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FISH INVASION RESTRUCTURES STREAM AND FOREST FOOD WEBS BY INTERRUPTING RECIPROCAL PREY SUBSIDIES

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Abstract. Habitat alteration and biotic invasions are the two leading causes of global environmental change and biodiversity loss. Recent innovative experiments have shown that habitat disturbance can have drastic effects that cascade to adjacent ecosystems by altering the flow of resource subsidies from donor systems. Likewise, exotic species invasions could alter subsidies and affect distant food webs, but very few studies have tested this experimentally. Here we report evidence from a large-scale field experiment in northern Japan that invasion of nonnative rainbow trout (*Oncorhynchus mykiss*) interrupted reciprocal flows of invertebrate prey that drove stream and adjacent riparian forest food webs. Rainbow trout usurped terrestrial prey that fell into the stream, causing native Dolly Varden charr (*Salvelinus malma*) to shift their foraging to insects that graze algae from the stream bottom. This indirectly increased algal biomass, but also decreased biomass of adult aquatic insects emerging from the stream to the forest. In turn, this led to a 65% reduction in the density of riparian-specialist spiders in the forest. Thus, species invasions can interrupt flows of resources between interconnected ecosystems and have effects that propagate across their boundaries, effects that may be difficult to anticipate without in-depth understanding of food web relationships.

Key words: food webs; Hokkaido, Japan; invasion ecology; large-scale field experiment; *Oncorhynchus mykiss*; resource subsidies; riparian ecology; *Salvelinus malma*; stream ecology.

INTRODUCTION

Habitat destruction and biotic invasions are the two leading agents of global environmental change (Vitousek et al. 1997) and both are important in streams and their adjacent riparian forests. Habitat in nearly all stream and riparian ecosystems worldwide has been degraded by human activities (Benke 1990, Naiman and Décamps 1997). These disturbances can interrupt flows of resources that link the two ecosystems (Likens and Bormann 1974), so that habitat destruction in riparian forests has strong potential to alter stream ecosystems, and vice versa (Nakano et al. 1999b, Sabo and Power 2002). Ecologists have long recognized that most of the energy in headwater streams is derived from the surrounding riparian forest, and that inputs of dissolved organic matter, leaves, and wood strongly influence communities of stream biota (Hynes 1975, Vannote et al. 1980, Wallace et al. 1997). However, researchers have only recently appreciated the importance of two other resource subsidies, terrestrial invertebrates that fall directly into streams and feed fish (Wipfli 1997, Nakano et al. 1999b, Kawaguchi et

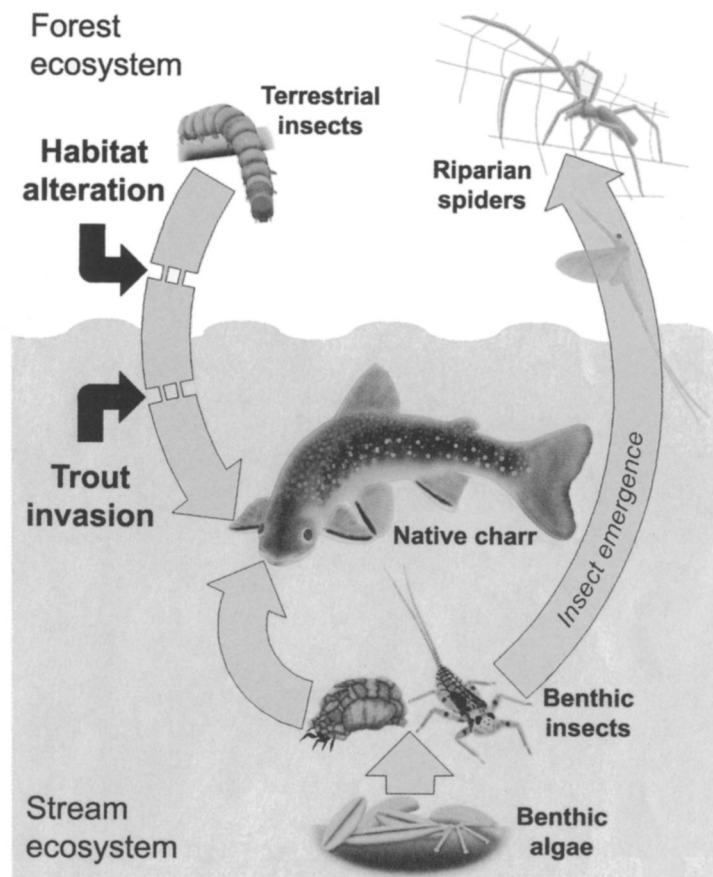
al. 2003), and the reciprocal flow of adult aquatic insects that emerge into forests and feed riparian consumers like birds and spiders (Nakano and Murakami 2001, Kato et al. 2003, Sanzone et al. 2003). As a result of such connectivity, streams and forests are likely to be coupled in their vulnerability to habitat degradation, because it can sever fluxes of resources across the boundary between them and markedly change community structure and function in the adjacent ecosystem (Polis et al. 2004).

