
EXPLORING NUTRIENT AVAILABILITY AND HERBIVOROUS INSECT POPULATION DYNAMICS ACROSS MULTIPLE SCALES

A PREPRINT

2024-09-17

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
 44 co-limiting factors [Tyrrell, 1999, , Vitousek et al. [2010]], and are often investigated as limiting factors for higher
 45 trophic levels to determine the consequences to animal growth and reproduction [Andersen et al., 2004]. For example,
 46 bluegrass fields supplemented with high quality (e.g. increased nitrogen) food pellets increase vole (*Microtus ochrom-*
gaster) densities compared to control fields by supporting higher adult survival, increased breeding, and growth rate
 48 [Cole and Batzli, 1978]. Less phosphorus in a dryland insect herbivore's (*Sabinia setosa*) host plant, velvet mesquite
 49 (*Prosopis velutina*), leads to individuals having decreased RNA content (slower growth) and lower abundance [Schade
 50 et al., 2003]. More broadly, nitrogen and phosphorus limitation has been shown in mammals [Randolph et al., 1995,
 51 White, 1993], birds [Forero et al., 2002, Granbom and Smith, 2006], and insects [Floyd, 1996, Huberty and Denno,
 52 2006, Marsh and Adams, 1995, Perkins et al., 2004] which is discussed further in White [2008] and Andersen et al.
 53 [2004]. However, not all animal populations respond positively to increasing environmental nutrients. For example,
 54 studies from across the globe reveal that the abundances of many grasshopper species are positively [Joern et al., 2012,
 55 Ozment et al., 2021, Welti et al., 2020a,b, Zhu et al., 2020, 2019], or not related [Heidorn and Joern, 1987, Jonas
 56 and Joern, 2008, Lenhart et al., 2015, Ozment et al., 2021] to plant nitrogen concentrations as reviewed in Cease
 57 [2024]. Can the relationship between herbivore abundance and environmental nutrients be explained by approaches
 58 that consider 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 low
 65 protein:carbohydrate ratio and eat about double the amount of carbohydrate relative to protein when given a choice of
 66 artificial diets [Behmer, 2009, Brosemann et al., 2023, Lawton et al., 2021, Le Gall et al., 2019]. Their high energy,
 67 relative to protein, demand is heightened by their impressive long-distance migration. Marching bands of South
 68 American locusts (*Schistocerca cancellata*) eat predominantly from dishes containing carbohydrates and largely ignore
 69 dishes containing protein [Cease et al., 2023], and have the highest survival and lipid gain when eating carbohydrate-
 70 biased plants [Talal et al., 2020]. As adults, flight increases carbohydrate, but not protein, consumption in migratory
 71 locusts (*Locusta migratoria*) and locusts eating carbohydrate-biased diets fly for longer times [Talal et al., 2023]. At
 72 a local scale, high-use agricultural areas that decrease soil and plant nitrogen promote *Oedaleus* locust outbreaks in
 73 Senegal and China [Cease et al., 2012, Giese et al., 2013, Le Gall et al., 2019, Word et al., 2019]. Less is known
 74 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 decorus asiaticus* in China show that locusts increase phosphorus excretion with increasing
 79 plant phosphorus content, suggesting that phosphorus may not be limiting in the Inner Mongolian Steppe for this
 80 species [Zhang et al., 2014]. Understanding the multi-scale flow of nitrogen and phosphorus from soils to continental
 81 scale population dynamics may reveal a connection between soil quality and locust plagues in Australia and further
 82 elucidate 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 erupt following
 85 periods of favorable climatic conditions. For example, preceding vegetation growth is an important factor for Australian
 86 plague locust population outbreaks [Lawton et al., 2022]. In addition to climatic variability, Australia is marked by
 87 poor natural soil fertility [Morton et al., 2011, Orians and Milewski, 2007]. Nutrients such as nitrogen and phosphorus
 88 are 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 Australian plague locust
 90 is the most widespread and economically damaging [Hunter et al., 2001]. As with many dryland animals, numerous
 91 studies have shown the relationship between climatic conditions and Australian plague locust population outbreaks
 92 [Clark, 1974, Deveson and Walker, 2005, Farrow, 1982, Key, 1945], however few have investigated the relationship
 93 between soil and plant 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 Australian plague locusts. We have three specific questions and subsequent predictions across scales:

- 96 1) What are the nutritional preferences of individuals from gregarious Australian plague locust field populations?
 97 We 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 Australian plague locusts when constrained to high nitrogen environments? We expect
 100 locusts to select particularly carbohydrate biased diets to redress a protein : carbohydrate imbalance in their
 101 local environment.
- 102 3) Can we use soil nutrients as a predictor of Australian plague locust nymph outbreaks at the continental scale?

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

108 2 METHODS

109 2.1 Field site and animals

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

116 2.2 Nutritional target and performance curve using synthetic diets

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

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

127 2.2.1 Nutrition target (choice diets)

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

137 2.2.2 Performance curve (no-choice diets)

138 We ran this experiment to determine the growth rate and development time to adulthood of Australian plague locust
 139 juveniles in response to different dietary p:c ratios. We isolated fourth instar nymphs from the Mendooran population
 140 and housed them in individual cages. Each day, we retrieved individuals that had molted into the fifth (final) stadium

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

154 **2.3 Field cage experiments**

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

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

171 We measured plant diversity and abundance in each locust cage and outside the cage within each fertilized plot. We
 172 also measured ground, litter, manure, and plant cover in each of the nine plots by randomly tossing three 0.25 x 0.25
 173 m quadrats within each of the nine plots. We took these ground cover and biodiversity measurements at the beginning
 174 and end of the experiment. We took plant leaf samples for nutrient analyses from each cage three times during the
 175 experiment on November 11th, November 25th, and December 1st, 2015. Plant species with resulting carbon, nitrogen,
 176 digestible carbohydrate and protein content as well as soil nitrogen (from 0-10 cm cores) can be seen in Table 6. Plant
 177 species ground cover for each cage can be seen in Table 7. The relationship between soil NO₃ and NO₄ within cage
 178 plots and cage plant carbohydrates and proteins are visualized in Supplementary Figure 1.

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

186 We collected all remaining field-cage locusts on Nov. 28, 2015 and recorded developmental stage and body mass.
 187 We calculated surviving proportion for each cage accounting for the locusts we removed for the nutritional status
 188 experiments (surviving proportion = # live locusts/(initial # added -# locusts removed for secondary experiment)). We
 189 calculated the proportion molted to adult of the surviving locusts (# adults/# live locusts).

190 **2.4 Correlating historical nymphal outbreaks with soil nitrogen and phosphorus**

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

194 **2.4.1 Locust outbreak data**

195 Australian plague locust data from 2000 - 2017 (~ 190,000 records) were used in this study. This database contains
 196 georeferenced points with a categorical ordinal variable 0-4 to represent approximate nymph densities. The value
 197 ranges for nymphs are: 0 = nil, 1 = < 5 m², 2 = 5-30 m², 3 = 31-80 m², and 4 = > 80 m². Population outbreaks are
 198 characterized by very high densities of gregarious nymphs (up to 1000 m²). We focused on nymphs as this life stage

cannot fly and can be used to assess prior local habitat conditions. While the database extends into the 1980s, we only used data collected between 2000-2017 as this period overlapped with the soil grid data which was released in 2015. Since climatic conditions and migration patterns are drivers in outbreak occurrence [Lawton et al., 2022, Veran et al., 2015] they likely mask the relationship between static environmental variables like soil nutrients. To account for this variability, we spatially aggregated the survey dataset to a 1 km² x 1 km² grid as can be seen in Supplementary Figure 2. This allowed us to model how often locust outbreaks occur in grid cells rather than the actual outbreak. We used a 1 km² x 1 km² grid as this reflects the estimated maximum dispersal distance from hatching to 5th instar [Hunter et al., 2008]. We counted the number of outbreaks (APLC nymph density code 4), the number of nil records (APLC nymph density code 0), and total number of survey observations. This resulted in approximately 12,000 grid cells for the final dataset. Overall APLC survey point distribution can be seen in Figure 1 A.

2.4.2 Soil grid of Australia data

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 APLC 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.

2.5 Statistics

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](#)

2.5.1 Intake Targets

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 of locust weight as either a non-linear or linear effect via Akaike information criterion (AIC), AIC adjusted for small sample size (AICc), and Bayesian information criterion (BIC). If weight was not an important variable, it was removed entirely from the model.

2.5.2 Field population

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).

2.5.3 Field Cage

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

2.5.4 Historical outbreaks and soil nutrient grid modeling

To relate nymph survey grids to soil nitrogen and phosphorus, we constructed two GAMMs (family: tweedie, link: log) predicting the number of outbreaks (APLC Survey Category 4) and nil observations (category 0). Since both soil nitrogen and mean annual precipitation are highly correlated (Pearson correlation = 0.93) with both variables decreasing going into the arid interior of Australia, we are unable to add precipitation directly to the model as it would bias the results. Instead, we built a comparison model with mean annual precipitation between 2000 and 2017 switched for soil nitrogen. To do this, we calculated the average precipitation between 2000 and 2017 for all survey grids using the European Centre for Medium-Range Weather Forecasts' ERA5 reanalysis dataset [Muñoz-Sabater

253 et al., 2021]. This allowed us to visually compare the effect differences of soil nitrogen and mean annual precipitation
 254 on locust outbreaks. In other words, if soil nitrogen and mean annual precipitation were so tightly correlated that
 255 the effects are indistinguishable, the modeled results should look very similar. The soil models had the following
 256 independent variables: soil nitrogen, phosphorus, latitude / longitude, bioregion, and the number of observations
 257 within each grid. For the precipitation model, all variables were the same except mean annual precipitation replaced
 258 soil nitrogen and phosphorus. The inclusion of bioregions as a random effect allowed us to account for variation due
 259 to vegetation community and soil characteristics. The inclusion of latitude and longitude allowed us to account for
 260 spatial autocorrelation [Clayton et al., 1993]. Lastly, the inclusion of the total number of observations allowed us to
 261 account for sampling intensity biases.

262 3 RESULTS

263 3.1 Field population

264 3.1.1 Choice experiment (nutritional target)

265 Australian plague locust individuals from the two outbreeding populations regulated to a specific ratio of 1 protein : 2
 266 carbohydrate (Figure 2 A, Table 1). Model selection can be seen in Table 8. Consumption in the two diet pairings did
 267 not differ, indicating non-random feeding (Supplementary Figure 3 A, Table 1). While the protein : carbohydrate ratio
 268 did not change, females consumed more food than males, likely due to being bigger overall (Supplementary Figure 3
 269 B, Table 1).

270 3.1.2 No choice experiment (performance curves)

271 Australian plague locusts had higher specific mass growth rates and shorter development times on the 1 protein : 2
 272 carbohydrate (14 protein : 28 carbohydrate) diet as compared to the other diets (Figure 2 B & C, Table 2, Table 9).
 273 Development time and specific growth rate did not differ between male and female locusts (Supplementary Figure 3
 274 C & D, Table 2).

