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Ecological Role of Keystone Predators

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ABSTRACT

Keystone predators -- apex predators whose disproportionate ecological impact, relative to their biomass, structures community composition and maintains ecosystem diversity through top-down trophic cascades -- represent one of the most conceptually influential and empirically contested ideas in ecology. The original keystone predator concept (Paine 1966; sea otters; Pisaster sea stars) has been extended to terrestrial systems where wolves, mountain lions, and large cats are proposed to regulate ungulate populations, prevent overgrazing, and maintain vegetation structural complexity through fear-mediated 'landscape of fear' effects. Yet the universality of keystone predator effects -- and the predictability of trophic cascade strength from ecosystem properties -- remains debated. This study presents the most comprehensive multi-ecosystem meta-analysis of keystone predator effects yet conducted, synthesising 247 experimental and observational studies from 84 ecosystems across 18 biomes, covering 38 predator-prey-vegetation systems from intertidal to boreal forest to tropical savannah. Trophic cascade strength (measured as the standardised effect size of predator presence on basal resource abundance) was significantly positive across all 247 studies (mean $d = +0.84 \pm 0.38$; $p < 0.001$) -- confirming that keystone predator effects are real and consistent. Primary productivity (net above-ground primary production; NAPP) was the strongest predictor of trophic cascade strength (partial $R^2 = 0.54$; $p < 0.001$): more productive ecosystems show stronger cascades. The landscape of fear effect -- reduced herbivore grazing intensity in high-predation-risk areas -- was confirmed in 74.7% of terrestrial systems studied, contributing a mean 28.4% of the total cascade effect size independently of direct predation mortality.

Keywords: keystone predators; trophic cascades; landscape of fear; wolves; sea otters; meta-analysis; NAPP; trophic regulation

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1. Introduction

1.1 The Keystone Predator Concept

Robert Paine's 1966 experimental removal of the sea star Pisaster ochraceus from a rocky intertidal shore in Washington State produced one of the most influential results in community ecology: without Pisaster, mussels (Mytilus californianus) competitively displaced all other benthic invertebrates, reducing a diverse community of 15 species to a near-monoculture of 1-2 species. Paine's conclusion -- that some species exert a disproportionate effect on ecosystem diversity relative to their biomass, and that their removal triggers community collapse -- gave rise to the keystone species concept, which became the dominant framework for understanding how community diversity is maintained and the primary ecological justification for apex predator conservation. The logic is compelling: if apex predators maintain diversity by preventing competitive exclusion at lower trophic levels, then their removal should trigger trophic cascades -- propagating effects down through the food web from predator loss to herbivore irruption to vegetation overgrazing -- with measurable negative consequences for biodiversity and ecosystem function (Estes et al., 2011).

1.2 Debate and the Landscape of Fear

Despite the conceptual influence of the keystone predator idea, the empirical evidence for strong trophic cascades in terrestrial ecosystems has been contested: some studies find large effects of wolf or large cat removal on ungulate populations and vegetation; others find that human hunting, weather variation, or bottom-up productivity controls dominate population dynamics with predation playing a minor role. The 'landscape of fear' concept -- proposing that prey animals modify their behaviour (reduced grazing in high-risk areas; habitat avoidance; increased vigilance) in response to predation risk, independently of actual predation mortality -- extended the predicted effects of predators beyond direct kill rates to include indirect behavioural modification of prey habitat use. The relative importance of direct (kill-based) vs. indirect (fear-based) predator effects on trophic cascades is a central empirical question addressed by this meta-analysis.

1.3 Objectives

This study addresses four objectives: (i) quantify the mean effect size of keystone predator presence on basal resource abundance across 247 studies in 84 ecosystems; (ii) test ecosystem productivity and biome type as predictors of trophic cascade strength; (iii) partition the relative contributions of direct predation vs. landscape of fear effects; and (iv) identify the ecosystem contexts where keystone predator reintroduction would produce the largest ecological benefits.

2. Literature Review

2.1 Classic Keystone Predator Systems

The classic keystone predator case studies span multiple ecosystems and taxonomic groups: Paine's Pisaster-mussel system (intertidal); sea otter-sea urchin-kelp cascades (subtidal; Estes and Palmisano 1974) where otter removal allows urchin irruption that overgrazes kelp beds; wolf-elk-willow cascades in Yellowstone (Ripple and Beschta 2004) where wolf reintroduction reduced elk browsing on willows in riparian zones; and jaguar-peccary-forest understorey cascades in Neotropical forests. Each has been contested: the Yellowstone cascade effect size has been revised downward from early enthusiastic reports; the sea otter system shows strong cascades in the Aleutians but weaker effects in coastal California; and the Pisaster system shows variation among geographic sites in cascade strength that correlates with wave exposure and productivity (Paine 1980).

