
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 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, 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 ochingaster*)
 42 densities compared to control fields by supporting higher adult survival, increased breeding, and growth rate [Cole and
 43 Batzli, 1978]. A decrease in phosphorus in the host plant of the dryland insect herbivore *Sabinia setosa*—velvet
 44 mesquite (*Prosopis velutina*)—results in lower RNA content, slower growth, and reduced abundance in the in-
 45 sect population [Schade et al. [2003]. Nonlinear relationships between phosphorus availability and herbivore
 46 abundance has been documented, for example insufficient phosphorus limits RNA production and growth, while
 47 excessive phosphorus disrupts nutrient homeostasis and reduces fitness, as demonstrated in laboratory studies
 48 of locusts [Cease et al., 2016]. Phosphorus plays a vital role in RNA synthesis, energy storage and transfer via
 49 ATP, and numerous cellular processes, making it essential for animal growth and reproduction. For herbivo-
 50 rous insects, phosphorus-rich plant tissue is particularly important, as it supports their rapid growth and high
 51 reproductive rates [Sterner and Elser, 2003, Andersen et al., 2004]. More broadly, nitrogen and phosphorus limita-
 52 tion has been shown in mammals [Randolph et al., 1995, White, 1993], birds [Forero et al., 2002, Granbom and Smith,
 53 2006], and insects [Floyd [1996]; Huberty and Denno [2006]; Marsh and Adams [1995]; ; Perkins et al. [2004]] which
 54 is discussed further in White [2008] and Andersen et al. [2004]. However, not all animal populations respond posi-
 55 tively to increasing environmental nutrients. For example, studies from across the globe reveal that the abundances of
 56 many grasshopper species are positively [Joern et al., 2012, Ozment et al., 2021, Welti et al., 2020a,b, Zhu et al., 2020b,
 57 2019], or not related [Heidorn and Joern, 1987, Jonas and Joern, 2008, Lenhart et al., 2015, Ozment et al., 2021] to
 58 plant nitrogen concentrations as reviewed in Cease [2024]. Can the relationship between herbivore abundance and
 59 environmental nutrients be explained by approaches that consider nutritional physiology at the organismal level, in
 60 addition to population and landscape ecology?

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

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

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

- 99 1) What are the nutritional preferences of individuals from gregarious *C. terminifera* field populations? We
 100 expect individuals to be carbohydrate biased based on their active lifestyle, and to keep a constant intake
 101 target between populations.
- 102 2) **What happens to *C. terminifera* when constrained to high-nitrogen environments?** Since at the individual level, locusts are often confronted with sub-optimal nutritional situations like high-nitrogen
 103 environments, locusts will prefer carbohydrate-rich diets to correct protein-carbohydrate imbalances.
- 104 3) **Can we use soil nutrients as a predictor of *C. terminifera* nymph outbreaks at the continental scale?** We expect outbreaks to be negatively correlated with soil nitrogen at this level.
- 105 4) **What are the large-scale patterns of *C. terminifera* outbreaks, accounting for climatic factors?** We expect outbreaks to be associated with low-nitrogen areas, as terrestrial herbivores
 106 often require significantly more nitrogen than phosphorus [elser_nutritional_2000]. Given locusts' capacity to post-ingestively regulate phosphorus within natural ranges [cease_dietary_2016;
 107 zhang_grasshoppers_2014], we predict nitrogen to be a stronger predictor of population dynamics
 108 at the continental scale.

113 2 METHODS

114 Details regarding the scales of inference, the application of factors of interest, and the corresponding replicates can be
 115 found in Table 1. This table outlines the hierarchical structure of our experimental design across individual, population,
 116 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

117 2.1 Field site and animals (Question 2 and 3)

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

124 2.2 Nutritional target and performance curve using synthetic diets (Question 2 and 3)

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

129 We collected fourth and fifth instar nymphs from outbreeding populations on Nov. 12, 2015 from two locations: near
 130 Mendooran (31°40.791' S, 149°04.209' E) and Guntawang (32°23.988' S, 149°28.649' E), New South Wales. The
 131 Mendooran population was forming marching bands while the Guntawang population was at high density but was not
 132 actively marching during the collection period. Both populations were collected along dirt roads flanked by livestock
 133 grazing pastures containing a mix of grasses and forbs. We transported locusts back to the Trangie Agricultural
 134 Research Centre and kept them in large plastic bins with holes along with an assortment of grasses and forbs cut
 135 from the same field locusts were collected until experiments were started. For both experiments, locusts were housed
 136 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
 137 (nutritional target) or one (performance curve) artificial diets, a water tube capped with cotton, and a perch.

138 **2.2.1 Nutrition target (choice diets)**

139 We ran this experiment to determine the preferred dietary p:c ratio of *C. terminifera* field populations. We selected
 140 equal numbers of males and females from both Mendooran and Guntawang populations and individuals that had no
 141 visible wing bud separation to ensure they were early in the fifth instar. Locusts were heated with incandescent light
 142 bulbs on a 14:10 light:dark cycle. The average daytime and nighttime temperatures in the cages were 25.5°C and
 143 23.4°C respectively, recorded from an iButton (Maxim). We randomly assigned 80 locusts (20 individuals per diet pair
 144 per population) to one of two treatment groups receiving pairs of either 7p:35c & 28p:14c or 7p:35c & 35p:7c (% p :
 145 % c by dry mass). We used two different pairs to ensure that the selected p:c ratio was not the result of eating randomly
 146 between the two dishes. We let locusts eat from the dishes for three days (Nov. 12-15, 2015) and calculated the mass
 147 of protein and carbohydrate each locust ate by subtracting the final dish weights from the initial dish weights.

148 **2.2.2 Performance curve (no-choice diets)**

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

161 **2.3 Field cage experiments (Question 2)**

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

170 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
 171 ground by partially burying it and nailing thin slats of wood over the mesh edges. We removed any plant litter and
 172 arthropods (mostly spiders and locusts) so we could more easily count the locusts and limit predation. This removal
 173 may have also affected factors such as light availability for plants and soil temperature, which could have influenced
 174 plant growth and other ecological dynamics. We added 20 4th instar locust nymphs to each field cage on the evening of
 175 November 13th and morning of November 14th. We randomly selected these nymphs from the Mendooran population
 176 we collected on November 12th (see synthetic diet methods section above). Each fertilized plot had four cages, for a
 177 total of 12 cages per fertilization level, and 36 cages and 720 locusts in total. We checked the cages every 4-5 days
 178 and removed any spiders.

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

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

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

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

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

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

198 **2.4 Correlating historical nymphal outbreaks with soil nitrogen and phosphorus (Questions 3 and 4)**

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

202 **2.4.1 Locust outbreak data**

203 *Chortoicetes terminifera* data from 2000 - 2017 (~ 190,000 records) were used in this study. This database contains
 204 georeferenced points with a categorical ordinal variable 0-4 to represent approximate nymph densities. The value
 205 ranges for nymphs are: 0 = nil, 1 = < 5 m², 2 = 5-30 m², 3 = 31-80 m², and 4 = > 80 m². Population outbreaks are
 206 characterized by very high densities of gregarious nymphs (up to 1000 m²). We focused on nymphs as this life stage
 207 cannot fly and can be used to assess prior local habitat conditions. While the database extends into the 1980s, we only
 208 used data collected between 2000-2017 as this period overlapped with the soil grid data which was released in 2015
 209 to account for any potential shifts in soil nutrient composition. Since climatic conditions and migration patterns are
 210 drivers in outbreak occurrence [Lawton et al., 2022, Veran et al., 2015] they likely mask the relationship between static
 211 environmental variables like soil nutrients. To account for this variability, we spatially aggregated the survey dataset
 212 to a 1 km² grid as can be seen in Supplementary Figure 2. This allowed us to model how often locust outbreaks occur
 213 in grid cells rather than the actual outbreak. We used a 1 km² grid as this reflects the estimated maximum dispersal
 214 distance from hatching to 5th instar [Hunter et al., 2008]. **Since it is often difficult to accurately assess categories**
 215 **2-3 given the small differences in densities, We counted the number of outbreaks (APLC nymph density code**
 216 **4), the number of nil records (APLC nymph density code 0), and total number of survey observations.** This
 217 resulted in approximately 67,000 grid cells for the final dataset. Overall APLC survey point distribution can be seen
 218 in Figure 1 A.

