

Does primary productivity modulate the indirect effects of large herbivores? A global meta-analysis

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Summary

1. Indirect effects of large mammalian herbivores (LMH), while much less studied than those of apex predators, are increasingly recognized to exert powerful influences on communities and ecosystems. The strength of these effects is spatiotemporally variable, and several sets of authors have suggested that they are governed in part by primary productivity. However, prior theoretical and field studies have generated conflicting results and predictions, underscoring the need for a synthetic global analysis.

2. We conducted a meta-analysis of the direction and magnitude of large mammalian herbivore-initiated indirect interactions using 67 published studies comprising 456 individual responses. We georeferenced 41 of these studies (comprising 253 responses from 33 locations on five continents) to a satellite-derived map of primary productivity. Because predator assemblages might also influence the impact of large herbivores, we conducted a similar analysis using a global map of large carnivore species richness.

3. In general, LMH reduced the abundance of other consumer species and also tended to reduce consumer richness, although the latter effect was only marginally significant.

4. There was a pronounced reduction in the strength of negative (i.e. suppressive, due e.g., to competition) indirect effects of LMH on consumer abundance in more productive ecosystems. In contrast, positive (facilitative) indirect effects were not significantly correlated with productivity, likely because these comprised a more heterogeneous array of mechanisms. We found no effect of carnivore species richness on herbivore-initiated indirect effect strength.

5. Our findings help to resolve the fundamental problem of ecological contingency as it pertains to the strength of an understudied class of multitrophic interactions. Moreover, these results will aid in predicting the indirect effects of anthropogenic wildlife declines and irruptions, and how these effects might be mediated by climatically driven shifts in resource availability. To the extent that intact ungulate guilds help to suppress populations of small animals that act as agricultural pests and disease reservoirs, the negative impacts of large mammal declines on human well-being may be relatively stronger in low-productivity areas.

Key-words: competition, context dependence, ecosystem engineers, large mammals, trophic cascades, ungulate herbivory

Introduction

Indirect effects, the impacts of one species on another via one-or-more intermediary species (Wootton 1994; Menge 1995; Abrams *et al.* 1996), are ubiquitous and affect diverse properties of communities and ecosystems worldwide (Pace *et al.* 1999; Werner & Peacor 2003; Estes, Brashares & Power 2013). Intensive research has focused on indirect effects driven by apex predators, such as keystone

predation (Paine 1966), apparent competition (Holt 1977) and especially trophic cascades, which have emerged as an organizing theme in community ecology (Hairston, Smith & Slobodkin 1960; Schmitz, Hambäck & Beckerman 2000; Terborgh & Estes 2010; Estes, Brashares & Power 2013).

Herbivores can also generate cascading indirect effects (Fig. 1a; Côté *et al.* 2004; Ohgushi 2005), for example by consuming or physically altering vegetation used as habitat or forage by other animal species (Wieren 1998). We refer to these as herbivore-initiated indirect interactions (HIII). Paine (2000) argued that HIII had been overlooked

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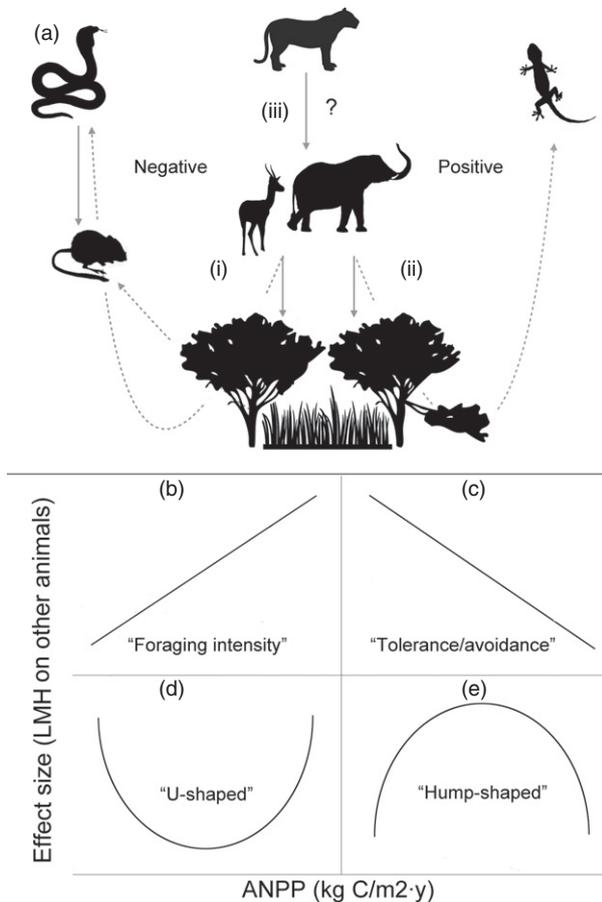


Fig. 1. (Top) Potential mechanistic pathways of herbivore-initiated indirect interactions (HIII) and (bottom) their hypothesized strengths as a function of above-ground net primary productivity (ANPP). (a) Pathways of negative (left) and positive (right) HIII that have been documented in African savannas: (i) large herbivores consume vegetation, competitively suppressing small mammals and negatively impacting snakes that prey on rodents (McCaughey *et al.* 2006); (ii) elephants are ecosystem engineers that increase microhabitat availability and quality for reptiles and amphibians by damaging trees (Nasseri, McBrayer & Schulte 2011; Pringle 2008); (iii) apex predators (e.g. leopards) may constrain the densities and/or behaviour of smaller bodied large herbivore species (Sinclair, Mduma & Brashares 2003; Ford *et al.* 2014), thereby limiting herbivores' effects on plants and dampening HIII. (b) Foraging-intensity hypothesis: effect strength increases with higher ANPP if strong plant defences (e.g. by thorny or toxic vegetation) limit herbivory at low ANPP (Coley, Bryant & Chapin 1985). (c) Tolerance/avoidance hypothesis: greater plant regrowth following herbivory and/or high assimilable vegetation biomass relative to herbivore intake rates may dampen HIII at high ANPP. (d, e) Non-monotonic responses of HIII strength to ANPP may result if plant defence and tolerance/avoidance of herbivory control herbivore impacts at different ends of the ANPP spectrum.

