A rodent herbivore reduces its predation risk through ecosystem engineering

Graphical abstract

Highlights

- Voles modified habitat structure by destroying a large, unpalatable bunchgrass

- Damage activities of voles decreased the plant volume of the bunchgrasses

- Vole damage activities were enhanced at the presence of the predatory birds

- Habitat modifications by voles reduced predation risk and increased vole survival
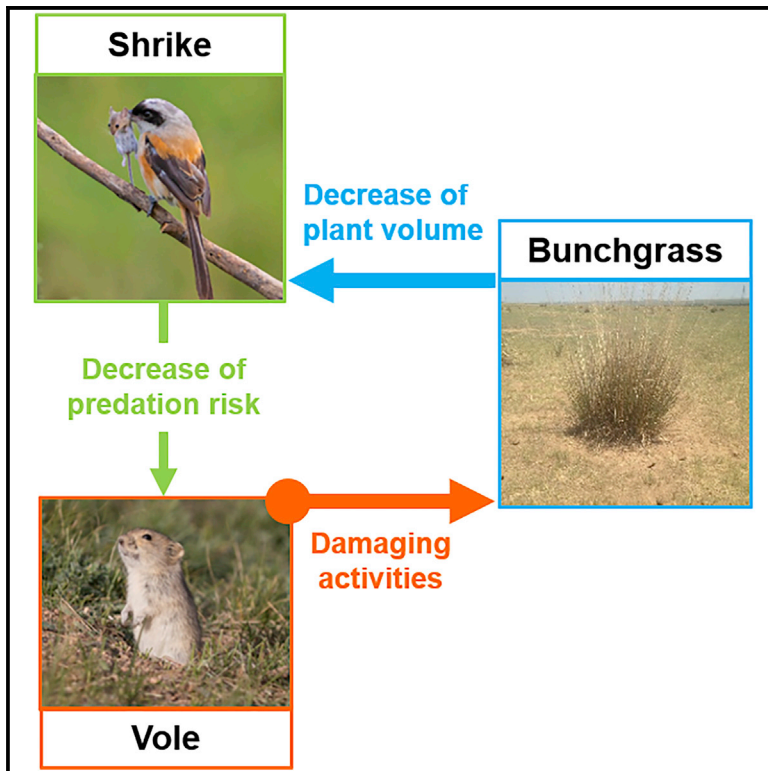
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In brief

Zhong et al. show that by damaging a large, unpalatable bunch grass, Brandt's voles in steppe grasslands in China can reduce the predation risk from avian predators (*Lanius* spp.) probably due to improved vision. Habitat modifications by voles can reduce the visiting frequency of avian predators and thus increase the survival of voles.

CellPress

Report

A rodent herbivore reduces its predation risk through ecosystem engineering

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SUMMARY

Predator-prey interactions are ubiquitous and powerful forces that structure ecological communities.[1–3] Habitat complexity has been shown to be particularly important in regulating the strength of predator-prey interactions.[4–6] While it is well established that changes in habitat structure can alter the efficacy of predatory and anti-predatory behaviors,[7–9] little is known about the consequences of engineering activity by prey species who modify the external environment to reduce their own predation risk. Using field surveys and manipulative experiments, we evaluated how habitat modification by Brandt's voles (*Lasiopodomys brandtii*) influences predation risk from a principal avian predator (shrike; *Lanius* spp.) in a steppe grassland, located in Inner Mongolia, China. We found that voles actively modify habitat structure by cutting down a large, unpalatable bunchgrass species (*Achnatherum splendens*) in the presence of shrikes, a behavior that disappeared when these avian predators were excluded experimentally. The damage activities of these voless dramatically decreased the volume of unpalatable grasses, which in turn reduced visitations by shrikes and thus mortality rates. Our study shows that herbivorous prey that act as ecosystem engineers can directly reduce their own predation risk by modifying habitat structure. Given the ubiquity of predation risks faced by consumers, and the likely ability of many consumers to alter the habitat structure in which they live, the interplay between predation risk and ecosystem engineering may be an important but unappreciated mechanism at play in natural communities.

RESULTS

We tested the hypothesis that Brandt's voles (*L. brandtii*) damage large individuals of an unpalatable bunchgrass species (*A. splendens*) and thereby reduce the predation risk they face from their primary avian predators (shrikes; *Lanius* spp.) in a steppe grassland in Inner Mongolia, China (Figure 1). The shrike uses bunchgrasses both as perches when seeking vole prey and as places to hoard their captures. We carried out a large-scale field survey to investigate the impact of Brandt's vole activities on the growth of large *A. splendens* and the association between the abundance of these large bunchgrasses and predation on Brandt's voles by predatory birds. These correlative results suggest hypotheses which we then assessed experimentally. We conducted two manipulative experiments to explicitly test (1) the effects of risk from predatory birds on amplifying the damaging behaviors exerted by voles on the large *A. splendens* and (2) the effects of changes in vegetation structure caused by the voles on their own predation risk from the predatory birds.

Field survey: The interrelationships among Brandt's voles, *A. splendens* grass, and predation risk

Using natural variation in vole and bunchgrass abundance in our study system, we assessed correlations between vole presence/absence, bunchgrass growth rates, and avian predator visits. We found that the average plant volume (calculated by multiplying the ground surface area covered by an individual bunchgrass by its height) of the unpalatable *A. splendens* grass, given vole presence, was reduced by 0.63 m³, whereas the average plant volume of *A. splendens* in the absence of voles increased by 0.49 m³, as compared to the initial conditions ($F_{1, 14}$ = 15.09; p = 0.0017; Figure 2A). Moreover, the total number of visits by predatory birds per plot was positively correlated with the coverage of *A. splendens* grass (pseudo-R^2 = 0.252; z-ratio = 2.185; p = 0.029; Figure 2B).
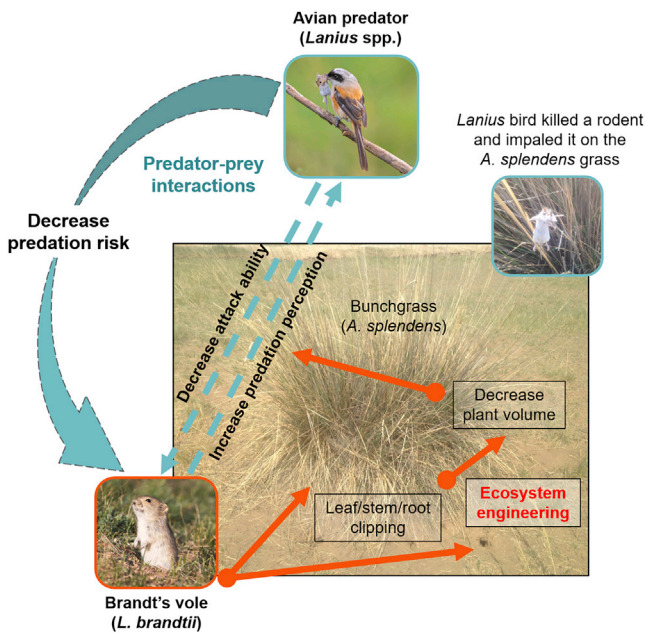
Figure 1. The hypothesized interactions among avian predators (*Lanius* spp.), Brandt's voles (*Lasiopodomys brandtii*), and bunchgrasses (*Achnatherum splendens*) in the Inner Mongolia steppe grassland of northern China