275 3.2 Field Cage

276 For the first 11 days of the 14 day field cage experiment, plant protein and carbohydrate contents remained consistently
 277 protein-biased for all treatments (Figure 3 A-C, Table 3), and only showed differences in protein content by the last
 278 sample period on December 1, which was after the end of the locust cage experiment. Accordingly, there was no effect
 279 of fertilizer on locust survival and adult proportion, though locusts in the medium level nitrogen fertilizer treatment
 280 were heavier than locusts in the high nitrogen fertilizer treatment (TukeyHSD: difference: -0.043, p-value: < 0.001)
 281 ((Figure 3 D-F, Table 4)). Locusts that were retrieved from field cages after nine days and were given a choice to
 282 regulate protein and carbohydrate intake showed a pattern consistent with rebalancing a shortage of carbohydrates
 283 (Figure 4, Table 5, Supplementary Figure 4). Irrespective of fertilizer treatment group, locusts initially selected very
 284 carbohydrate biased diets, but gradually, after 9 days, their trajectory returned close to the predicted intake target of 1p
 285 : 2c (Figure 4, Supplementary Figure 4).

286 3.3 Locust outbreaks

287 Australian plague locust outbreaks were negatively associated with soil nitrogen, which supports the hypothesis that
 288 nitrogen (in excess) acts as a limiting factor for population upsurges (Table 6, Fig. 5A). Australian plague locusts had
 289 a nonlinear relationship with soil phosphorus with outbreaks occurring more often in areas with approximately 4%
 290 soil phosphorus and were strongly negatively associated with increasing phosphorus afterwards (Fig. 5B). For both
 291 nutrients, the absence models had a very weak relationship with soil nutrient in comparison to the outbreak models,
 292 demonstrating little model bias due to APLC survey protocol. There were significant nonlinear relationships between
 293 coordinates and the total number of observations in all models (Supplementary Figs. 5 & 6). The relationship between
 294 locust outbreaks and mean annual precipitation (e.g. nonlinear) was very different from the relationship with soil
 295 nitrogen (e.g. linear; Fig. 5, Supplementary Fig. 7). Soil nitrogen and phosphorus show weak positive correlations
 296 with woody vegetation cover, while mean annual precipitation exhibits high variation in its relationship with soil
 297 nitrogen and weak correlation with soil phosphorus (Supplementary Figure 8). Thus, the relationship between soil
 298 nitrogen and locust outbreaks cannot be fully explained by differences in woody vegetation.

299 4 DISCUSSION

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

305 as energetically-costly migration, as well as organism-environment interactions should be considered. For forecasting
 306 pest populations dynamics, adding variables describing the nutritional quality of landscapes can inform seasonal
 307 scouting surveys. We hope that this study spurs future interest in multi-scale experiments and modeling of nutrient
 308 availability with animal population dynamics.

309 **4.1 Field populations**

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

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

320 Importantly, all field cage plants were protein biased (roughly 1p : 1c to 2p : 1c) as compared to the desired locust
 321 intake target of 1p : 2c. When locusts were subsampled from the field cages mid-experiment and given the opportunity
 322 to select carbohydrate or protein diets, they selected extremely carbohydrate-biased diets for more than a week. This
 323 behavior indicated that locusts in the small field cages were highly carbohydrate-limited, driving them to overeat carbo-
 324 hydrates to redress the imbalance. Interestingly, multiple studies have shown that the Australian nutritional landscape
 325 is often too protein-biased relative to what the Australian plague locust prefers [Lawton et al., 2020, 2021]. Regardless,
 326 populations are still persistent and outbreaks can occur at lower frequencies in these areas [Deveson, 2013, Key, 1945].
 327 How this species can achieve the optimal balance of nutrients within an unfavorable nutritional environment merits
 328 further investigation, but may include post-ingestive regulation and/or large-range foraging. Migratory locusts (*Locusta*
 329 *migratoria*) can choose microclimates that favor higher efficiency of carbohydrate or protein absorption depending on
 330 their host plant and nutritional status [Clissold et al., 2013]. For this study, we collected free-living locusts from the
 331 same region and a similar environment as where we built the field cages, yet those confined to field cages selected a
 332 10 x decrease in p:c (1p : 20c vs 1p : 2c). This result suggests that free-living locusts are able to persist in high protein
 333 regions by foraging over a larger range to seek out pockets of carbohydrate-rich plants and that the limited foraging
 334 range of the field cages precluded field-cage locusts from finding sufficient carbohydrates. Similarly, these results
 335 suggest that, while Australian plague locusts can persist in low numbers in nitrogen rich regions, those environments
 336 are unlikely to support extreme outbreaks due to a limitation of carbohydrate-rich resources. We tested this prediction
 337 using historical outbreak and large-scale soil nutrient modeling.

338 **4.2 Historical outbreak modeling**

339 This is the first time to our knowledge that terrestrial animal population dynamics have been modeled with nutrients at
 340 the continental level, allowing nutrient limitation to be tested at a scale not previously investigated. Locust outbreaks
 341 are associated with decreasing soil nitrogen (Fig. 5A), suggesting that nitrogen acts as a limiting factor not due to
 342 its deficit [White, 1993] but its excess. Plants growing in high nitrogen environments tend to have high p:c ratios,
 343 which force locusts to either undereat carbohydrates (limiting their energy to support growth and migration) or overeat
 344 protein (which can be toxic) to acquire sufficient carbohydrates [Behmer, 2009, Cease, 2024]. On the other end of
 345 the performance curve, Australian plague locusts do have a lower p:c range that limits performance, as shown using
 346 artificial diets (Fig. 2B-C). However, our outbreak models found no lower limit (Fig 5A), suggesting that locusts
 347 do not often encounter environments where protein deficit limits their growth. This result is consistent with other
 348 research that found most grasses across New South Wales tend to have higher p:c ratios than locusts require [Lawton
 349 et al., 2021]. Even when locusts have access to low p:c plants it is more difficult for them to extract carbohydrate
 350 than protein [Clissold et al., 2006], further exacerbating the problem of relative protein excess. Interestingly, this
 351 relationship between nitrogen and locusts stays consistent throughout multiple spatial levels which suggests that it
 352 scales linearly; an uncommon characteristic in ecology [Levin, 1992, Wiens, 1989]. We also show that outbreaks
 353 are correlated with a low level of soil phosphorus, however, outbreaks peak at approximately 4%, suggesting that
 354 while locusts generally do well in low phosphorus environments, phosphorus deficit can be limiting for locusts in
 355 extremely phosphorus poor soils (Fig. 5B). Because Australian soils are characteristically phosphorus poor [Donald,
 356 1964], Australian animals like this locust are adapted to phosphorus poor environments and potentially having too
 357 much phosphorus is deleterious [Morton et al., 2011]. Locust populations may be more tightly correlated with soil
 358 nitrogen than phosphorus because terrestrial herbivores require 5-50 times more nitrogen than phosphorus [Elser et al.,
 359 2000], meaning they can more readily balance phosphorus by eating a few foods rich or poor in phosphorus but
 360 cannot as quickly regulate protein and carbohydrate energy because they make up the bulk of their required nutrients.

Indeed, laboratory studies have revealed that short-term limitations in dietary phosphorus have no apparent impact on grasshopper growth [Cease et al., 2016], suggesting that these mobile herbivores could seek out phosphorus-rich diets intermittently to overcome potential phosphorus limitation in field environments. However, in this study, we only tested this relationship with phosphorus at the continental level; further field and laboratory experiments are needed to explore this non-linear relationship between locust outbreaks and soil phosphorus. While we only looked at nitrogen and phosphorus, it is also important to note that animals require a suite of nutrients. Other nutrients such as potassium and sodium [Joern et al., 2012] warrant further investigation. Comparing locust outbreaks between continents would further show the relationship between nutrient availability and animal population dynamics. One excellent dataset for this would be SoilGrids (<https://www.isric.org/explore/soilgrids>) which provides soil nitrogen estimates globally at a 250-meter resolution.

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

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

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

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

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

418 locally among optimal patches, whereas herbivore populations with extreme numbers (i.e., irruptions) may be more
 419 limited by nutritionally unfavorable environments across scales.

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

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

441 4.5 Synthesis and Application

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

456 5 REFERENCES

- 457 Tom Andersen, James J. Elser, and Dag O. Hessen. Stoichiometry and population dynamics. *Ecology Letters*, 7
 458 (9):884–900, September 2004. ISSN 1461-023X, 1461-0248. doi: 10.1111/j.1461-0248.2004.00646.x. URL
 459 <https://onlinelibrary.wiley.com/doi/10.1111/j.1461-0248.2004.00646.x>.
- 460 Achyut Aryal, Sean C. P. Coogan, Weihong Ji, Jessica M. Rothman, and David Raubenheimer. Foods, macronutrients
 461 and fibre in the diet of blue sheep (*Psuedois nayaur*) in the Annapurna Conservation Area of Nepal. *Ecology*
 462 and Evolution, 5(18):4006–4017, September 2015. ISSN 2045-7758, 2045-7758. doi: 10.1002/ece3.1661. URL
 463 <https://onlinelibrary.wiley.com/doi/10.1002/ece3.1661>.
- 464 George O. Batzli. Nutritional Ecology of the California Vole: Effects of Food Quality on Reproduction. *Ecology*, 67(2):
 465 406–412, April 1986. ISSN 0012-9658, 1939-9170. doi: 10.2307/1938583. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1938583>.
- 467 Spencer T. Behmer. Insect Herbivore Nutrient Regulation. *Annual Review of Entomology*, 54(1):165–187, Jan-
 468 uary 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>.

