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Evaluating the contribution of individual variation in parasite-mediated anorexia to trophic cascades

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Abstract

Recent evidence suggests that parasite-mediated reductions in food intake (i.e., anorexia) in herbivores can trigger trophic cascades that increase producer biomass. This outcome assumes homogeneous host responses to parasite infection; however, individual variation in parasite-mediated anorexia is common. To understand the potential consequences of such variation, we quantified individual variation in host feeding responses to parasitism empirically using a wild herbivore–helminth system. We then evaluated the impact of ecologically relevant levels of variation in anorexia on producers using stochastic individual-based models composed of parasites, herbivores, and plants. Our empirical data showed that although higher helminth burdens were associated with lower population-level feeding rates, there was considerable individual variation in the presence and magnitude of anorexia. Our models revealed a pronounced effect of variation in anorexia prevalence but not magnitude on plants. Plant biomass increased as anorexia became prevalent in the herbivore population, and there was a strong dampening effect of anorexia prevalence on plant biomass variance, suggesting that parasite-mediated anorexia in herbivores can stabilize producer population dynamics. Interestingly, the association between higher anorexia prevalence and lower variance in plant biomass was due, in part, to negative feedback between herbivore feeding rates and helminth ingestion, suggesting that negative feedback between host behavior and parasitism, a phenomenon that can help stabilize certain host–parasite interactions, may have stabilizing effects that extend to other members of the ecological community via trophic cascades.

KEYWORDS
behavioral variation, feedback, feeding behavior, gastrointestinal helminths, trait-mediated effect, trophic cascade

INTRODUCTION

Parasites that infect herbivores can trigger trophic cascades that indirectly affect producer populations (Buck & Ripple, 2017). The most frequently described producer–herbivore–parasite cascades emerge when direct negative effects of parasites on herbivore densities are coupled with indirect positive effects of declines in herbivore numbers on producer biomass (Bogdziewicz et al., 2022; Buck & Ripple, 2017; Holdo et al., 2009). However, parasites also have nonlethal effects on their hosts, including effects on host traits such as physiology or behavior (Buck, 2019), which, similar to effects on host density, can also affect producers (Buck & Ripple, 2017; Koltz et al., 2022). In fact, for sublethal parasites that rarely cause mortality, these trait-mediated effects may be as strong, if not stronger, drivers of trophic cascades than density-mediated effects (Koltz et al., 2022).

One well-known host trait affected by parasitism is feeding behavior. A variety of parasites, ranging from viruses and bacteria to fungi and helminths, cause reductions in food consumption in hosts, a phenomenon known as parasite-mediated anorexia (Hite et al., 2020; Kyriazakis et al., 1998). In vertebrates, anorexia is modulated by a complex set of physiological and immunological mechanisms, with consequences for both individual-level disease severity and population-level disease transmission (Dynes et al., 1990; Hite et al., 2020). In addition, when hosts are consumers, parasite-mediated anorexia might also have broader scale ecological effects. For example, indirect effects of parasites on producer biomass, caused by changes in host feeding behavior, have been described experimentally in several aquatic host–parasite systems (Bernot & Lamberti, 2008; Harjoe et al., 2022; Morton & Silliman, 2020; Wood et al., 2007). Recently, a mathematical model focusing on helminth parasites, caribou (*Rangifer tarandus*), and lichen, a dominant caribou food resource, also showed that parasite-induced reductions in herbivore resource intake can lead to increases in producer biomass (Koltz et al., 2022). These and other studies of parasite-associated trophic cascades typically focus on how mean effects of parasites on host traits translate to producers, yet parasite-mediated changes in host traits are known to be highly variable (Hoye et al., 2012). Accounting for this variability may be key to understanding the conditions under which parasite effects on hosts are most likely to trigger trophic cascades.

Effects of parasites on host feeding behavior are notoriously variable, differing at the individual, population, and species levels (Hite et al., 2020; Koltz et al., 2022; Kyriazakis, 2010). As an example, in laboratory rats (*Rattus norvegicus*) infected with the parasitic nematode, *Nippostrongylus brasiliensis*, food consumption declined by 37% on average, but individual-level declines ranged from 6% to 80%, suggesting substantial individual variation in the magnitude of anorexia (Horbury et al., 1995). Such variation in individual anorexia responses can be attributed to a range of factors, including parasite dose, host nutrition, host susceptibility, or host/parasite genotype (Kyriazakis, 2010; Pfenning-Butterworth et al., 2023). Over the past two decades, the importance of host heterogeneity in shaping outcomes of host–parasite interactions at population and community scales has become increasingly clear (e.g., Paull et al., 2012; VanderWaal & Ezenwa, 2016). For example, individuals who have high contact rates can contribute disproportionately to large disease outbreaks (Lloyd-Smith et al., 2005). Here, we extend this idea to food chain dynamics, focusing on parasite-induced variation in host feeding behavior and trophic cascades. To do this, we use a simulation model parameterized with empirical data from a wild herbivore to examine trait-mediated effects of parasites on plants when herbivores experience parasite-mediated anorexia. Many herbivore populations can have strong impacts on plant communities (Estes et al., 2011). Here, we focused on a wild herbivore–helminth system (Grant's gazelle [*Nanger granti*] and strongyle nematodes [Nematoda: Strongylida]) where an anthelmintic treatment experiment was conducted and parasite-mediated reductions in feeding rate have been described (Ezenwa & Worsley-Tonks, 2018; Worsley-Tonks & Ezenwa, 2015). Specifically, we (i) examined the degree to which helminths generate individual variation in the presence and magnitude of host anorexia; (ii) investigated factors that explain variation in anorexia; and (iii) explored the potential consequences of variation in anorexia prevalence and magnitude for both plants and parasites.

METHODS

Study design and data collection

We used data on gastrointestinal helminth parasitism and feeding behavior collected as part of a prior anthelmintic treatment study of Grant's gazelles. Following procedures described in detail in Worsley-Tonks and Ezenwa (2015) and Ezenwa and Snider (2016), animals were captured at the Mpala Research Centre, Kenya (0°17′ N, 36°52′ E) in June 2011, ear tagged for individual recognition, and a random subset were given a subcutaneous injection of the anthelmintic drug moxidectin (0.05 mL/kg, Cydectin Long-Acting Injection for Sheep, Virbac Animal Health). Capture protocols were approved by the Institutional Animal Care and Use Committee of the University of Georgia (protocol number A2010 10-188), and captures were performed under the supervision of the Kenya Wildlife Service and approved by the Kenya National Council for Science and Technology.

Following capture and anthelmintic treatment, the behavior of study animals was monitored for 10 months (July 2011–April 2012). We used the percent time an individual spent feeding, derived from behavioral observations, as a proxy for food intake (Muruthi et al., 1991).