Like habitat destruction, invasions of nonnative fishes could also interrupt resource flows and have far-reaching effects on interconnected ecosystems. Fish invasions have also occurred worldwide and severely altered stream communities through direct predation on and competition with native species, as well as indirect effects on food webs (Moyle 1986, Flecker and Townsend 1994). However, the effects of fish invasions on food web linkages among ecosystems are unstudied. If fish invaders alter resource subsidies to and from terrestrial ecosystems, their effects, like those of habitat destruction, could propagate across ecosystem boundaries. Here we used a large-scale field experiment to test the hypothesis that a nonnative stream fish interrupts reciprocal flows of invertebrate prey, and drives changes in both the stream community and riparian consumers such as spiders (Fig. 1).

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FIG. 1. A generalized diagram showing flows of invertebrate prey that drive food web relationships in stream and riparian forest ecosystems of northern Japan. These reciprocal food web subsidies are subject to interruption via habitat alteration or exotic fish species invasion, with consequences that propagate within and between the interconnected ecosystems.



Ideal systems in which to study these complex interactions are spring-fed streams of Hokkaido, northern Japan, a region being rapidly invaded by nonnative rainbow trout (*Oncorhynchus mykiss*; Fausch et al. 2001; see Plate 1). Previous research in one such stream (Nakano et al. 1999b, Kawaguchi and Nakano 2001, Nakano and Murakami 2001, Kawaguchi et al. 2003) showed that the deciduous riparian forest supported abundant terrestrial invertebrates that not only fed forest consumers, but also fell into the stream and made up about 50% of the annual energy budgets of native fishes such as Dolly Varden charr (*Salvelinus malma*). In turn, emergence of adult aquatic insects from the stream created a reciprocal subsidy that made up 26% of the annual energy intake of forest birds (Nakano and Murakami 2001) and was also important to the diets and distribution of web-building spiders (Kato et al. 2003). Decoupling the subsidy of terrestrial prey using a greenhouse cover over the stream (Fig. 2), which mimicked one consequence of riparian forest habitat alteration, caused native charr to deplete herbivorous stream invertebrates and thereby indirectly increase stream algae (Nakano et al. 1999b). However, it is unknown whether severing this flow of terrestrial prey to the stream would also reduce aquatic insect emergence that subsidizes the riparian forest food web. Rainbow

trout forage preferentially on terrestrial invertebrates that fall into streams (Nakano et al. 1999a), suggesting that they might also interrupt this prey subsidy and have strong indirect effects that could propagate throughout the stream food web and across the ecosystem boundary into the riparian forest. If so, the problem could be pervasive because rainbow trout are not only invading throughout Hokkaido, but are also the most widely introduced fish species in the world (Fausch et al. 2001).

METHODS

Hypotheses and study design

We conducted a large-scale field experiment in southwestern Hokkaido (Japan) to test the effects of rainbow trout invasion on flows of invertebrate prey between stream and riparian forest ecosystems, and the consequences for both systems (Fig. 1). We designed the experiment to test three specific hypotheses: (a) experimentally interrupting the subsidy of terrestrial prey from forest to stream causes indirect effects in the stream food web that ultimately increase attached algae (cf. Nakano et al. 1999b), but also reduce aquatic insect emergence that drives abundance of riparian consumers like spiders; (b) invading rainbow trout have a similar effect on the stream food web and riparian consumers



PLATE 1. Nonnative rainbow trout (*Oncorhynchus mykiss*) like this one are rapidly invading streams of Hokkaido, Japan. Their presence was experimentally manipulated in reaches of the study stream. Photo credit: C. V. Baxter.

as experimentally decoupling the terrestrial prey subsidy; and (c) the two factors combined have a greater effect than either alone. We manipulated terrestrial prey input and invading rainbow trout in a 2×2 factorial design, with four replicates of the four treatments: control (native wild Dolly Varden charr at natural density), a mesh greenhouse cover that reduced terrestrial prey input to the stream and aquatic insect emergence to the forest (Fig. 2; Nakano et al. 1999b), wild rainbow trout added at natural densities, and both greenhouse cover and rainbow trout added.