in the development of community ecology and that increased attention was needed to elucidate the frequency and strength of HIII – especially those of large mammalian herbivores (LMH), which he argued should be especially strong. The intervening years have seen an

increasing number of empirical studies of mammalian HIII (e.g. Suominen *et al.* 2008; Young *et al.* 2015), revealing that HIII may have either negative (e.g. competition for forage; Young, Palmer & Gadd 2005) or positive (e.g. creation of micro-habitat via ecosystem engineering; Pringle 2008; Pringle *et al.* 2015) effects on co-occurring taxa. Several reviews of HIII have also been published (Suominen & Danell 2006; Pringle *et al.* 2011; Foster, Barton & Lindenmayer 2014; Keesing & Young 2014). However, little research, and no review or meta-analysis of which we are aware, has assessed the environmental factors governing HIII strength.

Identifying the environmental drivers of context dependence, or contingency, in the strength of species interactions is a major goal in community ecology, both in general (Agrawal *et al.* 2007; Schmitz 2010) and for indirect interactions in particular (Shurin & Seabloom 2005). Primary productivity is among the most fundamental potential sources of such contingency, as it determines the availability of basal resources and thus can augment or attenuate the strength of species interactions between consumers utilizing those resources (e.g. Oksanen *et al.* 1981; Leibold 1989; Persson *et al.* 1996). In the case of predator-initiated trophic cascades, theoretical predictions of stronger effects in more productive systems (Shurin & Seabloom 2005) have received mixed empirical support (Schmitz 1994; Chase 2003; Borer *et al.* 2005; Borer, Halpern & Seabloom 2006; Bridgeland *et al.* 2010; Kurle & Cardinale 2011; Peckarsky *et al.* 2013), and a consensus remains elusive.

For HIII, the relationship between productivity and effect strength is even less clear. Although multiple studies have reported local correlations between HIII strength and productivity (Pringle *et al.* 2007; Suominen *et al.* 2008; Vesterlund *et al.* 2012; Goheen *et al.* 2013; Young *et al.* 2015), there has been no synthetic or cross-ecosystem treatment of this issue. Moreover, classic ecological theory provides grounds for contrasting predictions about how primary productivity might modify HIII. For example, low-productivity environments have less plant biomass and are predicted to filter out fast-growing, poorly defended plant species and select for slow-growing, well-defended ones (Coley, Bryant & Chapin 1985); in turn, limited availability of palatable forage in these resource-poor habitats should constrain the biomass, intake rates and per capita impacts of herbivores relative to resource-rich environments (Janzen 1974; McNaughton 1985; Grant & Scholes 2006). Thus, the strength of direct and indirect effects might be positively correlated with productivity, reflecting the distribution of herbivores and their feeding activity (Fig. 1b); we call this the 'foraging-intensity' hypothesis. Apparent support for this hypothesis comes mainly from studies showing stronger direct effects of herbivores on plants in more productive areas (Bakker *et al.* 2006; Endara & Coley 2011; Lezama *et al.* 2014), which may or may not translate into stronger indirect effects.

Alternatively, because primary productivity may increase plants' ability to tolerate or compensate following herbivory (Maschinski & Whitham 1989; Strauss & Agrawal 1999; Chase *et al.* 2000), weaker HIII might be expected in high-productivity systems where herbivore damage is repaired more rapidly (Fig. 1c). Additionally, herbivores may only be able to consume a small fraction of total plant biomass in the most productive ecosystems such as tropical rain forests, which should likewise dampen HIII. We refer to this idea as the 'tolerance/avoidance' hypothesis. Results consistent with this prediction come from African savannas, where prior studies have found stronger indirect effects of LMH in lower productivity habitats (Pringle *et al.* 2007; cf. Asner *et al.* 2009; Young *et al.* 2015).

It is also possible that interactions between the foraging-intensity and tolerance/avoidance mechanisms might produce non-monotonic relationships between productivity and HIII strength. A concave-up, U-shaped relationship is possible if weak plant defences translate into strong LMH impacts at high productivity while slow regrowth produces the same outcome at low productivity (Fig. 1d). Likewise, a unimodal, hump-shaped relationship is conceivable if strong plant defences limit herbivory in low-productivity habitats while high tolerance and/or avoidance dampens HIII strength in high-productivity habitats, generating the strongest effects at intermediate productivities (Fig. 1e).

Finally, top-down effects of apex carnivores might also influence the strength of HIII. Trophic cascades limit large herbivores' impacts on plants by suppressing herbivore densities and/or altering their behaviour (Schmitz 2008; Ford *et al.* 2014; Ripple *et al.* 2014), and this might dampen HIII. However, trophic cascades are not universal in large mammal-dominated systems (Ford *et al.* 2015), and top-down effects on species >150 kg are typically weak-to-negligible (Sinclair, Mduma & Brashares 2003). Moreover, the strengths of trophic cascades are themselves contingent on factors such as ecosystem productivity (as noted above) and predator diversity, and the direction of these contingencies is difficult to predict *a priori*. For example, high carnivore species richness might dampen cascades if intraguild predation relaxes top-down control (Finke & Denno 2004), but might strengthen them if the effects of multiple predator species are additive (Byrnes *et al.* 2006).