While the original treatment study tracked female and male study subjects and included both anthelmintic-treated and control individuals, here, we focused exclusively on treated females, since parasite-mediated changes in feeding behavior were found to be present in females (Worsley-Tonks & Ezenwa, 2015) but not males (Sabey et al., 2024). Following treatment, individual parasite burdens generally dropped to zero and then increased over time (Appendix S1: Figure S1), and we leveraged this treatment followed by rapid parasite reaccumulation process to quantify changes in feeding behavior at the within-individual level. Notably, because parasite burdens for all individuals approached their peak during the 10-month study window (Appendix S1: Figure S1), this method allowed us to characterize feeding behavior across a full range of relevant parasite intensities for each study subject. To quantify behavior, animal groups were located by vehicle, and tagged individuals were randomly selected for focal observation (Worsley-Tonks & Ezenwa, 2015). During each observation period, five behavioral states were recorded: feeding, vigilance, resting, moving, and other, as described in Worsley-Tonks and Ezenwa (2015). Nine anthelmintic-treated females were observed over the 10-month study period. The average observation period was 19.9 ± 2.00 (mean ± SD) minutes, and individuals were observed on average 3.43 ± 0.51 (mean ± SD) times per month.

Fecal samples collected from study individuals during the behavioral observations were used to track helminth infection status. All samples were collected within 10 min of observing a focal individual defecate, stored in a cooler with ice packs in the field, and processed in the laboratory later the same day. For each sample, the strongyle nematode fecal egg count (FEC) was measured using a modified McMaster egg counting technique (Ezenwa, 2003). We used strongyle FEC as an estimate of individual parasite burden.

To explore potential drivers of variation in parasite-mediated anorexia in gazelles, we focused on the role of predation risk, which is known to have strong effects on feeding behavior in herbivores (Hutchings et al., 2006; McArthur et al., 2014). We used four metrics: group size, vigilance behavior, tree cover, and heterogeneity in tree cover, as proxies of predation risk. Increases in group size and vigilance rates are well-documented responses to increased predation pressure in African savanna ungulates (Creel et al., 2014). Likewise, habitat features such as tree density and habitat heterogeneity are known modifiers of ungulate predation risk (Ford et al., 2014; Gorini et al., 2011; Hebblewhite & Merrill, 2009). Data on group size and time spent vigilant were derived from behavioral observations. GPS coordinates collected during these observations were used to derive animal locations, and based on these locations, estimates of tree cover (percent of a pixel covered by the tree canopy) were extracted from Moderate Resolution Imaging Spectroradiometer (Terra MODIS; MOD44B) imagery (DiMiceli et al., 2015), downloaded from the National Aeronautics and Space Administration (NASA) Land Processes Distributed Active Archive Center using the R package MODIStsp (Busetto & Ranghetti, 2016). Tree cover for the entire study period was derived from a single 250 × 250 m resolution image captured on March 6, 2012. For each study individual, the average tree cover present across all locations where it was sighted during a single month was used to estimate average tree cover, and the SD of the values across these locations in a month was used as an estimate of heterogeneity in tree cover (henceforth, habitat heterogeneity).

Statistical analysis

To examine the extent to which there was variation in the presence and magnitude of parasite-mediated anorexia among gazelles, we first tested for a population-level effect of strongyle burden on gazelle feeding behavior. To do this, we used a generalized linear mixed model (GLMM) with the mean proportion of time spent feeding by an individual per month included as the response variable, monthly mean strongyle FEC included as a fixed effect, and individual identity included as a random intercept and slope. We used monthly averages for feeding rate (percent time feeding [FT]) and FEC because there was not a corresponding fecal sample collected for each behavioral observation. We modeled time spent feeding using a quasi-binomial distribution because the data distribution was wider than could be accommodated by a binomial distribution. Random intercepts and slopes were included to allow for different levels of effects of FEC on feeding rate among individuals. Next, we ran separate analyses for each individual using quasi-binomial generalized linear models (GLMs) with the same response (mean monthly time spent feeding) and predictor (monthly strongyle FEC) variables as the population-level model. Since the coefficients from these models represent the mean individual-level effect of FEC on feeding rate, we compared the mean effect among individuals to assess the degree of variation. Finally, to account for potential temporal trends in the dataset, we also performed additional population- and individual-level analyses including timepoint—represented by the order of the observation month (from July 2011 to April 2012)—as a covariate in the models outlined above.

To examine whether variation in anorexia could be explained by predation risk, we tested for an effect of strongyle FEC, one of four predation risk proxy variables (group size, time spent vigilant, tree cover and habitat heterogeneity), and the interaction between FEC and each proxy on gazelle feeding time using population-level quasi-binomial GLMMs. Individual identity was included as a random intercept and slope in all models, and timepoint (month order) was included as a covariate. The timepoint covariate could account for the time lag between the date of tree cover image capture (March 6, 2012) and the FEC sample dates.

All analyses were performed in R 4.3.2 (R Core Team, 2023). GLMs and GLMMs were fit with the packages stats (R Core Team, 2023) and MASS (Venables & Ripley, 2002), respectively. In all cases, we used the exclusion of zero from the 95% CI as a criterion for statistical significance.

Individual-based modeling

Model structure

To explore how parasite-mediated anorexia might affect producers, we used a stochastic individual-based modeling framework to simulate a closed population of herbivores infected by helminths and consuming the focal plant. We parameterized the model using our empirical data on gazelle feeding and helminth burdens. In our model, plant biomass (PB_t) accumulated via logistic growth (Tsoularis & Wallace, 2002) with growth rate (r) and carrying capacity (K), and was lost via herbivore consumption estimated by a maximum intake rate (MaxIntake), herbivore feeding rate (FT), and maximum time spent feeding (MaxFT) (Figure 1, Equation 1). The abundance of helminth parasites in the environment (EP_t) was determined by parasite survival in the environment ($\text{Survival}_{\text{env}}$), depletion, and addition of parasites. The depletion of environmental parasite stages by host ingestion was estimated by transmission probability (β_P), and the addition of parasites to the environment by host shedding of parasite propagules was determined by daily fecal production (FecProd) and FEC (Figure 1, Equation 2). Individual herbivore percent time feeding (FT_{it}) depended on FEC (Figure 1, Equation 3). In Equation (3), $\eta(FT_{it})$ represents individual feeding rate transformed with an inverse logit link function of a quasi-binomial model; α is the intercept and β is the coefficient for the FEC effect, with deviance ε. The intercept (α) and coefficient (β) were randomly generated from normal distributions fit to individual intercepts and coefficients from the GLM results, respectively. If an individual coefficient was positive, we replaced it with zero to prevent a positive overall effect of helminth burden on feeding time as we found no empirical evidence that helminth infection significantly increased gazelle feeding rate on average (see *Results*). Because the intercept and coefficient were not independent from one another in the empirical dataset (Pearson correlation $r = -0.214$), we generated these two correlated parameters together using the package faux (DeBruine, 2023), instead of generating them separately from the corresponding normal distributions. The deviance (ε_i) was generated from a normal distribution with mean and SD equal to 0 and 0.271, respectively. This SD was obtained from the average SD of the residuals of the quasi-binomial models used to test for an individual-level effect of FEC on feeding rate. We parameterized the feeding responses based on our individual-level GLMs instead of the population-level model to capture the variation in feeding responses among individuals. Finally, individual FEC (FEC_{it}), which reflects helminth burden, was affected by parasite survival inside the host ($\text{Survival}_{\text{within}}$) and host ingestion of environmental parasites (Figure 1, Equation 4). Equation (4) also captures a feedback effect of feeding responses on helminth infection where ingestion of parasites was affected by feeding rate.

