
EXPLORING NUTRIENT AVAILABILITY AND HERBIVOROUS INSECT POPULATION DYNAMICS ACROSS MULTIPLE SCALES

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ABSTRACT

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

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

22 1 INTRODUCTION

23 Plant nutrients are usually more variable than animal body composition both in their total amounts and ratios, which
24 can make it challenging for herbivores to acquire an optimal nutritional balance. This topic has been well-explored us-
25 ing Ecological Stoichiometry, which looks at the relative amounts of elements moving through different ecological and
26 biological levels and their consequences [Elser et al., 2000]. Nutrient balance affects individual performance [Batzli,
27 1986, Bernays et al., 1994] and—by extension through changes in growth, reproduction, and death rates—influences
28 population dynamics [Elser et al., 2000]. While studies have investigated this trend between available nutrients and
29 animal populations, they usually happen at one scale and biological level. For example, much grasshopper nutri-
30 tion research has been done at the organismal or local population level using lab and/or field studies [Behmer, 2009,
31 Cease, 2024, Le Gall et al., 2019], with a few separate larger scale modeling endeavors [Zhou et al., 2019, Welti
32 et al. [2020b]]. To our knowledge, no study has integrated individual herbivorous animal nutrition to continental level
33 patterns in nutrient availability. Here we work across spatial scales, bridging field observations and cage manipula-
34 tions with continental-scale insect pest outbreak modeling to see how the animal-nutrient relationship changes across
35 multiple scales.

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

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

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

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

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

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

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

- 119 1. What are the nutritional preferences and performance curves of individuals from gregarious *C. terminifera*
 120 field populations? We expect individuals to select and perform best on carbohydrate-biased diets based on
 121 their active lifestyle, and to keep a constant intake target between populations.
- 122 2. How does *C. terminifera* respond physiologically and behaviorally when constrained to high-nitrogen envi-
 123 ronments? We expect locusts to exhibit higher mass, survivorship, and adult proportion in lower-nitrogen
 124 environments. To redress the nutritional imbalance of a high-protein:carbohydrate (P:C) diet, we also expect
 125 locusts to behaviorally select carbohydrate-biased foods if such options are available.
- 126 3. Can we use soil nutrients as a predictor of *C. terminifera* nymph outbreaks at the continental scale, account-
 127 ing for climatic factors? We expect outbreaks to be negatively correlated with soil nitrogen at this level
 128 because low nitrogen environments generally promote growth of low p:c vegetation. Given locusts’ capac-
 129 ity to post-ingestively regulate phosphorus (e.g. regulate phosphorous intake after ingestion) within natural
 130 ranges [[Cease et al., 2016](#), [Zhang et al., 2014](#)], we predict nitrogen to be a stronger predictor of population
 131 dynamics at the continental scale

132 2 METHODS

133 Details regarding the scales of inference, the application of factors of interest, and the corresponding replicates can be
 134 found in Table 1. This table outlines the hierarchical structure of our experimental design across individual, population,
 135 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

136 2.1 Field site and animals (Questions 1 and 2)

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

143 2.2 Nutritional target and performance curve using synthetic diets (Question 1)

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

148 We collected fourth and fifth instar nymphs from outbreaking populations on Nov. 12, 2015 from two locations: near
149 Mendooran (31°40.791' S, 149°04.209' E) and Guntawang (32°23.988' S, 149°28.649' E), New South Wales. The
150 Mendooran population was forming marching bands while the Guntawang population was at high density but was not
151 actively marching during the collection period. Both populations were collected along dirt roads flanked by livestock
152 grazing pastures containing a mix of grasses and forbs. We transported locusts back to the Trangie Agricultural
153 Research Centre and kept them in large plastic bins with holes along with an assortment of grasses and forbs cut
154 from the same field locusts were collected until experiments were started. For both experiments, locusts were housed
155 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
156 (nutritional target) or one (performance curve) artificial diets, a water tube capped with cotton, and a perch.

157 2.2.1 Nutrition target (choice diets)

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

167 2.2.2 Performance curve (no-choice diets)

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

180 2.3 Field cage experiments (Question 2)

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

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

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

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

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

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

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

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

217 2.4 Correlating historical nymphal outbreaks with soil nitrogen and phosphorus (Questions 3)

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

221 2.4.1 Locust outbreak data

222 *Chortoicetes terminifera* data from 2000 - 2017 (~ 190,000 records) were used in this study. This database contains
 223 georeferenced points with a categorical ordinal variable 0-4 to represent approximate nymph densities. The value
 224 ranges for nymphs are: 0 = nil, 1 = < 5 m², 2 = 5-30 m², 3 = 31-80 m², and 4 = > 80 m². Population outbreaks are
 225 characterized by very high densities of gregarious nymphs (up to 1000 m²). We focused on nymphs as this life stage
 226 cannot fly and can be used to assess prior local habitat conditions. While the database extends into the 1980s, we only
 227 used data collected between 2000-2017 as this period overlapped with the soil grid data which was released in 2015
 228 to account for any potential shifts in soil nutrient composition. Since climatic conditions and migration patterns are
 229 drivers in outbreak occurrence [Lawton et al., 2022, Veran et al., 2015] they likely mask the relationship between static
 230 environmental variables like soil nutrients. To account for this variability, we spatially aggregated the survey dataset
 231 to a 1 km² grid as can be seen in Supplementary Figure 2. This allowed us to model how often locust outbreaks occur
 232 in grid cells rather than the actual outbreak. We used a 1 km² grid as this reflects the estimated maximum dispersal
 233 distance from hatching to 5th instar [Hunter et al., 2008]. Since it is often difficult to accurately assess categories
 234 2-3 given the small differences in densities, We counted the number of outbreaks (APLC nymph density code 4),
 235 the number of nil records (APLC nymph density code 0), and total number of survey observations. This resulted in
 236 approximately 67,000 grid cells for the final dataset. Overall APLC survey point distribution can be seen in Figure 1
 237 A.

238 2.4.2 Soil grid of Australia data

239 The soil and landscape grid of Australia is a modeled raster of 12 soil variables at a 90 m² resolution. These soil charac-
 240 teristics are available at multiple depths from surface to two meters below the surface. These depths and methodology
 241 are consistent with the specifications of the Global Soil Map project (<http://www.globalsoilmap.net>) [Grundy et al.,
 242 2015]. We extracted this data from Google Earth Engine [Gorelick et al., 2017]. In this data set both phosphorus
 243 and nitrogen units are the mass fraction of total nutrient in the soil by weight. We took the average of nitrogen and
 244 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
 245 grasses and forbs. Then, for each APLC survey grid we calculated the mean mass fraction of nitrogen and phosphorus

246 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
247 C respectively.

248 2.5 Statistics

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

253 2.5.1 Intake Targets (Question 1 and 2)

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

260 2.5.2 Field population (Question 1)

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

264 2.5.3 Field Cage Experiments (Question 2)

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

275 2.5.4 Historical outbreaks and soil nutrient grid modeling (Question 3)

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

292 3 RESULTS

293 3.1 Field population (Question 1)

294 3.1.1 Choice experiment (nutritional target)

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

299 consumption (Supplementary Figure 3 A, Table 2). While the protein : carbohydrate ratio did not change, females
 300 consumed more food than males, likely due to being bigger overall (Supplementary Figure 3 B, Table 2).

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

Table 2: Generalized additive model results for macronutrient consumption (carbohydrate and protein) of two out-breaking populations of *C. terminifera* in Mendooran and Guntawang. Models were selected via AIC, AICc and BIC which can be seen in Supplementary Table 3. Diet pair A and B had the following protein to carbohydrate ratios: 7p:35c & 28p:14c and 7p:35c & 35p:7c respectively. Family: multivariate gaussian distribution, link: identity, SE: standard error.