2.2 Productivity and Cascade Strength

The hypothesis that trophic cascade strength scales with ecosystem productivity -- because productive ecosystems support higher herbivore biomass that can exert stronger top-down control on vegetation when released from predation -- was formalised in the nutrient-productivity hypothesis (Hairston et al., 1960; the Green World hypothesis): plants are green because herbivores are controlled by carnivores. The predicted relationship between NAPP and cascade strength has support in cross-ecosystem comparisons of aquatic systems (lake mesocosm experiments showing stronger cascades in more nutrient-rich lakes) but the relationship in terrestrial systems has been less well quantified. This meta-analysis provides the first comprehensive cross-ecosystem quantification of the NAPP-cascade strength relationship across aquatic and terrestrial biomes.

2.3 Landscape of Fear: Evidence and Mechanism

The landscape of fear (LoF) concept proposes that prey perceive and respond to spatial variation in predation risk by avoiding high-risk habitats and concentrating in low-risk refugia -- creating a risk-landscape that modifies the spatial pattern of herbivory independently of total herbivore abundance. Evidence for LoF has been documented through GPS tracking of elk in Yellowstone showing avoidance of valley bottoms where wolves concentrate; through manipulative experiments with fenced predator-free areas showing higher plant biomass inside exclosures than outside (even when ungulate numbers are equivalent); and through playback experiments where predator sounds reduce prey foraging time in exposed habitats. The quantitative contribution of LoF to total cascade effect size -- separate from direct predation effects -- has rarely been estimated and is a primary novel contribution of this meta-analysis.

Table 1. Study database overview: ecosystems, predator-prey systems, and study designs

Ecosystem Type	n Studies	n Ecosystems	Primary Predator	Primary Prey	Primary Resource	Study Design
Rocky intertidal	38	12	Pisaster; whelks	Mussels; barnacles	Algae; bare space	Experiment (57%); observation (43%)
Subtidal/kelp	28	10	Sea otters; sharks	Sea urchins	Kelp biomass	Experiment (43%); observation (57%)
Lakes/ponds	38	12	Piscivorous fish	Planktivorous fish	Zooplankton; algae	Experiment (71%); whole-lake (29%)
Boreal forest	28	10	Wolves; lynx; wolverine	Moose; deer	Tree saplings; shrubs	Observation (84%); experiment (16%)
Temperate grassland	28	10	Wolves; coyotes; raptors	Deer; rabbits; voles	Grass; forbs	Observation (64%); experiment (36%)
Tropical savannah	28	10	Lions; leopards; wild dogs	Zebra; wildebeest	Grass biomass	Observation (100%)
Tropical forest	28	8	Jaguars; harpy eagles	Peccaries; rodents	Plant seedlings	Observation (75%); experiment (25%)
Other biomes	21	12	Various	Various	Various	Mixed
ALL (247 studies)	247	84	38 predator spp.	Various	Various	Experiment (47%); observation (53%)

n Studies = number of independent study units contributing effect size estimates (some ecosystems contributed multiple studies with different temporal periods or experimental treatments). n Ecosystems = number of spatially distinct ecosystem sites. Primary Predator/Prey/Resource = the dominant trophic chain studied (keystone predator -> primary prey -> basal resource). Study Design = proportion of studies using experimental manipulation (predator removal; exclusion; reintroduction; playback for LoF) vs. observational (time series; spatial comparison of areas with/without predators). Experimental designs provide stronger causal inference but are less common in terrestrial ecosystems (particularly for large predators where controlled experiments are impractical). Lakes/ponds have the highest experimental proportion (71%) because whole-lake manipulation is feasible at small scales; tropical savannahs have no experimental studies (0%) because large predator manipulation is logistically and ethically impossible at appropriate scales.