For simplicity, there was no birth, death, immigration, and emigration in the herbivore population. Second, herbivore plant consumption and parasite ingestion were modeled as linearly related to herbivore feeding time (Type I functional response) (Koprivnikar et al., 2023; Rauw et al., 2006), which in this model assumes that the spatial distribution of parasites, foraging patches, or host–parasite encounter probabilities is even. Third, plant carrying capacity and growth rate, and the coefficient for the parasite effect on host feeding rate (β in Equation 3) were time-invariant (i.e., no seasonal changes were assumed). Additionally, herbivore daily fecal production did not vary with feeding time in our model, which means that the number of parasites shed by hosts into the environment was solely determined by helminth burden. Because a major component of the Grant's gazelle diet at the study site is legumes (family: Fabacea) (Pansu et al., 2022), we used an average value for legume growth, 1.08 kg/kg × day as the plant growth rate (Reich et al., 2003). Survival rates of adult parasites and eggs were based on *Haemonchus contortus* (Coyne & Smith, 1992; Saccareau et al., 2017), a common gastrointestinal nematode of herbivores, known to infect Grant's gazelle (Pester & Laurence, 1974). Details of model parameter values derived from this study and prior literature are summarized in Table 1.

For all simulations, herbivore population size was set to 100. Initial environmental parasite abundance (EP_0) was set to 1×10^8, and parasite transmission probability (β_P) was set to 1×10^{-4}. Plant carrying capacity (K) as well as initial plant biomass (PB_0) were set to 200 kg/assigned

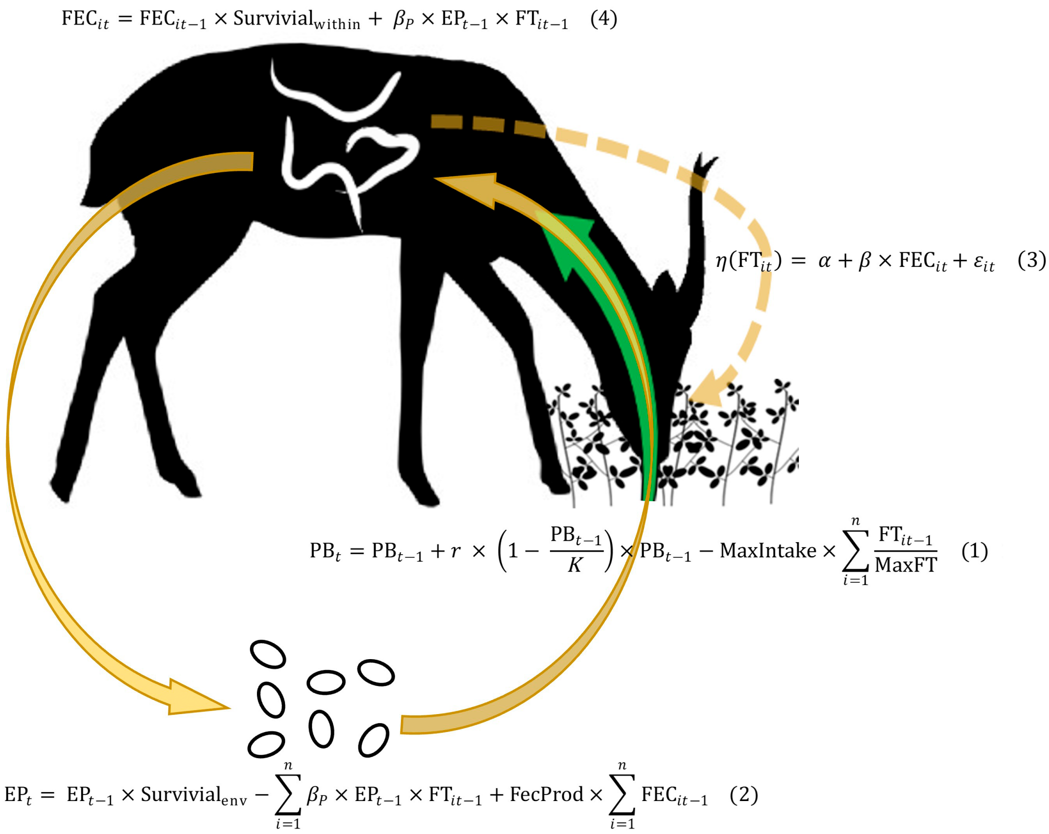

FIGURE 1 Model structure and equations. Individual-based modeling framework for evaluating the effects of individual variation in herbivore feeding responses to gastrointestinal helminth infection on other trophic levels. Solid lines indicate fluxes between compartments for either ingestion/excretion or life-cycle transitions; a dashed line indicates an effect of helminth infection on feeding rate. Fecal egg count is used as an index of individual herbivore infection burden. Definitions and values of parameters can be found in Table 1. Image silhouettes were downloaded and modified from the website PhyloPic (http://phylopic.org/) under a CC0 1.0 universal public domain dedication license.

area, which was the lowest possible value (adding 25 kg/assigned area starting from 0 kg/assigned area) at which plant biomass did not crash due to herbivory. FEC data from non-anthelmintic-treated gazelles were fit with a negative binomial distribution, which was used to randomly generate initial FECs ($\mu = 1674.33$, $\text{size} = 1.22$). This distribution generated nearly 100% prevalence of helminth infection (only 0.0014%–0.0015% individuals were not infected), which mirrors the ubiquitous nature of helminth parasitism in Grant's gazelle and other Africa savanna herbivores (Ezenwa, 2003; Titcomb et al., 2022). To explore the effects of variation in herbivore anorexia on trophic interactions, we ran a series of simulations described in detail in the following sections. All simulations were run over a 360-day timestep, and results for the 360th day were used for comparisons. We examined both the mean and variance of the 360th day outcomes to evaluate mean effects and the variability of outcomes. Finally, we drew inferences about system-level stability from the plant biomass variance results, following research using the invariability of plant biomass production as a measure of ecosystem-level stability (Craven et al., 2018).

