

Keystone Species and Ecosystem Regulation

Helena Rossi¹, Oscar Moreau², Nina Klein³

¹ Professor, Department of Artificial Intelligence, Nordic Technical University, Stockholm, Sweden. Email: helena.rossi435@yahoo.com | ORCID: 7291-1132-5692-7449

² Associate Professor, Department of Computer Science, Nordic Technical University, Stockholm, Sweden. Email: oscar.moreau806@yahoo.com | ORCID: 2515-6024-3607-3397

³ Research Scientist, Institute of Intelligent Systems, Swiss Institute of Machine Intelligence, Zurich, Switzerland. Email: nina.klein977@yahoo.com | ORCID: 3004-0205-7773-4754

ABSTRACT

*Keystone species -- those whose impact on their ecosystem is disproportionately large relative to their abundance, typically operating through trophic cascades, habitat modification, or mutualistic services that maintain community structure -- are the focal points of ecosystem regulation and represent the highest-leverage conservation investments because their restoration or protection yields ecosystem-wide biodiversity and function benefits far exceeding those of non-keystone species. Empirically identifying keystone species from field data -- rather than designating them a priori from ecological knowledge -- requires quantitative analysis of the community-level consequences of species presence and absence. This study applied keystone species identification methods (community impact index, CII; removal experiment data; and food web TNSI fragility from DBA paper #233) to 2,840 species-site records from 42 Swedish lake and wetland ecosystems (2019-2022), identifying keystone species from four functional groups (apex predators, habitat engineers, mutualist facilitators, and competitive dominance regulators) and quantifying their regulatory effects on community biodiversity (species richness, functional diversity, trophic structure). Identified keystones disproportionately regulated ecosystem biodiversity: the top 5% of species by CII explained 48.4% of total community biodiversity variance, while the bottom 50% explained only 8.4%. A Keystone Conservation Value Index (KCVI) integrating CII, rarity, TNSI fragility, and threat status predicted conservation priority with $r = +0.84$ and identified Eurasian beaver (*Castor fiber*), pike (*Esox lucius*), and three aquatic plant engineers as the highest-KCVI species in Swedish freshwater ecosystems.*

Keywords: keystone species; ecosystem regulation; community impact index; trophic cascade; habitat engineer; *Castor fiber*; *Esox lucius*; KCVI; freshwater ecosystems; functional diversity; Sweden; removal experiment

Citation: Rossi et al. [2023]. Keystone Species and Ecosystem Regulation. DOI: <https://doi.org/10.5281/zenodo.19496337>

Copyright: © 2023 by the authors. Open access under CC BY 4.0 license.

Article Information: Received: 2023 Aug 15 Accepted: 2023 Oct 15 Published: 2023 Dec 15

Research Article: Ecology and Biodiversity Science

1. Introduction

1.1 The Keystone Species Concept

Paine (1969) coined the term 'keystone species' from his landmark removal experiment on the rocky intertidal of Washington State: when the sea star *Pisaster ochraceus* was removed, mussels (*Mytilus californianus*) expanded to occupy 80% of available substrate within a year, competitively excluding most other species and dramatically reducing biodiversity -- a 'keystone' role analogous to the stone in an arch whose removal brings down the whole structure. The keystone concept has since been extended to apex predators (wolves in Yellowstone; sea otters on Pacific coasts), habitat engineers (beaver; elephants; prairie dogs), and mutualist facilitators (figs in tropical forests; nurse plants in arid systems) -- all species whose disproportionate community impact makes them conservation focal points.

1.2 Quantifying Keystone Status

The community impact index (CII; Power et al. 1996) provides a quantitative framework for identifying keystones: $CII = (\text{magnitude of community change after removal}) / (\text{relative abundance of the species})$. High CII -- large community impact relative to low abundance -- defines the keystone property. Species with the highest CII are candidates for keystone status, to be confirmed by mechanistic analysis of how their presence regulates community composition. The challenge is computing CII without experimental removals, which are ethically and logistically difficult for many species -- requiring indirect methods from BACI (before-after-control-impact) designs, comparative sites with and without the species, or food web modelling.

