# Chapter 4
# Ecosystem Engineers, Keystone Species

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## Glossary

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| Connectance | The proportion of possible ecological interaction links between species that are realized. |
| Ecosystem engineer | An organism that creates or modifies its habitat [19]. |
| Ecosystem functioning | The way ecosystems work related to abiotic and biotic components, such as chemicals, water, soil, microbes, plants, and animals. |
| Keystone species | A species that has a disproportionate effect on its environment relative to its biomass (Paine 1995). |
| Trophic level | The position a species occupies in a food chain. |

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## Definition of the Subject

This entry focuses on two ecological phenomena. The first is "keystone species" which is defined by Paine [1] as a species (mostly of high trophic status) whose activities exert a disproportionate influence on the patterns of species occurrence, distribution, and density in a community. The second is the concept of "ecosystem engineers" defined by Jones et al. [2] as organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials.

## Introduction: Keystone Species and Ecosystem Engineers: Analysis of Concepts

Paine's definition of keystone species was inspired from the large effects of the removal of the carnivorous starfish (*Pisaster ochraceus*) from intertidal habitat, which reduced prey species diversity due to intense competition from mussel prey [3], and represents now a classic textbook in ecology. The original keystone species concept of Paine [1, 4] thus identified a very specific mechanism: the top-down regulation of community structure and diversity by a top predator (Fig. 4.1). The concept of keystone species has been later extended to a broader definition and now includes any species whose effect on ecosystems is disproportionately large relative to its low biomass in the community as a whole [5]. Keystone species are thus species which have large effects on communities and ecosystems through many different processes such as trophic interactions, pollination, or habitat modification [6, 7]. Examples include rabbits that can increase abundance and diversity of lizards

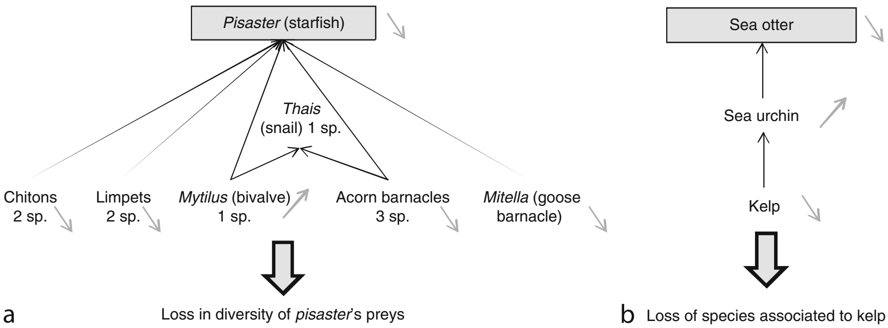


**Fig. 4.1** Two examples of keystone species impacts. (**a**) Effects of the removal of *Pisaster* on prey species diversity as a consequence of mussel population explosion. (**b**) Consequences of the removal of sea otters on species diversity due to overgrazing of kelp by sea urchins. Keystone species are represented in *grey boxes*. Small *grey arrows* indicate the direction of species abundance changes following the removal of the keystone species. The large *grey arrows* indicate the global consequences of keystone species loss on the ecosystem

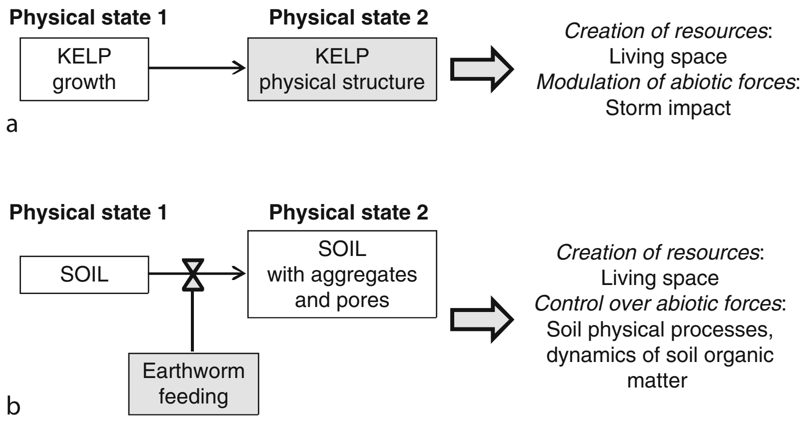


**Fig. 4.2** Two examples of ecosystem engineering with kelp (**a**) and earthworms (**b**) as ecosystem engineers. Ecosystem engineering corresponds to changes in physical state (state 1–2) of biotic (i.e., kelp for **a**) or abiotic (i.e., soil for **b**) materials. Ecosystem engineers are represented in *grey boxes*. (**a**) Case of autogenic engineering, the engineer is part of the new physical state (via growth here). (**b**) Case of allogenic engineering, the new physical state is caused by the engineer (⧗, caused via feeding here), but the engineer is not part of the new physical state

