A theoretical framework for multispecies coexistence in large herbivores based on functional traits and dietary data

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Abstract

Modern Coexistence Theory (MCT) has long aimed to predict community structure, but empirical support remains scattered across unconnected case-studies from a narrow subset of systems where it is possible to quantify niche and fitness differences (e.g., pairwise interactions between fast-growing plants or protists). We sought a framework to apply MCT to a broader range of ecological scenarios by combining eDNA dietary data with life-history traits of mammal herbivores from diverse communities across three African savannas. Although this first application of the framework treated dietary niche differentiation as the sole mechanism for coexistence, it unveiled three conclusions about multispecies coexistence. First, dietary niche differentiation promoted coexistence but was insufficient to explain observed coexistence for all species. Second, modelled coexistence patterns in herbivore communities could not be predicted from species-level traits or pairwise comparisons. Third, herbivore diversity is generally robust to reductions in the number of plant resources, particularly when there is more dietary specialisation.

Key words: Coexistence, DNA metabarcoding, equalising effects, mammal herbivores, niche partitioning, stabilising effects.

Introduction

Among the most fundamental questions in ecology is how many different species can coexist on a limited number of resources (Hutchinson 1959, 1961). Extensions of this basic question are (1) how different species must be to coexist stably and, its corollary, (2) how many resource types are sufficient to support multiple species? Modern empirical techniques – including stable-isotope analysis (Crawford *et al.* 2008) and DNA metabarcoding (Pansu *et al.* 2019; Potter *et al.* 2022; Pringle 2021) – make it possible to measure how free-ranging animals use resources and have shown that dietary niche differences are ubiquitous in various consumer guilds. But such techniques cannot answer whether measured niches are different enough to allow coexistence, resulting in a gulf that has persisted more than sixty years between the theoretical understanding of coexistence and empirical data on niche differentiation.

Modern Coexistence Theory (MCT) addresses the question of how different the niches of two or more species must be for them to coexist. In the simplest case of two competing species, the dominant competitor excludes the weaker if they consume identical resources (i.e., occupy the same niche). To avoid this fate, weaker competitors must differentiate their niches. According to MCT, species can coexist as long as their niches are different enough to overcome disparities in competitive abilities (i.e., fitness differences: Barabás *et al.* 2018; Chesson 2000, 2018). While this interpretation of coexistence is intuitively appealing and heuristically valuable, connecting it to ecological scenarios in the real world remains a struggle.

Empirical support for MCT is scattered across case-studies from a subset of systems that can be manipulated in carefully designed experiments (e.g., mostly pairwise interactions between fast-growing plants or protists: Buche *et al.* 2022). In the absence of a consistent definition of the niche that maps onto the predictions of MCT (Mittelbach & McGill 2019), specific competition models must be tailored to the characteristics of a given system (Broekman *et al.* 2019; Godwin *et al.* 2020). This makes it hard to synthesise empirical support for MCT – so much so that applying different analytical approaches to the same dataset leads to estimates of niche and fitness differences that vary so much that they can change the interpretation of coexistence (Spaak *et al.* 2023b).

At their core, existing empirical approaches to quantifying niche and fitness differences follow the same general approach: measure population growth rates from experimental or observation studies where competitor densities vary, then use these measurements to infer vital demographic parameters (Godwin *et al.* 2020). These demographic parameters – which include intrinsic growth rates, competition coefficients, or relative yields – can be rearranged to quantify niche and fitness differences and interpret coexistence (García-Callejas *et al.* 2020; Godwin *et al.* 2020). This general approach restricts empirical studies of MCT to systems where demographic rates can be estimated through experimental manipulation or observational studies that span at least one generation. Experimental approaches grow populations in treatments that vary the density of competing species (Broekman *et al.* 2019; HilleRisLambers *et al.* 2012), and are most common for communities with annual recruitment (Hallett *et al.* 2019; Levine & HilleRisLambers 2009; Wainwright *et al.* 2019) or microcosm communities with fast dynamics (e.g., Descamps-Julien & Gonzalez 2005; Letten *et al.* 2018; Narwani *et al.* 2013). By comparison, observational approaches estimate demographic parameters from time-series (Adler 2013; HilleRisLambers *et al.* 2012) and work best for communities with detailed historical data spanning multiple generations (e.g., Adler *et al.* 2010; Usinowicz *et al.* 2017). Neither approach lends itself to studying MCT in communities of large and long-lived species. These communities cannot be manipulated feasibly or ethically in experiments, and their community dynamics are too slow relative to the length of most historical time-series.

Here we ask whether it is possible to flip the conventional approach to quantifying niche and fitness differences. Rather than measuring population growth rates to infer vital demographic parameters, can we instead measure demographic parameters and infer population growth rates? For instance, there is a growing wealth of data on resource use and consumption patterns in communities of large and long-lived species, like mammals (e.g., Pansu *et al.* 2019, 2022; Potter *et al.* 2022; Pringle 2021). Similarly, troves of trait data (e.g., Jones *et al.* 2009) can be used to estimate intrinsic monoculture growth rates (Cole 1954) and minimum resource requirements based on metabolic scaling (Capellini *et al.* 2010). Using these data to model population growth rates would make it possible to quantify niche and fitness differences according to a generalisable approach proposed by Spaak & De Laender (2020), which redefines niche ($\mathcal{N}$) and fitness ($\mathcal{F}$) differences based on population growth rates instead of vital demographic parameters (**Figure 1**).

To implement this approach, we developed a novel analytical framework to quantify $\mathcal{N}$ and $\mathcal{F}$ for multispecies assemblages of large mammal herbivores across protected areas in southern and eastern Africa: Gorongosa National Park, Mozambique; Serengeti National Park, Tanzania; and Laikipia, Kenya (comprising Mpala Research Centre and Ol Jogi Conservancy), Kenya (**Figure 1**). This first application of the framework focused exclusively on dietary resource partitioning, to the exclusion of other stabilising factors (e.g., fluctuation-dependent, dispersal-based, or predator-mediated mechanisms). Then, using data on functional traits and diet composition, we estimated population growth rates and quantified multispecies $\mathcal{N}$ and $\mathcal{F}$ in each community. We simulated how reducing plant resource diversity might affect herbivore coexistence by altering the persistence probability of individual species. Ultimately, our study offers a step towards achieving the infamously elusive goal of how dietary niche partitioning contributes to multispecies coexistence.

Methods

MacArthur's consumer-resource model for mammal herbivores

We modelled herbivore densities using MacArthur's consumer-resource model (Chesson 1990; MacArthur 1970; Sakarchi & Germain 2025), where the population dynamics of the mammal consumers, N, and their plant resources, R, are:

$$\frac{1}{N_i}.\frac{dN_i}{dt} = b_i(\Sigma_l u_{il} w_l R_l - m_i) \qquad (1)$$

$$\frac{1}{R_l}.\frac{dR_l}{dt} = r_l(K_l - R_l) - \Sigma_i u_{il} N_i \qquad (2)$$

Here, N_i is the abundance of species i; b_i is the factor by which excess resources are converted into population growth; u_{il} is the rate at which species *i* consumes resource *l* per unit abundance of resource; w_l is a ratio of the reproductive benefit received from one unit of resource *l*; R_l is the edible biomass of plant resource *l*; and m_i is the minimum resource requirement of species *i* to maintain a population growth rate of exactly 0. The plant species' growth rates, r_l, are scaled by units of carrying capacity K_l (i.e., $r_l = g_l/K_l$, where g_l is the intrinsic growth rate). All the parameters used here and elsewhere in this study are described in Table 1.

We assumed that resources R_l are at equilibrium because their dynamics are faster than those of the consumers (e.g., grass growth in the case of grazers, and leaf production in the case of browsers), and that r_l is the same for all species (i.e., species with higher intrinsic growth rates, g_l, have proportionally higher carrying capacities, K_l, so that their ratios, r, remain consistent across species). These assumptions allowed us to substitute the equilibrium resource density into Equation 1 so that:

$$\frac{1}{N_i}.\frac{dN_i}{dt} = b_i(\overbrace{\Sigma_l u_{il} w_l K_l - m_i}^{\substack{resource\\consumption}} - \overbrace{\frac{1}{r}\Sigma_l \Sigma_i u_{il}^2 w_l N_i}^{\substack{intraspecific\\competition}} - \overbrace{\frac{1}{r}\Sigma_l \Sigma_j u_{il} u_{jl} w_l N_j}^{\substack{interspecific\\competition}}) \qquad (3)$$

Parameterising the MacArthur consumer-resource model

Equation 3 contained several unknown parameters that had to be estimated using empirical field data or species trait data. The first of these parameters was the factor by which excess resource consumption is turned into population growth rate, which we defined as $b_i = \frac{0.1}{M_i}$, where M_i is mean adult body mass (kg) from the PanTHERIA trait database (Jones *et al.* 2009). This definition assumes that excess resource consumption is converted into population growth rate with a transfer efficiency of 10% – i.e., 100 kg of herbivore is sustained by 1000 kg of plant (Barneche *et al.* 2021; Lindeman 1942; Pauly & Christensen 1995) – and is in units of abundance rather than biomass.

The first term in Equation 3 is the contribution of resource consumption to population growth. We lacked information on the true values of K_l, but overcame this using an alternative understanding of herbivore biology. If we were to assume that $N_i \approx N_j \approx 0$, Equation 3 would reflect the species' intrinsic growth rate (i.e., the growth rate in the absence of competition), $\mu_i = b_i(\sum_l u_{il} w_l K_l - m_i)$. Because mammal life histories are well characterised, μ_i can be estimate from life history traits by numerically solving Cole's (1954) equation:

$$1 = e^{-\mu_i} + \lambda. e^{-\mu_i \kappa} - \lambda. e^{-\mu_i(\delta+1)} \quad (4)$$

Here κ is the age of first reproduction, λ is the mean litter size, and δ is the reproductive lifespan; obtained from the PanTHERIA trait database (Jones *et al.* 2009).

The second and third terms in Equation 3 represent the reductions in growth rate due to intra- and interspecific competition, respectively. As demonstrated in subsequent sections, the scaled resource growth rate, r, does not affect the estimates of niche ($\mathcal{N}$) and fitness ($\mathcal{F}$) differences because it scales the magnitudes, but not the signs, of herbivore equilibrium densities. This ensures that the *relative* equilibrium densities are unaffected by values of r, a property that allowed us to set $r = 1$ for simplicity. Similarly, we set $w_i = 1$ because our empirical estimates of resources consumption (explained in the proceeding paragraphs) were in units of dry vegetation biomass, rather than wet consumed biomass. Thus, the benefit species *i* received from consuming one unit of resource did not need to be adjusted.

To measure species consumption rates, we used previously published empirical data for 20 antelope species from three African protected areas: 11 species from Gorongosa National Park, Mozambique (Pansu *et al.* 2019); eight species from Serengeti National Park, Tanzania (Pansu *et al.* 2022); and 12 species from Laikipia (Mpala and Ol Jogi), Kenya (Pansu *et al.* 2022). Although data were available for more species in the original studies, we limited our analysis to antelope (Bovidae) and zebras (Equidae: *Equus* spp.) with ≥10 faecal samples per species per protected area. Briefly, fresh faecal samples were collected during road surveys in seasonal bouts, reflecting a series of snapshots in time. Faecal DNA was extracted, amplified (*trn*L-P6 locus), sequenced, and analysed according to an established metabarcoding workflow. For details of sampling and laboratory protocols, bioinformatic processing, and quality-control procedures, we refer readers to the comprehensive descriptions in the original peer-reviewed studies (Pansu *et al.* 2019, 2022). Taxonomic assignment used local reference databases, resulting in 144 molecular operational taxonomic units (mOTUs) for Gorongosa, 91 mOTUs from Serengeti, and 121 mOTUs from Laikipia. This yielded three separate matrices (11 × 144 Gorongosa; 8 × 91 Serengeti; 12 × 121 Laikipia), where each element, p_{il}, is the proportional contribution of plant species *l* to the diet of herbivore species *i*.

We then multiplied each p_{il} by the estimated daily per capita dietary intake, m_i ($kg.d^{-1}$ dry matter) using the metabolic scaling relationship $m_i = 0.05.M_i^{0.77}$ (Clauss *et al.* 2007). Thus, proportional consumption of different resources summed to an individual's total daily consumption.

Analysing mammal herbivore coexistence through niche ($\mathcal{N}$) and fitness ($\mathcal{F}$) differences

Following Spaak & Schreiber (2023), we separately examined the coexistence of all 2^S possible combinations of herbivore species in each community (where S is the number of species in each assemblage). For each combination of n species, using matrix algebra we calculated equilibrium densities in the absence of invader species i (i.e., $N_j^{-i,*}$, where $-i$ denotes the absence of focal species i and * denotes equilibrium) by solving Equation 3, which simplifies to $0 = \mu_i - \frac{b_i w}{r} \; {}_{l} \; {}_{j} u_{il} u_{jl} N_j^{-i*}$. This formulation shows why r scales the magnitude but not the sign of equilibrium densities, enabling us to set $r = 1$ for simplicity. If all n species had positive equilibrium densities, we plugged the vector of equilibrium densities back into Equation 3 to calculate the invasion growth rates of each of the remaining $S - n$ species. The sub-community of n species was considered stable if all potential invaders had negative invasion growth rates (i.e., the growth rate when at low density, $N_i = 0$).