Study site and experimental treatments

The experiment was conducted in Horonai Stream, a small spring stream (2–5 m wide, 14 km long, 15.4 km² drainage area, gradient <1%) draining a watershed within the Hokkaido University Tomakomai Experimental Forest (42°43' N, 141°36' E; Nakano et al. 1999b). The riparian forest is dominated by oak (*Quercus crispula*), ash (*Fraxinus mandshurica*), and maple (*Acer mono*), and the canopy covers >95% of the stream width for most of its length (Nakano and Murakami 2001). Groundwater input creates stable temperature (annual range = 6–10°C) and discharge regimes (mean annual = 0.24 m³/s) with few flood disturbances (Nakano et al. 1999b).

We used a randomized complete-block design in which 16 fenced reaches (length 27.5 ± 0.69 m [mean ± 1 SE], 100-m² surface area) along a 1.7-km segment of stream were divided into four blocks, from upstream to downstream. The four treatments were randomly assigned to the four reaches in each block. Reaches were enclosed using 6-mm plastic mesh fences supported by steel pipe frames that allowed passage of drifting invertebrates, but not fish >3 cm fork length. All fish were removed from the reaches by four passes of depletion electrofishing (Model 12 Electrofisher, [Smith-Root, Vancouver, Washington, USA]). Native Dolly

Varden charr were added to each reach in equal numbers ($n = 40$ individuals) and sizes (fork length, 134.1 ± 0.9 mm [mean ± 1 SE]) to achieve densities of 0.4 charr/m², about average for undisturbed Hokkaido streams (Fausch et al. 1994, Nakano et al. 1999b). Rainbow trout ($n = 20$ individuals) of similar size (144.9 ± 2.3 mm) were added to half the reaches at 0.2 trout/m², the density previously estimated for Horonai Stream (Nakano et al. 1999a). Electrofishing reaches before the experiment apparently had little effect on benthic invertebrates, because biomass from natural substrates in control reaches and three unmanipulated reaches interspersed among the experimental reaches was similar (C. Baxter, K. Fausch, M. Murakami, and N. Kuhara, unpublished data).

To exclude input of terrestrial prey to the stream and aquatic insect emergence to the forest, half the reaches received greenhouse covers made of transparent 1-mm nylon mesh supported by aluminum frames (Fig. 2). The covers also extended 25 m upstream to reduce terrestrial prey drifting into the reaches, because fish upstream of the experimental reaches were expected to consume most of them (Nakano et al. 1999b, Kawaguchi et al. 2003). At least 50 m of unmanipulated stream separated reaches. Both ends of greenhouse covers were blocked with mesh to prevent flying terrestrial insects from entering, but roof windows (1 \times 4 m) at each end allowed emerging aquatic insects to escape (Nakano et al. 1999b). In a previous study (Nakano et al. 1999b), average air temperatures under greenhouse covers were $\sim 1^\circ\text{C}$ higher than outside, but water temperatures did not differ. In our study, paired measurements of relative photon flux showed that covers reduced light by $11.9 \pm 1.0\%$ (mean ± 1 SE, $n = 10$) on average, which was within the range of natural variation in light among reaches. Relative photon-flux density at the water surface did not differ significantly among treatments (means ranged from 1.9% to 5.2%,



FIG. 2. The mesh greenhouse cover used to experimentally reduce flux of aquatic and terrestrial invertebrates between the riparian forest and the stream. The greenhouse cover is $5 \times 2.5 \times 55$ m and is shown covering one of the study reaches.