The presence of large unpalatable *A. splendens* grass can hinder the risk perception of voles from their major avian predators, *Lanius* spp., but increase attack ability of avian predators by providing perching sites. However, the ecosystem engineering (including clipping of stems and leaves and burrowing and other root-damaging activities) of *L. brandtii* voles can reduce the coverage of *A. splendens* grass and thus increase the ability of voles to detect predators and deter visits by predators, thus reducing mortality from predation. The interactions between avian predators and voles via bunchgrass are denoted by the steel gray lines. The ecosystem engineering effects of voles are denoted by orange lines. The *Lanius* bird photo capturing a rodent was provided by Guoyong Li. See also Figure S1.

Semi-natural manipulative experiment #1: Effects of predation risk on the damage activities of Brandt's voles on *A. splendens* grass

Net enclosures (predatory bird exclusion) significantly reduced the visiting frequency of predatory birds across vole treatments (χ^2 = 11.93; df = 1; p < 0.001), while the presence of voles had the opposite effects across predator treatments (χ^2 = 9.66; df = 1; p = 0.002; Figure 3A). In the plots without net protection (predatory birds were thus potentially present), the presence of voles significantly increased the visiting frequency of birds (216% increase in plots with voles versus plots without voles; z-ratio = 2.76; p = 0.006). However, in the plots with net protection (preventing attacks by predatory birds), the visiting frequency of birds was similar between vole and no-vole treatments (z-ratio = 0.98; p = 0.341; Figure 3A).

The growth of plant volume of *A. splendens* was significantly affected by the interaction between predatory birds and voles ($F_{1, 20}$ = 10.87; p = 0.004). Specifically, the presence of voles significantly reduced the growth of aboveground plant volume when predators were present (t-ratio = 5.80; p < 0.001), but when predatory birds were excluded, the
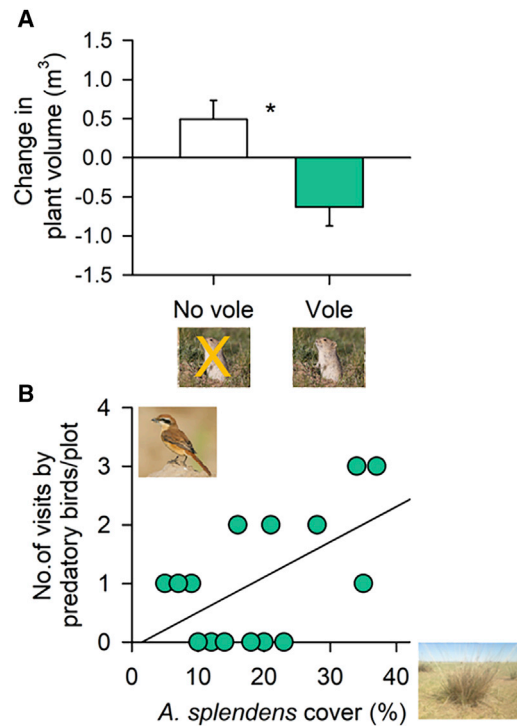

Figure 2. Field survey: The interrelationships among Brandt's voles, *A. splendens* grass, and predation risk

(A and B) (A) Effects of vole activities on plant growth of 15 pairs of *A. splendens* grasses (one with voles present, while another had them absent) during a 1-year period (from July 2019 to August 2020) and (B) the effects of *A. splendens* cover on the total number of visits by predatory birds per plot in the 15 plots (10 × 10 m) during the peak of growing seasons (June to August) of 2019 (see STAR Methods). The net growth rate of *A. splendens* was calculated as the differences in plant volume between the two sampling dates in July 2019 and August 2020. The *Lanius* bird photo was provided by Wenke Duan. An asterisk (*) between the bars indicates significant differences between treatments. Error bars represent ± 1 SE. See also Figure S1.

growth of plant volume was similar between plots with and without voles (t-ratio = 1.15; p = 0.464; Figure 3B). In contrast to plant volume, the growth of root biomass of *A. splendens* grass was not significantly affected by the treatments (Figure 3C).

Semi-natural manipulative experiment #2: Effects of *A. splendens* grass coverage on behaviors of Brandt's voles and predatory birds