We estimated niche, $\mathcal{N}$, and fitness, $\mathcal{F}$, differences for the stable community using the general definitions by Spaak *et al.* (2021b) (**Figure 1**). These definitions rely on a standard notation of the per capita growth rate of a focal invader species i as a function of its density (N_i) and the densities of the resident community: $\frac{1}{N_i}\frac{dN_i}{dt} = f_i(N_i, \mathbf{N^{-i}})$. Here, the bold font $\mathbf{N^{-i}}$ denotes a vector of densities for resident species $N_{j \neq i}$. $\mathcal{N}$ and $\mathcal{F}$ are defined as (Spaak *et al.* 2021a; Spaak & De Laender 2020):

$$\mathcal{N}_i = \frac{f_i(0, \mathbf{N}^{-\mathbf{i},*}) - f_i(\sum_{j \neq i} c_{ij} N_j^{-i,*}, \mathbf{0})}{f_i(0, \mathbf{0}) - f_i(\sum_{j \neq i} c_{ij} N_j^{-i,*}, \mathbf{0})} \quad (5)$$

$$\mathcal{F}_i = \frac{-f_i(\sum_{j \neq i} c_{ij} N_j^{-i,*}, \mathbf{0})}{f_i(0, \mathbf{0}) - f_i(\sum_{j \neq i} c_{ij} N_j^{-i,*}, \mathbf{0})} \quad (6)$$

Here, $f_i(0, \mathbf{N}^{-\mathbf{i},*})$ is the invasion growth rate (c.f., Grainger *et al.* 2019) of the focal species i when it is at ~0 density and the resident community is at equilibrium densities, $\mathbf{N}^{-\mathbf{i},*}$; $f_i(0, \mathbf{0})$

is the intrinsic growth rate of focal species i in monoculture; and $f_i(\sum_{j \neq i} c_{ij} N_j^{-i,*}, \mathbf{0})$ is the no-niche growth rate, which represents a counterfactual scenario in which all species have exactly the same dietary niche as the focal species i, while still consuming the same quantity of resources (**Figure 1**). A correction factor c_{ij} converts the quantity of resources consumed by species j into units of species i so that $c_{ij} = \frac{1}{c_{ji}}$ (i.e., if species j consumes tenfold more than species i, then $c_{ij} = 10$ and $c_{ji} = 0.1$). The correction factor was estimated from species' relative resource consumption rates as (Spaak *et al.* 2021a; Spaak & De Laender 2020):

$$c_{ij} = \sqrt{\frac{\sum u_{jl}^2}{\sum u_{il}^2}} \qquad (7)$$

According to this formulation, coexistence is stable when $\mathcal{N}_{\mathrm{i}} > \mathcal{F}_i$, (Spaak *et al.* 2021b).

For the three herbivore assemblages, we calculated $\mathcal{N}$ and $\mathcal{F}$ using Equations 5 and 6 following Spaak & Schreiber (2023). For the $S - n$ species not in the stable community (the invaders), we solved Equation 3 using the equilibrium densities for the n resident species. For the n species in the stable community (the residents), we set each species as an invader one at a time, recalculated new equilibrium densities for the remaining $n - 1$ species in the sub-community, then solved Equations 5 and 6 with the recalculated equilibrium densities. In two instances (described in Supplementary Appendix 1), removing one of the resident species led to the extirpation of a second resident species (i.e., species A could only persist in the presence of species B, but not *vice versa*). This occurred because in these instances community assembly was path-dependent and varied depending on the sequence of species being added. To deal with this, we set the negative equilibrium densities for the extirpated species to zero before calculating $\mathcal{N}$ and $\mathcal{F}$ (noting that $\mathcal{N}$ and $\mathcal{F}$ do not strictly exist for these species: Spaak & Schreiber (2023).

We also quantified $\mathcal{N}$ and $\mathcal{F}$ for all pairs of species within each of the three protected areas to compare these to multispecies estimates. Multispecies $\mathcal{N}$ can be inferred from the mean of pairwise estimates: $\mathcal{N}_i \approx \frac{\Sigma_j \mathcal{N}_{ij}^{(2)}}{S-1}$, where S is the number of species in the assemblage and the superscript $^{(2)}$ denotes pairwise estimates. Multispecies $\mathcal{F}$ relates to the sum of pairwise estimates, scaled by the relative yield (RY): $\mathcal{F}_i \approx 1 - \Sigma\left(1 - \mathcal{F}_{ij}^{(2)}\right)RY_j$, where RY_j is the ratio between the equilibrium density of species j in a multispecies community when species i is absent (numerator) and present (denominator) (Spaak *et al.* 2021a).

Simulating the effect of resource loss on herbivore coexistence

To evaluate how resource richness affects coexistence, we simulated random removal of plant species to estimate the number of herbivore species able to coexist given fewer plant resources. For each community separately, we randomly sampled, without replacement, levels of plant species richness in increments of 10 species: iterating the process 100 times for each level of plant species richness. For each iteration, herbivore consumption rates, p_{il}, were standardised to always sum to one, assuming that the relative proportional consumption of the remaining resources remained unchanged.

For each sub-sample of plant richness, we examined every combination of herbivore species to identify the stable community. Because herbivore richness varied between random iterations of plant richness, we explored whether this variation could be attributed to higher or lower dietary specialisation using Blüthgen's standardised specialisation index, d', where higher values correspond to more specialisation (Blüthgen *et al.* 2006). We calculated d' for plant resources (i.e., a plant is specialised if it is only consumed by few herbivores) and herbivores (i.e., a herbivore is specialised if it only consumes few plant species).

We inferred the persistence probability for each herbivore species at every level of plant resource richness as the proportion of the 100 iterations in which the species was present in the stable community. Lastly, we observed that the relationship between the number of coexisting herbivores, S, and the number of plant resource species, P, was non-linear, so we modelled this relationship using a power curve ($S = \alpha P^{\beta}$, where α and β are estimated constants: Brown *et al.* 2002). We also fitted an asymptotic curve to these relationships but found that it fitted the data worse than the power curve in two of the three sites (according to AIC comparisons) and predicted an asymptote that was consistently lower than the observed herbivore richness.

Results

Modelled herbivore growth rates

Our model predicted that between four (Serengeti) and eight (Gorongosa) herbivore species coexisted stably, showing that resource partitioning could explain the coexistence of many, but not all, species. The level of dietary resource partitioning was not enough to ensure positive invasion growth rates for three species in Gorongosa (Impala, Reedbuck, Wildebeest: **Figure 2a**), four in Serengeti (Buffalo, Hartebeest, Plain's zebra, Thompson's gazelle: **Figure 2b**), and six in Laikipia (Dik-dik, Impala, Klipspringer, Kudu, Oryx, Plain's zebra: **Figure 2c**). These species included some of the most abundant species in each community. Notably, species with negative invasion growth rates were not those with the lowest intrinsic growth rates (**Figure 2**), nor did their minimum daily resource requirements (*m*) or dietary specialisation (Blüthgen's *d'*) differ from species with positive invasion growth rates (**Supplementary Figures S1-3**). Thus, our competition-based model makes intriguing predictions of coexistence that are not readily apparent from species-specific traits.

Niche ($\mathcal{N}$) and fitness ($\mathcal{F}$) differences

Computing niche and fitness differences for multispecies communities of mammal herbivores showed that most species were near the thresholds between coexistence and exclusion (**Figure 3**). Large discrepancies between $\mathcal{N}$ and $\mathcal{F}$ were uncommon, implying that there is little qualitative difference between species that coexisted and those that were excluded. Moreover, both $\mathcal{N}$ and $\mathcal{F}$ were generally uncorrelated to species-specific traits (**Supplementary Figures S4-6**). Niche differences were significantly higher for species with higher daily resource requirements in Gorongosa (**Figure S4**), but the reverse in Serengeti (**Figure S5**). In Serengeti, specialised species had higher niche differences (**Figure S5**). Fitness differences were uncorrelated to all traits (**Supplementary Figures S4-6**), further underscoring the limitations of inferring coexistence from species' traits.

Pairwise analyses of $\mathcal{N}$ and $\mathcal{F}$ remain the standard approach to MCT, yet our findings suggest that such comparisons are a poor proxy for multispecies coexistence. Almost all pairs of species were predicted to coexist stably (**Figure S7**): just 4 of 110 pairs (3.6%) in Gorongosa, 4 of 56 (7.1%) in Serengeti, and 2 of 132 (1.5%) in Laikipia resulted in competitive exclusion. Among the species expected to be excluded from pairs were those that persisted in multispecies communities (e.g., in Gorongosa, Oribi persisted in a multispecies community, but was excluded when paired with Waterbuck). And species able to coexist in pairs with all other species were among those excluded in multispecies communities (e.g., Wildebeest in Gorongosa; Buffalo and Thompson's gazelle in Serengeti; Dik-dik, Klipspringer, Kudu, and Oryx in Laikipia).

Mismatches between pairwise and multispecies coexistence arose overwhelmingly from fitness, rather than niche differences (**Figure 4**). Multispecies $\mathcal{N}$ was reasonably well approximated by the average of pairwise estimates (**Figures 4 a, c, d**), indicating that variation in species richness did not drastically change species' niche differences. By contrast, multispecies $\mathcal{F}$ is approximated by the sum of pairwise estimates (**Figure 3 c, d, f**), which increases with the number of species in the community.

The effect of reducing plant resource on herbivore coexistence and persistence

Reducing plant diversity had similarly non-linear effects on herbivore species richness across all three focal communities despite differences in the number of herbivores predicted to coexist at equilibrium (β exponents of 0.23 – 0.27: **Figure 5 a-c**). Herbivore richness was highly robust to removal of up to half of the plant taxa in each system (a 50% reduction in plant richness reduced the median number of herbivores in Gorongosa by a single species and had no effect Serengeti and Laikipia); collapsing rapidly from 3-4 herbivore species to 0 with the removal of the last 10 plant taxa. However, variability in the predicted number of coexisting herbivore species increased substantially when resources became scarce (**Figure 5 a–c**). Although some combinations of just 20 plant resources were enough to support 10 species in Gorongosa (**Figure 5a**), five in Serengeti (**Figure 5b**), and eight in Laikipia (**Figure 5c**); a different combination of 20 plant taxa could only support one herbivore species in each of the protected areas. Variation in herbivore richness was reflected in the persistence probabilities of individual species (**Figure 5 d – f**). Reducing the number of plant taxa generally increased the persistence probability of species that were absent from the stable community, but reduced the persistence probability of resident species.

Reducing the number of plant resources also increased the mean and variation of dietary specialisation (Blüthgen's *d'*: **Supplementary Figures S8-10**). However, dietary specialisation was only associated with higher herbivore richness at relatively low levels of plant richness (< 20 – 70 plant taxa: **Supplementary Figures S11 – 13**). Moreover, higher herbivore richness was predicted only by herbivore specialisation (i.e., when herbivores only ate specific plants:

Supplementary Figures S11-13), not by plant specialisation (i.e. when plants were only eaten by specific consumers: **Supplementary Figures S14-16**).

Discussion

Ecologists have compiled vast quantities of data at ever-increasing resolution on the differences between the dietary niches of large herbivores (Codron *et al.* 2019; Kleynhans *et al.* 2011; Shipley *et al.* 2009), yet these data remain unmoored to any framework for making predictions about coexistence. We applied principles of MCT to three species-rich herbivore communities, which has rarely been done for any group of vertebrates (Barabás *et al.* 2018; Chesson 2018; Godwin *et al.* 2020). We show that dietary resource partitioning – differences in the subset of plant taxa eaten by each herbivore – predicted coexistence for some, though not all, species. Invasion growth rates were consistently higher than would be expected if species shared a common dietary niche, but this effect was not strong enough to ensure mutual invisibility by all species. This raises new questions about how mammal herbivores coexist if not for dietary niche partitioning, and what answering these questions can teach us about MCT more broadly.

Lessons on herbivore coexistence

No-niche growth rates were consistently negative (**Figure 2**), indicating that without resource partitioning, the diverse large-herbivore communities in African savannas would collapse to a single dominant competitor. Yet resource partitioning alone could not explain the coexistence of all species sampled in the original dietary studies; often excluding species that typically occur in high densities in our systems (e.g., impala in Gorongosa; zebra and Thomson's gazelle in Serengeti; dik-dik and impala in Laikipia) and throughout African savannas more broadly (e.g., impala and wildebeest: Staver & Hempson 2020). To probe these counterintuitive patterns, we revisited five main assumptions of our MCT model.

The first and second model assumptions were that that only herbivory regulates the abundance of plant resources and that herbivores and plant taxa are evenly spread throughout the landscape. Neither of these assumptions holds in nature. With spatially heterogenous plant resources, herbivores can reduce interspecific competition locally via spatial habitat segregation or by migrating. For example, migratory Serengeti wildebeest, zebra, and gazelles avoid competition with 'resident' species, and they reduce competition with one another via spatial and temporal avoidance at smaller scales (Anderson *et al.* 2024; Hopcraft *et al.* 2014). When species' preferred food sources differ and are spatially concentrated, coexistence can be supported through the spatial storage effect (i.e., when species experience relatively higher competition in patches of high quality resources: Sears & Chesson 2007). Unlike for sessile organisms, where crowding at preferred patches can increase intraspecific competition beyond the relative benefits of higher quality resources, (Ellner *et al.* 2022), mammal herbivores are free to move. Therefore, movements in relation to unevenly distributed plant resources likely play a major role in herbivore coexistence.

A third assumption of the model is that aggregated population-level dietary profiles – which were derived from averaged consumption data across multiple years and species – faithfully represent herbivores' dietary niches. In reality, dietary niches are not static and can change seasonally. For instance, impala are known shift the relative proportion of graze and browse in their diets across seasons (Codron *et al.* 2007), which allows them to reach high densities (Staver & Hempson 2020) even in instances where they typically experience competition from other species (e.g., removal of buffalo due to poaching in Serengeti led to increases in impala: Arsenault & Owen-Smith 2002). Our results showed that even when species cannot coexist due to dietary partitioning alone, their persistence probability increased as plant resources were reduced. While this does not mimic effects of seasonality *per se*, the result is consistent with the possibility that seasonal reductions in the availability of different resources could enable coexistence of species that would otherwise have been excluded competitively.