219 **2.4.2 Soil grid of Australia data**

220 The soil and landscape grid of Australia is a modeled raster of 12 soil variables at a 90 m² resolution. These soil charac-
 221 teristics are available at multiple depths from surface to two meters below the surface. These depths and methodology
 222 are consistent with the specifications of the Global Soil Map project (<http://www.globalsoilmap.net>) [Grundy et al.,
 223 2015]. We extracted this data from Google Earth Engine [Gorelick et al., 2017]. In this data set both phosphorus
 224 and nitrogen units are the mass fraction of total nutrient in the soil by weight. We took the average of nitrogen and
 225 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
 226 grasses and forbs. Then, for each APLC survey grid we calculated the mean mass fraction of nitrogen and phosphorus
 227 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
 228 C respectively.

229 **2.5 Statistics**

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

234 **2.5.1 Intake Targets (Question one and two)**

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

241 **2.5.2 Field population (Question one)**

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

245 **2.5.3 Field Cage Experiments (Question 2)**

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

256 **2.5.4 Historical outbreaks and soil nutrient grid modeling (Questions 3 and 4)**

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

273 **3 RESULTS**

274 **3.1 Field population (Question 1)**

275 **3.1.1 Choice experiment (nutritional target)**

276 *Chortoicetes terminifera* individuals from the two outbreeding populations regulated to a specific ratio of 1 protein
 277 : 2 carbohydrate (Figure 2 A, Table 2). Model selection can be seen in Supplementary Table 3. **Consumption in**
 278 **the two diet pairings did not differ, indicating that instead of consuming between the diets randomly (which**
 279 **would be expected if nutrients had no impact on diet consumption) locusts were actively balancing their protein**
 280 **and carbohydrate consumption (Supplementary Figure 3 A, Table 2).** While the protein : carbohydrate ratio did
 281 not change, females consumed more food than males, likely due to being bigger overall (Supplementary Figure 3 B,
 282 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
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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.

3.1.2 No choice experiment (performance curves)

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).

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.

3.2 Field Cage (Question 2)

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

protein	s(cage)			3.442	0.130
	Intercept	0.209	0.017		0.000
	Medium	-0.001	0.014		0.928
	High	-0.034	0.014		0.014
	2015-11-25	0.026	0.010		0.014
	2015-12-01	-0.049	0.009		0.000
	Medium:2015-11-25	-0.012	0.015		0.422
	High:2015-11-25	-0.023	0.015		0.123
	Medium:2015-12-01	0.008	0.013		0.516
	High:2015-12-01	0.056	0.013		0.000
	s(species)			307.929	0.000
	s(plot)			214.489	0.000
	s(cage)			89.944	0.000

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

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

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

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

none	-0.001	0.001	0.475
s(id)		110.728	0.381

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

297 3.3 Locust outbreaks (Question 3 and 4)

298 *Chortoicetes terminifera* outbreaks were negatively associated with soil nitrogen, which supports the hypothesis that
 299 nitrogen (in excess) acts as a limiting factor for population upsurges (Table 7, Figure 5 A). *C. terminiferas* had a
 300 nonlinear relationship with soil phosphorus with outbreaks occurring more often in areas with approximately 4% soil
 301 phosphorus and were strongly negatively associated with increasing phosphorus afterwards (Figure 5 B). For both
 302 nutrients, the absence models had a very weak relationship with soil nutrient in comparison to the outbreak models,
 303 demonstrating little model bias due to APLC survey protocol. There were significant nonlinear relationships between
 304 coordinates and the total number of observations in all models (Supplementary Figure 6; Supplementary Figure 7).
 305 The relationship between locust outbreaks and mean annual precipitation was very different from the relationship with
 306 soil nitrogen (Figure 5, Supplementary Figure 8). Soil nitrogen and phosphorus show weak positive correlations with
 307 woody vegetation cover, while mean annual precipitation exhibits high variation in its relationship with soil nitrogen
 308 and weak correlation with soil phosphorus (Supplementary Figure 5). Thus, the relationship between soil nitrogen and
 309 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.

310 4 DISCUSSION

311 We show that herbivore diet preferences remain consistent between spatial levels, from individual foraging behavior
 312 and physiology to large scale population dynamics, with locust populations negatively related to environmental nitro-
 313 gen. Thus by going across scales, this study shows a consistent pattern of excess nitrogen limiting a pest herbivore
 314 and introduces a more nuanced view of phosphorus limitation on herbivore populations. Instead of the broad general-
 315 ization that animals are always negatively or positively associated with certain nutrients, specific life history traits,
 316 such as energetically-costly migration, as well as organism-environment interactions should be considered. **While this**
 317 **study advances our understanding of nutrient limitation across scales, future work should aim to explicitly as-**
 318 **sess phosphorus nutrient imbalances at finer scales. This could help elucidate whether phosphorus mismatches**
 319 **at smaller scales influence broader patterns of herbivore population dynamics.** Investigating multi-scale nutrient
 320 interactions, including a wider array of nutrients such as potassium and sodium, could also provide a more comprehen-
 321 sive framework for modeling herbivore responses to environmental heterogeneity. **For forecasting pest populations**
 322 **dynamics, describing the nutritional quality of landscapes can inform seasonal scouting surveys.** We hope that
 323 this study spurs future interest in multi-scale experiments and modeling of nutrient availability with animal population
 324 dynamics.

325 4.1 Field populations

326 Field populations of final instar *C. terminifera* behaviorally regulated to a 1 protein (p) : 2 carbohydrate (c) nutrient
 327 ratio, which supported the fastest nymphal growth and the lowest development time to adulthood (Figure 2 B & C),
 328 consistent with previous studies [Clissold et al., 2014, Lawton et al., 2021]. Locusts are highly mobile (*C. terminifera*

329 can fly up to 500 km in a single night, [Deveson and Walker, 2005]) and the demand for energy via carbohydrates and
 330 lipids likely increases relative to protein demand during the later life stages of these animals.

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

336 Importantly, all field cage plants were protein biased (roughly 1p : 1c to 2p : 1c) as compared to the desired locust
 337 intake target of 1p : 2c. When locusts were subsampled from the field cages mid-experiment and given the opportunity
 338 to select carbohydrate or protein diets, they selected extremely carbohydrate-biased diets for more than a week. This
 339 behavior indicated that locusts in the small field cages were highly carbohydrate-limited, driving them to overeat
 340 carbohydrates to redress the imbalance. Interestingly, multiple studies have shown that the Australian nutritional
 341 landscape is often too protein-biased relative to what the *C. terminifera* prefers [Lawton et al., 2020, 2021]. Regardless,
 342 populations are still persistent and outbreaks can occur at lower frequencies in these areas [Deveson, 2013, Key,
 343 1945]. How this species can achieve the optimal balance of nutrients within an unfavorable nutritional environment
 344 merits further investigation, but may include post-ingestive regulation and/or large-range foraging. Migratory locusts
 345 (*Locusta migratoria*) can choose microclimates that favor higher efficiency of carbohydrate or protein absorption
 346 depending on their host plant and nutritional status [Clissold et al., 2013]. For this study, we collected free-living
 347 locusts from the same region and a similar environment as where we built the field cages, yet those confined to field
 348 cages selected a 10x decrease in p:c (1p : 20c vs 1p : 2c). This result suggests that free-living locusts are able to persist
 349 in high protein regions by foraging over a larger range to seek out pockets of carbohydrate-rich plants and that the
 350 limited foraging range of the field cages precluded field-cage locusts from finding sufficient carbohydrates. Similarly,
 351 these results suggest that, while *C. terminifera* can persist in low numbers in nitrogen rich regions, those environments
 352 are unlikely to support extreme outbreaks due to a limitation of carbohydrate-rich resources.