The presence of *A. splendens* grass significantly changed the behavior of voles and predatory birds and their interactions. The coverage of *A. splendens* did not affect the total number of visits by predatory bird per plot (χ^2 = 2.32; df = 2; p = 0.314), though a trend of increase in the number of visits with increased coverage of *A. splendens* was observed (Figure 4A). However, coverage of *A. splendens* significantly altered the feeding behaviors ($F_{2,10}$ = 9.23; p = 0.005) and mortality rate (χ^2 = 7.55; df = 2; p = 0.023) of voles. With increased coverage by *A. splendens* grass, the feeding frequency of voles on palatable grasses was reduced, and the mortality rate of voles per plot was
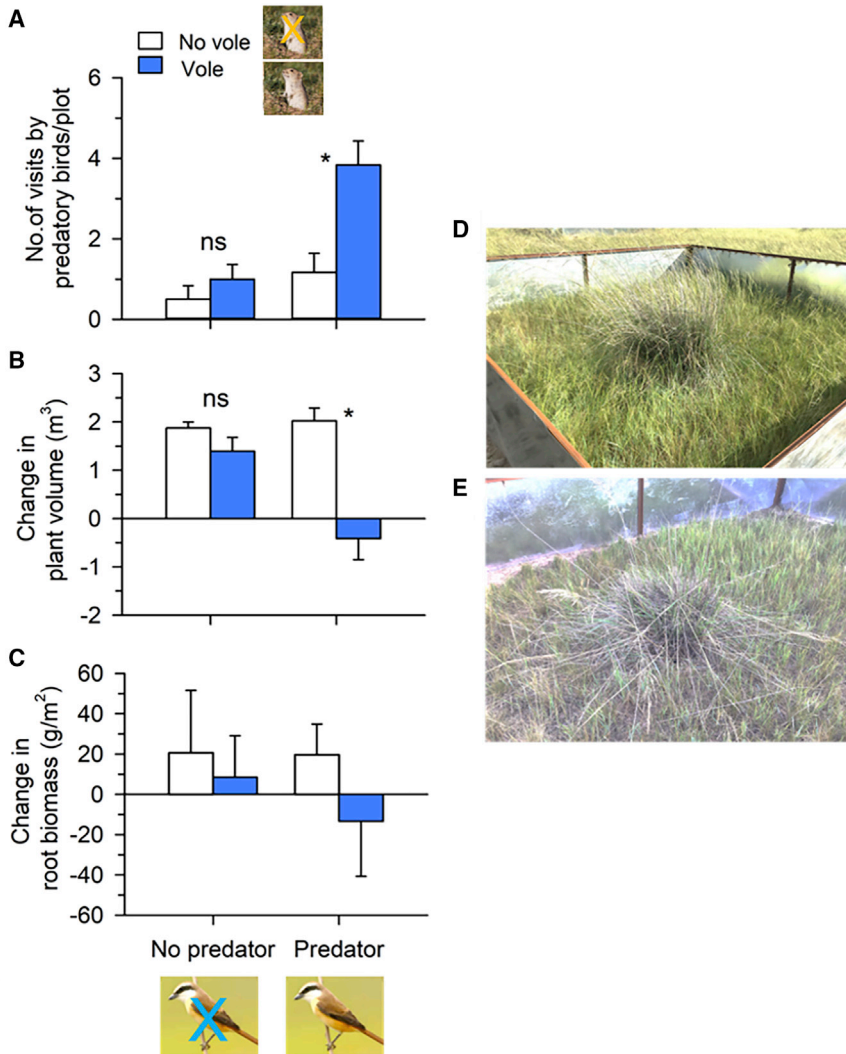
Figure 3. Semi-natural manipulative experiment #1: Effects of predation risk on the damage activities of Brandt's voles on *A. splendens* grass

(A–C) Left panels: effects of the manipulations of predatory birds (presence/absence) and voles (presence/absence) on (A) the total number of visits by predatory birds, (B) the growth of plant volume, and (C) root biomass of *A. splendens* grasses in the 24 enclosure plots (6 m × 6 m; 6 replicates for each treatment) during a 1-month period (July) in the growing seasons of 2020 (see STAR Methods). The net growth rate of *A. splendens* was calculated as the differences in plant volume and root biomass between the two sampling dates in early and late July 2020.

(D and E) Right panels: a comparison of the *A. splendens* bunchgrass (D) before and (E) after the 1-month manipulative experiment #1 due to the damage activities of voles in the plots under presence of both voles and predatory birds. The *Lanius* bird photo was provided by Wenke Duan. An asterisk (*) between the bars indicates significant and ns indicates nonsignificant differences between treatments. Error bars represent ± 1 SE. See also Figures S1 and S4A.

increased. Plots with a coverage of 100% *A. splendens* grass had a significantly lower frequency of palatable grass feeding by voles (t-ratio = 4.05; p = 0.006) and also a significantly higher mortality rate of voles (z = 2.57; p = 0.010) as compared to plots without *A. splendens* grass (i.e., 0% coverage) (Figures 4B and 4C).

DISCUSSION

We have shown that Brandt's voles actively reduce the higher predation risk associated with the presence of a large bunchgrass by damaging this unpalatable, dominant plant species. The negative effects on the bunchgrasses by voles markedly reduced their mortality rates. These observations provide novel insights into how ecosystem engineers can drive the dynamics and structure of food webs by the modification of habitat structure.[11]

The potential for predation risk drove the damaging activities of Brandt's voles on a large dominant grass utilized for perches by its main avian predator. Voles did not consume the *A. splendens* grass[12] but simply cut the basal parts of the stems and leaves and left them on the ground and dug burrows, which

led to cutting of the roots of the bunchgrass (Figure S1). These activities lead to negative growth for individual bunchgrasses, making them less suitable as perches and larders for the predatory bird but more suitable for voles to detect the avian predators due to improved vision. These findings, along with the fact that high predation risk is often associated with the presence of large individuals of the *A. splendens* grass, suggest that the damage activities of voles on *A. splendens* grass are an adaptive behavior aimed at habitat modification to reduce predation risk.

It is well documented that activities of herbivores can exert profound effects on habitat structure by acting as ecosystem engineers.[13–17] There is also growing evidence that such habitat modifications can have important consequences on trophic interactions in food webs because of how microhabitat structure influences both predatory tactics and prey escape behaviors. In a marine ecosystem in the Catalan coast, Pagès et al.[18] reported that grazing by the principal herbivorous fish, *Sarpa salpa*, significantly altered habitat structure by reducing the canopy height of seagrass, which in turn increased predation rates by predatory fishes such as *Sparus aurata* and *Diplodus sargus* on their herbivorous sea urchin prey *Paracentrotus lividus*. In African savannas, the key ecosystem engineer elephants (*Loxodonta africana*) can open up woody vegetation and maintain large areas of open grasslands. This in turn alters the perception of predation risk by different vertebrate herbivores and hence the ability of top predators such as lions to kill these prey.[19–21] These studies have focused on how habitat modifications by one herbivore species can indirectly modify
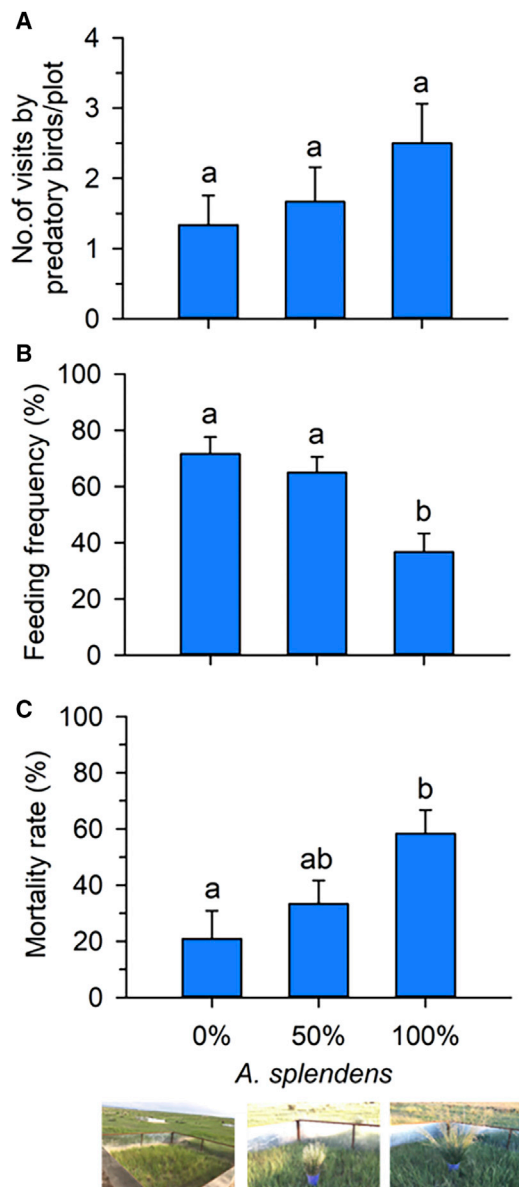
Figure 4. Semi-natural manipulative experiment #2: Effects of _A. splendens_ grass coverage on behaviors of Brandt's voles and predatory birds