We conducted a meta-analysis of field studies to quantify the magnitude of LMH indirect effects on the abundance and species richness of other consumers. We coupled the abundance analysis with (a) remotely sensed data to test how effect size varied as a function of annual above-ground net primary productivity (ANPP) and (b) a global map of large carnivore distributions (Ripple *et al.* 2014) to assess whether and how predator species richness influences HIII strength. We conducted separate analyses for (a) negative HIII, which may arise from competition between LMH and sympatric consumers for plants used

as food and/or habitat (Foster, Barton & Lindenmayer 2014; Keesing & Young 2014; Takagi & Miyashita 2014), and (b) positive HIII, which can occur due to a diverse array of facilitative mechanisms, including physical habitat engineering, resource provisioning through excreta and modification of plant secondary chemistry (McNeil & Cushman 2005; Suominen & Danell 2006; Barrett & Stiling 2007).

Following Paine (2000), we focused on LMH (>5 kg) because their large size leads to pronounced impacts on plant traits, biomass, and community composition, which in turn are likely to generate indirect effects. Understanding the environmental conditions that modulate the strength of HIII is important in accounting for and predicting the outcomes of anthropogenic activity and management actions world-wide: whereas diverse native LMH assemblages continue to decline in Africa (Craigie *et al.* 2010) and Asia (Corlett 2007), deer, macropod, and feral ungulate populations are increasing in many parts of the Americas, Europe, Australia and on islands (Coulson 2002; Côté *et al.* 2004; Kaji *et al.* 2010).

Materials and methods

QUANTIFYING EFFECT SIZES

We conducted a literature search using ISI Web of Science to find peer-reviewed field studies that reported the effects of ≥ 2 levels of density of at least one wild LMH species (i.e. >5 kg body mass) on the abundance and/or species richness of at least one other animal species. Additional references were collected from the works cited in these articles and from the few previous reviews of HIII (Wieren 1998; Suominen & Danell 2006; Foster, Barton & Lindenmayer 2014). The Web of Science search yielded approximately 1500 articles. By reviewing these abstracts and additional articles cited in relevant papers, we selected 111 studies for thorough evaluation. Of these, 64 studies comprising 442 responses (defined as a single taxon's abundance or species richness) were ultimately included. This initial set of studies did not include any from hyperproductive forested ecosystems, so to obtain a more globally representative sample, we conducted a more targeted search and identified three additional studies from Neotropical forests, yielding 14 additional responses. In total, the final data set included 67 studies spanning five continents and comprising 456 responses, with response taxa from six animal classes plus the phylum Arthropoda. Complete literature search and study inclusion criteria are in the electronic supplementary material (Text S1, Tables S1 & S2, Supporting information).

We included both manipulative ($N = 54$) and observational ($N = 13$) studies, defining two categorical treatment levels, 'high' and 'low', for the independent variable LMH density in each study. For studies that included >2 LMH densities, we used only the highest and lowest densities, allowing inclusion of the greatest number of studies using

consistent methods. If a study had a factorial design assessing factors additional to LMH density, we compared pairs of treatments that differed only in LMH density, and included separate responses for each combination of LMH density (high vs. low) and the interacting factor.

To obtain treatment means for response variables, we extracted numerical data from tables and text and used WebPlotDigitizer (Rohatgi 2011) to collect data from figures. When responses were given for >1 year of a study, we followed Gurevitch & Hedges (2001) and Borer *et al.* (2005) in using only the final time point to allow the longest possible time for treatment effects to emerge. We calculated effect sizes at the most taxonomically specific level enabled by the data reported in each study. When studies presented several responses at the same taxonomic level, we included separate effect sizes for each. In other words, when species-level responses were presented, we calculated an effect size for each species, and when multiple species were lumped within family- or order-level responses, we calculated effect sizes for these higher taxonomic categories; however, if studies provided responses for both individual species and the higher taxonomic categories to which they belonged, we used only the lower level (more specific) data.

Effect sizes were calculated as Hedges' d (Gurevitch & Hedges 2001):

$$d = J * [(\mu_H - \mu_L) / S] \quad \text{eqn 1.1}$$

where μ_H and μ_L are the mean values of the response for the high and low LMH density treatments, respectively. J is a scaling factor that reduces the influence of studies with small sample size:

$$J = 1 - [3 / (4 * (N_H + N_L - 2) - 1)] \quad \text{eqn 1.2}$$

where N_H and N_L are sample sizes for the two treatment levels. S is the pooled standard deviation of the two treatments:

$$S = \sqrt{[(N_H - 1)(s_H^2) + (N_L - 1)(s_L^2)] / (N_H + N_L - 2)} \quad \text{eqn 1.3}$$

where s_H and s_L are the simple standard deviations of the response for the high and low LMH density treatments. The variance of d was calculated following Gurevitch & Hedges (2001) as:

$$\text{var} = [(N_L + N_H) / (N_L \cdot N_H)] + [d^2 / (2 \cdot (N_L + N_H))] \quad \text{eqn 1.4}$$

QUANTIFYING PRIMARY PRODUCTIVITY AND CARNIVORE SPECIES RICHNESS

For the 64 studies that reported HIII on abundance, we collated information about site attributes, including

geographic coordinates, names of protected areas, plot size(s) and maps. In four cases, we obtained clarifying information by contacting authors. It was possible to locate 41 studies to within areas of $\leq 100 \text{ km}^2$ (Fig. 2); these 41 studies were from 33 localities, and included both suppressive and facilitative HIII. (Only eight geographically localizable studies reported HIII on species richness, which was insufficient for analysis.) For each study, we delineated a polygon encompassing the study area and calculated ANPP as the 2000–2013 average derived from a cloud cover- and aerosol-corrected version of the MODIS 17A3 product (1-km resolution, Fig. 2; Zhao *et al.* 2005) in ArcMap 10.0 (ESRI, Inc., Redlands, CA). We averaged the ANPP values for all pixels partially or fully overlapping each polygon.