Assumption four is that herbivores compete for plant *species*, which ignores the fact that different species feed on different tissues, phenological/ontogenetic stages, and at different vertical strata of the same plants. For instance, buffalo and zebra bulk-feed on taller swards and consume larger quantities of nutrient-poor stems relative to species such as wildebeest and Thomson's gazelle, which feed more selectively on shorter swards and nutrient-rich foliage (Anderson *et al.* 2024; Arsenault & Owen-Smith 2002, 2008). To some extent, these traits are also reflected in differences among plant species, some of which are taller, stemmier, and less nutritious than others (Potter *et al.* 2022). Nonetheless, focusing solely on differences in dietary species composition in faecal DNA may offer an incomplete and conservative indicator of dietary niche differences in real savannas.

Lastly, our MCT model considers only two trophic levels and is thus unable to capture top-down effects of predators or pathogens. Theoretically, predation and disease can have stabilising effects on coexistence that are analogous to resource-based niche differences (Chesson & Kuang 2008; Song & Spaak 2024; Spaak *et al.* 2023a). Resource-use overlap can be reduced when herbivores have different predator-avoidance behaviours (Dellinger *et al.* 2022). Coexistence can also be supported when predation pressure covaries with resource availability. For example, the relative predation from lions on buffalo and zebra varies between the wet and dry seasons (Funston & Mills 2006; Grange & Duncan 2006) and while zebra typically face less predation pressure than wildebeest and gazelles (Owen-Smith & Mills 2008; Sinclair *et al.* 2003), zebra can be more exposed to predators when they lead the grazing succession (Sinclair 1985).

Implications for Modern Coexistence Theory

Studies of animals, let alone large, long-lived vertebrates, are vanishingly rare in the MCT literature. Nearly 90% of $\mathcal{N}$ and $\mathcal{F}$ estimates in a recent meta-analysis of almost 1,000 two-species communities were from terrestrial plants or phytoplankton (Buche *et al.* 2022). By focusing on multispecies communities, our study moves beyond the predominant focus on pairwise estimates of niche and fitness differences, which likely misrepresent coexistence (Figure 4 and Spaak *et al.* 2021a)

We showed that herbivore diversity is relatively robust to the reduction of resources. The non-linear relationship between resource and consumer richness was remarkably consistent across three different protected areas. The exponents in these power functions – ranging between 0.23 and 0.27 – were strikingly similar to the ¼-power scaling common to many biological allometries (Brown *et al.* 2002, 2004; Hatton *et al.* 2015; West *et al.* 1997). Although this consistent pattern warrants further attention, it would be premature to attribute the way herbivore diversity scales predictably with plant diversity to metabolic processes. Multispecies fitness differences were higher than their pairwise equivalents, confirming earlier theoretical results that fitness differences increase with species richness (Spaak *et al.* 2021a). This suggests that, unlike what is expected from a power function, the accumulation of fitness differences will eventually set an upper limit to the total number of coexisting species. Reducing the number of plant resources increased variation in the number of coexisting herbivores; sometimes even improving the persistence probability of certain species. Such pattens support the view that the specific structure of competitive interactions determine patterns of secondary extirpations (Eichenwald *et al.* 2024; Emary & Evans 2021; Fowler 2010), which are not simply a deterministic outcome of allometric scaling.

Like previous studies, we were unable to identify simple trait-based indicators of which species can coexist in a given system (Levine *et al.* 2025). It is possible that the interaction between traits of different species, rather than the values of species-specific traits *per se*, ultimately determine coexistence. But the multitude of potential interactions soon become intractable in species-rich systems. Levine *et al.* (2025) make a convincing case for using 'process informed metrics' (quantifiable indicators that have straightforward relationships to the outcomes of mechanistic competition models) to predict pairwise coexistence from species traits. However, our findings question whether process informed metrics identified for pairs of species would necessarily extend to multispecies communities.

Future perspectives

Given the rapid growth of molecular dietary data (Pringle & Hutchinson 2020), it should be increasingly possible to apply MCT to various animal groups. This will not only deepen our understanding of the role of dietary resource partitioning in promoting multispecies coexistence but can open new empirical opportunities to test and develop MCT. An immediate opportunity would be evaluating coexistence, $\mathcal{N}$, and $\mathcal{F}$ based on repeated dietary measurements from the same site. This offers a major step-change in understanding fluctuation-dependent coexistence mechanisms because our framework makes it possible to construct a time-series of $\mathcal{N}$ and $\mathcal{F}$ (as opposed to using time-series data to quantify a single estimate of $\mathcal{N}$ and $\mathcal{F}$: e.g., Adler 2013). This could be coupled with wildlife census data, or even post-translocation monitoring (Gross *et al.* 2024), to validate the predictions of coexistence models using independently collected demographic data.

Should our framework be applied to new and existing molecular dietary data, it could give rise to a 'macroecology of Modern Coexistence Theory' by making it possible to examine how geographical or environmental covariates affect the relative strengths of niche and fitness differences. Even though our framework currently leaves room for refinement, it begins closing the significant gap between a 'theory of niche' and a 'theory of coexistence' (Letten *et al.* 2017; Mittelbach & McGill 2019); a gap that has, until now, remained particularly persistent in mammal herbivore communities.

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Table 1: A summary of the variables and parameters used in the theoretical framework to quantify niche ($\mathcal{N}$) and fitness ($\mathcal{F}$) differences for mammal herbivores.

Parameter or variable	**Description (units)**	**Source of information**
Herbivore dynamics		
N_i	The density of herbivore species *i* (number of individuals).	Modelled variable
b_i	Factor by which excess resources are converted into population growth (number of individuals supported by 1 kg of plant dry matter)	Estimated as $b_i = \frac{0.1}{M_i}$, assuming a 10% energy transfer efficiency across tropic levels.
u_{il}	Rate at which herbivore species *i* consumes plant resource *l* (kg of plant dry matter per individual herbivore per unit of time)	Calculated by multiplying p_{il} by m_i.
p_{il}	The proportion of plant resource *l* in the diet of herbivore species *i.* (unitless proportion)	Quantified empirically from eDNA field data.
w_l	The ratio of the reproductive benefit species *i* receives from one unit of resource *l* (unitless ratio)	We to set $w_i = 1$ because minimum dietary requirements (m_i) are already based on dry matter biomass, rather than consumed (wet) biomass.
m_i	Minimum resource requirement of species *i* to maintain a growth rate of exactly 0 (kg plant dry biomass per individual).	Estimated from the metabolic scaling relationship: $m_i = 0.05. M_i^{0.77}$ (Clauss *et al.* 2007).
M_i	Mean body mass of herbivore species *i* (kg)	PanTHERIA global database of mammal traits (Jones *et al.* 2009).
μ_i	Herbivore intrinsic growth rate when in monoculture (individuals per unit of time)	Inferred based on life-history traits (κ, λ, δ) using Cole's (1954) equation (Equation 4)

κ	The age of first reproduction (years).	PanTHERIA global database of mammal traits (Jones *et al.* 2009).
λ	Mean litter size (number of offspring)	PanTHERIA global database of mammal traits (Jones *et al.* 2009).
δ	Reproductive lifespan (years).	PanTHERIA global database of mammal traits (Jones *et al.* 2009).
Plant resource dynamics		
R_l	The density of edible plant biomass (kg plant dry biomass)	Modelled variable
r_l	The intrinsic growth rate of plant resource *l* scaled by its carrying capacity (kg plant dry biomass per unit of time).	Since the value of r_l is a constant scaling parameter when estimating equilibrium densities (meaning that *relative* equilibrium densities are unaffected), it had no effect when calculating niche and fitness differences. Therefore, we set $r_l = 1$ for simplicity.
K_l	The carrying capacity of plant resource *l* (kg plant dry biomass).	This parameter remains unknown, but the term that includes $K_l$can be replaced with parameter μ_i.

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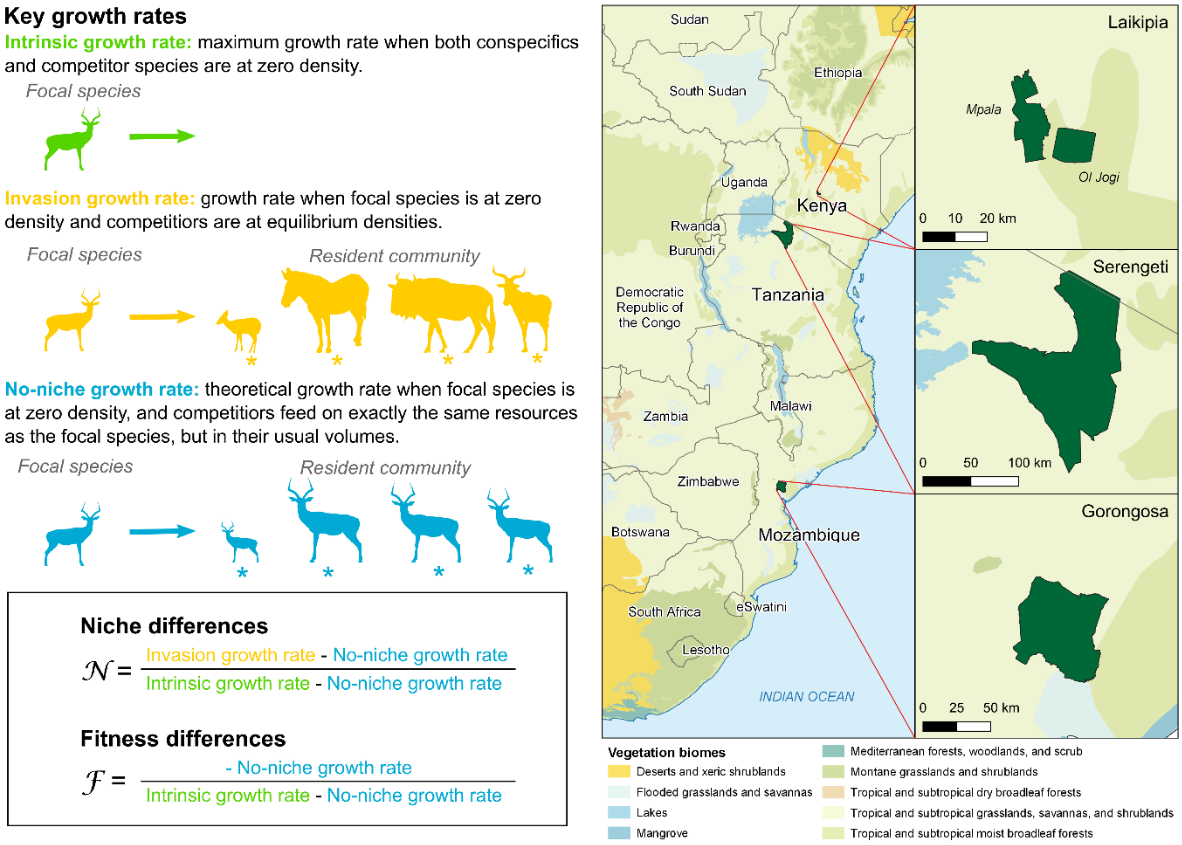
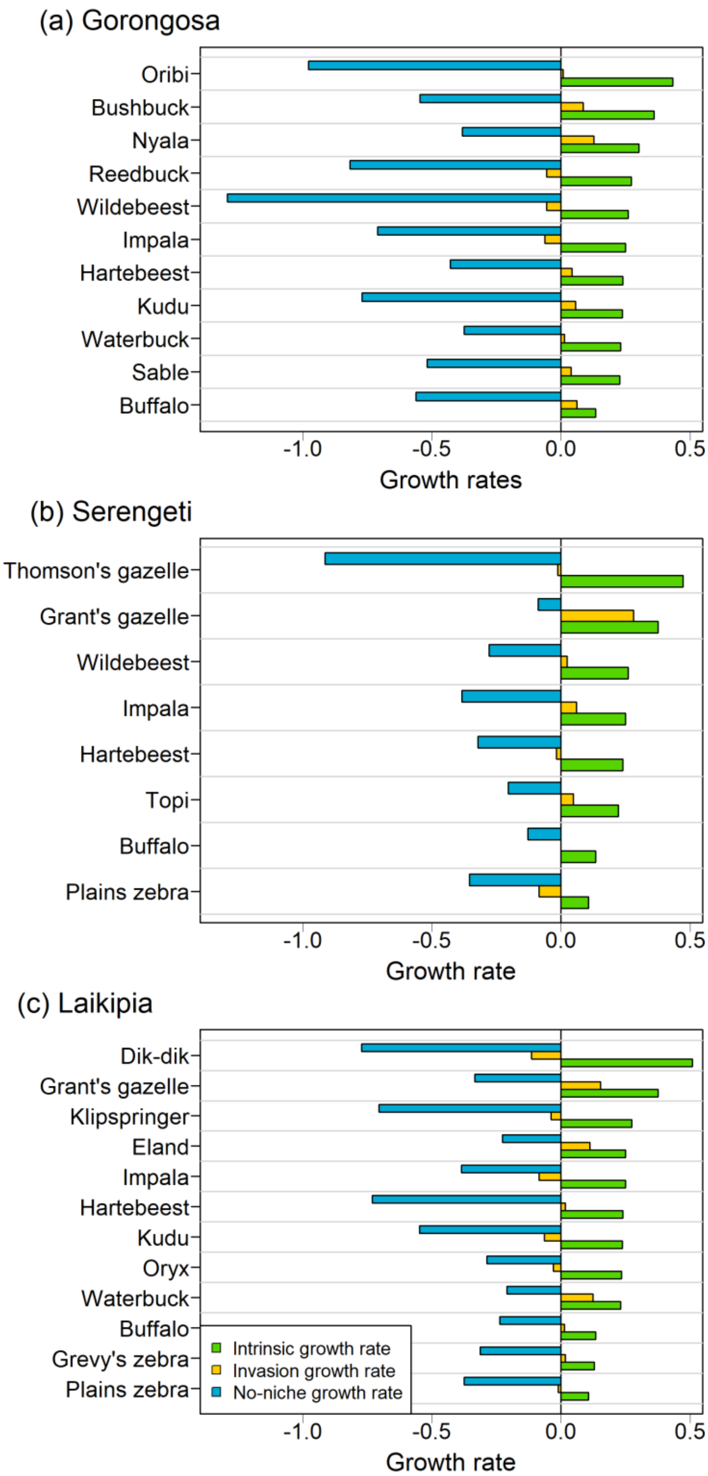


Figure 1. *Left*: a conceptual summary of how to quantify niche and fitness differences from herbivore growth rates. *Right*: the locations of the three savanna sites, Laikipia (Mpala Community Conservancy and Ol Jogi Private Ranch, central Kenya), Serengeti National Park (northern Tanzania), and Gorongosa National Park (central Mozambique), where niche and fitness differences were quantified for mammal herbivores. (Icons: Impala, *Six Plus by Libé* CC BY-SA; Common duiker, *Robert Hering* CC0; Zebra, *Kai Caspar* CC0; Wildebeest, *Six Plus by Libé* CC BY-SA; Hartebeest; *TeaandBiology* CC0. Biome data from: Olson *et al.* (2001).



