
EXPLORING NUTRIENT AVAILABILITY AND HERBIVOROUS INSECT POPULATION DYNAMICS ACROSS MULTIPLE SCALES

A PREPRINT

2024-09-23

ABSTRACT

1. Nutrient composition varies greatly across landscapes, which in turn influences the spatiotem-
2 poral variation and dynamics of populations. Yet few studies have investigated this pattern on
3 multiple scales.
4. We tested how nutrient limitation affects herbivore populations across spatial scales from indi-
5 vidual behavior to landscape level population dynamics using Australian plague locust, *Chor-*
6 *toicetes terminifera* (Walker), field populations and long-term survey data from across their
7 range.
8. At the individual level, juvenile locusts selected for a carbohydrate-biased intake target of 1
9 protein (p) 2 carbohydrate (c) and had the highest growth and shortest development time when
10 fed artificial diets with that same 1p:2c ratio over the duration of the 5th (final) juvenile instar.
11. At the field level, locusts kept in field cages with protein-biased plants redressed their nutritional
12 imbalance by selecting very carbohydrate-biased diets (up to a 1p:20c ratio) for more than a
13 week after being removed from the protein-biased environment. Once the deficiency was met,
14 locusts returned to the 1p:2c intake target.
15. Going up to the landscape level, outbreaks were negatively correlated with soil nitrogen and
16 showed a non-linear relationship with soil phosphorus peaking at approximately 4% soil phos-
17 phorus. We disentangled the relationship between mean annual precipitation and soil nitrogen
18 through leveraging both comprehensive locust surveys and remotely sensed soil and weather
19 data that spanned decades.
20. This paper is the first to integrate lab, field, and remote sensing approaches to demonstrate the
21 importance of nutrient balancing and acquisition across scales for herbivores. Specifically for
22 locusts, we show that low nitrogen environments promote outbreaks, likely by reducing plant
23 protein to carbohydrate ratios. Incorporating soil quality data into locust plague forecasting
24 models can help increase accuracy of predictions.

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

27 **1 INTRODUCTION**

28 Plant nutrients are usually more variable than animal body composition, which can make it challenging for herbivores
29 to acquire an optimal nutritional balance [Elser et al., 2000]. Nutrient balance affects individual performance [Batzli,
30 1986, Bernays et al., 1994] and, by extension, influences population dynamics [Elser et al., 2000]. One way many
31 primary consumers achieve an optimal blend of nutrients is through selecting different host plants or plant parts to
32 reach a specific amount and ratio, termed the intake target, IT [Simpson and Raubenheimer, 2012a]. For example,
33 giant pandas (*Ailuropoda melanoleuca*) synchronize their migration and reproduction cycles with seasonal nutrient
34 availability between different bamboo species [Nie et al., 2015]. While studies have investigated this trend between
35 available nutrients and animal populations, they usually happen at one scale and biological level. For example, much
36 grasshopper nutrition research has been done at the organismal or local population level using lab and/or field studies
37 [Behmer, 2009, Cease, 2024, Le Gall et al., 2019], with a few separate larger scale modeling endeavors [Welti et al.,

38 2020b, Zhou et al., 2019]. To our knowledge, no study has integrated individual herbivorous animal nutrition to
 39 continental level patterns in nutrient availability. Here we work across spatial scales, bridging field observations and
 40 cage manipulations with continental-scale insect pest outbreak modeling to see how the animal-nutrient relationship
 41 changes across multiple scales.

42 Food quality has long been considered an important predictor of animal population dynamics [Andersen et al., 2004,
 43 White, 1993]. Phosphorus and nitrogen commonly limit primary production in ecosystems, either separately or as co-
 44 limiting factors [Tyrrell, 1999, Vitousek et al., 2010], and are often investigated as limiting factors for higher trophic
 45 levels to determine the consequences to animal growth and reproduction [Andersen et al., 2004]. For example, blue-
 46 grass fields supplemented with high quality (e.g. increased nitrogen) food pellets increase vole (*Microtus ochrogaster*)
 47 densities compared to control fields by supporting higher adult survival, increased breeding, and growth rate [Cole and
 48 Batzli, 1978]. Less phosphorus in a dryland insect herbivore's (*Sabinia setosa*) host plant, velvet mesquite (*Prosopis*
 49 *velutina*), leads to individuals having decreased RNA content (slower growth) and lower abundance [Schade et al.,
 50 2003]. More broadly, nitrogen and phosphorus limitation has been shown in mammals [Randolph et al., 1995, White,
 51 1993], birds [Forero et al., 2002, Granbom and Smith, 2006], and insects [Floyd, 1996, Huberty and Denno, 2006,
 52 Marsh and Adams, 1995, Perkins et al., 2004] which is discussed further in White [2008] and Andersen et al. [2004].
 53 However, not all animal populations respond positively to increasing environmental nutrients. For example, studies
 54 from across the globe reveal that the abundances of many grasshopper species are positively [Joern et al., 2012, Ozment
 55 et al., 2021, Welti et al., 2020a,b, Zhu et al., 2020, 2019], or not related [Heidorn and Joern, 1987, Jonas and Joern,
 56 2008, Lenhart et al., 2015, Ozment et al., 2021] to plant nitrogen concentrations as reviewed in Cease [2024]. Can
 57 the relationship between herbivore abundance and environmental nutrients be explained by approaches that consider
 58 nutritional physiology at the organismal level, in addition to population and landscape ecology?

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

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

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

- 96 1) What are the nutritional preferences of individuals from gregarious *C. terminifera* field populations? We
 97 expect individuals to be carbohydrate biased based on their active lifestyle, and to keep a constant intake
 98 target between populations.
- 99 2) What happens to *C. terminifera* when constrained to high nitrogen environments? We expect locusts to select
 100 particularly carbohydrate biased diets to redress a protein : carbohydrate imbalance in their local environment.
- 101 3) Can we use soil nutrients as a predictor of *C. terminifera* nymph outbreaks at the continental scale?

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

107 2 METHODS

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

Scale of inference	Scale at which the factor of interest is applied	Number of replicates at the appropriate scale
individual	Populations	150 locusts
individual	cages	20 locusts in each cage
population	cages	36 cages in each fertilization treatment
Landscape	populations	67144 1 km ² grids throughout Australia

Table 1: Replication statement for all scales of interest

111 2.1 Field site and animals

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

117 2.2 Nutritional target and performance curve using synthetic diets

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

123 We collected fourth and fifth instar nymphs from outbreeding populations on Nov. 12, 2015 from two locations: near
 124 Mendooran (31°40.791' S, 149°04.209' E) and Guntawang (32°23.988' S, 149°28.649' E), New South Wales. The
 125 Mendooran population was forming marching bands while the Guntawang population was at high density but was not
 126 actively marching during the collection period. Both populations were collected along dirt roads flanked by livestock
 127 grazing pastures containing a mix of grasses and forbs. We transported locusts back to the Trangie Agricultural
 128 Research Centre and kept them in large plastic bins with holes along with an assortment of grasses and forbs cut
 129 from the same field locusts were collected until experiments were started. For both experiments, locusts were housed
 130 individually in plastic cages (ca. 18 cm L x 12 cm W x 4 cm H) with small holes for ventilation. Each cage had two
 131 (nutritional target) or one (performance curve) artificial diets, a water tube capped with cotton, and a perch.

132 **2.2.1 Nutrition target (choice diets)**

133 We ran this experiment to determine the preferred dietary p:c ratio of *C. terminifera* field populations. We selected
 134 equal numbers of males and females from both Mendooran and Guntawang populations and individuals that had no
 135 visible wing bud separation to ensure they were early in the fifth instar. Locusts were heated with incandescent light
 136 bulbs on a 14:10 light:dark cycle. The average daytime and nighttime temperatures in the cages were 25.5°C and
 137 23.4°C respectively, recorded from an iButton (Maxim). We randomly assigned 80 locusts (20 individuals per diet pair
 138 per population) to one of two treatment groups receiving pairs of either 7p:35c & 28p:14c or 7p:35c & 35p:7c (% p :
 139 % c by dry mass). We used two different pairs to ensure that the selected p:c ratio was not the result of eating randomly
 140 between the two dishes. We let locusts eat from the dishes for three days (Nov. 12-15, 2015) and calculated the mass
 141 of protein and carbohydrate each locust ate by subtracting the final dish weights from the initial dish weights.

142 **2.2.2 Performance curve (no-choice diets)**

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

155 **2.3 Field cage experiments**

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

164 We built 0.75 x 0.75 x 0.75 m cages with four steel fence posts and aluminum mesh. We secured the mesh to the
 165 ground by partially burying it and nailing thin slats of wood over the mesh edges. Before adding locusts to the cages,
 166 we removed any plant litter and arthropods (mostly spiders and locusts) so we could more easily count the locusts
 167 and limit predation. We added 20 4th instar locust nymphs to each field cage on the evening of November 13th and
 168 morning of November 14th. We randomly selected these nymphs from the Mendooran population we collected on
 169 November 12th (see synthetic diet methods section above). Each fertilized plot had four cages, for a total of 12 cages
 170 per fertilization level, and 36 cages and 720 locusts in total. We checked the cages every 4-5 days and removed any
 171 spiders.

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

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

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

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

190 We calculated the proportion molted to adult of the surviving locusts (# adults/# live locusts).

191 **2.4 Correlating historical nymphal outbreaks with soil nitrogen and phosphorus**

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

195 **2.4.1 Locust outbreak data**

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

210 **2.4.2 Soil grid of Australia data**

211 The soil and landscape grid of Australia is a modeled raster of 12 soil variables at a 90 m² resolution. These soil characteristics are available at multiple depths from surface to two meters below the surface. These depths and methodology are consistent with the specifications of the Global Soil Map project (<http://www.globalsoilmap.net>) [Grundy et al., 2015]. We extracted this data from Google Earth Engine [Gorelick et al., 2017]. In this data set both phosphorus and nitrogen units are the mass fraction of total nutrient in the soil by weight. We took the average of nitrogen and phosphorus of the top two depths (0 cm – 5 cm and 5 cm and 15 cm) as these are most relevant to nutrient content of grasses and forbs. Then, for each APC survey grid we calculated the mean mass fraction of nitrogen and phosphorus in the soil by weight to a 15 cm depth. Spatial distribution of soil nitrogen and phosphorus can be seen in Figure 1 B and Figure 1 C respectively.

220 **2.5 Statistics**

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

225 **2.5.1 Intake Targets**

226 To determine intake targets, we constructed GAM (family: Multivariate Normal Distribution, Link: Identity) with the following variables when possible: diet pairing (factor), locust sex (factor), time period interval (integer), locust initial weight (numeric) following roughly the procedure found in Lawton et al. [2021]. We selected the inclusion 227 of locust weight as either a non-linear or linear effect via Akaike information criterion (AIC), AIC adjusted for small 228 sample size (AICc), and Bayesian information criterion (BIC). If weight was not an important variable, it was removed 229 entirely from the model.

232 **2.5.2 Field population**

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

236 **2.5.3 Field Cage**

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

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

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

263 **3 RESULTS**

264 **3.1 Field population**

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

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

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

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

276 **3.2 Field Cage**

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

285 **3.3 Locust outbreaks**

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

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

4 DISCUSSION

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

4.1 Field populations

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

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

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

4.2 Historical outbreak modeling

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

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

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

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

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

388 **4.4 Comparing the relationship between plant macronutrients and herbivore abundance in other taxa**

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

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

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

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

433 4.5 Synthesis and Application

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

448 5 REFERENCES

- 449 Tom Andersen, James J. Elser, and Dag O. Hessen. Stoichiometry and population dynamics. *Ecology Letters*, 7
 450 (9):884–900, September 2004. ISSN 1461-023X, 1461-0248. doi: 10.1111/j.1461-0248.2004.00646.x. URL
 451 <https://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2004.00646.x>.
- 452 Achyut Aryal, Sean C. P. Coogan, Weihong Ji, Jessica M. Rothman, and David Raubenheimer. Foods, macronutrients
 453 and fibre in the diet of blue sheep (*Pseudois nayaur*) in the Annapurna Conservation Area of Nepal. *Ecology*