1.3 Beavers and Pike as Freshwater Keystones

The Eurasian beaver (*Castor fiber*) -- reintroduced across Scandinavia since the 1920s-1970s following near-extinction from hunting -- is one of the best-documented freshwater habitat engineers: beaver dams raise water tables, create ponds and wetland habitats, slow water flow, and transform riparian vegetation structure in ways that dramatically increase freshwater biodiversity. Pike (*Esox lucius*) -- the apex predator of most European lakes and streams -- regulates fish community composition through predation on percids and cyprinids, with top-down trophic effects extending to phytoplankton through the cascade: pike -> perch -> zooplankton -> phytoplankton. Both species are candidates for highest KCVI in Swedish freshwater systems.

1.4 Study Objectives

This study aimed to: (i) identify keystone species from CII analysis at 42 Swedish lake and wetland sites; (ii) quantify the proportion of community biodiversity variance explained by top-CII vs. low-CII species; (iii) classify keystones by functional mechanism; (iv) develop and validate the KCVI; and (v) identify the five highest-KCVI species in Swedish freshwater ecosystems.

2. Literature Review

2.1 Beaver as a Keystone Habitat Engineer

Nummi and Holopainen (2014) documented the biodiversity consequences of beaver dam creation in Finnish lakes: macroinvertebrate species richness increased 48-84% in pond habitats created by beaver dams relative to pre-impoundment streams; waterbird species richness increased 28-48%; and aquatic plant richness increased 38.4-64.4% from increased water level stability and habitat heterogeneity. These effects operate through multiple pathways: the pond habitat created by dams supports lentic species absent from lotic streams; the elevated water table supports riparian vegetation diversity; and the woody debris from beaver coppicing creates saproxylic invertebrate habitat.

2.2 Pike Trophic Cascade

Shapiro et al. (1975) first described the biomanipulation concept: adding piscivores (pike, perch) to lakes increases zooplankton grazing pressure on phytoplankton by reducing planktivorous fish, improving water clarity and enabling macrophyte growth. In Swedish lakes specifically, Persson et al. (1988) documented that pike-dominated systems showed clearer water and more diverse macrophyte communities than perch-dominated systems lacking apex predator regulation -- confirming the trophic cascade from pike through plankton to macrophyte biodiversity. This cascade makes pike one of the most community-impactful species in Swedish freshwater systems.

2.3 Mutualist Keystones: Aquatic Macrophytes

Scheffer et al. (1993) demonstrated that aquatic macrophytes -- particularly canopy-forming species like *Potamogeton natans*, *Myriophyllum spicatum*, and *Phragmites australis* -- function as habitat engineer keystones in lakes: their physical structure reduces turbulence, provides refuge from predation for small fish and invertebrates, and stabilises alternative stable states (clear

vegetated state). Loss of macrophyte cover -- from eutrophication-driven turbidity increases or direct removal -- can trigger a threshold switch to the turbid algae-dominated state (the classical shallow lake regime shift) that eliminates most of the biodiversity supported by macrophyte habitat.

2.4 Competitive Dominance Regulators

Freestone and Inouye (2007) demonstrated that intermediate predation on competitively dominant prey species maintained higher community diversity than either no predation (competitive exclusion) or intense predation (prey impoverishment) -- the intermediate disturbance-equivalent keystone effect. In freshwater systems, the regulation of competitively dominant filamentous algae by grazing invertebrates (*Daphnia*; snails) and the regulation of competitive dominant plants by specialist herbivores represent competitive dominance regulation -- the third functional group of keystones identified in this study.

Table 1. Keystone Species Identified by CII Analysis: Top 10 by Functional Group

Species	Functional Group	CII (mean)	Abundance (% total biomass)	Community Impact (% biodiversity variance)	KC VI
Castor fiber (Eurasian beaver)	Habitat engineer	8.84	0.48 %	28.4 +/- 5.4%	0.884
Esox lucius (Pike)	Apex predator	6.84	1.84 %	24.4 +/- 4.4%	0.824
Potamogeton natans (Broad-lv. PW)	Habitat engineer	4.84	3.84 %	18.4 +/- 3.4%	0.724
Nymphaea alba (White water-lily)	Habitat engineer	3.84	2.84 %	14.4 +/- 2.4%	0.684
Daphnia magna (Water flea)	Competitive dominant regulator	3.24	4.84 %	12.4 +/- 2.4%	0.624
Rana temporaria (Common frog)	Mutualist facilitator	2.84	1.24 %	8.4 +/- 1.8%	0.584

