Current Biology

Experimental Evidence for the Population-Dynamic Mechanisms Underlying Extinction Cascades of Carnivores

Highlights

- Initial carnivore extinctions can trigger extinctions of other carnivore species

- An experiment shows that these effects are transmitted by competition among hosts/prey

- These population-dynamic processes can be major drivers of extinction cascades

Authors

Dirk Sanders, Rachel Kehoe, F.J. Frank van Veen

Correspondence

d.sanders@exeter.ac.uk

In Brief

Sanders et al. demonstrate the mechanisms for horizontal extinction cascades at high trophic levels in a field experiment. They show that the loss of carnivores can increase extinction rates of other species at the same trophic level due to indirect population-dynamic effects that are rarely considered in this context.

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Experimental Evidence for the Population-Dynamic Mechanisms Underlying Extinction Cascades of Carnivores

Dirk Sanders,[1,*] Rachel Kehoe,[1] and F.J. Frank van Veen[1]
[1]Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Penryn Campus, Penryn, Cornwall, TR10 9FE, UK
*Correspondence: d.sanders@exeter.ac.uk
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SUMMARY

Species extinction rates due to human activities are high [1–3], and initial extinctions can trigger cascades of secondary extinctions, leading to further erosion of biodiversity [4]. A potential major mechanism for secondary extinction cascades is provided by the long-standing theory that the diversity of consumer species is maintained due to the positive indirect effects that these species have on each other by reducing competition among their respective resource species [5–7]. This means that the loss of one carnivore species could lead to competitive exclusion at the prey trophic level, leading to extinctions of further carnivore species. Evidence for these effects is difficult to obtain due to many confounding factors in natural systems, but extinction cascades that could be due to this mechanism have been demonstrated in simplified laboratory microcosms [8]. We established complex insect food webs in replicated field mesocosms and found that the over-harvesting of one parasitoid wasp species caused increased extinction rates of other parasitoid species, compared to controls, but only when we manipulated the spatial distribution of herbivore species such that the potential for interspecific competition at this level was high. This provides clear evidence for horizontal extinction cascades at high trophic levels due to the proposed mechanism. Our results demonstrate that the loss of carnivores can have widespread effects on other species at the same trophic level due to indirect population-dynamic effects that are rarely considered in this context.

RESULTS AND DISCUSSION

We assembled replicate food webs, consisting of herbivorous aphids and carnivorous insect species (Figure 1), in 40 field mesocosms. We applied to this a factorial experiment manipulating (1) human impact on one carnivore species (harvesting of the parasitoid wasp *Aphidius megourae* leading to functional extinction, which is defined as a significant reduction in its

abundance that markedly weakens the interaction strength with its host) and (2) the potential for interspecific competition among herbivores, by having all aphid species either uniformly distributed or aggregated (Figure 1). Interspecific competition was therefore manipulated without altering food web structure.

Sustained harvesting of the parasitoid *A. megourae* (Figure 1) led to its functional extinction and markedly increased the extinction rate of the two other indirectly linked parasitoid species *Lysiphlebus fabarum* and *Aphidius ervi* (Figure 2; Table S1; Cox proportional hazards model harvesting effect z = 3.53, p < 0.001), but only in the treatments with a uniform aphid distribution (Figure 2; Table S1; harvesting × aphid distribution z = 3.53, p = 0.0310). This demonstrates that interspecific competition at the herbivore level between the three aphid species was the mechanism by which extinction cascades were transmitted. Secondary extinction events happened 2–3 parasitoid generations (4–5 weeks) after the start of harvesting, with the parasitoid *A. ervi* becoming extinct in all harvesting communities that allowed for strong competition between aphids and with no extinctions in non-harvested communities. The parasitoid *L. fabarum* responded similarly (Figure 2; Table S1), although with fewer extinction events.