(A–C) (A) The total number of visits by the predatory birds, (B) the feeding frequency of Brandt's voles on their palatable host grass plants, and (C) the mortality rate of Brandt's voles in the 18 enclosure plots (6 m × 6 m) in the semi-natural manipulated experiment# 2, during a 3-week period (late July to mid-August) in the growing seasons of 2020 (see STAR Methods). Different letters above the bars indicates significant differences between treatments. Error bars represent ± 1 SE. See also Figures S1, S2, and S4B.

the predation risk for another herbivore species, a form of indirect interaction termed "interaction modification."[22] But none of these studies have considered the consequences of these habitat alterations on predation risk of the habitat manipulator itself. Yet many herbivore engineers themselves face pervasive predation risk in natural ecosystems.[23–26] In this study, we provide empirical evidence that herbivorous prey, when acting as

ecosystem engineers, can directly reduce their own predation risk by modifying habitat structure. Given that nearly every herbivore species faces predation risk and that all species can likely modify habitat structure at least to some degree, the ecosystem engineering effects of Brandt's voles on predation risk documented in our ecosystem may also exist in other ecosystems and herbivore species.

If individuals of a species can alter habitat structure and thus improves their individual fitness and this effect spills over to conspecifics, this can lead to an Allee effect (i.e., increased individual fitness at higher population densities).[27] This can generate alternative stable states and permit spatial patchiness. Avian predators are always present in our system, imposing mortality on voles even when voles are scarce. But these predators require bunchgrasses to effectively catch voles (e.g., as perches or impaling sites). Because voles remove bunchgrasses, the abundance of bunchgrasses likely declines with vole population size. At high vole numbers, there should be scant bunchgrasses, making predation harder and leading to reduced visits by avian predators. In the supplemental materials (Figure S2), we present a simple graphical model that illustrates how these processes could lead to alternative stable states. Birth rates of voles decline with density. At low densities, death rates rise because predators are attracted and bunchgrasses are common. But at high prey densities, the increasing degradation and thus scarcity of bunchgrasses hampers attacks, generating a component Allee effect in mortality. This can generate a "predator pit" at low density,[28] which can be escaped at high vole numbers. The complex vole-shrike interaction mediated by bunchgrasses provides empirical evidence that the transition between positive to negative effect of prey on predator would produce multiple stable equilibria that increase community diversity and stability.[29–31] This finding suggests that planting bunchgrasses would help to reduce damage of overabundant vole to pastureland.

The habitat-restructuring activities of these herbivorous voles on unfavorable plant structure almost surely are an adaptive behavior that arose through natural selection. Engineering activities may be costly for time and energy but can bring crucial benefits. In areas with high predation risk, a simple strategy for herbivore prey could be to leave and select a safer habitat with lower predation risk. Yet such a strategy may come at the expense of losing high food availability[32–35] or costs incurred simply by moving (and alternative habitats may not be available). If herbivorous prey as ecosystem engineers actively modify the vegetation structure so as to reduce their predation risk, this may allow them to continue to utilize favorable resource-rich patches, even in the potential presence of predators. In our study, in addition to lowered mortality, lowered predation risk increases foraging activities and so may facilitate vole population performance and fitness in the long run. It should be pointed out that the higher mortality rate of voles in the plots with abundant bunchgrass can be attributed to either direct predation (predators killing the voles) and the costs of avoiding predation risk (e.g., stress responses to perceived predation risks from shrikes). The relative contributions of these consumptive and non-consumptive impacts of predators are difficult to distinguish in the field. This issue warrants further investigation.

Our study highlights the importance of behavioral responses by prey to predation risk via ecosystem engineering activities.

While these activities may be costly, they can be outweighed by other fitness benefits for the engineer. Ecosystem engineering by changing the physical environment has been broadly shown to modify species interactions.[17–19,36,37] Our study demonstrates that Brandt's voles can reduce their own predation risk by modifying habitat structure. This finding underlines the importance of studying trophic and non-trophic interactions in concert to fully understand ecosystem dynamics and stability.[11,38,39]

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2022.02.074.

AUTHOR CONTRIBUTIONS

Z. Zhong and Z. Zhang designed the experiments. Z. Zhong and G.L. carried out the experiments. Z. Zhong, D.S., and G.L. analyzed the data. Z. Zhong, Z. Zhang, D.S., and R.D.H. wrote the first draft of the manuscript, and D.W. and G.L. helped to improve the manuscript. All authors contributed to draft review and editing.

DECLARATION OF INTERESTS

The authors declare no competing interests.

REFERENCES

1. Hairston, N.G., Smith, F.E., and Slobodkin, L.B. (1960). Community structure, population control, and competition. Am. Nat. 94, 421–425.

2. Schmitz, O.J., Hambäck, P.A., and Beckerman, A.P. (2000). Trophic cascades in terrestrial systems: a review of the effects of carnivore removals on plants. Am. Nat. 155, 141–153.

3. P. Barbosa, and I. Castellanos, eds. (2005). Ecology of predator-prey interactions (Oxford University Press).

4. Heck, K.L.J., and Crowder, L.B. (1991). Habitat structure and predator-prey interactions in vegetated aquatic systems. In Habitat structure: the physical arrangement of objects in space, S.S. Bell, E.D. McCoy, and H.R. Mushinsky, eds. (Chapman and Hall), pp. 281–299.