301 3.1.2 No choice experiment (performance curves)

302 *Chortoicetes terminifera* had higher specific mass growth rates and faster development times on the 1 protein : 2 car-
 303 bohydrate (14 protein : 28 carbohydrate) diet as compared to the other diets (Figure 2 B & C, Table 3, Supplementary
 304 Table 4). Development time and specific growth rate did not differ between male and female locusts (Supplementary
 305 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.

306 3.2 Field Cage (Question 2)

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

macronutrient	variable	estimate	SE	statistic	p-value
carbohydrate	Intercept	0.127	0.007		0.000
	Medium	-0.020	0.007		0.005
	High	-0.011	0.007		0.121
	2015-11-25	-0.009	0.007		0.181
	2015-12-01	-0.012	0.006		0.033
	Medium:2015-11-25	0.019	0.010		0.063
	High:2015-11-25	0.004	0.010		0.656
	Medium:2015-12-01	0.019	0.008		0.017
	High:2015-12-01	0.010	0.008		0.222
	s(species)			67.305	0.000
	s(plot)			1.643	0.207
	s(cage)			3.442	0.130
	protein	Intercept	0.209	0.017	
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 (Question 3)

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. terminifera*s 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). The relationship between locust outbreaks and mean annual precipitation was very different from the relationship with soil nitrogen (Figure 5, Supplementary Figure 8). Soil nitrogen and phosphorus show weak positive correlations with woody vegetation cover, while mean annual precipitation exhibits high variation in its relationship with soil nitrogen and weak correlation with soil phosphorus (Supplementary Figure 5). Thus, the relationship between soil nitrogen and locust outbreaks cannot be fully explained by differences in woody vegetation.

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.

4 DISCUSSION

We show that herbivore diet preferences remain consistent between spatial levels, from individual foraging behavior and physiology to large scale population dynamics, with locust populations negatively related to environmental nitrogen. Thus by going across scales, this study shows a consistent pattern of excess nitrogen limiting a pest herbivore and introduces a more nuanced view of phosphorus limitation on herbivore populations. Instead of the broad generalization that animals are always negatively or positively associated with certain nutrients, specific life history traits,

334 such as energetically-costly migration, as well as organism-environment interactions should be considered. While this
 335 study advances our understanding of nutrient limitation across scales, future work should explicitly assess phosphorus
 336 nutrient imbalances at finer scales to clarify their influence on broader patterns of herbivore population dynamics. In-
 337 vestigating multi-scale nutrient interactions, including a wider array of nutrients such as potassium and sodium, could
 338 also provide a more comprehensive framework for modeling herbivore responses to environmental heterogeneity. For
 339 forecasting pest populations dynamics, describing the nutritional quality of landscapes can inform seasonal scouting
 340 surveys. We hope that this study spurs future interest in multi-scale experiments and modeling of nutrient availability
 341 with animal population dynamics.

342 4.1 Field populations

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

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

353 Importantly, all field cage plants were protein biased (roughly 1p : 1c to 2p : 1c) as compared to the desired locust
 354 intake target of 1p : 2c. When locusts were subsampled from the field cages mid-experiment and given the opportunity
 355 to select carbohydrate or protein diets, they selected extremely carbohydrate-biased diets for more than a week. This
 356 behavior indicated that locusts in the small field cages were highly carbohydrate-limited, driving them to overeat
 357 carbohydrates to redress the imbalance. Interestingly, multiple studies have shown that the Australian nutritional
 358 landscape is often too protein-biased relative to what the *C. terminifera* prefers [Lawton et al., 2020, 2021]. Regardless,
 359 populations are still persistent and outbreaks can occur at lower frequencies in these areas [Deveson, 2013, Key,
 360 1945]. How this species can achieve the optimal balance of nutrients within an unfavorable nutritional environment
 361 merits further investigation, but may include post-ingestive regulation and/or large-range foraging. Migratory locusts
 362 (*Locusta migratoria*) can choose microclimates that favor higher efficiency of carbohydrate or protein absorption
 363 depending on their host plant and nutritional status [Clissold et al., 2013]. For this study, we collected free-living
 364 locusts from the same region and a similar environment as where we built the field cages, yet those confined to field
 365 cages selected a 10x decrease in p:c (1p : 20c vs 1p : 2c). This result suggests that free-living locusts are able to persist
 366 in high protein regions by foraging over a larger range to seek out pockets of carbohydrate-rich plants and that the
 367 limited foraging range of the field cages precluded field-cage locusts from finding sufficient carbohydrates. Similarly,
 368 these results suggest that, while *C. terminifera* can persist in low numbers in nitrogen rich regions, those environments
 369 are unlikely to support extreme outbreaks due to a limitation of carbohydrate-rich resources.

370 4.2 Historical outbreak modeling

371 This is the first time to our knowledge that terrestrial animal population dynamics have been modeled with nutrients
 372 at the continental level, allowing nutrient limitation to be tested at a scale not previously investigated. Locust out-
 373 breaks are associated with less soil nitrogen (Figure 5 A), suggesting that nitrogen acts as a limiting factor not due
 374 to its deficit [White, 1993] but its excess. Plants growing in high nitrogen environments tend to have high p:c ratios,
 375 which force locusts to either undereat carbohydrates (limiting their energy to support growth and migration) or overeat
 376 protein (which can be toxic) to acquire sufficient carbohydrates [Behmer, 2009, Cease, 2024]. On the other end of the
 377 performance curve, *C. terminifera* do have a lower p:c range that limits performance, as shown using artificial diets
 378 (Figure 2 B-C). We also show that outbreaks are correlated with a low level of soil phosphorus, however, outbreaks
 379 peak at approximately 4%, suggesting that while locusts generally do well in low phosphorus environments, phospho-
 380 rus deficit can be limiting for locusts in extremely phosphorus poor soils (Figure 5 B). Because Australian soils are
 381 characteristically phosphorus poor [Donald, 1964], Australian animals like this locust are adapted to phosphorus poor
 382 environments and potentially having too much phosphorus is deleterious [Morton et al., 2011]. Locust populations
 383 may be more tightly correlated with soil nitrogen than phosphorus because terrestrial herbivores require 5-50 times
 384 more nitrogen than phosphorus [Elser et al., 2000], meaning they can more readily balance phosphorus by eating a few
 385 foods rich or poor in phosphorus but cannot as quickly regulate protein and carbohydrate energy because they make up
 386 the bulk of their required nutrients. Indeed, laboratory studies have revealed that short-term limitations in dietary phos-
 387 phorus have no apparent impact on grasshopper growth [Cease et al., 2016], suggesting that these mobile herbivores
 388 could seek out phosphorus-rich diets intermittently to overcome potential phosphorus limitation in field environments.
 389 However, in this study, we only tested this relationship with phosphorus at the continental level; further field and lab-

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

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

401 **4.3 Locusts are more likely to be limited by high nitrogen environments than other grasshoppers**

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

422 **4.4 Comparing the relationship between plant macronutrients and herbivore abundance in other taxa**