[8] and sea otters whose hunting in the late nineteenth century caused a population explosion of their sea urchin prey and consequent overgrazing of kelp which led to numerous extinctions of local species [6].

The concept of ecosystem engineering was proposed two decades later than the "keystone species" concept by Jones and colleagues [2]. They defined ecosystem engineers as "organisms that directly or indirectly modulate the availability of resources (other than themselves) to other species by causing physical state changes in biotic or abiotic materials. In so doing they modify, maintain and/or create habitats" [2]. They further distinguish between two types of ecosystem engineers (Fig. 4.2): autogenic engineers that change the environment via their own physical structures, i.e., their living and dead tissues, and allogenic engineers that change the environment by transforming living or nonliving materials from one physical state to another via mechanical or other means. The idea that organisms can have important effects on abiotic processes occurring in the environment had been recognized before; indeed, Darwin devoted a whole book to the impact of earthworms on soil formation [9]. However, since the development of the concept of ecosystem engineer, engineering effects have been described for many organisms, from classic examples such as beavers, termites, or earthworms [10–12] to mollusks [13], fish [14], caterpillars [15], polychaete worms [16], grasses [17, 18], burrowing shrimp [19], ants [20], and many other species (see Table 1 of [21]).

Both the keystone species and the ecosystem engineer concepts point out to species which have important effects in ecological communities and ecosystems. Although these concepts partly overlap – an ecosystem engineer can be a keystone species – they however insist on different aspects: the keystone concept focuses on species which have disproportionate effects on community structure and ecosystem functioning ("outcome focused" sensu [22]) whereas the ecosystem engineering concept considers organisms which influence the abiotic environment with consequences on other species and related ecosystem processes ("process focused" sensu [22]). These differences between the two concepts are reflected in the literature: these concepts generally appear in distinct studies as less than 5% of the studies on these topics refer to both ecosystem engineers and keystone species (source: ISI Web of Science).

The keystone species concept has been strongly related to food web theory since its first definition [1, 23]. In particular, the identification of keystone species in food webs is an important issue. Theoretical studies have tried to pin down the characteristics of keystone species through food web models [24, 25] and several indices based on food web topology have been developed to identify keystones [26]. Models have shown that the loss of species with a large number of trophic interactions can trigger high numbers of secondary extinctions with serious consequences for species persistence; a result which highlights the potential keystone role of highly connected species in food webs [24, 27, 28].

In contrast, the concept of ecosystem engineering has been rarely related to food web studies. Recent studies acknowledge that ecosystem engineers may also play an important role in the network of trophic interactions but separating the trophic effects from the engineering effects to determine their relative importance is difficult [20, 29–31].

The importance of keystone species can also be strongly linked with ecosystem engineering. For example, the large impact of sea otters in kelp forest ecosystems results from the coupling between engineering effects and a trophic cascade [32]. In these ecosystems, kelp provides habitat for many species and dampens wave action; the keystone effect of sea otters is thus mediated through their indirect trophic effect on kelp densities which is a main ecosystem engineer.

## Issue-1: How to Find Keystone Species and Ecosystem Engineers in Communities?

Keystone species and ecosystem engineers may affect ecosystem processes, such as nutrient cycling, and thereby ecosystem functioning. In the face of rapid biodiversity loss, a considerable amount of studies were dedicated to investigate a possible link between species richness and ecosystem function [33] and the threat of diversity loss on the loss of ecosystem services to man. First indications show positive relationships between species richness and ecosystem productivity, stability, and sustainability, with more species being able to fully and complementarily run ecosystem functions due to niche differentiation and facilitative interactions (reviewed by [34]). However, there is now a growing consensus that functional diversity, rather than species numbers per se, strongly determines ecosystem functioning [35]. This means that the presence of a particular species with specific traits may play a larger role in determining ecosystem function than merely the number of species [36]. The apparent diversity-ecosystem function relationship can thus be partly caused by a greater chance of an influential species with particular traits being present in more diverse communities than in species-poor communities.