- 470 E. A. Bernays, K. L. Bright, N. Gonzalez, and J. Angel. Dietary Mixing in a Generalist Herbivore: Tests of Two
 471 Hypotheses. *Ecology*, 75(7):1997–2006, October 1994. ISSN 00129658. doi: 10.2307/1941604. URL <http://doi.wiley.com/10.2307/1941604>.
- 473 Jonah Brosemann, Rick Overson, Arianne J. Cease, Sydney Millerwise, and Marion Le Gall. Nutrient supply and
 474 accessibility in plants: effect of protein and carbohydrates on Australian plague locust (*Chortoicetes terminifera*)
 475 preference and performance. *Frontiers in Insect Science*, 3:1110518, July 2023. ISSN 2673-8600. doi: 10.3389/
 476 finsc.2023.1110518. URL <https://www.frontiersin.org/articles/10.3389/finsc.2023.1110518/full>.
- 477 Alison S. Scott Brown, Monique S. J. Simmonds, and Walter M. Blaney. Relationship between nutritional composition
 478 of plant species and infestation levels of thrips. *Journal of Chemical Ecology*, 28(12):2399–2409, 2002. ISSN
 479 00980331. doi: 10.1023/A:1021471732625. URL <http://link.springer.com/10.1023/A:1021471732625>.
- 480 Arianne J. Cease. How Nutrients Mediate the Impacts of Global Change on Locust Outbreaks. *Annual Review of
 481 Entomology*, 69(1):527–550, January 2024. ISSN 0066-4170, 1545-4487. doi: 10.1146/annurev-ento-120220-
 482 110415. URL <https://www.annualreviews.org/doi/10.1146/annurev-ento-120220-110415>.
- 483 Arianne J. Cease, James J. Elser, Colleen F. Ford, Shuguang Hao, Le Kang, and Jon F. Harrison. Heavy Livestock
 484 Grazing Promotes Locust Outbreaks by Lowering Plant Nitrogen Content. *Science*, 335(6067):467–469, January
 485 2012. ISSN 0036-8075, 1095-9203. doi: 10.1126/science.1214433. URL <https://www.science.org/doi/10.1126/science.1214433>.
- 487 Arianne J. Cease, James J. Elser, Eli P. Fenichel, Joleen C. Hadrich, Jon F. Harrison, and Brian E. Robinson. Living
 488 With Locusts: Connecting Soil Nitrogen, Locust Outbreaks, Livelihoods, and Livestock Markets. *BioScience*, 65
 489 (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>.
- 491 Arianne J. Cease, Michelle Fay, James J. Elser, and Jon F. Harrison. Dietary phosphate affects food selection, post-
 492 ingestive P fate, and performance of a polyphagous herbivore. *Journal of Experimental Biology*, page jeb.126847,
 493 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>.
- 495 Arianne J. Cease, Eduardo V. Trumper, Héctor Medina, Fernando Copa Bazán, Jorge Frana, Jon Harrison, Nelson
 496 Joaquin, Jennifer Learned, Mónica Roca, Julio E. Rojas, Stav Talal, and Rick P. Overson. Field bands
 497 of marching locust juveniles show carbohydrate, not protein, limitation. *Current Research in Insect Science*, 4:
 498 100069, 2023. ISSN 26665158. doi: 10.1016/j.cris.2023.100069. URL <https://linkinghub.elsevier.com/retrieve/pii/S2666515823000185>.
- 500 Ken Cheng, Stephen J. Simpson, and David Raubenheimer. A Geometry of Regulatory Scaling. *The American
 501 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>.
- 503 Dp Clark. The Influence of Rainfall on the Densities of Adult Chortoicetes Terminifera (Walker) in Central Western
 504 New South Wales, 1965-73. *Australian Journal of Zoology*, 22(3):365, 1974. ISSN 0004-959X. doi: 10.1071/
 505 ZO9740365. URL <http://www.publish.csiro.au/?paper=ZO9740365>.
- 506 D G Clayton, L Bernardinelli, and C Montomoli. Spatial Correlation in Ecological Analysis. *International Journal
 507 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>.
- 509 F. J. Clissold, G. D. Sanson, and J. Read. The paradoxical effects of nutrient ratios and supply rates on an outbreaking
 510 insect herbivore, the Australian plague locust. *Journal of Animal Ecology*, 75(4):1000–1013, July 2006. ISSN 0021-
 511 8790, 1365-2656. doi: 10.1111/j.1365-2656.2006.01122.x. URL <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-2656.2006.01122.x>.
- 513 Fiona J. Clissold, Nicole Coggan, and Stephen J. Simpson. Insect herbivores can choose microclimates to achieve
 514 nutritional homeostasis. *Journal of Experimental Biology*, page jeb.078782, January 2013. ISSN 1477-9145, 0022-
 515 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>.
- 517 Fiona J. Clissold, Helena Kertesz, Amelia M. Saul, Julia L. Sheehan, and Stephen J. Simpson. Regulation of water
 518 and macronutrients by the Australian plague locust, *Chortoicetes terminifera*. *Journal of Insect Physiology*, 69:35–
 519 40, October 2014. ISSN 00221910. doi: 10.1016/j.jinsphys.2014.06.011. URL <https://linkinghub.elsevier.com/retrieve/pii/S0022191014001267>.
- 521 F. R. Cole and G. O. Batzli. Influence of Supplemental Feeding on a Vole Population. *Journal of Mammalogy*, 59(4):
 522 809–819, November 1978. ISSN 1545-1542, 0022-2372. doi: 10.2307/1380145. URL <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1380145>.

- 524 Keith Cressman. Role of remote sensing in desert locust early warning. *Journal of Applied Remote Sensing*, 7(1):
 525 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>.
- 526
- 527 Darron A. Cullen, Arianne J. Cease, Alexandre V. Latchininsky, Amir Ayali, Kevin Berry, Camille Buhl, Rien
 528 De Keyser, Bert Foquet, Joleen C. Hadrich, Tom Matheson, Swidbert R. Ott, Mario A. Poot-Pech, Brian E.
 529 Robinson, Jonathan M. Smith, Hojun Song, Gregory A. Sword, Jozef Vanden Broeck, Rik Verdonck, Heleen
 530 Verlinden, and Stephen M. Rogers. From Molecules to Management: Mechanisms and Consequences of
 531 Locust Phase Polyphenism. In *Advances in Insect Physiology*, volume 53, pages 167–285. Elsevier, 2017.
 532 ISBN 978-0-12-811833-7. doi: 10.1016/bs.aiip.2017.06.002. URL <https://linkinghub.elsevier.com/retrieve/pii/S0065280617300231>.
- 533
- 534 R.H. Dadd. The nutritional requirements of locustsIV. Requirements for vitamins of the B complex. *Journal of
 535 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>.
- 536
- 537 Louis De Grandpré, Maryse Marchand, Daniel D. Kneeshaw, David Paré, Dominique Boucher, Stéphane Bourassa,
 538 David Gervais, Martin Simard, Jacob M. Griffin, and Deepa S. Pureswaran. Defoliation-induced changes in foliage
 539 quality may trigger broad-scale insect outbreaks. *Communications Biology*, 5(1):463, May 2022. ISSN 2399-3642.
 540 doi: 10.1038/s42003-022-03407-8. URL <https://www.nature.com/articles/s42003-022-03407-8>.
- 541
- 542 E. D. Deveson and P. W. Walker. Not a one-way trip: historical distribution data for Australian plague locusts support
 543 frequent seasonal exchange migrations. *Journal of Orthoptera Research*, 14(1):91–105, January 2005. ISSN 1082-
 544 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>.
- 545
- 546 Edward D. Deveson. Satellite normalized difference vegetation index data used in managing Australian plague locusts.
 547 *Journal of Applied Remote Sensing*, 7(1):075096, July 2013. ISSN 1931-3195. doi: 10.1117/1.JRS.7.075096. URL
<http://remotesensing.spiedigitallibrary.org/article.aspx?doi=10.1117/1.JRS.7.075096>.
- 548
- 549 Ted Deveson and David Hunter. THE OPERATION OF A GISBASED DECISION SUPPORT SYSTEM FOR
 550 AUSTRALIAN LOCUST MANAGEMENT. *Insect Science*, 9(4):1–12, December 2002. ISSN 1672-9609,
 551 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>.
- 552
- 553 Colin Donald. Phosphorus in Australian agriculture. *Journal of the Australian Institute of Agricultural Science*, 30
 (75):195, 1964.
- 554
- 555 Terry J. Doonan and Norman A. Slade. Effects of Supplemental Food on Population Dynamics of Cotton Rats,
 556 *Sigmodon Hispidus*. *Ecology*, 76(3):814–826, April 1995. ISSN 0012-9658, 1939-9170. doi: 10.2307/1939347.
 557 URL <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1939347>.
- 558
- 559 James J. Elser, William F. Fagan, Robert F. Denno, Dean R. Dobberfuhl, Ayoola Folarin, Andrea Huberty, Sebastian
 560 Interlandi, Susan S. Kilham, Edward McCauley, Kimberly L. Schulz, Evan H. Siemann, and Robert W. Sterner.
 561 Nutritional constraints in terrestrial and freshwater food webs. *Nature*, 408(6812):578–580, November 2000. ISSN
 562 0028-0836, 1476-4687. doi: 10.1038/35046058. URL <https://www.nature.com/articles/35046058>.
- 563
- 564 Ra Farrow. Population Dynamics of the Australian Plague Locust, Chortoicetes terminifera (Walker) in Central
 565 Western New South Wales III. Analysis of Population Processes. *Australian Journal of Zoology*, 30(4):569, 1982.
 566 ISSN 0004-959X. doi: 10.1071/ZO9820569. URL <http://www.publish.csiro.au/?paper=ZO9820569>.
- 567
- 568 R. B. Floyd, editor. *Frontiers of population ecology*. CSIRO Pub, Collingwood, VIC, Australia, 1996. ISBN 978-0-
 569 643-05781-4.
- 570
- 571 M. G. Forero, J. L. Tella, K. A. Hobson, M. Bertellotti, and G. Blanco. Conspecific food competition explains
 572 variability in colony size: a test in Magellanic penguins. *Ecology*, 83(12):3466–3475, December 2002. ISSN 0012-
 573 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).
- 574
- 575 M. Giese, H. Brueck, Y. Z. Gao, S. Lin, M. Steffens, I. Kögel-Knabner, T. Glindemann, A. Susenbeth, F. Taube,
 576 K. Butterbach-Bahl, X. H. Zheng, C. Hoffmann, Y. F. Bai, and X. G. Han. N balance and cycling of Inner Mongolia
 577 typical steppe: a comprehensive case study of grazing effects. *Ecological Monographs*, 83(2):195–219, May 2013.
 578 ISSN 0012-9615, 1557-7015. doi: 10.1890/12-0114.1. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/12-0114.1>.
- 579
- Noel Gorelick, Matt Hancher, Mike Dixon, Simon Ilyushchenko, David Thau, and Rebecca Moore. Google Earth
 Engine: Planetary-scale geospatial analysis for everyone. *Remote Sensing of Environment*, 202:18–27, December 2017. ISSN 00344257. doi: 10.1016/j.rse.2017.06.031. URL <https://linkinghub.elsevier.com/retrieve/pii/S0034425717302900>.