- 454 *and Evolution*, 5(18):4006–4017, September 2015. ISSN 2045-7758, 2045-7758. doi: 10.1002/ece3.1661. URL
 455 <https://onlinelibrary.wiley.com/doi/10.1002/ece3.1661>.
- 456 George O. Batzli. Nutritional Ecology of the California Vole: Effects of Food Quality on Reproduction. *Ecology*, 67(2):
 457 406–412, April 1986. ISSN 0012-9658, 1939-9170. doi: 10.2307/1938583. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1938583>.
- 459 Spencer T. Behmer. Insect Herbivore Nutrient Regulation. *Annual Review of Entomology*, 54(1):165–187, January
 460 2009. ISSN 0066-4170, 1545-4487. doi: 10.1146/annurev.ento.54.110807.090537. URL <https://www.annualreviews.org/doi/10.1146/annurev.ento.54.110807.090537>.
- 462 E. A. Bernays, K. L. Bright, N. Gonzalez, and J. Angel. Dietary Mixing in a Generalist Herbivore: Tests of Two
 463 Hypotheses. *Ecology*, 75(7):1997–2006, October 1994. ISSN 00129658. doi: 10.2307/1941604. URL <http://doi.wiley.com/10.2307/1941604>.
- 465 LeAndra Luecke Bridgeman. The Feeding Ecology of YucatÁn Black Howler Monkeys (*Alouatta pigra*) in Man-
 466 grove Forest, Tabasco, Mexico. 2012. doi: 10.7936/K75T3HGP. URL <http://openscholarship.wustl.edu/etd/998>.
 467 Publisher: Washington University in St. Louis.
- 468 Jonah Brosemann, Rick Overton, Arianne J. Cease, Sydney Millerwise, and Marion Le Gall. Nutrient supply and
 469 accessibility in plants: effect of protein and carbohydrates on Australian plague locust (*Chortoicetes terminifera*)
 470 preference and performance. *Frontiers in Insect Science*, 3:1110518, July 2023. ISSN 2673-8600. doi: 10.3389/finsc.2023.1110518. URL <https://www.frontiersin.org/articles/10.3389/finsc.2023.1110518/full>.
- 472 Alison S. Scott Brown, Monique S. J. Simmonds, and Walter M. Blaney. Relationship between nutritional composition
 473 of plant species and infestation levels of thrips. *Journal of Chemical Ecology*, 28(12):2399–2409, 2002. ISSN
 474 00980331. doi: 10.1023/A:1021471732625. URL <http://link.springer.com/10.1023/A:1021471732625>.
- 475 Arianne J. Cease. How Nutrients Mediate the Impacts of Global Change on Locust Outbreaks. *Annual Review of
 476 Entomology*, 69(1):527–550, January 2024. ISSN 0066-4170, 1545-4487. doi: 10.1146/annurev-ento-120220-110415. URL <https://www.annualreviews.org/doi/10.1146/annurev-ento-120220-110415>.
- 478 Arianne J. Cease, James J. Elser, Colleen F. Ford, Shuguang Hao, Le Kang, and Jon F. Harrison. Heavy Livestock
 479 Grazing Promotes Locust Outbreaks by Lowering Plant Nitrogen Content. *Science*, 335(6067):467–469, January
 480 2012. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.1214433. URL <https://www.science.org/doi/10.1126/science.1214433>.
- 482 Arianne J. Cease, James J. Elser, Eli P. Fenichel, Joleen C. Hadrich, Jon F. Harrison, and Brian E. Robinson. Living
 483 With Locusts: Connecting Soil Nitrogen, Locust Outbreaks, Livelihoods, and Livestock Markets. *BioScience*, 65
 484 (6):551–558, June 2015. ISSN 1525-3244, 0006-3568. doi: 10.1093/biosci/biv048. URL <http://academic.oup.com/bioscience/article/65/6/551/303376/Living-With-Locusts-Connecting-Soil-Nitrogen>.
- 486 Arianne J. Cease, Michelle Fay, James J. Elser, and Jon F. Harrison. Dietary phosphate affects food selection, post-
 487 ingestive P fate, and performance of a polyphagous herbivore. *Journal of Experimental Biology*, page jeb.126847,
 488 January 2016. ISSN 1477-9145, 0022-0949. doi: 10.1242/jeb.126847. URL <https://journals.biologists.com/jeb/article/doi/10.1242/jeb.126847/262050/Dietary-phosphate-affects-food-selection-post>.
- 490 Arianne J. Cease, Eduardo V. Trumper, Héctor Medina, Fernando Copa Bazán, Jorge Frana, Jon Harrison, Nelson
 491 Joaquin, Jennifer Learned, Mónica Roca, Julio E. Rojas, Stav Talal, and Rick P. Overton. Field bands
 492 of marching locust juveniles show carbohydrate, not protein, limitation. *Current Research in Insect Science*, 4:
 493 100069, 2023. ISSN 26665158. doi: 10.1016/j.cris.2023.100069. URL <https://linkinghub.elsevier.com/retrieve/pii/S2666515823000185>.
- 495 Ken Cheng, Stephen J. Simpson, and David Raubenheimer. A Geometry of Regulatory Scaling. *The American
 496 Naturalist*, 172(5):681–693, November 2008. ISSN 0003-0147, 1537-5323. doi: 10.1086/591686. URL <https://www.journals.uchicago.edu/doi/10.1086/591686>.
- 498 Dp Clark. The Influence of Rainfall on the Densities of Adult Chortoicetes Terminifera (Walker) in Central Western
 499 New South Wales, 1965-73. *Australian Journal of Zoology*, 22(3):365, 1974. ISSN 0004-959X. doi: 10.1071/
 500 ZO9740365. URL <http://www.publish.csiro.au/?paper=ZO9740365>.
- 501 D G Clayton, L Bernardinelli, and C Montomoli. Spatial Correlation in Ecological Analysis. *International Journal
 502 of Epidemiology*, 22(6):1193–1202, 1993. ISSN 0300-5771, 1464-3685. doi: 10.1093/ije/22.6.1193. URL <https://academic.oup.com/ije/article-lookup/doi/10.1093/ije/22.6.1193>.
- 504 Fiona J. Clissold, Nicole Coggan, and Stephen J. Simpson. Insect herbivores can choose microclimates to achieve
 505 nutritional homeostasis. *Journal of Experimental Biology*, page jeb.078782, January 2013. ISSN 1477-9145, 0022-
 506 0949. doi: 10.1242/jeb.078782. URL <https://journals.biologists.com/jeb/article/doi/10.1242/jeb.078782/258075/Insect-herbivores-can-choose-microclimates-to>.

- 508 Fiona J. Clissold, Helena Kertesz, Amelia M. Saul, Julia L. Sheehan, and Stephen J. Simpson. Regulation of water
 509 and macronutrients by the Australian plague locust, *Chortoicetes terminifera*. *Journal of Insect Physiology*, 69:35–
 510 40, October 2014. ISSN 00221910. doi: 10.1016/j.jinsphys.2014.06.011. URL <https://linkinghub.elsevier.com/retrieve/pii/S0022191014001267>.
- 512 F. R. Cole and G. O. Batzli. Influence of Supplemental Feeding on a Vole Population. *Journal of Mammalogy*, 59(4):
 513 809–819, November 1978. ISSN 1545-1542, 0022-2372. doi: 10.2307/1380145. URL <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1380145>.
- 515 Keith Cressman. Role of remote sensing in desert locust early warning. *Journal of Applied Remote Sensing*, 7(1):
 516 075098, May 2013. ISSN 1931-3195. doi: 10.1117/1.JRS.7.075098. URL <http://remotesensing.spiedigitallibrary.org/article.aspx?doi=10.1117/1.JRS.7.075098>.
- 518 Darron A. Cullen, Arianne J. Cease, Alexandre V. Latchininsky, Amir Ayali, Kevin Berry, Camille Buhl, Rien
 519 De Keyser, Bert Foquet, Joleen C. Hadrich, Tom Matheson, Swidbert R. Ott, Mario A. Poot-Pech, Brian E.
 520 Robinson, Jonathan M. Smith, Hojun Song, Gregory A. Sword, Jozef Vanden Broeck, Rik Verdonck, Heleen
 521 Verlinden, and Stephen M. Rogers. From Molecules to Management: Mechanisms and Consequences of
 522 Locust Phase Polyphenism. In *Advances in Insect Physiology*, volume 53, pages 167–285. Elsevier, 2017.
 523 ISBN 978-0-12-811833-7. doi: 10.1016/bs.aiip.2017.06.002. URL <https://linkinghub.elsevier.com/retrieve/pii/S0065280617300231>.
- 525 R.H. Dadd. The nutritional requirements of locustsIV. Requirements for vitamins of the B complex. *Journal of Insect Physiology*, 6(1):1–12, February 1961. ISSN 00221910. doi: 10.1016/0022-1910(61)90086-5. URL <https://linkinghub.elsevier.com/retrieve/pii/0022191061900865>.
- 528 Louis De Grandpré, Maryse Marchand, Daniel D. Kneeshaw, David Paré, Dominique Boucher, Stéphane Bourassa,
 529 David Gervais, Martin Simard, Jacob M. Griffin, and Deepa S. Pureswaran. Defoliation-induced changes in foliage
 530 quality may trigger broad-scale insect outbreaks. *Communications Biology*, 5(1):463, May 2022. ISSN 2399-3642.
 531 doi: 10.1038/s42003-022-03407-8. URL <https://www.nature.com/articles/s42003-022-03407-8>.
- 532 E. D. Deveson and P. W. Walker. Not a one-way trip: historical distribution data for Australian plague locusts support
 533 frequent seasonal exchange migrations. *Journal of Orthoptera Research*, 14(1):91–105, January 2005. ISSN 1082-
 534 6467, 1937-2426. doi: 10.1665/1082-6467(2005)14[91:NAOTHD]2.0.CO;2. URL <http://www.bioone.org/doi/abs/10.1665/1082-6467%282005%2914%5B91%3ANAOTHD%5D2.0.CO%3B2>.
- 536 Edward D. Deveson. Satellite normalized difference vegetation index data used in managing Australian plague locusts.
 537 *Journal of Applied Remote Sensing*, 7(1):075096, July 2013. ISSN 1931-3195. doi: 10.1117/1.JRS.7.075096. URL
 538 <http://remotesensing.spiedigitallibrary.org/article.aspx?doi=10.1117/1.JRS.7.075096>.
- 539 Ted Deveson and David Hunter. THE OPERATION OF A GISBASED DECISION SUPPORT SYSTEM FOR
 540 AUSTRALIAN LOCUST MANAGEMENT. *Insect Science*, 9(4):1–12, December 2002. ISSN 1672-9609,
 541 1744-7917. doi: 10.1111/j.1744-7917.2002.tb00167.x. URL <https://onlinelibrary.wiley.com/doi/10.1111/j.1744-7917.2002.tb00167.x>.
- 543 Colin Donald. Phosphorus in Australian agriculture. *Journal of the Australian Institute of Agricultural Science*, 30
 544 (75):195, 1964.
- 545 Terry J. Doonan and Norman A. Slade. Effects of Supplemental Food on Population Dynamics of Cotton Rats,
 546 *Sigmodon Hispidus*. *Ecology*, 76(3):814–826, April 1995. ISSN 0012-9658, 1939-9170. doi: 10.2307/1939347.
 547 URL <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1939347>.
- 548 James J. Elser, William F. Fagan, Robert F. Denno, Dean R. Dobberfuhl, Ayoola Folarin, Andrea Huberty, Sebastian
 549 Interlandi, Susan S. Kilham, Edward McCauley, Kimberly L. Schulz, Evan H. Siemann, and Robert W. Sterner.
 550 Nutritional constraints in terrestrial and freshwater food webs. *Nature*, 408(6812):578–580, November 2000. ISSN
 551 0028-0836, 1476-4687. doi: 10.1038/35046058. URL <https://www.nature.com/articles/35046058>.
- 552 Ra Farrow. Population Dynamics of the Australian Plague Locust, *Chortoicetes Terminifera* (Walker) in Central
 553 Western New South Wales Iii. Analysis of Population Processes. *Australian Journal of Zoology*, 30(4):569, 1982.
 554 ISSN 0004-959X. doi: 10.1071/ZO9820569. URL <http://www.publish.csiro.au/?paper=ZO9820569>.
- 555 R. B. Floyd, editor. *Frontiers of population ecology*. CSIRO Pub, Collingwood, VIC, Australia, 1996. ISBN 978-0-
 556 643-05781-4.
- 557 M. G. Forero, J. L. Tella, K. A. Hobson, M. Bertellotti, and G. Blanco. Conspecific food competition explains
 558 variability in colony size: a test in Magellanic penguins. *Ecology*, 83(12):3466–3475, December 2002. ISSN 0012-
 559 9658. doi: 10.1890/0012-9658(2002)083[3466:CFCEVI]2.0.CO;2. URL [http://doi.wiley.com/10.1890/0012-9658\(2002\)083\[3466:CFCEVI\]2.0.CO;2](http://doi.wiley.com/10.1890/0012-9658(2002)083[3466:CFCEVI]2.0.CO;2).

