LETTERS

Trophic cascades across ecosystems

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Predation can be intense, creating strong direct and indirect effects throughout food webs[1–4]. In addition, ecologists increasingly recognize that fluxes of organisms across ecosystem boundaries can have major consequences for community dynamics[5,6]. Species with complex life histories often shift habitats during their life cycles[7] and provide potent conduits coupling ecosystems[5,6]. Thus, local interactions that affect predator abundance in one ecosystem (for example a larval habitat) may have reverberating effects in another (for example an adult habitat). Here we show that fish indirectly facilitate terrestrial plant reproduction through cascading trophic interactions across ecosystem boundaries. Fish reduce larval dragonfly abundances in ponds, leading to fewer adult dragonflies nearby. Adult dragonflies consume insect pollinators and alter their foraging behaviour. As a result, plants near ponds with fish receive more pollinator visits and are less pollen limited than plants near fish-free ponds. Our results confirm that strong species interactions can reverberate across ecosystems, and emphasize the importance of landscape-level processes in driving local species interactions.

Trophic cascades arise when predators reduce prey abundance, indirectly relaxing consumption on lower trophic levels[8]. For example, in a three-level food chain, predators can reduce herbivore abundance, indirectly benefiting plants. Studies of food-web interactions and trophic cascades have traditionally focused on the antagonistic interactions between species[1–4,8]. However, mutualists are also embedded within food webs. Many plant species either fail to reproduce or produce fewer seeds or seeds of lower quality if mutualist pollinators, including multitudes of insects, birds and mammals, fail to visit[9]. As a result, pollinators can be crucial drivers of plant population and community dynamics[10]. However, pollinators also have important predators; such predators can have an indirect negative effect on plants by harming mutualists[11–13].

The strength and ubiquity of trophic cascades has been the focus of a sustained debate in ecology, and considerable effort has focused on quantifying their strength in aquatic and terrestrial ecosystems[14]. However, only recently have ecologists explicitly examined how organisms with complex life histories can dynamically couple aquatic and terrestrial ecosystems[15–17], leading to trophic cascades that transcend ecosystem boundaries. The larval stages of many freshwater organisms (for example dragonflies and frogs) are vulnerable to a suite of aquatic predators, whereas the adult stages are important consumers in the terrestrial habitat. The intensity of predation experienced by juveniles in the aquatic habitat can therefore be predicted to indirectly influence the intensity of predation imposed in turn by adults in terrestrial habitats.

Here we show how strong direct effects of organisms with complex life histories can create trophic cascades that transcend terrestrial and aquatic ecosystem boundaries. Specifically, we demonstrate that freshwater fish indirectly facilitate plant reproduction by means of a cascade of species interactions, mediated by dragonflies switching during their life history between aquatic and terrestrial habitats (Fig. 1). Fish predation often strongly limits the abundance and

the size distribution (favouring smaller species) of larval odonates (dragonflies and damselflies) in aquatic habitats[18,19] Although detailed diet studies on adult dragonflies are rare, published accounts from the general region of our study have shown that the adults of many dragonfly species are voracious predators of bees and other pollinators[20–22]. We proposed that fish would reduce larval and adult dragonfly abundances and that this would permit a higher abundance of insect pollinators, thus indirectly increasing the pollination and reproductive success of nearby terrestrial plants.

Our study took place at the University of Florida's Katharine Ordway Preserve/Carl Swisher Memorial Sanctuary in northern Florida. This site contains 18 permanent ponds (retain standing water in most years) that differ in whether or not they contain fish. We chose eight ponds; four contained a community of fish (such as Centrarchid sunfishes) and four lacked fish. We found no systematic differences between ponds in surface area or in the amount of sunlight or vegetation structure near the pond margins (Supplementary Information).