353 4.2 Historical outbreak modeling

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

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

384 **4.3 Locusts are more likely to be limited by high nitrogen environments than other grasshoppers**

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

405 **4.4 Comparing the relationship between plant macronutrients and herbivore abundance in other taxa**

406 The effect of plant protein and carbohydrate on herbivore populations is predicted to depend on the herbivore's p:c
 407 intake target (IT) relative to its nutritional landscape (Le Gall et al., 2020). If there are sufficient plants on either side
 408 of the IT, herbivores can select from between them to achieve their IT. This complementary feeding has been recorded
 409 for field populations of blue sheep (*Pseudois nayaur*) in the Himalayan Mountains [Aryal et al., 2015], Black Howler
 410 Monkeys (*Alouatta pigra*) in Yucatán [Bridgeman, 2012], and other primates [Raubenheimer and Rothman, 2013].
 411 There would be a predicted impact on populations if the nutritional landscape were to become more constricted or
 412 not overlap with the IT. For example, lab colonies of tobacco hornworms (*Manduca sexta* larvae) have an IT around
 413 1:1 or sometimes slightly carbohydrate-biased [Wilson et al., 2019a] and their host plants tend to be carbohydrate-
 414 biased relative to their IT [Wilson et al., 2019b]. However, this does not seem to translate to population level effects,
 415 potentially due to secondary metabolites affecting growth more strongly than macronutrient balance and/or larvae may
 416 be able to compensate by overeating carbohydrates to acquire sufficient protein [Wilson et al., 2019a]. Overeating
 417 carbohydrates is not as detrimental as overeating protein, at least in the short term, and animals tend to be willing
 418 to overeat carbohydrates to a greater extent than protein [Cheng et al., 2008, Simpson and Raubenheimer, 2012b].
 419 Therefore, herbivores facing a nutritional landscape with a p:c generally lower than their IT (i.e., carbohydrate excess)
 420 may not be as negatively impacted as herbivores facing one higher than their IT (i.e., protein excess). However,
 421 there are several examples of higher localized densities of herbivores in response to higher plant nitrogen and protein
 422 contents with thrips [Brown et al., 2002] and spruce budworm (*Choristoneura*) [De Grandpré et al., 2022] being two
 423 examples. These examples suggest that low p:c diets limit population growth of some herbivores, but more studies
 424 are needed to determine if this relationship is only localized or if it scales up. It may be that herbivore populations
 425 with lower numbers are not limited by a nutritional landscape at a large scale because they can differentially disperse
 426 locally among optimal patches, whereas herbivore populations with extreme numbers (i.e., irruptions) may be more
 427 limited by nutritionally unfavorable environments across scales.

428 **Herbivore responses to nutrient variation often exhibit species-specific patterns, even among closely related species
 429 within the same feeding guild. For instance, generalist grasshoppers (*Melanoplus* spp.) coexist by occupying dis-
 430 tinct nutritional niches, varying their protein-to-carbohydrate intake ratios despite consuming overlapping host plants
 431 [Behmer and Joern, 2008]. Similarly, *Euchorthippus cheui* and *E. unicolor* display opposing preferences for nitrogen-
 432 enriched versus nitrogen-depleted host plants, leading to divergent population responses to fertilization and grazing
 433 pressure [*zhu_phenology_2020; Zhu et al. [2023]]. These examples highlight how phenological or physiological
 434 differences shape responses to shared nutritional landscapes. Building on these findings, we hypothesize that
 435 related locust species, including *Chortoicetes terminifera*, may also exhibit distinct nutrient preferences, poten-
 436 tially driven by local adaptations to environmental conditions. Investigating these differences could provide
 437 insights into how nutrient availability influences herbivore population dynamics across ecological scales.

438 There is evidence for phosphorus limitation in some species, but limited research showing a detrimental effect of excess
 439 phosphorus [Cease et al., 2016]. In aquatic insects such as *Daphnia* species, there is a strong positive association
 440 with phosphorus available and population dynamics Andersen et al. [2004]. However this trend is not seen in field

441 cricket populations (*Gryllus veletis*) [Harrison et al., 2014] and other terrestrial insects. Loaiza et al. [2011] found
 442 no effect of phosphorus fertilization (but a positive effect of N fertilization) on Kansas tallgrass prairie grasshopper
 443 population distributions, whereas Joern et al. [2012] found consistent positive correlations between plant phosphorus
 444 and Nebraskan grassland grasshopper populations.

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

459 4.5 Synthesis and Application

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

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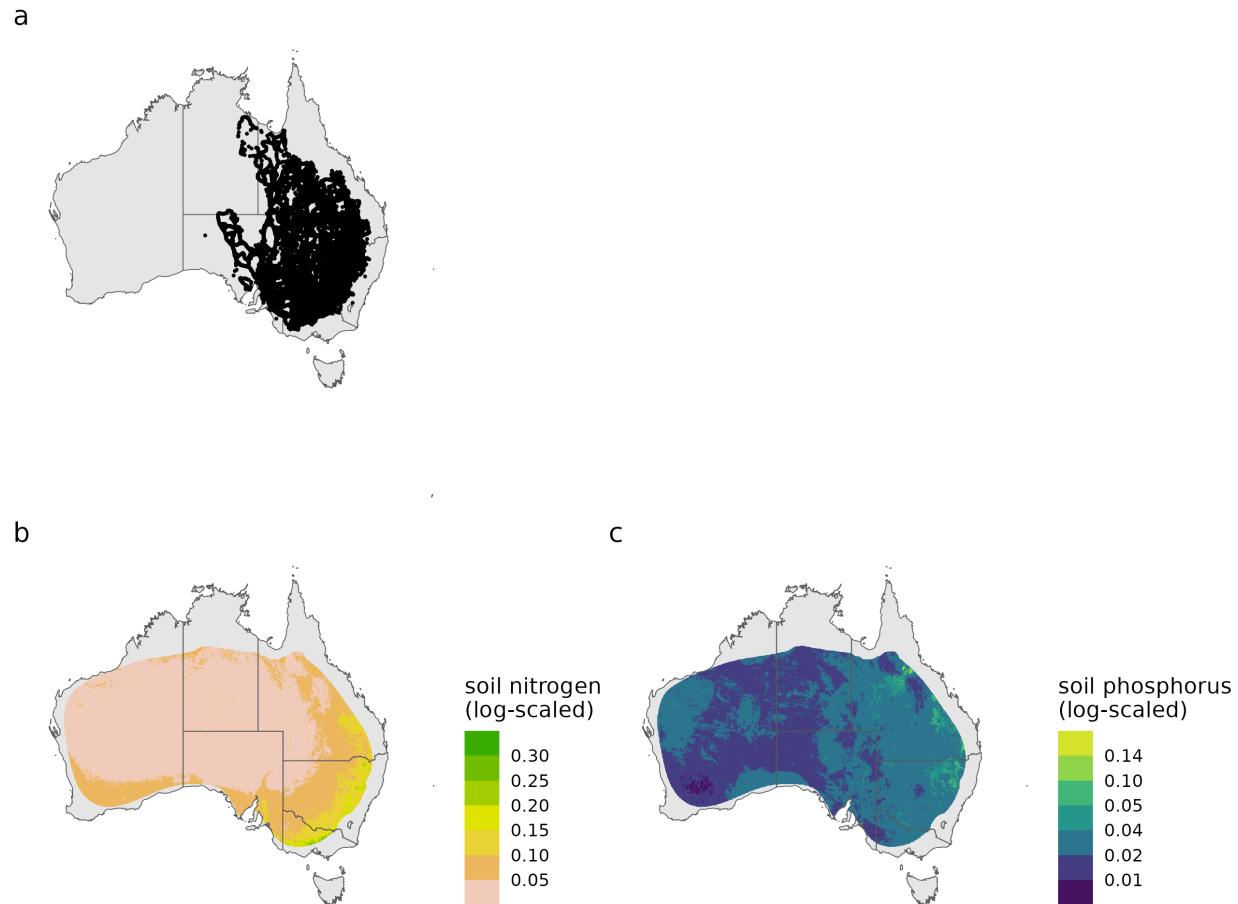
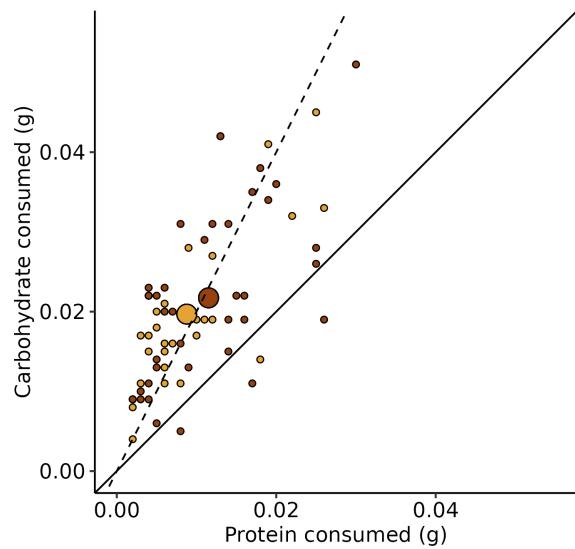


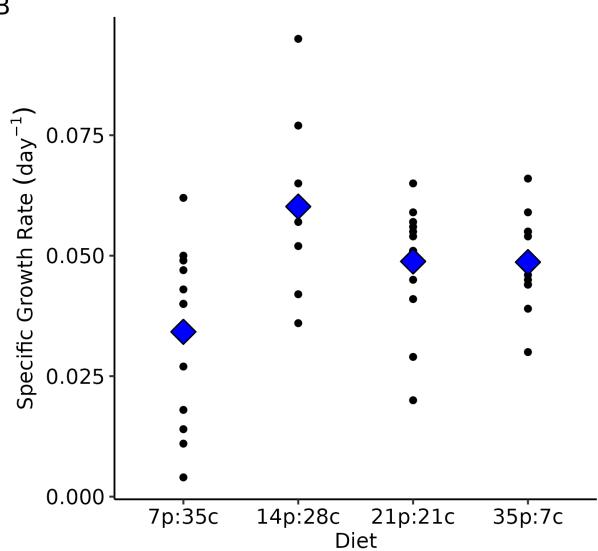
Figure 1: Locust survey data map and soil nutrients throughout the *C. terminifera* distribution. A: APLC survey dataset, B: mean proportion of nitrogen at 0-15 cm deep, C: mean proportion phosphorous at 0-15cm deep.