Effects of variation in anorexia prevalence

To quantify effects of variation in the prevalence of parasite-mediated anorexia (i.e., percent individuals affected) on plants, we ran simulations with different proportions of herbivores exhibiting parasite-mediated anorexia. We explored five prevalence scenarios: 0%, 25%, 50%, 75%, and 100%. For example, when anorexia prevalence was 25%, only 25% of individuals changed their feeding behavior in response to infection, while the other 75% did not. The presence of a feeding response in an individual was fixed for all 360-day time steps of a simulation. For individuals with no feeding response to infection, FT was calculated by using zero as the FEC value in Equation (3) (Figure 1). Each scenario (0%–100%) was replicated 200 times, and we used

TABLE 1 Parameter descriptions and values for simulation models involving parasite burden and environmental abundance, herbivore feeding rate, and producer biomass (Figure 1, Equations 1–4).

Parameter	Description	Value	Reference
PB	Plant biomass		
EP	Environmental parasite abundance		
FEC_i	Herbivore individual fecal egg count		
FT_i	Herbivore individual percent time feeding		
r	Plant growth rate	1.08 kg/kg × day	Average legume growth rate (Reich et al., 2003)
K	Plant carrying capacity	200 kg/assigned area	
MaxIntake	Herbivore maximum individual intake	0.86 kg/day	Estimated from 99% quantile at 22°C with water restricted (Maloiy et al., 2008)
MaxFT	Herbivore maximum time spent feeding	0.8	Arbitrarily set as the maximal recorded value in our dataset was 0.795
FecProd	Herbivore daily fecal production	230 g	Estimated from average food intake minus average food digested at 22°C with water restricted (Maloiy et al., 2008)
$\mathrm{Survival}_{\mathrm{within}}$	Parasite within-host survival rate	0.979/day	Saccareau et al. (2017)
$\mathrm{Survival}_{\mathrm{env}}$	Parasite environmental survival rate	0.917/day	Estimated from egg survival at 15°C (Coyne & Smith, 1992)
β_P	Parasite transmission probability given parasite abundance and feeding rate	1×10^{-4}	
a_i	Individual intercept for a GLM		Randomly generated from a normal distribution fit to GLM intercepts[a]
β_i	Individual coefficient for a GLM		Randomly generated from a normal distribution fit to GLM coefficients[a]
ε_i	Deviance from predicted feeding time		Randomly generated from a normal distribution fit to residuals of GLM residuals[a]

[a] Individual-level generalized linear models (GLMs) with quasi-binomial distributions, with fecal egg count as a fixed effect and percent time feeding as the response variable.

permutation tests to examine whether variable prevalence led to differences in the means (permutation analysis of variance) or variances (permutation Bartlett's test) of the effects on other trophic levels. In each case, we performed 10,000 permutations implemented using the package RVAideMemoire (Hervé, 2023). Finally, to evaluate whether results were consistent across model parameter values, we performed sensitivity analyses using different values for parasite transmission probability, initial FEC, and plant carrying capacity. We also ran a scenario with no feedback effect of feeding rate on parasite infection (i.e., consistent parasite ingestion rate; see Appendix S1: Section S1).

Effects of variation in anorexia magnitude

To quantify the effects of variation in the magnitude of parasite-mediated anorexia (i.e., the size of the response) on plants, we compared two simulation scenarios, one with and one without individual variation in the magnitude of anorexia. For the scenario with variation in individual responses, the coefficient of the helminth effect on individual feeding time was randomly drawn from a normal distribution fit to individual gazelle coefficients but replacing positive values with zero, the same process mentioned above under model structure. For the scenario with no variation in feeding responses, we set the coefficient as constant (-9.49×10^{-4}) across all individuals, which was equivalent to the mean value of the coefficient generated in the first scenario. Both scenarios had the same average FEC effect (coefficient value), but the first included among-individual variation in magnitude of feeding responses while the second did not. Anorexia prevalence was set at 100% for both scenarios, and all other parameter values were the same as described above. We simulated 200 replicates for both scenarios and performed permutation tests with 10,000 permutations for differences in the means (permutation Student's *t* test) and variances (permutation *F* test) of the trophic effects between the scenarios.

RESULTS

Variation in the presence and magnitude of anorexia

Overall, there was a negative population-level trend between gazelle feeding rate and strongyle fecal egg count ($n = 65$ samples and 9 individuals; estimate: −0.00027; 95% CI: −0.00063 to 0.000086; Figure 2a,b). After removing two data points from an individual with extremely high parasite burdens (FEC > 2500) or including timepoint (order of observation month) as a covariate, the mean population-level trend remained negative (without FEC outliers: estimate [95% CI]: −0.00029 [−0.00072 to 0.00014]; with timepoint included: −0.000083 [−0.00045 to 0.00029]; Appendix S1: Figure S2a,b).

Our individual-level analyses revealed that feeding responses to infection varied among individuals. Individual coefficient estimates for the relationship between FEC and feeding rate ranged from negative to slightly positive (individual GLMs: n [range] = 4–9; estimate [range] = −0.0031 to 0.000041; Figure 2a,b). Two out of nine (~22%) gazelles showed a significant decline in percent time spent feeding with increasing FEC (95% CI of coefficients: −0.0018 to −0.00015 and −0.0057 to −0.00073) while none showed a significant increase (Figure 2a,b). Individual coefficient estimates still ranged from negative to positive after FEC outliers were removed (estimate [range] = −0.0031 to 0.0015; Appendix S1: Figure S2a) or timepoint was accounted for (estimate [range] = −0.0045 to 0.00056; Appendix S1: Figure S2b).

Drivers of variation in the magnitude of anorexia

We tested whether factors related to predation risk (group size, vigilance behavior, percent tree cover, habitat heterogeneity) could explain among-individual variation in the magnitude of anorexia we observed. Neither group size, vigilance, tree cover, nor their interactions with strongyle FEC explained significant variation in gazelle feeding rate (Appendix S1: Table S1). However, the interaction between habitat heterogeneity, measured as the SD of tree cover, and strongyle FEC was a significant predictor of time spent feeding (estimate [95% CI]: −0.024 [−0.049 to −0.000025]; Appendix S1: Table S1). As habitat heterogeneity increased, the relationship between FEC and feeding rate became more negative (Figure 2c,d). A negative trend remained after the removal of high FEC outliers (estimate [95% CI]: −0.036 (−0.073 to 0.00024); Appendix S1: Figure S2c).

