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MYCORRHIZAL FUNGI AS DRIVERS AND MODULATORS OF ECOSYSTEM PROCESSES

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Mycorrhizal symbioses influence the trophic structure of the Serengeti

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Abstract

1. It is known that tropical grasslands such as Serengeti host large populations of arbuscular mycorrhizal (AM) fungi and that they respond to abiotic and biotic factors. It is also known that AM symbioses are important for the uptake of essential plant nutrients, which, in turn, influences the biomass and nutritional quality of herbivores and their predators. The purpose of this study was to investigate the influence of AM symbioses on the biomass of different trophic levels of an ecosystem.
2. To do this, we first measured the neutral lipid fatty acid biomarker 16:1ω5 to estimate the biomass of AM fungi in a long-term grazing exclusion experiment. Then, we used model selection of Bayesian linear regressions to infer the primary factors that influence AM fungal biomass. Using model selection of different combinations of soil characteristics, we selected the best model using the leave-one-out cross-validation information criterion. Finally, we used the Madingley model to simulate the influence of AM fungi on higher trophic levels. We combined spatially explicit information about soil phosphorus and AM fungal biomass to explore the emergent patterns of the Serengeti resulting from AM symbioses.
3. Our Bayesian analysis indicated that total soil phosphorus was the strongest predictor of AM fungal biomass, and there were significant interactions with grazing. Arbuscular mycorrhizal fungal biomass is lowest in soil where phosphorus is limited and increases with increasing phosphorus concentration. Biomass was also significantly higher in plots that were not grazed. The Madingley model indicated that nutritional benefits of AM symbioses maintain a substantial proportion of the biomass across all trophic levels.
4. *Synthesis.* Our analysis shows that inputs of phosphorus through arbuscular mycorrhizal symbioses substantially increase the ability of plants to grow and maintain nutritional quality, cascading through the biomass of consumers and predators in the ecosystem. Although they account for less than 1% of the total modelled biomass, the predicted nutritional benefit provided by arbuscular mycorrhizal fungi increased the biomass of macro-organisms in the Serengeti by 48%. When considering the management of biodiversity, future ecosystem models should account for the influence of arbuscular mycorrhizal fungi on all trophic levels.

KEYWORDS
arbuscular mycorrhizas, ecosystem function, environmental gradients, Madingley model, phosphorus, Serengeti National Park, trophic structure, ungulate grazing

1 | INTRODUCTION

Organisms that provide essential ecosystem functions are often taken for granted, and only when their functions are compromised or eliminated do we recognise and value their importance. It is easy to take arbuscular mycorrhizal (AM) fungi for granted. These fungi are hidden inside plant roots and their extensive hyphal networks in the soil are microscopic. Nevertheless, AM fungi account for a major portion of soil microbial biomass in most terrestrial ecosystems (Olsson, Thingstrup, Jakobsen, & Bååth, 1999; Zhu & Miller, 2003). More than 70% of all angiosperm families form AM symbioses (Brundrett, 2009), and these symbioses are often essential for plant nutrition (Marschner & Dell, 1994). Mycorrhizal symbioses also improve plant tolerance to drought (Augé, 2001) and resistance to pathogens (Cameron, Neal, van Wees, & Ton, 2013). Furthermore, enormous hyphal networks of AM fungi structure soils and support below-ground food webs (Antunes & Koyama, 2016). Experiments have demonstrated that AM symbioses influence plant community composition and mediate the cycling of carbon and nutrients (Johnson, Wolf, & Koch, 2003; Leake et al., 2004; van der Heijden, de Bruin, Luckerhoff, van Logtestijn, & Schlaeppi, 2016; Wubs, van der Putten, Bosch, & Bezemer, 2016). Ecosystem models may inform our understanding of the ecosystem functions provided by mycorrhizas (Johnson et al., 2006). The purpose of this study is to incorporate empirical measurements of AM fungal biomass into a recently developed General Ecosystem Model (GEM) to estimate the benefit of nutritional services provided by mycorrhizas to the Serengeti ecosystem.

Mycorrhizas often ameliorate nutrient limitation in plants and have been called *Nature's answer to the Law of the Minimum* because fungi are capable of acquiring soil resources that are inaccessible to plant roots (Read, 1991). Arbuscular mycorrhizas are often critical to plant phosphorus nutrition, especially in ecosystems with moderately weathered soils (Lambers, Raven, Shaver, & Smith, 2008). This study quantifies the importance of phosphorus inputs from AM fungi to the biomass of an entire ecosystem. Plant taxa vary in the degree to which they depend upon mycorrhizas; but in general, AM symbioses are essential for the nutrition of tropical plants, and warm season grasses are often highly dependent on mycorrhizas, acquiring up to 90% of their phosphorus requirements from AM fungi (Hartnett & Wilson, 2002; van der Heijden, 2003; Wilson & Hartnett, 1998). One can expect that the evolution of tropical grassland ecosystems that support large herds of ungulate grazers would be very different without nutritional symbioses of all kinds. Below-ground symbioses among roots, mycorrhizal fungi and diazotrophic prokaryotes relieve resource limitation in plants. Above-ground symbiotic communities in mammalian rumens convert low-quality forage into a nutritious diet (Hooper, Midtvedt, & Gordon, 2002). This study focuses on the influence of arbuscular mycorrhizas on the total biomass of different trophic levels in the Serengeti grassland.