A

population Guntawang Mendooran



B



C

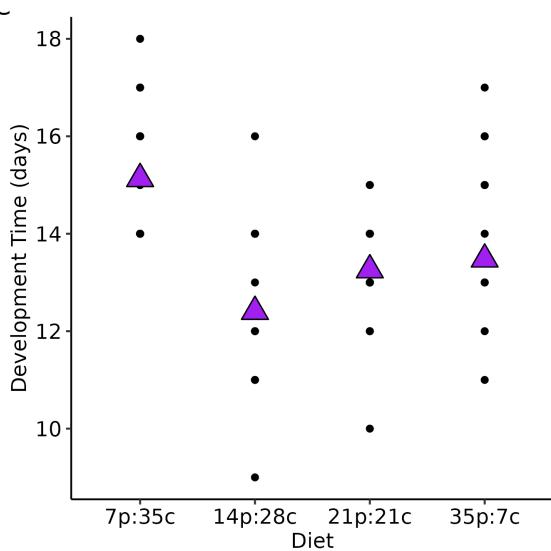


Figure 2: The nutritional preference (A) and physiological performance (B & C) of *C. terminifera* individuals that were collected from two marching bands of 5th instars. Raw data is shown as black dots with modeled estimated marginal means as large diamonds or triangles.

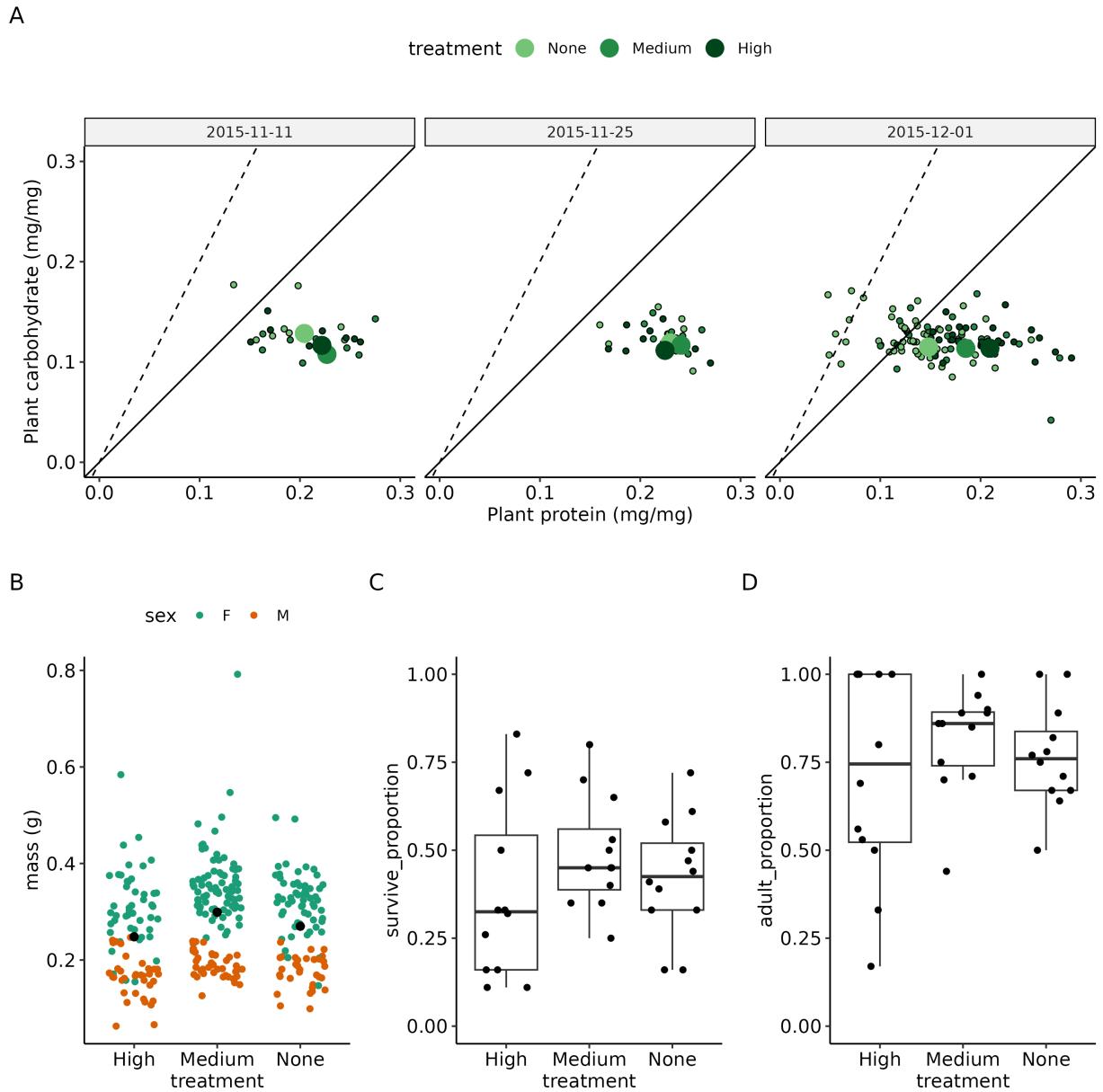


Figure 3: Nitrogen addition field cage experiments with plant nutrient change through time (A) and grasshopper performance metrics (B-C) are shown. Dashed line represents a 1p : 2c ratio, the solid line represents a 1p : 1c ratio. Black dots in B represent overall means whereas boxplots represent the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