Trophic effects generated by helminth-mediated anorexia

Variation in anorexia prevalence

Our simulation models showed a substantial positive effect of the prevalence of anorexia in the herbivore population on plants and a negative effect on helminths. As a greater proportion of herbivores were affected by parasite-mediated anorexia (from 0% to 100%), they spent less time feeding on average, and plant biomass increased (Figure 3a,b, Table 2). Specifically, when anorexia was at 100% compared to absent (0%), average plant biomass increased by over 16% (from 0%, 25%, 50%, 75%, to 100%: 135.6, 147.4 [+8.7%], 153.6 [+13.3%], 156.8 [+15.7%], and 158.4 kg [+16.8%]), and variance decreased by 60% (from 0%, 25%, 50%, 75%, to 100%: 17.19, 11.14 [−35.2%], 9.86 [−42.7%], 6.98 [−59.4%], 6.88 kg^2 [−60.0%]; Figure 3b). Anorexia was also negatively associated with FEC and environmental helminth abundance (Figure 3c,d, Table 2). Moving from the complete absence (0%) to complete presence (100%) of anorexia, the mean and variance of FEC decreased by 87.8% and 99.4%, respectively (mean: 656 vs. 5,400, variance: 4925 vs. 827,126), and for environmental helminth abundance, these two statistics decreased by 87.1% and 99.3%, respectively (mean: 9.04×10^7 vs. 6.99×10^8, variance: 9.13×10^{13} vs. 1.32×10^{16}).

Sensitivity analyses indicated that these trends remained the same when parameter values were varied (Appendix S1: Section S1, Figures S3–S5). Interestingly, when varying the maximum sustainable plant biomass (i.e., carrying capacity), we found that high anorexia prevalence (≥50%) in herbivores could prevent plant population crashes at low levels of carrying capacity (150 and 175 kg/assigned area; Appendix S1: Figure S5b). Finally, when the feedback effect of feeding rate on parasite transmission was removed, anorexia prevalence no longer influenced the mean or variance of FEC and environmental helminth abundance (Appendix S1: Figure S6, Table S2). In contrast, effects on the mean and variance of plant biomass remained (Appendix S1: Figure S6, Table S2), although the variance in plant biomass decreased by over 20% less in the absence of feedback (decline in variance from 0% to 100% anorexia prevalence: 37.7% without feedback vs. 60.0% with feedback). The decline in variance of plant biomass as anorexia prevalence increased, which was

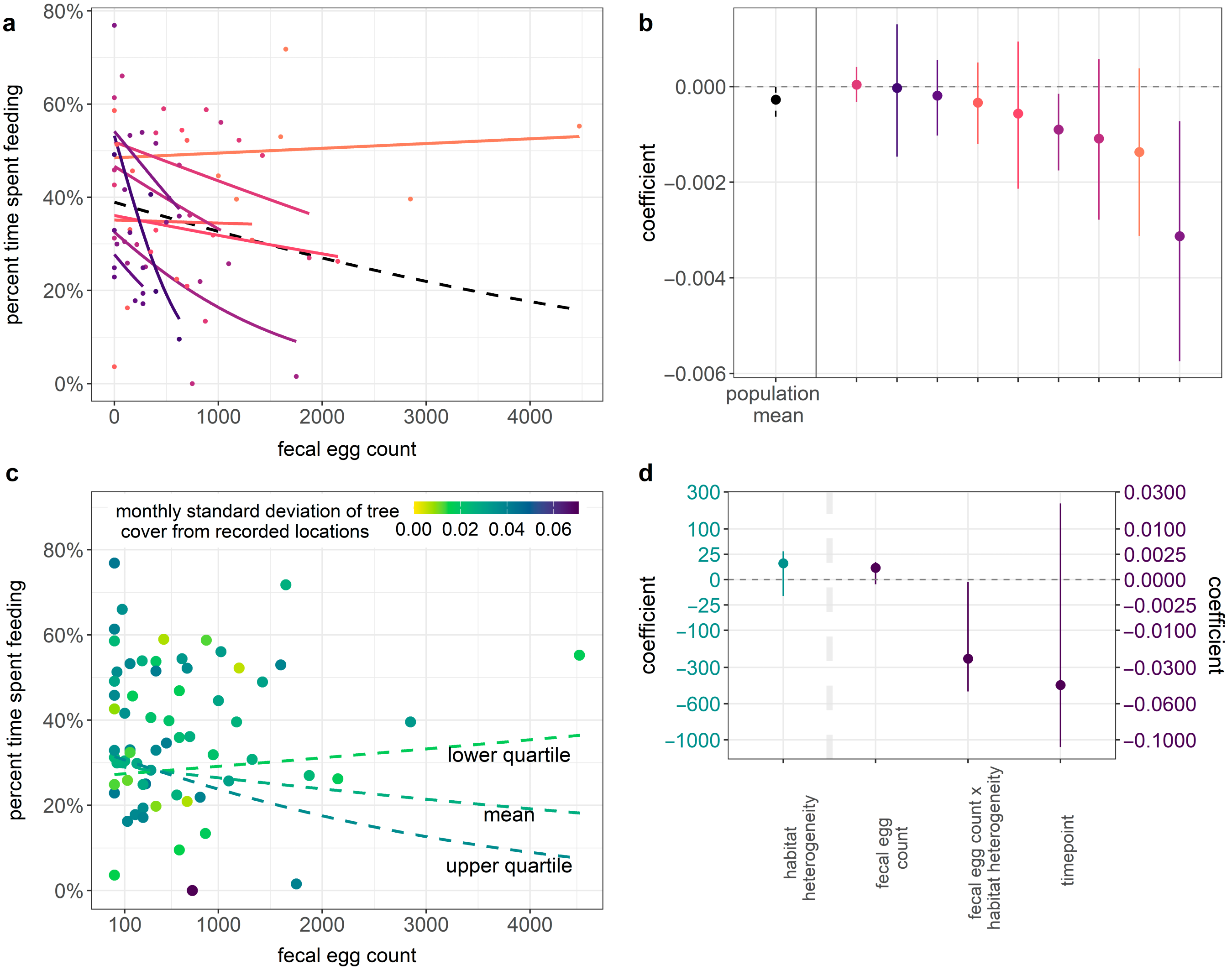

FIGURE 2 Variation in feeding responses to helminth infection. Effect of helminth burden on feeding rate in female Grant's gazelle (*Nanger granti*) without (a, b) and with (c, d) modulation effect by habitat heterogeneity: (a) Proportion of time spent feeding as related to fecal egg count, showing best-fit lines for the population (dashed) and individuals (solid) predicted by a generalized linear mixed model and individual generalized linear models. (b) Coefficients and 95% CIs for the effect of fecal egg count on feeding time estimated for the population (dashed) and individuals (solid). In addition to the population coefficient (left), one column represents a coefficient for one individual. (c) Feeding time as related to fecal egg count, with lines showing different values of SD of percent tree cover (habitat heterogeneity). Lines include the upper quartile (75% quantile), mean, and lower quartile (25% quantile) of monthly SD of tree cover across observations, predicted by a generalized linear mixed model. (d) Coefficients and 95% CIs for the effects of SD of tree cover (habitat heterogeneity), fecal egg count, their interaction, and a covariate, timepoint, on feeding time. For plot (d), *y*-axes on the left and right are for habitat heterogeneity (green) and other variables (purple), respectively, and these axes are square-root transformed for better visualization.