In addition, we manually extracted the number of large carnivore species (>15 kg) whose current ranges overlap each study site by georeferencing a published map of global carnivore species richness (Ripple *et al.* 2014). These data represent distributional extents derived from the IUCN Red List (IUCN 2012; Ripple *et al.* 2014).

ANALYSIS

To test the direction and strength of HIII on the (a) abundance and (b) species richness of response taxa, we conducted separate multilevel random-effects meta-analyses, with effect sizes weighted by the inverse of their variances (Gurevitch & Hedges 2001; Nakagawa & Santos 2012). Random-effects meta-analyses do not assume a single 'true' effect size within groups of studies, making them well-suited to ecological phenomena likely to differ in magnitude across systems. Because multiple effects reported from a single study or taxon may not be entirely independent (Nakagawa & Santos 2012), we included a random-effects term for study ID in each model. Likewise, because closely related taxa may respond in similar ways, we included a second random effect for the taxonomic affiliation of the response group (i.e. vertebrate class, or phylum in the case of Arthropoda).

In addition to these overall meta-analyses, we conducted separate tests for each taxon with ≥ 5 effect sizes (for abundance: birds, mammals, amphibians, reptiles and arthropods; for richness: arthropods). These taxon-specific meta-analyses included a random-effects term for study ID. We computed the total heterogeneity within each meta-analysis as I^2 (the percentage of variation across effect sizes due to true differences, not chance) following Higgins *et al.* (2003):

$$I^2 = (100) * (Q - \text{d.f.}) / Q \quad \text{eqn 1.5}$$

where Q is Cochran's heterogeneity statistic and df is the degrees of freedom (the number of studies - 1). To quantify how much heterogeneity was present among the effect sizes for different taxa and study IDs, we calculated

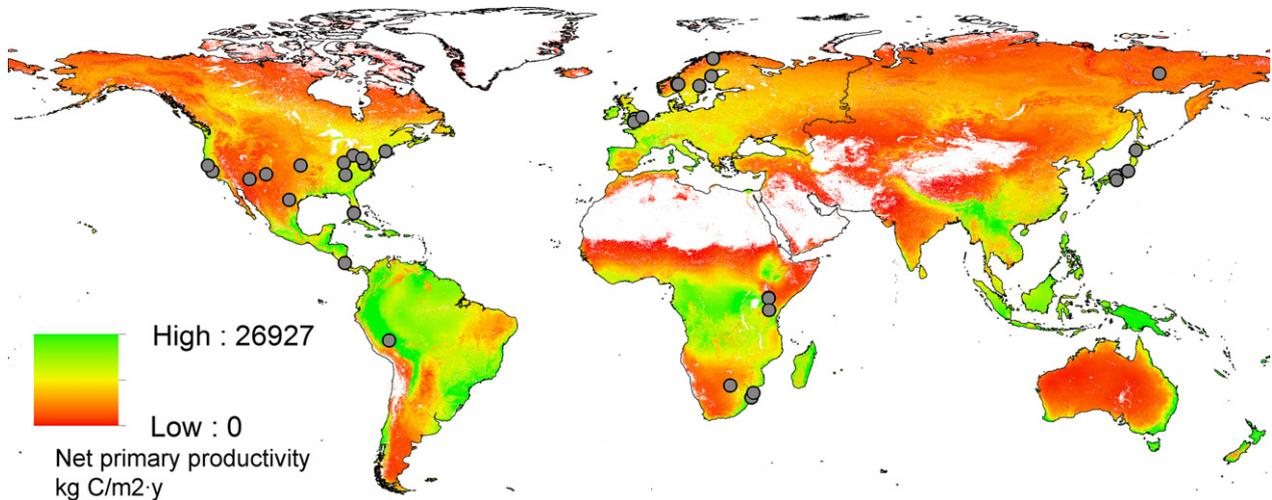


Fig. 2. Locations of studies included in the meta-regressions overlaid on a global map of average ANPP over the years 2000–2013 (Zhao *et al.* 2005).

the percentage of heterogeneity due to these random-effects groups, following Nakagawa & Santos (2012).

Publication bias, including the failure to capture unpublished non-significant results, is a risk in all data syntheses, including meta-analysis (Borenstein *et al.* 2009). To assess the possibility of publication bias in our data set, we created contour-enhanced funnel plots (Peters *et al.* 2008). If statistically significant studies are more likely to be published than are non-significant results, the plots should show larger effects sizes associated with larger standard errors. We also used Egger's regression to test for an association between the meta-analytic residuals and standard errors of the effect sizes within our data set (Nakagawa & Santos 2012; Koricheva & Gurevitch 2014). This is a more specific test for publication bias than the funnel plot examination, because the meta-analytic residuals take random-effects groupings into account. We found no indication of publication bias in our data and report the details and results of these assessments in the online supplement (Text S3, Table S3 & Fig. S1, Supporting information).