- 579 Martin Granbom and Henrik G. Smith. Food Limitation During Breeding in a Heterogeneous Landscape. *The Auk*,
 580 123(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>.
- 582 M. J. Grundy, R. A. Viscarra Rossel, R. D. Searle, P. L. Wilson, C. Chen, and L. J. Gregory. Soil and Landscape Grid
 583 of Australia. *Soil Research*, 53(8):835, 2015. ISSN 1838-675X. doi: 10.1071/SR15191. URL <http://www.publish.csiro.au/?paper=SR15191>.
- 585 Lennart Hansson. Food as a limiting factor for small rodent numbers: Tests of two hypotheses. *Oecologia*, 37(3):
 586 297–314, January 1979. ISSN 0029-8549, 1432-1939. doi: 10.1007/BF00347907. URL <http://link.springer.com/10.1007/BF00347907>.
- 588 Sarah J. Harrison, David Raubenheimer, Stephen J. Simpson, Jean-Guy J. Godin, and Susan M. Bertram. Towards
 589 a synthesis of frameworks in nutritional ecology: interacting effects of protein, carbohydrate and phosphorus on
 590 field cricket fitness. *Proceedings of the Royal Society B: Biological Sciences*, 281(1792):20140539, 2014. doi:
 591 10.1098/rspb.2014.0539. URL <https://doi.org/10.1098/rspb.2014.0539>.
- 592 T. J. Heidorn and A. Joern. Feeding Preference and Spatial Distribution of Grasshoppers (Acrididae) in Response
 593 to Nitrogen Fertilization of Calamovilfa longifolia. *Functional Ecology*, 1(4):369, 1987. ISSN 02698463. doi:
 594 10.2307/2389793. URL <https://www.jstor.org/stable/2389793?origin=crossref>.
- 595 Andrea F. Huberty and Robert F. Denno. Consequences of nitrogen and phosphorus limitation for the performance of
 596 two planthoppers with divergent life-history strategies. *Oecologia*, 149(3):444–455, September 2006. ISSN 0029-
 597 8549, 1432-1939. doi: 10.1007/s00442-006-0462-8. URL <http://link.springer.com/10.1007/s00442-006-0462-8>.
- 598 D. M. Hunter, P. W. Walker, and R. J. Elder. Adaptations of locusts and grasshoppers to the low and variable
 599 rainfall of Australia. *Journal of Orthoptera Research*, 10(2):347–351, December 2001. ISSN 1082-6467, 1937-
 600 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>.
- 602 D.M. Hunter, L. McCulloch, and P.A. Spurgin. Aerial detection of nymphal bands of the Australian plague
 603 locust (Chortoicetes terminifera (Walker)) (Orthoptera: Acrididae). *Crop Protection*, 27(1):118–123, January
 604 2008. ISSN 02612194. doi: 10.1016/j.cropro.2007.04.016. URL <https://linkinghub.elsevier.com/retrieve/pii/S0261219407001159>.
- 606 Anthony Joern, Tony Provin, and Spencer T. Behmer. Not just the usual suspects: Insect herbivore populations and
 607 communities are associated with multiple plant nutrients. *Ecology*, 93(5):1002–1015, May 2012. ISSN 0012-9658,
 608 1939-9170. doi: 10.1890/11-1142.1. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/11-1142.1>.
- 609 Jayne L. Jonas and Anthony Joern. Hostplant quality alters grass/forb consumption by a mixedfeeding insect herbivore,
 610 *Melanoplus bivittatus* (Orthoptera: Acrididae). *Ecological Entomology*, 33(4):546–554, August 2008. ISSN 0307-
 611 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>.
- 613 Lloyd B. Keith. Role of Food in Hare Population Cycles. *Oikos*, 40(3):385, May 1983. ISSN 00301299. doi:
 614 10.2307/3544311. URL <https://www.jstor.org/stable/3544311?origin=crossref>.
- 615 K.H.L. Key. The general ecological characteristics of the outbreak areas and outbreak years of the Australian plague
 616 locust (Chortoicetes terminifera Walk.). 1945. doi: 10.25919/RTPX-F935. URL <https://publications.csiro.au/publications/publication/PIprocite:8058408f-539f-4540-b888-0dda1e0c113d>. Publisher: Melbourne, Vic., Council
 617 for Scientific and Industrial Research.
- 619 Douglas Lawton, Cathy Waters, Marion Le Gall, and Arianne Cease. Woody vegetation remnants within pastures
 620 influence locust distribution: Testing bottom-up and top-down control. *Agriculture, Ecosystems & Environment*,
 621 296:106931, July 2020. ISSN 01678809. doi: 10.1016/j.agee.2020.106931. URL <https://linkinghub.elsevier.com/retrieve/pii/S016788092030116X>.
- 623 Douglas Lawton, Marion Le Gall, Cathy Waters, and Arianne J. Cease. Mismatched diets: defining the nutritional
 624 landscape of grasshopper communities in a variable environment. *Ecosphere*, 12(3):e03409, March 2021. ISSN
 625 2150-8925, 2150-8925. doi: 10.1002/ecs2.3409. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1002/ecs2.3409>.
- 627 Douglas Lawton, Peter Scarth, Edward Deveson, Cyril Piou, Allan Spessa, Cathy Waters, and Arianne J. Cease. Seeing
 628 the locust in the swarm: accounting for spatiotemporal hierarchy improves ecological models of insect populations.
 629 *Ecography*, 2022(2):ecog.05763, February 2022. ISSN 0906-7590, 1600-0587. doi: 10.1111/ecog.05763. URL
 630 <https://nsojournals.onlinelibrary.wiley.com/doi/10.1111/ecog.05763>.
- 631 Marion Le Gall, Rick Overton, and Arianne Cease. A Global Review on Locusts (Orthoptera: Acrididae) and Their
 632 Interactions With Livestock Grazing Practices. *Frontiers in Ecology and Evolution*, 7:263, July 2019. ISSN 2296-
 633 701X. doi: 10.3389/fevo.2019.00263. URL <https://www.frontiersin.org/article/10.3389/fevo.2019.00263/full>.

- 634 Paul A. Lenhart, Micky D. Eubanks, and Spencer T. Behmer. Water stress in grasslands: dynamic responses of plants
 635 and insect herbivores. *Oikos*, 124(3):381–390, March 2015. ISSN 0030-1299, 1600-0706. doi: 10.1111/oik.01370.
 636 URL <https://onlinelibrary.wiley.com/doi/10.1111/oik.01370>.
- 637 Simon A. Levin. The Problem of Pattern and Scale in Ecology: The Robert H. MacArthur Award Lecture. *Ecology*,
 638 73(6):1943–1967, December 1992. ISSN 0012-9658, 1939-9170. doi: 10.2307/1941447. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.2307/1941447>.
- 640 Viviana Loaiza, Jayne L. Jonas, and Anthony Joern. Grasshoppers (orthoptera: Acrididae) select vegetation patches
 641 in local-scale responses to foliar nitrogen but not phosphorus in native grassland: Grasshopper distribution and
 642 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>.
- 644 Nr Marsh and Ma Adams. Decline of Eucalyptus tereticornis Near Bairnsdale, Victoria: Insect Herbivory and Nitrogen
 645 Fractions in Sap and Foliage. *Australian Journal of Botany*, 43(1):39, 1995. ISSN 0067-1924. doi: 10.1071/BT9950039. URL <http://www.publish.csiro.au/?paper=BT9950039>.
- 647 William J. Mattson. Herbivory in Relation to Plant Nitrogen Content. *Annual Review of Ecology and Systematics*,
 648 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>.
- 650 Ali Abdalla Millist, Nicola. Benefitcost analysis of Australian plague locust control operations for 201011,
 651 2011. URL <https://www.agriculture.gov.au/sites/default/files/sitecollectiondocuments/animal-plant/aplc/research-papers/locust-control-11.pdf>.
- 653 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.
 654 Roshier, M.A. Smith, F.J. Walsh, G.M. Wardle, I.W. Watson, and M. Westoby. A fresh framework for the ecology
 655 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>.
- 657 Joaquín Muñoz-Sabater, Emanuel Dutra, Anna Agustí-Panareda, Clément Albergel, Gabriele Arduini, Gianpaolo
 658 Balsamo, Souhail Boussetta, Margarita Choulga, Shaun Harrigan, Hans Hersbach, Brecht Martens, Diego G.
 659 Miralles, María Piles, Nemesio J. Rodríguez-Fernández, Ervin Zsoter, Carlo Buontempo, and Jean-Noël Thé-
 660 paut. ERA5-Land: a state-of-the-art global reanalysis dataset for land applications. *Earth System Science
 661 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/>.
- 663 Yonggang Nie, Zejun Zhang, David Raubenheimer, James J. Elser, Wei Wei, and Fuwen Wei. Obligate herbivory
 664 in an ancestrally carnivorous lineage: the giant panda and bamboo from the perspective of nutritional geometry.
 665 *Functional Ecology*, 29(1):26–34, January 2015. ISSN 0269-8463, 1365-2435. doi: 10.1111/1365-2435.12302.
 666 URL <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2435.12302>.
- 667 Immanuel Noy-Meir. Desert Ecosystems: Higher Trophic Levels. *Annual Review of Ecology and Systematics*, 5(1):
 668 195–214, 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>.
- 670 Gordon H. Orians and Antoni V. Milewski. Ecology of Australia: the effects of nutrientpoor soils and intense fires.
 671 *Biological Reviews*, 82(3):393–423, August 2007. ISSN 1464-7931, 1469-185X. doi: 10.1111/j.1469-185X.2007.00017.x. URL <https://onlinelibrary.wiley.com/doi/10.1111/j.1469-185X.2007.00017.x>.
- 673 Katerina A. Ozment, Ellen A. R. Welti, Monica Shaffer, and Michael Kaspari. Tracking nutrients in space and time:
 674 Interactions between grazing lawns and drought drive abundances of tallgrass prairie grasshoppers. *Ecology and
 675 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>.
- 677 Adam F. Parlin, Mitchell J. Kendzel, Orley R. Taylor, Theresa M. Culley, Stephen F. Matter, and Patrick A.
 678 Guerra. The cost of movement: assessing energy expenditure in a long-distant ectothermic migrant under cli-
 679 mate change. *Journal of Experimental Biology*, 226(21):jeb245296, November 2023. ISSN 0022-0949, 1477-9145.
 680 doi: 10.1242/jeb.245296. URL <https://journals.biologists.com/jeb/article/226/21/jeb245296/334654/The-cost-of-movement-assessing-energy-expenditure>.
- 682 Marc C. Perkins, H. Arthur Woods, Jon F. Harrison, and James J. Elser. Dietary phosphorus affects the growth of larval
 683 *Manduca sexta*. *Archives of Insect Biochemistry and Physiology*, 55(3):153–168, March 2004. ISSN 0739-4462,
 684 1520-6327. doi: 10.1002/arch.10133. URL <https://onlinelibrary.wiley.com/doi/10.1002/arch.10133>.
- 685 J. C. Randolph, G. N. Cameron, and P. A. McClure. Nutritional Requirements for Reproduction in the Hispid Cotton
 686 Rat, *Sigmodon hispidus*. *Journal of Mammalogy*, 76(4):1113–1126, December 1995. ISSN 1545-1542, 0022-2372.
 687 doi: 10.2307/1382603. URL <https://academic.oup.com/jmammal/article-lookup/doi/10.2307/1382603>.