As predicted, larval (Fig. 2a) and adult (Fig. 2b) dragonflies were much more abundant in and around fish-free ponds than at ponds with fish. The species composition of dragonflies also differed between ponds with and without fish; large and medium-sized dragonflies dominated in and around fish-free ponds, whereas small species were more prevalent in and around ponds with fish (Fig. 2).
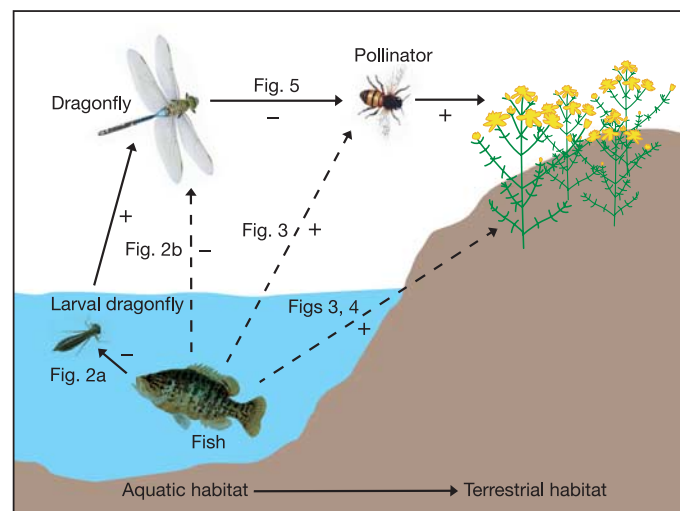
Figure 1 | Interaction web showing the pathway by which fish facilitate plant reproduction. Solid arrows indicate direct interactions; dashed arrows denote indirect interactions. The sign refers to the expected direction of the direct or indirect effect (see the text). Figure numbers indicate which figure presents data supporting each of the predicted effects. (Figure created by S. White and C. Stierwalt.)
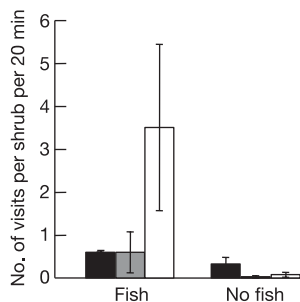
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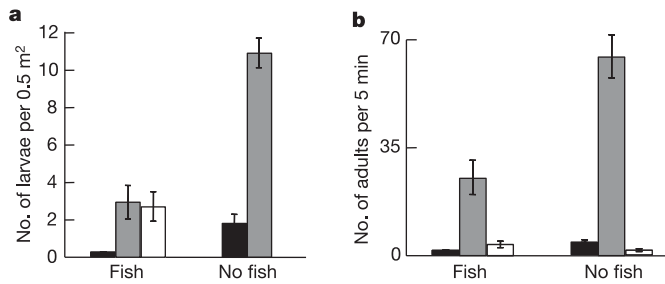
Figure 2 | **Surveyed dragonfly abundances in and near fish-containing and fish-free ponds.** We sorted dragonfly species into three size categories, small, medium and large (see Methods for dragonfly genera in each category). **a**, There were more larval individuals from the medium (grey bars) and large (black bars) size classes of dragonfly species, and fewer individuals from the small size classes (white bars), in ponds without fish than in ponds with fish (MANOVA: Pillai trace = 0.99, $F_{3,4}$ = 19.96, $P < 0.01$; univariate F-tests for large species, $F_{1,6}$ = 93.12, $P < 0.001$; for medium species, $F_{1,6}$ = 85.67, $P < 0.002$; and for small species, $F_{1,6}$ = 114.42, $P < 0.001$). **b**, The abundance of adult dragonflies was lower near ponds with fish (ANOVA: $F_{1,6}$ = 10.85, $P < 0.02$). There was a difference between the abundances of adult medium and large dragonfly species near fish-free ponds and near ponds with fish (MANOVA: Pillai trace = 0.82, $F_{3,4}$ = 5.89, $P = 0.06$; univariate F-tests for large species, $F_{1,6}$ = 22.97, $P < 0.003$; and for medium species, $F_{1,6}$ = 7.50, $P < 0.03$); there was no difference in small dragonfly density between fish-containing and fish-free ponds ($F_{1,6}$ = 1.52, $P > 0.26$). Results are shown as means ± s.e.m.

To assess the correlation of fish presence with pollinator visitation, we observed pollinator visitation on one of the most common flowering shoreline plants at these ponds, *Hypericum fasciculatum* (Hypericaceae; St John's wort). Pollinator visitation rates were much higher on *H. fasciculatum* shrubs near ponds with fish than near fish-free ponds (Fig. 3), and there was a difference in the composition of pollinator species; most visitors near ponds with fish were hymenopterans (mostly bees), whereas most visitors near fish-free ponds were dipterans (flies) (Fig. 3). Hypericaceae have evolved traits that attract bees[23]; bees may therefore be more effective than flies at pollinating *Hypericum*. Thus, the effect of reduced pollinator visits near fish-free ponds might be magnified, because those few visits that did occur were primarily from less effective pollinators.