Mycorrhizas function within a complex web of biotic and abiotic interactions that give rise to emergent patterns, such as animal migration. For example, higher soil phosphorus in the southern Serengeti may be the cause of migratory patterns where ungulates move to the nutrient-rich plants in the south for the gestational period (Murray, 1995). The difficulty in untangling this web of interactions and feedbacks has led ecologists to develop models that aim to simulate the flow of matter and energy across trophic levels through entire ecosystems (Lindeman, 1942; Mace, 2013; Purves et al., 2013). Ecosystem models are coming into favour with scientists interested in understanding holistic processes, and mycorrhizas are beginning to be incorporated in these models (Brzostek, Rebel, Smith, & Phillips, 2016). The Madingley model is a spatially explicit ecosystem model in the early stages of development that provides the opportunity to simulate the trophic structure of the Serengeti ecosystem with and without the effects of AM symbioses (Harfoot et al., 2014).

Because the relationships between plants and AM fungi have co-evolved in the Serengeti for millions of years with minimal human disturbance, we assume that the patterns of AM fungal biomass in relation to resource availability will provide a useful context for exploring the effects of AM fungi on trophic structure of grassland ecosystems. The biomass and composition of the plant community is strongly influenced by gradients in rainfall and soil nutrients (Anderson, Ritchie, & McNaughton, 2007; McNaughton, 1988). Ngorongoro volcanic highlands in the southeast generate a rain shadow and also deposit mineral-rich ash over highly weathered soils to create a precipitation gradient superimposed on an antiparallel edaphic gradient, with soil phosphorus more than 10 times higher in the south than in the north (Anderson & Talbot, 1965; Ruess & Seagle, 1994). Previous studies have shown that AM fungi are influenced by these rainfall and edaphic gradients (Antoninka, Ritchie, & Johnson, 2015; McNaughton & Oesterheld, 1990). Also, there is evidence that the growth of both AM fungi and plants are phosphorus limited, particularly in the north where there has been little or no input of volcanic ash (Propster & Johnson, 2015). Consequently, the standing crop of AM fungal hyphae is positively correlated with soil phosphorus availability (Antoninka et al., 2015), which conforms with the expectations of the model proposed by Treseder and Allen (2002) (Propster & Johnson, 2015; Teste et al., 2016). In this model, AM fungal abundance is predicted to have a quadratic relationship with soil nutrients, where abundance is positively correlated with the availability of limiting soil nutrients and negatively correlated with soil nutrients when plant hosts are no longer nutrient limited (Treseder & Allen, 2002).

The purpose of this study is to (1) measure the standing biomass of AM fungi in the Serengeti and compare it to biomass estimates of

plants and animals, (2) estimate the influence of grazing on the standing biomass of AM fungi, and (3) estimate the importance of AM fungi to primary and secondary production in the Serengeti ecosystem. To do this, we measured the biomass of AM fungi and environmental variables inside and outside fences that are part of a long-term grazing exclusion experiment (Anderson et al., 2007). Bayesian linear models were used to examine the relative importance of environmental variables and grazing on the biomass of AM fungi across the environmental gradients. These empirical data were used in a spatially explicit model to quantify the influence of AM fungi on the biomass of plants and herbivorous, omnivorous and carnivorous animals. We predicted that phosphorus inputs from AM fungi maintain a large portion of the biomass in the Serengeti, including most of the iconic migratory herds and large predators.

2 | MATERIALS AND METHODS

2.1 | Study sites

In 1999, a long-term grazing experiment was established in the Serengeti National Park, Tanzania, in which six plots (4 × 4 m) were arranged linearly at eight different sites (Anderson et al., 2007). Due to the rain shadow effect from the Ngorongoro highlands, mean annual precipitation (MAP) is lowest in the south and highest in the north (498–779 mm; Table 1), and volcanic inputs and different rates of weathering generate an antiparallel soil phosphorus gradient ranging from 0.01% in the north to 0.56% in the south (Table 1 and Figure 1a). At each site, three pairs of plots in closest proximity were randomly assigned to be normally grazed or fenced with 2-m tall chain-link that effectively excludes all ungulate grazers (Anderson et al., 2007). Originally, eight sites were set up for this long-term study; however, two sites in the western corridor were omitted because the fences at one of the sites had been lost to theft.

Soil organic matter is highest at the Barafu site (BRS; 16.21%) and lowest at Balanites (BAL) and Togora Plains (TOG), with 6.87% and 7.23%, respectively (Table 1). Total soil nitrogen is not correlated with the environmental gradient, and all sites had statistically similar nitrogen concentrations, except BRS and Soit Olowotonyi (SOT) were different (Table 1). Phosphorus was highly correlated with calcium (r^2 = .97) and iron (r^2 = .94) concentrations (Table 1). Sites BRS and SOT were mostly silty (55.24% and 51.75%), while all other sites were sandy (between 47.28% and 67.21%; Table 1).

2.2 | Sample collection

During the wet season in May 2012, six sites within the long-term experiment were sampled (Table 1; Figure 1). Composite rhizosphere soil samples (n = 36) were collected from holes *c*. 30 cm deep that were created when digging up roots of grasses used in a different study (Davison et al., 2015). To account for variable plant community composition across the six sites, soil samples were collected beneath two dominant plant species (*Digitaria macroblephara* and *Themeda triandra*). To minimise the influence of compaction and trampling from

TABLE 1 Locations and MAP of the six study sites in the Serengeti National Park. Letters to the right of soil characteristics indicate Tukey's honest significance, $p < .05$

Sites	Site code	Latitude (S)	Longitude (E)	MAP (mm)	pH	Total N (%)	Total P (%)	SOM (%)	Clay (%)	Silt (%)	Sand (%)	Total Ca (%)	Total Fe (%)
Barafu	BRS	2°42′0″	35°12′0″	498	7.62a	0.26a	0.56a	16.21a	24.76a	55.24a	20.00d	1.86a	2.21a
Soit Olowotonyi	SOT	2°36′0″	35°9′0″	537	7.80a	0.11b	0.46b	11.79b	24.95a	51.75a	23.30d	1.61b	1.77b
Togora Plains	TOG	2°12′30″	35°6′0″	676	6.42bc	0.15ab	0.09d	7.23d	12.79b	39.93b	47.28c	0.25c	0.67c
Balanites	BAL	2°4′30″	35°6′0″	710	6.67bc	0.20ab	0.05e	6.87d	9.74bc	30.38cd	59.88ab	0.19c	0.60c
Klein's Camp West	KCW	1°52′0″	35°11′30″	766	6.91b	0.22ab	0.01f	10.23bc	8.02c	24.77d	67.21a	0.21c	0.62c
Kuku Hills	KUH	1°47′30″	35°15′0″	779	6.29c	0.13ab	0.01f	7.76cd	10.37bc	34.78bc	54.85bc	0.18c	0.44c

MAP, mean annual precipitation; SOM, soil organic matter.