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

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

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

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

477 4.5 Synthesis and Application

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

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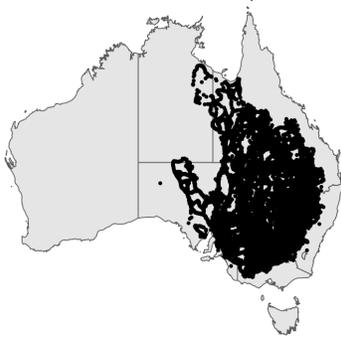
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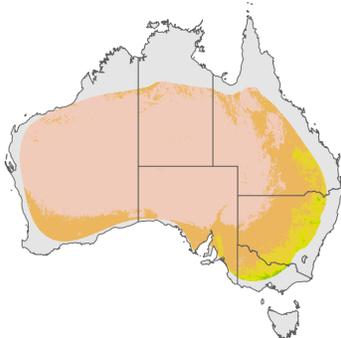
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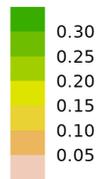
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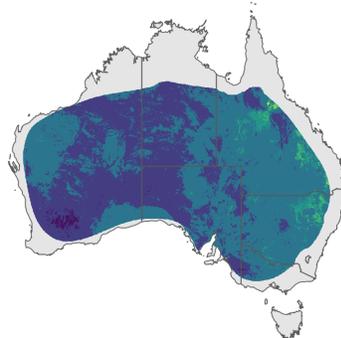
b



soil nitrogen
(log-scaled)



c



soil phosphorus
(log-scaled)

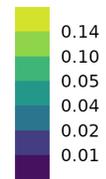


Figure 1: Locust survey data map and soil nutrients throughout the *C. terminifera* distribution. A: APLC survey dataset, B: mean proportion of nitrogen at 0-15 cm deep, C: mean proportion phosphorous at 0-15cm deep.

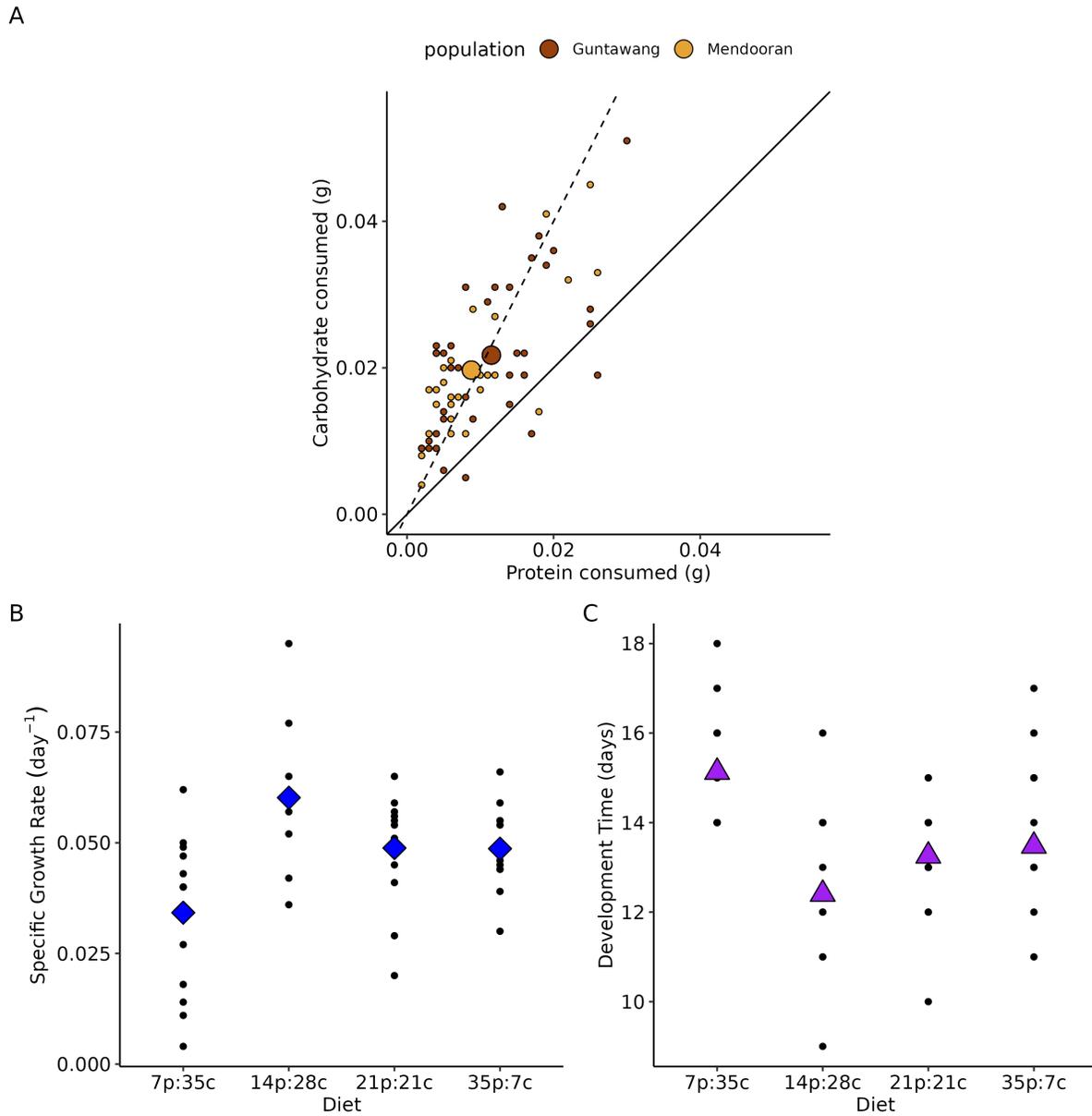


Figure 2: The nutritional preference (A) and physiological performance (B & C) of *C. terminifera* individuals that were collected from two marching bands of 5th instars. Raw data is shown as black dots with modeled estimated marginal means as large diamonds or triangles.