- 688 D. Raubenheimer and S. J. Simpson. Integrative models of nutrient balancing: application to insects and ver-
 689 tebrates. *Nutrition Research Reviews*, 10(1):151–179, January 1997. ISSN 0954-4224, 1475-2700. doi: 10.
 690 1079/NRR19970009. URL https://www.cambridge.org/core/product/identifier/S0954422497000103/type/journal_article.
- 692 David Raubenheimer and Jessica M. Rothman. Nutritional Ecology of Entomophagy in Humans and Other Primates.
 693 *Annual Review of Entomology*, 58(1):141–160, January 2013. ISSN 0066-4170, 1545-4487. doi: 10.1146/annurev-
 694 ento-120710-100713. URL <https://www.annualreviews.org/doi/10.1146/annurev-ento-120710-100713>.
- 695 John D. Schade, Marcia Kyle, S. E. Hobbie, W. F. Fagan, and J. J. Elser. Stoichiometric tracking of soil nutrients
 696 by a desert insect herbivore. *Ecology Letters*, 6(2):96–101, February 2003. ISSN 1461-023X, 1461-0248. doi:
 697 10.1046/j.1461-0248.2003.00409.x. URL <https://onlinelibrary.wiley.com/doi/10.1046/j.1461-0248.2003.00409.x>.
- 698 S. J. Simpson and J. D. Abisgold. Compensation by locusts for changes in dietary nutrients: behavioural mechanisms.
 699 *Physiological Entomology*, 10(4):443–452, December 1985. ISSN 0307-6962, 1365-3032. doi: 10.1111/j.1365-
 700 3032.1985.tb00066.x. URL <https://resjournals.onlinelibrary.wiley.com/doi/10.1111/j.1365-3032.1985.tb00066.x>.
- 701 Stephen J Simpson and David Raubenheimer. *The nature of nutrition: a unifying framework from animal adaptation
 702 to human obesity*. Princeton university press, 2012a.
- 703 Stephen J. Simpson and David Raubenheimer. *The Nature of Nutrition: A Unifying Framework from Animal Adap-
 704 tation to Human Obesity*. Princeton University Press, 1 edition, July 2012b. ISBN 978-0-691-14565-5 978-1-
 705 4008-4280-3. doi: 10.23943/princeton/9780691145655.001.0001. URL [https://academic.oup.com/princeton-scholarship-online/book/23993](https://academic.oup.com/princeton-

 706 scholarship-online/book/23993).
- 707 Stav Talal, Arianne J. Cease, Jacob P. Youngblood, Ruth Farington, Eduardo V. Trumper, Hector E. Medina, Julio E.
 708 Rojas, A. Fernando Copa, and Jon F. Harrison. Plant carbohydrate content limits performance and lipid accumula-
 709 tion of an outbreaking herbivore. *Proceedings of the Royal Society B: Biological Sciences*, 287(1940):20202500,
 710 December 2020. ISSN 0962-8452, 1471-2954. doi: 10.1098/rspb.2020.2500. URL <https://royalsocietypublishing.org/doi/10.1098/rspb.2020.2500>.
- 712 Stav Talal, Arianne Cease, Ruth Farington, Hector E. Medina, Julio Rojas, and Jon Harrison. High carbohydrate diet
 713 ingestion increases post-meal lipid synthesis and drives respiratory exchange ratios above 1. *Journal of Experi-
 714 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>.
- 716 Stav Talal, Jon F. Harrison, Ruth Farington, Jacob P. Youngblood, Hector E. Medina, Rick Overson, and Arianne J.
 717 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>.
- 719 Toby Tyrrell. The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature*, 400(6744):
 720 525–531, August 1999. ISSN 0028-0836, 1476-4687. doi: 10.1038/22941. URL <https://www.nature.com/articles/22941>.
- 722 Boris Petrovi Uvarov. *Grasshoppers and locusts. 2: Behaviour, ecology, biogeography population dynamics*. Univ.
 723 Press, Cambridge, 1977. ISBN 978-0-85135-072-1.
- 724 Sophie Veran, Stephen J. Simpson, Gregory A. Sword, Edward Deveson, Sylvain Piry, James E. Hines, and Karine
 725 Berthier. Modeling spatiotemporal dynamics of outbreaking species: influence of environment and migration in
 726 a locust. *Ecology*, 96(3):737–748, March 2015. ISSN 0012-9658, 1939-9170. doi: 10.1890/14-0183.1. URL
 727 <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/14-0183.1>.
- 728 Peter M. Vitousek, Stephen Porder, Benjamin Z. Houlton, and Oliver A. Chadwick. Terrestrial phosphorus limita-
 729 tion: mechanisms, implications, and nitrogen-phosphorus interactions. *Ecological Applications*, 20(1):5–15, January
 730 2010. ISSN 1051-0761, 1939-5582. doi: 10.1890/08-0127.1. URL <https://esajournals.onlinelibrary.wiley.com/doi/10.1890/08-0127.1>.
- 732 Ellen A. R. Welti, Rebecca M. Prather, Nathan J. Sanders, Kirsten M. De Beurs, and Michael Kaspari. Bottomup when
 733 it is not topdown: Predators and plants control biomass of grassland arthropods. *Journal of Animal Ecology*, 89(5):
 734 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>.
- 736 Ellen A. R. Welti, Karl A. Roeder, Kirsten M. De Beurs, Anthony Joern, and Michael Kaspari. Nutrient dilution
 737 and climate cycles underlie declines in a dominant insect herbivore. *Proceedings of the National Academy of
 738 Sciences*, 117(13):7271–7275, March 2020b. ISSN 0027-8424, 1091-6490. doi: 10.1073/pnas.1920012117. URL
 739 <https://pnas.org/doi/full/10.1073/pnas.1920012117>.
- 740 T. C. R. White. The importance of a relative shortage of food in animal ecology. *Oecologia*, 33(1):71–86, 1978. ISSN
 741 0029-8549, 1432-1939. doi: 10.1007/BF00376997. URL <http://link.springer.com/10.1007/BF00376997>.

- 742 T. C. R. White. The role of food, weather and climate in limiting the abundance of animals. *Biological Reviews*,
 743 83(3):227–248, August 2008. ISSN 1464-7931, 1469-185X. doi: 10.1111/j.1469-185X.2008.00041.x. URL
 744 <https://onlinelibrary.wiley.com/doi/10.1111/j.1469-185X.2008.00041.x>.
- 745 Thomas C. R. White. *The Inadequate Environment*. Springer Berlin Heidelberg, Berlin, Heidelberg, 1993. ISBN 978-
 746 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>.
- 748 W. G. Whitford. *Ecology of desert systems*. Academic Press, San Diego, 2002. ISBN 978-0-12-747261-4.
- 749 J. A. Wiens. Spatial Scaling in Ecology. *Functional Ecology*, 3(4):385, 1989. ISSN 02698463. doi: 10.2307/2389612.
 750 URL <https://www.jstor.org/stable/2389612?origin=crossref>.
- 751 J. Keaton Wilson, L. Ruiz, and G. Davidowitz. Dietary Protein and Carbohydrates Affect Immune Function and
 752 Performance in a Specialist Herbivore Insect (*Manduca sexta*). *Physiological and Biochemical Zoology*, 92(1):
 753 58–70, January 2019a. ISSN 1522-2152, 1537-5293. doi: 10.1086/701196. URL <https://www.journals.uchicago.edu/doi/10.1086/701196>.
- 755 Jerome Keaton Wilson, Laura Ruiz, Jesse Duarte, and Goggy Davidowitz. The nutritional landscape of host plants
 756 for a specialist insect herbivore. *Ecology and Evolution*, 9(23):13104–13113, December 2019b. ISSN 2045-7758,
 757 2045-7758. doi: 10.1002/ece3.5730. URL <https://onlinelibrary.wiley.com/doi/10.1002/ece3.5730>.
- 758 Mira L. Word, Sharon J. Hall, Brian E. Robinson, Balanding Manneh, Alioune Beye, and Arianne J. Cease. Soil-
 759 targeted interventions could alleviate locust and grasshopper pest pressure in West Africa. *Science of The Total
 760 Environment*, 663:632–643, May 2019. ISSN 00489697. doi: 10.1016/j.scitotenv.2019.01.313. URL <https://linkinghub.elsevier.com/retrieve/pii/S0048969719303560>.
- 762 Zijia Zhang, James J. Elser, Arianne J. Cease, Ximeい Zhang, Qiang Yu, Xingguo Han, and Guangming Zhang.
 763 Grasshoppers Regulate N:P Stoichiometric Homeostasis by Changing Phosphorus Contents in Their Frass. *PLoS
 764 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>.
- 766 Xiaolong Zhou, Xudong Liu, Pengfei Zhang, Zhi Guo, and Guozhen Du. Increased community compositional dissim-
 767 ilarity alleviates species loss following nutrient enrichment at large spatial scales. *Journal of Plant Ecology*, 12(2):
 768 376–386, March 2019. ISSN 1752-993X. doi: 10.1093/jpe/ryt035. URL <https://academic.oup.com/jpe/article/12/2/376/5096732>.
- 770 Hui Zhu, Venuste Nkurunziza, Jingting Wang, Qinfeng Guo, Hang Ruan, and Deli Wang. Effects of large herbivore
 771 grazing on grasshopper behaviour and abundance in a meadow steppe. *Ecological Entomology*, 45(6):1357–1366,
 772 December 2020. ISSN 0307-6946, 1365-2311. doi: 10.1111/een.12919. URL <https://resjournals.onlinelibrary.wiley.com/doi/10.1111/een.12919>.
- 774 Yu Zhu, Zhiwei Zhong, Jordi F. Pagès, Deborah Finke, Deli Wang, Quanhui Ma, Nazim Hassan, Hui Zhu, and Ling
 775 Wang. Negative effects of vertebrate on invertebrate herbivores mediated by enhanced plant nitrogen content. *Jour-
 776 nal of Ecology*, 107(2):901–912, March 2019. ISSN 0022-0477, 1365-2745. doi: 10.1111/1365-2745.13100. URL
 777 <https://besjournals.onlinelibrary.wiley.com/doi/10.1111/1365-2745.13100>.

778 **6 SUPPLEMENTARY**

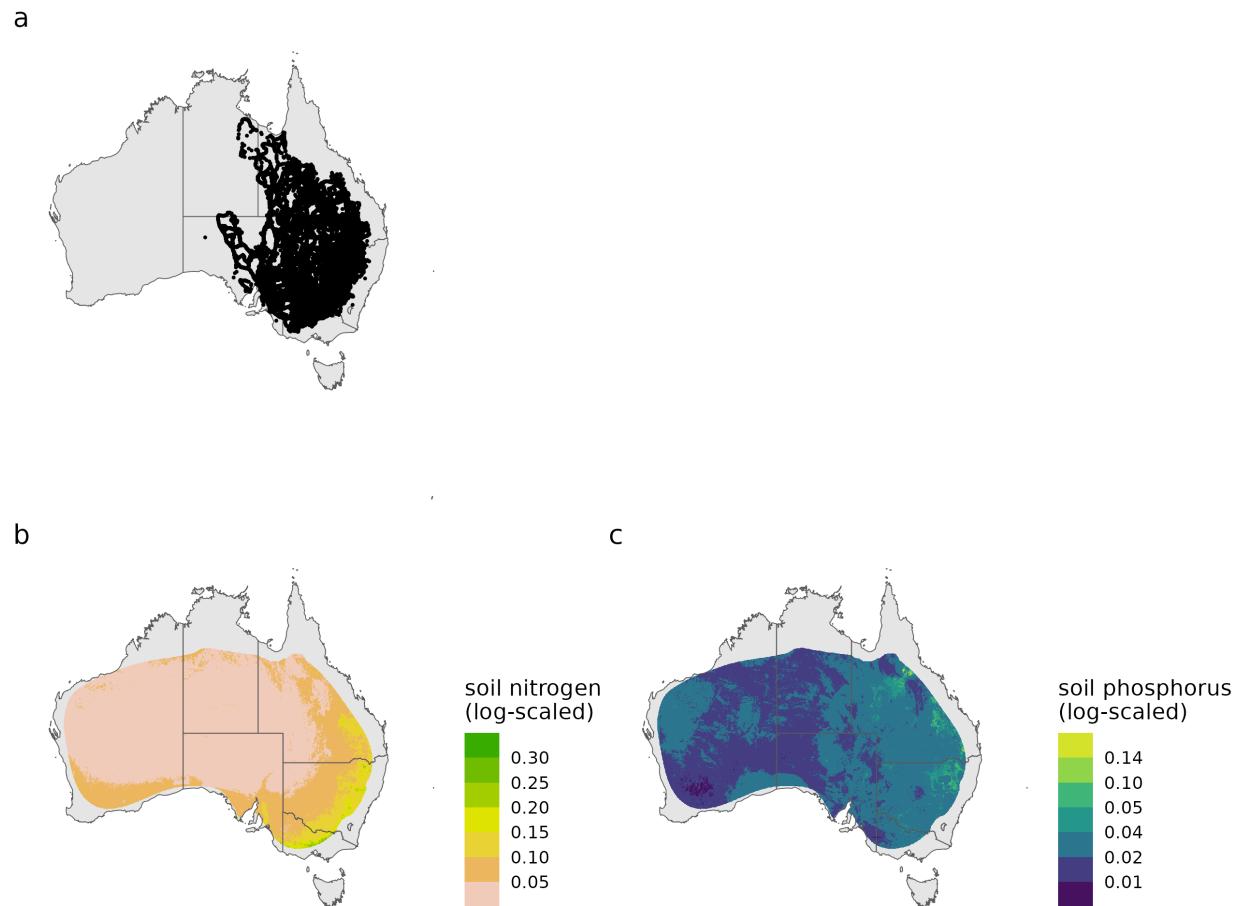
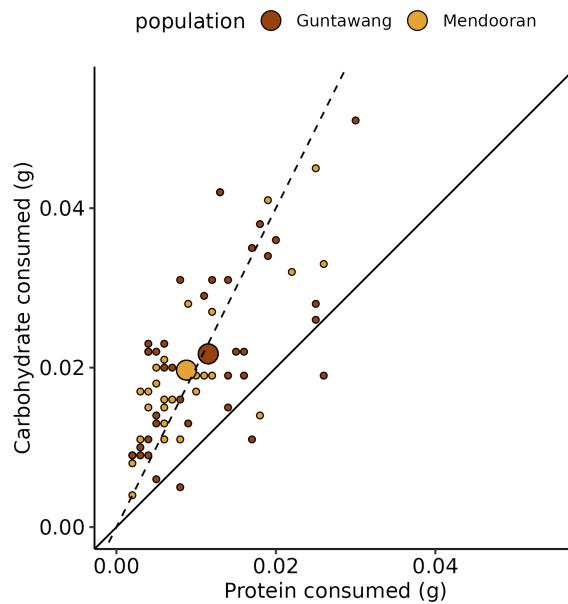