$P = 0.35$ by one-way ANOVA). Water temperature measured during the experiment using a data logger in each block was virtually identical (range of means: $8.5\text{--}9.0^{\circ}\text{C}$). Physical habitat features such as number of pools in each reach (range: 2–5 pools) and pieces of large wood ($\geq 30\text{-cm}$ diameter, $\geq 1\text{-m}$ length, range: 0–4 pieces), and stream discharge (range: $0.095\text{--}0.195$ m^3/s) did not differ among treatments ($P \geq 0.30$ by ANOVA), though discharge increased in downstream blocks ($P < 0.001$).

Sampling and analyses of food web components

The experiment was conducted for six weeks, from 11 June to 22 July 2002, when terrestrial prey input to the stream was increasing and emergence of adult aquatic insects was reaching its peak (Nakano and Murakami 2001). In each reach we measured the biomass of falling and drifting terrestrial invertebrates, terrestrial and aquatic prey in fish diets, benthic stream invertebrates, stream periphyton (attached algae), and emerging adult aquatic insects, as well as density of spiders in the adjacent riparian forest. Methods generally followed previous research (Nakano et al. 1999b, Kawaguchi and Nakano 2001, Nakano and Murakami 2001). Input of terrestrial invertebrates falling into each reach was estimated each of the last two weeks of the experiment using two 1-m^2 pan traps filled with water and 2–3 drops of surfactant, positioned midstream and adjacent to the bank. Pan contents were sieved ($250\text{-}\mu\text{m}$ mesh) after a three-day deployment. Biomass of terrestrial invertebrates drifting into each reach was estimated once during the last week using three drift nets (30×40 cm mouth, 1 m long, $250\text{-}\mu\text{m}$ mesh) set across the upstream end for 20 minutes at dusk (19:00) with their openings extending just above the water surface. Water volume filtered was estimated from the current velocity measured at the center of each net opening.

To estimate terrestrial and aquatic prey in fish diets, fish were captured by electrofishing during the last week of the experiment. Diet contents were collected from 10–15 fish per species in each reach using a pipette to flush prey items from the stomach. Biomass of stream benthic invertebrates and periphyton was measured using brick substrates ($20 \times 20 \times 5$ cm high; see Nakano et al. 1999b). Twenty bricks were placed in each reach 20 days before the experiment began, to allow colonization. At the end, 16 bricks were selected randomly from each reach. Each brick was quickly removed into a $100\text{-}\mu\text{m}$ mesh Surber net (Miura-Rika, Sapporo, Japan) placed just downstream, which captured aquatic invertebrates that were displaced, and then placed in a pan where all remaining invertebrates were collected. Subsequently, periphyton was sampled by placing a rubber template with a 5-cm^2 hole at two random locations on the brick and scouring the exposed brick surface with an acrylate fiber cloth (Tanida et al. 1999). When patches of periphyton were present, bricks were stratified into patchy and non-patchy areas and one sample was randomly located in each. Samples from each brick were combined and frozen. Pigments were later extracted from the cloths with 90% ethanol and chlorophyll *a* was measured using a spectrophotometer (U-1500 [Hitachi, Tokyo, Japan]).

The flux of adult aquatic insects emerging from each reach was estimated each of the last three weeks using two 1-m^2 floating emergence traps (1-mm mesh) positioned over representative pool and riffle habitats. Traps were deployed for three days, and insects were removed using an aspirator. All invertebrate and fish diet samples were preserved (70% ethanol), sorted to Order (pan and drift samples) or the taxonomic level required to identify trophic guilds (benthos, fish diet, and emergence samples), and wet mass converted to dry mass via regressions from previous research (Kawaguchi and Nakano