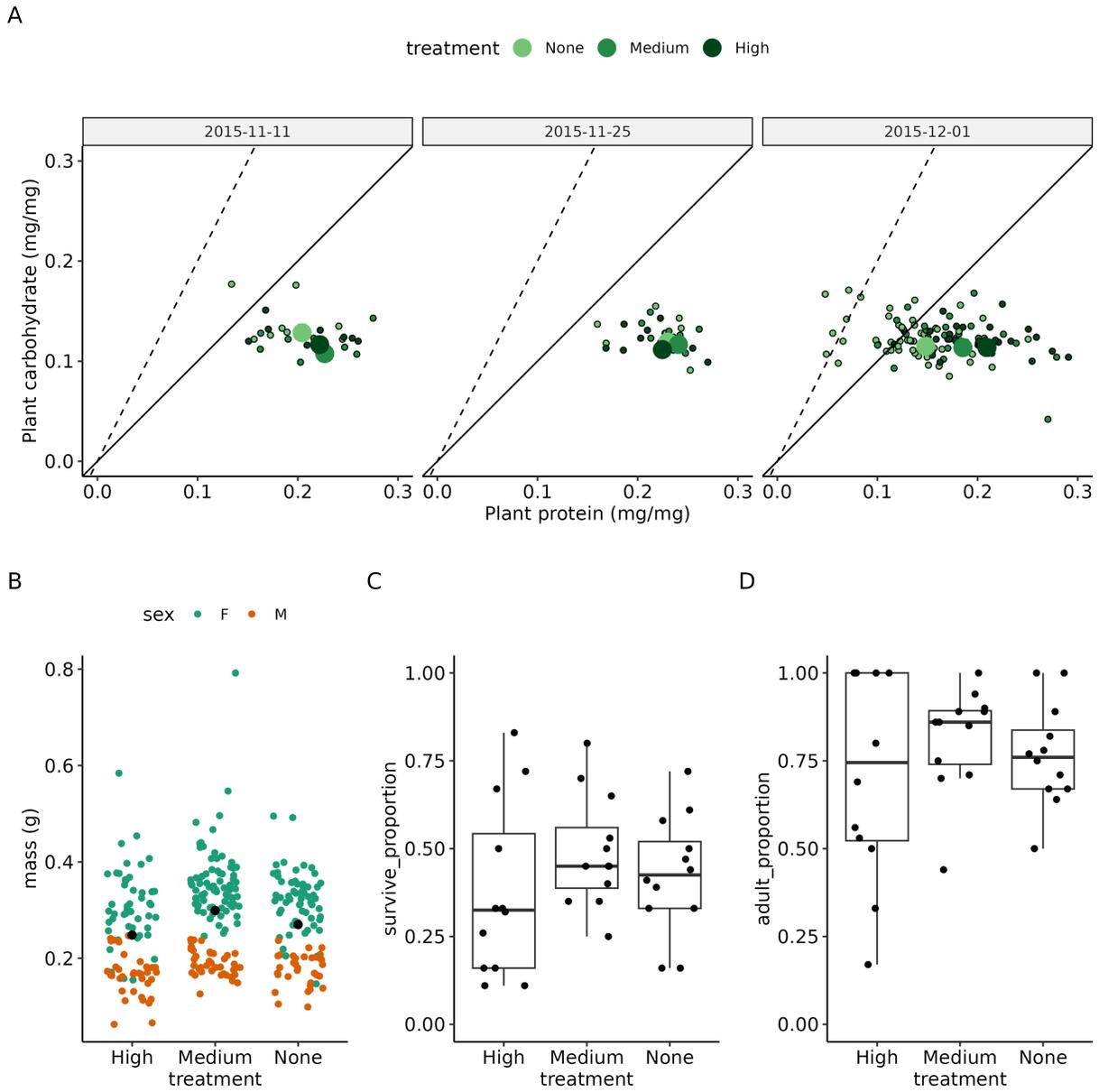


Figure 3: Nitrogen addition field cage experiments with plant nutrient change through time (A) and grasshopper performance metrics (B-C) are shown. Dashed line represents a 1p : 2c ratio, the solid line represents a 1p : 1c ratio. Black dots in B represent overall means whereas boxplots represent the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

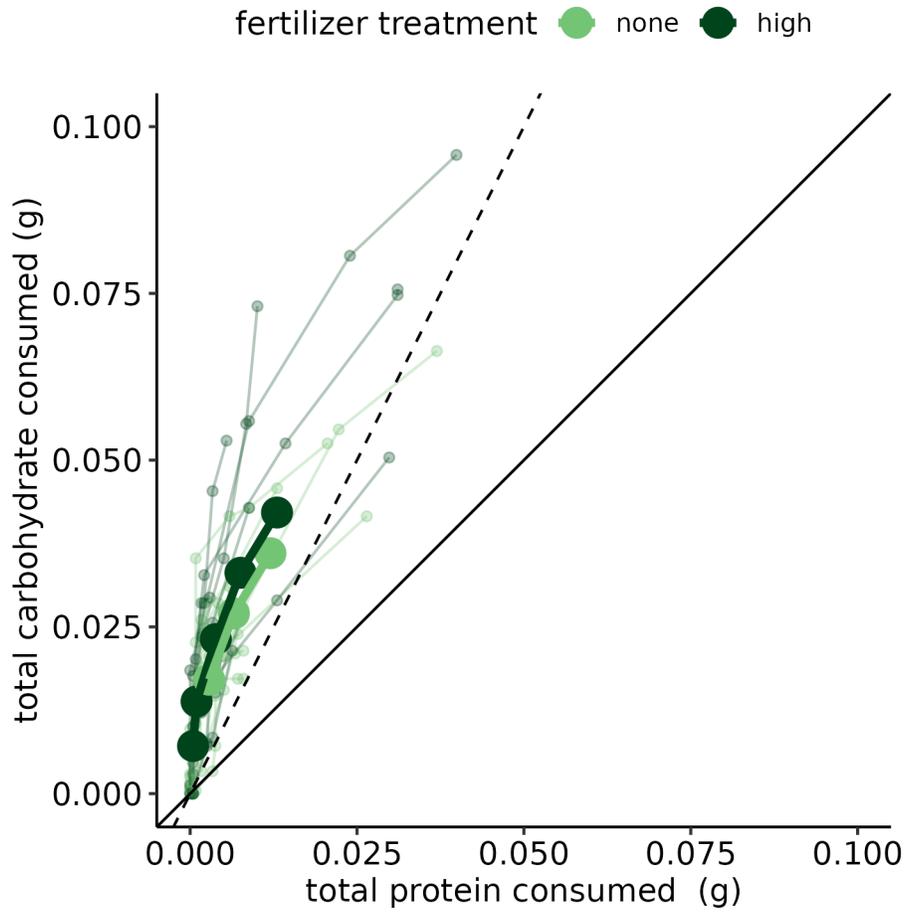


Figure 4: Nutrient imbalance redressing with artificial diet mixing of *C. terminifera* individuals taken from fertilized treatment cages. Colors represent fertilizer treatment. Smaller lines represent raw individual locust intake targets; large lines and points represent estimated marginal means. Points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