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611 **Figure 2.** Intrinsic (green), invasion (gold), and no-niche (blue) growth rates of mammal herbivores from (**a**)
612 Gorongosa National Park, Mozambique; (**b**) Serengeti National Park, Tanzania; and (**c**) Laikipia, Kenya. Species
613 are ordered from top to bottom based on the intrinsic growth rates. Invasion growth rates are positive for most,
614 though not all species, while no-niche growth rates were strongly negative for all species, demonstrating the

important of niche partitioning for coexistence. Consistently negative no-niche growth rates also show that no species had higher fitness than all its competitors combined. The lack of clear association between invasion and intrinsic growth rates indicates that coexistence is not simply determined by species traits alone, but by how these traits interact with those of competitors.

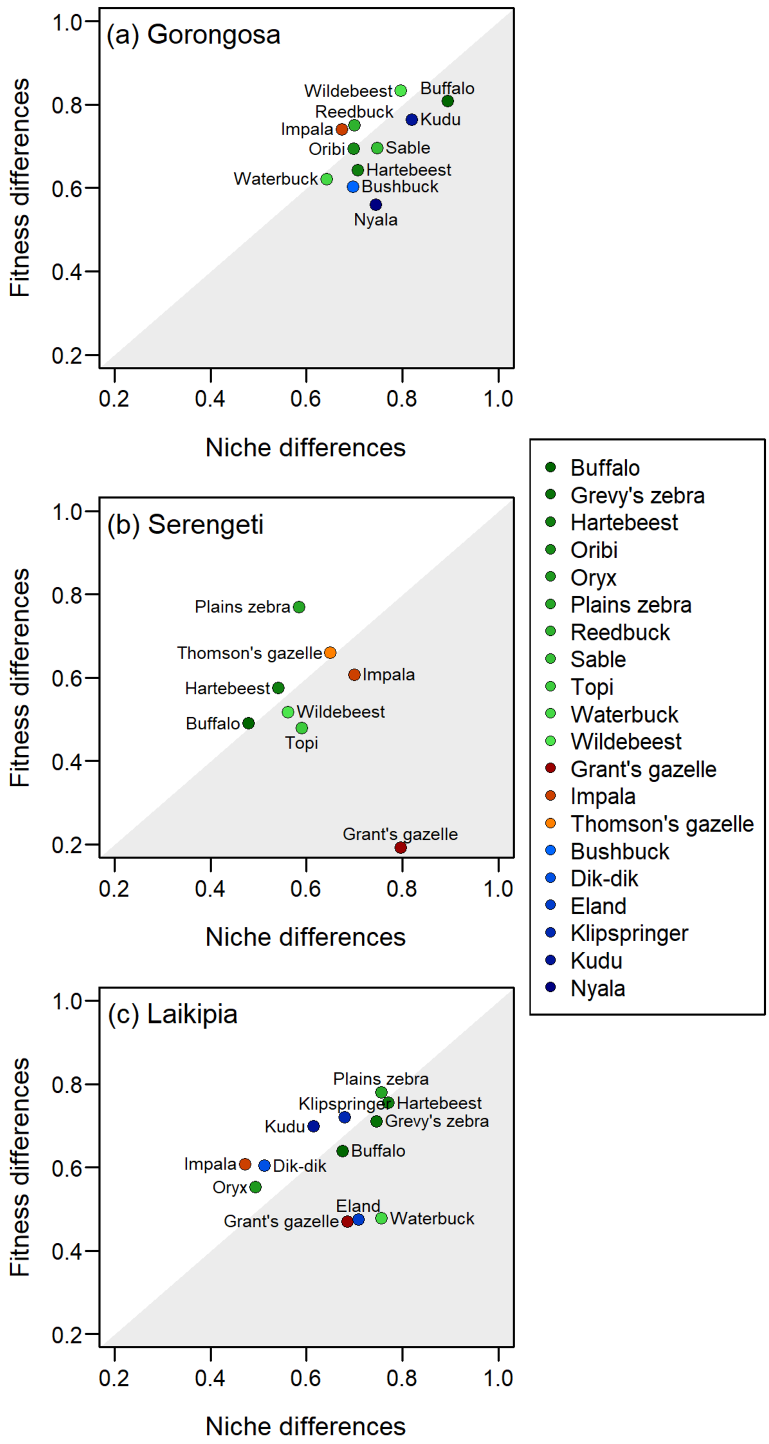

Figure 4: Multispecies niche and fitness differences of herbivore communities from (**a**) Gorongosa National Park, Mozambique; (**b**) Serengeti National Park, Tanzania; and (**c**) Laikipia, Kenya. Species could coexist in the grey zone, where niche differences exceeded fitness differences. Species were coloured based on broad diet type (greens = grazers; blue = browsers; reds = mixed feeders).

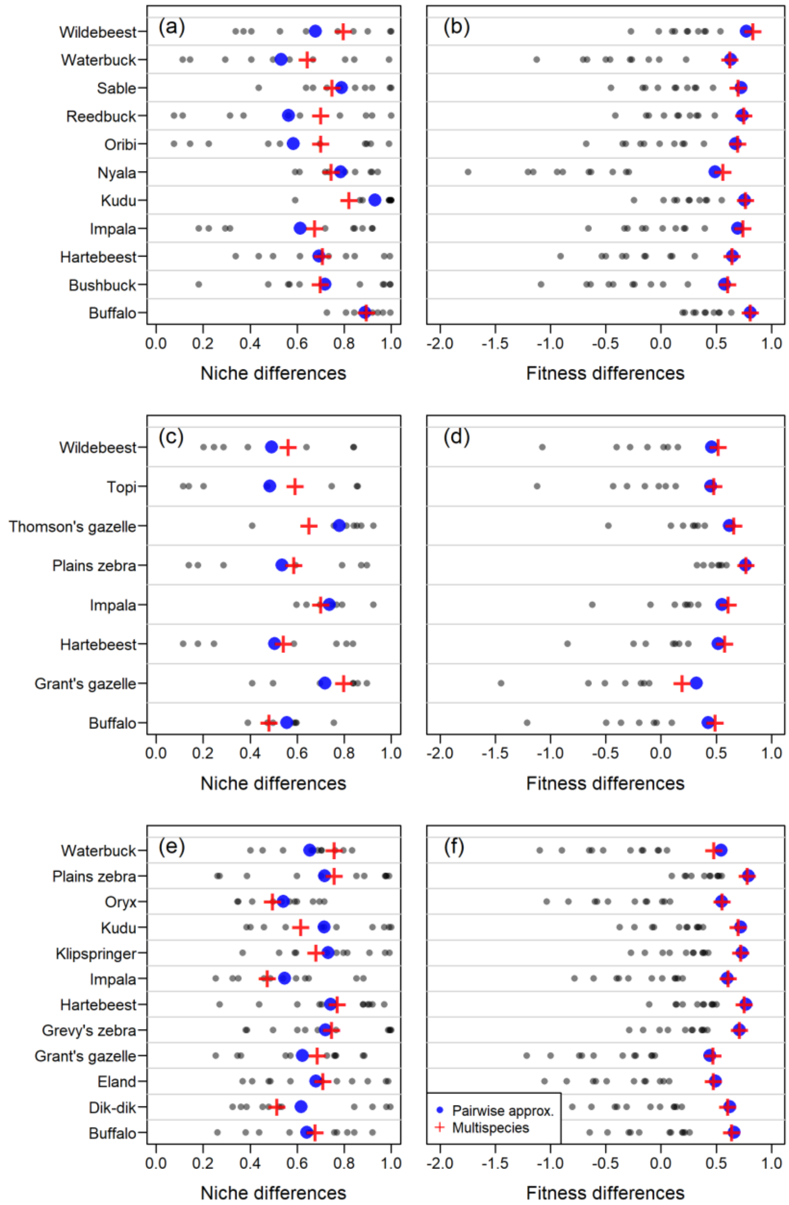

Figure 3: Comparisons of pairwise and multispecies niche (**a,c,e**) and fitness (**b,d,f**) differences for mammal herbivores in Gorongosa National Park, Mozambique (**a,b**); Serengeti National Park, Tanzania (**c,d**); and Laikipia, Kenya (**e,f**). Grey points indicate pair-wise niche and fitness differences, red crosses indicate the multispecies niche and fitness differences, and blue circles show multispecies noch and fitness differences as estimated from pairwise estimates. Multispecies niche differences are within the range of pairwise niche estimates (a,c,e), whereas multispecies fitness differences are consistently higher than pairwise estimates (b,d,f). Therefore, multispecies coexistence cannot easily be inferred from pairwise comparisons, which underestimate fitness differences.

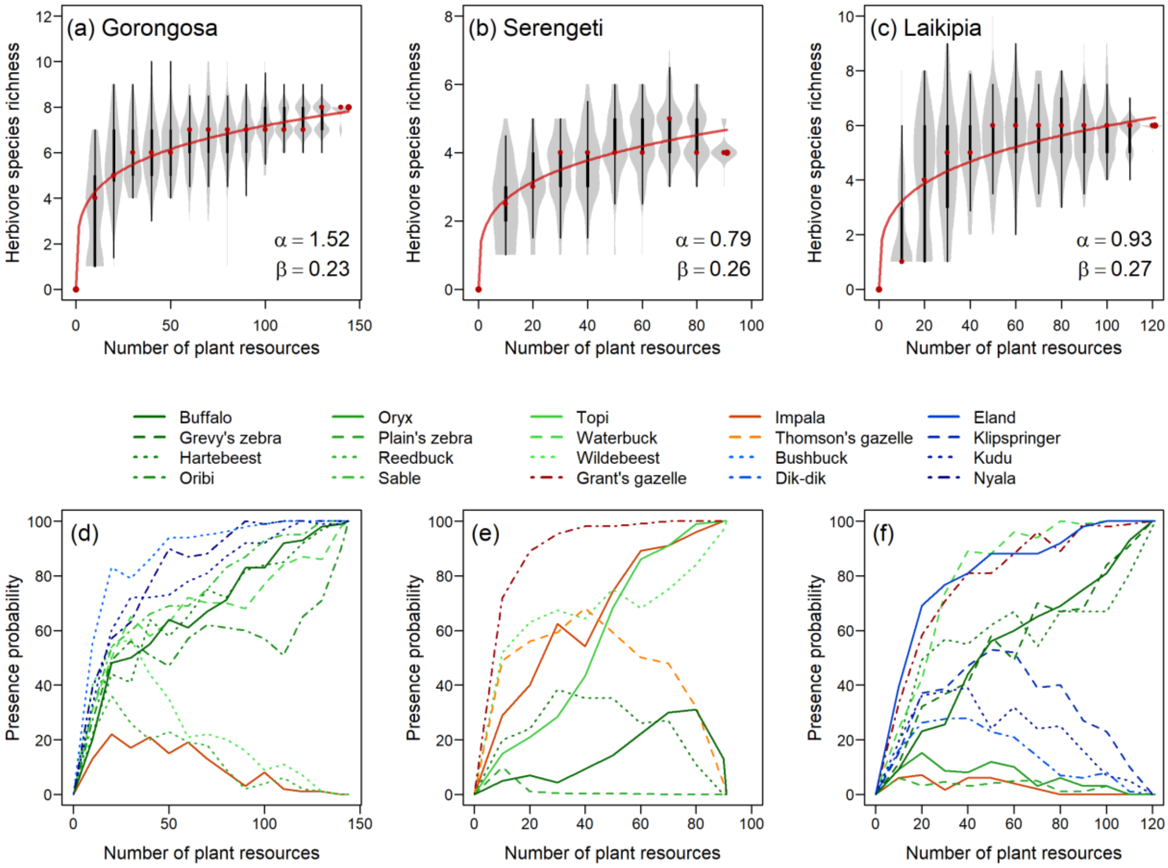

Figure 5. The non-linear response of herbivore richness (**a-c**) and species persistence (**d-e**) to the removal of plant resources in Gorongosa National Park, Mozambique; Serengeti National Park, Tanzania; and Laikipia, Kenya. (**a-c**) Grey violin plots show the distribution of herbivore richness across 100 random sub-samples at each level of plant resources (red circles = median richness, thick black line = interquartile range, thin line = 95% confidence intervals), and red lines show the modelled relationship between herbivore and plant richness. Parameters show the estimated coefficients from a power function of plant species richness (i.e., reversed x-axis, where the number of herbivores is 0 when the number of plant resources is 0). (**d–f**) Persistence probabilities of individual herbivore species at each level of plant richness in each system, based on their proportional presence in stable communities across the 100 iterations.