If it is possible to predict and identify a priori a set of species traits that determine keystone interactions in a system, this would greatly benefit management and conservation purposes. Species' traits determine how species contribute to ecosystem processes, so the presence and distribution of such traits can be utilized to indicate aspects of ecosystem functioning [37]. To identify keystone species various methods have been used ranging from experimental removal or addition manipulations to comparative studies and natural history observations [5]. Partly because of these methodological issues, identifying keystone species has so far proved elusive [5, 38] although some progress has been made and its concept now widely investigated in the context of complex ecological networks [25, 39–41]. Some examples of specific traits are for instance trophic level, body size, connectance, or traits concerning tolerance and resilience to disturbances. Organisms that influence their environment strongly and contribute disproportionately to the functioning of ecosystems often seem to occupy higher trophic levels in food webs [5]. Top predators have been described as highly interactive keystone species [42], have been shown to play an important role in stabilizing food webs [43], and play important roles in marine ecosystems [44] and terrestrial ecosystems [45].

Also, the loss of top predators has been linked to secondary extinctions [46, 47]. This has been attributed to their ecological role as suppressors of medium-sized predators (mesopredators) (e.g., [48, 49]) and generalist herbivores [50, 51]. In terrestrial ecosystems, organisms that influence their environment strongly also often seem to be large bodied (e.g., [52]). Larger bodied organisms require a high resource and energy use per individual [53, 54] and have greater mobility, home ranges, and longevity [55, 56] and, thereby, control more resources over greater and coarser spatial scales [52, 57]. It is also proposed that well-linked and interacting species as key interactors are more important for the community [28, 58–62]. This approach characterizes the interaction structure of species placed in an ecological network. Among plants, on the other hand, some studies have shown that species within the same functional types but with different requirements and tolerances may provide insurance to the system in the form of long-term resilience against changes in environmental factors, such as global warming, grazing, drought or frost [35].

The latter example indicates that the keystone status of a species often appears to be context dependent, and may change with successional status, productivity, diversity, and other ecosystem traits [63]. It is therefore important to identify how the importance of traits that define keystone species change across a gradient of conditions, measuring environmental factors, community composition, trophic dynamics, and distribution of strong and weak links in the community (e.g., [24]). Without droughts, a specific plant species may not play an important role in maintaining community composition or ecosystem functioning. The Australian brushtail possum (*Trichosurus vulpecula*) may function as a keystone species in rata-kamahi forests by defoliating and killing canopy trees, but not in beech-dominated forests where floristic composition, but not forest structure, is typically affected [64–66]. A species in its native grounds may play no specific role in the system, whereas an invasive species may have devastating effects in the system it got introduced into, e.g., feral cats and rats on islands [67], Alewife (*Alosa pseudoharengus*) in nonnative freshwater lakes and ponds [68], and Cheatgrass (*Bromus tectorum*) in nonnative grasslands [69].

Identifying keystone species therefore is not without its problems. It is also important to notice that ecologically important species might not necessarily be the ones that are also considered important by traditional conservationists (i.e., rare species; [70]).

## Issue-2: Usefulness for Management

Because of the limited resources available in comparison to conservation needs, it has been proposed to design protection of single species in the aim of indirectly protecting the regional biota. These "surrogate species" are roughly of three categories [71]: (1) flagships, charismatic species that attract public support; (2) umbrellas, species requiring such habitats that their protection might protect other species; and (3) biodiversity indicators, taxa whose presence may indicate high species richness. However the effectiveness of these policies has been questioned and [70] suggested that single-species management might be more effective when directed toward keystone species. Indeed, the importance of keystone species and ecosystem engineers in communities make these species particularly important conservation targets, since the loss of these species can affect entire communities and ecosystems [72]. However, the main difficulty for applying these concepts to conservation issues lays on both the identification of keystone species and ecosystem engineers in communities and on the context dependence of their impacts, as discussed in the previous section. Thus, although these concepts appear relevant for conservation policies, it is still a long way from providing general and practical recommendations for conservationists and managers [71].