5. Gorini, L., Linnell, J.D.C., May, R., Panzacchi, M., Boitani, L., Odden, M., and Nilsen, E.B. (2012). Habitat heterogeneity and mammalian predator-prey interactions. Mammal Rev. 42, 55–77.

6. Arthur, A.D., Pech, R.P., and Dickman, C.R. (2004). Habitat structure mediates the non-lethal effects of predation on enclosed populations of house mice. J. Anim. Ecol. 73, 867–877.

7. Orrock, J.L., Holt, R.D., and Baskett, M.L. (2010). Refuge-mediated apparent competition in plant-consumer interactions. Ecol. Lett. 13, 11–20.

8. Dickman, C.R. (1992). Predation and habitat shift in the house mouse, *Mus domesticus*. Ecology 73, 313–322.

9. Wheatley, R., Pavlic, T.P., Levy, O., and Wilson, R.S. (2020). Habitat features and performance interact to determine the outcomes of terrestrial predator-prey pursuits. J. Anim. Ecol. 89, 2958–2971.

10. Zhong, Z., Li, G., Sanders, D., Wang, D., Holt, R., and Zhang, Z. (2022). A rodent herbivore reduces its predation risk through ecosystem engineering (Dryad). https://doi.org/10.5061/dryad.cvdncjt57.

11. Sanders, D., Jones, C.G., Thébault, E., Bouma, T.J., van der Heide, T., van Belzen, J., and Barot, S. (2014). Integrating ecosystem engineering and food webs. Oikos 123, 513–524.

12. Li, G., Li, J., Kohl, K.D., Yin, B., Wei, W., Wan, X., Zhu, B., and Zhang, Z. (2019). Dietary shifts influenced by livestock grazing shape the gut microbiota composition and co-occurrence networks in a local rodent species. J. Anim. Ecol. 88, 302–314.

13. Jones, C.G., Lawton, J.H., and Shachak, M. (1994). Organisms as ecosystem engineers. Oikos 69, 373–386.

14. Wright, J.P., and Jones, C.G. (2006). The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. Bioscience 56, 203–209.

15. Hastings, A., Byers, J.E., Crooks, J.A., Cuddington, K., Jones, C.G., Lambrinos, J.G., Talley, T.S., and Wilson, W.G. (2007). Ecosystem engineering in space and time. Ecol. Lett. 10, 153–164.

16. Zhang, Y., Zhang, Z., and Liu, J. (2003). Burrowing rodents as ecosystem engineers: the ecology and management of plateau zokors *Myospalax fontanierii* in alpine meadow ecosystems on the Tibetan Plateau. Mammal Rev. 33, 284–294.

17. Zhong, Z., Li, X., Pearson, D., Wang, D., Sanders, D., Zhu, Y., and Wang, L. (2017). Ecosystem engineering strengthens bottom-up and weakens top-down effects via trait-mediated indirect interactions. Proc. Biol. Sci. 284, 20170894.

18. Pagès, J.F., Farina, S., Gera, A., Arthur, R., Romero, J., and Alcoverro, T. (2012). Indirect interactions in seagrasses: fish herbivores increase predation risk to sea urchins by modifying plant traits. Funct. Ecol. 26, 1015–1023.

19. Tambling, C.J., Minnie, L., Adendorff, J., and Kerley, G.I.H. (2013). Elephants facilitate impact of large predators on small ungulate prey species. Basic Appl. Ecol. 14, 694–701.

20. Fležar, U., Le Roux, E., Kerley, G.I.H., Kuijper, D.P.J., te Beest, M., Druce, D.J., Prinsloo, D., and Cromsigt, J.P.G.M. (2019). Simulated elephant-induced habitat changes can create dynamic landscapes of fear. Biol. Conserv. 237, 267–279.

21. Ferry, N., Mbizah, M.M., Loveridge, A.J., Macdonald, D.W., Dray, S., Fritz, H., and Valeix, M. (2020). Can an herbivore affect where a top predator kills its prey by modifying woody vegetation structure? Oecologia *192*, 779–789.

22. Wootton, J.T. (1993). Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. Am. Nat. *141*, 71–89.

23. Lima, S.L. (1998). Nonlethal effects in the ecology of predator-prey interactions: What are the ecological effects of anti-predator decision-making? Bioscience *48*, 25–34.

24. Brown, J.S., Laundré, J.W., and Gurung, M. (1999). The ecology of fear: optimal foraging, game theory, and trophic interactions. J. Mammal. *80*, 385–399.

25. Laundré, J.W., Hernández, L., and Ripple, W.J. (2010). The landscape of fear: ecological implications of being afraid. Open Ecol. J. *3*, 1–7.

26. Holt, R.D., and Barfield, M. (2013). Direct plant-predator interactions as determinants of food chain dynamics. J. Theor. Biol. *339*, 47–57.

27. Allee, W.C. (1938). The social life of animals (W.W Norton and Company).

28. Clark, T.J., Horne, J.S., Hebblewhite, M., and Luis, A.D. (2021). Stochastic predation exposes prey to predator pits and local extinction. Oikos *130*, 300–309.

29. Zhang, Z., Yan, C., Krebs, C.J., and Stenseth, N.C. (2015). Ecological non-monotonicity and its effects on complexity and stability of populations, communities and ecosystems. Ecol. Modell. *312*, 374–384.

30. Zhang, Z., Yan, C., and Zhang, H. (2021). Mutualism between antagonists: its ecological and evolutionary implications. Integr. Zool. *16*, 84–96.

31. Yan, C., and Zhang, Z. (2014). Specific non-monotonous interactions increase persistence of ecological networks. Proc. Biol. Sci. *281*, 20132797.

32. Brown, J.S., and Kotler, B.P. (2004). Hazardous duty pay and the foraging cost of predation. Ecol. Lett. *7*, 999–1014.

33. Burkepile, D.E., Burns, C.E., Tambling, C.J., Amendola, E., Buis, G.M., Govender, N., Nelson, V., Thompson, D.I., Zinn, A.D., and Smith, M.D. (2013). Habitat selection by large herbivores in a southern African savanna: the relative roles of bottom-up and top-down forces. Ecosphere *4*, 1–19.

34. Ripple, W.J., and Beschta, R.L. (2006). Linking wolves to willows via risk-sensitive foraging by ungulates in the northern Yellowstone ecosystem. For. Ecol. Manage. *230*, 96–106.