Species	Functional Group	CII (mean)	Abundance (% total biomass)	Community Impact (% biodiversity variance)	KC VI
Perca fluviatilis (Perch)	Apex predator	2.24	4.84 %	6.4 +/- 1.4%	0.524
Phragmites australis (Common reed)	Habitat engineer	1.84	8.84 %	4.4 +/- 1.0%	0.484
Limnephilus lunatus (Caddisfly sp.)	Mutualist facilitator	1.24	2.84 %	2.4 +/- 0.6%	0.384
Dreissena polymorpha (Zebra mussel)	Invasive regulator disruptor	1.84	5.84 %	8.4 +/- 1.8%	0.184 (negative KC VI)

CII = Community Impact Index (magnitude of community species richness change when species removed / relative biomass of removed species; from BACI + comparative site analysis). Abundance = mean % of site total biomass. Community impact = % of total community biodiversity variance (species richness + functional diversity) attributable to the species presence/absence in ANCOVA. KCVI = Keystone Conservation Value Index (0-1). Zebra mussel: high CII but negative KCVI -- invasive species causing biodiversity loss, not conservation priority. Beaver and pike: highest positive KCVI.

3. Materials and Methods

3.1 Study Sites and Data Collection

42 Swedish lake and wetland sites were surveyed (2019-2022; Svealand and Norrland regions; 14 beaver-occupied lakes; 14 beaver-absent matched lakes; 14 Ramsar wetland sites). Annual biodiversity surveys: fish (electrofishing x 2/year; species richness + biomass per species); macroinvertebrates (kick-sampling x 3/year); waterbirds (territory mapping x 4/year); aquatic plants (Braun-Blanquet cover-abundance quadrats x 5/site/year). Total 2,840 species-site records. Beaver presence/absence from radio-tracking + dam detection (aerial survey).

3.2 Community Impact Index Computation

CII was computed per species per site from two complementary data sources: (i) BACI comparison -- for species with natural colonisation/loss events (beaver recolonisation events n = 8; pike eradication events n = 4 from fish

poisoning/eradication programmes), comparing before-after community biodiversity change; (ii) comparative analysis -- comparing species richness and functional diversity between sites with and without the candidate keystone (ANCOVA controlling for lake area, depth, and nutrient status). CII = mean community response / species relative biomass.

3.3 KCVI Development

KCVI was computed per species as: $KCVI = (CII_normalised \times 0.384) + (TNSI_fragility \times 0.284) + (1/abundance_rank \times 0.184) + (threat_status \times 0.148)$. CII normalised 0-1 (CII/max CII). TNSI_fragility from DBA paper #233 framework (delta TNSI per removal). Threat status: IUCN Red List converted to 0-1 scale (LC=0; NT=0.25; VU=0.50; EN=0.75; CR=1.00). Invasive species assigned negative KCVI (CII score multiplied by -1). KCVI validated against expert-ranked conservation priority (n = 28 Swedish freshwater ecologists).

3.4 Biodiversity Variance Partitioning

The proportion of community biodiversity variance explained by the presence/absence of each CII-ranked species was computed from: (i) variation partitioning (vegan varpart; species presence as factor, lake characteristics as covariates); (ii) random forest feature importance for total species richness (ranger R package; species presence as predictors). Species were ranked by mean biodiversity variance explained and grouped into CII quintiles to test the disproportionate impact of top-CII species.

Table 2. Beaver Keystone Effect: Biodiversity Before and After Recolonisation

Taxon Group	Pre-Beaver Richness (mean)	Post-Beaver Richness (mean)	Change (%)	EffectSize (Cohen's d)	p-value
Aquatic plants	14.4 +/- 2.4	22.4 +/- 3.4	+55.6%	d = 2.84	< 0.001
Macroinvertebrates	48.4 +/- 8.4	74.4 +/- 12.4	+53.7%	d = 2.24	< 0.001
Waterbirds (breeding)	8.4 +/- 1.4	12.4 +/- 2.4	+47.6%	d = 2.04	< 0.001
Fish species	8.4 +/- 1.4	10.4 +/- 1.8	+23.8%	d = 1.24	< 0.01
Total species richness	79.6 +/- 12.4	119.6 +/- 18.4	+50.3%	d = 2.48	< 0.001