Supplementary information

A theoretical framework for multispecies coexistence in large herbivores based on functional traits and dietary data.

Falko T. Buschke, Daryl Codron, Robert M. Pringle, and Jürg Spaak

Supplementary Appendix 1: Handling invalid community assembly pathways

As described in the methods section, we quantified $\mathscr{N}$ and $\mathscr{F}$ for the n-species stable community by sequentially removing each species from the community, recalculating the equilibrium for the remaining n-1 species, and then quantifying the invasion growth rate of the removed species. However, this process was not possible in two instances because removing one of the species led to the knock-on extirpation of a second species (i.e., one of the species in the $n - 1$ species community had a negative equilibrium density).

In Gorongosa, removing Sable or Nyala during the invasion analysis led to the co-extirpation of Oribi. Despite having the highest intrinsic growth rate among the 11 species analysed from Gorongosa, Oribi's invasion growth rate was only marginally positive, while its no-niche growth rate was the most negative of all the resident species (main text, Figure 2a). This suggests that the presence of Sable or Nyala dampen the relative competitive superiority of other resident species (Buffalo, Bushbuck, Hartebeest, Kudu, Waterbuck); a necessary condition for Oribi to maintain positive invasion growth rates.

In Laikipia, removing Eland led to co-extirpation of Grevy's zebra. These two species had amongst the highest pairwise niche differences (0.987), which suggests that the presence of Eland dampened the relative competitive strength of other species in the resident community (Buffalo, Grant's gazelle, Hartebeest, Waterbuck) without affecting the Grevy's zebra.

Strictly speaking $\mathcal{N}$ and $\mathcal{F}$ do not exist for Sable and Nyala in Gorongosa, or Eland in Laikipia because of the lack of $n - 1$ species sub-communities. However, to include these species in Figure 4 of the main text, we simply set the equilibrium densities of the extirpated species (i.e. Oribi in Gorogosa, and Grevy's zebra in Laikipia) to zero, leaving the densities of the other species unchanged. We then calculated invasion and no-niche growth rates (and, by extension, $\mathcal{N}$ and $\mathcal{F}$) based on these equilibrium densities.

We also considered an approach where we removed the extirpated species completely and recalculated the equilibrium densities for the species remaining in the n-2 species stable community. However, we chose not to present the results from this approach because (i) it led to quantitatively similar estimates of $\mathcal{N}$ and $\mathcal{F}$, and (ii) this approach only considered one possible configuration of $n - 2$ communities when alternative configurations with positive equilibrium densities could exist.

Spaak & Schreiber (2023) proposed an invasion graph analysis that makes explicit the (non)existence of all sub-communities. While this approach would not have allowed for the straightforward quantification of $\mathcal{N}$ and $\mathcal{F}$ either, it has the benefit of showing all the valid pathways that could lead to the stable end states.

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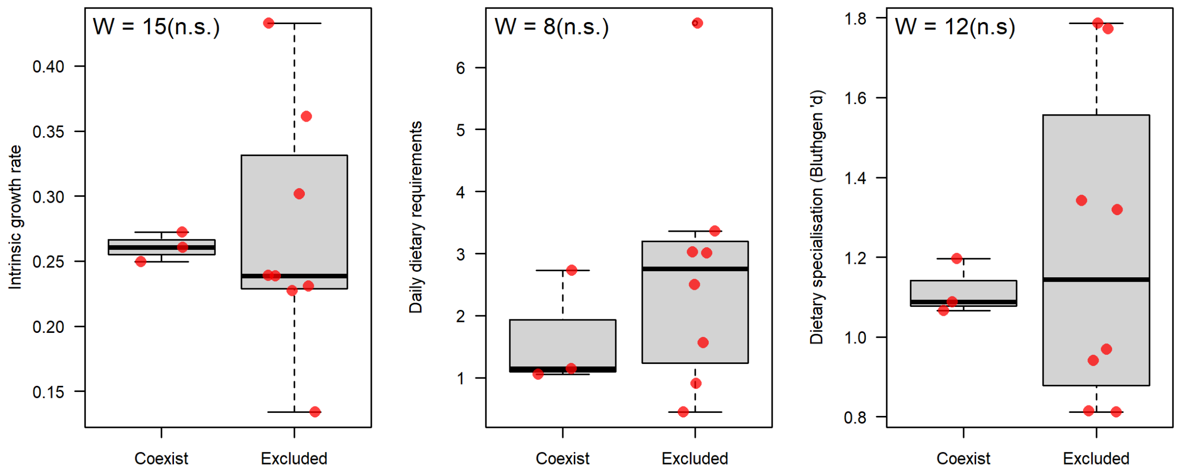

Figure S1: The intrinsic growth rates (left), daily dietary resource requirements (middle), and dietary specialisation measured using Blüthgen's *d'* (right) for species able or unable to coexist stably in Gorongosa National Park, Mozambique. Red circles show individual species, and boxes show the median, first- and third quartiles, and minimum and maximum values. Reported numbers represent the test statistic from a non-parametric Mann-Whitney U test (n.s. = statistically non-significant at $\alpha = 0.05$).

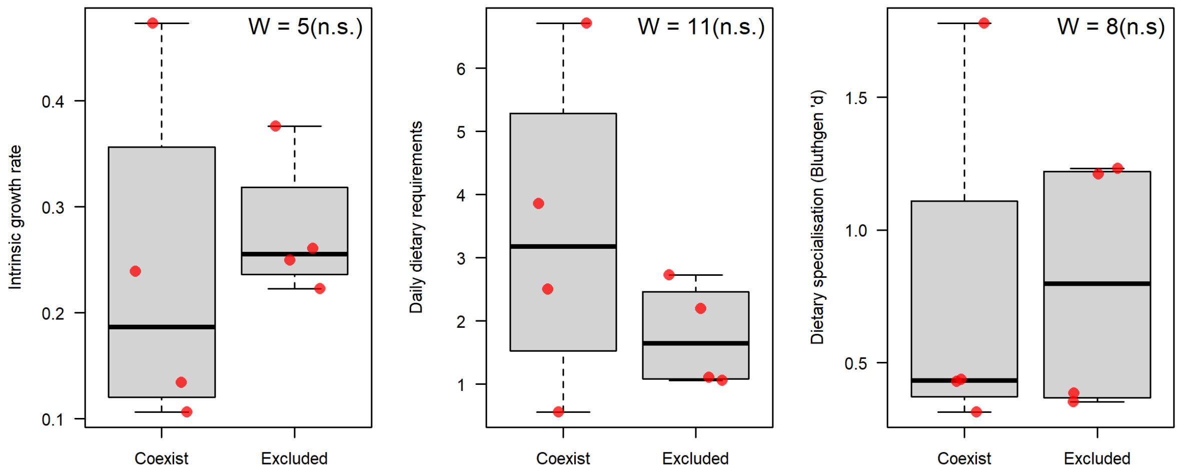

Figure S2: The intrinsic growth rates (left), daily dietary resource requirements (middle), and dietary specialisation measured using Blüthgen's *d'* (right) for species able or unable to coexist stably in Serengeti National Park, Tanzania. Red circles show individual species, and boxes show the median, first- and third quartiles, and minimum and maximum values. Reported numbers represent the test statistic from a non-parametric Mann-Whitney U test (n.s. = statistically non-significant at $\alpha = 0.05$).

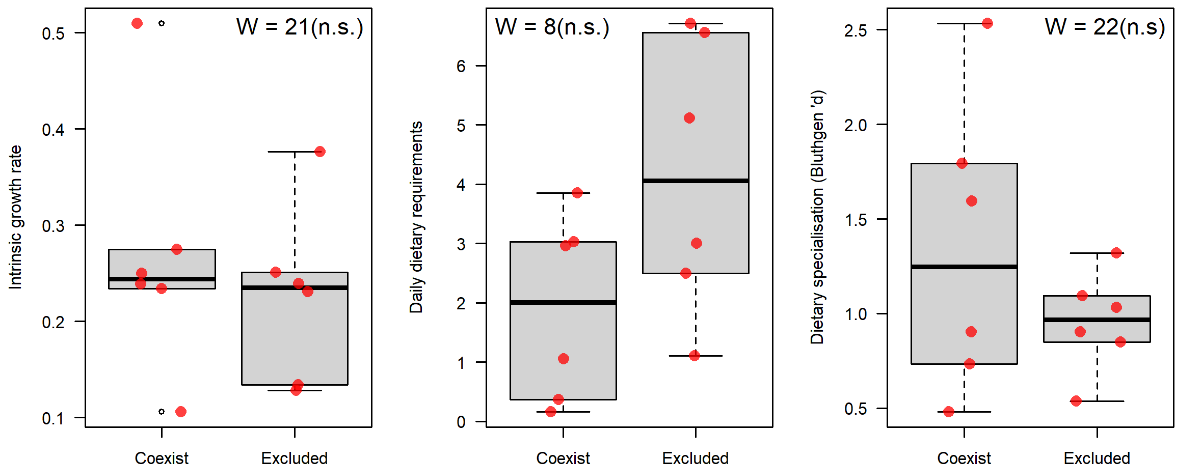

Figure S3: The intrinsic growth rates (left), daily dietary resource requirements (middle), and dietary specialisation measured using Blüthgen's *d'* (right) for species able or unable to coexist stably in Laikipia, Kenya. Red circles show individual species, and boxes show the median, first- and third quartiles, and minimum and maximum values. Reported numbers represent the test statistic from a non-parametric Mann-Whitney U test (n.s. = statistically non-significant at $\alpha = 0.05$).

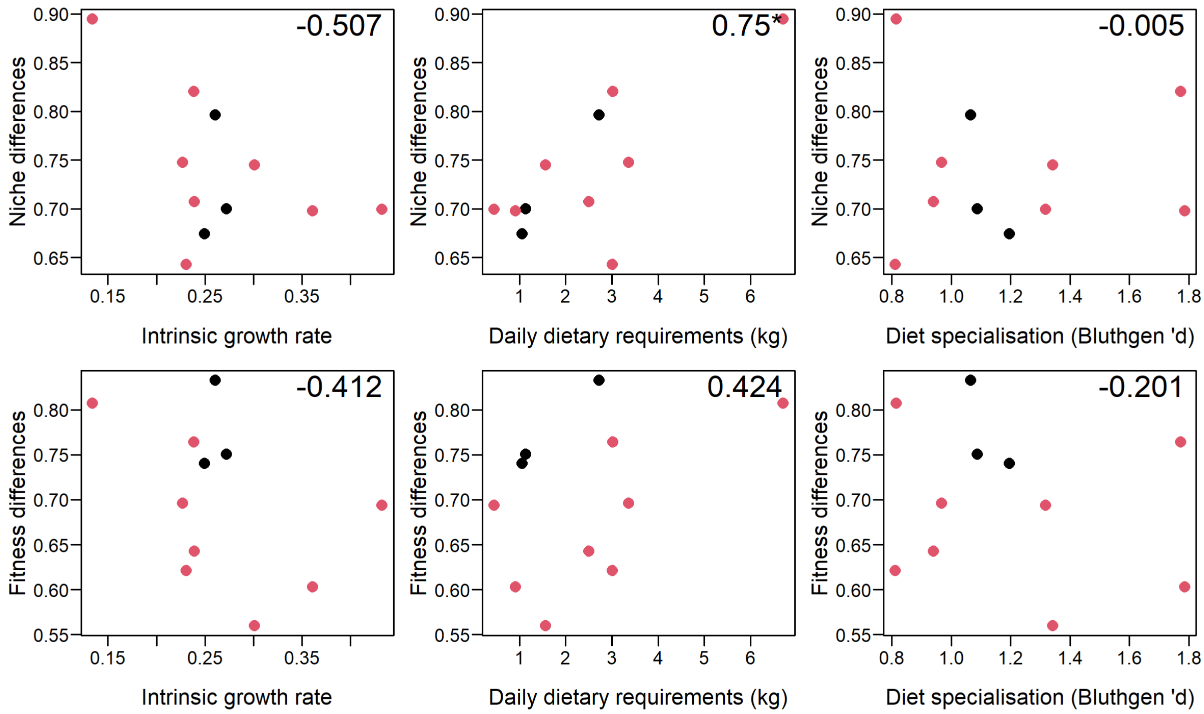

Figure S4: The relationships between niche (top row) and fitness (bottom row) differences and intrinsic growth rates (left column), daily dietary resource requirements (middle column), and dietary specialisation measured using Blüthgen's *d'* (right column) for mammal herbivores in Gorongosa National Park, Mozambique. Red points are species that can coexist stably, while black points are species that are excluded competitively. The number in each panel is the Pearson's correlation coefficient (* = statistically significant at α = 0.05).