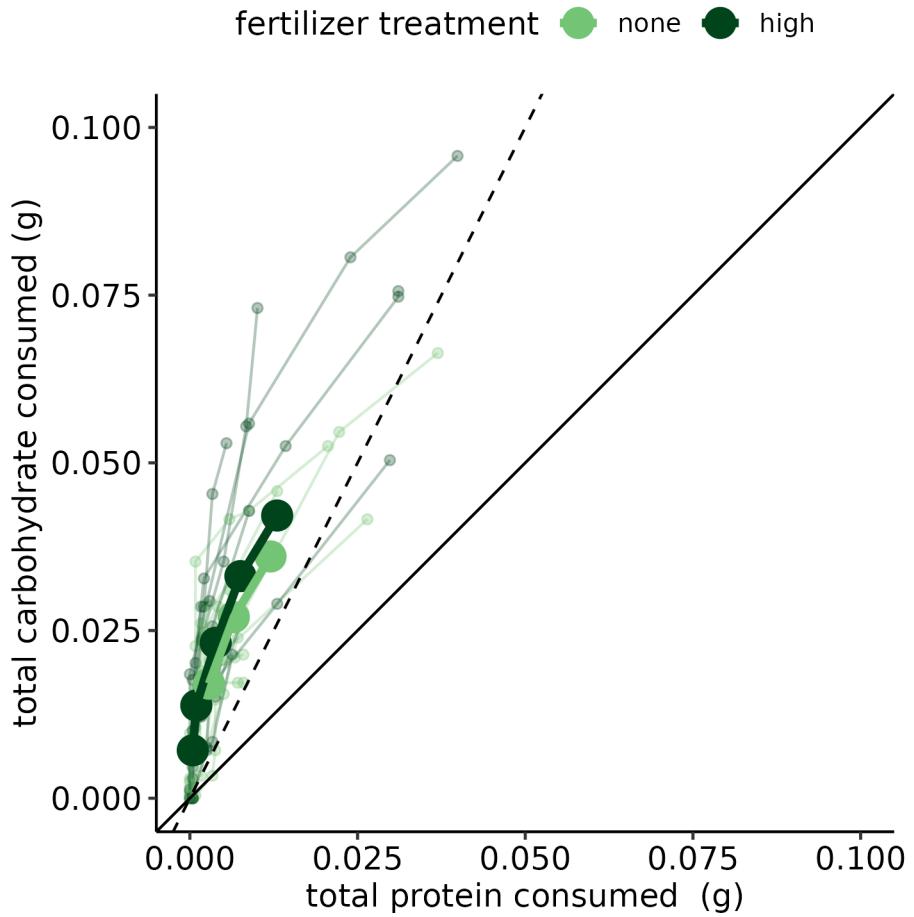
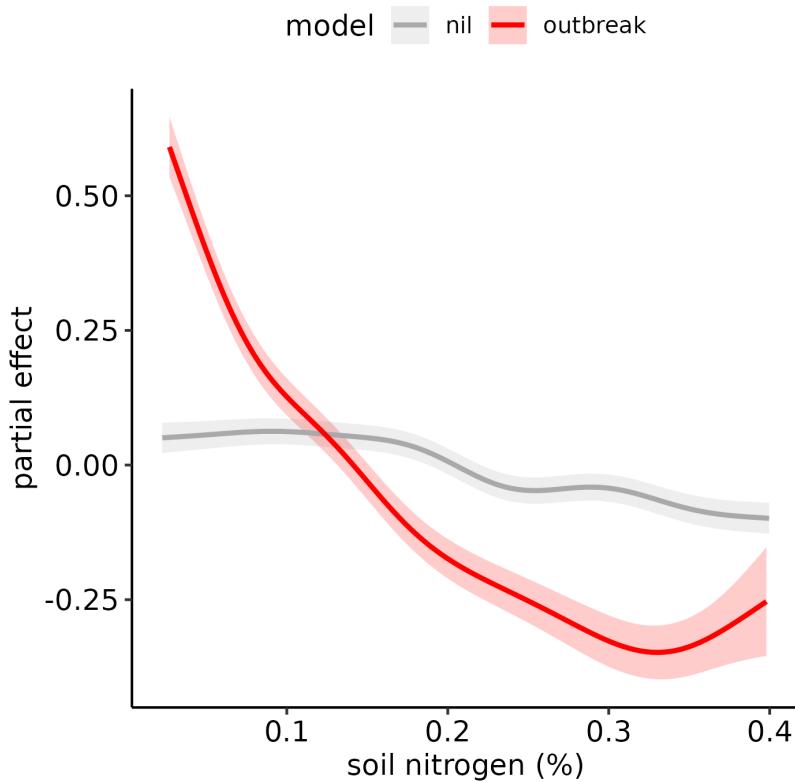


Figure 4: Nutrient imbalance redressing with artificial diet mixing of *C. terminifera* individuals taken from fertilized treatment cages. Colors represent fertilizer treatment. Smaller lines represent raw individual locust intake targets; large lines and points represent estimated marginal means. Points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

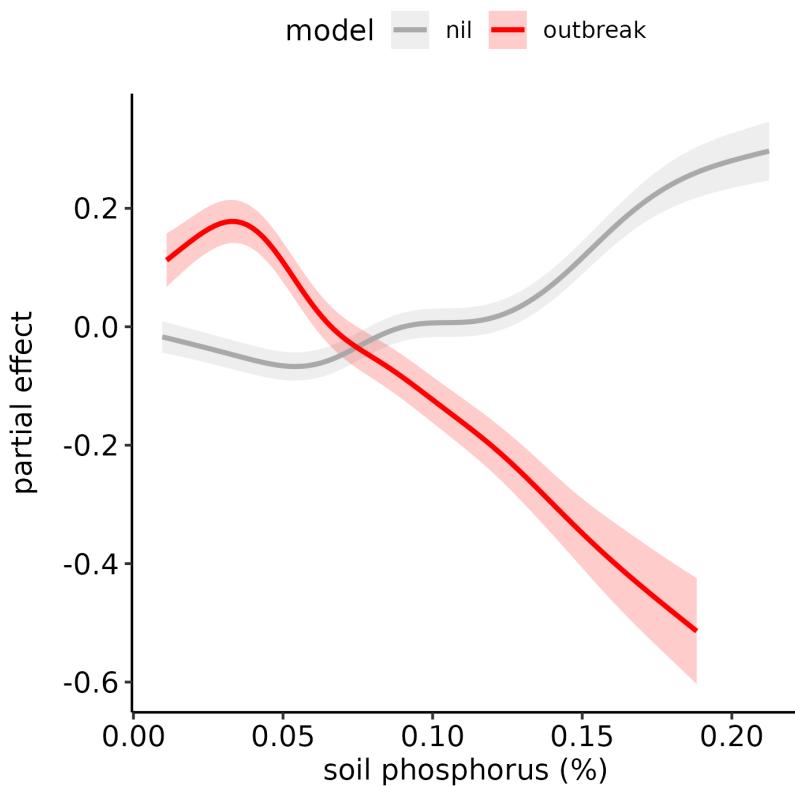
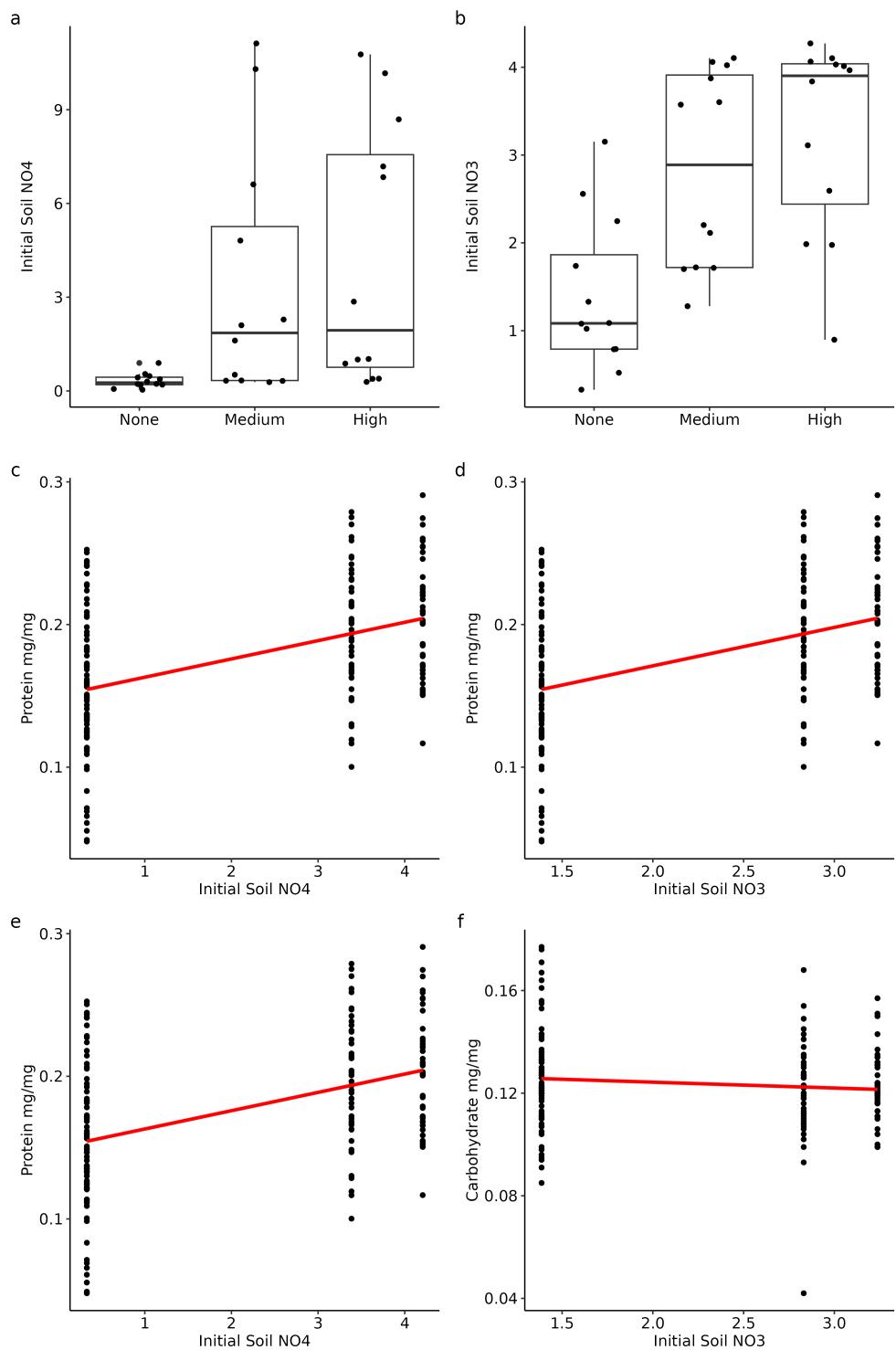
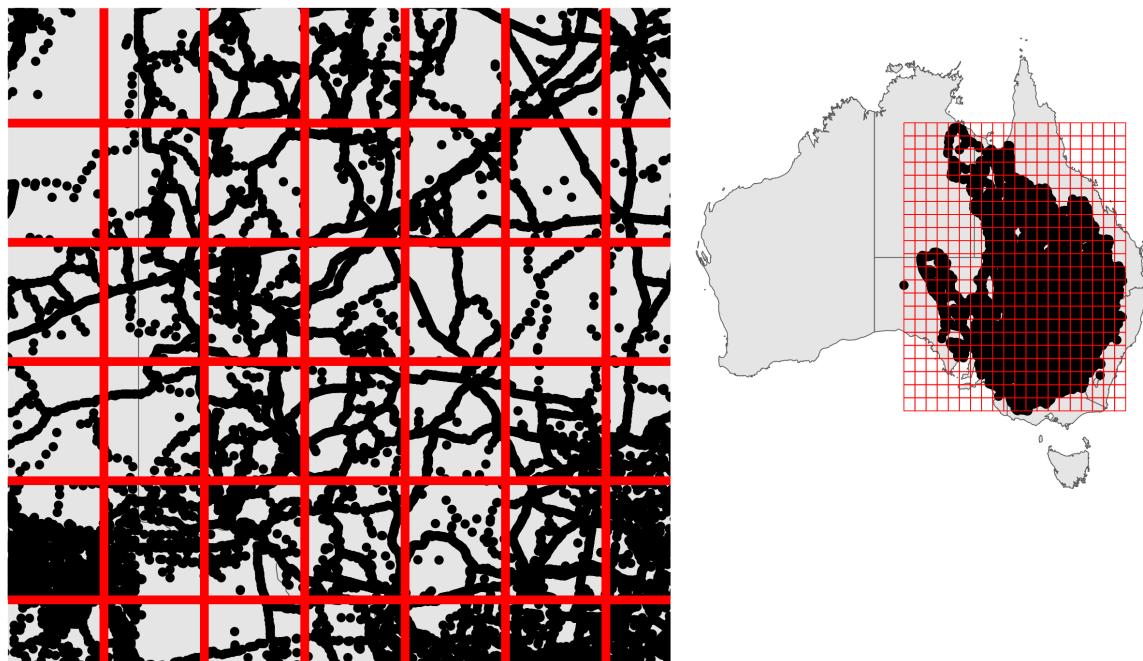