Harvesting the parasitoid *A. megourae* reduced its abundance by 58.8% compared to the non-harvesting treatments over the course of the experiment (Figure S1B, $t_{1,28} = -3.69$, p = 0.0015 for harvesting effect), whereas manipulating the aphid distributions did not affect *A. megourae* abundance ($t_{1,28} = 0.07$, p < 0.94). We detected no extinction events for *A. megourae*, but the reduction in its density significantly reduced the top-down control of its host: in the harvesting treatments, population density of the aphid *Megoura viciae* was 143.0% (average over the course of the experiment) compared to non-harvesting treatments (harvesting × week interaction, $t_{1,277} = 2.52$, p = 0.0125; Figure S1A). Overall, *M. viciae* abundance in mesocosms was not affected by the different aphid distributions ($t_{1,28} = 1.16$, p > 0.25 for effect of aphid distribution). Differences in interspecific competition between the aphid distribution treatments are therefore due not to differences in overall density in the mesocosm (Figure S1A) but to the aggregation of aphid species on certain trays. The other two aphids, *Aphis fabae* and *Acyrthosiphon pisum*, maintained higher densities on their respective trays in harvesting treatments with aggregated aphid distribution when compared to treatments with uniform aphid distribution (Figures S2C and S2E; $t_{1,97} = 3.83$, p < 0.001 for *A. fabae* and
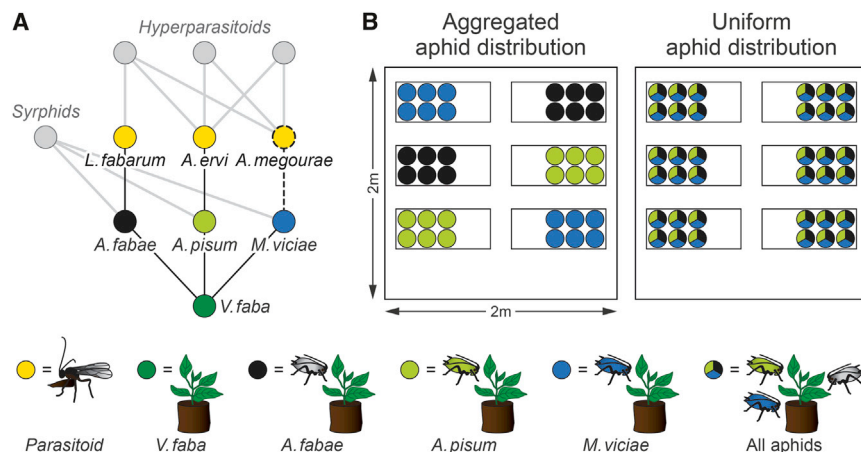
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Figure 1. Design of the Mesocosm Experiment

(A) Experimental insect communities with three aphid species feeding on bean plants and each aphid being attacked by a specialist parasitoid (see Figure S1 for population dynamics). The dashed line indicates the harvested parasitoid species *Aphidius megourae* and the functionally extinct interaction with its host *Megoura viciae* in the harvesting treatments. Other naturally occurring food web interactions that were observed in the mesocosms (predatory Syrphidae and hyperparasitoids) are shown in gray. We tested for secondary extinctions at the parasitoid trophic level in the species *Lysiphlebus fabarum* and *Aphidius ervi*.

(B) Arrangement of trays and pots inside the field cages with aggregated and uniform aphid distribution (see Figure S2 for aphid densities). Circles indicate pots with *M. viciae* (blue), *Aphis fabae* (black), *Acyrthosiphon pisum* (green), and all three aphid species (all three colors).

$t_{1,97} = 2.84$, $p < 0.01$ for *A. pisum*). This indicates that these species were released from competition with *M. viciae*.