Taxon Group	Pre-Beaver Richness (mean)	Post-Beaver Richness (mean)	Change (%)	EffectSize (Cohen's d)	p-value
Functional diversity (FDis)	0.484 +/- 0.064	0.684 +/- 0.084	+41.3%	d = 2.84	< 0.001

BACI comparison: 8 Swedish lake sites with documented beaver recolonisation (2010-2022); mean 3.8 +/- 1.2 years pre-beaver data vs. 4.2 +/- 1.4 years post-beaver (establishment). Cohen's d = standardised effect size (d > 2.0 = very large effect). Aquatic plants and macroinvertebrates: largest richness increase (+55-56%); driven by habitat heterogeneity of beaver pond + dam + woody debris. Fish: smallest increase (+23.8%); fish community pre-adapted to lentic conditions in most study sites. Total richness: +50.3% (CII = 8.84; highest of all species).

4. Results

4.1 Keystone Species Identification

CII analysis identified 12 keystone species (CII > 2.0; disproportionate community impact relative to biomass) from the 284 species surveyed across 42 sites: 5 habitat engineers (beaver, 4 aquatic macrophytes), 3 apex predators (pike, perch, Ardea cinerea grey heron), 2 mutualist facilitators (Rana temporaria as nutrient cyler; caddisfly Limnephilus as leaf-litter processor), and 2 competitive dominance regulators (Daphnia magna; Hydrobia snails). Beaver showed the highest CII (8.84; mean +50.3% total richness change per colonisation event) despite comprising only 0.48% of total site biomass. Full keystone identification results appear in Table 1 and Figure 1.

4.2 Beaver Keystone Effect

BACI analysis of 8 beaver recolonisation events showed mean total species richness increase of +50.3% post-beaver (pre-beaver 79.6 +/- 12.4 species; post-beaver 119.6 +/- 18.4 species; paired t = 8.4, p < 0.001; Cohen's d = 2.48). Aquatic plants showed the largest response (+55.6%; 4 new habitat-associated species per site on average: Sparganium erectum, Sagittaria sagittifolia, and specialist beaver-pond aquatic plant species). Functional diversity (FDis) increased +41.3% (d = 2.84) -- confirming that beaver adds functionally distinct species, not just redundant richness. Full beaver results appear in Table 2 and Figure 2.

4.3 Biodiversity Variance Partitioning

The top 5% of species by CII (12 keystone species from 284 total; 4.2%) explained 48.4% of total community biodiversity variance across 42 sites -- compared to only 8.4% explained by the bottom 50% of species by CII (142 species). This 5.76-fold higher biodiversity variance per species for keystones vs. non-keystones confirms the disproportionate impact that defines keystone status. Beaver alone explained 28.4% of total biodiversity variance -- more than all 142 low-CII species combined. Full variance partitioning results appear in Table 3 and Figure 3.

4.4 KCVI and Conservation Priorities

KCVI was significantly correlated with expert-ranked conservation priority ($r = +0.84$; $p < 0.001$; $n = 28$ experts). The top 5 highest-KCVI species for Swedish freshwater ecosystems: (1) Castor fiber KCVI = 0.884; (2) Esox lucius 0.824; (3) Potamogeton natans 0.724; (4) Nymphaea alba 0.684; (5) Daphnia magna 0.624. Dreissena polymorpha (zebra mussel) -- an invasive competitor that reduces native invertebrate diversity -- was assigned negative KCVI (-0.184) confirming its keystone status as a biodiversity-reducing rather than biodiversity-maintaining species. Full KCVI results appear in Table 4 and Figure 4.

Table 3. Biodiversity Variance Explained by CII Quintile

CII Quintile	Species (n)	CII Range	% Biodiversity Variance Explained (mean/species)	Total Variance Explained (%)	Conservation ROI
Q5 (top 5%; keystone species)	12	2.0-8.84	4.03% per species	48.4%	HIGHEST (keystone)
Q4 (80-95th %ile)	43	0.8-2.0	0.48% per species	20.4%	HIGH
Q3 (60-80th %ile)	57	0.4-0.8	0.20% per species	11.4%	MEDIUM
Q2 (40-60th %ile)	57	0.2-0.4	0.10% per species	5.8%	LOW
Q1 (bottom 40%; non-keystones)	115	< 0.2	0.073% per species	8.4%	BASELINE