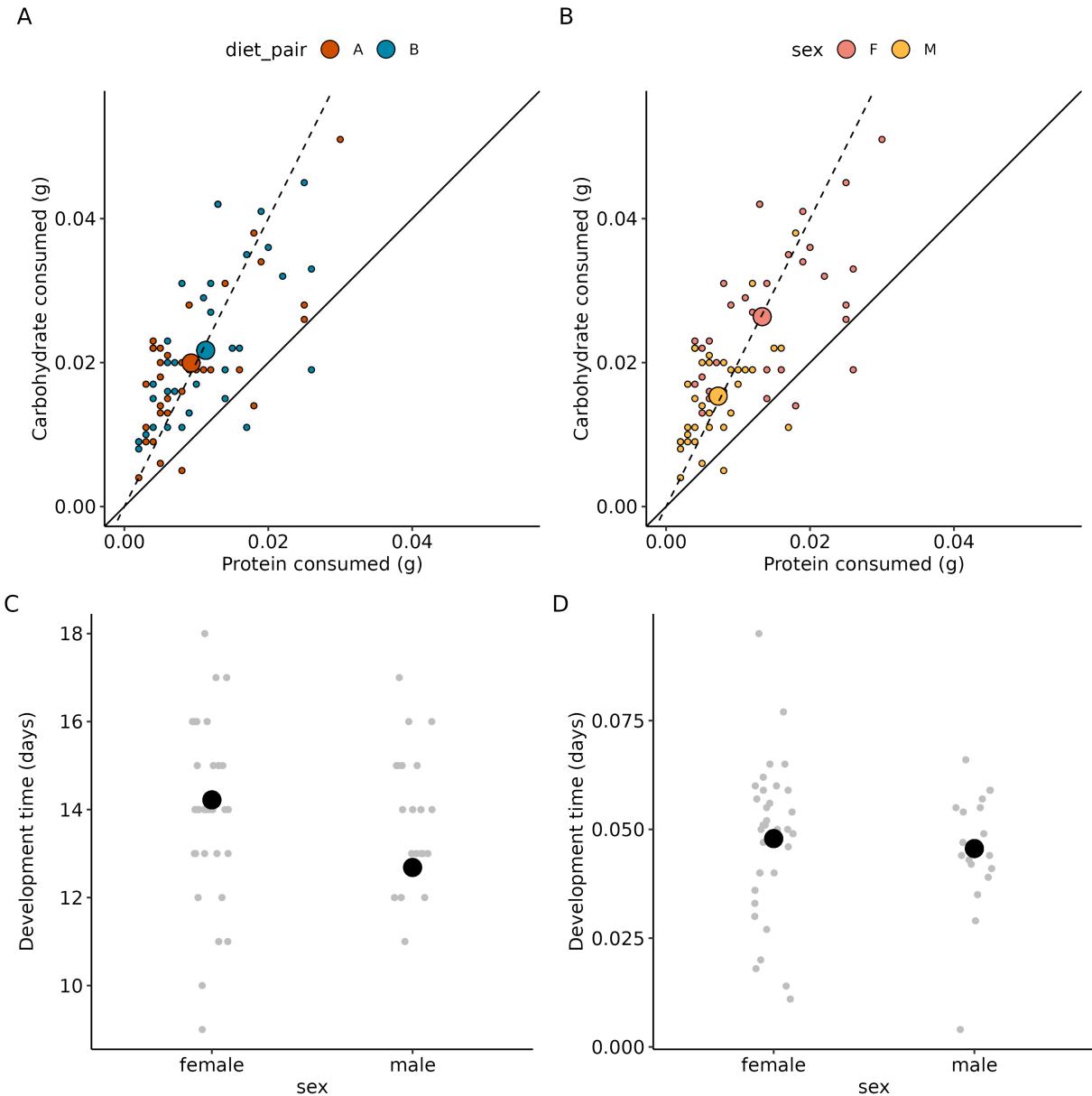
Figure 5: Relationship between outbreaks and nil observations for both soil nitrogen (A) and phosphorus (B). Partial effect is the modeled predictions after accounting for bioregion and spatial autocorrelation.



