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Ecology of alien species with special reference to stream salmonids

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Because of their economical value, salmonid fishes have been transferred across national boundaries everywhere in the world. Here, we review the invasion patterns and mechanisms of successful invasions in stream-dwelling salmonids. The high invasion success of salmonids may partly result from extremely high propagule pressure (number of individuals introduced and number of introduction events). Interspecific interactions may also play a role, and the close ecological similarity among salmonids may result in niche overlap and interspecific aggressions. Often newly invading species take advantage of their species-specific core habitats, forcing other fishes to species-specific refugia where their fundamental niche requirements are met. This may result in disruption of the original distribution patterns of species along the headwater-to-mainstream continuum. Moreover, salmonid introductions may have wide-reaching impacts on the trophic organization of stream communities and, further, on terrestrial organisms such as insects, spiders, amphibians, reptiles, birds and mammals.

Introduction

Invasions by nonindigenous species are recognized as a major threat to global biodiversity, leading to species extinctions and worldwide homogenization of the biota (e.g., Rahel 2000, Olden 2006). Invaders can also alter fundamental ecological properties of the host ecosystems, such as species dominance, nutrient cycling, and productivity (Simon and Townsend 2003). For the next few decades, management and control of invasive species is indeed one of the biggest challenges conservation biologists will face (Allendorf and Lundquist 2003).

For tens of millions of years, species incapable of long-range dispersal have diverged evolutionarily behind geographical barriers, coming together only through, for example, continental movements. Such barriers no longer exist, because human-aided dispersal is overcoming the effects of geographical isolation. Ancient human migrations and trade led to an early spread of some domesticated species and their parasites. Growth of global commerce has provided scope for a corresponding increase in biotic invasions which is now up to 50 000 times higher than it was without human-aided movement of species (Crooks 2005).

Our purpose in this article is to (i) review the general mechanisms underlying successful invasions and, more specifically, to (ii) examine invasion patterns in stream-dwelling salmonid fishes, a commercially valuable group of freshwater fish that has been transferred from their original ranges to all major continents of the world.

Successful invasions: patterns and mechanisms

Ecological traits, diversity and propagule pressure

Hierro *et al*. (2004) reviewed seven potential mechanisms explaining invasion success: (1) release from natural enemies, (2) rapid genetic changes during invasion, (3) empty niches in the recipient system, (4) novel attributes or weapons possessed by the invader, (5) disturbance promoting invasion, (6) diverse systems keeping invaders out, and (7) high propagule pressure (i.e., number of individuals introduced and number of introduction events). Further, the invasional meltdown hypothesis suggests that the presence of one invader facilitates subsequent invasions, whereas the opposite view emphasizing biotic resistance states that communities become more resistant to additional invaders as these are added to the species pool (*see* Parker *et al*. 1999).

Many authors attempted to identify general characteristics shared by all successful invaders. For example, Lodge (1993) suggested that successful invaders are characterized by (1) r-selected traits, (2) high dispersal rate, (3) single-parent reproduction, (4) vegetative reproduction, (5) high genetic variability, (6) phenotypic plasticity, (7) large native range, and (8) human commensalisms. Correspondingly, invasible habitats are: (1) climatically similar to native habitats, (2) at an early successional phase, (3) disturbance-prone, (4) species-poor, and (5) lack predators. However, as all successful invaders are unlikely to share a common set of characters, it has been suggested that each trait must rather suit the specific conditions of the new environment as a key-to-lock mechanism, making invasions highly context-dependent (Lodge 1993, Heger and Trepl 2003).

Darwin already suggested that alien organisms closely related to native species are unlikely to become successful invaders, as they will be excluded by native competitors, predators and pathogens (‘naturalization hypotheses’ or ‘phylogenetic repulsion’). Indeed, it has been shown that native-like invaders often encounter more enemies that regulate their abundance in the new environment (Shea and Chesson 2002, Ricciardi and Atkinson 2004). For example, in Olden *et al*’s (2006) study, successful invaders had life-history and niche characteristics that differed from those of native species. Darwin also presented an opposing idea, however: owing to similarities in many ecologically important traits, native-like invaders are more likely to establish in the novel environment than are more distantly related invaders (‘phylogenetic attraction’) (e.g., Strauss *et al*. 2006). For example, a native-like invader may develop mutualistic interactions with local species (Richardson *et al*. 2000).