The concepts of keystone species and of ecosystem engineers could also be useful for other management issues in natural and anthropized ecosystems, such as for ecosystem restoration or agriculture. For example, in agro-ecosystems, several well-known ecosystem engineers have been used to improve soil fertility and crop yield. In some countries, farmers make use of the soil fertilizing effect of termites by spreading termite mound soil in their field [73]. Similarly, earthworm inoculation has generally positive effects on crop yield [74].

## Future Directions

The notions of ecosystem engineers and keystone species have been playing prominent roles in ecology for several decades, still many questions and uncertainties ask for further investigations. Three of them are briefly described here. The first is how keystone roles and engineering effects are related to body-size: Do larger organisms have larger effects than smaller organisms? The second regards the context dependence of keystone roles and engineering effects: As the composition and structure of ecological communities are dynamic both in terms of species composition and species abundances, what does that imply for the role species have in communities and ecosystem functioning? The third line of research might be the most relevant for our society: How can the concepts for nature conservation, biodiversity protection, and the enhancement of environmental quality be used?

## Bibliography

### *Primary Literature*


1. Paine RT (1969a) A note on trophic complexity and community stability. Am Nat 103:91–93
2. Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386
3. Paine RT (1966) Food web complexity and species diversity. Am Nat 100:65–75
4. Paine RT (1969b) The *Pisaster-Tegula* interaction: prey patches, predator food preference, and intertidal community structure. Ecology 50:950–961
5. Power ME, Tilman D, Estes JA, Menge BA, Bond WJ, Mills LS, Daily G, Castilla JC, Lubchenco J, Paine RT (1996) Challenges in the quest for keystones. Bioscience 46:609–620
6. Estes JA, Palmisano JF (1974) Sea otters: their role in structuring nearshore communities. Science 185:1058–1060
7. Terborgh J (1986) Keystone plant resources in tropical forest. In: Soulé ME (ed) Conservation biology. Sinauer Associates, Sunderland, pp 330–344
8. Bravo LG, Belliure J, Rebollo S (2009) European rabbits as ecosystem engineers: warrens increase lizard density and diversity. Biodivers Conserv 18:869–885
9. Darwin CR (1881) The formation of vegetable mould through the action of worms, with observations of their habits. John Murray, London
10. Dangerfield JM, McCarthy TS, Ellery WN (1998) The mound-building termite *Macrotermes michaelseni* as an ecosystem engineer. J Trop Ecol 14:507–520
11. Eisenhauer N (2010) The action of an animal ecosystem engineer: identification of the main mechanisms of earthworm impacts on soil microarthropods. Pedobiologia 53:343–352
12. Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. Oecologia 132:96–101
13. Gutiérrez JL, Jones CG, Strayer DL, Iribarne OO (2003) Mollusks as ecosystem engineers: the role of shell production in aquatic habitats. Oikos 101:71–90
14. Flecker AS, Taylor BW (2004) Tropical fishes as biological bulldozers: density effects on resource heterogeneity and species diversity. Ecology 85:2267–2278
15. Lill JT, Marquis RI (2003) Ecosystem engineering by caterpillars increases insect herbivore diversity on white oak. Ecology 84:682–690
16. Schwindt E, De Francesco C, Iribarne OO (2004) Individual and reef growth of the non-native reef-building polychaete *Ficopomatus enigmaticus* in a south-western Atlantic coastal lagoon. J Mar Biol Assoc UK 84:987–93
17. Perelman SB, Burkart SE, León RJC (2003) The role of native tussock grass (*Paspalum quadrifarium* Lam.) in structuring plant communities in the Flooding Pampa grasslands, Argentina. Biodivers Conserv 12:225–238