We examined whether the effects of fish on dragonflies (Fig. 2) and their cascading effects on pollinator visits (Fig. 3) indirectly
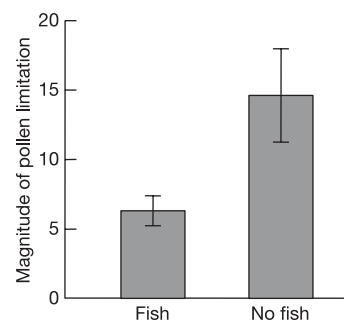
influenced plant reproductive output. We performed pollen supplementation experiments to determine the degree to which *H. fasciculatum* seed production was limited by pollen receipt at each pond. Plants near fish-free ponds were more than twice as pollen limited than plants near ponds with fish (Fig. 4). Complementary experiments with a second plant species (*Sagittaria latifolia*) also showed enhanced pollinator visitation and reproductive output at the margins of ponds with fish (Supplementary Information), indicating that the indirect effect of fish upon plant reproductive success might be general.

Our results indicate that fish presence might have led to low larval and adult dragonfly abundances in and around ponds, causing cascading indirect effects on pollinator visitation rates and plant reproductive output in an adjacent terrestrial community. The decrease in adult dragonfly numbers near ponds with fish probably reflects a combination of demographic effects, in which fish predation reduces larval dragonfly density[18,19], and behavioural effects, in which dragonflies avoid ovipositing in ponds with fish. However, because our study did not experimentally manipulate fish presence we cannot discern the relative magnitudes of the possible mechanisms.

We found evidence that pollinator visitation was lower near fish-free ponds, both because adult dragonflies predate on pollinators and because pollinators behaviourally avoid foraging near adult dragonflies. At our study site, over a seven-day period, we observed several predation events by two common species of dragonflies (*Anax junius* and *Erythemis simplicicollis*)[24] known to attack large insect species including pollinators; four of eight of those observed predation events were on pollinators (bees, moths and flies; Fig. 5a). To examine the behavioural influence of dragonfly presence on pollinator visitation, we put cages around naturally occurring *H. fasciculatum* near a pond with fish; the mesh size allowed free access by most pollinators but precluded escape by enclosed *E. simplicicollis*. We found that fewer visitors entered cages containing dragonflies than control cages (paired *t*-test: $t = -4.2$, $P = 0.002$), and visitors that did enter cages with dragonflies foraged on fewer flowers than visitors that entered cages not containing dragonflies ($t = -3.8$, $P = 0.009$). This resulted in *H. fasciculatum* flowers receiving fewer overall visits in the presence of a dragonfly (Fig. 5b).

Strong linkages between consumers in aquatic and terrestrial ecosystems are not limited to this special case in which an aquatic consumer (fish) affects terrestrial predators of mutualists. Many terrestrial predators, herbivores and pollinators have larval aquatic phases. Aquatic predators might therefore have a variety of consequences for interactions in neighbouring terrestrial ecosystems. Similarly, many organisms (for example salamanders) with terrestrial life-stages are important aquatic predators, and thus interactions in

Figure 3 | **Pollinator visitation rates to *Hypericum fasciculatum*.** The total number of pollinator visits to *Hypericum fasciculatum* was higher near ponds with fish (ANOVA: $F_{1,6}$ = 11.45, $P < 0.02$). There was a marginally significant difference between the compositions of pollinators at fish-containing and fish-free ponds (MANOVA, Pillai trace = 0.79, $F_{3,4}$ = 4.9, $P = 0.07$). The number of visits by all three groups of pollinators (black bars, Diptera; grey bars, Lepidoptera; white bars, Hymenoptera) was less near ponds with fish (univariate F-tests: Diptera (primarily Syrphidae, Bombyliidae) $F_{1,6}$ = 4.62, $P < 0.07$; Hymenoptera (primarily *Agapostemon* spp. (Halictidae)) $F_{1,6}$ = 15.50, $P < 0.05$; Lepidoptera (primarily Noctuidae) $F_{1,6}$ = 5.72, $P = 0.05$). Results are shown as means ± s.e.m.