Some of the early authors (e.g., Elton 1958) argued that high species diversity begets community stability. Such diverse communities can resist invasions, while species-poor communities with numerous vacant niches could easily be entered by an invading species. However, evidence about successful invasions into species-rich communities, and about failed invasions into species-poor communities, has now accumulated, especially in freshwater fish communities (Moyle and Light 1996). Many studies show that species richness of the target community is not a key factor explaining invasion success because the very same processes that increase local species richness may also enhance colonization by alien species (Levine 2000, Levine *et al*. 2004). This often leads to a scale-dependent pattern, where the alien and native species are negatively related at small spatial scales, whereas at larger scales this relationship is positive (e.g., Pauchard and Shea 2006). Moreover, Moyle and Light (1996) suggested that successful invasions into simple systems are simply more conspicuous than those into more complex ones, thus biasing our conclusions. Therefore, as stated by Herbold and Moyle (1986), it is more likely that introduced species rearrange the community rather than enter an empty slot.

Lockwood *et al*. (2005) and Colautti (2005) offered a simple "null-model" explanation for the establishment of alien species: high propagule pressure. The great importance of propagule pressure has also been shown experimentally (Von Holle and Simberloff 2005) and through meta-analysis (Colautti *et al.* 2006). Colautti *et al.* (2006) pointed out that introduced species are a nonrandom sample of the global species pool, being affected by man and spreading vectors. Such active selection by man may challenge current paradigms of invasion biology and impair the prediction of high-risk invaders based on characteristics of the invaders or systems invaded. For example, Miller *et al.* (2002) showed that interpreting the big size of bivalves as an important ecological trait facilitating invasion success may be misleading, because intentionally introduced species are often selected for their large body size.

Disturbance and resistance

Many successful invasions have occurred in systems where some kind of human or natural disturbance has changed habitat conditions (Moyle and Light 1996, Kennard *et al.* 2005). For example, if the invader arrives at a time when resources are in short supply and competition is intense, this should hinder establishment, and conversely, establishment may be facilitated if unused resources are available (Davis 2003). Melbourne *et al.* (2007) concluded that biotic resistance should be strongest in homogenous, non-fluctuating environments. To be established in such systems, alien species must possess superior competitive abilities, resulting in hostile takeover. By contrast, in spatiotemporally variable environments, a more variable set of species is able to invade, because the fluctuating resource base creates constantly new niche opportunities (Shea and Chesson 2002, Melbourne *et al.* 2007). In such systems, the adverse effects of invaders should be weaker, with a higher potential for co-existence and low extinction risk. It has thus been argued that alien species are not a primary cause of biodiversity loss but mere passengers of (human-induced) environmental change (MacDougall and Turkington 2004, Didham *et al.* 2005).

Distinguishing the proximate and ultimate causes of invasion is challenging, owing to the numerous environmental correlates and multiple threats acting synergistically (Gurevitch and Padilla 2004, Didham *et al.* 2005). For example, Hierro *et al.* (2006) studied the effect of disturbance on the colonization success of annual plants in their native and nonnative ranges. They concluded that disturbance had a stronger effect in the nonnative range, suggesting that disturbance acts in concert with other factors; in their case, probably the simultaneous escape of invaders from native soil pathogens. Infrequent disturbances, however, pose another selective agent that favors native species with long-term adaptations to such rare events, whereas introduced species new to the environment cannot have such evolved adaptations. Therefore, invasion success of nonnative species may sometimes be only transient, and this is particularly so if they have insufficient storages through, for example, long-lived adults (Allendorf and Lundquist 2003).

Predicting invasions

Simberloff (2006) argued recently that the ability to predict invasions and its impacts on the native biota is the "Holy Grail" of invasion biology. For this purpose, Kolar and Lodge (2001, 2002) introduced a model based on transition stages: transportation, release, establishment and spread. At each stage, an invasive species must possess certain characteristics to succeed, and these characteristics may differ between stages. Williamson (1996) suggested the 1:10 rule: that is, about 10% of alien species manage from one stage to another and only about one percent of potential invaders get through the invasion chain (*see* also Williamson 2006). This categorical view has been challenged, however, as much higher establishment rates (up to 50%) have been observed in many organisms (García-Berthou *et al.* 2005, Jeschke and Strayer 2005). The transition-stage model considers invasion as a dynamic process, containing lag phases between stages (Heger and Trepl 2003, Crooks 2005). Difficulties in predicting invasion outcomes partly arise from such time lags. Early stages of invasions may be relatively invisible, but an alien species not detected as a nuisance earlier may suddenly show an unexpected boost (Crooks 2005).

Peterson and Vieglais (2001) suggested that projecting niche characteristics of a potential invader onto environmental characteristics of a target landscape could provide a means of predicting invasion success. However, species' niches are highly flexible and environmental conditions may differ profoundly between the recipient and native systems. Such variation produces error to predictions based on niche conservatism (native niche as absolute tolerance limit). For example, Fitzpatrick *et al.* (2007) found that nonnative fire ants first established in areas similar to their native environment, but then expanded into harsh environments not inhabited in their native range. The authors explained this by rapid evolution in the new environment, and by release from natural enemies and competitors, cautioning against uncritical use of niche models in predicting range expansions of alien species. Overall, the predictive ability of invasion biology seems rather limited thus far (Cadotte *et al.* 2006, Williamson 2006), mainly because of insufficient information about autecology of the invading species, target community and stage of invasion. Nevertheless, distinguishing a priori invaders likely to have a major impact is important for prioritizing management efforts (Copp *et al.* 2005), because prevention and eradication are likely to be effective only at the early stages of invasion (Crooks 2005).