Due to the presence of hyperparasitoids in the mesocosms, primary parasitoid species could potentially also have affected each other via natural enemy-mediated indirect effects (so-called "apparent competition"). Hyperparasitism rates for *L. fabarum* and *A. ervi* were in the order of 50%–60% in week 12 of the experiment but were not affected by either aphid distribution or harvesting treatment (*L. fabarum*, harvesting effect $z = -0.62$, $p = 0.534$; aphid distribution effect $z = 1.18$, $p = 0.235$; *A. ervi*, harvesting effect $z = -1.39$, $p = 0.1630$; aphid distribution effect $z = -0.47$, $p = 0.6366$). Therefore, our treatments did not affect any hyperparasitoid-mediated apparent competition that may have occurred in the mesocosms.

These results demonstrate that the effect of the functional extinction of one parasitoid species, as a result of overharvesting, is transmitted to other parasitoids via competitive interactions between hosts. The risk of horizontal secondary extinctions therefore depends strongly on the degree of competition at the lower trophic level, which may be affected by resource overlap and by factors such as spatial distribution. These horizontal extinction cascades at the consumer level are the result of a combination of a top-down and a bottom-up cascade, despite there being no extinctions at the lower trophic levels. The secondary extinctions of parasitoids can occur before the extinction of their host species due to decreased foraging efficiency when host densities are low relative to non-host densities [9, 10].

The experiment provides an important mechanistic insight, allowing researchers to predict horizontal extinction cascades following the decline in population size of consumer species where there is a degree of specialization. This includes host-parasitoid systems but also, for example, plant-herbivore systems and aquatic systems where predators may specialize on different prey sizes, such as the classic example of a positive indirect effect of a salamander (feeding on large zooplankton) on *Chaoborus* midge larvae (feeding on small zooplankton), with smaller zooplankton species being released from competition with larger plankton species when salamanders are present [7]. In reality, most ecosystems will consist of a mixture of specialist

and generalist consumers, just like our experimental communities (which contained generalist predatory syrphid larvae and generalist hyperparasitoids in addition to specialized primary parasitoids), and the mechanism that we report here may act in the more specialized components of any ecosystem.

Interestingly, the harvested parasitoid *A. megourae* declined in abundance but never went extinct in any of the communities, while the two non-harvested parasitoid species showed strong responses and went extinct in most of the harvested communities that allowed for the transmission of the effect among the herbivores. This provides empirical support for the theoretical prediction [11] that considering functional extinctions also means shifting the conservation focus away from extinction-threatened target species only, as other species in the community may be far more likely to go extinct as an indirect consequence of a reduction in population size of the target species.

Our results provide the first experimental evidence for horizontal extinction cascades in communities with realistic food web structure and, crucially, the first experimental evidence for the underlying mechanism. This is particularly significant because it demonstrates that the loss of species at higher trophic levels (carnivores) can have widespread effects on other species at the same level, something that would not be predicted by the bottom-up secondary extinction mechanisms that are most commonly focused on ("co-extinctions" [4]). So far, past and ongoing secondary extinctions have been difficult to quantify; many might have gone unnoticed, while in other cases, secondary extinctions might be inevitable but simply have not happened yet [4]. Our study suggests that while extinction events up or down the food chain may occur after the functional extinction of a consumer, indirect interactions among consumers mixing top-down and bottom-up effects can occur rapidly and may be major drivers of extinction cascades.