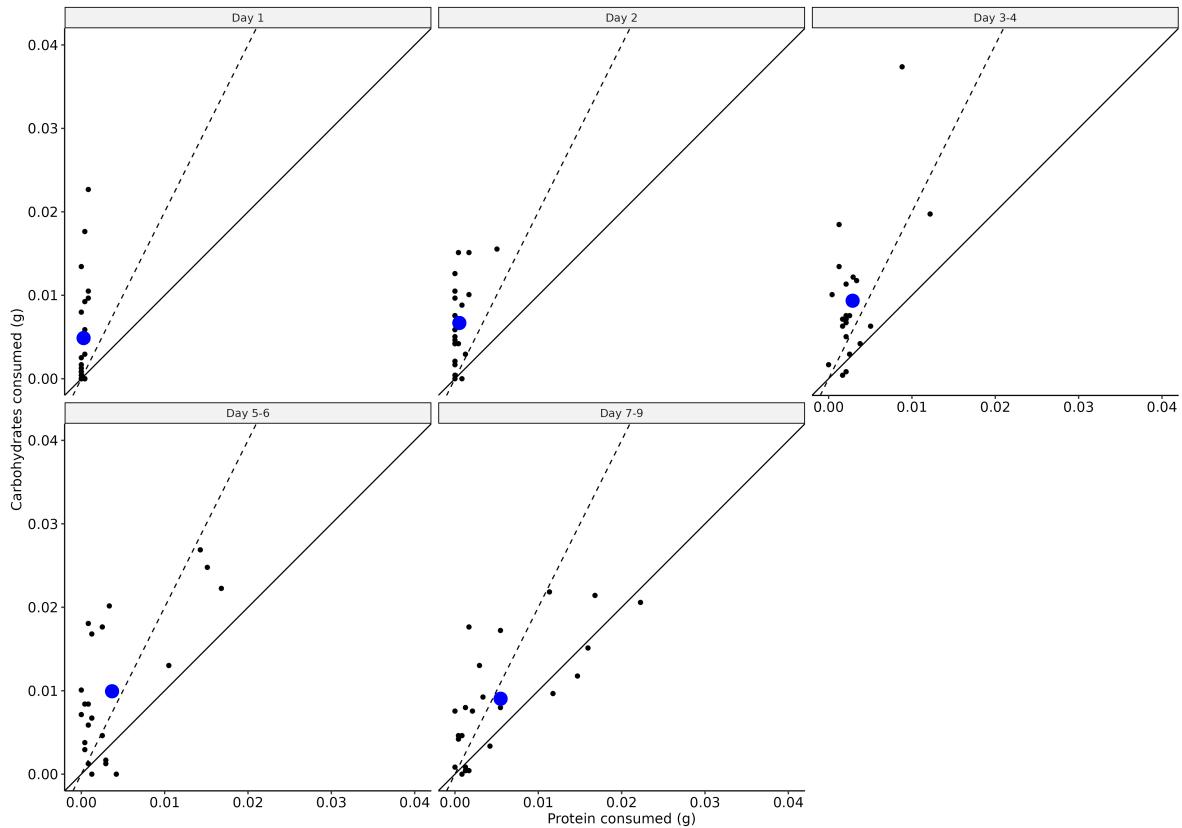
Supplementary Figure 1: Field cage soil nitrogen content by treatment (A & B) and regressed with plant carbohydrates and protein (C-F).



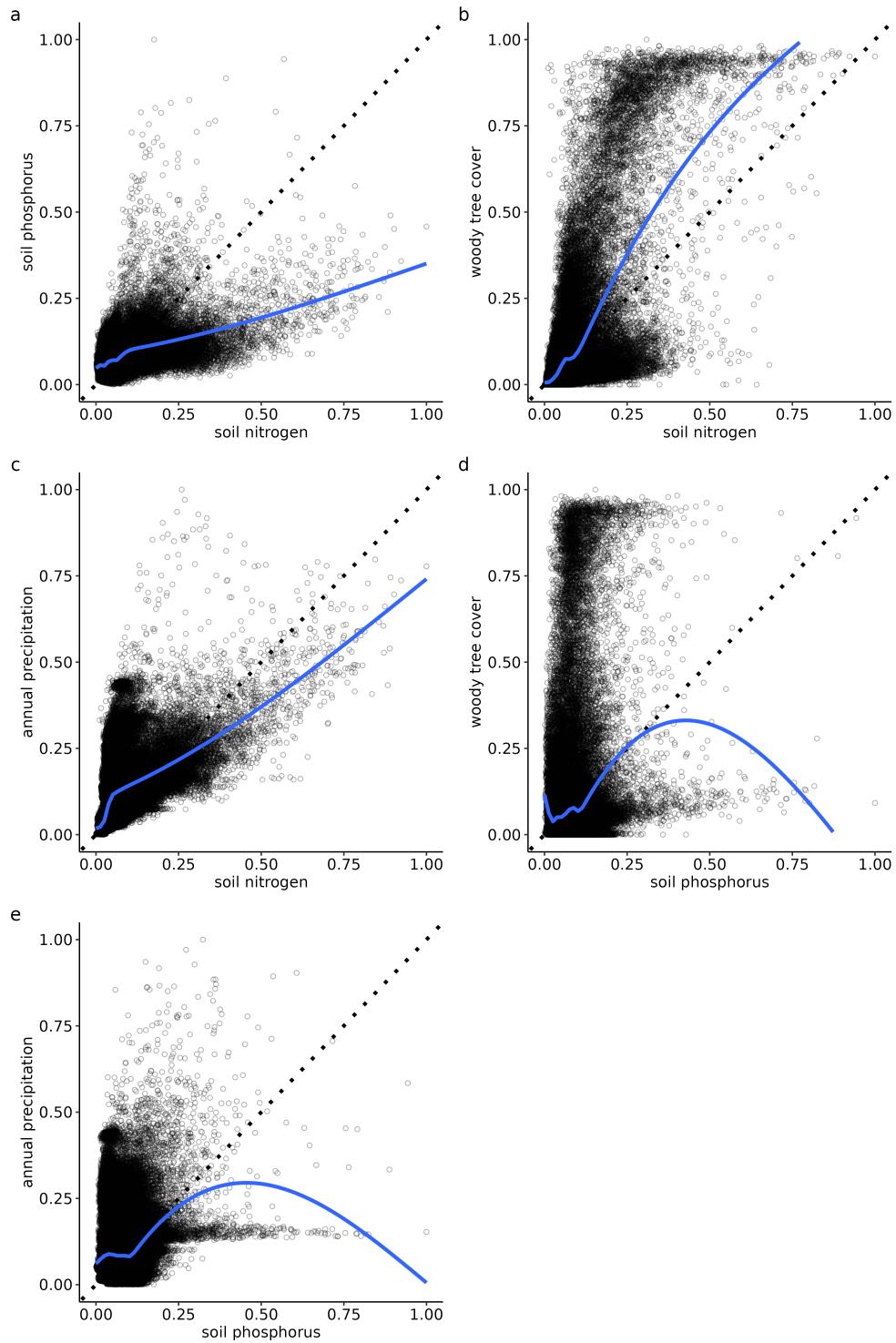
Supplementary Figure 2: Map illustrating the summarization of point observation data into a fishnet grid across eastern Australia. The full extent is shown in the inset map. We summed the number of outbreak, nil, and total observations. The grid in this figure is not at a 1 km^2 scale for demonstration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



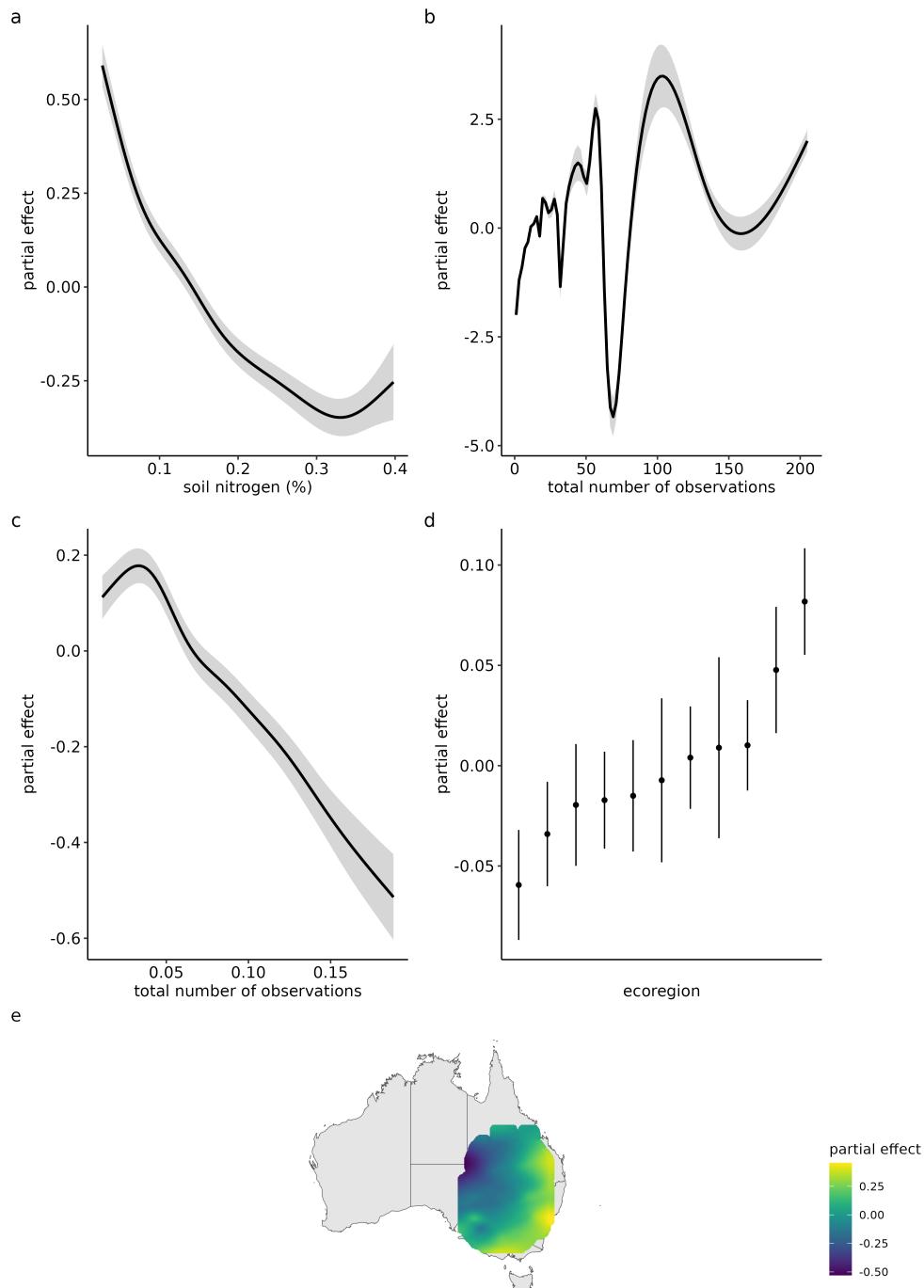
Supplementary Figure 3: Nutrient consumption for outbreaking field populations of *C. terminifera* by diet pair (A) and sex (B) and development time (C) specific growth rate (D) by sex. The P:C ratio did not differ between diet pairing and sex. Females consumed more diet (but kept the same ratio) than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