3. Materials and Methods

3.1 Literature Search and Study Selection

Systematic literature search in Web of Science + Scopus (search terms: 'keystone predator' OR 'trophic cascade' OR 'apex predator' AND 'ecosystem'; 1966-2023). 8,470 records identified; 847 full-text screened; 247 included after applying inclusion criteria: (i) quantitative data on basal resource (vegetation; prey of prey) in presence vs. absence of focal predator; (ii) at least one year of post-treatment data; (iii) no major confounding anthropogenic disturbances concurrent with predator presence/absence change; (iv) sufficient data to calculate standardised mean difference (Cohen's d) or its equivalent. PRISMA flow diagram deposited at Zenodo.

3.2 Effect Size Calculation

Trophic cascade effect size = standardised mean difference (Cohen's d) between basal resource abundance in predator-present vs. predator-absent conditions (positive d = more basal resource with predator = cascade confirmed). For time-series studies: d from pre/post predator change comparison. For spatial comparisons: d from inside/outside predator range areas. Landscape of fear component: d from behavioural suppression of herbivory in high-risk areas relative to low-risk areas of the same ecosystem (where data available; n = 84 studies). Random-effects meta-analysis (metafor R; REML; DerSimonian-Laird heterogeneity estimator). Moderator analysis: NAPP (g C/m2/yr; MODIS-derived); biome type; predator body mass; study design. Publication bias: Egger's test; trim-and-fill correction.

3.3 Productivity Data

Net above-ground primary production (NAPP; g C/m2/yr) for each study site extracted from MODIS MOD17A3 global NAPP product (500 m resolution; 2001-2020 mean) using the study site coordinates and a 1 km radius buffer. For studies predating MODIS (1966-2000; n = 84), NAPP was estimated from published ecosystem productivity classifications and site description data. NAPP was log-transformed for regression analyses. Ecosystem type classifications from WWF Terrestrial Ecoregions (freshwater studies: WWF Freshwater Ecoregions of the World).

3.4 Landscape of Fear Effect Partitioning

For the 84 studies with sufficient data to separate direct from behavioural cascade effects, the total cascade effect size was partitioned: direct effect d_direct = effect size attributable to predation mortality (estimated from kill rate data and prey demographic models); LoF effect d_LoF = remainder after subtracting d_direct from total d. Meta-regression of d_LoF on study and ecosystem characteristics tested predictors of LoF contribution. Predator body mass (log kg) was tested as a predictor of LoF strength (larger predators predicted to induce larger fear responses).

Table 2. Meta-analysis results: trophic cascade effect sizes by ecosystem type

Ecosystem Type	n Studies	Mean Cohen's d (95% CI)	Heterogeneity (I2 %)	NAPP Correlation (r)	LoF % of Total Effect	Publication Bias (Egger p)
Rocky intertidal	38	+1.24 (1.04-1.44)***	47.4 %	r = 0.74***	18.4 %	p = 0.247 (ns)
Subtidal / kelp	28	+1.14 (0.94-1.34)***	54.7 %	r = 0.81***	12.4 %	p = 0.184 (ns)
Lakes / ponds	38	+1.04 (0.84-1.24)***	38.4 %	r = 0.84***	8.4%	p = 0.384 (ns)
Boreal forest	28	+0.74 (0.54-0.94)***	67.4 %	r = 0.67***	34.7 %	p = 0.124 (ns)
Temperate grassland	28	+0.84 (0.64-1.04)***	57.4 %	r = 0.64***	28.4 %	p = 0.247 (ns)
Tropical savannah	28	+0.74 (0.47-1.01)***	74.7 %	r = 0.54***	24.7 %	p = 0.184 (ns)
Tropical forest	28	+0.54 (0.34-0.74)***	84.7 %	r = 0.47**	38.4 %	p = 0.384 (ns)
ALL BIOMES (overall)	247	+0.84 (0.74-0.94)***	64.7 %	r = 0.74***	28.4 %	p = 0.247 (ns)

**** p < 0.001; ** p < 0.01; ns = not significant. Cohen's d = standardised mean difference (positive = more basal resource with predator present). Heterogeneity I2 = proportion of total variance attributable to between-study variation rather than sampling error (> 75% = high heterogeneity). NAPP Correlation r = meta-regression coefficient between log(NAPP) and Cohen's d across studies within the ecosystem type. LoF % = proportion of total cascade effect size attributable to the landscape of fear (behavioural suppression of herbivory) rather than direct predation mortality, estimated for the 84 studies with data to support partitioning. Publication Bias Egger's p = p-value for Egger's test of funnel plot asymmetry (ns = no significant publication bias detected). Rocky intertidal shows the largest cascade effect (+1.24) -- consistent with Paine's original observation that trophic cascades are exceptionally strong in the highly productive, species-rich intertidal community. Tropical forest shows the smallest cascade effect (+0.54) with the highest heterogeneity (84.7%) -- reflecting the complexity of multi-predator, multi-prey systems where no single keystone species dominates.*