strengthened in the presence of feedbacks, suggests that both the presence of anorexia and feedback between feeding rate and parasite transmission contributed to low levels of variance in plant biomass.

Variation in anorexia magnitude

Our simulation models showed that individual variation in anorexia magnitude increased helminth infection compared to the scenario when the magnitude of anorexia was constant, but did not significantly affect plant biomass. When the magnitude of anorexia changed from constant to variable, neither the mean nor variance of herbivore feeding time and plant biomass changed significantly (Figure 4a,b, Table 2). Specifically, the mean and variance of plant biomass were 158.41 kg and 6.89 kg^2 at variable magnitude compared to 158.37 kg and 8.62 kg^2 at constant magnitude. On the other hand, when the magnitude of anorexia changed from constant to variable, there

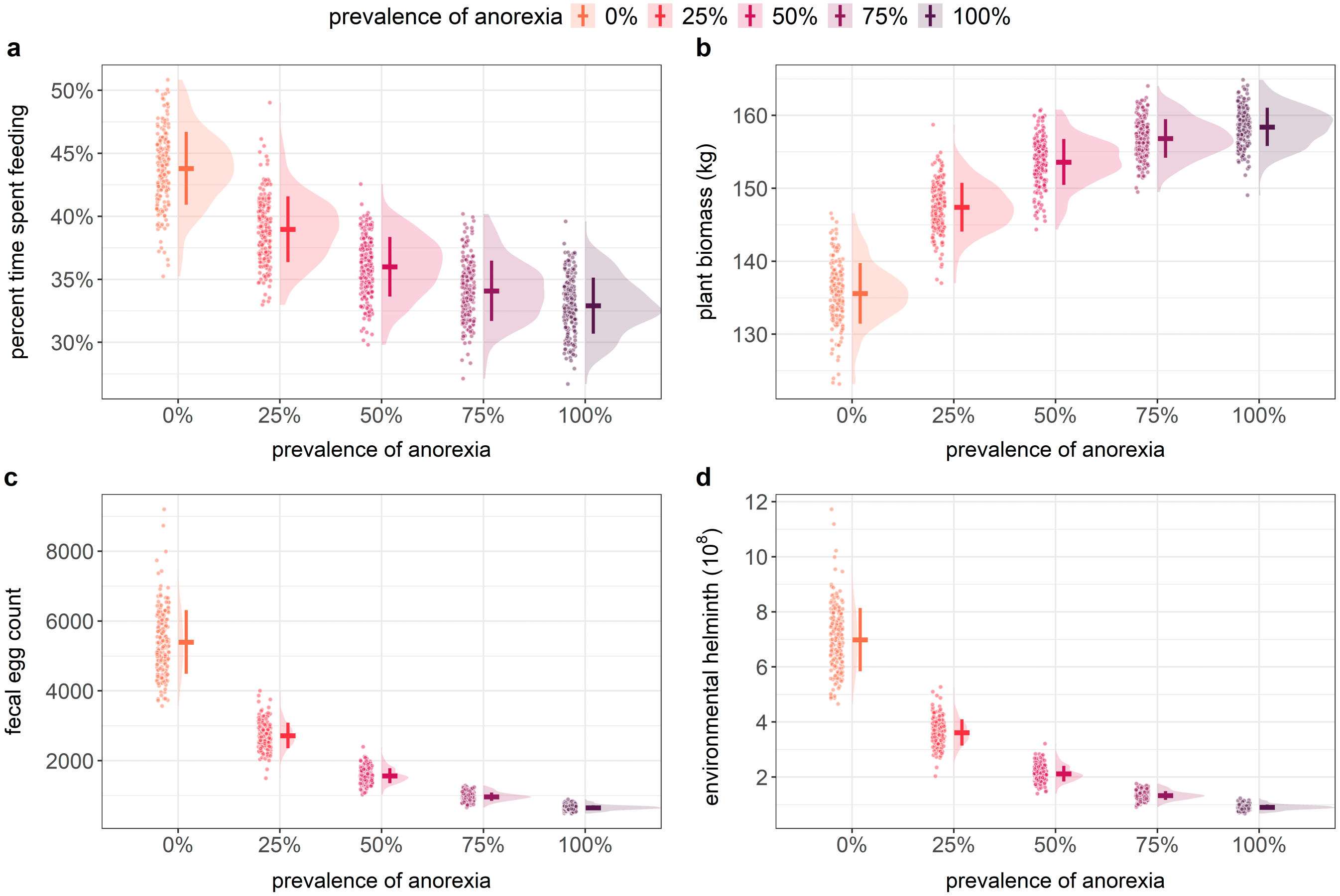

FIGURE 3 Simulation results with varying anorexia prevalence. Two hundred replicate simulations run for five anorexia prevalence scenarios (0%, 25%, 50%, 75% and 100%). Results on the 360th day are shown for: (a) average herbivore individual feeding time, (b) plant biomass, (c) average herbivore fecal egg count, and (d) environmental helminth abundance. Each graph includes a density distribution (violin plot) and a bar showing mean (tick) ± SD (upper and lower lengths) on the right, and data points representing replicates on the left.

was a 26% increase in both mean FEC and environmental helminth abundance (FEC: 656 vs. 520; environmental helminth abundance: 9.04×10^7 vs. 7.16×10^7; Figure 4c,d). At the same time, variance in helminth abundance increased by nearly 500% both within the host and in the environment (FEC: 4925 vs. 828; environmental helminth abundance: 9.13×10^{13} vs. 1.50×10^{13}; Figure 4c,d).