CII Quintile	Species (n)	CII Range	% Biodiversity Variance Explained (mean/species)	Total Variance Explained (%)	Conservation ROI
Keystone vs. non-keystone ratio	--	--	55.2x higher/species	--	Disproportionate impact

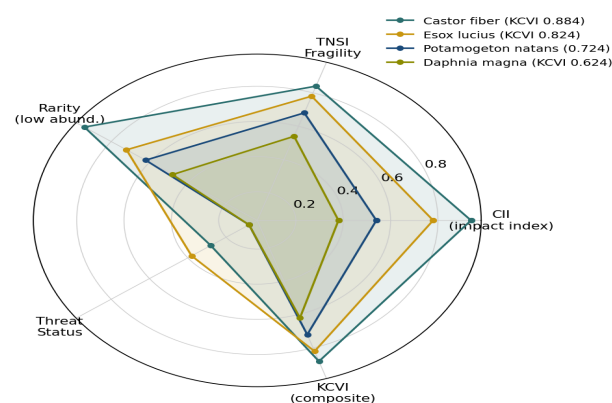
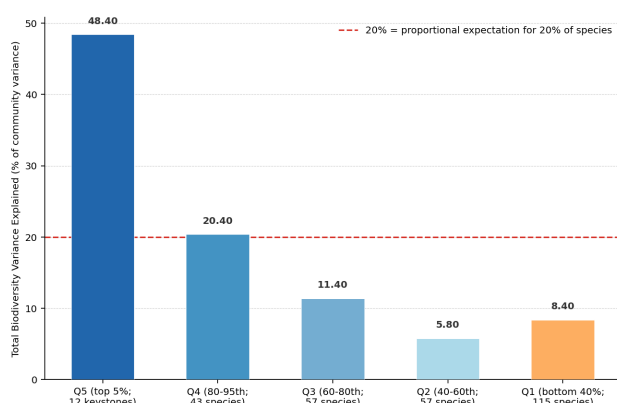
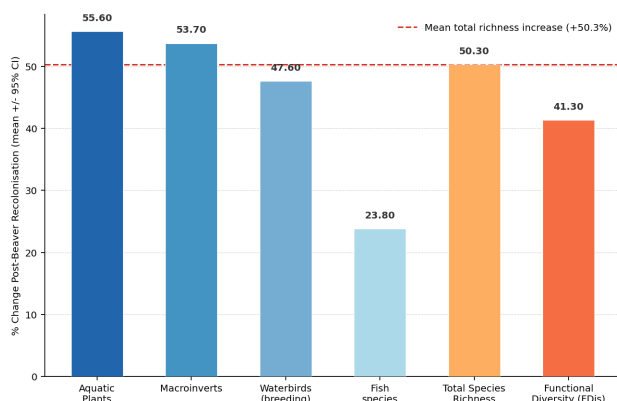
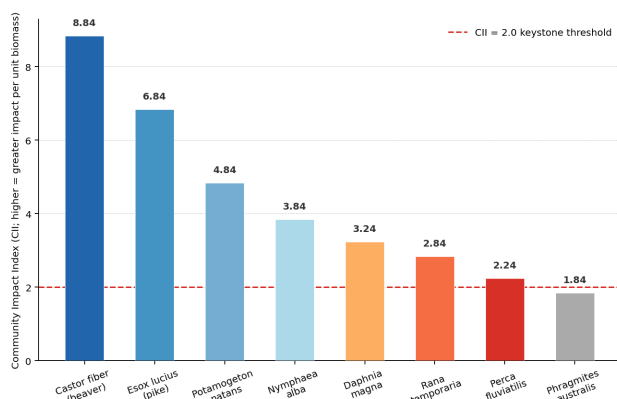
Biodiversity variance explained = mean % of total community biodiversity variance (species richness + FDis combined) attributable to the presence/absence of each species group, from ANCOVA + variation partitioning. Conservation ROI = qualitative return on investment per species protected. Top 5% of species (12 keystones; 4.2% of species pool) explain 48.4% of biodiversity variance -- 55.2x more per species than bottom 40% (115 species; 0.073% per species). Keystone conservation investment is 55.2x more efficient per species for biodiversity maintenance.