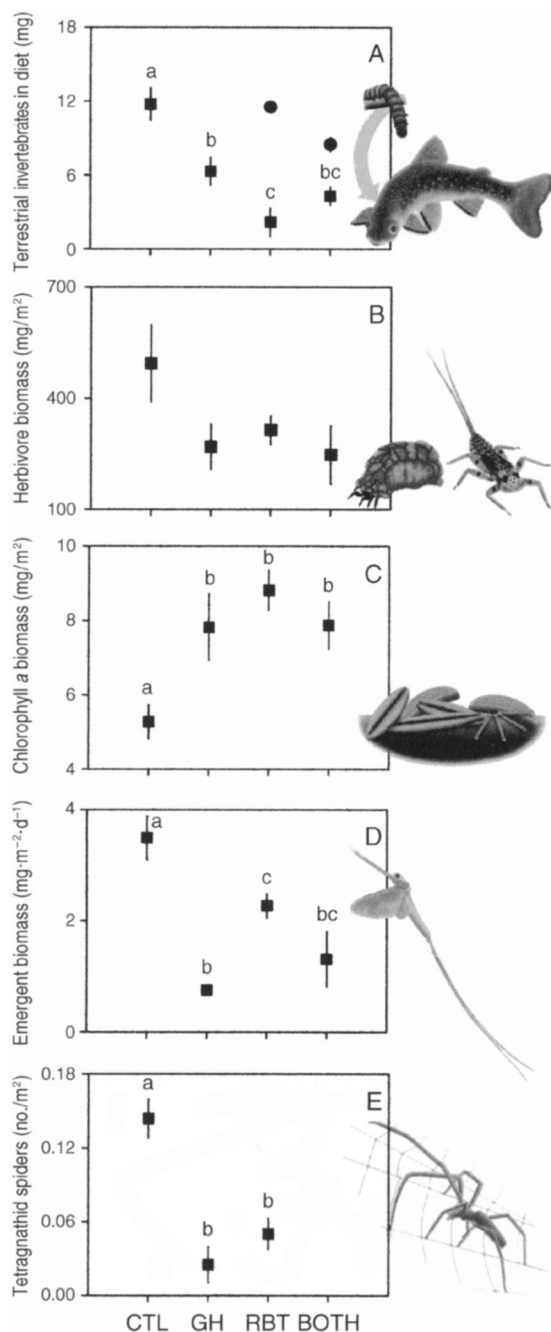


FIG. 3. Changes in five food web components in reaches of Horonai Stream caused by four treatments (CTL = control with native fish only, GH = greenhouse cover, RBT = rainbow trout added, BOTH = both greenhouse cover and rainbow trout) after six weeks during summer 2002. (Data are means \pm 1 SE, n = 4 replicates [except n = 3 for rainbow trout treatment]). Bars with different lowercase letters indicate significant differences (P < 0.05) among treatments based on LSD comparisons after ANOVA of log-transformed data (except square-root transformation for spider counts), when the interaction effect was significant (all except herbivore biomass). In (A) the different symbols represent biomass of terrestrial invertebrates in the diets of native Dolly Varden charr (squares) and nonnative rainbow trout (circles).

2001). Herbivorous taxa of stream invertebrates were designated from previous research (Nakano et al. 1999b), and are hereafter termed "herbivores," though they likely derived some energy from detrital-based biofilms in addition to periphyton. Two taxa of terrestrial insects, Lucanidae and Raphidophoridae, were too large for fish to consume and were excluded. Initial analysis showed that a large proportion of the biomass of benthic herbivores consisted of pupae and larvae of the caddisfly, *Glossosoma* spp. When they pupate, *Glossosoma* cement their stone cases to rocks, stop actively grazing, and are largely invulnerable to fish predation. Therefore, only *Glossosoma* larvae were included in further analysis, because the pupae had little influence on the food web during the experiment.

Web-weaving riparian spiders were collected within a 2×20 m transect positioned 2–4 m from the stream bank along each reach. During the final week, all web-building spiders found to a maximum height of 2 m were collected by hand at night (20:00–22:00), when the spiders were most active and visible (Kato et al. 2003). Because greenhouse covers reduced biomass of emergent aquatic insects reaching the riparian zone to similar levels whether rainbow trout were added or not, reaches with both greenhouse cover and rainbow trout were not sampled for spiders. Spiders were preserved in 70% ethanol and sorted to Family.

Data were analyzed using a two-way ANOVA for randomized complete-block designs (SAS Institute 1999). One reach with the rainbow trout treatment suffered heavy predation on fish by mink (*Mustela vison*), which resulted in an ineffective treatment, so it was excluded. All biomass data (except emergence) were transformed using logarithms, and spider count data were transformed using square root. When a significant interaction between main effects was detected (for all components except herbivore biomass), differences among treatments were assessed using least significant difference (LSD) comparisons.