- 561 M. Giese, H. Brueck, Y. Z. Gao, S. Lin, M. Steffens, I. Kögel-Knabner, T. Glindemann, A. Susenbeth, F. Taube,
 562 K. Butterbach-Bahl, X. H. Zheng, C. Hoffmann, Y. F. Bai, and X. G. Han. N balance and cycling of Inner Mongolia
 563 typical steppe: a comprehensive case study of grazing effects. *Ecological Monographs*, 83(2):195–219, May 2013.
 564 ISSN 0012-9615, 1557-7015. doi: 10.1890/12-0114.1. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/12-0114.1>.
- 566 Noel Gorelick, Matt Hancher, Mike Dixon, Simon Ilyushchenko, David Thau, and Rebecca Moore. Google Earth
 567 Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, 202:18–27, December 2017.
 568 ISSN 00344257. doi: 10.1016/j.rse.2017.06.031. URL <https://linkinghub.elsevier.com/retrieve/pii/S0034425717302900>.
- 570 Martin Granbom and Henrik G. Smith. Food Limitation During Breeding in a Heterogeneous Landscape. *The Auk*,
 571 123(1):97–107, January 2006. ISSN 1938-4254, 0004-8038. doi: 10.1093/auk/123.1.97. URL <https://academic.oup.com/auk/article/123/1/97/5562605>.
- 573 M. J. Grundy, R. A. Viscarra Rossel, R. D. Searle, P. L. Wilson, C. Chen, and L. J. Gregory. Soil and Landscape Grid
 574 of Australia. *Soil Research*, 53(8):835, 2015. ISSN 1838-675X. doi: 10.1071/SR15191. URL <http://www.publish.csiro.au/?paper=SR15191>.
- 576 Lennart Hansson. Food as a limiting factor for small rodent numbers: Tests of two hypotheses. *Oecologia*, 37(3):
 577 297–314, January 1979. ISSN 0029-8549, 1432-1939. doi: 10.1007/BF00347907. URL <http://link.springer.com/10.1007/BF00347907>.
- 579 Sarah J. Harrison, David Raubenheimer, Stephen J. Simpson, Jean-Guy J. Godin, and Susan M. Bertram. Towards
 580 a synthesis of frameworks in nutritional ecology: interacting effects of protein, carbohydrate and phosphorus on
 581 field cricket fitness. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792):20140539, 2014. doi:
 582 10.1098/rspb.2014.0539. URL <https://doi.org/10.1098/rspb.2014.0539>.
- 583 T. J. Heidorn and A. Joern. Feeding Preference and Spatial Distribution of Grasshoppers (Acrididae) in Response
 584 to Nitrogen Fertilization of Calamovilfa longifolia. *Functional Ecology*, 1(4):369, 1987. ISSN 02698463. doi:
 585 10.2307/2389793. URL <https://www.jstor.org/stable/2389793?origin=crossref>.
- 586 Andrea F. Huberty and Robert F. Denno. Consequences of nitrogen and phosphorus limitation for the performance of
 587 two planthoppers with divergent life-history strategies. *Oecologia*, 149(3):444–455, September 2006. ISSN 0029-
 588 8549, 1432-1939. doi: 10.1007/s00442-006-0462-8. URL <http://link.springer.com/10.1007/s00442-006-0462-8>.
- 589 D. M. Hunter, P. W. Walker, and R. J. Elder. Adaptations of locusts and grasshoppers to the low and variable
 590 rainfall of Australia. *Journal of Orthoptera Research*, 10(2):347–351, December 2001. ISSN 1082-6467, 1937-
 591 2426. doi: 10.1665/1082-6467(2001)010[0347:AOLAGT]2.0.CO;2. URL <http://www.bioone.org/doi/abs/10.1665/1082-6467%282001%29010%5B0347%3AAOLAGT%5D2.0.CO%3B2>.
- 593 D.M. Hunter, L. McCulloch, and P.A. Spurgin. Aerial detection of nymphal bands of the Australian plague
 594 locust (Chortoicetes terminifera (Walker)) (Orthoptera: Acrididae). *Crop Protection*, 27(1):118–123, January
 595 2008. ISSN 02612194. doi: 10.1016/j.cropro.2007.04.016. URL <https://linkinghub.elsevier.com/retrieve/pii/S0261219407001159>.
- 597 Anthony Joern, Tony Provin, and Spencer T. Behmer. Not just the usual suspects: Insect herbivore populations and
 598 communities are associated with multiple plant nutrients. *Ecology*, 93(5):1002–1015, May 2012. ISSN 0012-9658,
 599 1939-9170. doi: 10.1890/11-1142.1. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/11-1142.1>.
- 600 Jayne L. Jonas and Anthony Joern. Hostplant quality alters grass/forb consumption by a mixedfeeding insect herbivore,
 601 *Melanoplus bivittatus* (Orthoptera: Acrididae). *Ecological Entomology*, 33(4):546–554, August 2008. ISSN 0307-
 602 6946, 1365-2311. doi: 10.1111/j.1365-2311.2008.01004.x. URL <https://resjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2311.2008.01004.x>.
- 604 Lloyd B. Keith. Role of Food in Hare Population Cycles. *Oikos*, 40(3):385, May 1983. ISSN 00301299. doi:
 605 10.2307/3544311. URL <https://www.jstor.org/stable/3544311?origin=crossref>.
- 606 K.H.L. Key. The general ecological characteristics of the outbreak areas and outbreak years of the Australian plague
 607 locust (Chortoicetes terminifera Walk.). 1945. doi: 10.25919/RTPX-F935. URL <https://publications.csiro.au/publications/publication/PIprocite:8058408f-539f-4540-b888-0dd1e0c113d>. Publisher: Melbourne, Vic., Council
 608 for Scientific and Industrial Research.
- 610 Douglas Lawton, Cathy Waters, Marion Le Gall, and Arianne Cease. Woody vegetation remnants within pastures
 611 influence locust distribution: Testing bottom-up and top-down control. *Agriculture, Ecosystems & Environment*,
 612 296:106931, July 2020. ISSN 01678809. doi: 10.1016/j.agee.2020.106931. URL <https://linkinghub.elsevier.com/retrieve/pii/S016788092030116X>.

- 614 Douglas Lawton, Marion Le Gall, Cathy Waters, and Arianne J. Cease. Mismatched diets: defining the nutritional
 615 landscape of grasshopper communities in a variable environment. *Ecosphere*, 12(3):e03409, March 2021. ISSN
 616 2150-8925, 2150-8925. doi: 10.1002/ecs2.3409. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.3409>.
- 618 Douglas Lawton, Peter Scarth, Edward Deveson, Cyril Piou, Allan Spessa, Cathy Waters, and Arianne J. Cease. Seeing
 619 the locust in the swarm: accounting for spatiotemporal hierarchy improves ecological models of insect populations.
 620 *Ecography*, 2022(2):ecog.05763, February 2022. ISSN 0906-7590, 1600-0587. doi: 10.1111/ecog.05763. URL
 621 <https://nsojournals.onlinelibrary.wiley.com/doi/10.1111/ecog.05763>.
- 622 Marion Le Gall, Rick Overton, and Arianne Cease. A Global Review on Locusts (Orthoptera: Acrididae) and Their
 623 Interactions With Livestock Grazing Practices. *Frontiers in Ecology and Evolution*, 7:263, July 2019. ISSN 2296-
 624 701X. doi: 10.3389/fevo.2019.00263. URL <https://www.frontiersin.org/article/10.3389/fevo.2019.00263/full>.
- 625 Paul A. Lenhart, Micky D. Eubanks, and Spencer T. Behmer. Water stress in grasslands: dynamic responses of plants
 626 and insect herbivores. *Oikos*, 124(3):381–390, March 2015. ISSN 0030-1299, 1600-0706. doi: 10.1111/oik.01370.
 627 URL <https://onlinelibrary.wiley.com/doi/10.1111/oik.01370>.
- 628 Viviana Loaiza, Jayne L. Jonas, and Anthony Joern. Grasshoppers (orthoptera: Acrididae) select vegetation patches
 629 in local-scale responses to foliar nitrogen but not phosphorus in native grassland: Grasshopper distribution and
 630 food quality. *Insect Science*, 18(5):533–540, 10 2011. doi: 10.1111/j.1744-7917.2010.01376.x. URL <https://onlinelibrary.wiley.com/doi/10.1111/j.1744-7917.2010.01376.x>.
- 632 Nr Marsh and Ma Adams. Decline of Eucalyptus tereticornis Near Bairnsdale, Victoria: Insect Herbivory and Nitrogen
 633 Fractions in Sap and Foliage. *Australian Journal of Botany*, 43(1):39, 1995. ISSN 0067-1924. doi: 10.1071/
 634 BT9950039. URL <http://www.publish.csiro.au/?paper=BT9950039>.
- 635 William J. Mattson. Herbivory in Relation to Plant Nitrogen Content. *Annual Review of Ecology and Systematics*,
 636 11(1):119–161, November 1980. ISSN 0066-4162. doi: 10.1146/annurev.es.11.110180.001003. URL <https://www.annualreviews.org/doi/10.1146/annurev.es.11.110180.001003>.
- 638 Ali Abdalla Millist, Nicola. Benefitcost analysis of Australian plague locust control operations for 201011,
 639 2011. URL <https://www.agriculture.gov.au/sites/default/files/sitecollectiondocuments/animal-plant/aplc/research-papers/locust-control-11.pdf>.
- 641 S.R. Morton, D.M. Stafford Smith, C.R. Dickman, D.L. Dunkerley, M.H. Friedel, R.R.J. McAllister, J.R.W. Reid, D.A.
 642 Roshier, M.A. Smith, F.J. Walsh, G.M. Wardle, I.W. Watson, and M. Westoby. A fresh framework for the ecology
 643 of arid Australia. *Journal of Arid Environments*, 75(4):313–329, April 2011. ISSN 01401963. doi: 10.1016/j.jaridenv.2010.11.001. URL <https://linkinghub.elsevier.com/retrieve/pii/S0140196310003010>.
- 645 Joaquín Muñoz-Sabater, Emanuel Dutra, Anna Agustí-Panareda, Clément Albergel, Gabriele Arduini, Gianpaolo
 646 Balsamo, Souhail Boussetta, Margarita Choulga, Shaun Harrigan, Hans Hersbach, Brecht Martens, Diego G.
 647 Miralles, María Piles, Nemesio J. Rodríguez-Fernández, Erwin Zsoter, Carlo Buontempo, and Jean-Noël Thé-
 648 paut. ERA5-Land: a state-of-the-art global reanalysis dataset for land applications. *Earth System Science
 649 Data*, 13(9):4349–4383, September 2021. ISSN 1866-3516. doi: 10.5194/essd-13-4349-2021. URL <https://essd.copernicus.org/articles/13/4349/2021/>.
- 651 Yonggang Nie, Zejun Zhang, David Raubenheimer, James J. Elser, Wei Wei, and Fuwen Wei. Obligate herbivory
 652 in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry.
 653 *Functional Ecology*, 29(1):26–34, January 2015. ISSN 0269-8463, 1365-2435. doi: 10.1111/1365-2435.12302.
 654 URL <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.12302>.
- 655 Immanuel Noy-Meir. Desert Ecosystems: Higher Trophic Levels. *Annual Review of Ecology and Systematics*, 5(1):
 656 195–214, November 1974. ISSN 0066-4162. doi: 10.1146/annurev.es.05.110174.001211. URL <https://www.annualreviews.org/doi/10.1146/annurev.es.05.110174.001211>.
- 658 Gordon H. Orians and Antoni V. Milewski. Ecology of Australia: the effects of nutrientpoor soils and intense fires.
 659 *Biological Reviews*, 82(3):393–423, August 2007. ISSN 1464-7931, 1469-185X. doi: 10.1111/j.1469-185X.2007.
 660 00017.x. URL <https://onlinelibrary.wiley.com/doi/10.1111/j.1469-185X.2007.00017.x>.
- 661 Katerina A. Ozment, Ellen A. R. Welti, Monica Shaffer, and Michael Kaspari. Tracking nutrients in space and time:
 662 Interactions between grazing lawns and drought drive abundances of tallgrass prairie grasshoppers. *Ecology and
 663 Evolution*, 11(10):5413–5423, May 2021. ISSN 2045-7758, 2045-7758. doi: 10.1002/ece3.7435. URL <https://onlinelibrary.wiley.com/doi/10.1002/ece3.7435>.
- 665 Adam F. Parlin, Mitchell J. Kendzel, Orley R. Taylor, Theresa M. Culley, Stephen F. Matter, and Patrick A.
 666 Guerra. The cost of movement: assessing energy expenditure in a long-distant ectothermic migrant under cli-
 667 mate change. *Journal of Experimental Biology*, 226(21):jeb245296, November 2023. ISSN 0022-0949, 1477-9145.