For both negative (suppressive) and positive (facilitative) HIII, we constructed separate sets of candidate meta-regression models (Table 1). We used a linear [$d = \beta \cdot ANPP + \text{intercept}$] and a power function model [$d = 1/(\beta \cdot ANPP) + \text{intercept}$] to test for the monotonic relationships predicted by our foraging intensity and plant tolerance hypotheses, respectively (Fig. 1b,c). To test for non-monotonic (i.e. U- or hump-shaped) responses of HIII strength to ANPP (Fig. 1d,e), we used the model $d = \beta_1 \cdot ANPP^2 + \beta_2 \cdot ANPP + \text{intercept}$. Each of these three models was specified both as described above, and also with the addition of a predator richness term (i.e. six total models including ANPP). The seventh model included predator species richness as the only predictor. All candidate models were multilevel random-effects meta-regression models including a random-effects term

for responding taxon. Because all studies in the meta-regressions were georeferenced, we nested taxonomic effects within a random-effects term for study location, instead of including a random study ID term as in the meta-analyses described above. Two locations hosted more than one study: Wytham Woods in the UK (two studies) and Mpala Research Centre in Kenya (nine studies). We accounted for potential spatial autocorrelation among effect sizes by forcing a correlated structure to the random-effect variances (Viechtbauer 2015) as defined by a set of spatial weights calculated in ArcMap from the inverse of the distances between locations. This procedure assumes effect sizes from sites that are geographically close together to be less independent than those from sites that are farther apart. We also included a null model in both the positive and negative HIII candidate sets for comparison with the ANPP-parameterized models; this null model was fit with only the random-effects terms and was included to ensure that parameterized models provided an improved fit. We used the small sample size bias-corrected form of Akaike's information criterion (AIC_c) to define the top-performing model for each of the positive and negative HIII sets and assessed each model's relative likelihood of being the best in the candidate set using Akaike weights (w_i) (Burnham, Anderson & Burnham 2002; Anderson 2008).

All meta-analyses and meta-regressions were conducted in R v3.2.2 with the function *rma.mv* in the package *metafor* (Viechtbauer 2010; R Core Team 2013) and included a residual error term to account for the distance between each data point and the model-predicted d values.

Results

LMH had significantly negative overall effects on the abundance of other animals (Fig. 3; mean $d = -0.37$, 95% CI $[-0.72, -0.01]$, $N = 424$). Effect sizes from

Table 1. Meta-regression model specifications, coefficients, and model selection for (top) negative HIII (top) and positive HIII (bottom)

Rank		Model specification	B	SE	AIC _c	ΔAIC _c	w _i	% Deviance
Negative HIII								
1	Power	$\sim 1/(\beta \cdot ANPP)$			449.76	–	0.43	2.29
		ANPP	–0.40	0.13				
		Intercept	–0.41	0.27				
2	Power + CR	$\sim 1/(\beta_1 \cdot ANPP) + \beta_2 \cdot CR$			450.65	0.89	0.28	2.72
		ANPP	–0.53	0.16				
		CR	0.09	0.07				
		Intercept	–0.40	0.27				
3	Linear	$\sim \beta \cdot ANPP$			453.29	3.53	0.07	1.21
		ANPP	0.87	0.41				
		Intercept	–1.75	0.32				
4	Quadratic	$\sim \beta_1 \cdot ANPP^2 + \beta_2 \cdot ANPP$			453.32	3.56	0.07	1.91
		ANPP ²	–3.40	2.16				
		ANPP	5.76	3.08				
		Intercept	3.16	0.91				
5	Quadratic + CR	$\sim \beta_1 \cdot ANPP^2 + \beta_2 \cdot ANPP + \beta_3 \cdot CR$			453.36	3.6	0.07	2.61
		ANPP ²	–5.03	2.29				
		ANPP	8.65	3.44				
		CR	0.14	0.09				
		Intercept	4.53	1.22				
6	Null	$\sim NULL$			454.99	5.23	0.03	–
		Intercept	–1.09	0.13				
7	Linear + CR	$\sim \beta_1 \cdot ANPP + \beta_2 \cdot CR$			455.21	5.45	0.03	1.34
		ANPP	1.11	0.54				
		CR	0.05	0.08				
		Intercept	–2.04	0.55				
8	CR	$\sim \beta \cdot CR$			456.62	6.86	0.01	0.20
		CR	–0.05	0.06				
		Intercept	–0.98	0.19				
Positive HIII								
1	Null	$\sim NULL$			339.64	0	0.43	–
		Intercept	0.77	0.12				
2	Power	$\sim 1/(\beta \cdot ANPP)$			341.71	2.07	0.15	0.10
		ANPP	0.08	0.14				
		Intercept	0.67	0.24				
3	CR	$\sim \beta \cdot CR$			341.90	2.26	0.14	0.02
		CR	0.012	0.07				
		Intercept	0.75	0.15				
4	Linear	$\sim \beta \cdot ANPP$			341.94	2.30	0.14	0.00
		ANPP	0.02	0.17				
		Intercept	0.75	0.21				
5	Power + CR	$\sim 1/(\beta_1 \cdot ANPP) + \beta_2 \cdot CR$			344.02	4.38	0.05	0.11
		ANPP	0.08	0.14				
		CR	0.01	0.07				
		Intercept	0.65	0.25				
6	Linear + CR	$\sim \beta_1 \cdot ANPP + \beta_2 \cdot CR$			344.26	4.62	0.04	0.02
		ANPP	0.00	0.18				
		CR	0.01	0.07				
		Intercept	0.75	0.21				
7	Quadratic	$\sim \beta_1 \cdot ANPP^2 + \beta_2 \cdot ANPP$			344.29	4.65	0.04	0.01
		ANPP ²	0.04	0.49				
		ANPP	–0.10	1.34				
		Intercept	0.81	0.67				
8	Quadratic + CR	$\sim \beta_1 \cdot ANPP^2 + \beta_2 \cdot ANPP + \beta_3 \cdot CR$			346.66	7.02	0.01	0.02
		ANPP ²	–0.03	0.64				
		ANPP	0.10	1.71				
		CR	0.02	0.10				
		Intercept	0.70	0.89				