DISCUSSION

Variation in host behavior and its effects on population-level transmission dynamics are well documented (VanderWaal & Ezenwa, 2016). However, the role of similar variation in shaping community and higher level outcomes of host–parasite interactions is underexplored. In this study, we documented individual differences in feeding responses to helminth parasitism in a wild herbivore population and evaluated the potential influence of this variation on trophic interactions using individual-based simulation models. First, our empirical data revealed that there was individual variation in anorexia presence and magnitude. Second, our models showed that variation in anorexia prevalence (i.e., proportion of individuals experiencing anorexia) affected both average and variance in plant biomass, while there was no effect of variation in anorexia magnitude (i.e., size of the anorexia effect) on plant biomass. Third, we found that both types of anorexia variation had strong feedback effects on helminth abundance, with increasing anorexia prevalence decreasing parasite abundance and variance and increasing variation in anorexia magnitude increasing parasite abundance and variance. In combination, our results suggest that individual differences in herbivore feeding responses to parasites can trigger trophic cascades that affect producer biomass, parasite abundances, and the stability of both.

Helminth-associated reductions in feeding have been documented in a range of domestic and wild herbivore species (Koltz et al., 2022). However, despite an overall

TABLE 2 Results of permutation tests used for comparing means and variances between or among different simulation scenarios.

Comparison variable	*F* statistic	*t* statistic	X^2 statistic	*p* value
Prevalence of anorexia (0%, 25%, 50%, 75%, and 100%)				
Permutation analysis of variance[a]				
Feeding time	**607.7**			**<0.001**
Plant biomass	**1651.8**			**<0.001**
Fecal egg count	**3605.6**			**<0.001**
Environmental helminth abundance	**3666.7**			**<0.001**
Permutation Bartlett's test[b]				
Feeding time			**16.8**	**<0.001**
Plant biomass			**59.35**	**<0.001**
Fecal egg count			**1381.0**	**<0.001**
Environmental helminth abundance			**1310.6**	**<0.001**
Magnitude of anorexia: variation versus constant				
Permutation Student's *t* test[a]				
Feeding time		−1.50		0.13
Plant biomass		0.14		0.89
Fecal egg count		**25.4**		**<0.001**
Environmental helminth abundance		**25.7**		**<0.001**
Permutation *F* test[b]				
Feeding time	0.79			0.086
Plant biomass	0.80			0.110
Fecal egg count	**5.95**			**<0.001**
Environmental helminth abundance	**6.10**			**<0.001**

Note: Ten thousand permutations were run to test differences. Significant differences are bolded.

[a] Comparison for means.

[b] Comparison for variances.

negative population-level association between helminth burden and feeding rate in gazelles, we found that the presence and magnitude of individual gazelle feeding responses to helminth parasitism varied considerably. This individual variation in feeding behavior was significantly modulated by habitat use, with higher heterogeneity in habitat use associated with more intense parasite-mediated anorexia. Utilizing a variety of habitats can increase refuge availability, and is a strategy some ungulates use to avoid predators (Hebblewhite & Merrill, 2009). However, an increase in refuge availability can trade off with low forage availability in refuges (Hopcraft et al., 2010; Verdolin, 2006). Moreover, the magnitude of anorexia can be amplified by poor forage quality (Van Dam, Hofs, et al., 1998; Van Dam, Van der Heide, et al., 1998). Thus, gazelles using more heterogeneous habitats potentially experience lower predation risk, but higher parasite-mediated anorexia. Alternatively, a negative association between habitat heterogeneity and feeding responses to parasitism could reflect variation in plant community composition and forage palatability across habitats (Mogashoa et al., 2021), or a high energetic cost of exploiting a variety of habitats (Bélichon et al., 1996). Indeed, both low forage quality in a plant community and high energetic costs of habitat use can lead to reduced food intake (Trevail et al., 2019; Van Dam, Hofs, et al., 1998; Van Dam, Van der Heide, et al., 1998). Irrespective of the mechanisms generating individual variation in host feeding responses to parasite infection, our data highlight the extent to which helminth infection generates variable anorexia responses among hosts.

Our simulation models, which were guided by the empirical findings in gazelle, explored the broader consequences of host feeding responses to parasite infection. Model results revealed a pronounced effect of variation in anorexia prevalence, but not variation in magnitude, on plants. Specifically, as the prevalence of anorexia in the herbivore population increased from 0% to 100%, reductions in herbivore feeding led to substantial increases in plant biomass (>16%) and more stable plant