- 668 doi: 10.1242/jeb.245296. URL <https://journals.biologists.com/jeb/article/226/21/jeb245296/334654/The-cost-of-movement-assessing-energy-expenditure>.
- 670 Marc C. Perkins, H. Arthur Woods, Jon F. Harrison, and James J. Elser. Dietary phosphorus affects the growth of larval
671 *Manduca sexta*. *Archives of Insect Biochemistry and Physiology*, 55(3):153–168, March 2004. ISSN 0739-4462,
672 1520-6327. doi: 10.1002/arch.10133. URL <https://onlinelibrary.wiley.com/doi/10.1002/arch.10133>.
- 673 J. C. Randolph, G. N. Cameron, and P. A. McClure. Nutritional Requirements for Reproduction in the Hispid Cotton
674 Rat, *Sigmodon hispidus*. *Journal of Mammalogy*, 76(4):1113–1126, December 1995. ISSN 1545-1542, 0022-2372.
675 doi: 10.2307/1382603. URL <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1382603>.
- 676 D. Raubenheimer and S. J. Simpson. Integrative models of nutrient balancing: application to insects and ver-
677 tebrates. *Nutrition Research Reviews*, 10(1):151–179, January 1997. ISSN 0954-4224, 1475-2700. doi: 10.
678 1079/NRR19970009. URL https://www.cambridge.org/core/product/identifier/S0954422497000103/type/journal_article.
- 680 David Raubenheimer and Jessica M. Rothman. Nutritional Ecology of Entomophagy in Humans and Other Primates.
681 *Annual Review of Entomology*, 58(1):141–160, January 2013. ISSN 0066-4170, 1545-4487. doi: 10.1146/annurev-
682 ento-120710-100713. URL <https://www.annualreviews.org/doi/10.1146/annurev-ento-120710-100713>.
- 683 John D. Schade, Marcia Kyle, S. E. Hobbie, W. F. Fagan, and J. J. Elser. Stoichiometric tracking of soil nutrients
684 by a desert insect herbivore. *Ecology Letters*, 6(2):96–101, February 2003. ISSN 1461-023X, 1461-0248. doi:
685 10.1046/j.1461-0248.2003.00409.x. URL <https://onlinelibrary.wiley.com/doi/10.1046/j.1461-0248.2003.00409.x>.
- 686 S. J. Simpson and J. D. Abisgold. Compensation by locusts for changes in dietary nutrients: behavioural mechanisms.
687 *Physiological Entomology*, 10(4):443–452, December 1985. ISSN 0307-6962, 1365-3032. doi: 10.1111/j.1365-
688 3032.1985.tb00066.x. URL <https://resjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-3032.1985.tb00066.x>.
- 689 Stephen J Simpson and David Raubenheimer. *The nature of nutrition: a unifying framework from animal adaptation
690 to human obesity*. Princeton university press, 2012a.
- 691 Stephen J. Simpson and David Raubenheimer. *The Nature of Nutrition: A Unifying Framework from Animal Adap-
692 tation to Human Obesity*. Princeton University Press, 1 edition, July 2012b. ISBN 978-0-691-14565-5 978-1-
693 4008-4280-3. doi: 10.23943/princeton/9780691145655.001.0001. URL <https://academic.oup.com/princeton-scholarship-online/book/23993>.
- 695 Stav Talal, Arianne J. Cease, Jacob P. Youngblood, Ruth Farington, Eduardo V. Trumper, Hector E. Medina, Julio E.
696 Rojas, A. Fernando Copa, and Jon F. Harrison. Plant carbohydrate content limits performance and lipid accumula-
697 tion of an outbreaking herbivore. *Proceedings of the Royal Society B: Biological Sciences*, 287(1940):20202500,
698 December 2020. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2020.2500. URL <https://royalsocietypublishing.org/doi/10.1098/rspb.2020.2500>.
- 700 Stav Talal, Arianne Cease, Ruth Farington, Hector E. Medina, Julio Rojas, and Jon Harrison. High carbohydrate diet
701 ingestion increases post-meal lipid synthesis and drives respiratory exchange ratios above 1. *Journal of Experi-
702 mental Biology*, 224(4):jeb240010, February 2021. ISSN 0022-0949, 1477-9145. doi: 10.1242/jeb.240010. URL <https://journals.biologists.com/jeb/article/224/4/jeb240010/237230/High-carbohydrate-diet-ingestion-increases-post>.
- 704 Stav Talal, Jon F. Harrison, Ruth Farington, Jacob P. Youngblood, Hector E. Medina, Rick Overson, and Arianne J.
705 Cease. Body mass and growth rates predict protein intake across animals, June 2023. URL <http://biorxiv.org/lookup/doi/10.1101/2023.06.20.545784>.
- 707 Toby Tyrrell. The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature*, 400(6744):
708 525–531, August 1999. ISSN 0028-0836, 1476-4687. doi: 10.1038/22941. URL <https://www.nature.com/articles/22941>.
- 710 Boris Petrovi Uvarov. *Grasshoppers and locusts. 2: Behaviour, ecology, biogeography population dynamics*. Univ.
711 Press, Cambridge, 1977. ISBN 978-0-85135-072-1.
- 712 Sophie Veran, Stephen J. Simpson, Gregory A. Sword, Edward Deveson, Sylvain Piry, James E. Hines, and Karine
713 Berthier. Modeling spatiotemporal dynamics of outbreaking species: influence of environment and migration in
714 a locust. *Ecology*, 96(3):737–748, March 2015. ISSN 0012-9658, 1939-9170. doi: 10.1890/14-0183.1. URL
715 <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/14-0183.1>.
- 716 Peter M. Vitousek, Stephen Porder, Benjamin Z. Houlton, and Oliver A. Chadwick. Terrestrial phosphorus limita-
717 tion: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications*, 20(1):5–15, January
718 2010. ISSN 1051-0761, 1939-5582. doi: 10.1890/08-0127.1. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/08-0127.1>.

- 720 Ellen A. R. Welti, Rebecca M. Prather, Nathan J. Sanders, Kirsten M. De Beurs, and Michael Kaspari. Bottomup when
 721 it is not topdown: Predators and plants control biomass of grassland arthropods. *Journal of Animal Ecology*, 89(5):
 722 1286–1294, May 2020a. ISSN 0021-8790, 1365-2656. doi: 10.1111/1365-2656.13191. URL <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2656.13191>.
- 724 Ellen A. R. Welti, Karl A. Roeder, Kirsten M. De Beurs, Anthony Joern, and Michael Kaspari. Nutrient dilution
 725 and climate cycles underlie declines in a dominant insect herbivore. *Proceedings of the National Academy of
 726 Sciences*, 117(13):7271–7275, March 2020b. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1920012117. URL
 727 <https://pnas.org/doi/full/10.1073/pnas.1920012117>.
- 728 T. C. R. White. The importance of a relative shortage of food in animal ecology. *Oecologia*, 33(1):71–86, 1978. ISSN
 729 0029-8549, 1432-1939. doi: 10.1007/BF00376997. URL <http://link.springer.com/10.1007/BF00376997>.
- 730 T. C. R. White. The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews*,
 731 83(3):227–248, August 2008. ISSN 1464-7931, 1469-185X. doi: 10.1111/j.1469-185X.2008.00041.x. URL
 732 <https://onlinelibrary.wiley.com/doi/10.1111/j.1469-185X.2008.00041.x>.
- 733 Thomas C. R. White. *The Inadequate Environment*. Springer Berlin Heidelberg, Berlin, Heidelberg, 1993. ISBN 978-
 734 3-642-78301-2 978-3-642-78299-2. doi: 10.1007/978-3-642-78299-2. URL <http://link.springer.com/10.1007/978-3-642-78299-2>.
- 736 W. G. Whitford. *Ecology of desert systems*. Academic Press, San Diego, 2002. ISBN 978-0-12-747261-4.
- 737 J. Keaton Wilson, L. Ruiz, and G. Davidowitz. Dietary Protein and Carbohydrates Affect Immune Function and
 738 Performance in a Specialist Herbivore Insect (*Manduca sexta*). *Physiological and Biochemical Zoology*, 92(1):
 739 58–70, January 2019a. ISSN 1522-2152, 1537-5293. doi: 10.1086/701196. URL <https://www.journals.uchicago.edu/doi/10.1086/701196>.
- 741 Jerome Keaton Wilson, Laura Ruiz, Jesse Duarte, and Goggy Davidowitz. The nutritional landscape of host plants
 742 for a specialist insect herbivore. *Ecology and Evolution*, 9(23):13104–13113, December 2019b. ISSN 2045-7758,
 743 2045-7758. doi: 10.1002/ece3.5730. URL <https://onlinelibrary.wiley.com/doi/10.1002/ece3.5730>.
- 744 Mira L. Word, Sharon J. Hall, Brian E. Robinson, Balanding Manneh, Alioune Beye, and Arianne J. Cease. Soil-
 745 targeted interventions could alleviate locust and grasshopper pest pressure in West Africa. *Science of The Total
 746 Environment*, 663:632–643, May 2019. ISSN 00489697. doi: 10.1016/j.scitotenv.2019.01.313. URL <https://linkinghub.elsevier.com/retrieve/pii/S0048969719303560>.
- 748 Zijia Zhang, James J. Elser, Arianne J. Cease, Ximeи Zhang, Qiang Yu, Xingguo Han, and Guangming Zhang.
 749 Grasshoppers Regulate N:P Stoichiometric Homeostasis by Changing Phosphorus Contents in Their Frass. *PLoS
 750 ONE*, 9(8):e103697, August 2014. ISSN 1932-6203. doi: 10.1371/journal.pone.0103697. URL <https://dx.plos.org/10.1371/journal.pone.0103697>.
- 752 Xiaolong Zhou, Xudong Liu, Pengfei Zhang, Zhi Guo, and Guozhen Du. Increased community compositional dissim-
 753 ilarity alleviates species loss following nutrient enrichment at large spatial scales. *Journal of Plant Ecology*, 12(2):
 754 376–386, March 2019. ISSN 1752-993X. doi: 10.1093/jpe/ryt035. URL <https://academic.oup.com/jpe/article/12/2/376/5096732>.
- 756 Hui Zhu, Venuste Nkurunziza, Jingting Wang, Qinfeng Guo, Hang Ruan, and Deli Wang. Effects of large herbivore
 757 grazing on grasshopper behaviour and abundance in a meadow steppe. *Ecological Entomology*, 45(6):1357–1366,
 758 December 2020. ISSN 0307-6946, 1365-2311. doi: 10.1111/een.12919. URL <https://resjournals.onlinelibrary.wiley.com/doi/10.1111/een.12919>.
- 760 Yu Zhu, Zhiwei Zhong, Jordi F. Pagès, Deborah Finke, Deli Wang, Quanhui Ma, Nazim Hassan, Hui Zhu, and Ling
 761 Wang. Negative effects of vertebrate on invertebrate herbivores mediated by enhanced plant nitrogen content. *Jour-
 762 nal of Ecology*, 107(2):901–912, March 2019. ISSN 0022-0477, 1365-2745. doi: 10.1111/1365-2745.13100. URL
 763 <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.13100>.

764 **6 SUPPLEMENTARY**

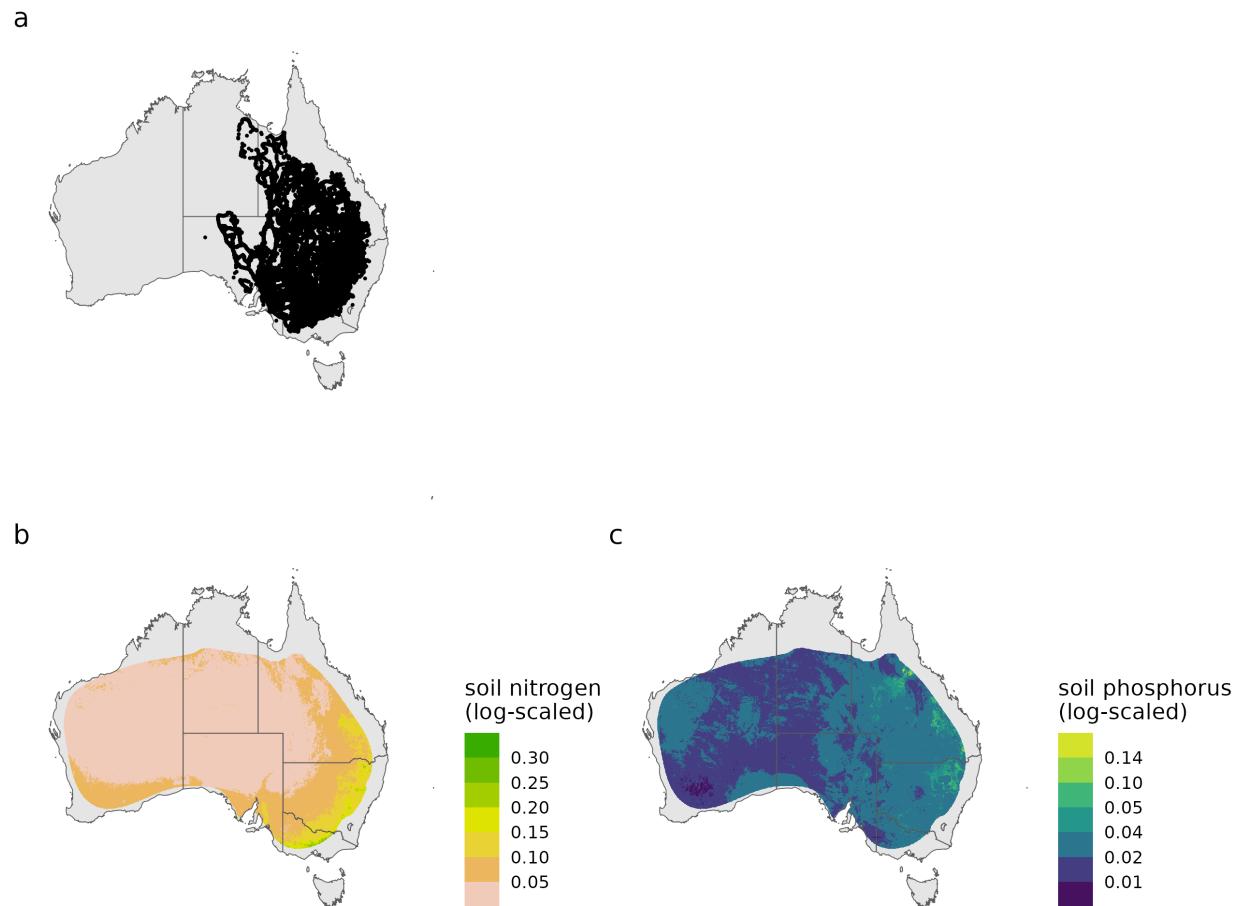
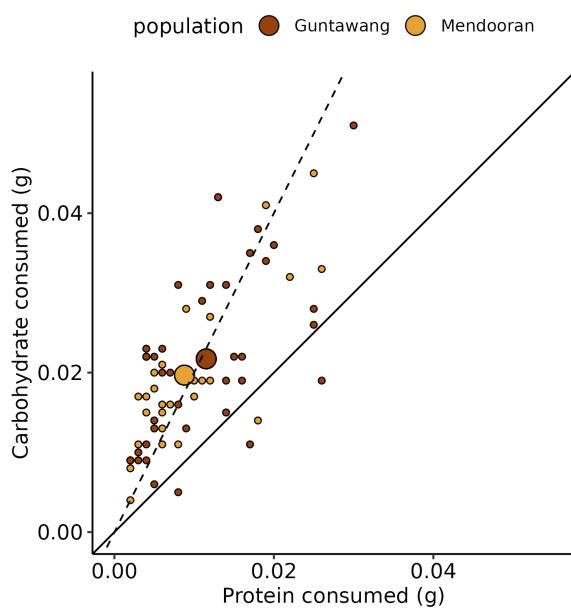


Figure 1: Locust survey data map and soil nutrients throughout the *C. terminifera* distribution. A: APLC survey dataset, B: mean proportion phosphorous at 0-15cm deep, C: mean proportion of nitrogen at 0-15 cm deep.