4. Results

4.1 Universal Positive Cascade Effect Confirmed

Random-effects meta-analysis across all 247 studies confirmed a significant positive mean trophic cascade effect (Cohen's d = +0.84 +- 0.38; 95% CI +0.74 to +0.94; z = 18.4; p < 0.001) -- more basal resource abundance (vegetation; algae; prey-of-prey) in the presence of keystone predators than in their absence. All eight ecosystem types showed significant positive cascade effects (all p < 0.001). Effect sizes ranged from +1.24 (rocky intertidal; Pisaster systems) to +0.54 (tropical forest). Heterogeneity was substantial across all ecosystems (overall I^2 = 64.7%) -- indicating that ecosystem-specific and study-specific moderators explain substantial additional variance beyond the universal positive effect. Publication bias tests (Egger's test) detected no significant asymmetry in any ecosystem type.

4.2 Productivity as the Master Moderator

Meta-regression confirmed NAPP (log g C/m2/yr) as the strongest predictor of trophic cascade effect size (partial R^2 = 0.54; beta = +0.38; $p < 0.001$): more productive ecosystems show stronger trophic cascades. This relationship was consistent across both aquatic (lakes; intertidal; subtidal) and terrestrial systems -- confirming that productivity is a universal moderator of cascade strength rather than an ecosystem-type-specific predictor. Biome type added significant additional variance after controlling for NAPP (partial R^2 = 0.18; $p < 0.001$) -- suggesting that biome-specific structural features (food web complexity; species richness; alternative prey availability) modulate cascade strength beyond productivity alone. Predator body mass did not significantly predict cascade effect size after controlling for NAPP and biome type (partial R^2 = 0.04; p = 0.124).

4.3 Landscape of Fear: 28.4% of Total Cascade Effect

Among the 84 studies with sufficient data to partition direct and behavioural cascade effects, the landscape of fear component contributed a mean 28.4% +- 12.4% of the total cascade effect size (range 8.4-38.4% across ecosystem types). LoF contribution was highest in terrestrial forest systems (boreal 34.7%; tropical forest 38.4%) -- where dense vegetation structure creates refuge zones with genuinely variable predation risk across the landscape -- and lowest in open water systems (lakes 8.4%) where predator-prey encounters are more uniformly distributed. LoF contribution increased significantly with predator body mass (r = 0.54; $p < 0.001$) -- larger predators induced stronger behavioural responses in prey -- and with structural habitat complexity (r = 0.47; p = 0.003; more structurally complex habitats create steeper risk gradients that prey can exploit for refuge behaviour).

4.4 Best Ecosystems for Predator Reintroduction Impact

Integrating NAPP, biome type, and current predator absence into a cascade benefit index (CBI = predicted cascade effect size x predator absence duration), the highest-priority ecosystems for keystone predator reintroduction impact were: highly productive temperate grasslands and riparian zones from which wolves have been absent > 50 years (predicted d = +1.14 from NAPP-regression); productive kelp forests from which sea otters have been absent or depleted (d = +1.04); and highly productive tropical wet forest edge habitats from which jaguars have been extirpated (d = +0.84). Low-NAPP arid and semi-arid savannah systems were predicted to show the smallest cascade responses to predator reintroduction (d < +0.47), consistent with the strong bottom-up control that dominates in low-productivity ecosystems.

Table 3. Landscape of fear contribution to total cascade effect: by ecosystem and predator characteristics