EXPERIMENTAL PROCEDURES

Study System

The plant-aphid-parasitoid communities consisted of bean plants (*Vicia faba*, L., var. the Sutton) as food resource for three aphid species *Aphis fabae*
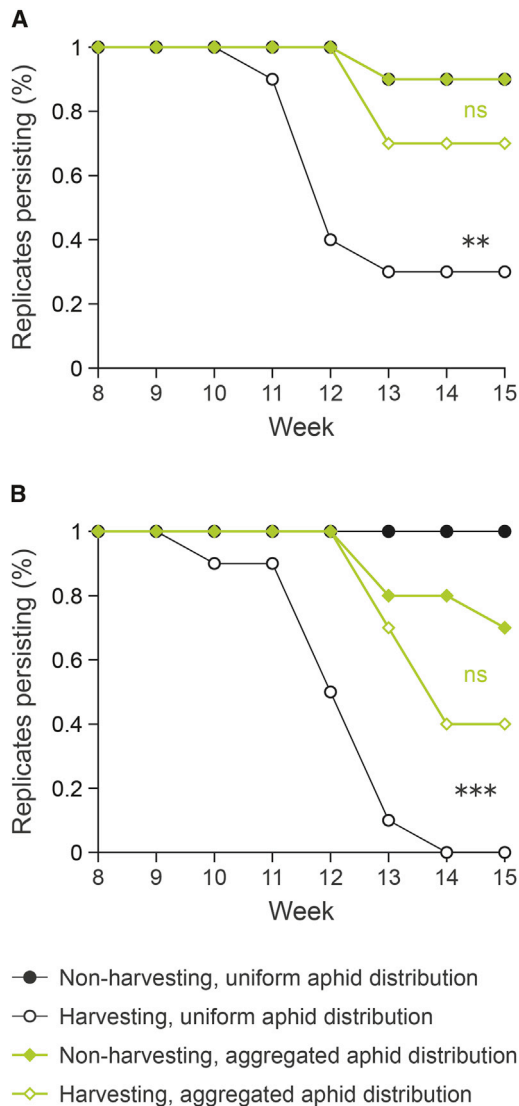
Figure 2. Secondary Extinction Events

Persistence of experimental parasitoid populations for *L. fabarum* (A) and *A. ervi* (B) in harvested (open black circles and green diamonds) and non-harvested (filled black circles and green diamonds) insect communities either with uniform (black line and circles) or aggregated (green line and diamonds) aphid distribution. Each treatment was replicated ten times. To allow all species to become established, we started harvesting at week 8 of the experiment (after four parasitoid generations). Significance levels for Kaplan-Meier survival curves between harvesting and non-harvesting treatments with the same aphid distribution are indicated ns, non-significant; **p < 0.01; ***p < 0.001. See Table S1 for survival analysis.

(Scopoli), *Acyrthosiphon pisum* (Harris), and *Megoura viciae* (Buckton), each attacked by a specialist parasitoid, these being *Lysiphlebus fabarum* (Marshall), *Aphidius ervi* (Haliday), and *Aphidius megourae* (Stary), respectively (see Figure 1).

Mesocosm Experiment

The experiment was conducted in a secure field on the Penryn Campus of the University of Exeter. We experimentally simulated the functional loss of the parasitoid species *A. megourae* by harvesting its mummies twice weekly and manipulated interspecific competition between aphid species by their

spatial distribution: (1) either all three aphid species were uniformly distributed over all plants or (2) aphid species were aggregated within the mesocosms. The uniform distribution ensured maximum interspecific competition, while the aggregated treatment resulted in higher intraspecific and reduced interspecific competition. Crossing the two factors "*A. megourae* harvesting" and "aphid distribution" in a full factorial design resulted in four treatments: (1) aggregated aphid distribution and non-harvested, (2) uniform aphid distribution and non-harvested, (3) aggregated aphid distribution and harvested (4), and uniform aphid distribution and harvested.

Insect communities were established in outdoor mesocosms (2 × 2 × 2 m Agro Quick Field Cages, Rovero) with a mesh size of 0.22 × 0.31 mm (thrips mesh) and a light-transmission ability of 77%. Structural poles and the base of the mesocosms were buried 20 cm into the ground for stability, along with ground sheeting to prevent the introduction of invertebrates. In each mesocosm, two wooden 80-cm-high tables each supported three trays, each of which contained six pots with bean plants of varying age (36 pots per cage). Each week, the two oldest plant pots from each tray were replaced with 2-week-old plants, while leaving the plant matter and all insects in the cage. Aggregated aphid distribution treatments had five adults of each of the three aphid species placed on the plants of each tray on the first week of the experiment, while the uniform aphid distribution treatments had 15 aphids of one species introduced per tray (see Figure 1). Insects were introduced on April 21, 2014, week 1 of the experiment. Although some movement existed, aggregation was still maintained (see Figure S2). Two adult mated female parasitoids were released into each mesocosm on the third and fourth week of the experiment.