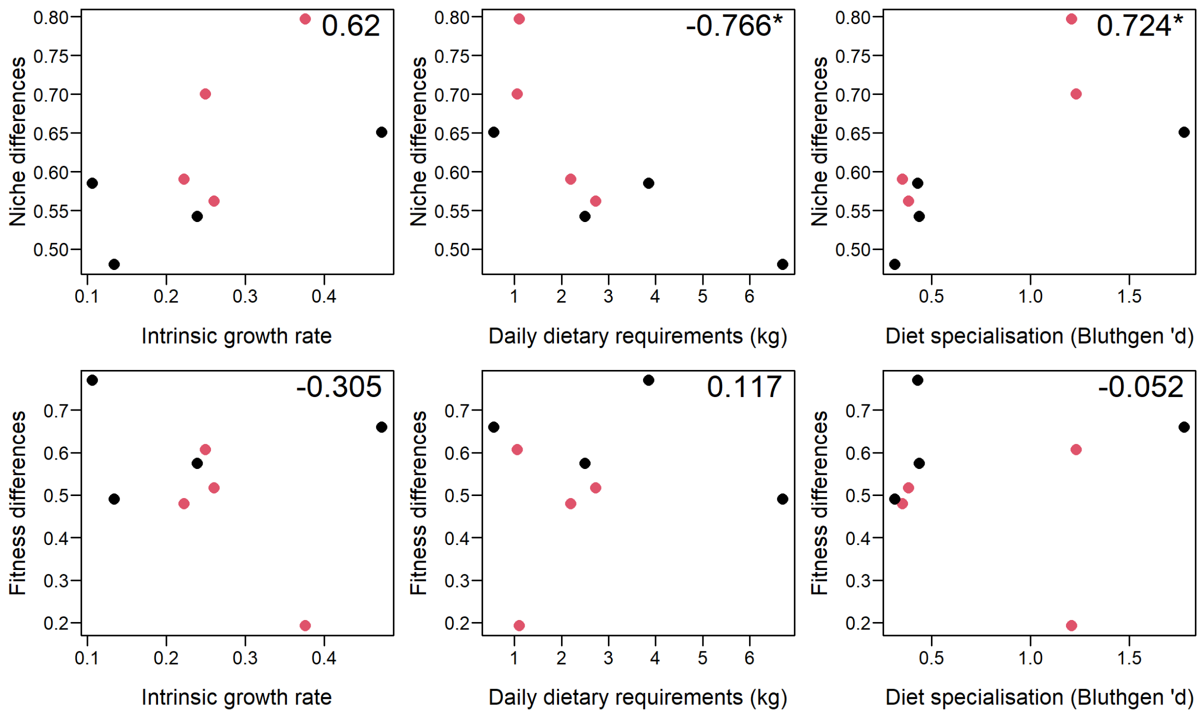

Figure S5: The relationships between niche (top row) and fitness (bottom row) differences and intrinsic growth rates (left column), daily dietary resource requirements (middle column), and dietary specialisation measured using Blüthgen's *d'* (right column) for mammal herbivores in Serengeti National Park, Tanzania. Red points are species that can coexist stably, while black points are species that are excluded competitively. The number in each panel is the Pearson's correlation coefficient (* = statistically significant at $\alpha = 0.05$).

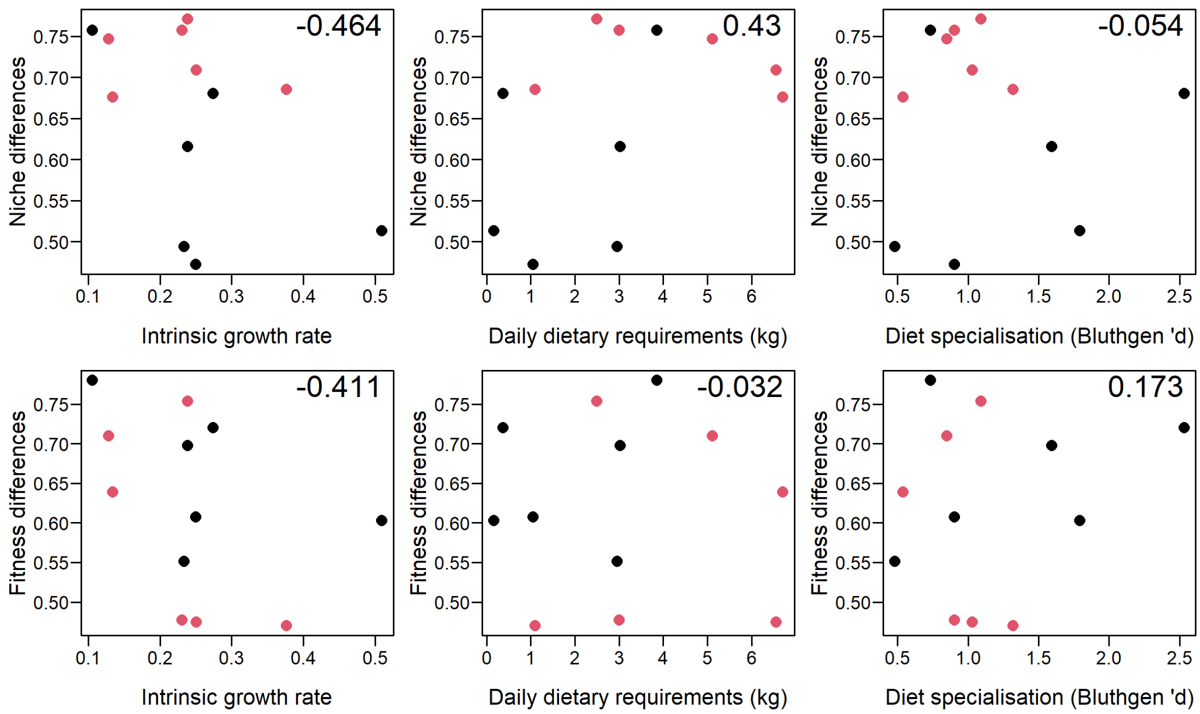

Figure S6: The relationships between niche (top row) and fitness (bottom row) differences and intrinsic growth rates (left column), daily dietary resource requirements (middle column), and dietary specialisation measured using Blüthgen's *d'* (right column) for mammal herbivores in Laikipia, Kenya. Red points are species that can coexist stably, while black points are species that are excluded competitively. The number in each panel is the Pearson's correlation coefficient (* = statistically significant at $\alpha = 0.05$).

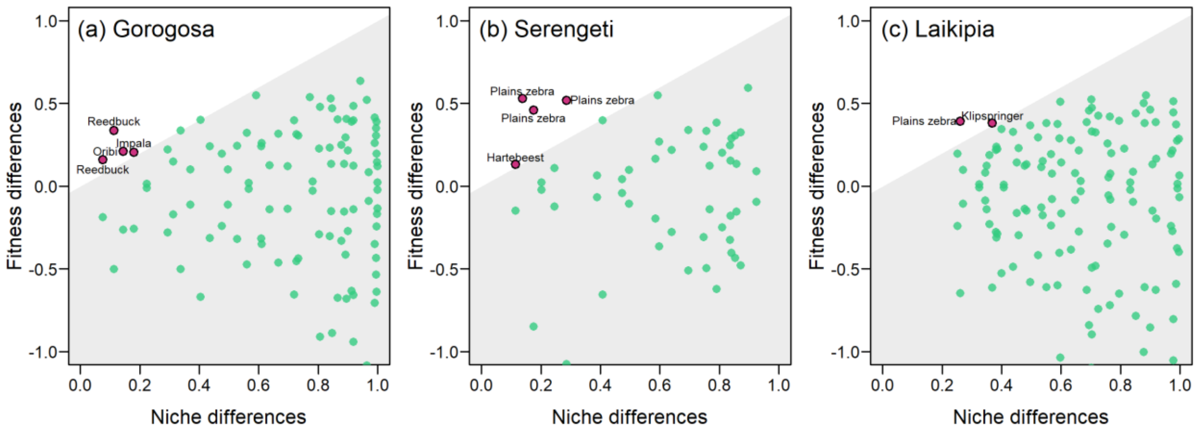

Figure S7: Niche and fitness differences for pairs of mammal herbivores in (**a**) Gorongosa National Park, Mozambique; (**b**) Serengeti National Park, Tanzania; and (**c**) Laikipia, Kenya. Green points show species whose niches are sufficiently different to overcome fitness differences, allowing for coexistence (grey zone). Labelled purple points show species unable to coexist because they are excluded by a superior competitor.

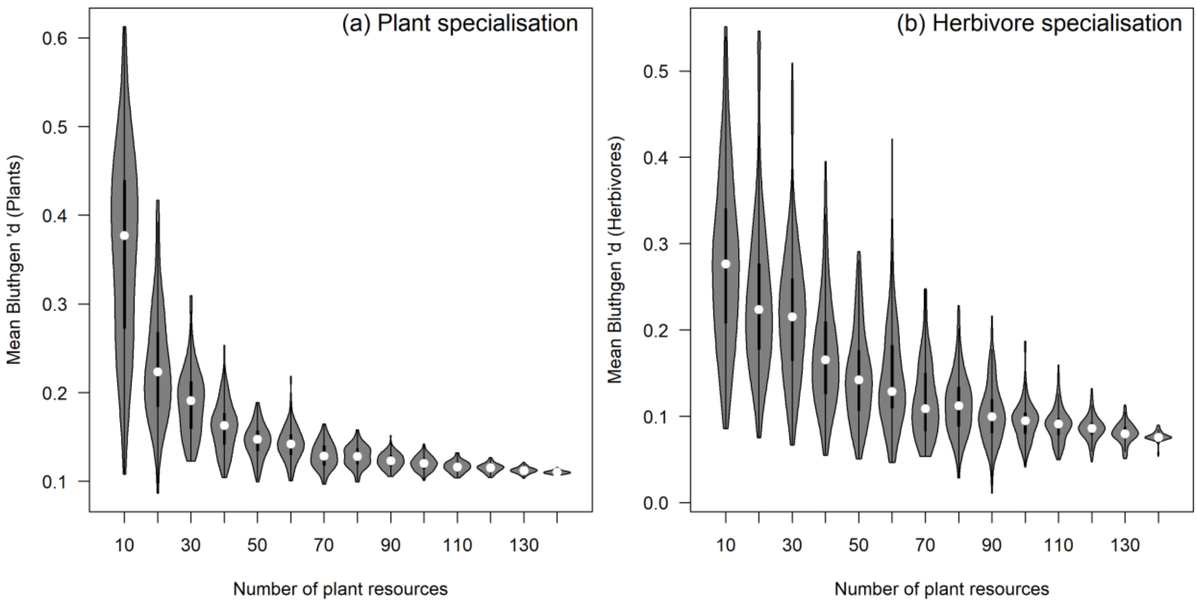

Figure S8: The specialisation of (**a**) plant resources and (**b**) mammal herbivories in Gorongosa National Park, Mozambique, for different levels of plant resources. Specialisation is measured using Blüthgen's *d'*, where higher values correspond to more specialisation: for plants, higher value mean that each plant resources is eaten by fewer herbivores; for herbivores, higher values mean that each consumer feeds on fewer plants. Violin plods show the distribution from 100 random iterations at each level of plant resources, where white circles show the median values, thick black lines show the interquartile range, and thin black lines denote the minimum and maximum values.

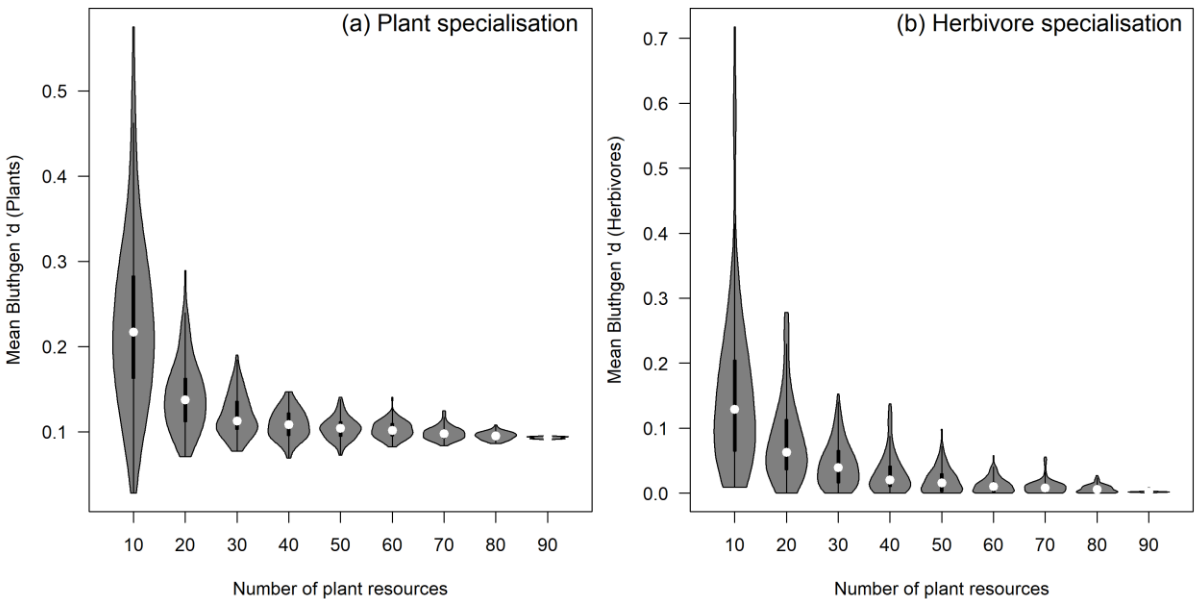

Figure S9: The specialisation of (**a**) plant resources and (**b**) mammal herbivories in Serengeti National Park, Tanzania, for different levels of plant resources. Specialisation is measured using Blüthgen's *d'*, where higher values correspond to more specialisation: for plants, higher value mean that each plant resources is eaten by fewer herbivores; for herbivores, higher values mean that each consumer feeds on fewer plants. Violin plods show the distribution from 100 random iterations at each level of plant resources, where white circles show the median values, thick black lines show the interquartile range, and thin black lines denote the minimum and maximum values.