Figure 1: Locust survey data map and soil nutrients throughout the Australian plague locust distribution. A: APLC survey dataset, B: mean proportion phosphorous at 0-15cm deep, C: mean proportion of nitrogen at 0-15 cm deep.

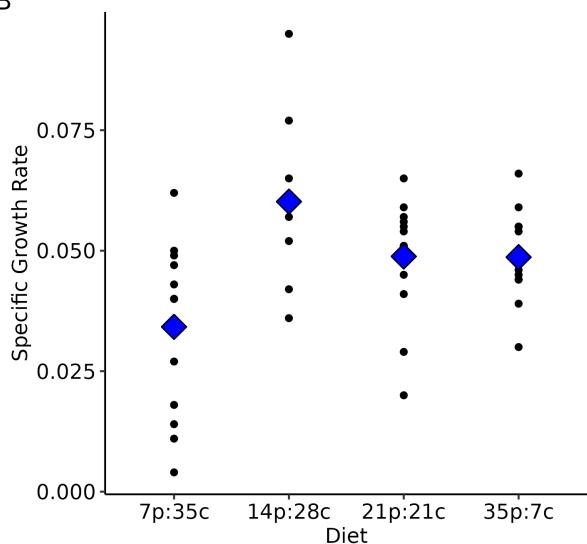
macronutrient	variable	estimate	SE	statistic	p-value
carbohydrate	Intercept	0.013	0.004		0.001
	male	-0.011	0.004		0.009
	day 2	0.007	0.003		0.008
	day 3-4	0.016	0.003		0.000
	day 5-6	0.026	0.003		0.000
	day 7-9	0.035	0.003		0.000
	none	-0.006	0.004		0.136
	s(id)			484.706	0.000
protein	Intercept	0.002	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		0.001		0.000
	day 7-9		0.001		0.000
	none	-0.001	0.001		0.475
	s(id)			110.728	0.381

Table 1: Generalized additive model results for macronutrient consumption (carbohydrate and protein) of two out-breaking populations of Australian plague locust in Mendooran and Guntawang. Models were selected via AIC, AICc and BIC which can be seen in Table 8. Family: multivariate gaussian distribution, link: identity, SE: standard error.

A



B



C

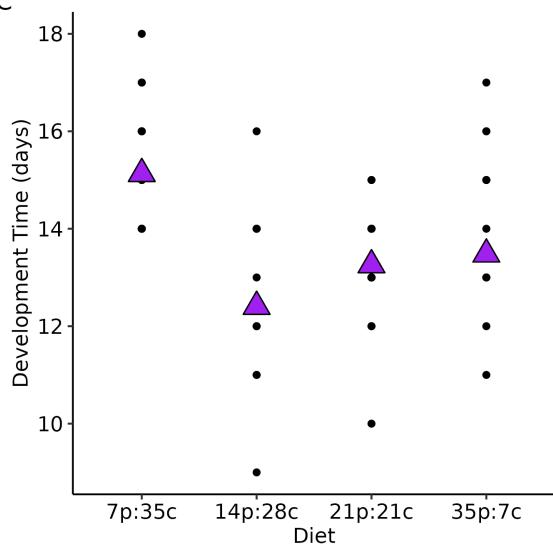


Figure 2: The nutritional preference (A) and physiological performance (B & C) of *C. terminifera* individuals were collected from two marching bands of 5th instars.

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 2: Australian plague locust 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 Table 9.

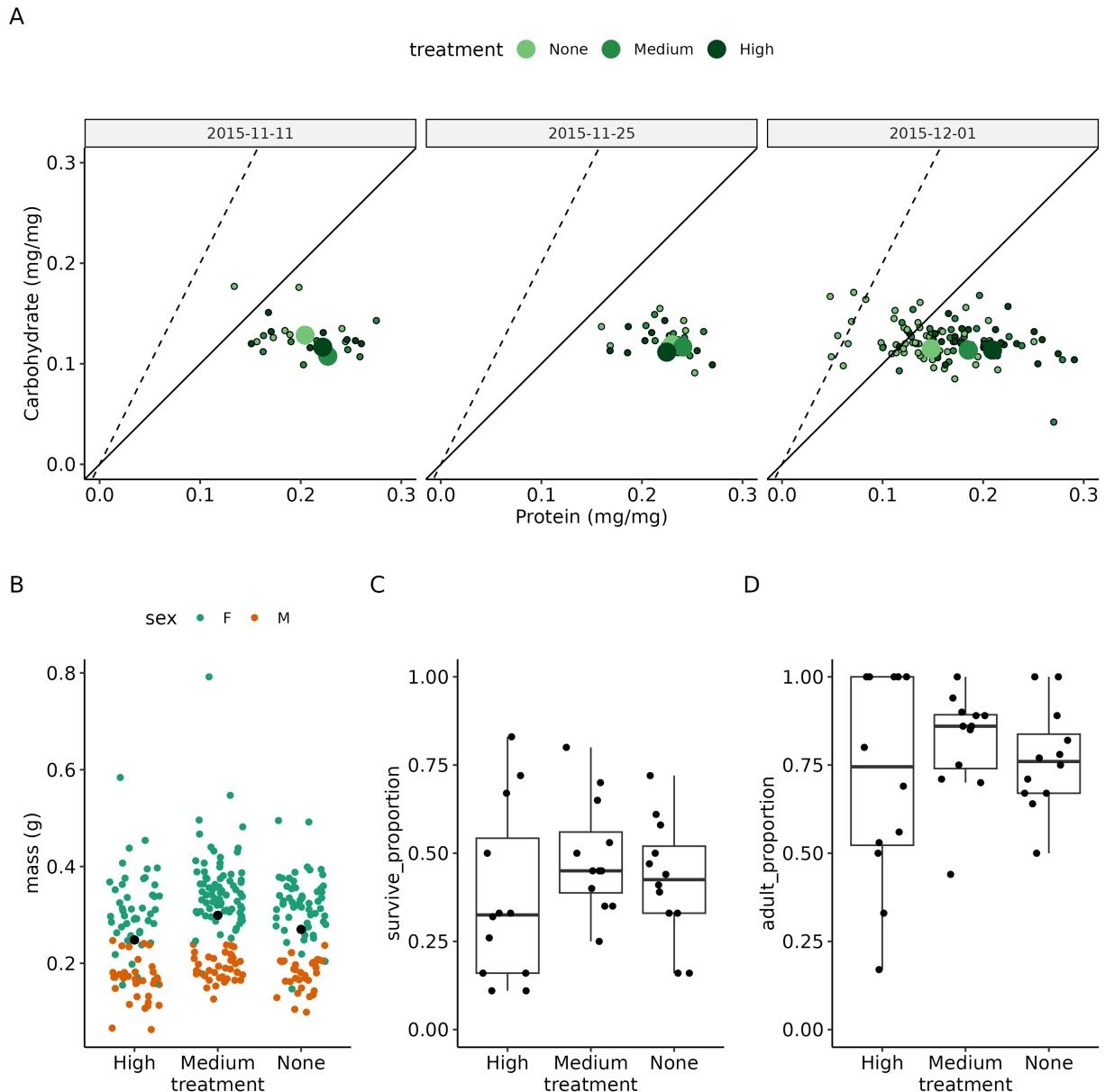


Figure 3: Nitrogen addition field cage experiments with plant nutrient change through time (A-C) and grasshopper performance metrics (D-F) are shown. Dashed line represents a 1p : 2c ratio, the solid line represents a 1p : 1c ratio.

