took their study one step further. After releasing the birds in flocks, the authors then split the groups up again, and re-released birds individually one last time. During these second solo flights, almost all birds had improved their navigational efficiency as compared to their first solo flight. This was presumably because they had learnt new information about their routes home when in groups. However, leaders had improved their navigational efficiency significantly more than followers. Hence, whilst leaders were initially no better navigators than their followers, by the time they had finished their flock flights, they had become more informed than their other group members.

The costs and benefits associated with different positions in the group have usually been attributed to predation risks or foraging rewards [18]. This is the first demonstration that the spatial position an individual occupies in a group can affect how it learns information about its environment. But why might followers be ineffective learners compared to leaders? Perhaps individuals in the back of the flock pay more attention to social information, and less attention to environmental landmarks during flight. This lends important insights into the cognitive demands individuals are under when trying to maintain flock cohesion, but at the same time navigate home. Indeed, other studies have recently highlighted the need for individuals in groups to balance their own goal-orientated behaviours with social cohesion [19]. The new study [2] also raises new questions surrounding the processes underlying collective decisions. Even though these groups have hierarchical leader–follower relationships, and initially do not follow the most informed individuals, groups still outperform singletons in a navigational challenge. How individuals integrate information in these hierarchical flocks, and exactly how much influence different individuals have in the collective decision, are the next key challenges to understand.

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Ecology: Dynamics of Indirect Extinction

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The experimental identification of the mechanism by which extinctions of predators trigger further predator extinctions emphasizes the role of indirect effects between species in disturbed ecosystems. It also has deep consequences for the hidden magnitude of the current biodiversity crisis.

Species do not go extinct one at a time. Instead, it looks as though ecosystems change in a kind of chain reaction, just like in bowling. The impact of the ball knocks down one or two pins, but they hit other pins and this ultimately

Figure 1. Predator and prey.
Parasitoid wasp *Aphidius megourae* ready to attack its herbivore host *Megoura viciae.* Photograph by Dirk Sanders.

determines your score. Likewise, when in an ecosystem one species goes extinct many others may follow even if they are not directly affected by the initial disturbance. The complex combination of direct and indirect effects resulting from species interactions determines the fate of the remaining species. To predict the conditions under which extinctions beget further extinctions is a major scientific and societal challenge under the current biodiversity crisis [1,2]. A new study by Sanders and colleagues [3] in this issue of *Current Biology* shows how and why initial extinctions of predators trigger cascades of secondary extinctions of the remaining predators.

Sanders and colleagues [3] performed a fascinating experiment using complex insect food webs that comprise multiple predators and prey species (Figure 1). In particular, they performed controlled mesocosms where different parasitoid wasp species (i.e., predators' trophic level) were specialized on attacking different species of pea aphids (i.e., herbivores' trophic level) all of which feed on the same plant species. In their experiments, they over-harvested wasps of one species at the top of the food web until it was functionally extinct, i.e., its effect on the pea aphid prey it was specialized on became negligible. Then, the authors waited and assessed whether further wasp species from the predators' trophic level became extinct. Secondary extinctions occurred quite often, with increased predator extinction rates compared to non-harvested food webs. But they only increased when multiple herbivore species did compete with each other. Consider the simplest, but representative food web that consists of wasp A feeding on aphid B, and wasp C feeding on aphid D. Then, the reduction of wasp A's population allows for aphid B to increase in abundance. If aphids B and D coexist and compete for a given plant resource, then the increase in B's abundance will decrease D's abundance, which in turn will decrease the abundance of its parasitic wasp A, eventually leading to its extinction. If aphids B and D do not compete, then no further extinctions happen.

The results presented by Sanders and colleagues [3] may seem like common wisdom. They are to some extent. In ecological theory it is well established that the diversity of predators is maintained due to the positive indirect effects they have on each other by reducing competition among the prey species they feed upon [4]. But so far, the theory lacked tests in the controlled conditions required for the indirect effects mechanism to manifest.
However, testing such a long-standing theory is not the only merit of Sanders and colleagues [3]. Their experiment also raises many important questions in the light of the current biodiversity crisis.