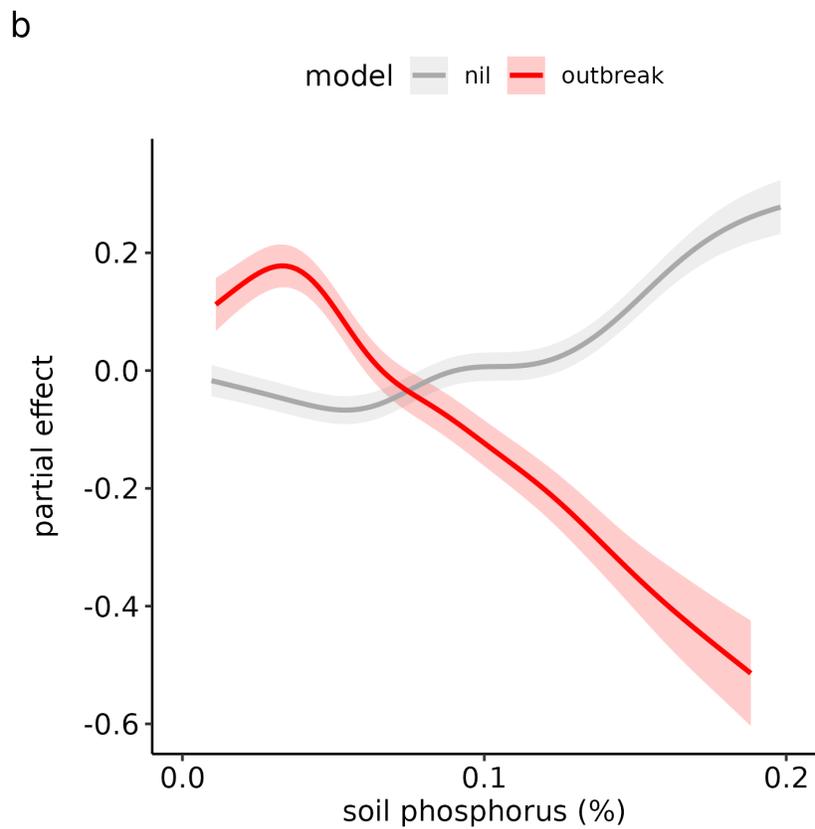
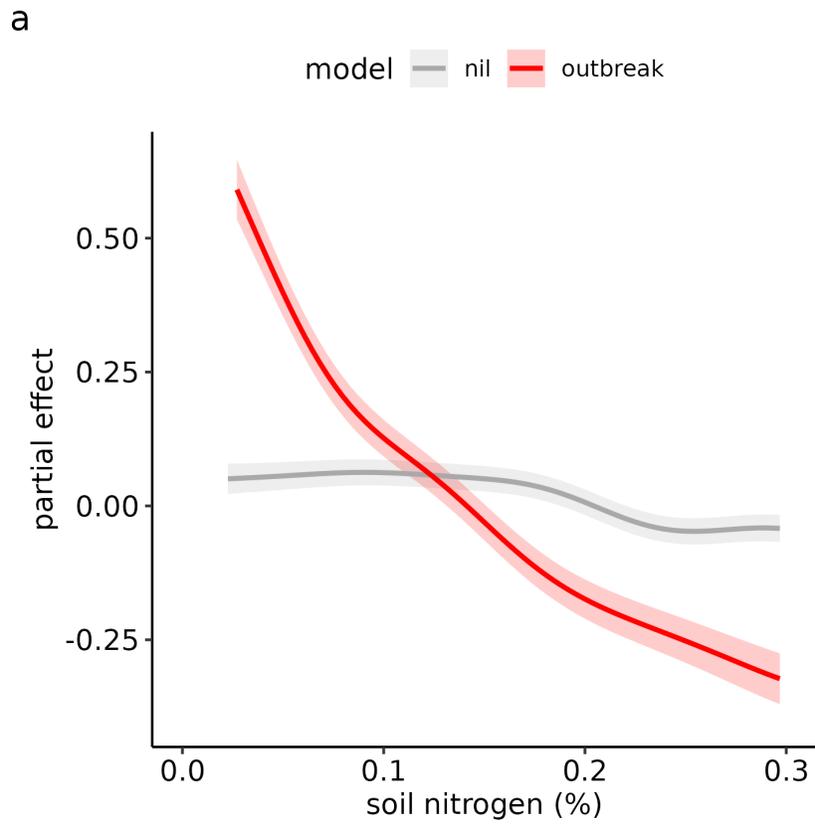
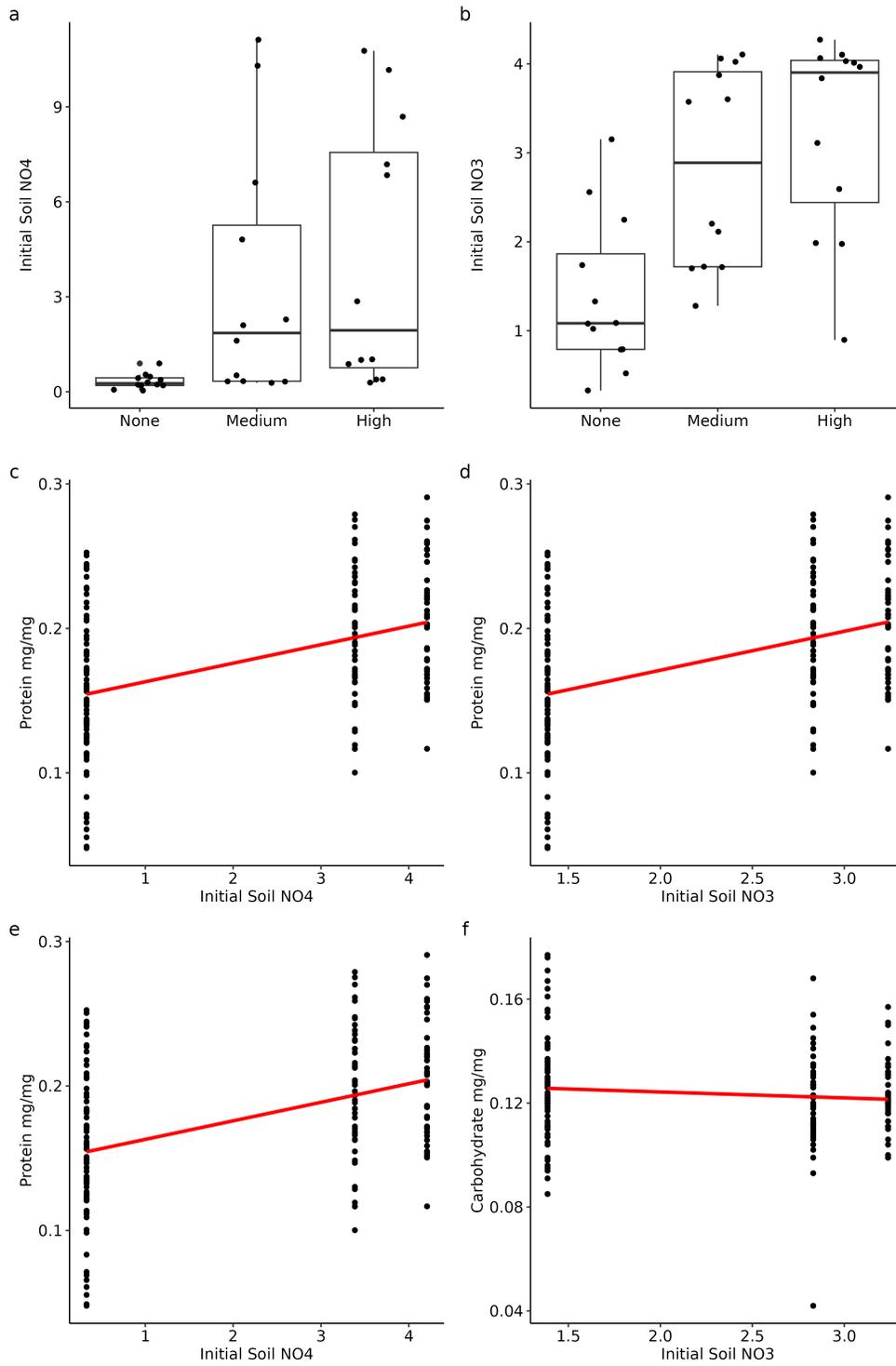
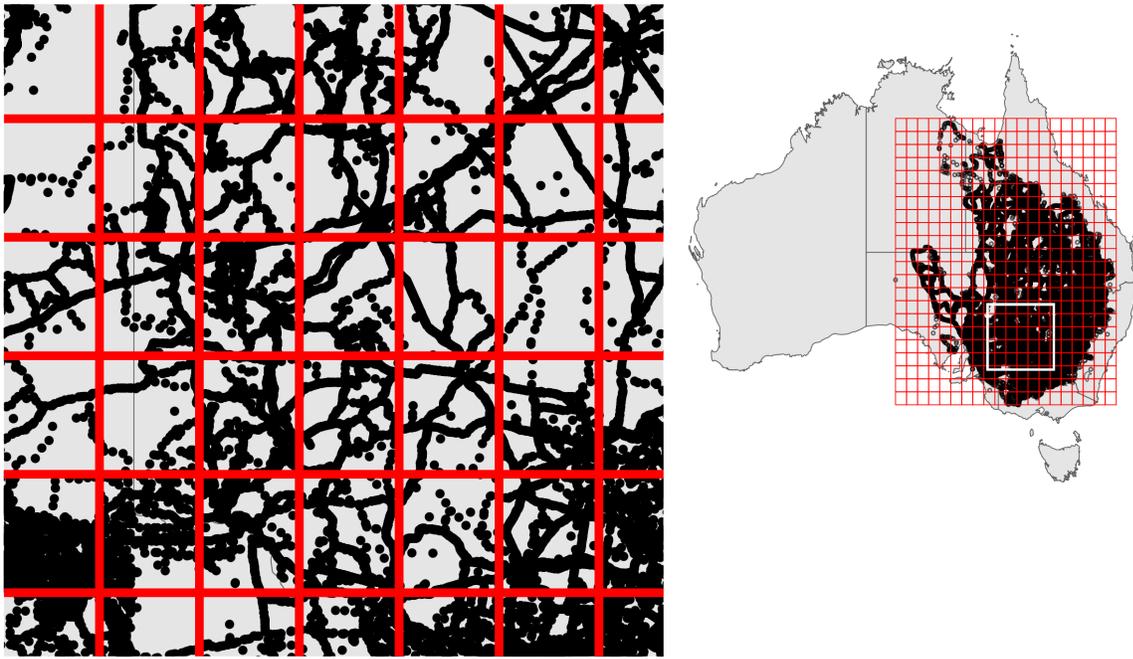