18. Fogel BN, Crain CM, Bertness MD (2004) Community level engineering effects of *Triglochin maritima* (seaside arrowgrass) in a salt marsh in northern New England, USA. J Ecol 92:589–597
19. Berkenbusch K, Rowden AA (2003) Ecosystem engineering – moving away from 'just-so' stories. New Zeal J Ecol 27:67–73
20. Sanders D, van Veen FJF (2011) Ecosystem engineering and predation: the multi-trophic impact of two ant species. J Anim Ecol 80:569–765
21. Wright JP, Jones CG (2004) Predicting effects of ecosystem engineers on patch-scale species richness from primary productivity. Ecology 85:2071–2081
22. Wright JP, Jones CG (2006) The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56:203–209
23. De Ruiter PC, Wolters V, Moore JC, Winemiller KO (2005) Food web ecology, playing Jenga and beyond. Science 309:68–71
24. Christianou M, Ebenman B (2005) Keystone species and vulnerable species in ecological communities: strong or weak interactors? J Theor Biol 235:95–103
25. Libralato S, Christensen V, Pauly D (2006) A method for identifying keystone species in food web models. Ecol model 195:153–171
26. Jordán F, Liu W-C, Davis AJ (2006) Topological keystone species: measures of positional importance in food webs. Oikos 112:535–546
27. Solé RV, Montoya JM (2001) Complexity and fragility in ecological networks. P Roy Soc B-Biol Sci 268:2039–2045
28. Dunne JA, Williams RJ, Martinez ND (2002) Network structure and biodiversity loss in foodwebs: robustness increases with connectance. Ecol Lett 5:558–567
29. Wilby A, Shachak M, Boeken B (2001) Integration of ecosystem engineering and trophic effects of herbivores. Oikos 92:436–444
30. Zhang YX, Richardson JS, Negishi JN (2004) Detritus processing, ecosystem engineering, and benthic diversity: a test of predator-omnivore interference. J Anim Ecol 73:756–766
31. De Visser SN, Freymann BP, Olff H (2011) The Serengeti food web: empirical quantification and analysis of topological changes under increasing human impact. J Anim Ecol 80:484–494
32. Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957
33. Schwartz MW, Brigham CA, Hoeksema JD, Lyons KG, Mills MH, van Mantgem PJ (2000) Linking biodiversity to ecosystem function:implications for conservation ecology. Oecologia 122:297–305
34. Giller PS, O'Donovan G (2002) Biodiversity and ecosystem function: do species matter? Biol Environ 102B:129–139
35. Diaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. Trends Ecol Evol 16:646–655
36. Sala OE, Lauenroth WK, McNaughton SJ, Rusch G, Zhang X (1996) Biodiversity and ecosystem functioning in grasslands. In: Mooney HA et al (eds) Functional role of biodiversity: a global perspective. Wiley, Chichester, pp 129–149
37. Bremner J (2008) Species' traits and ecological functioning in marine conservation and management. J Exp Marine Biol Ecol 366:37–47
38. Menge BA, Berlow EL, Balchette CA, Navarrete SA, Yamada SB (1994) The keystone species concept: variation in interaction strength in a rocky intertidal habitat. Ecol Monog 64:249–286
39. Brose U, Berlow EL, Martinez LD (2005) Scaling up keystone effects from simple to complex ecological networks. Ecol Lett 8:1317–1325
40. Mills LS, Soulé ME, Doak DF (1993) The keystone-species concept in ecology and conservation. Bioscience 43:219–224
41. Okey TA, Banks S, Born AF, Bustamante RH, Calvopiña M, Edgar GJ, Espinoza E, Fariña JM, Garske LE, Reck GK, Salazar S, Shepherd S, Toral-Granda V, Wallem P (2004) A trophic model of a Galapagos subtidal rocky reef for evaluating fisheries and conservation strategies. Ecol Model 172:383–401