Salmonid invasions in streams

Species introductions and impacts on native fish

Salmonid fishes are commercially valuable, which is the main reason for the extensive introduction of these originally holarctic fishes beyond their natural ranges. Salmonids are now present in, for example, South America, Africa, Australia, New Zealand and Japan, where they do not occur naturally. Fish species introductions have resulted in worldwide homogenization of the fish fauna (Rahel 2000, 2002) and it is therefore not surprising that brown trout (*Salmo trutta*) and rainbow trout (*Oncorhynchus mykiss*) are listed among the eight fish species included in the list of 100 of the world's worst invasive species (Lowe *et al.* 2000). Salmonid introductions are categorized into three types based on the origin of the fish used: inter-continental transfers, intracontinental transfers (stocking of native species within a continent but outside of their native ranges), and stock transfers (transfer of genetically differentiated stocks within the native ranges) (Krueger and May 1991).

The adverse effects of alien salmonids on native stream fish are of great concern. In North America, for example, the risk of alien salmonids replacing the native ones has lead to massive eradication efforts (e.g., Finlayson *et al.* 2005) and isolation management (Avenetti *et al.* 2006). The European brown trout and intra-continentally introduced rainbow trout have displaced the native brook trout (*Salvelinus fontinalis*) in many parts of the eastern North America, while brook trout and brown trout are similarly replacing native cutthroat trout subspecies (*Oncorhynchus clarki* sp.) and bull trout (*Salvelinus confluentus*) in western North American streams (Krueger and May 1991, Dunham *et al.* 2002). Recently, Atlantic salmon (*Salmo salar*) have been released in North American rivers draining to the Pacific Ocean. As a consequence, the native populations of several anadromous salmonids (*Oncorhynchus* sp.) are facing a risk of being detrimentally affected by the invader (Volpe *et al.* 2001). Reciprocally, Pacific salmonids have been transferred to Great Lakes where they hinder re-establishment of the native Atlantic salmon (Fausch 1998, Scott *et al.* 2005).

Conversely, brook trout and rainbow trout have been transferred from North America to European streams (Holčik 1991). However, the effects of these introductions on native fish fauna have been rather poorly documented, although risks are evident (Copp *et al.* 2005, Korsu *et al.* 2007). In Japan, North American rainbow trout is displacing the Japanese masu salmon (*Oncorhynchus masou*) (Taniguchi *et al.* 2002) and in New Zealand, European brown trout may have driven native grayling (*Prototroctes oxyrhynchus*) to extinction, and have fragmented the populations of native galaxiids by interference competition and predation (McDowall 2003, Townsend 2003). In South America, salmonids introduced into Lake Titicaca may have driven endemic fish species to extinction (Rodríguez 2001), and similar effects may also have occurred in Africa, but these cases are inadequately documented (Woodford and Impson 2004).

Explaining invasion success in salmonids: pre-adaptive niche segregation or hostile takeover?

Colautti (2005) showed convincingly that propagule pressure is often a key to the high establishment rate of salmonids in their new environments. Salmonid species chosen for introduction are a non-random sample of the global species pool, large-sized species with high economical value being typically preferred (propagule bias; Cambray 2003, Colautti 2005). The big size of introduced salmonids may be one of the main reasons for their high invasion success, as fish size is strongly related to social dominance (Nakano 1995, Young 2004).

Although stream-dwelling salmonids are relatively similar ecologically, some observations suggest that pre-adaptations of invaders to a certain position in the headwaters-to-mainstream continuum may help explain invasion success. For example, cutthroat trout, brook trout, brown trout, and rainbow trout are known to have dissimilar (but partially overlapping) distributions, with the two former species preferring high gradient, narrow channels and the latter two wider channels with lower gradient (Bozek and Hubert 1992). The novel species combinations following introductions have disrupted the original distribution patterns, as the alien species have located familiar conditions in the new environmental setting (De la Hoz Franco and Budy 2005, McHugh and Budy 2005). Thus, invasion success can sometimes be predicted simply by comparing the niche requirements of the invaders and natives and, subsequently, by screening for vacant niche space in the recipient system. Korsu *et al*. (2007) used this approach to explain the invasion success of North American brook trout in a North European watershed previously dominated by native brown trout. They were able to show that the pattern of coexistence among these two species is basically similar on both continents. In both areas, brook trout ultimately settles in small headwater streams, but the process of replacement differs profoundly: in northern Europe, brook trout replaces brown trout in headwater streams, whereas in North America, these same streams are the ultimate refuge area for brook trout under competition from the European invader (Rahel and Nibbelink 1999).