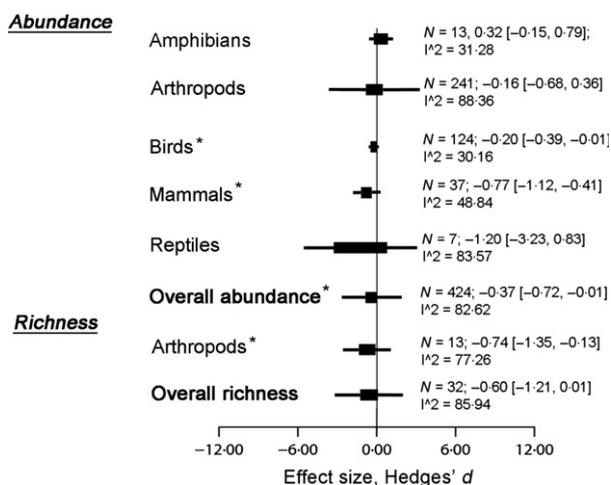


Fig. 3. Large mammalian herbivore effects on consumer abundance and species richness. Summary effects are shown for each taxonomic class with at least five responses, and for all taxa combined. Black rectangles represent the 95% confidence interval for the summary effect size (values in parentheses; asterisk indicates statistical significance), and whiskers represent the 95% credible interval (the range within which 95% of true effect sizes for the population of studies for each group are estimated to fall). Values of I^2 represent the percentage of variation across effect sizes due to true heterogeneity, not chance, calculated following (Higgins *et al.* 2003).

different studies were moderately heterogeneous (47.9% of total heterogeneity), with only minimal heterogeneity due to differences among taxonomic groups (3.4%). We also found a marginally significant negative overall effect of LMH on consumer species richness ($d = -0.60$, $[-1.27, 0.01]$, $N = 32$). As for the abundance effects, most of the heterogeneity in richness effects was among studies (55.5%), with little differentiation among taxonomic groups (<1%). When individual taxonomic groups were analysed separately, we found significantly negative HIII on bird and mammal abundance, and on arthropod species richness; the trends for arthropod and reptile abundance were negative but not statistically significant.

The ANPP of study sites in the data set ranged from 0.18 to 1.17 kg C m⁻² y, except for one study from the highly productive Peruvian Amazon (2.21 kg C m⁻² y; Beck, Thebpanya & Filiaggi 2010). Thus, our sample is broadly representative of the range of terrestrial ecosystems where substantial LMH populations occur, as <10% of the global land surface has ANPP > 1.17 kg C m⁻² y (although substantial desert and tundra regions have ANPP < 0.18 kg C m⁻² y).

The strength of negative HIII decreased with increasing ANPP, and there was greatest support for the ANPP power function fit to these data ($w_i = 0.43$; Fig. 4a-c; Table 1). The model with predator species richness alone was the worst-ranked model for negative HIII ($w_i = 0.01$; Fig. 4d), and models including predator richness were never ranked higher than the corresponding ANPP-only models. In contrast, there was no discernible relationship

between positive HIII strengths and either ANPP or predator richness (Fig. 4e,f); here, the null model was the best-supported ($w_i = 0.43$; Table 1).

Discussion

We found that LMH typically have suppressive indirect effects on consumer abundance, consistent with the few prior reviews of the topic (Wieren 1998; Suominen & Danell 2006; Foster, Barton & Lindenmayer 2014). We also detected a trend towards negative HIII on consumer richness, although this result was only marginally significant and may not be robust. When abundance responses of individual taxa to LMH were considered separately, the only groups with significant directional responses were mammals and birds, which declined with increasing LMH density. We suggest that these negative HIII stem from the consumption by LMH of resources required by these two groups. All but one of the 37 mammal responses were of small mammals, primarily herbivorous or omnivorous rodents that may compete with LMH for forage (e.g. Keesing 2000). Similarly, the 124 bird responses included many species that are at least partially granivorous, frugivorous or nectarivorous, and LMH have also been shown to negatively affect birds generally by reducing the availability of perch sites and safe spaces (Ogada *et al.* 2008). In contrast, adult amphibians and reptiles are almost exclusively carnivorous, and therefore unlikely to compete with LMH for food [although suppression of the rodent and insect prey of herpetofauna can have analogous effects (McCauley *et al.* 2006; Pringle *et al.* 2007), and LMH may be as likely to enhance habitat availability/quality for these species as to diminish it (see discussion of positive HIII below)]. The absence of consistent HIII on arthropod abundance may reflect the enormous ecological diversity subsumed within this group; we analysed arthropods together because many of the original studies did the same, but future studies should strive for greater taxonomic resolution.

Our finding of stronger negative HIII at lower productivity is consistent with our 'tolerance/avoidance' hypothesis (Fig. 1c). Indeed, meta-analyses from both terrestrial and marine systems confirm that regrowth following herbivory is slower at lower productivities (Chase *et al.* 2000; Burkepile & Hay 2006), suggesting that HIII involving taxonomically diverse herbivores across a diverse range of ecosystems may be moderated by the same mechanism. Likewise, the few primary studies reporting HIII strengths across productivity gradients within single ecosystems support the tolerance/avoidance hypothesis. In Lapland, Suominen *et al.* (2003) found stronger negative effects of reindeer on carabid and curculionid beetles at sites with lower productivity. Similarly, Pringle *et al.* (2007) and Young *et al.* (2015) found stronger negative effects of African LMH on arthropods, lizards and rodents at lower productivity sites. These localized (and our own global) results are collectively consistent with the expected