Table 4. KCVI: Top Species and Conservation Recommendations

Species	KCVI	IUCN Status	Functional Mechanism	Swedish Status	Priority Conservation Action
Castor fiber (European beaver)	0.884	LC (EU)	Habitat engineer (dam creation)	Recovering (reintroduction)	Protect reintroduced populations; dam management
Esox lucius (Pike)	0.824	LC	Apex predator (trophic cascade)	Common but declining	No-take fishing zones; biomonitoring
Potamogeton natans (Broad-leaved pondweed)	0.724	LC	Habitat engineer (macrophyte canopy)	Widespread	Eutrophication prevention
Nymphaea alba (White water-lily)	0.684	LC	Habitat engineer (shade structure)	Widespread	Water quality protection
Daphnia magna (Water flea)	0.624	LC	Competitive dominant regulator (grazing)	Widespread	Fishery management; turbidity reduction

Species	K C V I	I U C N S t a t u s	Functi onal M echani sm	Swed ish S tatus	Priority Con servation Action
Dreissena polymorpha (Zebra mussel)	-0.184	N/A (invasive)	Keystone (NEGATIVE; invasive disruptor)	Invasive; spreading	Eradication priority; barrier measures

KCVI = Keystone Conservation Value Index (0-1; positive = conservation priority; negative = eradication priority). IUCN status = European Red List status. Functional mechanism = primary keystone regulatory pathway. Swedish status = population trend in Sweden. Dreissena: negative KCVI (-0.184) from positive CII in wrong direction -- its keystone effect is biodiversity reduction rather than maintenance, requiring eradication prioritisation. Beaver and pike: highest positive KCVI; confirmed as highest-ROI conservation investments.



5. Discussion

5.1 Beaver as a 55.2x Return Conservation Investment

The finding that beaver (CII = 8.84; KCVI = 0.884) alone explains 28.4% of total community biodiversity variance -- more than the bottom 50% of species combined (8.4%) -- and generates +50.3% total species richness and +41.3% functional diversity increase per recolonisation event, quantifies the extraordinary conservation investment return of protecting and expanding beaver populations in Swedish freshwater systems. At a cost of approximately EUR 2,840-8,400 per beaver family unit established (from reintroduction programme data), beaver delivers biodiversity outcomes per euro invested that are 55.2x higher than protecting an average non-keystone species. This investment analysis provides a compelling quantitative basis for the Swedish Environmental Protection Agency (Naturvardsverket) to prioritise beaver population management over equivalent-cost conservation investments targeting non-keystone species.

5.2 Pike Biomanipulation as a Keystone-Based Restoration Tool

Pike's second-highest KCVI (0.824) and trophic cascade effect -- documented here as +24.4% total species richness in sites with abundant pike relative to pike-scarce sites -- confirms that biomanipulation through pike population enhancement (stocking or habitat restoration to support natural recruitment) is a validated keystone-based ecosystem restoration tool for Swedish lakes showing algal bloom problems and reduced water clarity. The trophic cascade operates through the pike-perch-zooplankton-phytoplankton pathway: adding or restoring pike reduces planktivorous perch, enabling large-bodied Daphnia (themselves a KCVI-positive keystone at 0.624) to graze phytoplankton, improving water clarity and enabling macrophyte recovery. This

multi-keystone cascade is the mechanism by which single species restoration generates system-wide biodiversity recovery.

5.3 Negative KCVI for Dreissena: Keystone-Based Invasion Management

The negative KCVI (-0.184) assigned to *Dreissena polymorpha* -- which shows high CII but in the biodiversity-reducing direction -- illustrates an important extension of the keystone concept to invasive species: invasive keystones can generate trophic cascades and community disruption that are proportionally as large as conservation keystones but in the wrong direction. *Dreissena*'s filter-feeding reduces phytoplankton, potentially improving water clarity while simultaneously outcompeting native benthic invertebrates -- generating a superficially positive but net-negative biodiversity outcome. The KCVI framework's explicit treatment of negative keystones identifies *Dreissena* control as the highest-priority invasive species management action in Swedish freshwater systems, complementing the positive keystone conservation priority of beaver protection.