There is ample evidence that human-driven loss of species triggers cascades of secondary extinctions, which may exceed the number of primary extinctions [1,5]. Even if a small fraction of these secondary extinctions is accounted for, the current biodiversity crisis indicates that the sixth mass extinction on Earth is already under way, with extinction rates orders of magnitude larger than background extinction rates [2,6]. Most secondary extinctions concern species that have lost obligate mutualists, prey, or host. Examples include specialized predators such as black-footed ferrets (*Mustela nigripes)* becoming extinct after the decline of prairie dogs (*Cynomys* sp.), their sole prey [7], or the paradigmatic example of the extinction of the moa birds of New Zealand that led to the loss of several internal parasite species [8]. As such, they focus on bottom-up secondary extinction mechanisms, i.e. extinctions of consumers after the initial loss of their specialized resources. However, the kind of secondary extinctions mediated by top-down indirect effects mechanisms reported in the experiment of Sanders *et al.* [3] is rarely considered. More specifically, secondary extinctions of further predators following the well-known initial extinction of predators due to human actions are actually seldom reported [1,9]. If this mechanism is universal, how come predator secondary extinctions are not more prevalent in nature?

Part of the answer relies on the difficulties of detection and the time it may take for secondary extinctions to happen. Past and ongoing secondary extinctions of predators have been difficult to quantify, with many going un-noticed, and probably most of them have not happened yet. But it is also possible that the tested experimental mechanism does not manifest or it is counterbalanced by other processes in those natural ecosystems where secondary extinctions have been assessed. The mechanism investigated requires that different predators are specialized on different, competing prey species. Large natural ecosystems actually have a mix of specialized and generalist predators, although the proportion of diet specialists is much larger than the proportion of generalists [10,11]. This suggests that, in principle, secondary extinctions of predators should be more widespread than currently observed. Alternatively, it might be that specialized predators are not yet extinct, and thus expected secondary extinctions of predators are not observed. Several apex predators in decline, mostly terrestrial vertebrates, are generalists [9], but the most important components of global change, such as habitat loss, species invasion and climate change, are mostly affecting specialized species, predators in particular [12,13].

Importantly, Sanders and colleagues [3] found that secondary extinctions of predators can occur even if the initial predator extinction has not happened yet, but it is already functionally extinct (i.e., its effects on prey population dynamics are negligible). They show that reductions up to 70% of the initial population of the harvested wasp species triggered the extinction of non-targeted wasps. This result echoes recent empirical and theoretical approaches that suggest that functional extinctions and ‘real’ extinctions have very similar effects on community dynamics and co-extinction patterns [14,15]. The translation of these results into practical conservation initiatives is not straightforward, but at least it implies that we should monitor predators that are not directly threatened but belong to the same trophic level of the threatened species in order to minimize the likelihood of secondary extinctions.

A recurrent question in secondary extinction studies is to what extent ecological mechanisms and evolutionary adaptations may buffer species against the loss of their interaction partners. In the case of the study of Sanders *et al.* [3], what if the co-extinct predator could shift its diet when its prey decreases in abundance? It has been suggested that the establishment of new feeding links (known as ‘rewiring’) may buffer against bottom-up secondary extinctions [16] — e.g., if the parasitoid wasp attacks a new insect herbivore, its secondary extinction might be less likely to happen. However, recent theory shows that this is not the case when food web dynamics are taken into account [17]. New feeding links can lead to overexploitation of resources and further secondary extinctions of predators, especially when predators are efficient in exploiting novel prey and when species cannot escape predation when they are rare. Adaptation processes, such as rewiring, should be explored in more detail in experiments like the one conducted by Sanders and colleagues [3], but it seems clear that secondary extinctions of predators will become more prevalent.

Species interactions are as fundamental as species richness for understanding biodiversity dynamics and the response of ecosystems to global environmental change. Daniel H. Janzen beautifully expressed this: “*What escapes the eye, however, is a much more insidious kind of extinction: the extinction of ecological interactions*” [18]. Disrupting or distorting species interactions may result in species loss and ecosystem simplification. However, the complexity of the combination of direct and indirect biotic interactions in multispecies systems hinders predictions on the effects of the current biodiversity crisis. Studies like the one by Sanders and collaborators [3] show that informative predictions on expected secondary extinctions can be made even if subsequent complex direct and indirect effects are considered simultaneously. It is an optimistic perspective to tackle a daunting challenge: the characterization and consequences of the sixth mass extinction in Earth’s history.

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