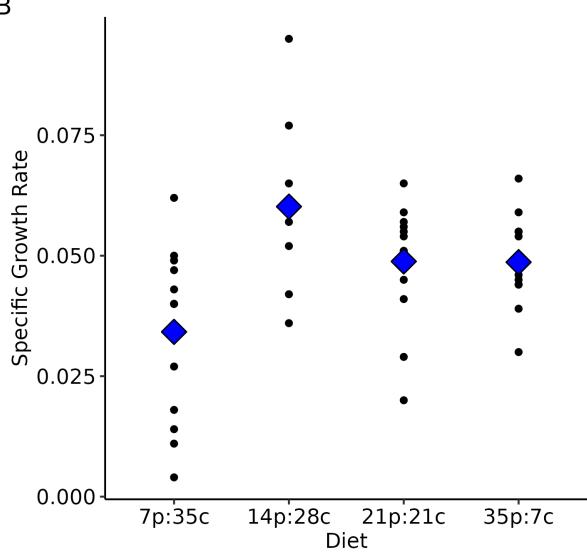
macronutrient	variable	estimate	SE	p-value
carbohydrate	Intercept	0.026	0.002	0.000
	Mendooran	-0.001	0.002	0.483
	diet pair B	0.001	0.002	0.573
	male	-0.011	0.002	0.000
protein	Intercept	0.014	0.001	0.000
	Mendooran	-0.002	0.002	0.122
	diet pair B	0.002	0.002	0.293
	male	-0.006	0.002	0.000

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

A



B



C

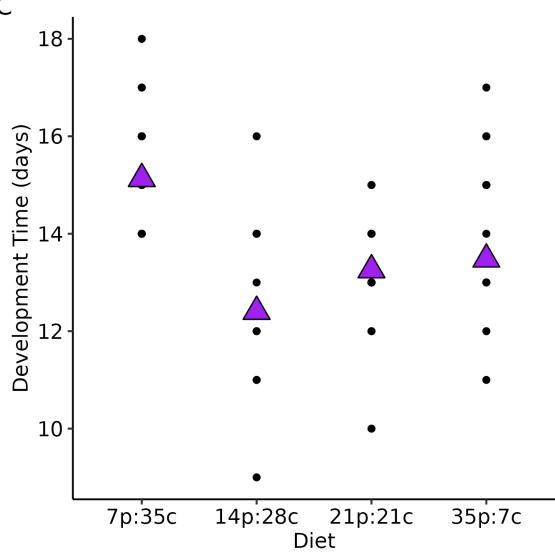


Figure 2: The nutritional preference (A) and physiological performance (B & C) of *C. terminifera* individuals were collected from two marching bands of 5th instars. Raw data is shown as black dots with modeled estimated marginal means as large diamonds or triangles.

variable	Specific Growth Rate			Development Time		
	estimate	SE	p-value	estimate	SE	p-value
Intercept	0.061	0.004	0.000	15.780	1.555	0.000
21p:21c	-0.011	0.005	0.040	0.917	0.624	0.149
35p:7c	-0.010	0.006	0.091	1.709	0.665	0.013
7p:35c	-0.026	0.005	0.000	2.716	0.603	0.000
male	-0.003	0.004	0.398	-1.615	0.829	0.057
initial weight (g)				-21.048	10.407	0.049

Table 3: *C. terminifera* physiological performance (specific growth rate and development time) when constrained to specific diets with varying protein and carbohydrate content. SE: standard error. Posthoc comparisons for both physiological performance metrics can be seen in Supplementary Table 4.

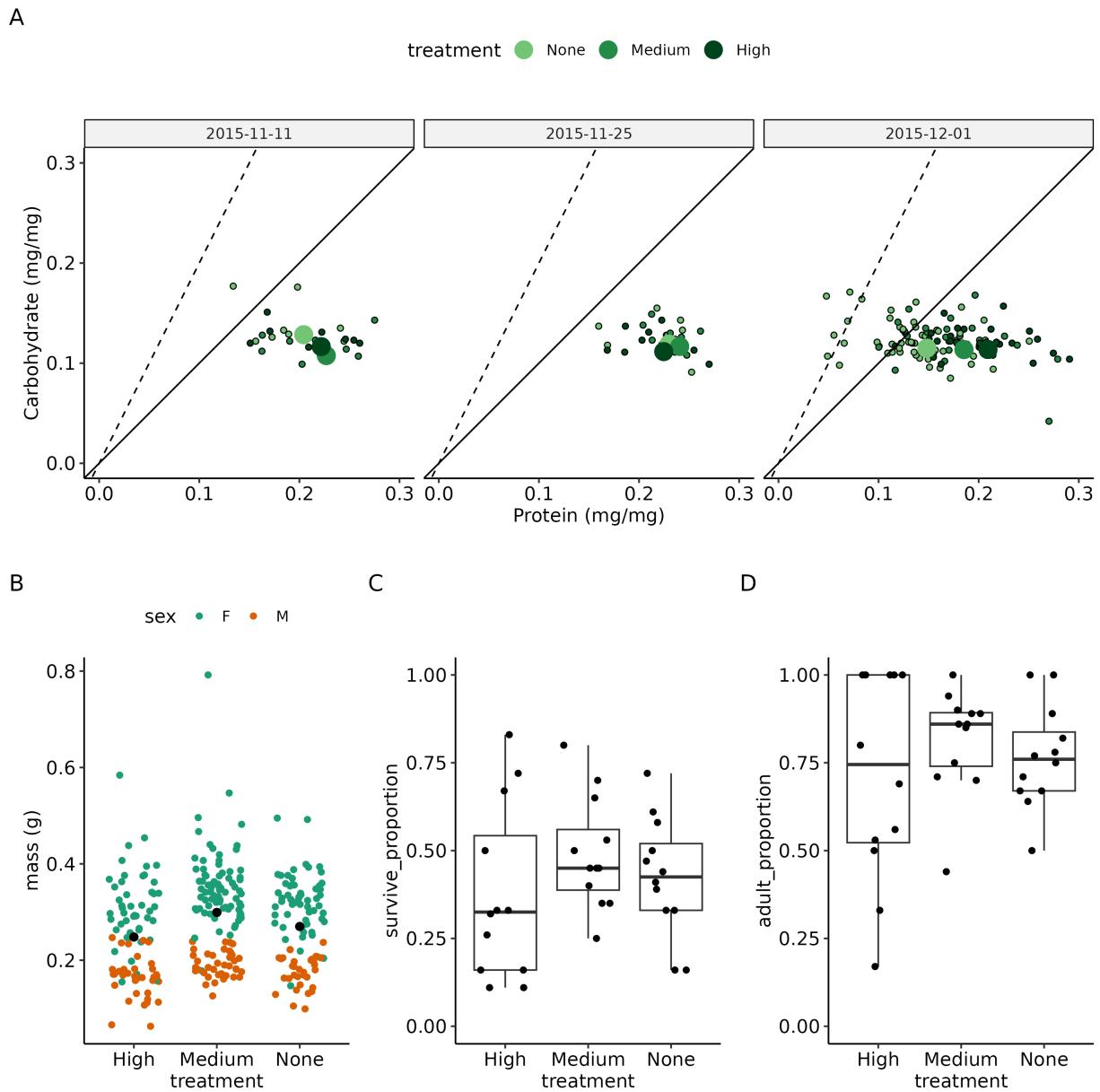


Figure 3: Nitrogen addition field cage experiments with plant nutrient change through time (A-C) and grasshopper performance metrics (D-F) are shown. Dashed line represents a 1p : 2c ratio, the solid line represents a 1p : 1c ratio. Black dots in B represent means.

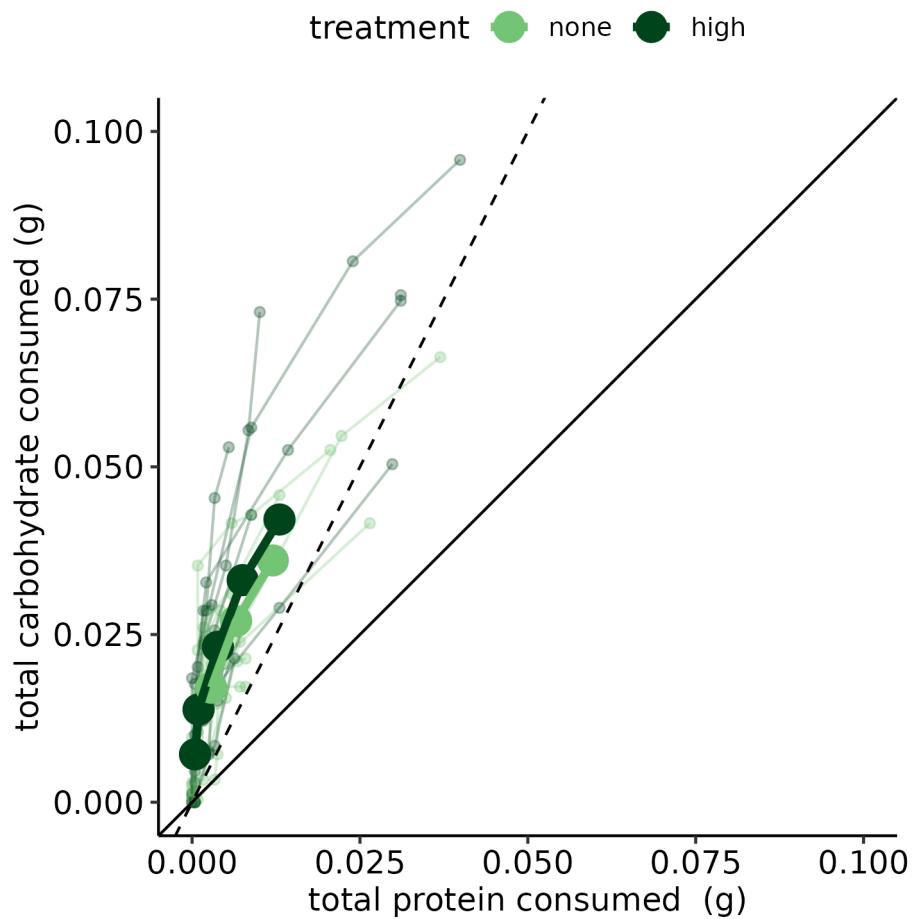


Figure 4: Nutrient imbalance redressing with artificial diet mixing of *C. terminifera* individuals taken from fertilized treatment cages. Colors represent treatment. Smaller lines represent raw individual locust intake targets with large lines and points representing estimated marginal means. Individual time step targets can be seen in Supplementary Figure 4.

macronutrient	variable	estimate	SE	statistic	p-value
carbohydrate	Intercept	0.127	0.007		0.000
	Medium	-0.020	0.007		0.005
	High	-0.011	0.007		0.121
	2015-11-25	-0.009	0.007		0.181
	2015-12-01	-0.012	0.006		0.033
	Medium:2015-11-25	0.019	0.010		0.063
	High:2015-11-25	0.004	0.010		0.656
	Medium:2015-12-01	0.019	0.008		0.017
	High:2015-12-01	0.010	0.008		0.222
	s(species)			67.305	0.000
	s(plot)			1.643	0.207
	s(cage)			3.442	0.130
protein	Intercept	0.209	0.017		0.000
	Medium	-0.001	0.014		0.928
	High	-0.034	0.014		0.014
	2015-11-25	0.026	0.010		0.014
	2015-12-01	-0.049	0.009		0.000
	Medium:2015-11-25	-0.012	0.015		0.422
	High:2015-11-25	-0.023	0.015		0.123
	Medium:2015-12-01	0.008	0.013		0.516
	High:2015-12-01	0.056	0.013		0.000
	s(species)			307.929	0.000
	s(plot)			214.489	0.000
	s(cage)			89.944	0.000

Table 4: Generalized additive model results for plant macronutrient (carbohydrate and protein) differences between fertilization treatment. Family: multivariate gaussian distribution, link: identity, SE: standard error, significance indicated in bold.