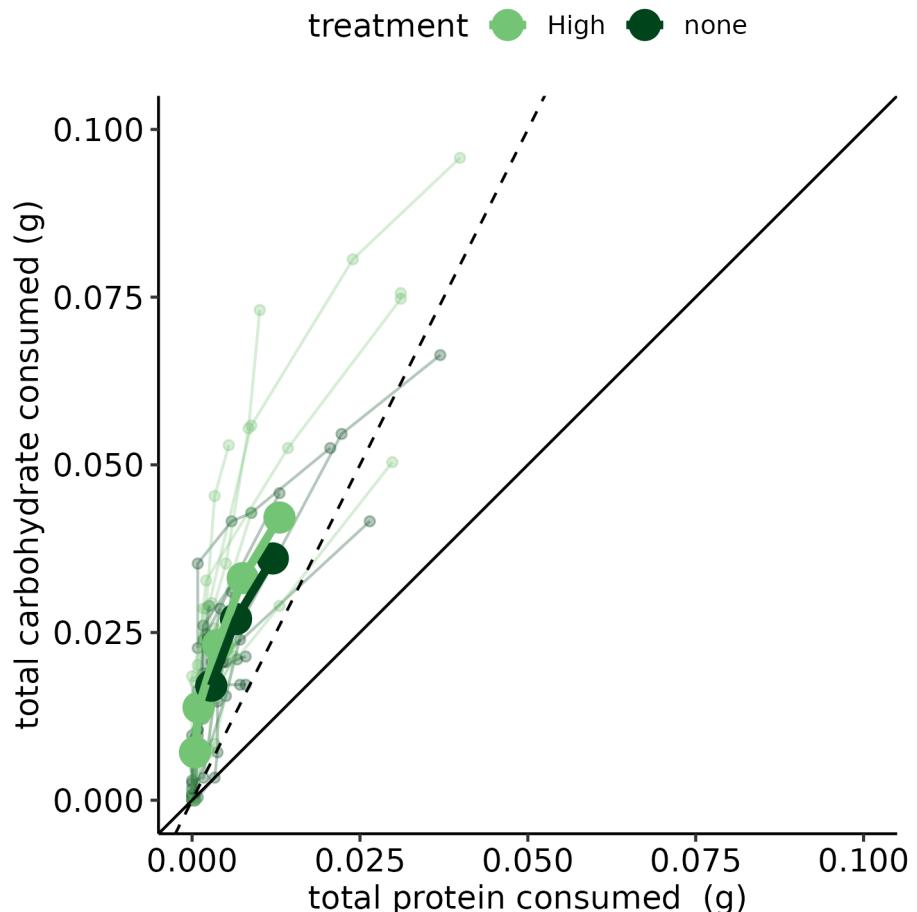


Figure 4: Nutrient imbalance redressing with artificial diet mixing of *C. terminifera* individuals taken from fertilized treatment cages. Colors represent treatment with large lines and points representing overall means. Individual time step targets can be seen in Supplementary Figure 4.

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

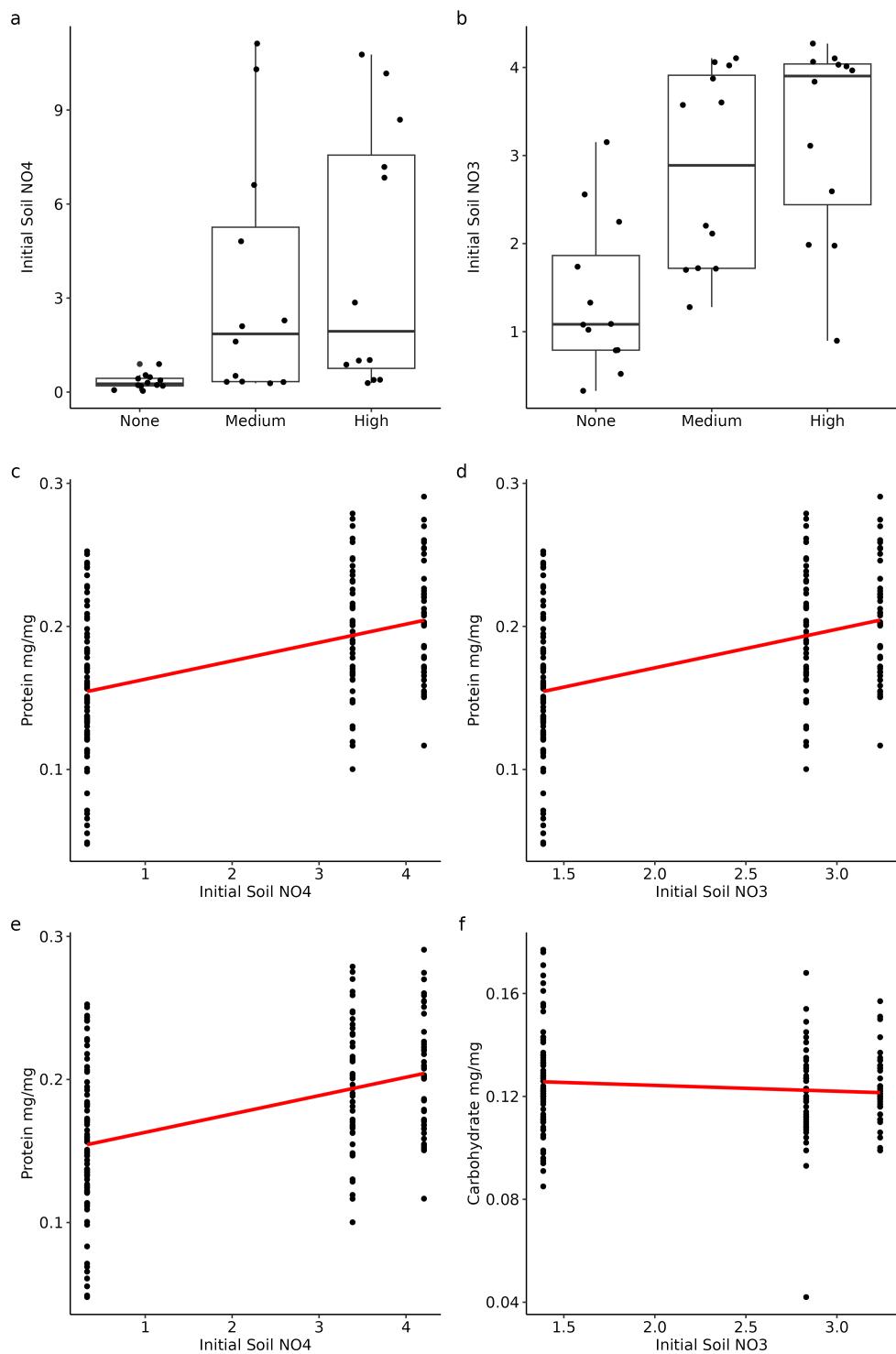
Table 3: Generalized additive model results for plant macronutrient (carbohydrate and protein) differences between fertilization treatment. Family: multivariate gaussian distribution, link: identity, SE: standard error, significance indicated in bold.

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

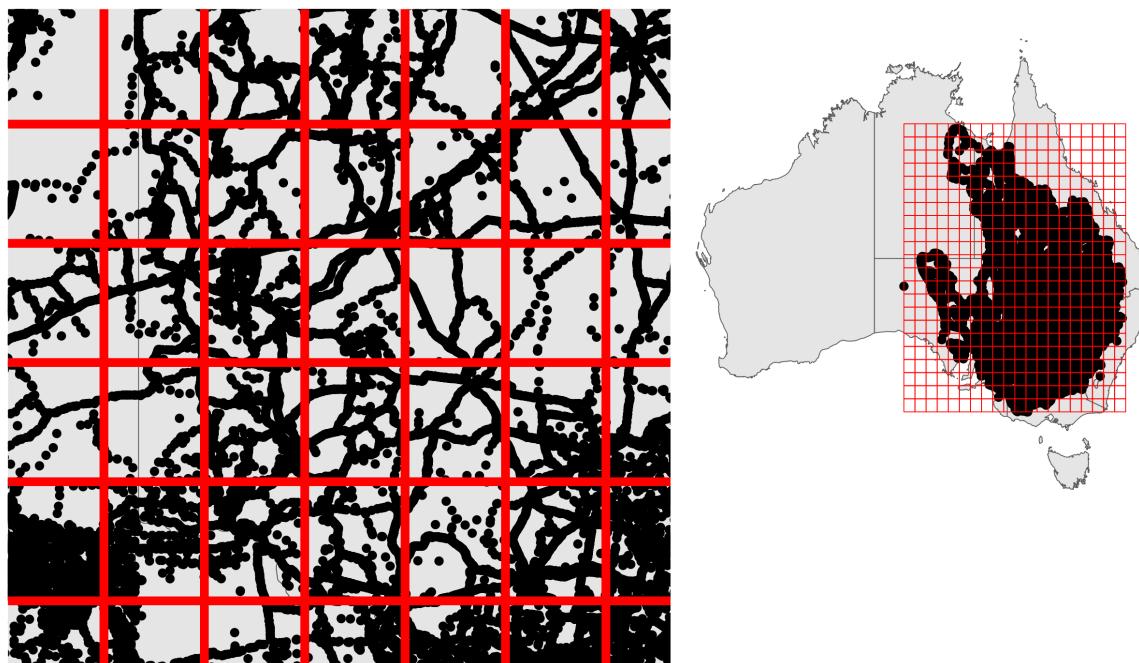
Table 4: Generalized additive model results for differences between final locust mass after the nitrogen fertilization experiment finished. Family: scaled T, link: identity, SE: standard error.

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

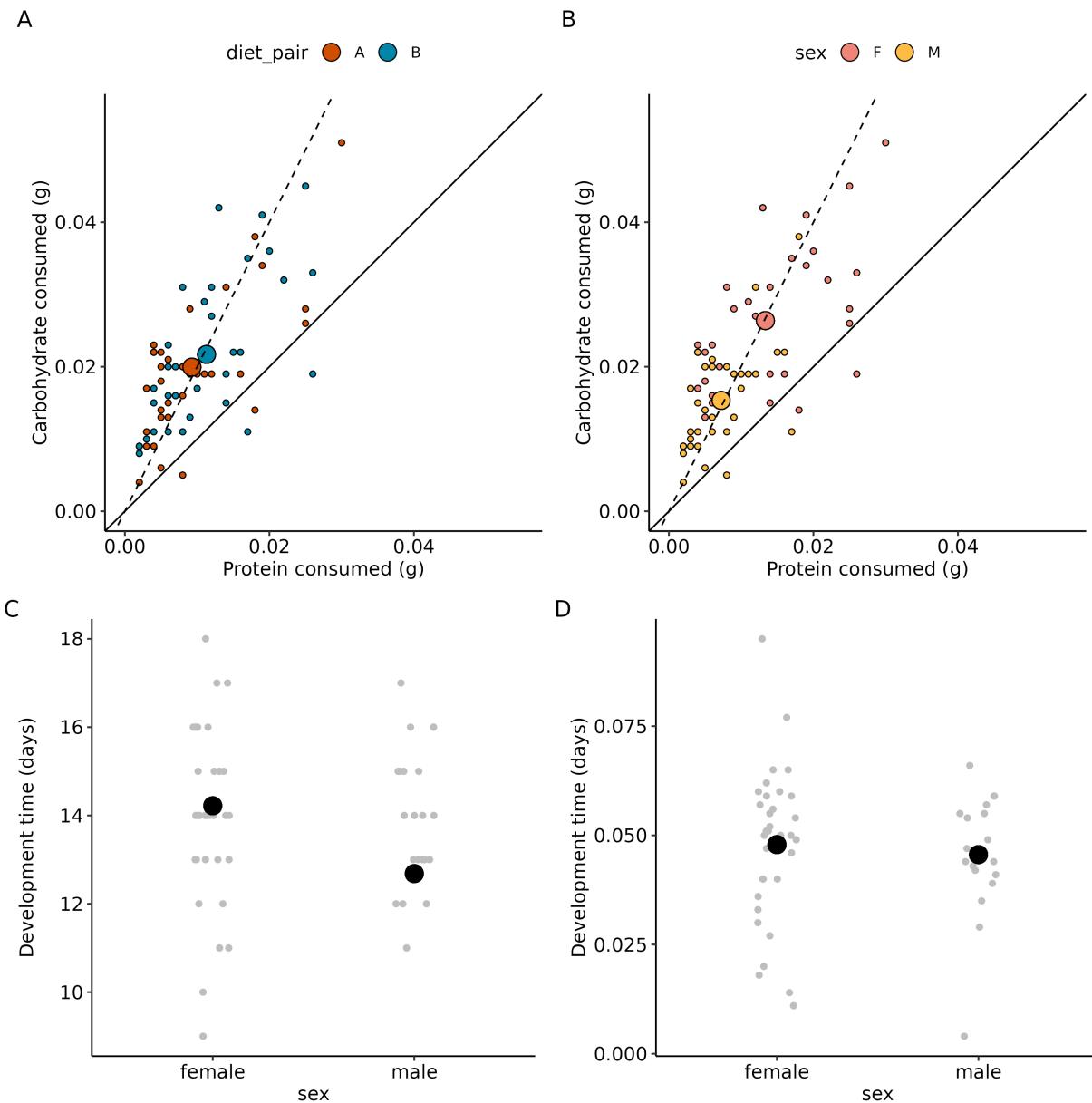
Table 5: Generalized additive model results for nutrient imbalance dressing of field cage Australian plague locust in the control and high fertilization treatments. Model also included interactive terms; however, none were significant and left out. SE: standard error