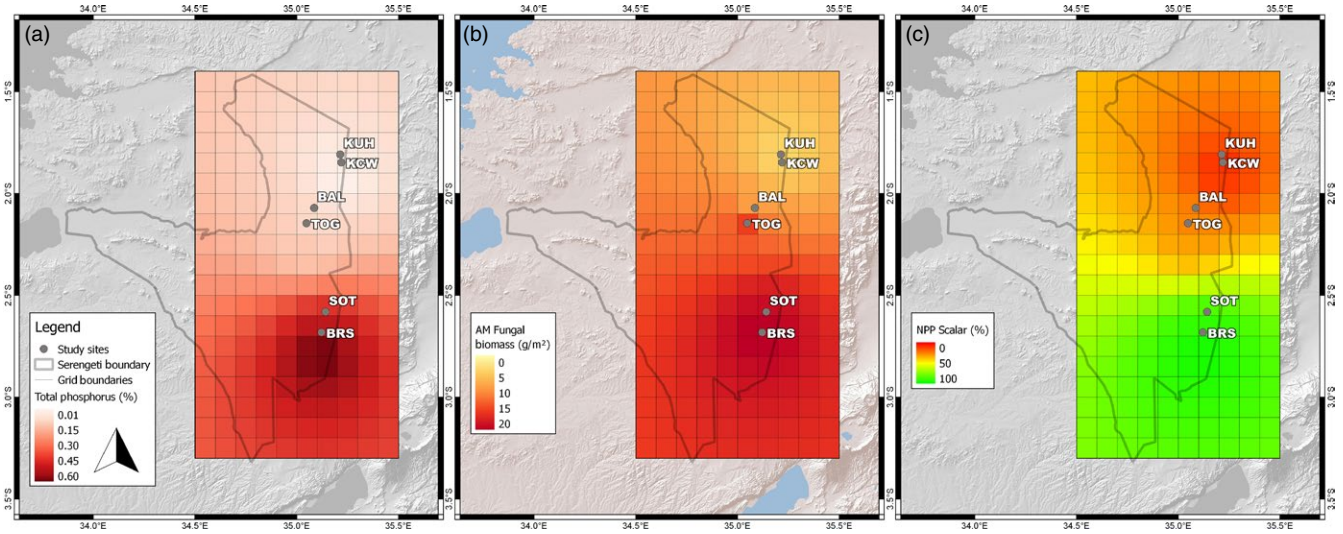

FIGURE 1 (a) Serengeti National Park soil phosphorus gradient ranging from high percent soil phosphorus (red) in the south to low percent phosphorus (white) in the north. (b) Arbuscular mycorrhizal (AM) fungal biomass (g/m^2), to a depth of 1 metre, based on the concentration of neutral lipid fatty acid 16:1ω5, which is a signature for AM fungi. (c) Changes to net primary productivity and plant biomass with no phosphorus acquisition benefits from AM fungi. In grid cells with high levels of plant available soil phosphorus, loss of AM fungi will have almost no effect on the total plant biomass (green). In contrast, AM fungi are essential in northern sites where phosphorus is very limiting, and without mycorrhizal symbioses, plants would produce almost no biomass (red). Sites included in this study are Kuku Hills (KUH), Klein's Camp West (KCW), Balanites (BAL), Togora (TOG), Soit le Motonyi (SOT) and Barafu (BRS). Madingley model grid boundaries (0.1° × 0.1°) display the resolution of the ecosystem model [Colour figure can be viewed at wileyonlinelibrary.com]

grazers, samples were collected below the soil surface. A Bayesian analysis verified that there was no significant difference in soil bulk density between grazed and ungrazed treatments (CI = −0.203, 0.049). Within 6 hr of collection, soils were dried for 48 hr using a solar oven which reached a maximum temperature of 90°C. After 2 weeks, the dry samples were transported to the laboratory and frozen for long-term storage (USDA-APHIS Permit number: P526P-15-00008).

2.3 | Soil analyses

To determine which factors predict the abundance of AM fungi, we analysed soil samples for nutrient concentrations of commonly influential soil characteristics. Frozen soil samples were dried at 103°C and sieved (<2 mm). Soil organic matter was measured using loss on ignition, 2 g subsamples were weighed, heated to 550°C for 24 hr in a Lindberg HB muffle furnace (Lindberg/MPH, Riverside, MI 49084) and then reweighed (Heiri, Lotter, & Lemcke, 2001). Soil pH was measured potentiometrically in a 1:2.5 water:soil paste at the Soil Science Laboratory of Sokoine University of Agriculture in Morogoro, Tanzania (Klute, 1986). To measure total phosphorus, calcium and iron, 0.3 g subsamples were ground and digested in 7 ml concentrated nitric acid and 3 ml 30% hydrogen peroxide in Milestone 900 Microwave Digestor (Ethos Inc., Bristol, UK). Samples were digested for 20 min and reached a maximum temperature of 425°C. Total phosphorus converted to orthophosphate was quantified via colourimetry (Grimshaw, 1987) on a QuikChem 8000 Series FIA+ (Lachat Instruments, Milwaukee, WI, USA) using QuikChem Method 10-115-01-1-A. Total iron and calcium were measured on a AAnalyst 100 Atomic Absorption Spectrophotometer (Perkin Elmer, Waltham, MA, USA). Samples were compared to in-house standards and external standards produced by Ricca Chemical Company (Arlington, TX, USA) and Hach Company (Loveland, CO, USA).