42. Soulé ME, Estes AJ, Miller B, Honnold DL (2005) Strongly interacting species: conservation policy, management and ethics. BioScience 55:168–176
43. Rooney N, McCann K, Gellner G, Moore JC (2006) Structural asymmetry and the stability of diverse food webs. Nature 442:265–269
44. Boyd I, Wanless S, Camphuysen CJ (eds) (2006) Top predators in marine ecosystems. Cambridge University Press, Cambridge, UK
45. Johnson CN (2010) Red in tooth and claw: how top predators shape terrestrial ecosystems. J Anim Ecol 79:723–725
46. Borrvall C, Ebenman B (2006) Early onset of secondary extinction in ecological communities following the loss of top predators. Ecol Lett 9:435–442
47. Henke SE, Bryant FC (1999) Effects of coyote removal on the faunal community in western Texas. J Wildlife Manage 63:1066–1081
48. Crooks JA, Soulé ME (1999) Lag times in population explosions of invasive species: causes and implications. In: Viken A (ed) Invasive species and biodiversity management. Kluwer, Dordrecht, pp 103–126
49. Letnic M, Koch F, Gordon C, Crowther MS, Dickman CR (2009) Keystone effects of an alien top-predator stem extinctions of native mammals. Proc Roy Soc Biol Sci 276:3249–3256
50. McLaren BE, Peterson RO (1994) Wolves, moose, and tree rings on isle royale. Science 266:1555–1558
51. Ripple WJ, Beschta RL (2003) Wolf reintroduction, predation risk, and cottonwood recovery in Yellowstone National Park. Forest Ecol Manag 184:299–313
52. Owen-Smith RN (1988) Megaherbivores: the influence of very large body size on ecology. Cambridge University Press, Cambridge, UK
53. Bush GL (1993) A reaffirmation of Santa Rosalia, or why are there so many kinds of small animals? In: Lees DR, Edwards D (eds) Evolutionary patterns and processes. Academic, London, pp 229–249
54. Olff H, Ritchie ME, Prins HHT (2002) Global environmental controls of diversity in large herbivores. Nature 415:901–904
55. Haskell JP, Ritchie ME, Olff H (2002) Fractal geometry predicts varying body size scaling relationships for mammal and bird home ranges. Nature 418:527–530
56. Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge, UK
57. Ritchie ME, Olff H (1999) Spatial scaling laws yield a synthetic theory of biodiversity. Nature 400:557–560
58. Allesina S, Bodini A, Bondavalli C (2006) Secondary extinctions in ecological networks: bottlenecks unveiled. Ecol Model 194:150–161
59. Dunne JA, Williams RJ, Martinez ND (2004) Network structure and robustness of marine food webs. Marine Ecol Prog Ser 273:291–302
60. Estrada E (2007) Characterisation of topological keystone species: local, global and "meso-scale" centralities in food webs. Ecol Complex 4:48–57
61. Jordán F, Benedek Z, Podani J (2007) Quantifying positional importance in food webs: a comparison of centrality indices. Ecol Model 205:270–275
62. Jordán F, Liu W-C, Mike A (2009) Trophic field overlap: a new approach to quantify keystone species. Ecol Model 220:2899–2907
63. De Ruiter PC, Neutel A, Moore JC (1995) Energetics, patterns of interaction strengths, and stability in real ecosystems. Science 269:1257–1260
64. Batcheler CL (1983) The possum and rata-kamahi dieback in New Zealand: a review. Pac Sci 37:415–426
65. Rose AB, Pekelharing CJ, Platt KH (1992) Magnitude of canopy dieback and implications for conservation of southern rata-kamahi (Metrosideros umbellate-Weinmannia racemosa) forests, central Westland, New Zealand. New Zeal J Ecol 16:23–32
66. Wardle JA (1984) The New Zealand beeches: ecology, utilization and management. New Zealand Forest Service, Christchurch, p 447

67. Holdaway RN (1999) A spatio-temporal model for the invasion of the New Zealand archipelago by the Pacific rat *Rattus exulans*. J Roy Soc New Zeal 29:91–105
68. Madenjian CP, Pothoven SA, Dettmers JM, Holuszko JD (2006) Changes in seasonal energy density of alewife (*Alosa pseudoharengus*) in Lake Michigan after invasion of dreissenid mussels. Can J Fish Aquat Sci 63:1–12
69. Knapp PA (1996) Cheatgrass (*Bromus tectorum* L.) dominance in the Great Basin desert. Global Environ Chang 6:37–52
70. Simberloff D (1998) Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? Biol Conserv 83:247–257
71. Boogert NJ, Paterson DM, Laland KN (2006) The implications of niche construction and ecosystem engineering for conservation biology. BioScience 56:1–9
72. Crain CM, Bertness MD (2006) Ecosystem engineering across environmental gradients: implications for conservation and management. BioScience 56:211–218
73. Black HIJ, Okwakol MJN (1997) Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of termites. Appl Soil Ecol 6:37–54
74. Fragoso C, Brown GG, Patron JC, Blanchart E, Lavelle P, Pashanasi B, Senapati B, Kumar T (1997) Agricultural intensification, soil biodiversity and agroecosystem function in the tropics: the role of earthworms. Appl Soil Ecol 6:17–35
75. Paine RT (1995) A conversation on refining the concept of keystone species. Conserv Biol 9(4):962–964