RESULTS

The greenhouse cover caused more than a four-fold reduction in the falling input of terrestrial invertebrates to the stream (5.4 ± 1.1 vs. 24.4 ± 3.3 $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$ [mean \pm 1 SE] in the eight reaches with vs. eight without greenhouses; P = 0.001 by t test) whereas drifting inputs were low and similar between these treatments (0.069 ± 0.017 vs. 0.049 ± 0.011 $\text{mg} \cdot \text{m}^{-2} \cdot \text{d}^{-1}$; P = 0.20 by t test). Consequently, adding the greenhouse cover caused a 47% reduction in the biomass of terrestrial prey consumed by native Dolly Varden charr compared to the control (Fig. 3A; P = 0.05 by LSD comparison after ANOVA), and drove them to shift their foraging to benthic stream insects, which increased greatly in their diets (1.20 ± 0.38 vs. 0.16 ± 0.06 mg [mean \pm 1 SE], P < 0.006 by LSD). The stream insect assemblage was dominated by herbivores, which accounted for 75% of total biomass for all benthic samples com-

bined. Thus, in reaches with greenhouse covers this foraging shift by charr resulted in a 46% reduction in biomass of herbivores (Fig. 3B; $P = 0.02$ for greenhouse main effect; interaction not significant, $P = 0.16$), and subsequently, a 49% increase in biomass of chlorophyll *a* in periphyton on bricks (Fig. 3C; $P = 0.04$ by LSD) in an archetypal trophic cascade (Carpenter et al. 1985, Power 1990). Likewise in the treatment where rainbow trout were added, they apparently consumed most terrestrial prey, and reduced the terrestrial prey consumption of native charr by 82% compared to the control (Fig. 3A; $P = 0.0005$ by LSD). This also caused charr to increase the biomass of benthic stream insects they consumed (treatment, 0.72 ± 0.25 mg vs. control, 0.16 ± 0.06 mg [mean ± 1 SE], $P < 0.05$ by LSD), thereby decreasing herbivores (Fig. 3B; $P = 0.03$ for rainbow trout main effect) and increasing periphyton biomass (Fig. 3C; $P = 0.002$ by LSD) to levels similar to those of the greenhouse treatment.

The greenhouse-cover and rainbow trout treatments also lowered the biomass of adult aquatic insects emerging from the stream by 79% and 35%, respectively (Fig. 3D; $P = 0.0001$ and $P = 0.03$ by LSD). In turn, this lower emergent biomass resulted in 83% and 65% fewer spiders of the family Tetragnathidae in the riparian forest along the respective treatment reaches (Fig. 3E; $P = 0.001$ and $P = 0.005$ by LSD). Tetragnathid spiders weave horizontal orb webs, and a previous study along Horonai Stream showed that they depend on emerging aquatic insects for a large portion of their diet (Kato et al. 2003). Taken together, our results demonstrate that adding rainbow trout had as large an effect on the stream food web as excluding terrestrial prey input, and as large an effect on riparian spiders as cutting off emergent insects using a mesh greenhouse.

Adding both the greenhouse and rainbow trout treatments together produced similar results to adding either alone (Fig. 3). In these reaches, there was a similar reduction of terrestrial prey in charr diets ($P = 0.01$ by LSD), and a subsequent foraging shift by charr to benthic stream insects (treatment, 0.95 ± 0.45 mg vs. controls, 0.16 ± 0.06 mg [mean ± 1 SE], $P < 0.01$ by LSD) causing reduction in stream herbivores (see significant main effects above), increased periphyton ($P = 0.003$), and decreased emergent insect biomass ($P = 0.0006$). Although we predicted that the effects of the rainbow trout invasion might be amplified by excluding terrestrial prey, we instead found that either treatment alone caused the food web components we measured to reach thresholds beyond which the added treatment elicited no further response.

Underwater observations of fish feeding and aggressive behavior showed that when rainbow trout were present, they dominated Dolly Varden and occupied favorable locations for foraging on invertebrates drifting on the surface or in the water column, which were

otherwise used by charr (D. J. Jordan and C. V. Baxter, *unpublished data*). For example, in the eight reaches with rainbow trout, Dolly Varden exhibited 49% fewer drift-foraging attempts than in those without rainbow trout. In addition, in the rainbow trout treatment, rainbow trout consumed more terrestrial invertebrates than did Dolly Varden (Fig. 3A; $P = 0.0006$ by LSD), though this difference was not as strong in the treatment with both the greenhouse cover and rainbow trout ($P = 0.08$). Previous studies demonstrated that rainbow trout forage selectively on terrestrial invertebrates (Nakano et al. 1999a) and that Dolly Varden can quickly shift to foraging on benthos when drifting prey are reduced (Fausch et al. 1997, Nakano et al. 1999b). Our study indicates that these differences in behavior have important food web implications.