To measure soil texture, we determined particle size via laser diffraction (Beuselinck, Govers, Poesen, Degraer, & Froyen, 1998). Undried, unsieved frozen soil samples were suspended in water and analysed on a LS 13 320 Series Laser Diffraction Particle Size Analyzer (Beckman Coulter, Brea, CA, USA). Particle sizes were grouped according USDA soil texture classification. To standardise for variable densities across plots, our measurements of soil organic matter, soil texture, total phosphorus, nitrogen, calcium and iron were adjusted by bulk density. Soil bulk density and total soil nitrogen were obtained from previous analyses of soil from the same plots (Antoninka et al., 2015).

2.4 | Neutral lipid fatty acid analysis

To measure AM fungal biomass, we performed a neutral lipid fatty acid (NLFA) assay, which is a common measure of AM fungal abundance (Olsson, Bååth, Jakobsen, & Söderström, 1995). Samples were freeze-dried and finely ground with a mortar and pestle, and 5 g was mixed with a phosphate buffer, methanol and chloroform. The soil-solvent mixture was separated by centrifugation and then decanted with 1:2 mix of chloroform and methanol. Phosphate buffer was added and left for phase separation to occur overnight, and then the chloroform layer containing the lipids was recovered and reduced by nitrogen flow at 50°C. Lipids were separated into neutral lipids, glycolipids and phospholipids by solid-phase extraction by eluting with chloroform, acetone and methanol, respectively. Lipids were hydrolysed and methylated. The methylated fatty acids were

extracted with hexane and evaporated under nitrogen at 37°C. The NLFA analysis was performed using an Agilent 7890A gas chromatograph with an Agilent 5975C series mass selective detector. The NLFA biomarker 16:1ω5 was used to estimate AM fungal biomass (Olsson et al., 1995), and NLFA data are reported as percent of the total mole fraction. Total AM fungal biomass of each sample was calculated from NLFA concentrations according to Olsson and Johansen (2000). One sample was removed from further analyses due to methodological errors.

Biomass of AM fungi (g/m^2) to a depth of 1 m was calculated from the NLFA measurements. NLFA concentrations in soil samples (nmol/g) were converted to biomass based on the molar mass of tripalmitin and average percent NLFA of AM fungal tissue (36.3%, van Aarle & Olsson, 2003). Total AM fungal biomass was then estimated to the top metre of soil at each site. Arbuscular mycorrhizal fungal biomass was assumed to decrease exponentially with depth, similar to host plant biomass measured in previous studies (Antoninka et al., 2015; McNaughton, Banyikwa, & McNaughton, 1998). All biomass estimates were adjusted by soil bulk density (Antoninka et al., 2015).

2.5 | Statistical analyses

To determine significant differences in environmental variables among sites, a Tukey's honest significance test was performed on the results of an ANOVA using R version 3.4.1 (Table 1). Many of the environmental variables were highly correlated, so to reduce collinearity, a principal component (PC) analysis was performed on MAP, pH, iron, calcium, sand, silt and clay using the "prcomp" function in R. Principal component axis one explained 87.8% variation and represented long-term influence of volcanic ash deposits from the Ngorongoro highlands on soil characteristics (clay = 0.40, silt = 0.37, sand = −0.39, pH = 0.33, iron = 0.38, calcium = 0.39, MAP = −0.39). With 8.1% explained variation, the second axis (PC2) was largely influenced by pH (−0.70), silt (0.51) and sand (0.38). The third axis was mainly iron (−0.66) and pH (0.58) with 2.2% variation. For all three axes, undescribed variables had a loading of less than 0.30. The first three axes were included in all subsequent analyses (cumulative variation explained = 98.1%).

To determine the best linear estimate of AM fungal biomass, model selection was performed on all combinations of linear and categorical variables. Predictors included phosphorus, soil organic matter, soil nitrogen, net primary productivity (NPP), the first three PC axes and grazing treatment. Phosphorus was predicted to have a quadratic relationship with AM fungal abundance (Propster & Johnson, 2015; Treseder & Allen, 2002), so our model selection included a squared term for phosphorus. Model selection also included predictors variables for interactions between grazing and linear predictors (17 total predictor variables; n = 131,071 models). All continuous variables were standardised with a mean (M) of 0 and standard deviation (SD) of 1. Bayesian models with random effects for site were performed using the "stan_glmer" from the "rstanarm" package (version 2.15.3; Stan Development Team, 2017). All models used three chains with default parameters (family = Gaussian, prior = normal, iterations = 2,000). To determine the best model, the leave-one-out cross-validation information criterion (LOOIC) of each model was compared, where a lower LOOIC indicates a model with better fit and lower error. From the top 20 models (LOOIC between 255.61 and 257.04), the best model was selected by choosing the model with the least parameters without collinear variables (r^2 > .65). The best model converged for all monitored variables (Rhat < 1.01). Plant species richness is significantly lower in our ungrazed plots (Anderson et al., 2007), so to determine if plant community composition is important in predicting AM fungal abundance, we performed an additional Bayesian linear mixed effect model that included plant species richness. However, including plant species richness in our best model did not improve our linear model predictions (LOOIC increased by 2.7, resulting species richness credible interval = [−5.3, 5.6]).