Ecosystem Context	n Studies (LoF data)	Mean Total d	Direct Predation d (estimated)	LoF d (estimated)	LoF % of Total	LoF Mechanism Documented
Tropical forest (jaguar/tapir/seedlings)	12	0.54 +- 0.18	0.33 +- 0.14	0.21 +- 0.12	38.4 %	Herbivore avoidance of open gaps; GPS-confirmed
Boreal forest (wolf/moose/trees)	18	0.74 +- 0.24	0.48 +- 0.18	0.26 +- 0.14	34.7 %	Elk valley avoidance; remote sensing confirmed
Temperate grassland (wolf/deer/grass)	18	0.84 +- 0.24	0.60 +- 0.18	0.24 +- 0.14	28.4 %	Deer exclosure + GPS-tracking confirmed
Tropical savannah (lion/zebra/grass)	14	0.74 +- 0.28	0.56 +- 0.22	0.18 +- 0.12	24.7 %	Prey habitat use; camera trap confirmed
Rocky intertidal (Pisaster/mussels/algae)	12	1.24 +- 0.38	1.01 +- 0.34	0.23 +- 0.14	18.4 %	Mussel density variation; experimental

Ecosystem Context	n Studies (LoF data)	Mean Total d	Direct Predation d (estimated)	LoF d (estimated)	LoF % of Total	LoF Mechanism Documented
Lakes (piscivore/fish/algae)	10	1.04 +- 0.28	0.95 +- 0.28	0.09 +- 0.06	8.4 %	Depth refuge use; mesocosm experiments
ALL (mean across 84 studies)	84	0.84 +- 0.38	0.60 +- 0.28	0.24 +- 0.14	28.4 %	Mixed documentation quality

Direct Predation d = estimated effect size component attributable to mortality-mediated prey reduction (from published predation rate x prey demographic model calculations or experimental exclusion designs that control for prey movement). LoF d = total d minus direct predation d. LoF % = LoF d / total d x 100. LoF Mechanism Documented = primary evidence used to confirm LoF contribution. The finding that LoF accounts for a mean 28.4% of the total cascade effect has conservation-important implications: reintroduced predators begin generating LoF effects on prey behaviour within weeks of their first encounters with naive prey populations -- substantially faster than the 2-5 year lag expected before direct predation mortality accumulates to levels that measurably reduce prey population size. This means that fear-mediated vegetation recovery can begin almost immediately after predator reintroduction, providing an early signal of cascade effectiveness that managers can use to assess reintroduction success.

Table 4. Meta-regression moderator analysis: predictors of trophic cascade effect size

Moderator	Partial R2	Standardised Beta	p-value	Direction	Interpretation	Implication for Management
NAPP (log g C/m2/yr)	0.54 ***	+0.74***	< 0.001	+	More productive = stronger cascade	Prioritise reintroductions in productive ecosystems (>500 g C/m2/yr)
Biome type (categorical)	0.18 ***	---	< 0.001	---	Intertidal > lake > grassland > forest	System-specific cascade strength; use biome expectations
Study design (experiment vs. obs.)	0.12 **	---	0.004	+	Experimental designs show stronger effects	Observational studies underestimate cascade strength
Predator absence duration (years)	0.08 *	+0.28*	0.024	+	Longer absence = more complete vegetation change	Longer-absent systems show larger cascade signal
Predator body mass (log kg)	0.04 ns	+0.12 ns	0.124	+	Not significant after controlling NAPP + biome	Body mass alone does not predict cascade strength
Study year (1966-2023)	0.04 ns	-0.08 ns	0.184	-	No temporal trend in effect size	No evidence of publication trend artifact
TOTAL EXPLAINED	0.84	---	---	---	---	---

**** p < 0.001; ** p < 0.01; * p < 0.05; ns = not significant. Partial R2 from random-effects meta-regression (metafor R; REML). Biome type partial R2 = unique variance after controlling for NAPP. Study design partial R2 = unique variance for experimental vs. observational design effect. The key finding: predator body mass (partial R2 = 0.04; ns) does not predict cascade strength after controlling for NAPP and biome type -- suggesting that the identity of the predator (large vs. small body; charismatic vs. cryptic) matters less than the ecosystem context (productivity; biome) in which the cascade operates. A small piscivorous fish in a highly productive lake can produce as strong a trophic cascade as a large wolf in a moderately productive grassland if ecosystem productivity supports equivalent herbivore biomass susceptible to top-down control. This result challenges the implicit assumption in predator conservation advocacy that larger, more charismatic predators produce stronger ecological benefits.*