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_num)		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.

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

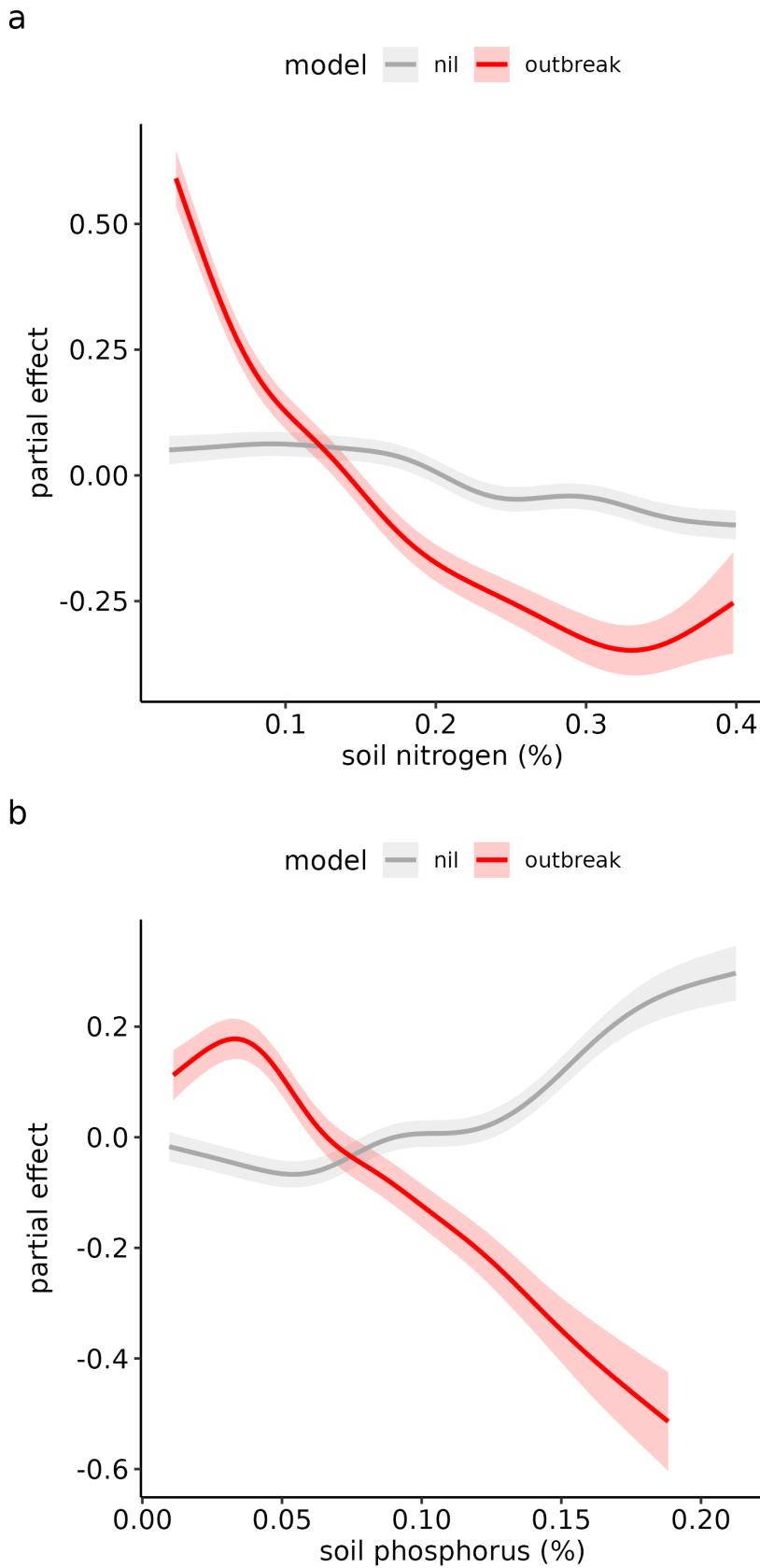
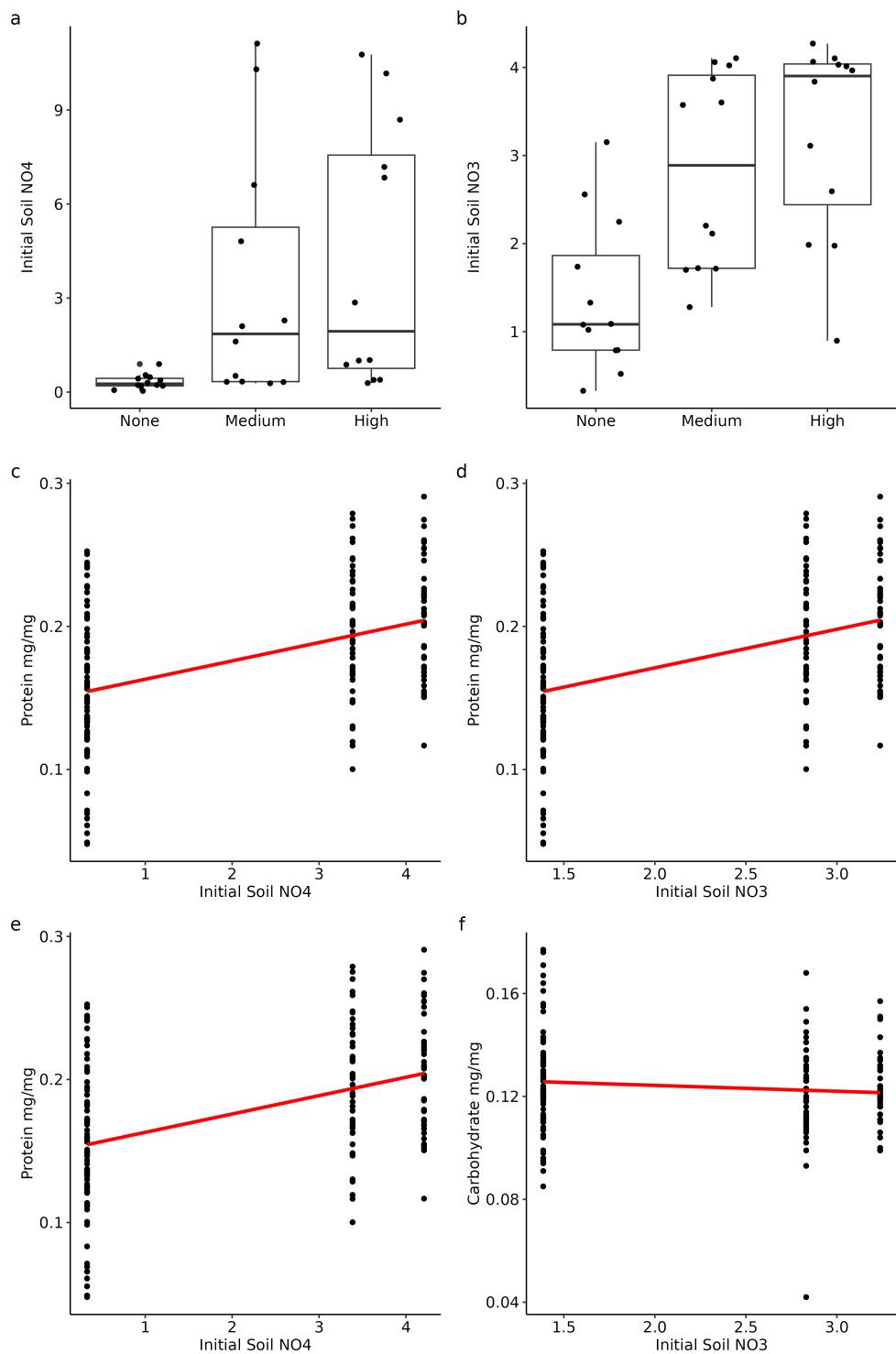


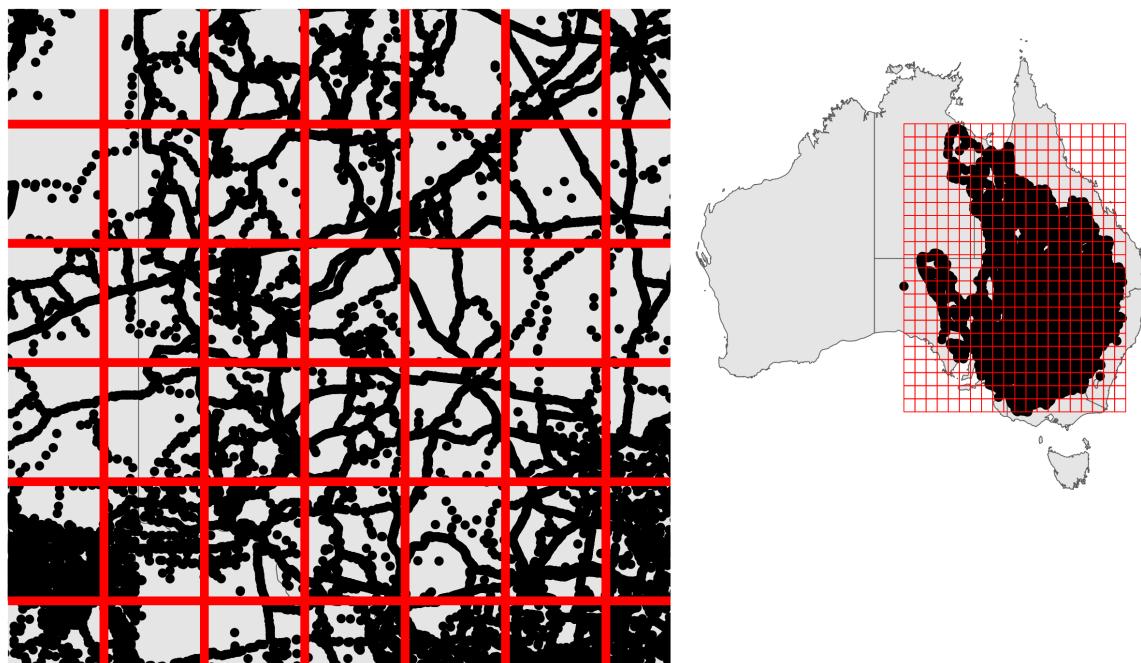
Figure 5: Relationship between outbreaks and nil observations for both soil nitrogen (A) and phosphorus (B). Partial effect is the modeled predictions after accounting for bioregion and spatial autocorrelation.

variable	outbreak model			nil model		
	EDF	statistic	p-value	EDF	statistic	p-value
s(nitrogen)	6.273	25.620	0.000	6.426	35.340	0.000
s(phosphorus)	5.372	15.521	0.000	6.407	28.867	0.000
s(number of observations)	22.547	630.896	0.000	22.408	3,199.357	0.000
te(longitude,latitude)	56.140	1.148	0.012	131.476	3.302	0.000
s(ecoregion)	6.498	4.802	0.000	2.726	0.361	0.035

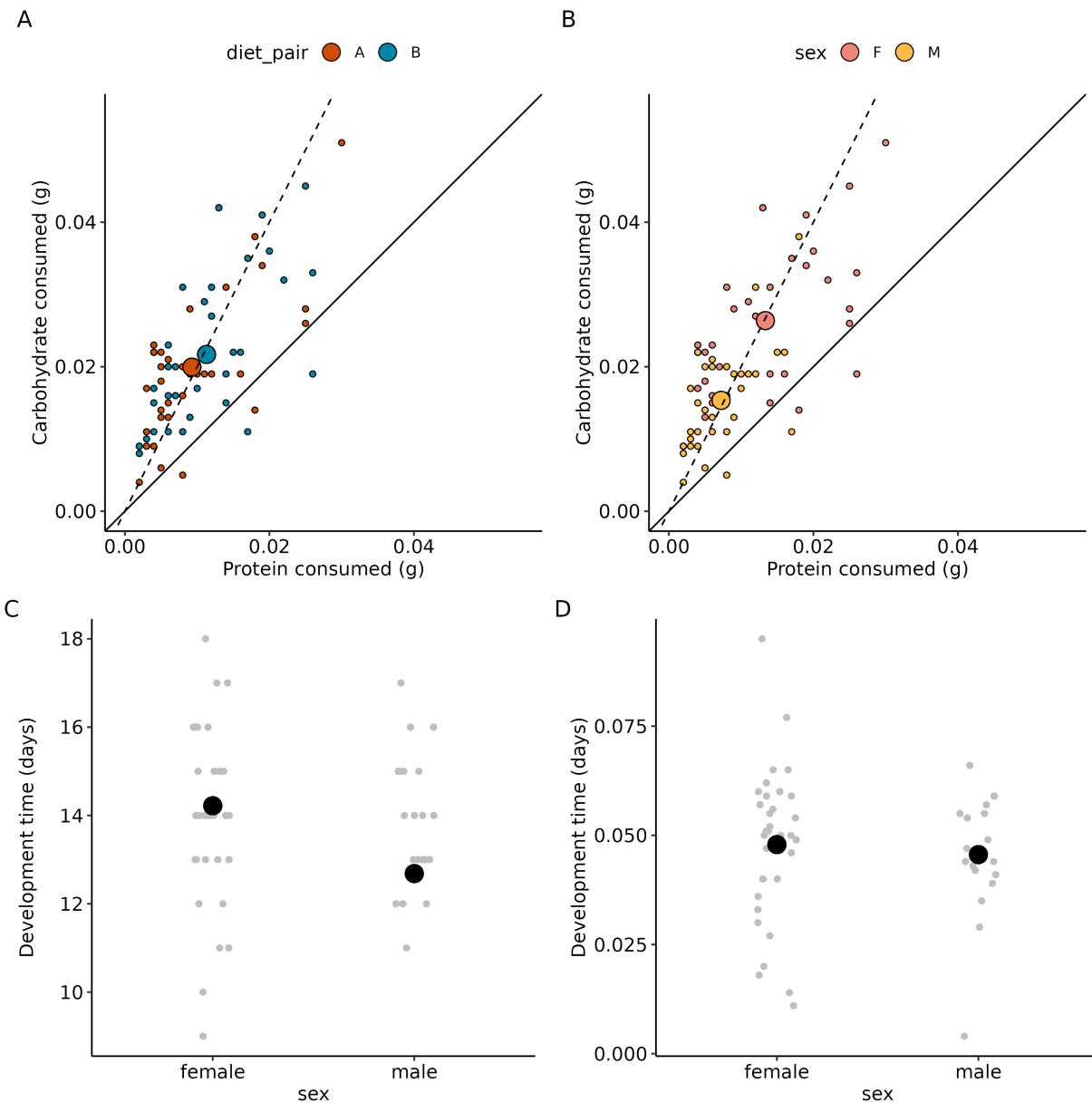
Table 7: Historical locust presence data modeling with soil nitrogen for outbreak, low presence, and no observation records with r-square and deviance explain reported. Family: tweedie, link: log, edf = estimated degrees freedom.