2.6 | Madingley model

To quantify the biomass of plants and animals in the Serengeti, we used the Madingley model, which is a GEM capable of representing macro-organisms within entire ecosystems at regional to global scales (Purves et al., 2013). To test the influence of AM fungi on the trophic structure of the ecosystem, a manipulated terrestrial carbon model was nested within the Madingley model. By explicitly representing key biological and ecological processes for both plants and animals (see Harfoot et al., 2014 for further details), this novel modelling approach allows an examination of possible ecosystem-wide transformations as a result of two contrasting scenarios within the Serengeti: (1) a model with AM fungi (default) and (2) a model without the effects of AM fungi on plant growth.

In the Madingley model, NPP is calculated by either temperature or precipitation, whichever is most limiting (Harfoot et al., 2014 for further details). This first-order approximation of plant growth subsequently drives the spatial and temporal differences in the biomass of heterotrophic populations. For comparison, a Serengeti Madingley model with AM fungi was performed with default settings (hereafter referred to as "With AM"). Madingley uses broad ecological models to predict plant biomass where benefits from AM fungal phosphorus are implicit in the model because mycorrhizal symbioses are essential to obtaining the predicted plant biomass. To quantify the effects of AM fungi on the Serengeti ecosystem, a raster was created to represent the percent change in plant biomass with no mycorrhizas ("Without AM"). We used only AM biomass measurements from samples without grazing exclosures. The nutritional benefit of AM fungi varies across the soil phosphorus gradient and is highest in soils from the north and lowest in soils from the south (Propster & Johnson, 2015). It is difficult to sufficiently sterilise soil in the Serengeti to measure plant growth in the absence of AM fungi and quantify their influence on plant biomass, so as a substitute, we used empirical measurements of the growth of *Andropogon gerardii* with and without AM symbioses in soils from Konza Prairie, Kansas. *Andropogon* is a C_4 grass in the same taxonomic tribe as *Themeda*, a dominant grass species in our plots throughout the Serengeti. Konza soil is similar to Serengeti

soil in the north with a pH between 6 and 7, and low available phosphorus (18.5 mg/kg available PO_4^{3-} in Konza, 5.66 mg/kg available PO_4^{3-} in the northern Serengeti; Johnson, Wilson, Bowker, Wilson, & Miller, 2010; Propster & Johnson, 2015). *Andropogon gerardii* grown with AM fungal symbionts in Konza soil grew 20 times larger than plants without AM fungi (Johnson, Wilson, Wilson, Miller, & Bowker, 2015). Based on experimental removal of AM fungi from *A. gerardii* grown in soil from Konza, a conservative estimate of 10% normal growth (i.e. 90% reduction in vegetation biomass without AM symbioses) was used for the lowest phosphorus soils in our models. Values of phosphorus and PC2 were calculated using an inverse distance weighted interpolation (QGIS 2.18.9) for all 0.1° grid cells with a rectangular boundary approximately covering the Serengeti grassland (1.4°S, 3.3°S, 34.5°E and 35.5°E). Using coefficients from the best Bayesian linear fixed-effects model, AM biomass was predicted for all grid cells. For each grid, AM fungal biomass was converted to percent change in NPP by scaling biomass to between 10% and 95%. Plant growth benefits from phosphorus acquired by AM fungal partners are greatest in phosphorus-limited ecosystems (Lambers et al., 2008). Because Madingley models predict NPP solely from precipitation and temperature and do not yet incorporate nutrient limitation, we scaled NPP by the biomass of AM fungi, which is highly correlated with phosphorus concentration (Antoninka et al., 2015). To estimate NPP, the nested terrestrial carbon model in Madingley was multiplied by a percent change layer for "Without AM," simulating plant biomass without the benefits of AM fungal partners under grazed conditions. By changing NPP based on these conversions, changes to the modelled biomass of plants, herbivores, omnivores and carnivores residing within the Serengeti region were compared. For both scenarios, five simulations were run for 100 years with monthly time steps. To ensure biomass estimates represented populations at equilibrium and minimised potential noise from random simulations, the last 5 years of each replicate simulation were averaged. All models used default Madingley parameters for animal cohorts (Harfoot et al., 2014).

The Madingley model has not yet incorporated nutrient cycles into biomass predictions. Therefore, we modified the "Without AM" model to predict the effects of plant nutritional quality on the biomass of animals, which we refer to as our "Predicted" model. Because AM fungi have been shown to consistently increase tissue phosphorus concentration in their host plants across a phosphorus gradient (Johnson, 1998; Johnson et al., 2015), the effects of decreased nutritional quality of plant material in the absence of mycorrhizas were estimated to decrease animal biomass by an additional 25% across the entire Serengeti. A reduction in biomass resulting from less phosphorus assumes that ungulates in the Serengeti are at the minimum level of phosphorus intake required for maintenance, which is the case for pregnant wildebeest in the northern ranges (Murray, 1995). For example, in the Konza Prairie, plants in soil with no AM symbioses contain half the tissue phosphorus in addition to lower biomass (Johnson et al., 2010). Therefore, herbivores would have to eat, on average, 25% more plant material to meet nutritional requirements, reducing their population and the populations of higher trophic levels. Plant biomass is unchanged in our "Predicted" model because its change is already accounted for in the "Without AM" model. The additional adjustment in the "Predicted" model simply accounts for the response of animals to a change in the stoichiometry of plant tissues.

3 | RESULTS

Based on the NLFA biomarker 16:1ω5, the estimated biomass of AM fungi (g/m^2) averaged 11.9 (±3.53) and ranged between 3.9 and 17.6 to a depth of 1 m (Figure 1b). Average biomass of AM fungi varied from 9.2 (±2.6) nmol/g at Kuku Hills (KUH) to 63.5 (±14.1) at SOT (Figure 2). Model selection indicated that grazing treatment, phosphorus and the second principal component axis (PC2) were important predictors of AM fungal biomass in the Serengeti (Table 2). Statistics for the means and 95% credible intervals of the best model are reported (Table 2). PC2, mainly pH, sand and silt, was in the best model, yet was not a significant predictor of AM fungal biomass (CI = −8.5, 2.8). There was no significant difference between the intercepts of each treatment; however, interactions with phosphorus and grazing treatment were significant (phosphorus CI = 59.7, 370.7, and phosphorus^2 CI = −630.3, −114.5).