Abundance of all six species on and around two pots per tray that were typical for the communities of that tray were counted weekly. In case of low numbers, we extended the search to the whole mesocosm to confirm extinctions. Harvesting treatments had all visible *A. megourae* mummies removed using tweezers for 20 min per mesocosm twice a week. We also recorded the presence of predatory Syrphidae and hyperparasitoids in all mesocosms. In week 12 of the experiment, we collected aphid mummies from all three species in each cage to estimate hyperparasitism rate. We did not collect mummies from species that were present with low number in a certain cage (below 20 mummies per cage), to ensure that we did not cause any extinctions. Samples ranged from 10–50 mummies per cage depending on the parasitoid densities.

Each treatment was replicated ten times, with mesocosms located 1.5 m apart from each other, in a block design. A block was formed of four mesocosms in a row, and each mesocosm was randomly assigned to one of the four treatments, allowing us to separate the variation based on any potential environmental gradients such as wind exposure and exposure to hyperparasitoids from the treatment variation in the data. We placed temperature data loggers inside and outside of one mesocosm in each of the ten blocks to test for temperature differences. The mean temperature inside the mesocosms did not differ from the outside ($t_{1,9} = -1.76$, p = 0.1127 for linear mixed-effects model with location of the data logger as fixed factor and block included as random factor). The experiment ran for 15 weeks, with the last count on August 6, 2014. The complete data are available in Data S1.

Statistical Analysis

To compare extinction probability between the different treatments, we recorded the number of weeks that the parasitoid species persisted in each of the 40 mesocosms. Species that persisted in mesocosms until the end of the experiment were treated as censored data. We used the Cox proportional hazards model from the package "survival" [12] in R v3.1.0 [13] to test for the impact of the factors (1) harvesting and (2) aphid distribution and their interaction on parasitoid species persistence in the communities. We further included parasitoid species identity of the non-harvested parasitoids (*L. fabarum* and *A. ervi*) and the interaction with the treatments harvesting and aphid distribution in the model to test for species-specific differences in response to the treatments. Proportional hazard assumptions were tested by inspecting Kaplan-Meier survival curves and with a cox.zph test [14]. Single treatments were compared with Kaplan-Meier survival curves and a log-rank test as implemented in the R function "survdiff" [15].

Aphid and parasitoid population dynamics were analyzed with linear mixed-effects models. The density data as dependent variables were log or square-root transformed to normalize the distribution. Models were checked for

homoscedasticity and normality of the residuals, and all models fulfilled the assumptions. Harvesting treatment, aphid distribution treatment, and the interaction between the two treatments were included as fixed factors. To account for systematic trends over time, we included week and week squared as covariates. Mesocosm identity nested in block was used as random intercept in the model. Because the residuals of these models showed a significant partial temporal autocorrelation, we included a first-order autoregression for the residuals. This was done using the R function "lme" from the package "nlme" [16]. We used generalized linear mixed-effects models (package "lme4" [17]) with binomial error structure to test for the impact of harvesting and aphid distribution on the hyperparasitism rate for *L. fabarum* and *A. ervi*. As response variable, the number of (1) hatched hyperparasitoids and (2) hatched primary parasitoids for each mesocosm for each of the two parasitoid species was combined. Harvesting treatment, aphid distribution treatment, and the interaction between the two treatments were included as fixed factors, and block was included as a random effect.

SUPPLEMENTAL INFORMATION

Supplemental Information includes two figures, one table, and one field dataset and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2015.10.017.

AUTHOR CONTRIBUTIONS

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