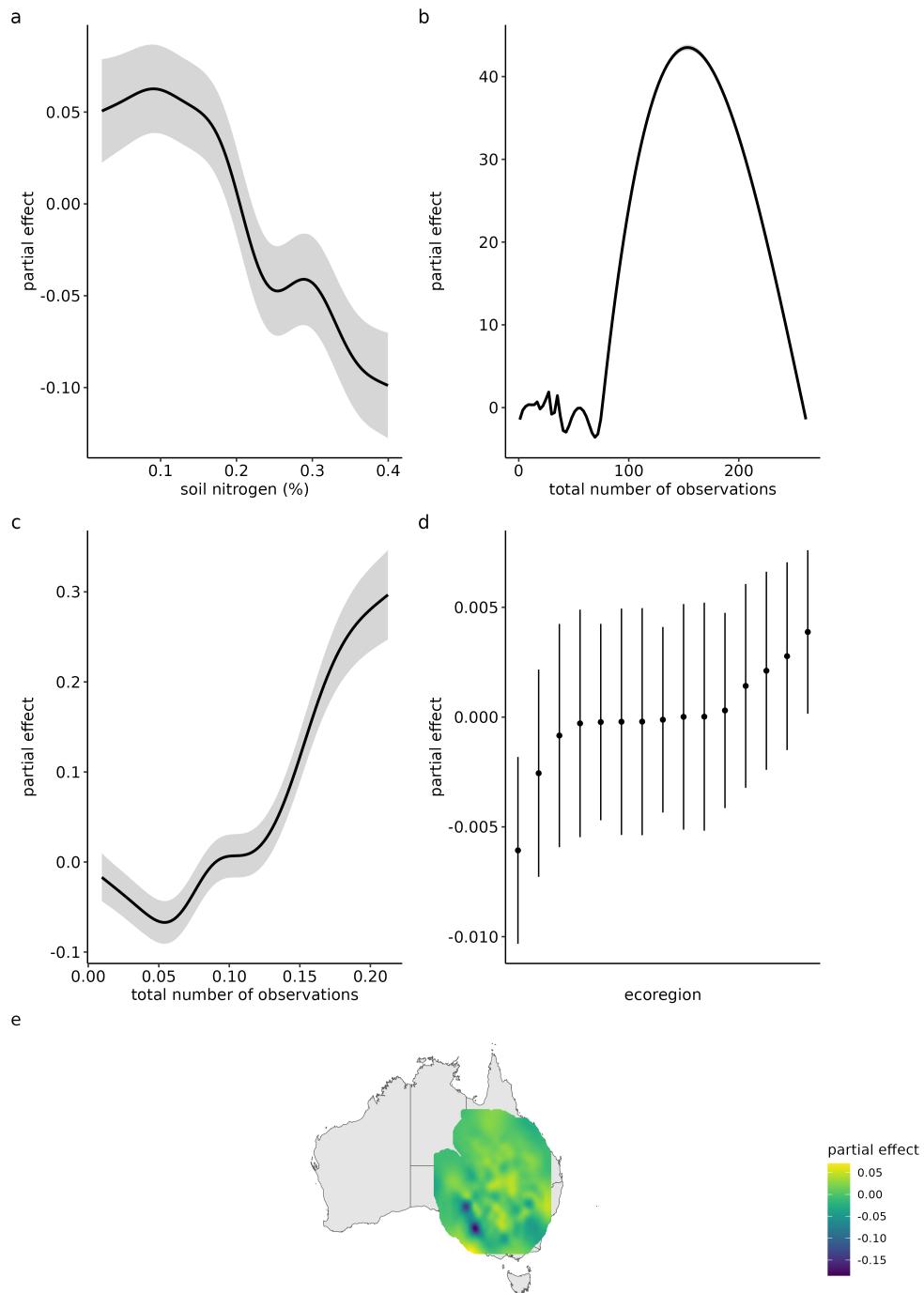
Supplementary Figure 4: Individual time step intake targets for grasshoppers kept in both high nitrogen fertilization and control cages. Blue dots represent estimated marginal means from the model while blacks dots represent raw individual intake targets.



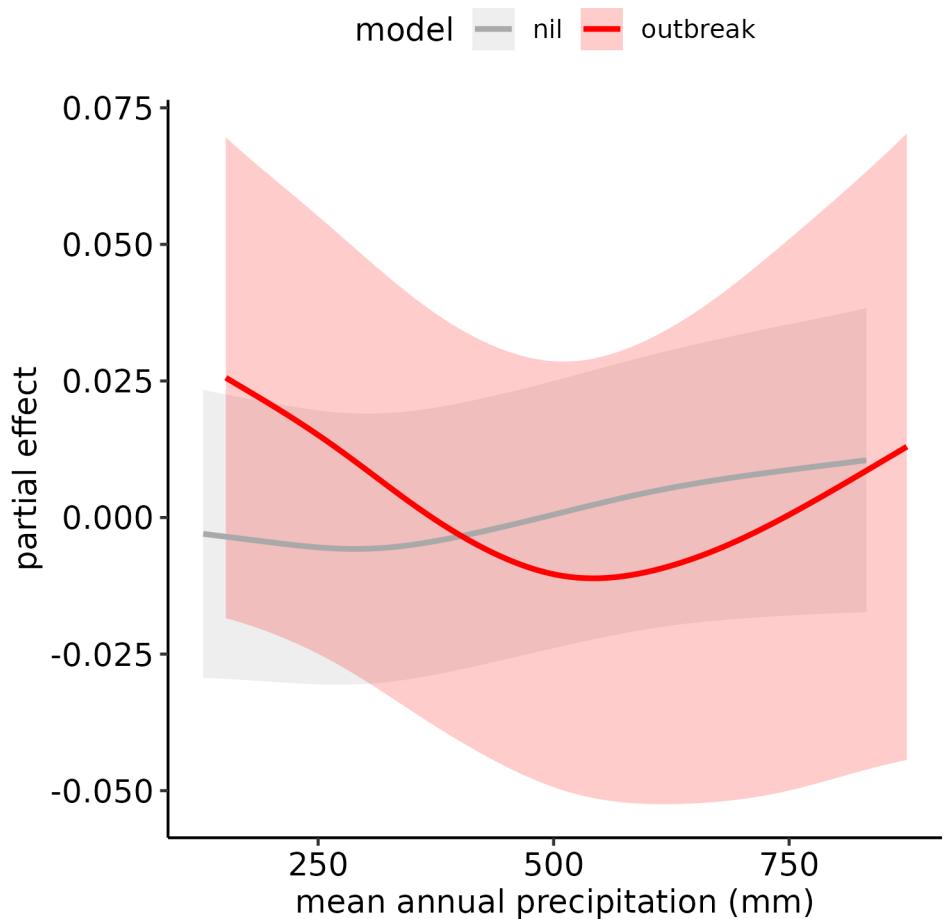
Supplementary Figure 5: Environmental variable correlations between mean annual precipitation, soil nitrogen, soil phosphorus, and woody vegetation pixel coverage. Mean annual precipitation was sourced from WorldClim V1 Bio-clim, soil nitrogen and phosphorus was sourced from Soil and Landscape Grid of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