35. Valeix, M., Loveridge, A.J., Chamaillé-Jammes, S., Davidson, Z., Murindagomo, F., Fritz, H., and Macdonald, D.W. (2009). Behavioral adjustments of African herbivores to predation risk by lions: spatiotemporal variations influence habitat use. Ecology *90*, 23–30.

36. Gribben, P.E., and Wright, J.T. (2014). Habitat-former effects on prey behaviour increase predation and non-predation mortality. J. Anim. Ecol. *83*, 388–396.

37. Pearson, D.E. (2010). Trait- and density-mediated indirect interactions initiated by an exotic invasive plant autogenic ecosystem engineer. Am. Nat. *176*, 394–403.

38. Ohgushi, T. (2005). Indirect interaction webs: herbivore-induced effects through trait change in plants. Annu. Rev. Ecol. Evol. Syst. *36*, 81–105.

39. Kéfi, S., Berlow, E.L., Wieters, E.A., Navarrete, S.A., Petchey, O.L., Wood, S.A., Boit, A., Joppa, L.N., Lafferty, K.D., Williams, R.J., et al. (2012). More than a meal… integrating non-feeding interactions into food webs. Ecol. Lett. *15*, 291–300.

40. Li, G., Yin, B., Wan, X., Wei, W., Wang, G., Krebs, C.J., and Zhang, Z. (2016). Successive sheep grazing reduces population density of Brandt's voles in steppe grassland by altering food resources: a large manipulative experiment. Oecologia *180*, 149–159.

41. Fang, J., and Sun, R. (1991). Seasonal dynamics of spatial patterns of Brandt's voles. Shou Lei Xue Bao *11*, 111–116.

42. T. Guo, ed. (1995). Practical development technology of economic plants for soil and water conservation (Yellow River Conservancy Press), pp. 379–380.

43. R Core Team (2020). R: A language and environment for statistical computing (R Foundation for Statistical Computing). https://www.R-project.org/.

44. Pinheiro, J., Bates, D., DebRoy, S., and Sarkar, D.; R Core Team (2020). nlme: Linear and Nonlinear Mixed Effects Models (R package version 3.1-150).

45. Lenth, R.V. (2016). Least-Squares Means: The R Package lsmeans. J. Stat. Softw. *69*, 1–33.

STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
Raw and analyzed data	This paper	https://doi.org/10.5061/dryad.cvdncjt57
Software and algorithms		
R Statistical Software	R Project	https://www.r-project.org
Contributed R packages	Comprehensive R Archive Network (CRAN)	https://cran.r-project.org

RESOURCE AVAILABILITY

Lead contact
Further information and requests should be directed to and will be fulfilled by the lead contact, Zhibin Zhang (zhangzb@ioz.ac.cn).

Materials availability
The study did not generate new unique reagents. More detail information about plant and animal species are listed in this work which will be made available by the lead contact upon reasonable request.

Data and code availability
The datasets that support these findings are deposited at Dryad Digital Repository: https://doi.org/10.5061/dryad.cvdncjt57.[10]

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethics statement
All vole and bird manipulations were carried out in accordance with regulations on animal experiments of Institute of Zoology, Chinese Academy of Science (IOZ-IACUC-2020-074).

Study site
The field study was conducted at the Maodeng grassland (44°11′ N, 116°27′ E) in the Xilinhot, Xilingol League of Inner Mongolia in northern China. The study area has a long history of low-intensity livestock grazing and mowing, yet it was fenced with little human disturbances since 2010 when it became a research site. This site has a semiarid continental monsoon climate, where temperatures vary from a mean winter (December-February) minimum of −16.5°C to a mean summer (June-August) maximum of 20.7°C. The mean precipitation for winter and summer is 10.4 mm and 169.1 mm.[40] The perennial grasses *Leymus chinensis*, *Stipa grandis*, and *Cleistogenes squarrosa* are the dominant plant species, accounting for > 60% of total plant biomass. The large perennial bunchgrass *Achnatherum splendens* mature adult range from (about 1.3 to 2.5 m height) is another dominant plant species, accounting for about 20% of total plant biomass; individual plants of bunchgrass are scattered across the site, and grow intermingled with other grassland plant species (including forage plants for the Brandt's vole; the bunchgrass is unpalatable for the vole) (Figure S1). The leaves and stems of *A. splendens* are very tough (with high fiber content) and difficult to harvest. Livestock generally avoid feeding on this grass species. *A. splendens* has a cylindrical-shape three-dimensional structure, and its plant volume is positively correlated with aboveground biomass (Figures S1 and S3A). Other common plants include the forbs *Artemisia scoparia*, grasses *Setaria viridis* and *Chloris virgata*, and sedge *Carex duriuscula*.

The grassland hosts a moderate density (ca 30–70 burrows every 1 hectare) of *Lasiopodomys brandtii* voles (mean ± SE weight, male: 37 ± 2 g, female: 52 ± 3 g). Overwintering *L. brandtii* voles breed twice yearly (in April and June), with 2-15 offspring per litter. The area of burrow system of a Brandt vole family (with 2-7 adult individuals) is about 4-9 m^2, and home range of individual vole is 50-100 m^2 in early spring, and 25-50 m^2 in summer and autumn.[41] *L. brandtii* voles prefer open habitats and generally avoid dense vegetation cover.[40,41] Voles prefer to feed on the dominant *L. chinensis* grass, and also feed on *S. grandis*, and *C. squarrosa*. The voles occasionally damage (but do not feed on) leaves of *A. splendens,* but they often burrow around this plant species and cause serious damage to its root systems, so that the aboveground portion of plants wither (also see Figure S1).[39,42] Voles often actively damage bunchgrasses nearby their burrow systems, and rarely affect bunchgrasses far away from their colonies (Zhong Z, personal observations).

There are ground-hunting predators such as foxes and yellow weasel present at the field site, but the principal predators of *L. brandtii* voles are the shrikes, *Lanius* spp., which are medium-sized predatory birds. There are mainly three shrike species

(i.e., *L. cristatus L. schach*, and *L. excubitor*) in the study area but it is hard to distinguish them under field conditions. Shrikes often perch on the branches and stems of shrubs and tall grasses (in particular *A. splendens* grass) and search for individual prey nearby (e.g., voles and large insects). Once a prey individual is targeted, shrikes swiftly pounce on it. Shrikes display a fascinating food storage behavior where they impale prey on a thorn or a stem, as if storing food on a meat hook (see Figure S1). The shrikes use the bunchgrasses for such food hoarding, as well as for perches to locate prey in the first place. Both voles and shrikes are only active in the daytime, and actively detect visually.[41] Other avian predators such as hawks and owls are present but are much less abundant.