Figure 4 | **Results from pollen supplementation experiments.** *Hypericum fasciculatum* plants near fish-containing ponds had significantly less pollen limitation (quantified as the difference in the average seed set between experimental supplementation and control treatments) than in plants near fish-free ponds (ANOVA: $F_{1,6}$ = 7.91, $P < 0.03$). Results are shown as means ± s.e.m.

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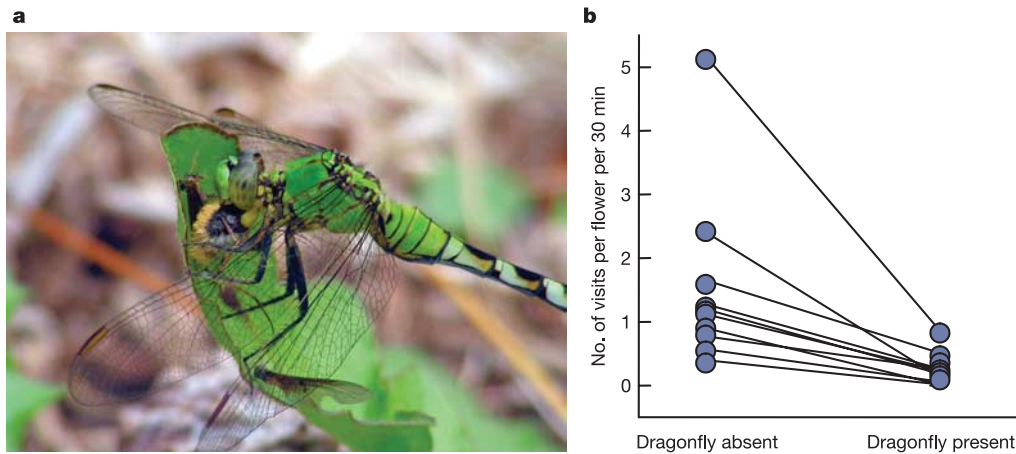
Figure 5 | **Effects of dragonflies on pollinators. a**, Photograph of a dragonfly (female *Erythemis simplicicollis*) consuming a bee-fly pollinator (*Bombylius* sp. (Diptera: Bombyliidae)) at our study site. Photo by M.W.McC. **b**, Results from the experiment comparing pollinator visitation rates in pairs of large-mesh cages placed around a *H. fasciculatum* shrub, one with a dragonfly (female *E. simplicicollis*) in it, and one as a control. Overall, visitation was much lower in the cage with the dragonfly than in the control cage (paired *t*-test: $t = -3.5$, $P = 0.007$).

the terrestrial ecosystem can cascade to the aquatic ecosystem. Determining the relative strengths of these interactions across ecosystem boundaries should be the focus of future empirical research.

Although the importance of habitat connectance for metacommunity structure has been well studied, this has primarily been restricted to cases involving patches of a single ecosystem type[25]. Understanding interactions across ecosystem types may be crucial for gauging the effects of anthropogenic environmental change. Deliberate introductions of fish by humans are ubiquitous throughout the world (for example for recreation or pest control)[26,27]. Our results reveal that such introductions might have cascading effects on adjacent terrestrial ecosystems. By increasing the reproductive success of insect-pollinated plants, freshwater fish introductions potentially alter competitive relationships between terrestrial plants, putting plants not pollinated by insects at a competitive disadvantage. Wetland destruction can harm dragonfly populations, with similar consequences for terrestrial plants. Conversely, a decline in fish abundances (and consequent increase in dragonflies) due to eutrophication, hydroperiod modification or pollution could indirectly harm insect-pollinated plants. Our findings emphasize how consumer flows across radically disparate ecosystems can affect landscape-level processes and drive local interactions between species.

METHODS

Study site and choice of ponds. In May 2003 we chose eight ponds within the Katharine Ordway Preserve/Swisher Memorial Sanctuary (managed by the University of Florida), in Putnam County, Florida. The average distance between study ponds was about 1,000 m (range 200–2,500 m). Four ponds were fish-free; four had abundant fish species (M.W.McC., unpublished observations), including several members of the Centrachidae, which are known predators of larval odonates[18]. Fish-containing and fish-free ponds were interspersed throughout this site and did not differ in surface area (*t*-test: $t = 1.46$; d.f. = 6; $P > 0.20$) or in the structural features of their surrounding vegetation (Supplementary Information).