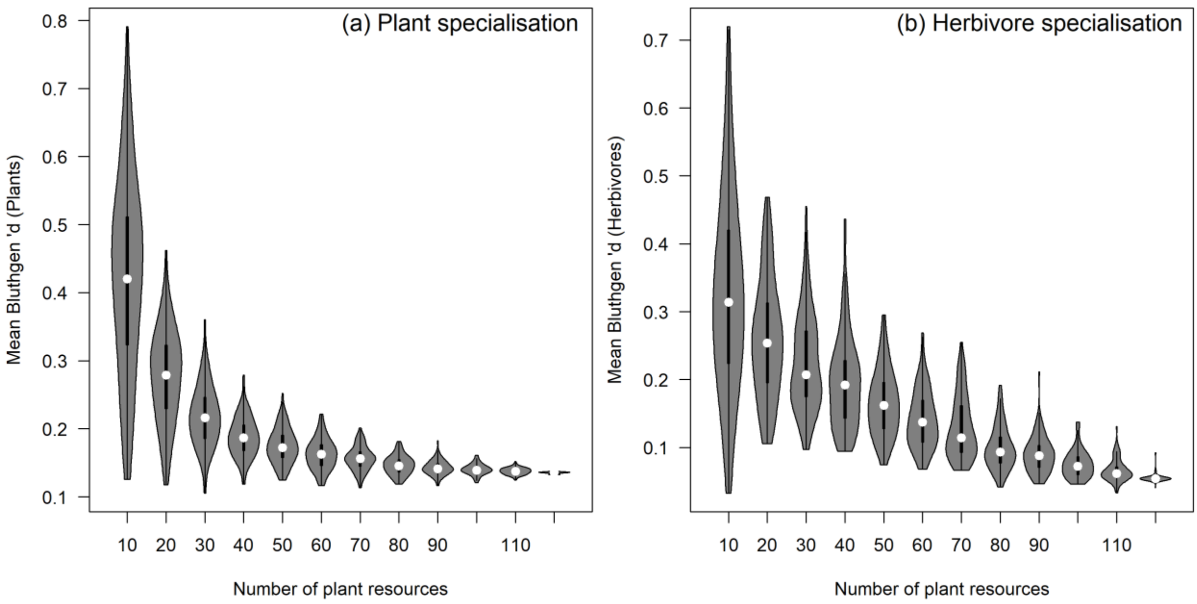

Figure S10: The specialisation of (**a**) plant resources and (**b**) mammal herbivories in Laikipia, Kenya, for different levels of plant resources. Specialisation is measured using Blüthgen's *d'*, where higher values correspond to more specialisation: for plants, higher value mean that each plant resources is eaten by fewer herbivores; for herbivores, higher values mean that each consumer feeds on fewer plants. Violin plods show the distribution from 100 random iterations at each level of plant resources, where white circles show the median values, thick black lines show the interquartile range, and thin black lines denote the minimum and maximum values.

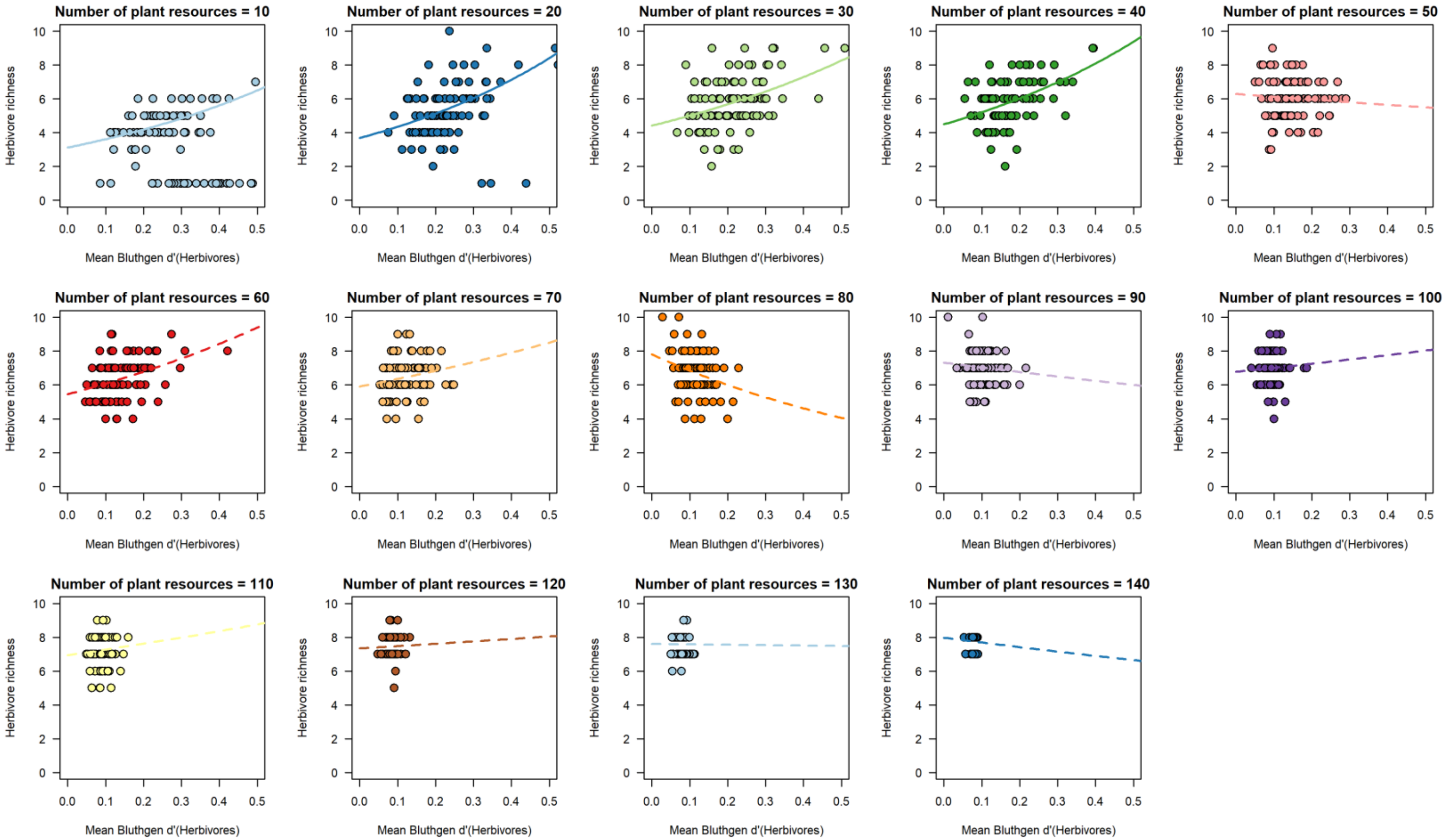

Figure S11: The relationship between mammal herbivore richness and herbivore consumption specialisation (measured using Blüthgen's *d'*) for different levels of plant resource richness in Gorongosa National Park, Mozambique. Trend lines show the relationship modelled using a generalised linear model with a Poisson error distribution, where solid lines reflect models where the slope parameters differed significantly from zero (at $\alpha = 0.05$).

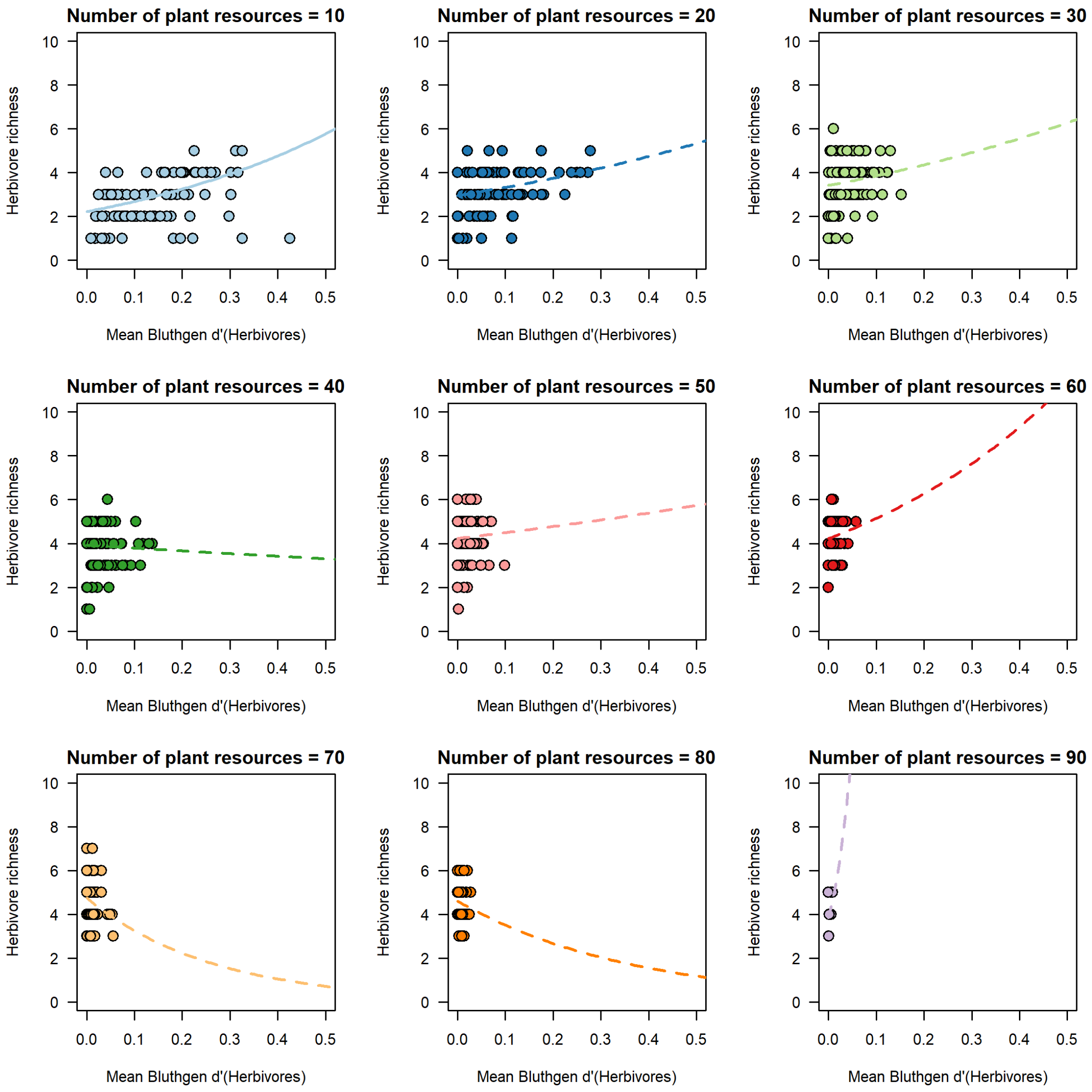

Figure S12: The relationship between mammal herbivore richness and herbivore consumption specialisation (measured using Blüthgen's *d'*) for different levels of plant resource richness in Serengeti National Park, Tanzania. Trend lines show the relationship modelled using a generalised linear model with a Poisson error distribution, where solid lines reflect models where the slope parameters differed significantly from zero (at $\alpha = 0.05$).

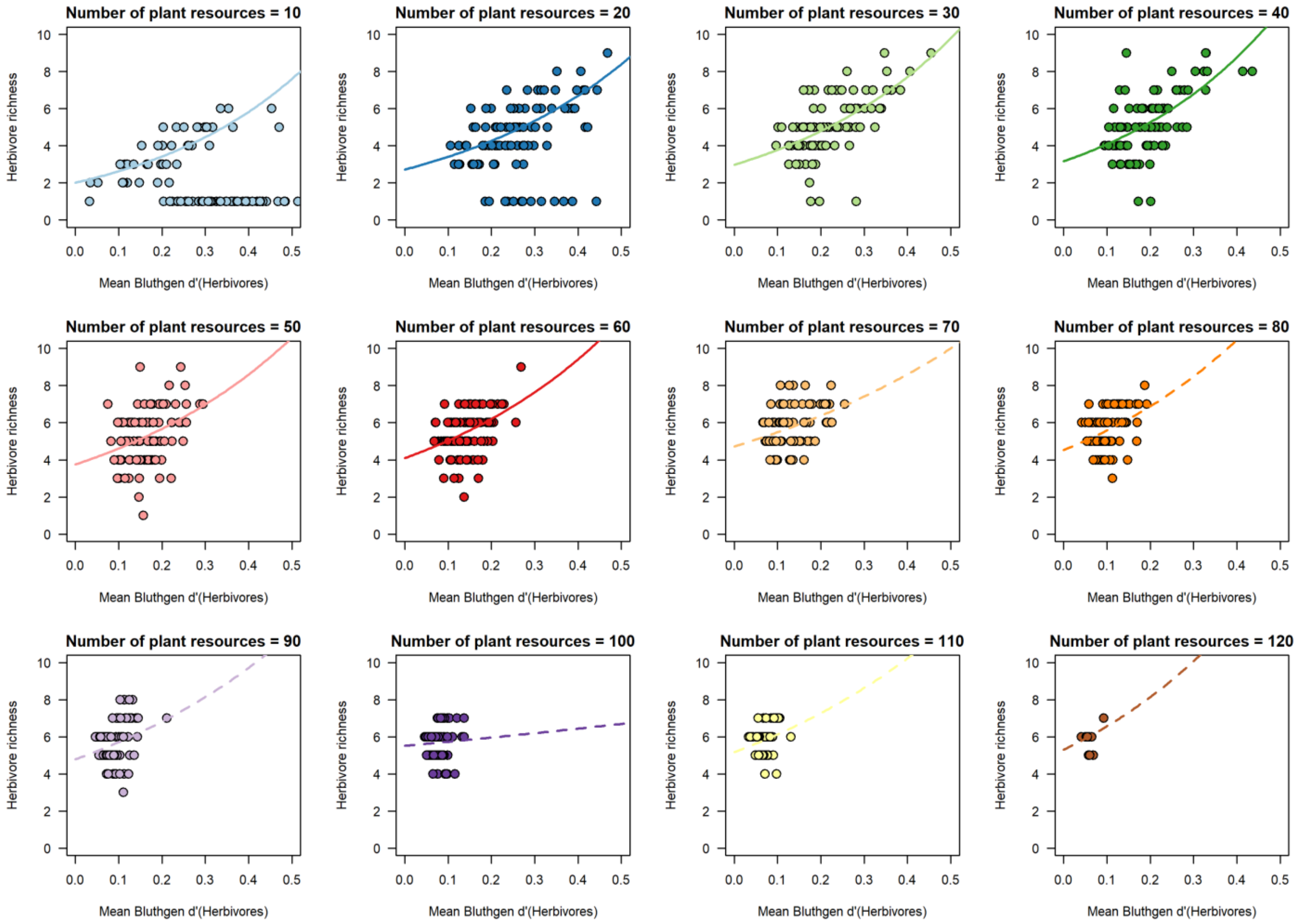

Figure S13: The relationship between mammal herbivore richness and herbivore consumption specialisation (measured using Blüthgen's *d'*) for different levels of plant resource richness in Laikipia, Kenya. Trend lines show the relationship modelled using a generalised linear model with a Poisson error distribution, where solid lines reflect models where the slope parameters differed significantly from zero (at $\alpha = 0.05$)