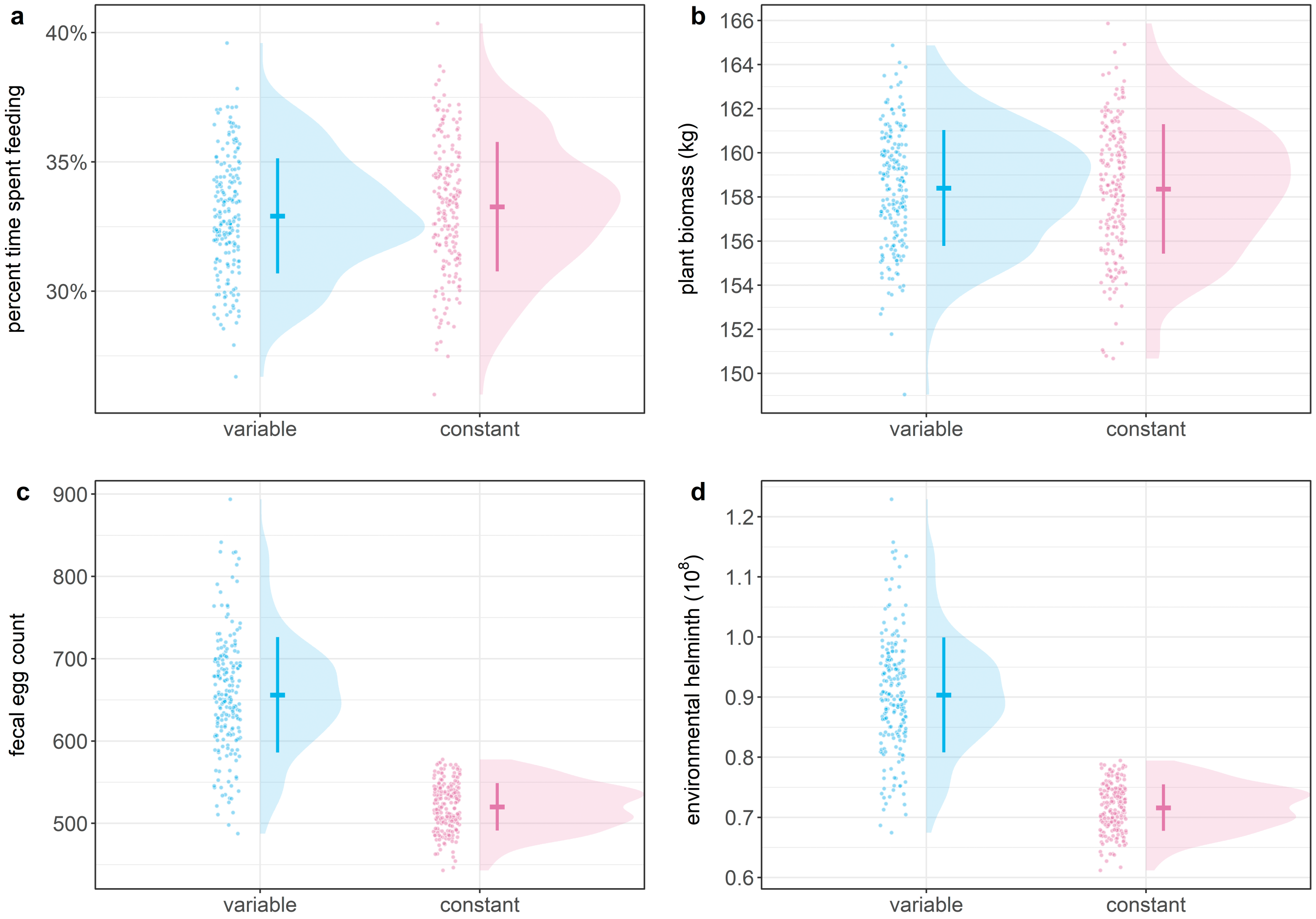

FIGURE 4 Simulation results showing different anorexia magnitude scenarios. Two hundred replicate simulations run for two scenarios where individuals had variable and constant magnitude of anorexia, respectively. Results on the 360th day are shown for: (a) average herbivore individual feeding time, (b) plant biomass, (c) average herbivore fecal egg count, and (d) environmental helminth abundance. Each graph includes a density distribution (violin plot) and a bar showing mean (tick) ± SD (upper and lower lengths) on the right, and data points representing replicates on the left.

dynamics, as reflected by a decline in the variance of plant biomass of 60%. Even when anorexia prevalence was relatively low, as in our gazelle dataset (~22%), the model (25% prevalence, see Figure 3) still produced an increase in average plant biomass of nearly 10% and a decrease in biomass variance of over 30% when compared to the complete absence of anorexia. The increase in plant biomass in our model in the presence of anorexia is consistent with prior research on parasite-induced trait-mediated trophic cascades (Bernot & Lamberti, 2008; Harjoe et al., 2022; Koltz et al., 2022; Morton & Silliman, 2020; Wood et al., 2007). In addition, our results extend this past work by showing that ecologically relevant levels of variation in the prevalence of parasite-mediated anorexia in herbivores can influence the degree of fluctuation in plant biomass. Plant biomass variance, as quantified in our model, can be translated as spatial or temporal variation in producer biomass (Lévesque et al., 2010). Consequently, reduced variance indicates less spatial or temporal fluctuations in producer population dynamics in response to herbivory. This result implies that parasite-mediated anorexia can act as a stabilizing force in plant-herbivore systems, a finding that is congruent with the results of a recent deterministic model of plant-caribou-helminth interactions showing that parasite-mediated anorexia stabilized producer–herbivore population dynamics (Koltz et al., 2022).

For parasites, as anorexia prevalence increased and variation in anorexia magnitude decreased in our models, declines in helminth abundance both within hosts and in the external environment were even more pronounced than changes in plant biomass. The declines in host helminth burden with increasing anorexia prevalence align with the hypothesis that helminth-mediated anorexia hinders transmission and protects hosts from more severe infection (Hite et al., 2020; Kyriazakis et al., 1998; Rao et al., 2017). In our models, this effect emerged, in part, because of the inclusion of a feedback effect linking host feeding rate to parasite ingestion. This negative feedback also enhanced the stability of plant biomass, as reflected by a ~20% decrease in plant biomass variance across levels of anorexia prevalence when the feedback was present compared to absent (Figure 3b vs. Appendix S1: Figure S6b). This observation that negative feedback between host behavior and parasitism contributes to stability in host–parasite relationships may be common (Hawley & Ezenwa, 2022; Sih et al., 2015; Silk & Fefferman, 2021). Intriguingly, our models suggest that such stabilizing effects of host behavior–parasite feedbacks may extend beyond host and parasite populations to other members of the ecological community via trophic cascades.

In combination, our results highlight the variable nature of both host behavioral responses to parasitism and parasite-induced trophic interactions. First, we detected high levels of variation in herbivore feeding responses to helminth parasitism. Second, by incorporating variation and stochasticity in herbivore responses to infection into simulation models, we identified a dampening effect of anorexia-triggered trophic cascades on variability in producer biomass. Importantly, the reduced variation in producer biomass suggests that fluctuating amplitudes in spatial or temporal plant dynamics can be mitigated by parasite-mediated anorexia in herbivores. Indeed, ecological models suggest that reduced stochastic variability in population dynamics can prevent population crashes (Johnson et al., 2022), and we observed this phenomenon in our models at low levels of plant carrying capacity (Appendix S1: Figure S5). It is important to note that our models make several simplifying assumptions. For example, we assumed a linear relationship between feeding rate and ingestion of plants and parasites. Other relationships (e.g., Type II or Type III functional responses) could result in more complex dynamics, as has been observed for predator–prey interactions (Bairagi et al., 2007; Kalinkat et al., 2013); however, we believe that linear relationships generate sufficient variation to draw insight. Another key assumption was that the magnitude of parasite-mediated anorexia is consistent over time within an individual. While within-individual variation in anorexia is plausible (e. g., associated with changes in habitat use), incorporating this form of variation into our models was beyond the scope of the current study. More generally, our work represents a first step toward accounting for variation in host responses in the context of parasite-induced trophic cascades. However, our models were guided by data derived from females of a single herbivore species, and given intriguing evidence that males in the same host population did not show feeding changes associated with helminth parasitism (Sabey et al., 2024), a deeper understanding of variation in parasite-mediated anorexia is needed across herbivore systems to fully appreciate the relevance of such variation for trophic cascades, plant and parasite dynamics. Despite the limitations, our study ties empirical evidence of variation in host behavioral responses to parasitism to theoretical support for parasite-induced trophic cascades on plants, emphasizing a potentially key role for parasites in stabilizing plant–herbivore systems.

AUTHOR CONTRIBUTIONS

Yen-Hua Huang and Vanessa O. Ezenwa conceived the research ideas and designed the study. Yen-Hua Huang performed the analyses and modeling. Vanessa O. Ezenwa oversaw the empirical data collection and supervised the work. Both authors wrote the paper and approved the final manuscript.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Huang & Ezenwa, 2025) are available in Zenodo at https://doi.org/10.5281/zenodo.16579419.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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