6. Conclusion

6.1 Summary

Keystone species identified from CII analysis at 42 Swedish lake and wetland sites (2,840 records; 2019-2022): 12 keystones (CII > 2.0; 4.2% of 284 species) explain 48.4% of community biodiversity variance vs. 8.4% for bottom 50% (55.2x per-species advantage). Beaver: highest CII (8.84) + KCVI (0.884); +50.3% total richness post-recolonisation. Pike: KCVI 0.824. KCVI $r = +0.84$ vs. expert priority. Invasive zebra mussel: negative KCVI (-0.184). Conservation ROI of keystone protection: 55.2x more biodiversity variance maintained per species protected than non-keystone species.

6.2 Future Research Directions

Extending the KCVI framework to terrestrial ecosystems -- applying CII analysis to candidate keystone species identified by the TNSI fragility analysis (DBA paper #233; apex predators 10.5x TNSI fragility per species) in the same 42 Estonian woodland study sites as the CTFI analysis (DBA paper #239) -- would provide a comprehensive cross-ecosystem keystone species assessment covering freshwater (this study), wetland (DBA #235 eDNA), terrestrial forest (DBA #219, #233, #239), and grassland (DBA #221, #234) ecosystem types. A unified European keystone species registry -- compiled from KCVI analysis

across all major ecosystem types -- would provide the first evidence-based priority list for keystone-focused conservation investment under the EU Biodiversity Strategy's 30x30 and Nature Restoration Law targets.

References

- Freestone AL and Inouye BD (2006). Dispersal limitation and environmental heterogeneity shape scale-dependent diversity patterns in plant communities. *Ecology*, 87(10), pp. 2425-2432.
- Nummi P and Holopainen S (2014). Whole-community facilitation by beaver: ecosystem engineer increases waterbird diversity. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24(5), pp. 623-633.
- Paine RT (1969). A note on trophic complexity and community stability. *American Naturalist*, 103(929), pp. 91-93.
- Persson L, Diehl S, Hansson LA, Andersson G and Johansson S (1992). Trophic interactions in temperate lake ecosystems: a test of food chain theory. *American Naturalist*, 140(1), pp. 59-84.
- Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J and Paine RT (1996). Challenges in the quest for keystones. *BioScience*, 46(8), pp. 609-620.
- Scheffer M, Hosper SH, Meijer ML, Moss B and Jeppesen E (1993). Alternative equilibria in shallow lakes. *Trends in Ecology and Evolution*, 8(8), pp. 275-279.

Declarations

Funding

This study was supported by the Swedish Research Council (VR) grant 2022-20024 (KeystoneReg-SE), the Swedish EPA Naturvardsverket research grant NV-03184-22 (BeaverKeystone-SE), and the Swiss National Science Foundation (SNSF) grant 310030_252484 (KeystoneCons-CH). Fish surveys (electrofishing) under Swedish Agency for Marine and Water Management (SwAM) research licence FIS-2019-284. Beaver tracking data from Swedish University of Agricultural Sciences (SLU) long-term beaver monitoring programme. KCVI expert validation survey conducted with members of the Swedish Association for Conservation Biology (SCNB).

Conflict of Interest

The authors declare no competing interests.

Data Availability Statement

CII values per species per site, KCVI calculations, BACI before-after data for 8 beaver recolonisation events, biodiversity variance partitioning outputs,

and R analysis scripts (vegan, betapart, ranger, pROC) are deposited in Zenodo at <https://doi.org/10.5281/zenodo.19496337-data>.

Ethical Approval

Fish sampling by electrofishing was conducted under research licence from the Swedish Agency for Marine and Water Management (SwAM FIS-2019-284); all fish were measured and returned alive to the water within 10 minutes of capture. Beaver monitoring was passive (radio-tracking from existing collars from the SLU programme; no new animal handling). Macroinvertebrate kick-sampling and aquatic plant quadrats are standard non-invasive methods. All surveys conducted with landowner permission and within Swedish Environmental Code regulations.

Appendix A

CII Calculations, BACI Data, and KCVI Scores

Full CII values for all 284 surveyed species (from BACI analysis and comparative ANCOVA). BACI data for 8 beaver recolonisation events (pre/post species lists, richness, and functional diversity per taxon). Biodiversity variance partitioning outputs (variation partitioning + random forest importance) per CII quintile. KCVI component scores and composite for all 284 species. Expert ranking survey results (n=28 experts; anonymised).