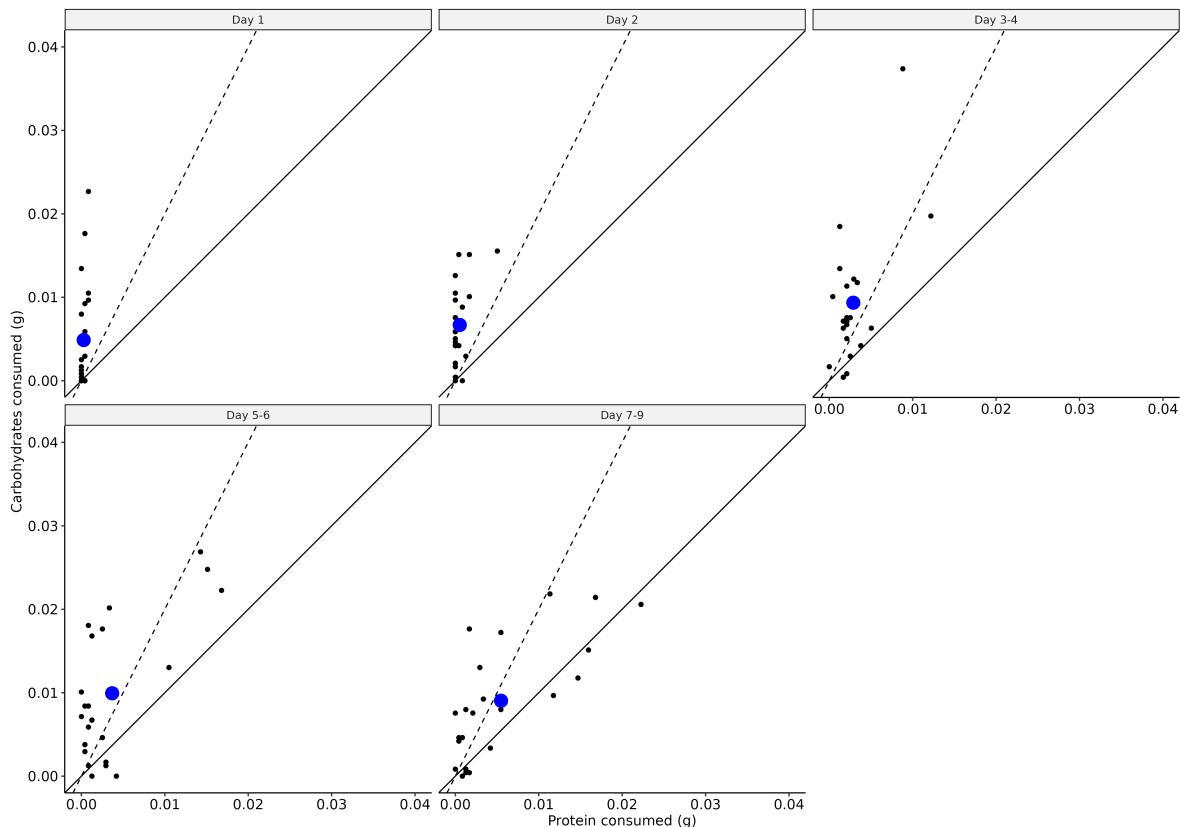
Supplementary Figure 1: Field cage soil nitrogen content by treatment (A & B) and regressed with plant carbohydrates and protein (C-F).



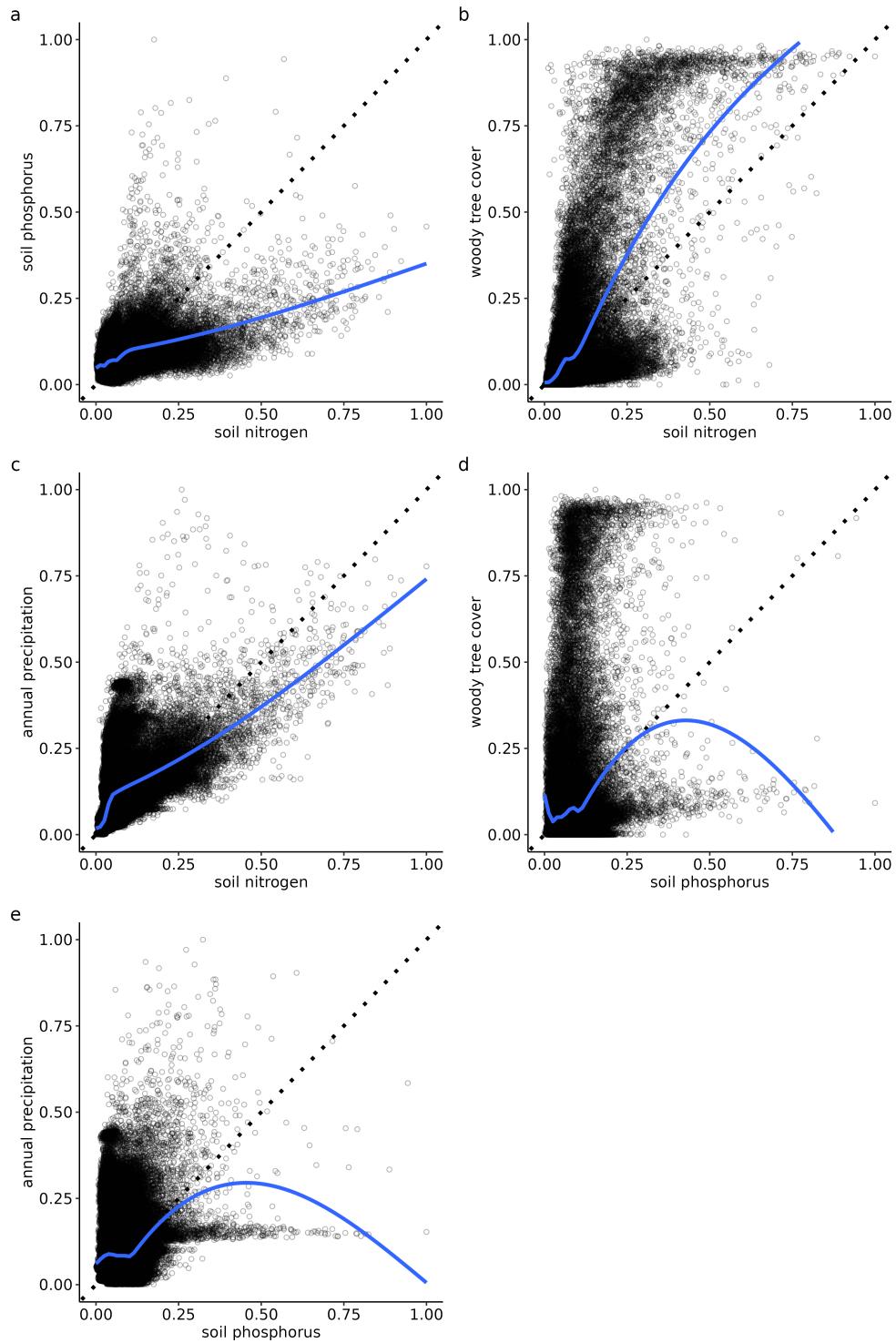
Supplementary Figure 2: Map showing how we summarized point observation data to a fishnet grid throughout eastern Australia. Entire extent can be seen in the inlet map. We summed the number of 4 (outbreak) observations, nil observations (0), and the total observations. Grid not at a 1 km² scale in this figure for demonstration purposes as the cells would be too small to see.



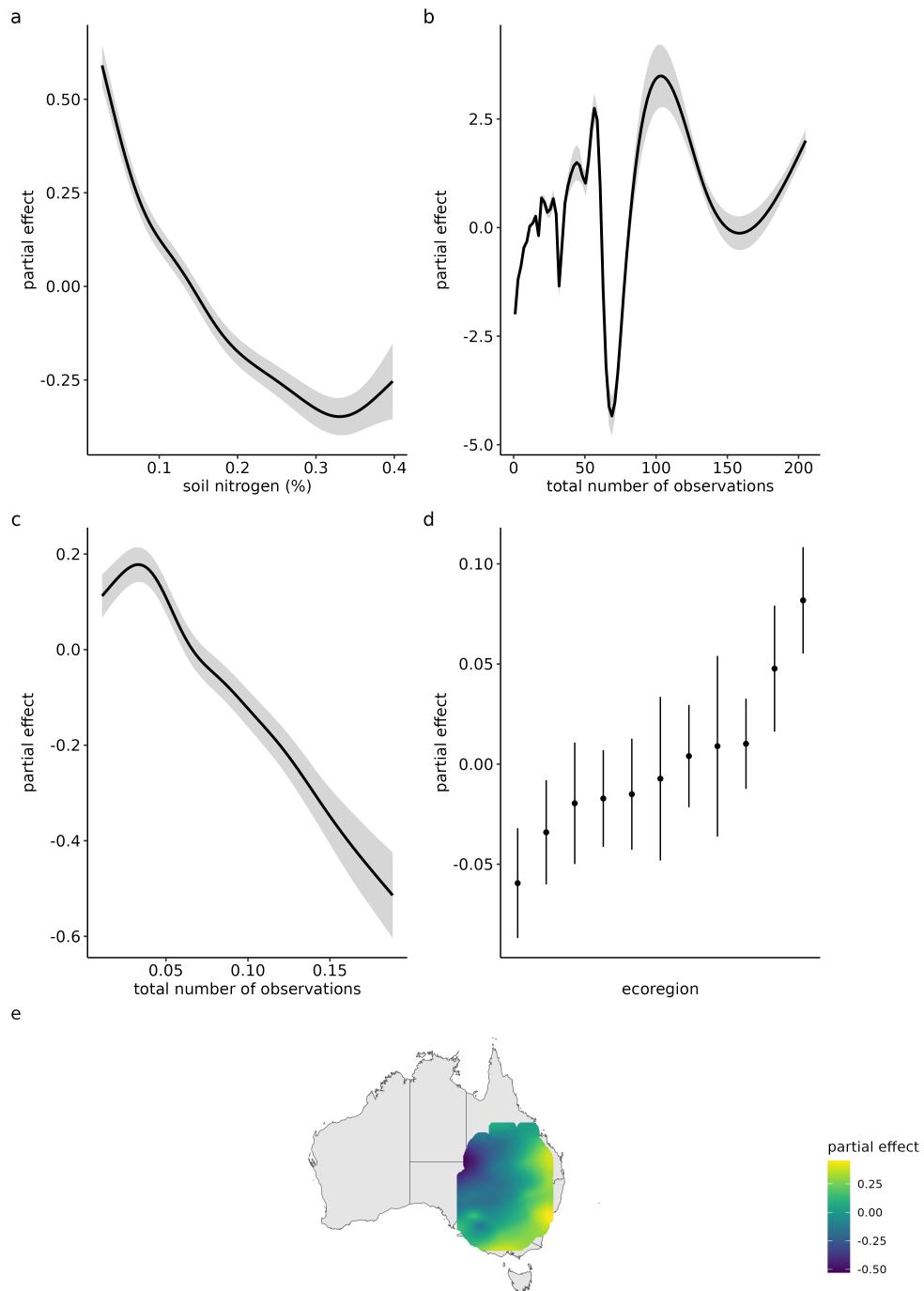
Supplementary Figure 3: Nutrient consumption for outbreaking field populations of *C. terminifera* by diet pair (A) and sex (B) and development time (C) specific growth rate (D) by sex. The P:C ratio did not differ between diet pairing and sex. Females consumed more diet (but kept the same ratio) than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



