works. Although its techniques have long been exploited, there is increasing recognition of the need to test the theory as it applies to animal patterns [12]. With Cuthill *et al.*'s work, we have some of the best insights yet into the adaptive significance of disruptive patterns in the natural world.

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# Are scared prey as good as dead?

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**Predators affect prey and their resources by changing the density and traits (e.g. morphology and behavior) of those prey. Ecological studies and models of community dynamics, however, typically only incorporate how changes in prey densities, rather than their traits, affect community dynamics. In a recent meta-analysis, Preisser *et al.* show that trait effects are as large, if not larger than density effects. This strongly suggests that trait effects should be integrated into empirical and theoretical studies.**

### The significance of fear
Historically, ecologists have characterized species interactions by the density effects that species have on each other. For example, when carnivores consume herbivores, they directly reduce herbivore densities and might indirectly affect plant densities by reducing or shifting herbivory (Box 1). Predators not only eat their prey, but also scare them [1]. By scaring prey and causing them to alter their traits, such as foraging effort or defensive morphologies, predators can have significant impacts on prey and their resources. For example, herbivores hiding from carnivores might feed less on plants, thus decreasing their own growth and reproduction, and increasing plant densities. A recent meta-analysis by Preisser *et al.* of

166 studies from 49 publications is the best evidence yet that trait effects are generally important and could rival and even exceed the importance of density effects [2].

Although the existence of trait effects has been well documented [3,4], their importance and extent are still largely unclear. Human experience suggests that changes caused by the fear of events might have larger effects on our

> **Box 1. Terminology and primary mechanisms of effects**
>
> Preisser *et al.* used the terminology of density- and trait-mediated interactions for both direct and indirect effects and distinguished between the two by noting whether the effects were for two- and three-level food chains, respectively [2]. In other papers, indirect effects have been referred to as density- and trait-mediated indirect interactions [4]. We define the terminology used here as follows:
> - **Density effects**: consumptive effects resulting from predators killing prey.
>   *Direct density effects:* changes in prey density caused by predation.
>   *Indirect density effects:* changes in the resource density of the prey caused by predation reducing prey density.
> - **Trait effects**: non-consumptive effects resulting from changes in prey behavior or morphology in response to predation risk.
>   *Direct trait effects:* changes in prey density caused by changes in prey behavior or morphology in response to predation risk. It is caused primarily by prey starving, emigrating, or being consumed more often by other predators.
>   *Indirect trait effects:* changes in the resource density of the prey resulting from changes in behavior or morphology of prey. It is caused primarily by prey reducing their foraging, switching their diets, or emigrating.

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societies than the occurrence of those events. For example, although few children are abducted by strangers, the fear of this event has driven how parents monitor and restrict where their children are allowed to play. Likewise, because predators can scare and thus alter the behavioral or morphological traits of more prey than they can consume, trait effects might often be larger than density effects.

### How large are trait effects and when are they largest?

Preisser *et al.* found that the direct density and trait effects of predators on prey are roughly equal in size [2]; that is, on average, the mere presence of predators has just as much of an effect on prey survival or population density as predation does (Table 1). Thus, studies that do not include trait effects are essentially missing half of the effects of predators. The results for indirect effects are even more striking. Indirect trait effects of predators on prey resources are 85% as large as the overall effect (both density and trait) that predators have on resources. This means that, on average, the presence of a predator that is scaring but not consuming prey has a similar effect on the density of the resource of their prey as does a predator that is both scaring and consuming prey. This might occur because changes in prey traits (e.g. reduced foraging) have a similar effect on resource consumption as removing prey. Or it might occur because predators scare more prey than they consume. Thus, multi-trophic studies that do not include indirect trait effects might be ignoring the main driving force in certain systems. These results are not that surprising, given that it is well known that prey can alter their behavior and morphology in response to predation risk [5]. Yet, this is the first analysis to show that these effects are consistently important at a community level across several different systems.

The apparently large magnitude of trait effects leads to the questions of when and where these effects are the largest. Preisser *et al.* compared the sizes of trait effects between terrestrial and aquatic systems and found them to be significantly larger in aquatic systems (Table 1). In terrestrial systems, direct trait effects were 40% of the total effect that predators had the on the survival or population density of their prey. This effect was larger in freshwater and marine systems, 63% and 77%, respectively (Table 1). Differences in the relative sizes of indirect trait effects are even larger. In freshwater systems, indirect trait effects were 93% of the total effect that the predator had on the density of the resources of their prey, compared with 57% in terrestrial systems. This suggests that, in freshwater systems, most of the impacts of predators on the resources of their prey are the result of the presence of predators causing prey to alter their

traits (either through behavior or morphology) and consume fewer resources. This might explain why trophic cascades, in which the presence of a top carnivore has a positive influence on plant biomass, appear to be stronger in aquatic systems than in terrestrial systems [6,7].