DISCUSSION

These results are among the first experimental evidence that invasion of a nonnative species in one environment can have strong, unanticipated ecological consequences in an adjacent ecosystem (cf. Kennedy and Hobbie 2004). Cascading interactions have been reported following invasions in several field-observational studies (Spencer et al. 1991, Roemer et al. 2002). However, our reach-scale field experiment clearly demonstrated that a nonnative fish caused strong indirect effects that not only cascaded down to the base of the aquatic food web to increase stream algae (cf. Flecker and Townsend 1994), but also extended across the terrestrial-aquatic boundary via emerging insects to depress riparian spider abundance (Fig. 1). Trophic cascades have been shown to occur rapidly in aquatic systems (Carpenter et al. 1985, Power 1990), but the effects we found were especially striking in their speed and magnitude, occurring within only a 6-wk period. These results indicate that nonnative species can have pervasive impacts that propagate rapidly through as many as four trophic linkages, and extend beyond the habitat in which they were introduced. Such cross-system effects may be common, but difficult to anticipate without in-depth understanding of organism behavior and food web connections. Moreover, our results indicate that the effects of invasive species on linked food webs can be as strong as those caused by experimentally severing prey subsidies between them (Nakano et al. 1999b, Sabo and Power 2002).

We measured the effects of adding rainbow trout on Dolly Varden foraging, and cascading effects on the linked stream-forest food web, but more treatments would be needed to address the full complexity of invasion impacts. The additive design we used is recommended for measuring the effects of nonnative fishes (Fausch 1998, Peterson and Fausch 2003) because it mimics the initial stage of invasion when a species first arrives, and we used natural densities of both the native and invading species. However, in later stages rainbow trout may replace Dolly Varden to varying

degrees, so additional treatments holding density constant and manipulating species composition could be used to answer whether rainbow trout that replaced Dolly Varden had as large an effect as we measured. Nevertheless, our behavioral observations suggested that the foraging shift by Dolly Varden was driven by the presence of rainbow trout, not simply by higher fish densities. Overall, the behavioral and demographic effects of rainbow trout on Dolly Varden must be assessed over larger spatial and longer temporal scales to better understand the ultimate food web impacts of this invasion.

Invasion theory suggests that introduced species that fill unique ecological roles not present in recipient communities (e.g., nitrogen-fixing plants, filter-feeding animals) should have the largest impacts (Lodge 1993). However, our experiment showed that invasion by a fish that is closely related and functionally similar to native species can have strong ecosystem effects. Moreover, the mechanism that triggered the trophic cascade was not direct predation, as in most food webs, but instead an "interaction modification indirect effect" (Wootton 1994:445) whereby one predator alters the interaction of another with its prey (Sih et al. 1998). Thus, by simply modifying the foraging behavior of a native salmonid, nonnative rainbow trout caused a trophic cascade in the stream community that reduced emerging adult insects and, in turn, reduced the density of forest consumers. Although others have shown that interaction-modification indirect effects can drive trophic cascades in aquatic communities (Peacor and Werner 1997), our results demonstrate that such effects also can be transmitted to adjacent terrestrial ecosystems.

Finally, these findings emphasize that the structure and function of adjacent ecosystems can be driven by prey flux between them. Moreover, the effects of stream fish invasions on such resource subsidies may extend beyond riparian consumers such as spiders to influence the broader food web of the forest ecosystem. For example, other research at Tomakomai Experimental Forest showed that birds subsidized by emerging aquatic insects depress herbivorous insect abundance in the riparian forest, thereby reducing herbivory on plants in riparian vs. upland environments (Murakami and Nakano 2002). Consequently, human disturbances such as species introductions or habitat destruction that alter these reciprocal food web subsidies may change either or both systems. This connectivity deserves further exploration, and its implications should be integrated into policies governing the introduction of nonnative species and management of streams and forests, as well as other strongly linked ecosystems.

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