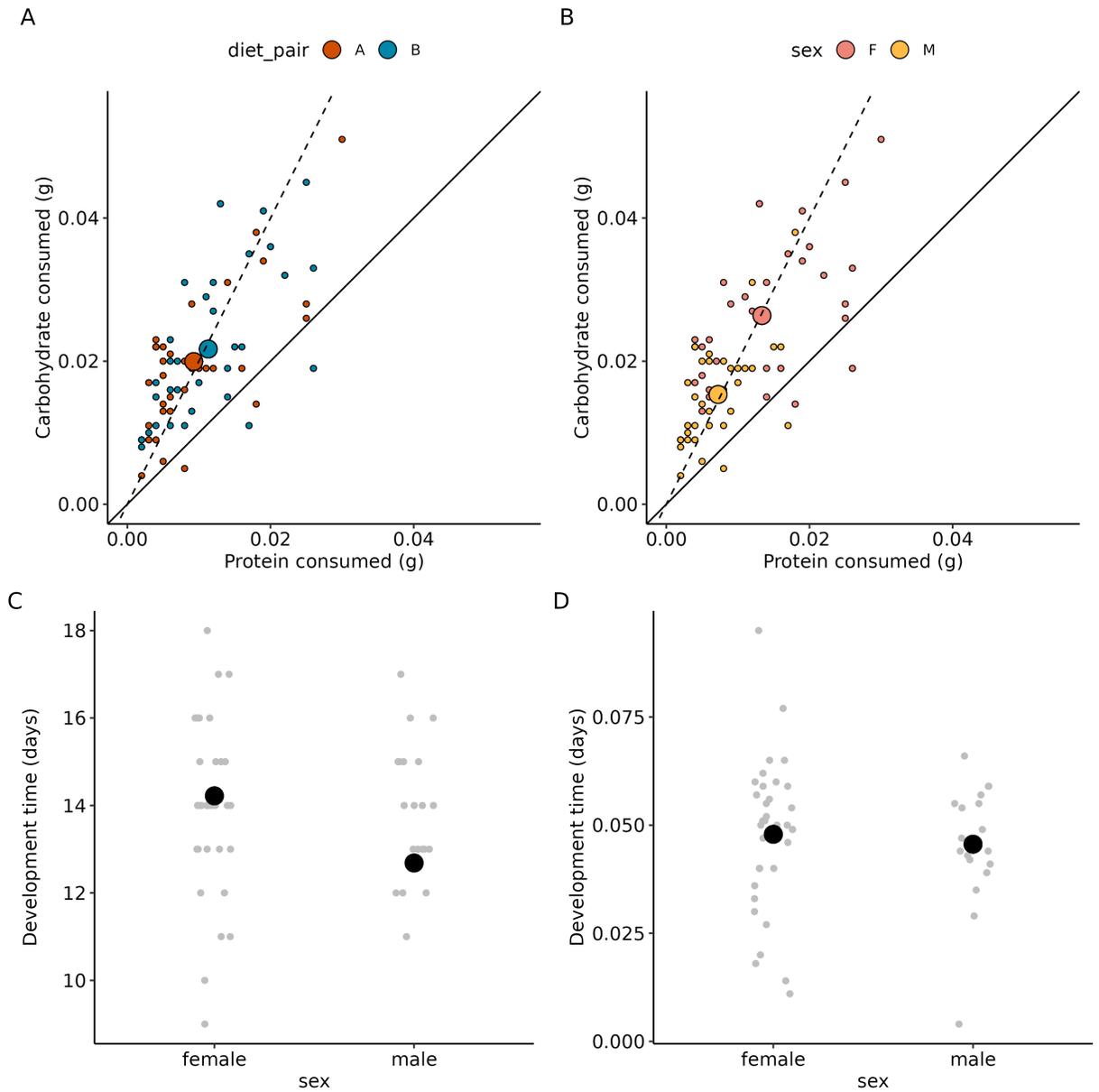
Figure 5: Relationship between outbreaks and nil observations for both soil nitrogen (A) and phosphorus (B). Partial effect is the modeled predictions after accounting for bioregion and spatial autocorrelation.



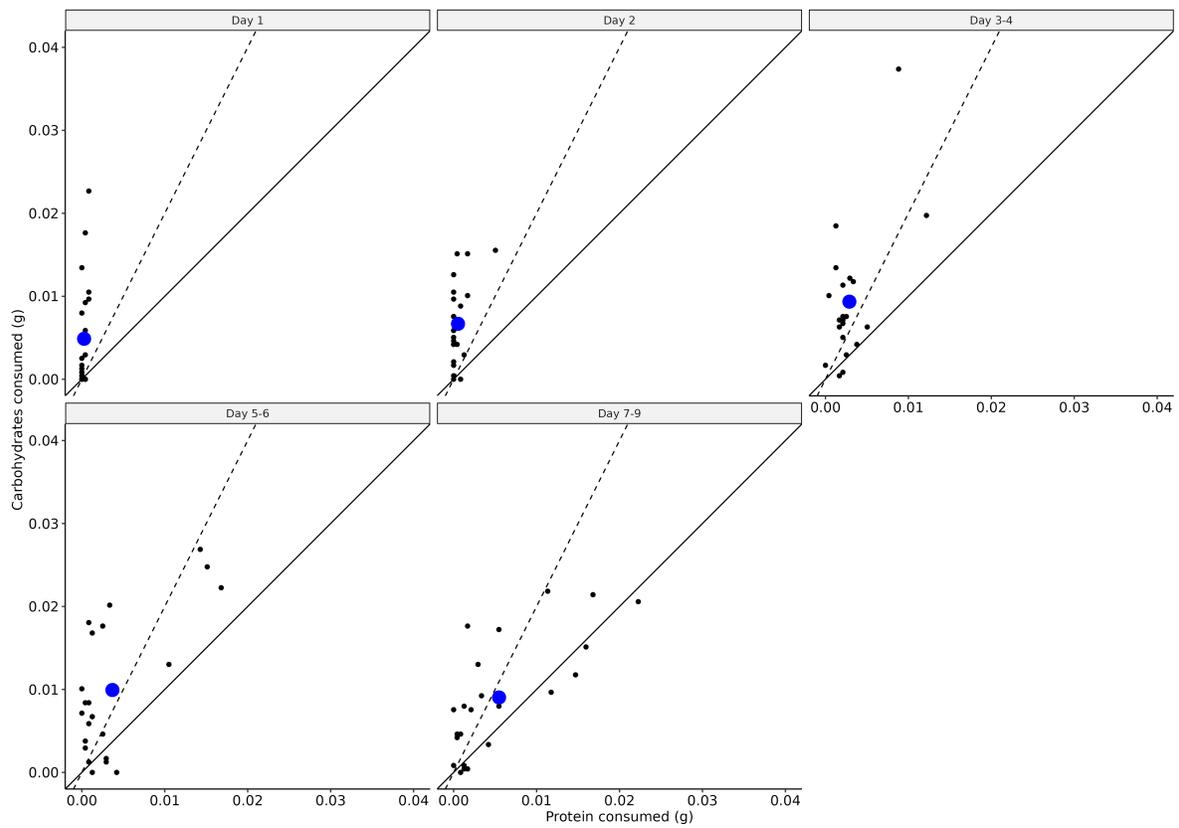
Supplementary Figure 1: Field cage soil nitrogen content by treatment (A & B) and regressed with plant carbohydrates and protein (C-F).