### Methodological issues

Although the findings of Preisser *et al.* are intriguing, there are methodological issues that should be considered when interpreting their results [8]. They found no evidence that publication biases and biases owing to different research methodologies were responsible for their results. However, research biases in the systems that researchers have chosen to measure trait and density effects are unavoidable and could be responsible for the reported large trait effects. In addition, the reported differences in trait and density effect sizes between terrestrial and aquatic systems could be due to some experimental methodologies being easier or more effective in aquatic systems, such as using chemical cues to elicit prey trait changes. Finally, the meta-analysis of Preisser *et al.* combines studies with different metrics of effect sizes, such as fecundity and mortality rates, which can make results less reliable [9]. However, in spite of these difficulties, we believe the meta-analysis is an important step in showing the relatively large magnitudes of trait effects and can be used to suggest patterns in trait and density effects that deserve further investigation.

### Future directions

For a better understanding of when and how traits effects significantly affect community dynamics, we need to know more about the optimality and mechanisms of how prey respond to changes in predation risk. One of the impediments to modeling trait effects in community dynamics has been the lack of empirical information about how the costs and benefits of prey foraging vary with predator, prey and resource densities [10]. We need more experiments that vary predator and resource densities and that measure how prey respond, and the resulting predation and foraging rates. In addition, a more mechanistic understanding of how and when prey respond to predation risk might lead to general predictions about when indirect trait effects are most likely to be important in the dynamics of predator–prey systems. More experiments are needed to explore details such as how prey perceive changes in predation risk and how their responses are shaped by factors such as the patterns of predation risk [11] and the abundance of resources [12].

Most models that incorporate trait effects into community dynamics have treated trait dynamics as a function of the densities of interacting species and have allowed the resulting traits to affect population and community dynamics [13]. This approach might be the best for producing general conclusions about the short- and long-term effects of trait effects. Trait dynamics, however, might often depend on more than the densities of interacting species. For example, prey behavior will often vary between individuals because non-homogenous environments produce differences in prey states (such as size and hunger). A way to explore whether this variation has lasting effects on the relative importance of

**Table 1. Mean proportion of the total effect of predators caused by density and trait effects on prey (a direct effect) and on the resource of that prey (an indirect effect)[a]**

| | Direct effect | | Indirect effect | |
|---|---|---|---|---|
| | Mean | *N* | Mean | *N* |
| Density effect/Total effect | 0.54 | 133 | 0.33 | 30 |
| Trait effect/Total effect | 0.58 | 136 | 0.85 | 30 |
| | | | | |
| Trait effect/Total effect | | | | |
|   Terrestrial | 0.40 | 23 | 0.57 | 8 |
|   Freshwater | 0.63 | 105 | 0.93 | 20 |
|   Marine | 0.77 | 8 | 0.97 | 2 |

[a]Data taken from [2].

indirect trait effects in community dynamics is to incorporate dynamic state variable models [14] into community models. Also, the traits of predators and prey often depend on the traits of other predators and prey; for example, where and when prey forage is shaped by the distributions and behaviors of other prey and predators [15]. Thus, in these cases, prey behavior is not only a function of the densities of interacting species, but also of the individual traits of those other species. How the dynamics of these games interact with changes in the densities of the players will require integrating game models into community models.

### Conclusions

Preisser *et al.* show that how a predator affects prey traits is often just as important as how many prey a predator eats. The size of trait effects will depend on the system, but can sometimes be similar to the total predator effect. Therefore, understanding community dynamics will often require understanding not only density impacts between predator and prey, but also how scared prey alter their interactions with other species. Changes in prey traits responding to predation risk have too large an effect to be ignored in either empirical or theoretical studies.

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Letters

# The future fate of the Antarctic marine biota?

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Antarctica has always been regarded as the most isolated marine environment, isolated physically by the circum-Antarctic Polar Front, which, as far we currently know, is also an effective physiological barrier to most marine life from either side of the Front. In their recent Research Focus article in *TREE*, Clarke *et al.* [1] questioned the isolation of Antarctica by summarizing little but intriguing evidence for faunal exchange through the Polar Front, possibly by means of mesoscale eddies or ship traffic in and out of Antarctica [2]. They argue that, under conditions of climate change, introduced invertebrate larvae [2] might be able to establish and threaten Antarctic marine communities.

I disagree with Clarke *et al.* [1], who assume that changes in Antarctic marine communities as a result of invasive species might soon be observed and reach the

same scale of changes as observed in the terrestrial fauna and flora at the Antarctic Peninsula through the impact of climate change. So far, there is no proof of any recently established populations of alien species in Antarctic waters. When considering the potential for non-native species to establish in Antarctic waters, it is important to distinguish between temperature adaptation on evolutionary timescales, which resulted in species such as lithodid king crabs being able to reconquer Antarctic benthic communities [3,4], and pelagic organisms occasionally being transported into Antarctic waters, but without being able to survive there [1–3,5]. For example, the successful speciation of limatulid bivalves across the Polar Front [6] is likely to have occurred only as a result of physiological preadaptations to the environmental conditions.

Unless there is considerable warming of the Southern Ocean above critical thresholds for non-native species, the Polar Front will continue to be an effective physiological

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