METHOD DETAILS

Field survey
Associations of Brandt's vole activities with A. splendens growth
In May 2019, we randomly selected 15 pairs of *A. splendens* grass individuals, one with voles (classified by the presence of active vole burrows around the base of the plants, see Figure S1B), the other with no voles, in an area of about 10 hectares within the study site. The two selected *A. splendens* grass individuals within a pair were spaced apart at least 15 m from each other. In late-July 2019, we visually counted and recorded the initial number of active vole burrows around the base of each *A. splendens* grass. We also estimated the initial plant volume of each *A. splendens* grass. Plant volume was calculated by multiplying the ground surface area covered by the bunchgrass by the height of that individual plant. In early-August 2020, we again measured the number of active vole burrows and plant volume of each *A. splendens* grass using the same methods. The net growth rate of *A. splendens* was calculated as the differences in plant volume between the two sampling dates.

At the beginning of the field survey in July 2019, there was an average of 2.9 vole burrows around each "vole-present" *A. splendens* grass, and no vole burrows were found around the "vole-absent" bunchgrasses. After one year, when we resampled in August 2020, the vole density showed no significant change (with an average of 3.4 and 0.3 vole burrows found around the vole-present and vole-absent *A. splendens* grasses, respectively), indicating that the observational contrasts were consistent over the course of this one-year field observational study (Figures S3B and S3C).

Associations of A. splendens abundance with predation risk of Brandt's voles
In May 2019, we randomly selected 15 plots (10 × 10 m) separated by at least 30 m from each other within the same 10-hectare area mentioned above. These plots have similar vole density (by visually estimating as above, about 4-7 vole burrows per plot), but with varying plant coverage of *A. splendens* grass (ranging from 5% to 37% percentage of coverage). From June to August, we conducted observations to assess the number of times that predatory birds (mainly shrikes, but sometimes hawks) visited (a "visit" is defined as a bird landing on the ground or on any of the plants within a plot) in each plot. We observed five days monthly, continually from 6:00 to 18:00, for a total of 12 h each day. We summed the total number of visits by predatory birds across the 15 days in each plot for statistical analyses. To estimate the potential variations in vole density, we visually surveyed the density of active vole burrows in each plot again by the end of the three-month field observation in August. Our data indicated that vole density (number of burrows) showed no significant change during the course of this three-month field observational experiment (see Table S1).

Semi-natural manipulative experiments
Experiment #1: Effects of predation risk on the damage activities of Brandt's voles on A. splendens grass
In early June 2020, we established six replicate blocks of experimental plots in a nearby site, for a total of 24 plots in an area with similar plant species composition (Table S2). Each plot contains one medium size (*ca* 4-5 m^3 in plant volume per individual) *A. splendens* grass located at the center, surrounded by abundant palatable grass species (e.g., *L. chinensis*, *S. grandis*, and *C. squarrosa*) used by the voles. The study site had not been occupied by voles prior to the experimental study. Each block had the following 2 × 2 factorial design: presence of voles and bird predators (V + P), voles only (V), bird predators only (P), and neither voles nor bird predators present (None). Plot treatments were randomly assigned within each block. The distances between the six replicate blocks were between 50 m and 200 m. Each of the four plots in a replicate block was separated by 10-20 m, each plot was 6 × 6 m (Figure S4A).

All plots, either with or without vole presence, were fenced by an iron sheet around the perimeter of each plot. The iron fences were 1.60 m height, with 0.80 m extended aboveground, and 0.80 m buried below the soil surface, to deter voles from burrowing underneath. To control for potential fence boundary effects, a 1-m buffer was designated between the fence and sampling areas within the study plots. For the plots with the "vole present" treatment, we placed a pair of subadult *L. brandtii* voles (one male and one female, with mean weight 10 ± 0.8 g and 15 ± 1.3g, mean ± s.e., respectively) into each plot (equal to a medium density of 556 individuals/ha). For the bird predator exclusion treatment, we used steel pipe frames enveloped within mesh nylon nets (Figure S1). The mesh size (16 cm^2 net) was small enough to exclude birds, but large enough to allow passage for large insects. Based on our field observations, birds could see voles in the enclosures covered with mesh covering, but birds could perceive net as a danger and generally avoid to approach to them (otherwise they may be trapped by the nets, we have observed a few such cases, see Figure S1H). Thus, birds would generally avoid approaching enclosures covered with nets after several failures of penetrating the nets. We initiated the vole and bird predator manipulation treatments from early-July through late-July, 2020, a total of one month of study duration. We chose to end the study within one month because we observed that voles in the experimental enclosures had already seriously damaged the *A. splendens* grasses (see Figure S1). To ensure food was not limited for voles, we put 1 kg of fresh

palatable *L. chinensis* grasses at the ground surface into each plot weekly during the study period; voles were observed to feed on these supplementary food plants.

In early July, 2020, we evaluated the initial plant volume and root biomass of *A. splendens* grass prior to the applications of experimental treatments. Plant volume was calculated by multiplying the ground area covered by the plant with the average height for each *A. splendens* individual. We then took two, 7.5-cm diameter, 50-cm deep cores under the canopy of *A. splendens* to determine their root biomass (*A. splendens* roots and rhizomes are typically concentrated within the top 50 cm of soils). Cores were pooled and sieved (2-mm mesh), then sorted into *A. splendens* roots or other plant material. We could identify *A. splendens* live roots visually, as they have a unique color and texture compared to other plant species in this grassland community. *A. splendens* roots were then dried for 48 h at 70°C and weighed. Analyses showed that the initial plant volume and root biomass of *A. splendens* grass were similar across the four treatments (Table S2). In late July, 2020, using the same methods, we measured the plant volume and root biomass of *A. splendens* grass in the plots to assess the effects of the voles on this plant species. The net growth rate of *A. splendens* was calculated as the differences in plant volume and root biomass between the two sampling dates.

During the one-month experimental period, we monitored the visiting frequency of shrikes in each plot to assess the effectiveness of nets in excluding bird predators. On the first two days of each week, we conducted observations to count the number of times that shrikes visited each plot (see the definition for "visit" above; but for the plots with nets, a "visit" is defined as a bird landing on the nets above the plots). The observations began from 6:00 to 18:00, for a total of 12 h each day. We summarized the total number of visits by predatory birds across the eight days in each plot for statistical analyses.