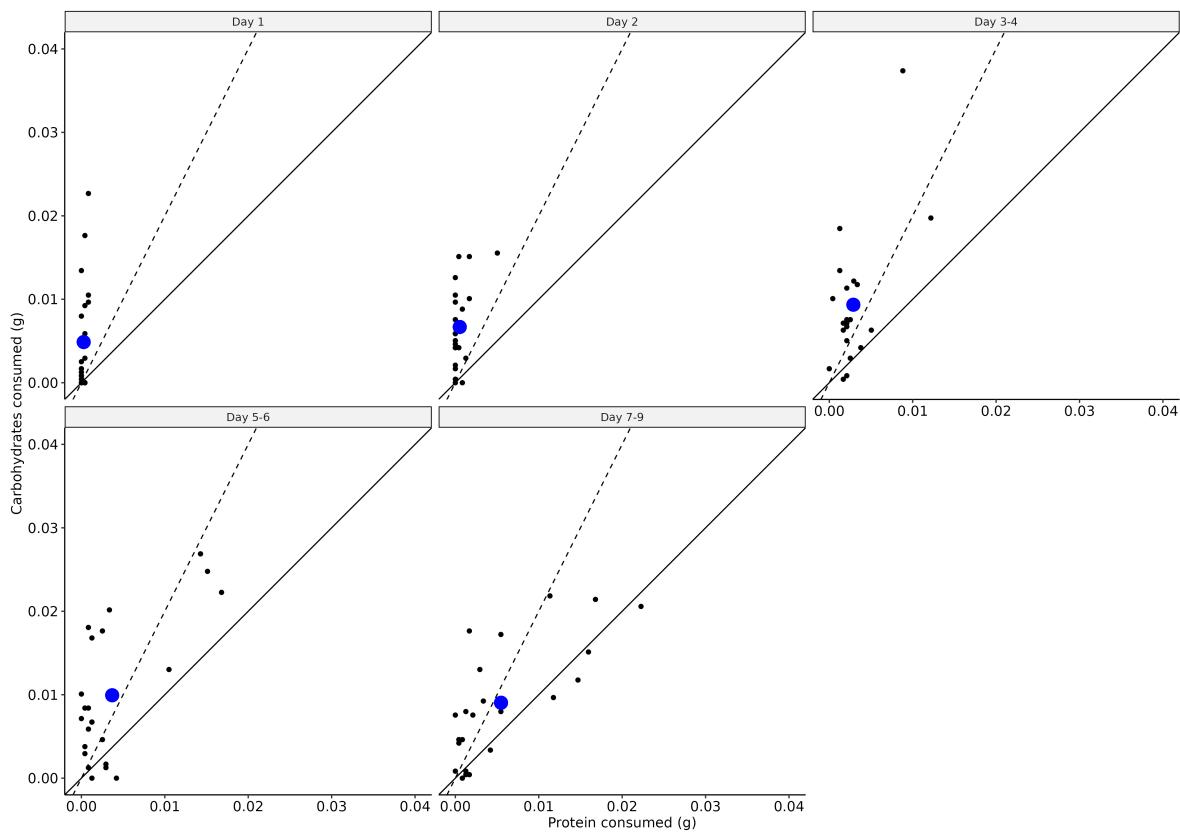
Supplementary Figure 1: Field cage soil nitrogen content by treatment (A & B) and regressed with plant carbohydrates and protein (C-F).



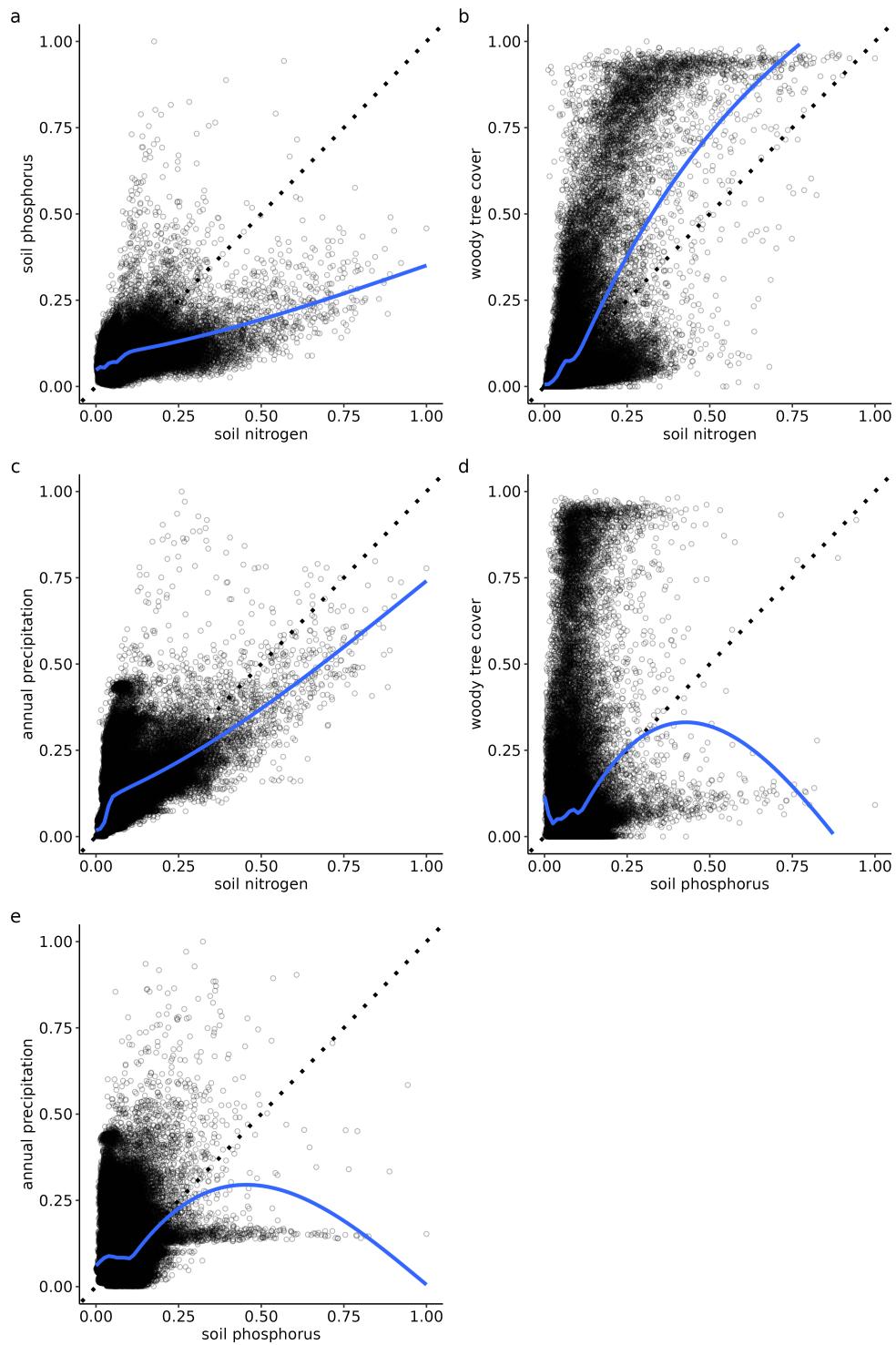
Supplementary Figure 2: Map showing how we summarized point observation data to a fishnet grid throughout eastern Australia. Entire extent can be seen in the inlet map. We summed the number of 4 (outbreak) observations, low presence observations (1-3), nil observations (0), and the total observations. Grid not at a 1 km² x 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 mean 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 overall mean while blacks dots represent 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. Dashed line represents a 1:1 slope and the blue line is a cubic spline with 10 knots.

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		
Medium	<i>Enteropogon spp.</i>	2015-11-11	0.431	0.042	0.209	0.126	2.831	3.385
	<i>Enteropogon spp.</i>	2015-11-25	0.417	0.026	0.210	0.137		
	<i>Enteropogon spp.</i>	2015-12-01	0.415	0.022	0.146	0.124		
	<i>Cyperus spp.</i>	2015-11-11	0.424	0.038	0.213	0.119		
	<i>Cyperus spp.</i>	2015-11-25	0.420	0.029	0.239	0.127		
	<i>Cyperus spp.</i>	2015-12-01	0.418	0.022	0.188	0.135		
	<i>Plasplodium spp.</i>	2015-12-01	0.414	0.020	0.243	0.094		
	<i>Rytidosperma spp.</i>	2015-11-11	0.422	0.037	0.227	0.106		
	<i>Rytidosperma spp.</i>	2015-11-25	0.420	0.028	0.242	0.115		
	<i>Rytidosperma spp.</i>	2015-12-01	0.422	0.021	0.181	0.116		
None	<i>Enteropogon spp.</i>	2015-11-11	0.432	0.031	0.164	0.145	1.387	0.331
	<i>Enteropogon spp.</i>	2015-11-25	0.414	0.021	0.194	0.115		
	<i>Enteropogon spp.</i>	2015-12-01	0.405	0.023	0.114	0.130		
	<i>Cyperus spp.</i>	2015-11-11	0.425	0.032	0.228	0.144		
	<i>Cyperus spp.</i>	2015-11-25	0.417	0.027	0.232	0.137		
	<i>Cyperus spp.</i>	2015-12-01	0.408	0.026	0.154	0.126		
	<i>Plasplodium spp.</i>	2015-12-01	0.399	0.028	0.183	0.095		
	<i>Austrostipa spp.</i>	2015-12-01	0.416	0.013	0.150	0.104		
	<i>Rytidosperma spp.</i>	2015-11-11	0.420	0.026	0.190	0.124		
	<i>Rytidosperma spp.</i>	2015-11-25	0.417	0.027	0.232	0.133		
	<i>Rytidosperma spp.</i>	2015-12-01	0.418	0.022	0.142	0.121		
	unknown	2015-12-01	0.413	0.031	0.168	0.101		

Table 6: 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

Table 7: 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

Table 8: 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. s() denotes a smoothing parameter was estimated. 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

Table 9: Posthoc comparisons for diet treatments for *C. terminifera* individual specific growth rate and development time. SE = standard error.