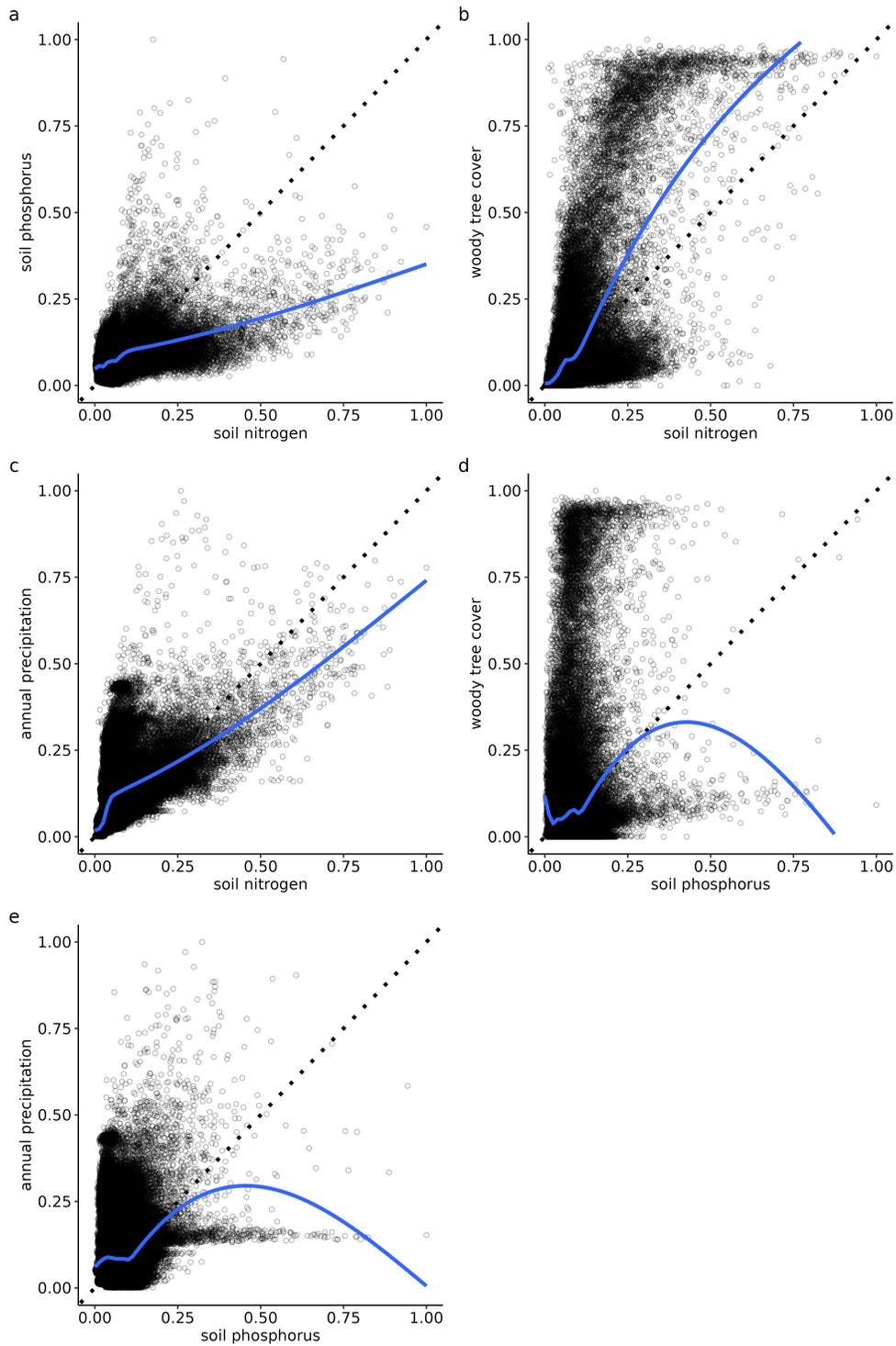
Supplementary Figure 2: Map illustrating the summarization of point observation data into a fishnet grid across eastern Australia. The inset map location is represented by the white box. We summed the number of outbreak, nil, and total observations. The grid in this figure is not at a 1 km² scale for demonstration purposes, as the cells would be too small to see.



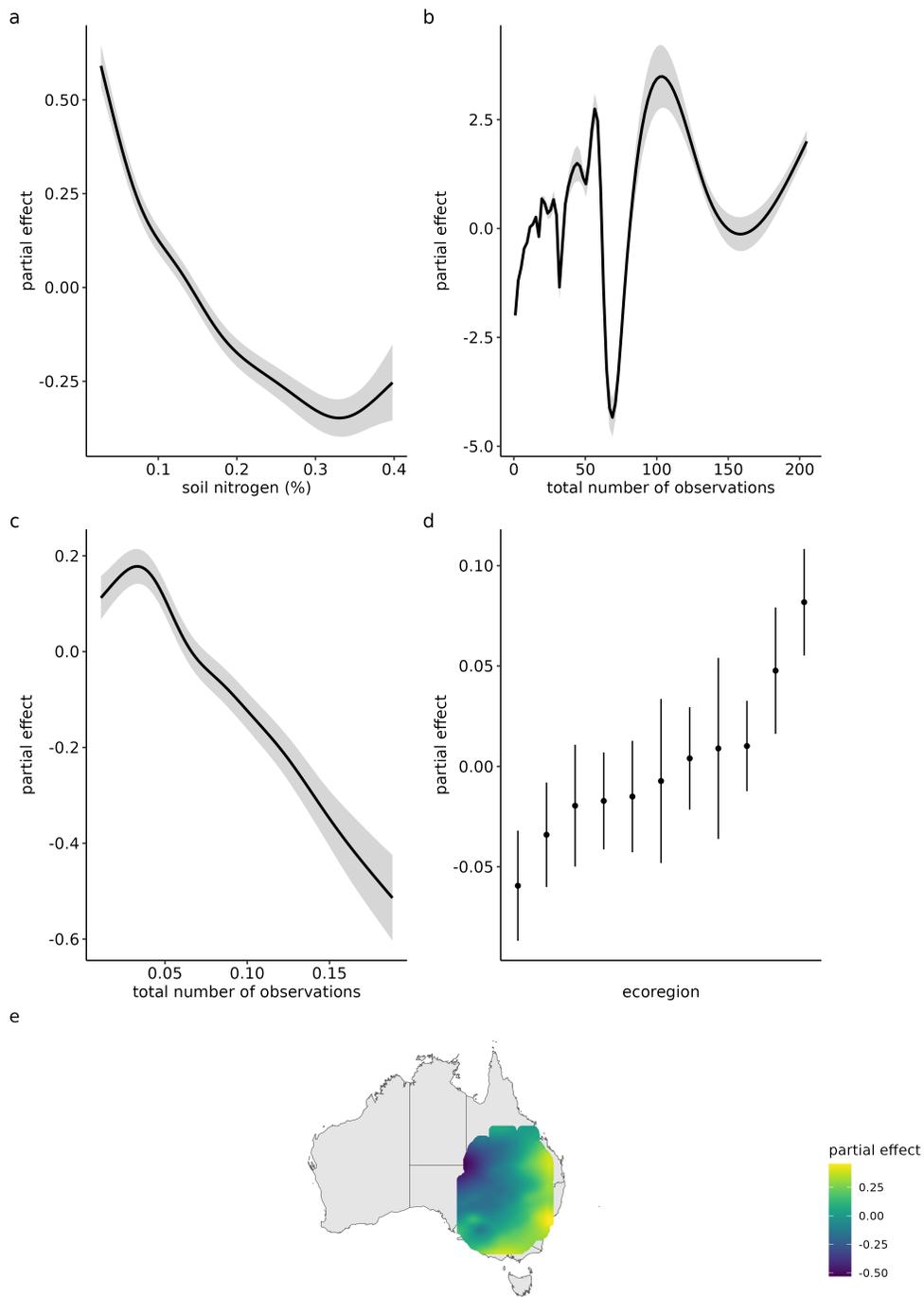
Supplementary Figure 3: Nutrient consumption for outbreaking field populations of *C. terminifera* by diet pair (A) and sex (B) and development time (C) specific growth rate (D) by sex. The P:C ratio did not differ between diet pairing and sex. Females consumed more diet (but kept the same ratio) than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