Experiment #2: Effects of *A. splendens* grass coverage on behaviors of Brandt's voles and predatory birds

In July 2020, we established six replicate blocks with a total of 18 plots covering 3 habitat structure treatments in an area with similar plant species composition in a site near the location of experiment #1 (Table S3). Each plot was fenced by iron sheets as described above. The study site was not occupied by voles prior to the initiation of the study. Each block had the following three habitat structure treatments: 0% *A. splendens* grass, 50% *A. splendens* grass, and 100% *A. splendens* grass (Figure S4B). For the 0% *A. splendens* grass treatment, we simply removed this grass from the plots; for the 50% *A. splendens* grass treatment, we assigned one *A. splendens* grass located at the center of the plot, and simulated the damage activities of voles on this grass by randomly removing half of the leaves and stems of this grass; for the 100% *A. splendens* grass, we assigned one *A. splendens* grass at the center of the plot and we simply kept the remaining grass undisturbed. For both the 50% and 100% *A. splendens* grass in the plots, we collected and transplanted plants from nearby sites into the treatment plots. We transplanted these grasses with soils into plastic buckets (0.05 m² basal area and 0.40 m height). We placed *A. splendens* grasses in plastic buckets for two reasons: 1) to prevent damage activities of voles on the grasses (voles are unable to climb up the buckets to damage *A. splendens* grasses), and 2) to tease out the potential confounding side effects of *A. splendens* grass as potential food resource for voles (though our evidence to date suggests that this species is not a significant food plant). Our goal was to evaluate the independent effects of *A. splendens* grass as a physical habitat structure in mediating the interactions between predatory birds and voles. Plot treatments were randomly assigned within each block. The distances between the six replicate blocks of plots were between 50 m and 150 m. Each of the three plots in a replicate block was separated by about 10-20 m, each plot was 6 × 6 m in size (Figure S4B). Two pairs of subadult *L. brandtii* voles (two males and two females) were placed into each plot (equal to a high-density of 1,111 individuals/ha). Based on our preliminary experiment, this high density of voles is sufficient to attract predatory birds, enabling us to detect the effects of *A. splendens* grass on the interactions between predatory birds and voles during this short-term study.

The study was conducted for three weeks from late-July to mid-August 2020. A preliminary study showed that this duration enabled us to detect the effects of experimental treatments on changed behavior of voles and predatory birds, before the host food plants have been eliminated by voles (which then creates a confounding factor, Z. Zhong., field observations). On the first two days of each week, we conducted observations to assess the number of times that predatory birds visited each plot. The observations began from 6:00 to 18:00, for a total of 12 h each day. We summed the total number of visits by predatory birds across the six days in each plot for statistical analyses. At the end of the experiment in mid-August, we recaptured the voles by setting up five live traps (10 cm high × 10 cm wide × 24 cm long) within each plot, and kept the traps present until we were confident all individuals were captured. We then calculated the mortality rate (%) of voles, calculated as ((initial number of voles– number of voles recaptured at the end of experiment) / initial number of voles) × 100%. We also assessed changes in feeding behaviors by measuring the feeding frequency of voles on the palatable grasses (i.e., *L. chinensis*, *S. grandis*, and *C. squarrosa*). Within each plot, we randomly laid out a transect (length × width = 2 m × 0.2 m) in the center of the plot. The transect consisted of 10 contiguous quadrats (0.2 m × 0.2 m) to assess the feeding intensity of voles on palatable grasses in each quadrat. Where palatable grass species (see above) were consumed (identified by the unique cutting plane left from vole feeding on leaves), we assigned the feeding intensity of the quadrat to be "1," otherwise, "0." Feeding intensity of all 10 quadrats were summed per transect, and divided by 10 to obtain a metric of feeding intensity, which ranged from 0% to 100%.

QUANTIFICATION AND STATISTICAL ANALYSIS

All data were analyzed using the open-source software R version 4.0.3.[43]

Field survey

For the field survey to explore associations of Brandt's vole activities with *A. splendens* growth, we first tested whether the vole density remained consistent over the course of the one-year field study. We used a linear mixed effects model provided by the nlme package[44] with the number of vole burrows found around the 15 pairs of *A. splendens* grasses in late-July 2019 (the beginning of the experiment) and early-August 2020 (the end of the experiment) as the response variable, and vole presence as the explanatory variable. Pair was included as a random factor in the model. Then, to test how vole activities can affect plant growth of *A. splendens*, we used the same models above with the change in plant volume of *A. splendens* grass as the response variable, and vole presence as the explanatory variable. Pair was included as a random factor in the model. All models were visually inspected for normality and homoscedasticity of variance.

For the field survey to explore associations of *A. splendens* abundance with predation risk of Brandt's voles, we first tested whether the vole density remained consistent over the course of the three-month field study. We simply presented the number of vole burrows found in May (the beginning of the study) and August 2019 (the end of the study) within each of the 15 plots (10 m × 10 m) to indicate the change in vole density during the field survey (Table S1). Then, we conducted a linear regression analysis to assess the effects of *A. splendens* coverage on the total number of visits by predatory birds in the 15 plots.

Semi-natural manipulated experiment [#]1

We used generalized linear models with a Poisson error structure to test for the effects of predatory birds, voles, and their interactions as explanatory variables on the visiting frequency of predatory birds (i.e., the effectiveness of nets in excluding birds). Block as random factor was removed from the model as it did not explain enough variation. We further tested difference of relative changes in plant volume and root biomass of *A. splendens* grass in vole and bird treatments using Linear mixed effects model. For these variables, we further conducted Tukey's tests within the package lsmeans[45] to evaluate how treatment means differed if a significant interaction effect was detected.

Semi-natural manipulated experiment [#]2

Similar to experiment [#]1, we used a generalized linear model with a Poisson error structure to test for effects of three different levels in coverage of *A. splendens* grass as a factorial fixed factor on the total number of visits by predatory birds per plot. We tested the effects of three different levels in coverage of *A. splendens* grass on the feeding intensity of voles on their palatable grasses by using a linear mixed effects model, while tested their effects on mortality rate of voles per plot by using a generalized linear model with a Binomial error structure. In the latter model, the response variable was a two-column dataset recording the number of dead and alive voles. If a significant effect was detected, we conducted Tukey's multiple comparison to assess the differences among specific treatments. The calculation of vole mortality rates at the plot level could be coarse, given that there were only 4 voles in each plot (i.e., mortality could only be 0, 25, 50, 75, or 100%). Nevertheless, we had 6 replicates for each treatment, which overall provided enough data to test out hypotheses.