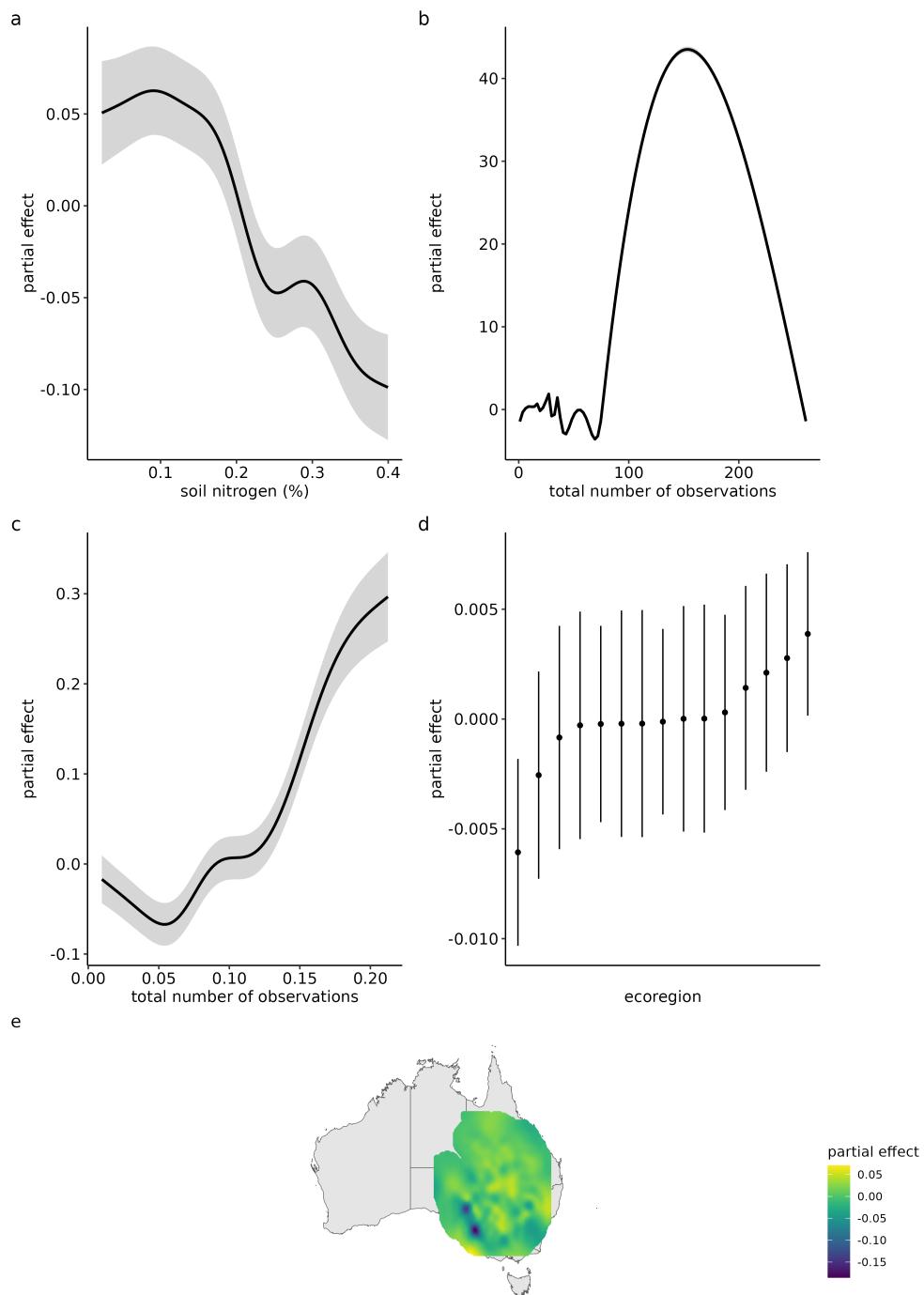
Supplementary Figure 4: Individual time step intake targets for grasshoppers kept in both high nitrogen fertilization and control cages. Blue dots represent estimated marginal means from the model while blacks dots represent raw individual intake targets.



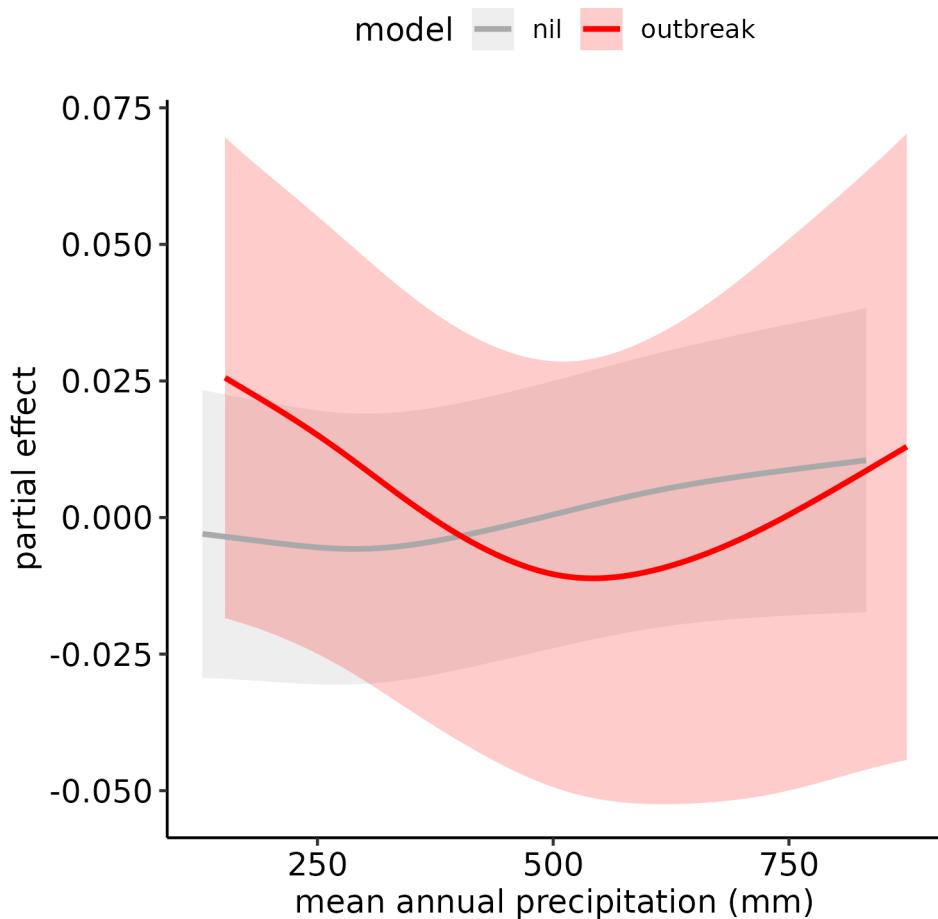
Supplementary Figure 5: Environmental variable correlations between mean annual precipitation, soil nitrogen, soil phosphorus, and woody vegetation pixel coverage. Mean annual precipitation was sourced from WorldClim V1 Bio-clim, soil nitrogen and phosphorus was sourced from Soil and Landscape Grid of Australia, and woody vegetation pixel coverage was sourced from Global Forest Cover Change dataset. We averaged woody coverage for each pixel between the years 2000 and 2017. For all rasters, we randomly sampled 100,000 georeferenced points and extracted values. All values have been scaled and min-max normalized (to fall within 0-1) for visual clarity otherwise, unit scales would mask relationships. Dashed line represents a 1:1 slope and the blue line is a cubic spline with 10 knots.



Supplementary Figure 6: Historical outbreaks record survey data modeling with soil nitrogen and phosphorus.



Supplementary Figure 7: Historical nil record survey data modeling with soil nitrogen and phosphorus.



Supplementary Figure 8: The relationship between locust outbreaks and nil observations and mean annual precipitation. This is included as a visual comparison for the soil nitrogen relationship seen in Figure 5

treatment	species	date	Plant C	Plant N	Plant Protein	Plant Carbohydrate	Soil NO3	Soil NO4
High	<i>Digitaria spp.</i>	2015-12-01	0.419	0.027	0.182	0.108	3.238	4.207
	<i>Enteropogon spp.</i>	2015-11-11	0.425	0.030	0.199	0.128		
	<i>Enteropogon spp.</i>	2015-11-25	0.414	0.028	0.180	0.120		
	<i>Enteropogon spp.</i>	2015-12-01	0.414	0.024	0.163	0.125		
	<i>Cyperus spp.</i>	2015-11-11	0.423	0.030	0.228	0.125		
	<i>Cyperus spp.</i>	2015-11-25	0.415	0.032	0.220	0.131		
	<i>Cyperus spp.</i>	2015-12-01	0.417	0.027	0.227	0.126		
	<i>Plasplodium spp.</i>	2015-12-01	0.400	0.029	0.233	0.120		
	<i>Rytidosperma spp.</i>	2015-11-11	0.424	0.023	0.206	0.125		
	<i>Rytidosperma spp.</i>	2015-11-25	0.422	0.029	0.243	0.112		
	<i>Rytidosperma spp.</i>	2015-12-01	0.419	0.025	0.217	0.117		
	<i>Enteropogon spp.</i>	2015-11-11	0.431	0.042	0.209	0.126	2.831	3.385
	<i>Enteropogon spp.</i>	2015-11-25	0.417	0.026	0.210	0.137		
	<i>Enteropogon spp.</i>	2015-12-01	0.415	0.022	0.146	0.124		
Medium	<i>Cyperus spp.</i>	2015-11-11	0.424	0.038	0.213	0.119		
	<i>Cyperus spp.</i>	2015-11-25	0.420	0.029	0.239	0.127		
	<i>Cyperus spp.</i>	2015-12-01	0.418	0.022	0.188	0.135		
	<i>Plasplodium spp.</i>	2015-12-01	0.414	0.020	0.243	0.094		
	<i>Rytidosperma spp.</i>	2015-11-11	0.422	0.037	0.227	0.106		
	<i>Rytidosperma spp.</i>	2015-11-25	0.420	0.028	0.242	0.115		
	<i>Rytidosperma spp.</i>	2015-12-01	0.422	0.021	0.181	0.116		
	<i>Enteropogon spp.</i>	2015-11-11	0.432	0.031	0.164	0.145	1.387	0.331
	<i>Enteropogon spp.</i>	2015-11-25	0.414	0.021	0.194	0.115		
	<i>Enteropogon spp.</i>	2015-12-01	0.405	0.023	0.114	0.130		
	<i>Cyperus spp.</i>	2015-11-11	0.425	0.032	0.228	0.144		
	<i>Cyperus spp.</i>	2015-11-25	0.417	0.027	0.232	0.137		
	<i>Cyperus spp.</i>	2015-12-01	0.408	0.026	0.154	0.126		
	<i>Plasplodium spp.</i>	2015-12-01	0.399	0.028	0.183	0.095		
None	<i>Austrostipa spp.</i>	2015-12-01	0.416	0.013	0.150	0.104		
	<i>Rytidosperma spp.</i>	2015-11-11	0.420	0.026	0.190	0.124		
	<i>Rytidosperma spp.</i>	2015-11-25	0.417	0.027	0.232	0.133		
	<i>Rytidosperma spp.</i>	2015-12-01	0.418	0.022	0.142	0.121		
	unknown	2015-12-01	0.413	0.031	0.168	0.101		

Supplementary Table 1: Field plot nutrient content for plant species collected from within the treatment plots but outside of the locust cages for three time points during the experiment. Soil nitrogen is also shown per each treatment. Trt = Treatment, C = carbon, N = Nitrogen, Prot = protein, Carb = Carbohydrates.

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

Supplementary Table 2: Averaged plant ground cover (%) across all cages per treatment. Ground cover was estimated on November 11th, 2015.

model	deltaBIC	deltaAIC	deltaAICc
macronutrient ~ population + diet_pair + sex + s(initial_mass_g, k=30)	0.01	0.00	0.01
macronutrient ~ population + diet_pair + sex + initial_mass_g	7.28	2.81	4.80
macronutrient ~ population + diet_pair + sex	0.00	0.00	0.00
macronutrient ~ 1	2.56	15.96	12.28

Supplementary Table 3: Model selection criteria via Akaike information criterion (AIC), AIC corrected for small sample size (AICc), and bayesian information criterion. Model formula with the dependent variable on the left side and independent variables on the right side of the equation. For all criteria, the lower the number, more negative in this case, the better fit model.

comparisons	Development Time			Specific Growth Rate		
	estimate	SE	adjusted p-value	estimate	SE	adjusted p-value
14p:28c - 21p:21c	-0.917	0.624	0.465	0.011	0.005	0.164
14p:28c - 35p:7c	-1.709	0.664	0.062	0.010	0.006	0.322
14p:28c - 7p:35c	-2.716	0.603	0.000	0.026	0.005	0.000
21p:21c - 35p:7c	-0.792	0.609	0.567	-0.001	0.005	0.997
21p:21c - 7p:35c	-1.799	0.571	0.014	0.015	0.005	0.020
35p:7c - 7p:35c	-1.007	0.619	0.374	0.016	0.005	0.029

Supplementary Table 4: Posthoc comparisons for diet treatments for *C. terminifera* individual specific growth rate and development time. SE = standard error