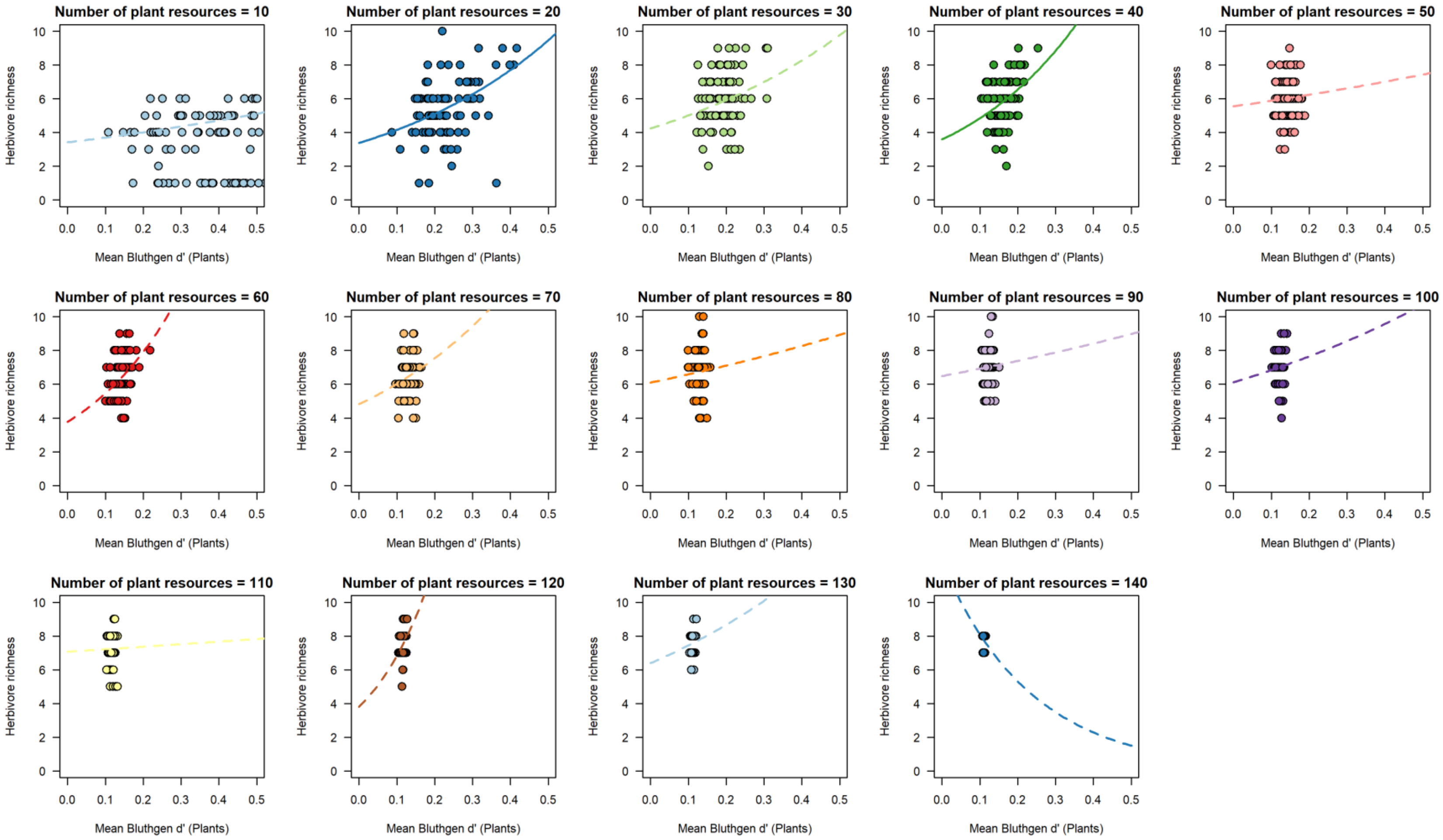

Figure S14: The relationship between mammal herbivore richness and plant resource specialisation (measured using Blüthgen's *d'*) for different levels of plant resource richness in Gorongosa National Park, Mozambique. Trend lines show the relationship modelled using a generalised linear model with a Poisson error distribution, where solid lines reflect models where the slope parameters differed significantly from zero (at $\alpha = 0.05$).

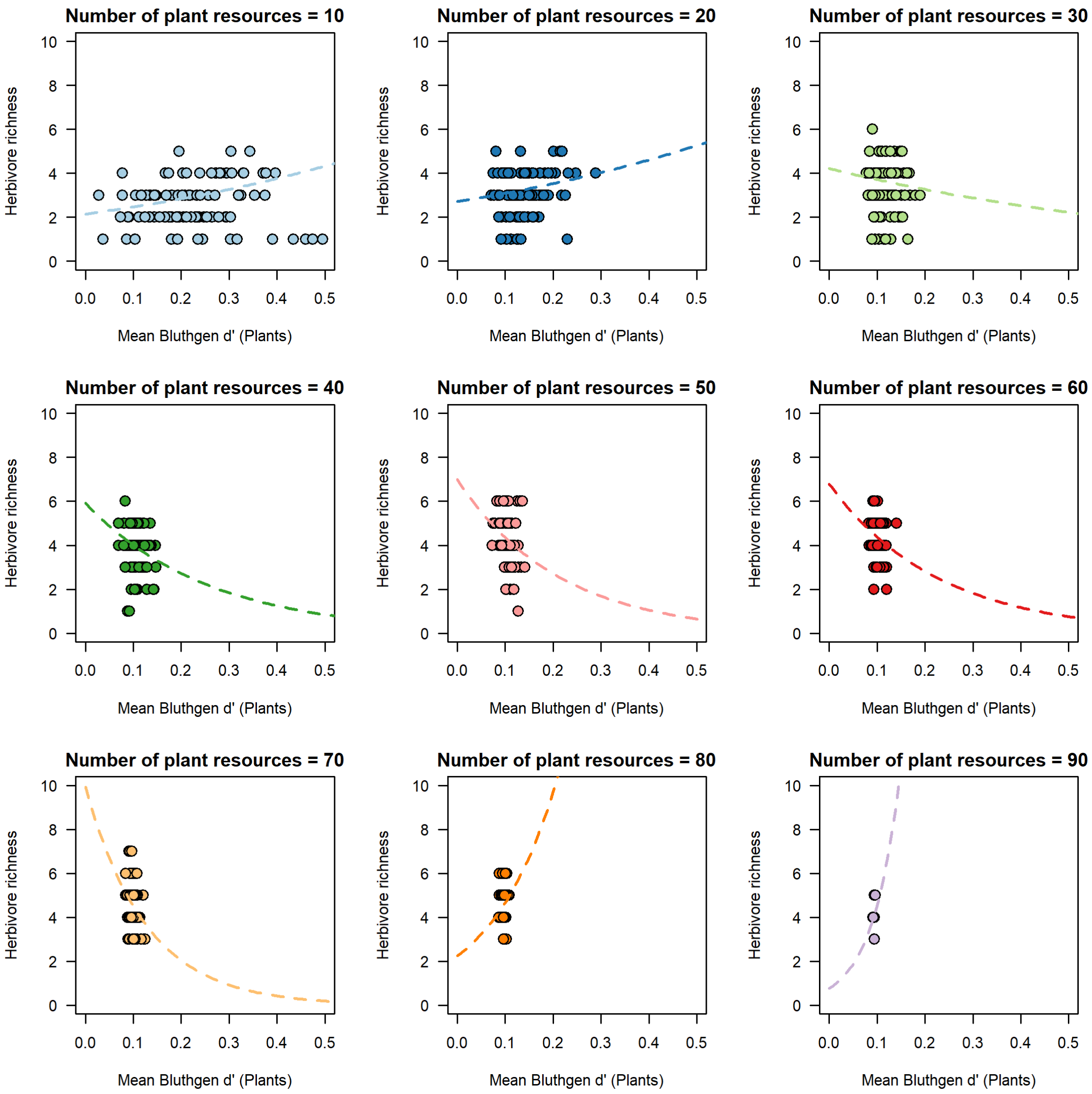

Figure S15: The relationship between mammal herbivore richness and plant resource specialisation (measured using Blüthgen's *d'*) for different levels of plant resource richness in Serengeti National Park, Tanzania. Trend lines show the relationship modelled using a generalised linear model with a Poisson error distribution, where solid lines reflect models where the slope parameters differed significantly from zero (at $\alpha = 0.05$).

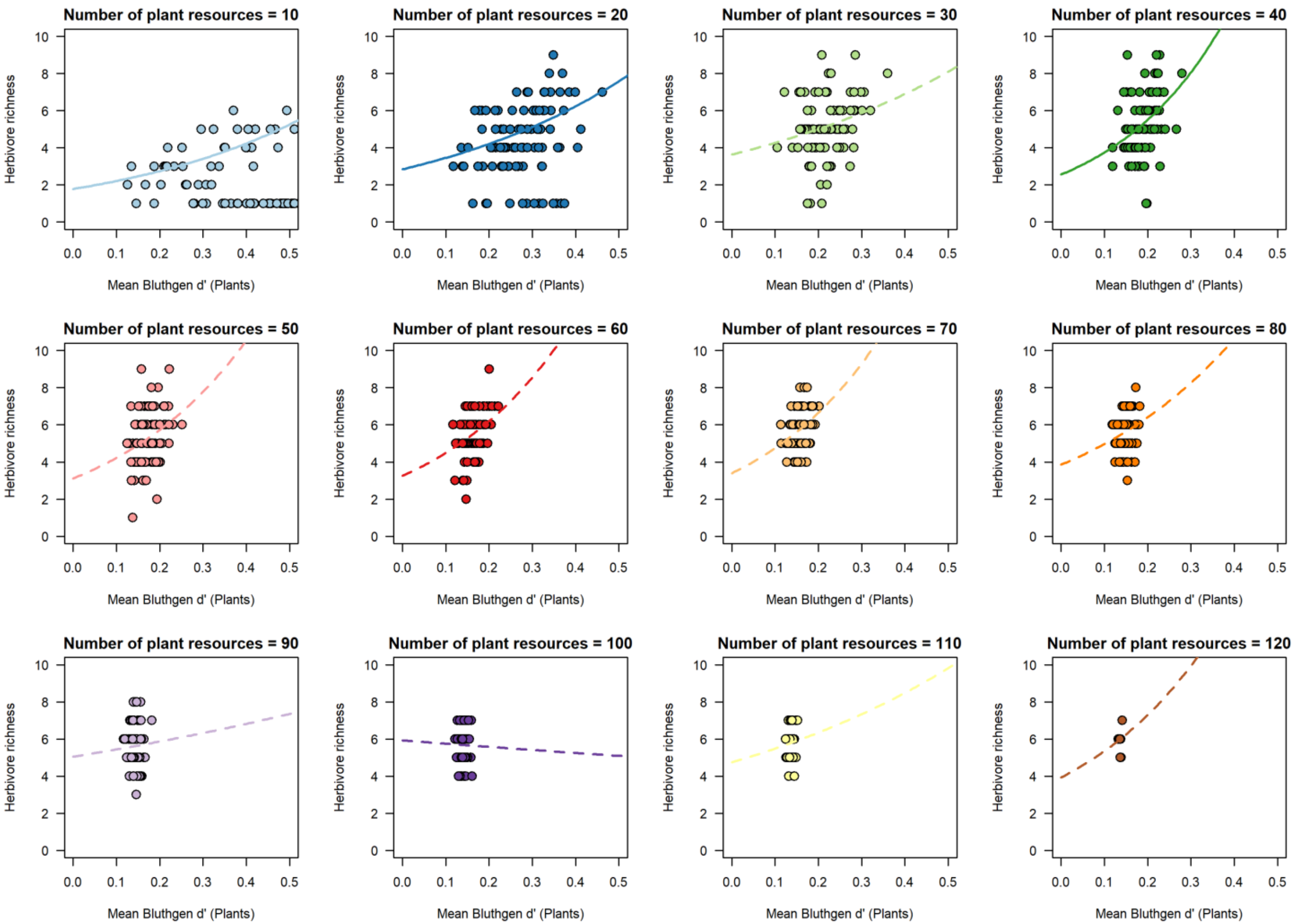

Figure S16: The relationship between mammal herbivore richness and plant resource specialisation (measured using Blüthgen's *d'*) for different levels of plant resource richness in Laikipia, Kenya. Trend lines show the relationship modelled using a generalised linear model with a Poisson error distribution, where solid lines reflect models where the slope parameters differed significantly from zero (at $\alpha = 0.05$).