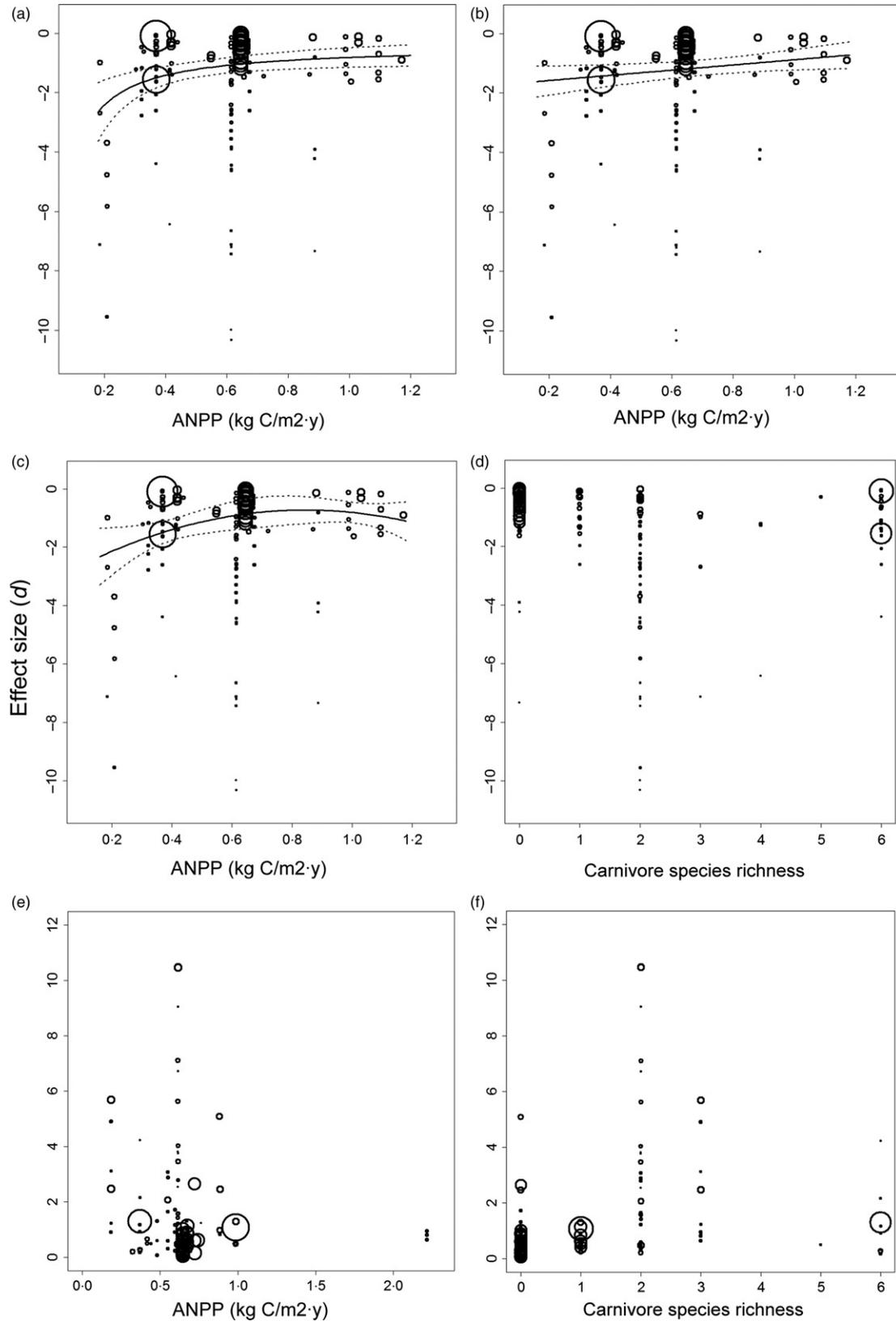


Fig. 4. Relationships between effect size (Hedge's d) of HIII on consumer abundance and ANPP or predator richness. The strength of negative (i.e. suppressive) HIII decreased (smaller magnitude) with increasing ANPP according to (a) power, (b) linear and (c) quadratic fits. The power function in panel A was the top-ranked model by AIC-based model selection (Table 1). (d) There was no detectable relationship between negative HIII strengths and carnivore species richness. Positive (i.e. facilitative) HIII were not significantly correlated with either (e) ANPP or (f) carnivore richness. For all panels, point size is proportional to $1/\sqrt{\text{var } d}$. In the regressions, points were weighted by $1/(\text{variance } d)$. Dashed lines are 95% CIs for average effect size at each value of ANPP.

positive relationship between tolerance/avoidance of herbivory and ANPP, and we posit that this is a primary mechanism governing HIII strength. Future work should focus on experimentally testing this mechanism, ideally in a range of ecosystem types with contrasting ANPP.

We found greatest support for the power function relationship between ANPP and negative HIII strengths. This suggests that although the strongest impacts of LMH on animal abundance occur in the lowest productivity systems, a greater ability of plants to tolerate and compensate for herbivory may be achieved with only moderate increases in productivity (Fig. 4a). For instance, Suominen, Danell & Bryant (1999) reported that moose browsing in low-productivity Alaskan boreal forest (ANPP = 0.18 kg C m⁻² y) shifted understorey vegetation towards mosses and grasses from a more pteridophyte- and forb-dominated state in the absence of browsing; in turn, curculionid and elaterid beetles at this Alaskan site were 31% and 40% more abundant, respectively, in unbrowsed areas. By contrast, soil arthropods in a comparatively high-productivity temperate forest (1.03 kg C m⁻² y) in Tennessee were only 4% more numerous when white-tailed deer (*Odocoileus virginianus*) were experimentally removed (Lessard *et al.* 2012).