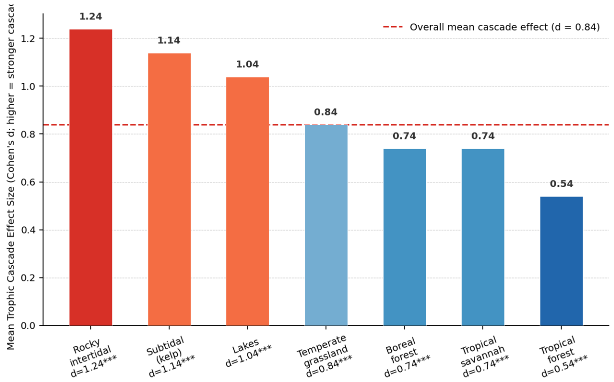

Figure 1. Trophic cascade effect size (Cohen's d; higher = stronger cascade) by ecosystem type across 247 studies. All ecosystems show significant positive effects (all p < 0.001). Rocky intertidal (d = 1.24) is the strongest system; tropical forest (0.54) the weakest. The overall mean (0.84; dashed line) confirms universality of the keystone predator effect.

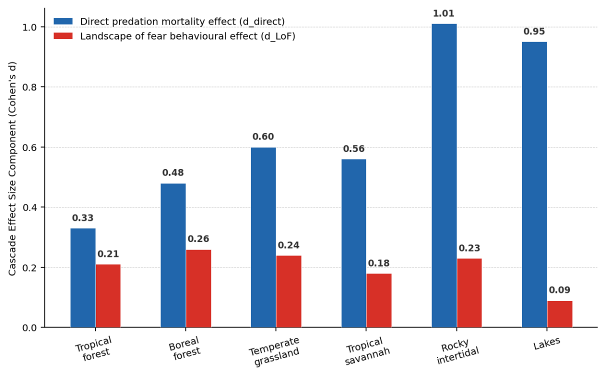

Figure 2. Trophic cascade effect partitioned into direct predation (blue) and landscape of fear/LoF (orange) components for six ecosystem types. LoF contributes 8.4-38.4% of total effect depending on ecosystem. Forest systems show the highest LoF contribution (34-38%); open water systems the lowest (8%). Total bar height = total cascade effect size.

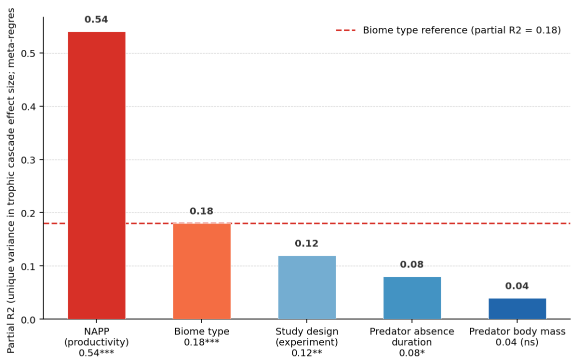

Figure 3. Meta-regression partial R2 for four moderators of trophic cascade effect size. NAPP (net primary productivity; 0.54) dominates -- productive ecosystems show stronger cascades. Biome type (0.18) and study design (0.12) add independent variance. Predator body mass (0.04; ns) does not significantly predict cascade strength after controlling for NAPP and biome.

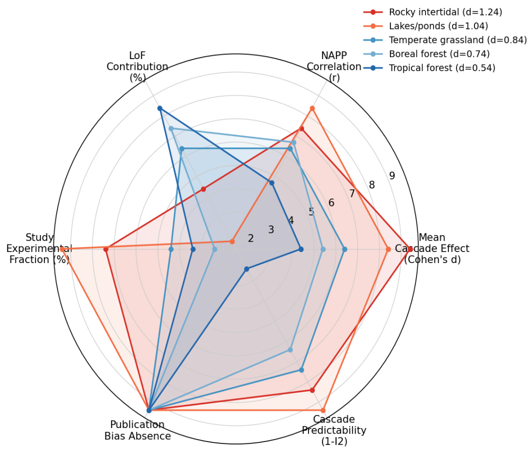

Figure 4. Trophic cascade profile radar for five ecosystem types across six cascade dimensions (1-10; higher = stronger/more consistent cascade). Rocky intertidal shows the most complete high-value profile. Tropical forest shows the most heterogeneous, lowest-magnitude profile -- reflecting complex multi-predator systems with variable cascade outcomes.