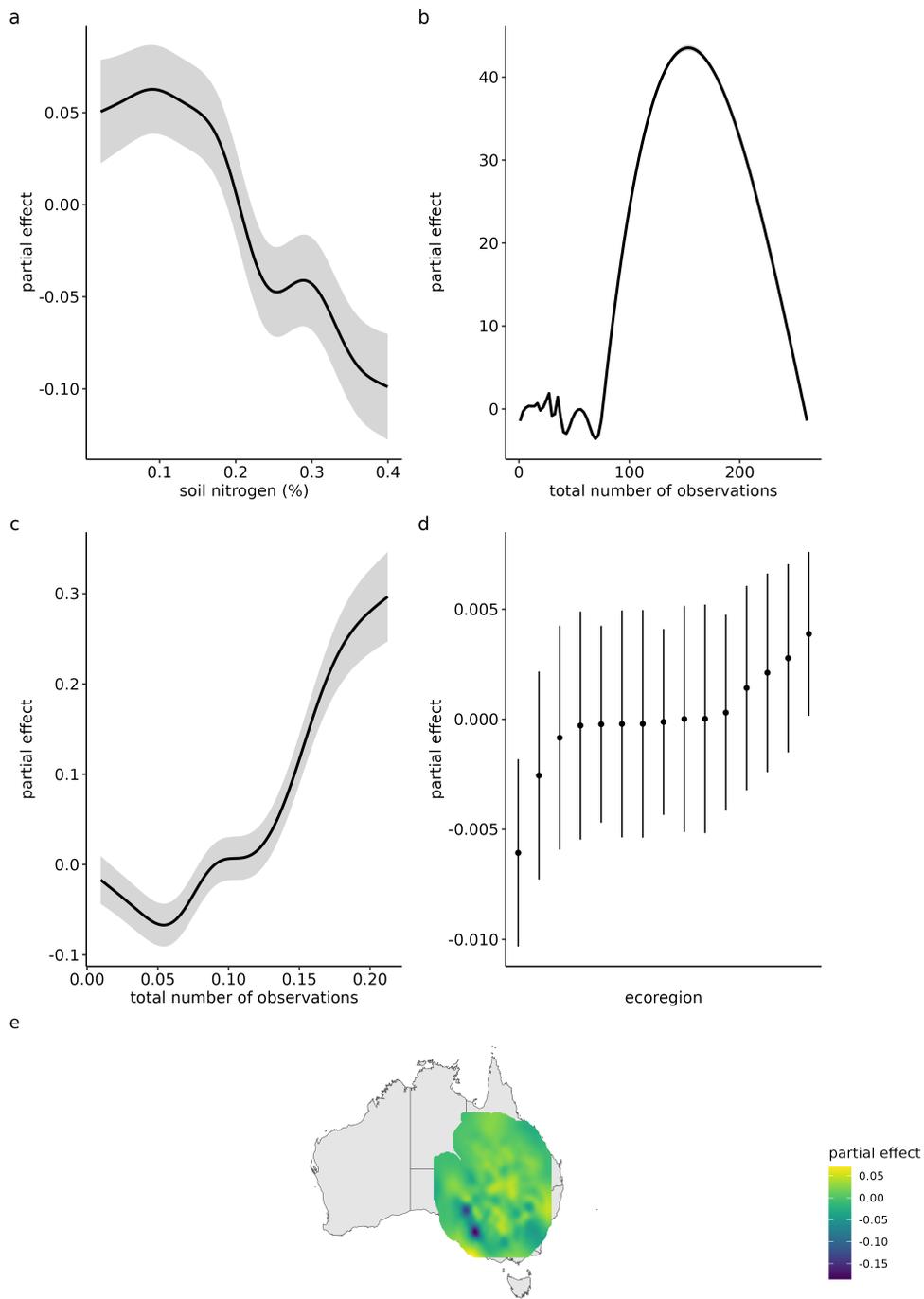
Supplementary Figure 4: Individual time step intake targets for grasshoppers kept in both high nitrogen fertilization and control cages. Blue dots represent estimated marginal means from the model while black dots represent raw individual intake targets.



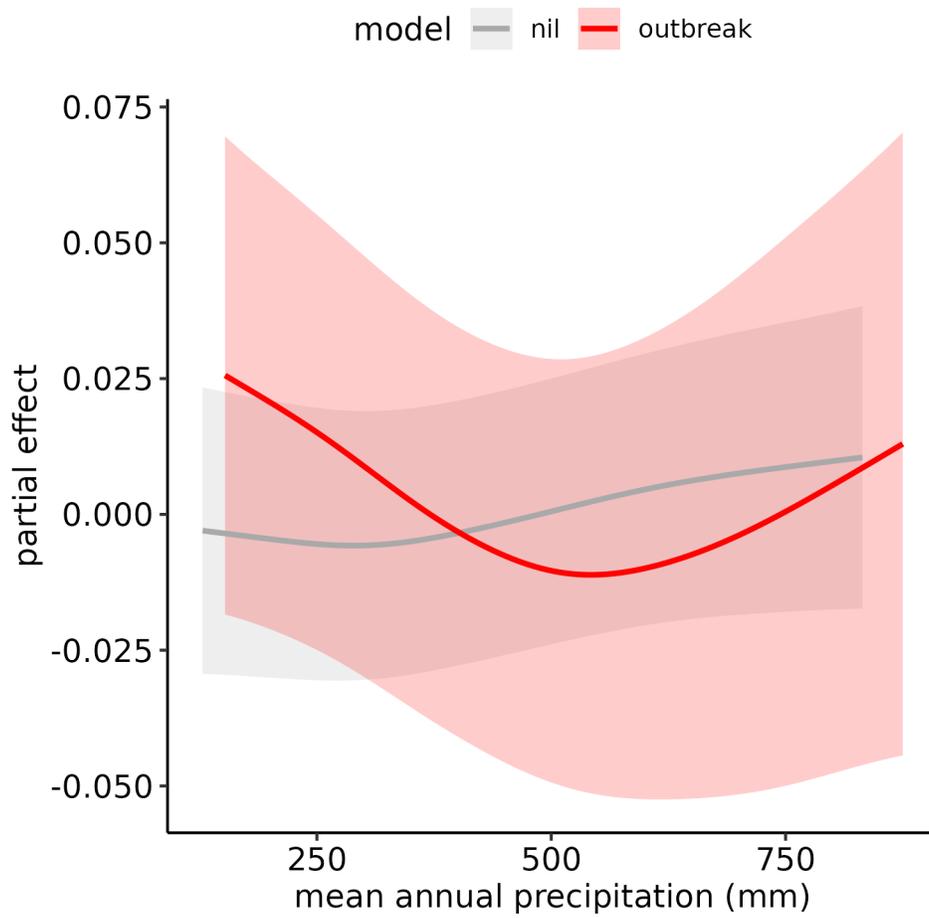
Supplementary Figure 5: Environmental variable correlations between mean annual precipitation, soil nitrogen, soil phosphorus, and woody vegetation pixel coverage. Mean annual precipitation was sourced from WorldClim V1 Bioclim, soil nitrogen and phosphorus was sourced from Soil and Landscape Grid of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