Quantifying larval and adult dragonflies. We estimated larval dragonfly densities by box sampling[18]. In each pond, a 0.5-m² metal box was deployed at five haphazardly chosen locations, and we determined the number of dragonfly larvae present by sweeping a 0.45 m × 0.25 m net until no additional dragonfly larvae were captured in five consecutive sweeps. We quantified adult dragonfly abundances by means of point counts, for which a single observer (M.W.McC.) counted the number of each species of dragonfly that entered the field of view during a 5-min observation period. At each pond, two counts were made from points each located 90° from the other.

We examined adult and larval dragonfly responses to fish presence in two ways (all data were square-root transformed before analyses to fit normality assumptions). First, we compared the total number of dragonflies between fish-containing and fish-free ponds with ANOVA. Second, to determine whether there were any compositional differences in response to fish, we separated dragonfly species into size classes (based on ref. 28). Genera in the small size class included *Erythrodiplax* and *Celithemus* (Libellulidae); the medium size class included *Libellula*, *Erythemis*, *Pachydiplax* and *Tramea* (Libellulidae); the large size class included *Anax* and *Coryphaesnae* (Aeshnidae). Here we first used MANOVA to determine whether there was an overall treatment effect. After a significant ($P < 0.05$) or marginally significant ($P < 0.08$) MANOVA, we examined univariate *F*-tests to discern differences for each size class.

Pollinator visitation rates. Over a two-week period from late May to early June, we observed pollinators at ten similar-sized *Hypericum fasciculatum* shrubs at each pond. We watched each focal shrub for 20 min and calculated the average number of pollinator visits per shrub per 20 min. First, we compared the visitation rate of plants near fish ponds with those of plants near fish-free ponds by using ANOVA. Second, we separated pollinators into their orders (Hymenoptera, Diptera and Lepidoptera) and used MANOVA to determine whether there was an overall treatment effect, and univariate *F*-tests to discern differences between pollinating taxa.

Pollen supplementation experiments. At each pond we chose ten *H. fasciculatum* shrubs that were similar in size and floral display and separated by at least 10 m from any other study plant. On each plant we chose two similar-sized branches and randomly selected one for the pollen supplement treatment and the other as a control. Flowers in the supplement treatment were rubbed with the anthers of flowers from another plant that was more than 5 m away. Branches were visited daily for one week until most (more than 60%) of the flowers had received pollen supplementation. For each shrub, we calculated the magnitude of pollen limitation as the difference in average seed set (counted under a dissecting microscope) between the supplemented and control flowers; we averaged those values to calculate the magnitude of pollen limitation for each pond. We used ANOVA to compare pollen limitation of shrubs near fish-containing and fish-free ponds.

Dragonfly predation observations. In April 2005, as we walked through the vegetation at the margins of each pond and flushed a variety of insects, we witnessed several predation events by two of the most common species of dragonflies at our study site, *Anax junius* and *Erythemis simplicicollis*. After we witnessed a predation event, we approached the dragonfly while it was consuming its prey and identified the prey to taxa (usually to order) by using close-focusing (about 5 m) binoculars.

Effects of dragonfly presence on pollinator visitation. We constructed cylindrical cages 1.5 m in diameter and 2 m tall from diamond-shaped, plastic mesh fencing 2.3 cm in width, designed to contain adult dragonflies (which cannot retract their wings), but to allow free access by most pollinators (except large lepidopterans, which were almost never observed visiting *H. fasciculatum*). At a single pond with fish, we paired two *H. fasciculatum* shrubs that were similar in size and floral display, and placed one of these cages over each shrub. We then introduced one adult female *E. simplicicollis* into one cage chosen at random and left the other as a caged control. This dragonfly was common at the study site,

especially at ponds without fish, and readily attacks large prey. Further, *E. simplicicollis* is a sit-and-wait predator, and its normal behaviour was not greatly altered by being caged. After 10 min, allowing time for the dragonfly to settle down, one observer watched each caged shrub and recorded the number and identity of pollinators that entered the cage and visited at least one flower, and the number of flowers each pollinator visited on a shrub before leaving. Each shrub was watched for 30 min. We then moved the cages to two new paired shrubs and repeated the experiment with a different dragonfly. In all we performed ten such paired experiments over a four-day period. We performed these experiments between 08:00 and 11:00 on mostly sunny days, so that pollinator activity rates would be comparable between paired experiments. We analysed these data with a paired *t*-test.

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