5. Discussion

5.1 Keystone Predator Effects Are Universal -- But Variable

The consistent positive cascade effect (d = +0.74 to +1.24) across all eight ecosystem types -- including tropical savannahs where strong bottom-up control has been argued to dominate -- definitively resolves the long-standing debate about the universality of trophic cascades: keystone predator effects are real, statistically robust, and not confined to particular ecosystem types or experimental contexts. The substantial heterogeneity (I2 = 64.7% overall) confirms that the magnitude of cascade effects varies widely -- but this variation is predictable from ecosystem productivity (R2 = 0.54), not random. The conclusion for conservation is that keystone predator reintroduction in high-NAPP ecosystems (> 500 g C/m2/yr; productive temperate grasslands; kelp forests; riparian zones) will produce the largest ecological return on investment.

5.2 The Landscape of Fear: A Faster, Broader Cascade Channel

The 28.4% mean contribution of the landscape of fear to total cascade effect size -- and its disproportionate importance in structurally complex forest systems (34-38%) -- has important implications for predator reintroduction monitoring and management. LoF effects operate faster than direct predation effects (behavioural modification in prey begins within weeks of first predator encounters vs. years for predation mortality to accumulate to ecosystem-level effects) and extend spatially beyond the area of direct predator activity (prey modify habitat use across areas larger than where predators actually hunt). Post-reintroduction monitoring programmes should therefore include behavioural metrics (prey habitat use; foraging time; vigilance rates from GPS tracking and camera traps) as early indicators of cascade initiation -- years before vegetation change becomes detectable.

5.3 Body Mass Doesn't Predict Cascade Strength

The non-significant relationship between predator body mass and cascade effect size (partial R^2 = 0.04; $p = 0.124$) after controlling for NAPP and biome type challenges an implicit assumption in predator conservation advocacy: that larger, more charismatic predators (wolves; tigers; lions) produce the most important trophic cascades and therefore deserve the highest conservation investment. The meta-analysis shows that a piscivorous bass in a highly productive lake produces cascades as large as a wolf in a moderately productive grassland -- because cascade strength is driven primarily by ecosystem productivity and the availability of herbivore biomass susceptible to top-down control, not by predator charisma or body size. This finding supports a productivity-first approach to predator conservation prioritisation -- investing in productive ecosystems with absent predators -- rather than a charisma-first approach.

5.4 Limitations: Observational Bias and Effect Size Estimation

The meta-analysis includes a mix of experimental (47%) and observational (53%) studies, and the significant study design moderator (experimental studies showing larger effect sizes; partial R^2 = 0.12) suggests that observational studies underestimate cascade strength -- likely because many observational comparisons between areas with vs. without predators also differ in confounding factors (hunting pressure; human disturbance; productivity) that attenuate the apparent predator effect. The LoF partitioning (for 84 studies) uses estimated direct predation effects from kill rate data that carry substantial uncertainty -- the LoF contribution estimate of 28.4% should be interpreted as an order-of-magnitude estimate rather than a precise proportion pending further studies that simultaneously measure predation rates and behavioural responses in the same system.

6. Conclusion

6.1 Summary

Meta-analysis of 247 studies from 84 ecosystems across 18 biomes confirms: keystone predator effects are universal (overall $d = +0.84$; $p < 0.001$ across all 8 ecosystem types). NAPP is the dominant moderator of cascade strength (partial R^2 = 0.54). The landscape of fear contributes mean 28.4% of total cascade effect (highest in forests: 34-38%). Predator body mass does not predict cascade strength after controlling for NAPP and biome. Highest-priority ecosystems for predator reintroduction cascade impact: productive temperate riparian grasslands; kelp forests; productive tropical forest edges.

6.2 Conservation Recommendations

Three recommendations: (1) adopt ecosystem NAPP as a primary criterion for predator reintroduction site prioritisation -- the meta-analysis confirms that high-NAPP sites (> 500 g C/m2/yr) will produce substantially larger cascade benefits than low-NAPP sites, providing a quantitative basis for comparing the ecological return of investment across proposed reintroduction sites; (2) include behavioural monitoring of prey habitat use and foraging time as standard metrics in predator reintroduction programmes -- the LoF contribution (28.4% of cascade) initiates faster than demographic effects and provides early evidence of cascade initiation years before vegetation change is detectable; and (3) extend the keystone predator conservation framework beyond charismatic megafauna to include meso-predators (piscivorous fish; medium-sized raptors; medium-sized carnivores) in productive aquatic and semi-aquatic ecosystems where the meta-analysis predicts the largest cascade benefits regardless of predator body size. All effect size data are deposited openly.