Two scenarios were modelled to examine the effects of AM fungi on the trophic structure of the Serengeti. A Madingley model without any modifications was used to represent a Serengeti with the benefits of mycorrhizal symbioses ("With AM"). A hypothetical Serengeti without the benefits of AM symbioses was simulated from the estimated change in plant biomass for normally grazed experimental plots ("Without AM"). The "Without AM" model had an average reduction in NPP of 53.8%. The capacity for NPP with no AM symbioses is visualised for all grid cells in the study area (Figure 1c). In the "With AM" model, mean total plant biomass (g/m^2) predicted by Madingley was

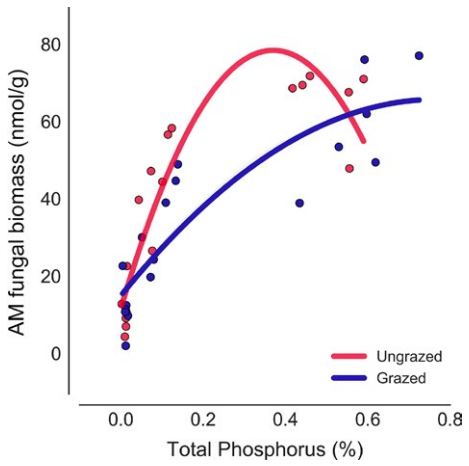

FIGURE 2 The best Bayesian linear model estimate for mean total arbuscular mycorrhizal (AM) fungal biomass in soil for grazed and ungrazed treatments. Biomass is based on the neutral lipid fatty acid 16:1ω5, a signature for AM fungi. Coefficients were determined for the best model based on the leave-one-out cross-validation information criterion. Lines represent predicted AM fungal biomass, and circles represent actual values [Colour figure can be viewed at wileyonlinelibrary.com]

TABLE 2 Results of the Bayesian linear fixed-effects model selected to predict arbuscular mycorrhizal fungal biomass. Data were not standardised for this table. *M*, *SD* and a 95% credible interval (2.5% and 97.5%) for posterior distribution are reported. Ungrazed coefficients are reported as the difference from grazed coefficients

Parameter	*M*	*SD*	2.5%	97.5%
Grazed	14.6	4.4	6.0	23.3
P	145.7	53.7	34.0	246.8
PC2	−2.9	2.9	−8.5	2.8
P^2	−109.3	81.4	−265.7	54.7
Ungrazed	−1.9	6.3	−14.4	10.5
P:Ungrazed	212.1	79.3	59.7	370.7
P^2:Ungrazed	−372.1	131.6	−630.3	−114.5

P, phosphorus (% of total soil); PC2, the second principal component axis.

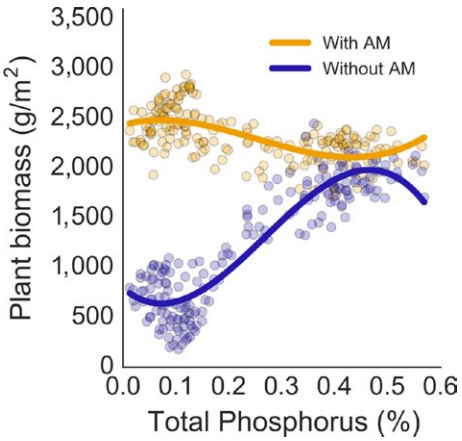

FIGURE 3 Average plant biomass (g/m^2) of five replicate Madingley simulations for 10 grids cells (0.1° × 0.1°) vs. phosphorus values for each grid. The Madingley model without modifications ("With arbuscular mycorrhizal [AM]") was used as the normal Serengeti model. Modifications to the Madingley model were performed to simulate the removal of arbuscular mycorrhizal fungi ("Without AM"). Lines represent third-order trends [Colour figure can be viewed at wileyonlinelibrary.com]

2255.7 (±74.8) in the south where precipitation is low but soil phosphorus is high, and 2,713.4 (±110.6) in the north where precipitation is high but soil phosphorus is low (Figure 3; yellow). For the model "Without AM," plant biomass (g/m^2) ranged from 1,987.8 (±245.2) to 781.4 (±194.0) in the south and north, respectively (Figure 3; blue).

We found that the nutritional benefits of AM symbioses are necessary to maintain a substantial proportion of NPP and biomass across all trophic levels. The Madingley Model estimated average biomass (g/m^2) across the model Serengeti "With AM" to be 2,320.9 (±255.5) for plants, 75.0 (±12.2) for herbivores, 16.8 (±10.8) for omnivores and 43.9 (±3.5) for carnivores (Figure 4, yellow). Average biomass (g/m^2) in the "Without AM" model was 1,202.0 (±610.6) for plants, 54.8 (±7.9) for herbivores, 12.3 (±6.5) for omnivores and 37.5 (±6.0) for carnivores (Figure 4, blue). Because the "Without AM" model does not account for the nutritional quality of forge when predicting biomass of animal consumers, we generated the "Predicted" model that used empirical data to