Whereas negative HIII strengths attenuated with increasing ANPP, positive HIII strengths were uncorrelated with ANPP. We hypothesize that this contrast is due to the different suites of mechanisms that generate negative and positive HIII. Negative HIII often result from 'first-order' exploitation competition and habitat degradation [e.g. ungulates reduce availability of food and antipredator concealment for rodents: (Keesing 1998)], as well as knock-on 'second-order' competition [e.g. lower rodent densities suppress snakes, yielding a negative HIII of ungulates on snakes (McCauley *et al.* 2006)]. Such higher order effects have also been called 'trophic ricochets' (Fig. 1a; Nuttle *et al.* 2011). Intuitively, and in line with our findings, such diffuse competitive interactions should be dampened by the greater ability of plants to avoid, compensate for, or otherwise tolerate herbivory.

Positive HIII, on the other hand, arise from diverse facilitative mechanisms. First, LMH may physically engineer habitat for specialist consumers; for example, frogs live in Amazonian peccary wallows (Beck, Thebpanya & Filiaggi 2010) and Sri Lankan elephant dung (Campos-Arceiz 2009), while geckos and other reptiles find shelter among elephant-damaged trees in African savannas (Pringle 2008; Nasser, McBrayer & Schulte 2011; Pringle *et al.* 2015). Secondly, fertilization by LMH excreta can yield bottom-up effects on consumer assemblages (e.g. Barrett & Stiling 2007). Thirdly, LMH-induced reductions in leaf C:N ratios may benefit smaller, more selective herbivores (McNeil & Cushman 2005; Huntzinger, Karban & Cushman 2008). Finally, positive HIII can result from indirect mutualism or commensalism, if herbivores consume the competitors of species that are resources for responding taxa (Dethier & Duggins 1984; Menge 1995; Tilman &

Borer 2015). This more varied suite of mechanisms for positive HIII may not all respond to productivity in consistent ways (if at all), which could obscure relationships between effect size and productivity. It would be interesting to analyse each of these mechanisms independently, but currently, there are too few studies for this to be possible. It may also be that the smaller number of positive HIII ($N = 80$ individual responses) in our data set reduced the power to detect an effect of ANPP, although we consider the former explanation more likely.

Generally speaking, herbivore biomass increases with productivity (Coe, Cumming & Phillipson 1976; McNaughton *et al.* 1989). Despite the expectation that greater densities of LMH feeding on concentrations of fast-growing, poorly defended plant species should lead to stronger HIII in productive regions (Fig. 1b), our results show a negative relationship between HIII and ANPP. Thus, we found no support for the 'foraging-intensity' hypothesis.

We also found no indication that predator species richness governs HIII strength. This does not mean that HIII are generally insensitive to predation – indeed, it is difficult to believe that strong trophic cascades do not also dampen HIII. If so, however, our analysis suggests that predator species richness alone is not the primary factor governing this relationship. Instead, the relevant variable might be predator density, predator species composition, behaviour, habitat structure or combinations of these factors (Schmitz 2007; Letourneau *et al.* 2009; Ford *et al.* 2014). Future research that more comprehensively investigates the impact of predator community attributes on HIII strength would help to evaluate these possibilities.

Although ANPP had only modest precision for prediction of negative HIII strength, it is instructive that despite the broad range of ecosystems, herbivores and response taxa in our data set, we were able to detect significant directional effects of productivity on HIII. We are not aware of any previous study quantifying context dependence of HIII. Additionally, the predictive power (i.e. percentage of deviance explained) of the models presented here is similar to those reported in another recent global meta-analysis of the effects of environmental context on trophic interactions (Rodríguez-Castañeda 2013). Our inclusion of observational along with manipulative studies may also partially account for the high variability of HIII strength we observed. In observational settings, changes in wild LMH abundance may be accompanied by other anthropogenic or natural confounds (Young *et al.* 2013), reducing the signature of HIII. Finally, the precision of our analysis was necessarily limited by the 1-km resolution of the MODIS-derived ANPP data. The strengths of HIII involving the smallest response taxa (e.g. insects) in our data set may be more tightly coupled to productivity over smaller spatial scales; such fine-scale data are not presently available in a global remotely sensed product.

Our results are relevant for predicting ecological consequences of the intersection of two types of anthropogenic global change, altered LMH densities and climate change.

Predator suppression and increased forage availability have led to irruptions of cervids across large parts of North America, Europe and Japan (Côté *et al.* 2004; Kaji *et al.* 2010); the same is true of macropods in parts of Australia (Coulson 2002). In contrast, LMH densities have declined by as much as 50% in recent decades throughout much of Africa (Craigie *et al.* 2010). Our results in conjunction with prior studies indicate that such changes in LMH abundance will likely generate strong cascading community-level impacts (Côté *et al.* 2004; Keesing & Young 2014), and we show here that the strengths of these impacts depend, in part, on the primary productivity of the habitat. Specifically, consumer populations in higher productivity ecosystems may be relatively buffered from the effects of irrupting or declining populations of large herbivores. In turn, change in climatic variables such as temperature and precipitation is expected to alter primary productivity in many habitats world-wide (Grimm *et al.* 2013), which our results suggest will modulate the impacts of any concurrent changes in LMH density. Accurately forecasting the effects of global change on biodiversity requires accounting for such context dependency in the strength of species interactions, as we have tried to do here for HIII.

Data accessibility

All raw data extracted from the articles included in the present meta-analysis are available in Dryad Digital Repository <http://dx.doi.org/10.5061/dryad.kh6j6> (Daskin & Pringle 2016). References for all articles are also in the Supporting Information (Text S2, Supporting information).

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Text S1, Tables S1 & S2. Literature search and inclusion criteria.

Text S2. Bibliography for all included studies.

Text S3, Table S3, Figure S1. Investigation of potential publication bias.