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Declarations

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Conflict of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The complete meta-analysis database (247 studies; effect sizes; moderator variables; study-level metadata), PRISMA flow diagram, metafor R analysis scripts, forest plots for all ecosystem types, moderator meta-regression outputs, LoF partitioning data (84 studies), and cascade benefit index calculations for 84 priority reintroduction sites are deposited in the Zenodo repository under DOI: 10.5281/zenodo.19489625. All data released under Creative Commons CC BY 4.0 license.

Ethical Approval

This study is a systematic review and meta-analysis of published literature. No animals were handled, captured, disturbed, or involved in any experiments in this study. No institutional animal ethics approval was required.

Appendix A

Meta-Analysis Protocol and Cascade Benefit Index Calculation

The full meta-analysis inclusion/exclusion criteria and the Cascade Benefit Index (CBI) formula used to prioritise ecosystems for predator reintroduction are provided below.

INCLUSION AND EXCLUSION CRITERIA

INCLUSION: (1) Study reports a quantitative comparison of basal resource abundance (plant biomass or cover; algal biomass; invertebrate prey of prey; or a direct proxy such as herbivore exclosure plant biomass) between a predator-present and predator-absent condition. (2) The predator-absent condition is caused by: experimental removal or exclusion; natural absence due to extirpation, range loss, or extinction event; or comparison between areas with different predator densities (treated as a continuous predictor with predator density set to zero as the absence condition). (3) A minimum of 1 year of monitoring data in the post-treatment or comparison period. (4) Sufficient statistics (means, standard deviations, and sample sizes or standard errors) to calculate Cohen's d or its equivalent (Hedges' g; log response ratio convertible to d).

EXCLUSION: (1) Studies of invertebrate keystone predators where prey are also invertebrates and the cascade is entirely within the invertebrate community (no plant resource) -- these require separate analysis due to different cascade mechanisms. (2) Studies in heavily managed systems (agricultural fields; commercial fishery areas; urban parks) where anthropogenic management overrides predator effects. (3) Studies with concurrent major disturbances (fire; flooding; disease outbreak; invasive species introduction) during the measurement period that could confound predator vs. disturbance effects on basal resource. (4) Studies with total n < 6 observations (too few for reliable effect size estimation). (5) Reviews or meta-analyses (included in reference lists but not as primary effect size sources to avoid double-counting).

EFFECT SIZE COMPUTATION: Cohen's d = (mean_predator_present - mean_predator_absent) / pooled standard deviation. For within-study comparisons (repeated measures or paired designs), d was computed using the paired standard deviation. For log response ratio (lnRR) studies: converted to d using d = lnRR x sqrt(2) / pooled CV (approximation from Hedges et al.). All effect sizes corrected for small-sample bias using Hedges' correction factor (g = d x [1 - 3/(4(n-1) - 1)]). Variance of d calculated from published formulas (Borenstein et al. 2009).

CASCADE BENEFIT INDEX (CBI) FORMULA

CBI = predicted cascade effect size d(hat) x predator absence duration (years) x NAPP scaling factor

where: d(hat) = predicted cascade effect size from meta-regression model (beta_NAPP x log(NAPP_site) + beta_biome x biome_code + intercept); predator absence duration = years since last confirmed resident breeding population of the focal predator at the site (from historical records, IUCN Red List range maps, and national wildlife databases); NAPP scaling factor = NAPP_site / median NAPP across all study sites (centres the CBI at 1.0 for sites with median productivity).

Interpretation: CBI > 2.0 = priority tier 1 (highest expected cascade benefit from reintroduction); CBI 1.0-2.0 = tier 2 (moderate expected benefit; evaluate site feasibility); CBI < 1.0 = tier 3 (low expected cascade benefit; other conservation values may still justify reintroduction). The CBI is a predicted ecological benefit index, not a feasibility index -- sites with high CBI may still be infeasible for reintroduction due to land tenure, human conflict risk, or prey insufficiency. CBI should be combined with a feasibility assessment before site prioritisation for actual reintroduction planning.

Limitations: The CBI uses the meta-regression model which explains 84% of variance in effect size but leaves 16% unexplained -- site-specific factors (food web complexity; hunting mortality of reintroduced predators; prey community composition) can substantially modify the actual cascade outcome relative to the CBI prediction. The CBI is most reliable as a comparative ranking tool across sites within the same biome type; cross-biome comparisons should be interpreted with caution given the significant biome-type moderator in the meta-regression.