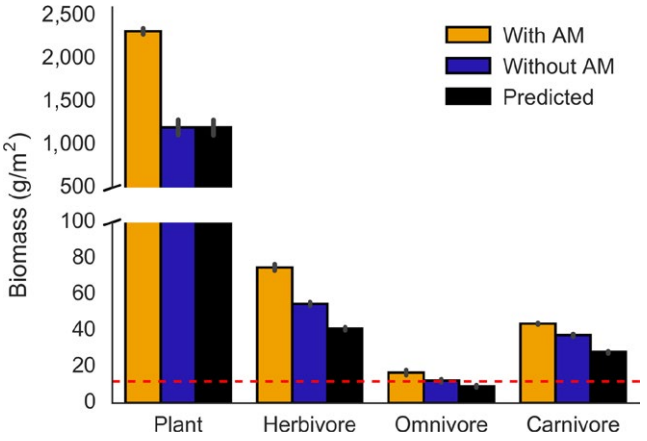

FIGURE 4 Average biomass (g/m^2) for four trophic levels estimated from a Serengeti model with arbuscular mycorrhizal (AM) fungi ("With AM"; yellow), a simulated Serengeti without arbuscular mycorrhizas ("Without AM"; blue), and the hypothesised effects of decreased nutritional quality of plants due to reduced phosphorus inputs in a Serengeti without mycorrhizas ("Predicted"; black). Error bars indicate a 95% confidence interval across the study area. For comparison, a dashed red line was added to indicate the average estimated AM fungal biomass (g/m^2) in the Serengeti. To improve visibility of smaller values, the y-axis was broken into two scales [Colour figure can be viewed at wileyonlinelibrary.com]

predict an additional loss in animal biomass that results from decreased plant tissue concentration of phosphorus. Taking into account the nutrient quality of the vegetation, average biomass (g/m^2) for the "Predicted" model was estimated to be 41.1 for herbivores, 9.2 for omnivores and 28.1 for carnivores (Figure 4, black). Total biomass for all trophic levels and AM fungi was 2,474.5 g/m^2 for a Serengeti with AM. Total biomass (g/m^2) was 1,306.6 in our "Without AM" model and 1,280.5 in our "Predicted" model, a change of −47.2% and −48.2% relative to the "With AM" model, respectively (Figure 4). In summary, the improved biomass production and nutritional quality of vegetation that results from AM symbioses contributes an estimated 45.2% of the herbivores', 45.1% of the omnivores', and 35.9% of the carnivores' biomass in the Serengeti (Figure 4). Overall, AM fungi were 0.72% and plants were 93.79% of the total modelled biomass, as illustrated by the line on Figure 4.

4 | DISCUSSION

Thirty years ago, McNaughton, Ruess, and Seagle (1988) concluded that large mammals have a major organising effect in the Serengeti ecosystem. From our analysis, we can conclude that AM fungi also play a critical role in the trophic structure of the Serengeti. Our model simulations suggest that although AM fungi account for less than 1% of the total biomass, phosphorus supplied by AM symbioses sustains half the vegetation biomass, and accordingly, half of the biomass of iconic migratory herbivores and one-third of the carnivore biomass (Figures 3 and 4). Arbuscular mycorrhizal fungi are particularly important the northern Serengeti where phosphorus acquired from mycorrhizas is essential to maintain most of the

plant biomass (Figure 3). Large mammals disproportionately influence an ecosystem in relation to their biomass by their redistribution of essential nutrients (Doughty et al., 2016). Africa has the largest mammal-driven nutrient diffusivity gradient (Doughty et al., 2016; Wolf, Doughty, & Malhi, 2013), and the Serengeti, in particular, is a hotspot for mammalian biodiversity with the largest terrestrial migration on Earth (Eby, Anderson, Mayemba, & Ritchie, 2014; Sandom, Faurby, Sandel, & Svenning, 2014). Millions of migrating ungulates have a significant and lasting impact on this ecosystem and may contribute to the high biodiversity of the Serengeti ecosystem (Anderson et al., 2007). The distribution of soil phosphorus in the Serengeti, transported through AM symbioses and accelerated by migratory ungulates, may be a significant driver of plant diversity and ultimately mammalian carrying capacity (Anderson et al., 2007; McNaughton, Zuniga, McNaughton, & Banyikwa, 1997). Without AM fungal inputs of phosphorus, these nutrient diffusion gradients would undoubtedly decline.

The Madingley model, which we used to estimate animal biomass, is in the early stages of development and has notable limitations. The model is populated with random animal behaviour and does not account for intelligent behaviour, such as pack hunting and migration (Harfoot et al., 2014). In addition, the Madingley model only distinguishes between broad plant functional groups for terrestrial evergreen and deciduous plant strategies (Harfoot et al., 2014). Functional differences of plant and microbial communities are an important, yet computationally limiting factor in ecosystem biomass estimates (Harfoot et al., 2014). Organic matter from detritivore nutrient cycles, which will be implemented in future versions of the Madingley model, can also influence the trophic structure and biodiversity (Moore et al., 2004). Despite the importance of ecological stoichiometry in determining the abundance of macro-organisms, the process for predicting the influence of forage quality is not yet incorporated in these models (Harfoot et al., 2014). While phosphorus is likely the most important benefit provided to grasses by AM fungi in the Serengeti, there are other factors like nitrogen uptake and drought tolerance that could influence grass biomass (Propster & Johnson, 2015). Our model is based on the assumption that a highly mycorrhizal-dependent C_4 grass from the Konza Prairie is a good proxy for Serengeti vegetation because the grasses in the Serengeti are C_4 (McNaughton, 1983). In the future, it would be ideal to use experimental data from multiple, dominant Serengeti plant species. Yet, regardless of these limitations, the Madingley model provides a first spatially explicit attempt to estimate the responses plant and animal biomass to variable environmental conditions (Harfoot et al., 2014). The model also provides an opportunity to examine how mycorrhizas may contribute to the trophic structure of a terrestrial ecosystem.

