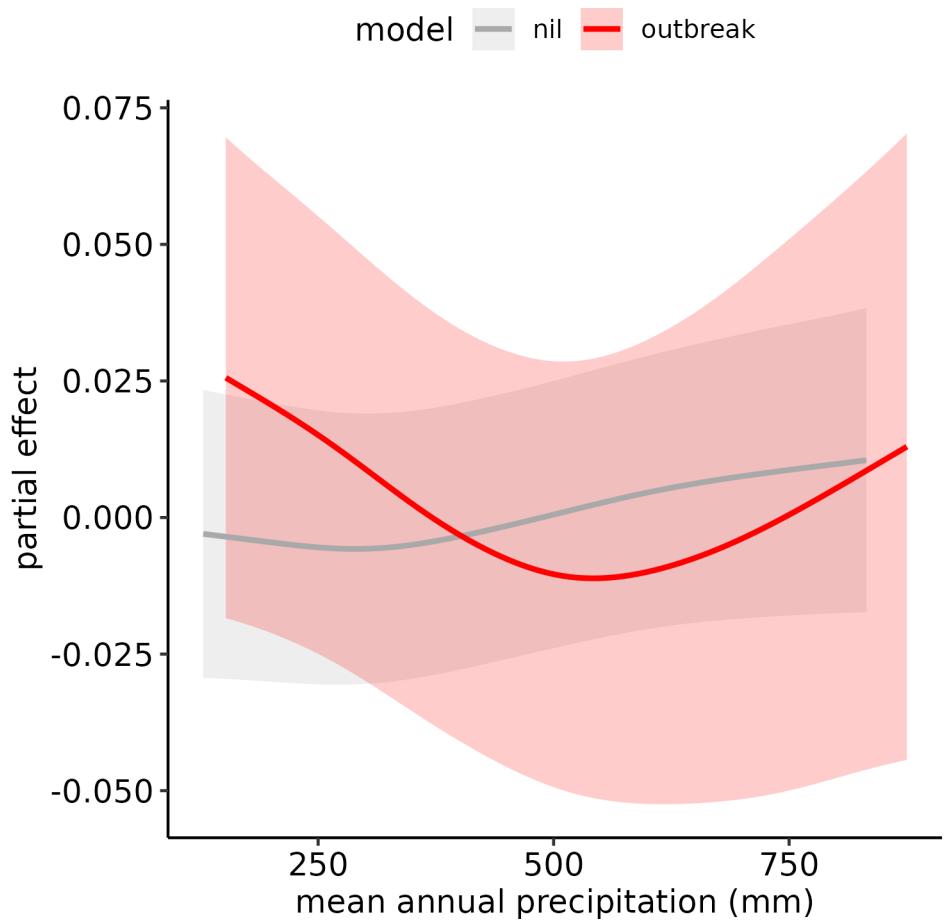
Supplementary Figure 5: Environmental variable correlations between mean annual precipitation, soil nitrogen, soil phosphorus, and woody vegetation pixel coverage. Mean annual precipitation was sourced from WorldClim V1 Bio-clim, soil nitrogen and phosphorus was sourced from Soil and Landscape Grid of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