Empirical measurements show that AM fungi are extremely abundant and diverse in the Serengeti grassland. Our findings using a NLFA signature fatty acid 16:1ω5 for AM fungal biomass corroborate patterns observed in previous studies in the long-term grazing experiment that measured the higher densities of AM fungal spores and hyphae in the southern than in the northern Serengeti (Antoninka et al., 2015). It is noteworthy that the highest diversity of AM fungal taxa reported anywhere in the world was observed in roots collected from our experimental plots (Davison et al., 2015). In the Serengeti, the extensive below-ground network of AM fungal hyphae is likely composed of ancient clones of fungi that have evolved in place to be locally adapted to their climatic and edaphic environments as well as their host plant communities (Ji et al., 2013; Johnson et al., 2010). Like all microscopic soil organisms, it is difficult to appreciate the ecosystem functions provided by AM fungi because they are hidden from view, but experimental evidence suggests that in phosphorus-limited soils from the north, AM symbioses have evolved to ameliorate plant phosphorus limitation and in the water-limited south they ameliorate drought stress (Propster & Johnson, 2015).

Our analysis shows that soil phosphorus and grazing are the most important determinants of AM fungal biomass (Table 2). Overall, biomass of AM fungi inside the fences has a concave-down relationship across the phosphorus gradient (Figure 2), similar to the Treseder and Allen (2002) model. In contrast to fenced (ungrazed) plots, the AM fungal biomass in grazed plots is lower, and the peak of the curve has shifted down and to the right, indicating a significant effect of grazing on the biomass of AM fungi in the Serengeti grassland. This finding corroborates many other empirical studies that have shown that as long as both plants and their fungal partners are phosphorus limited, an increase in soil phosphorus leads to an increase in both AM fungi and plant tissue phosphorus concentration (Johnson et al., 2010; Marschner & Dell, 1994). Even though we observed lower biomass of AM fungi in the north than the south, it should not be assumed that the symbiosis is less important in the north; experiments suggest just the opposite (Propster & Johnson, 2015). Lower fungal biomass in the north simply suggests that the fungi are phosphorus limited. Mutually beneficial carbon-for-phosphorus trade between host plants and AM fungi is expected to occur across the entire Serengeti phosphorus gradient, and future work on this relationship could yield important findings.

The biomass of AM fungi was higher inside the fenced plots compared with the grazed plots (Figure 2). At least two different possible mechanisms could cause grazing to reduce the abundance of AM fungi. First, nutrient enrichment from urine and manure could reduce the abundance of AM fungi because host plants generally allocate less photosynthate to nutritional symbionts as soil resources become less limiting (Bardgett, Wardle, & Yeates, 1998; Liu et al., 2012; McNaughton et al., 1997). Supporting evidence from previous work in the long-term grazing experiment is equivocal because the soil nitrogen and phosphorus were not consistently higher in the grazed plots than the ungrazed plots (Anderson et al., 2007). However, fertilisation may not increase the concentration of nutrients in the soil, but rather increase their concentration in plant tissues. More systematic measurements of nutrients in both soil and plant tissues are needed to effectively test this hypothesis. A second mechanism for reduced AM fungal biomass in the grazed plots could be that removal of photosynthetic shoots and leaves by grazing mammals could reduce the amount of carbon allocated below-ground to roots and AM fungi (Gehring & Whitham, 1994; Hartnett & Wilson, 2002). There is support for this hypothesis because at the end of the rainy season root biomass of *T. triandra*, a dominant grass at the experimental sites was generally

higher in the ungrazed exclosures compared with the grazed plots (Ritchie & Raina, 2016). It may be inferred that reduced allocation to roots results in less photosynthate available for root symbionts, but again more targeted measurements are necessary to adequately test this hypothesis.

In addition to phosphorus, other soil characteristics also influence the abundance of AM fungi in the Serengeti. We determined that an ordination of soil characteristics (mainly pH, silt and sand) improved our predictions of AM fungal abundance, but was not a significant contributor. Previous studies suggest that AM fungal communities are structured by soil properties. Soil pH has been shown to influence root colonisation and community composition (Hazard et al., 2013; Johnson, Zak, Tilman, & Pfleger, 1991; van Aarle, Olsson, & Söderström, 2002). At different levels of acidity, iron and calcium bind to phosphorus, modifying availability for plants (López-Bucio, de la Vega, Guevara-García, & Herrera-Estrella, 2000). Further, soil type and texture correlated with AM fungal communities (Antoninka et al., 2015; Hazard et al., 2013), possibly because AM fungi can increase plant uptake of calcium (Alizadeh, 2012) and clay can bind to phosphorus (Bolan, 1991).

5 | CONCLUSIONS

The results of our study show how ecosystem functions provided by AM symbioses may influence the trophic structure of an entire ecosystem. Mycorrhizas play a critical role in mobilising and conserving essential nutrients in most terrestrial ecosystems. Tropical grassland vegetation may be particularly dependent on AM symbioses because they moderate seasonal fluctuations in the essential resources that are required by primary producers. In particular, AM fungi can access phosphorus and water sources that are unavailable to plant roots, and in this way, they ameliorate phosphorus limitation and drought stress (Augé, 2001; Marschner & Dell, 1994). In this study, we demonstrated that nutrients supplied exclusively by mycorrhizal symbioses maintain much of the food web in the Serengeti. Because of the importance of AM fungi in sustaining ecosystem functions, they should be considered when managing for biodiversity.

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AUTHORS' CONTRIBUTIONS

B.S. contributed to the concept, data acquisition, analysis, interpretation, prepared figures and tables, and drafted and edited the manuscript; J.P. contributed to the data acquisition, analysis, interpretation and editing the manuscript; G.W.T.W. analysed the soils for neutral lipid fatty acids; A.A. contributed to the data analysis and interpretation; C.R. contributed to the concept, data analysis and interpretation; C.D. contributed to the concept, data analysis and interpretation; N.C.J. contributed to the concept, sample collection, interpretation, drafting and editing the manuscript.

DATA ACCESSIBILITY

Data associated with this manuscript are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.6fv68 (Stevens et al., 2018)

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