Alien species may not settle in the recipient system as key-to-lock, but they often must face some sort of niche adjustment after introduction. Thus, newly invading species primarily take advantage of their species-specific core habitats, forcing other species to those parts of river systems where their fundamental niche requirements are met (interactive niche segregation or “hostile takeover”). The role of aggressive behavior in explaining post-introduction niche adjustment in salmonids is often postulated because brown trout, for example, is a highly aggressive species having severe impacts on coexisting salmonids (DeWald and Wilzbach 1992). Aggression among stream salmonids is usually most intense during the first summer after hatching when they establish hierarchical and energetically optimal feeding positions in the current (Fausch 1984). Notably, the species that emerge earlier are free from interspecific competition until the competing species hatch. Rose (1986) showed that the growth of native brook trout during the first summer was normal, until it suddenly decreased after the emergence of the alien rainbow trout, due mainly to competition for feeding positions: more abundant and smaller rainbow trout alevins outcompeted bigger, but fewer brook trout. Importantly, these results indicate that demographic effects may, in some situations, overcome the often-cited “bigger size” advantage (Young 2004) in competitive interactions among salmonids.

Among adult stream salmonids, competition for spawning sites may have severe consequences: of two salmonid species with similar spawning habitat requirements, the earlier-spawning one faces a high risk of redd superimposition, and digging up and removal of eggs from the reddpocket, by the later-spawning species. For example, redd superimposition by the spring-spawning rainbow trout over the autumn-spawning brown trout leads to low egg survival in brown trout (Scott and Irvine 2000). Other reproductive interactions may be important as well. Sorensen *et al.* (1995) and Grant *et al.* (2002) reported interspecific spawning events in brown trout and brook trout reproducing in the same spawning ground. In such mixed-species spawning groups, heterospecific spawning can be frequent and lead to hybridization, competition for spawning places, or otherwise disturb species' reproductive outcome. Sexual interactions have indeed been evoked as a partial explanation for the replacement of native salmonids by alien fish in North America (Sorensen *et al.* 1995, Grant *et al.* 2002).

Moore *et al.* (1983) demonstrated the importance of competition in explaining the invasion success of rainbow trout by performing a large-scale population-level study, in which they removed alien salmonids from several streams. They noticed that native brook trout populations increased as a consequence, owing apparently to competitive release after the removal of rainbow trout. This notion, later highlighted by Fausch (1988), and Peterson and Fausch (2003), suggests that competition is the major cause of salmonid displacement. Competitive ability is, however, mediated by abiotic factors, such as temperature and water acidity, which in turn differ greatly along the river continuum (Taniguchi and Nakano 2000, De la Hoz Franco and Budy 2005, Kocovsky and Carline 2005). Thus, following interactive niche adjustment, salmonids with different niche optima are able to co-occur at the river-wide scale, but in different parts of the river system (*see* Korsu *et al.* 2007).

Vulnerability to invasions may be linked to habitat conditions, because streams are traditionally considered notoriously variable and disturbance-prone environments (e.g., flooding, drought, ice conditions) (Lake 2000). Successful invasions by alien fish have been often documented in systems where some kind of human-induced or natural disturbance has changed habitat conditions, creating niche opportunities for invaders (Moyle and Light 1996, Kennard *et al.* 2005). Conversely, environmental resistance in the form of flood-related disturbances can eliminate invaders because they often lack adaptations to the novel disturbance regime of the host ecosystem (Closs and Lake 1996, Leprieur *et al.* 2006). For example, high-flow events may flush developing eggs from gravel nests. Lacking well-developed adaptations to local disturbances, populations of introduced salmonids may easily collapse after an exceptional disturbance event (Strange *et al.* 1992, Fausch *et al.* 2001).

There have also been attempts to explain invasions through biological characteristics of successfully invaded salmonid species but this approach suffers from largely anecdotal observations and *a posteriori* argumentation. For example, invasion by brook trout of Rocky Mountain streams, where the native cutthroat trout has been largely displaced, was explained by several traits of the invader: (1) aggressiveness, (2) high predation capability, (3) size advantage, (4) disturbance-tolerance, (5) good visual ability in darkness (Dunham *et al.* 2002). Interestingly, the fact that brook trout has been displaced in large parts of its native range by brown trout was explained with the very same arguments (*see* DeWald and Wilzbach 1992, Waters 1983, 1999). This reasoning seems circular and underlines that listing adaptive characteristics *a posteriori* is highly problematic because invasion success of a given species is dependent not only on the biological traits of the invader, but also on the properties of the recipient system, which makes invasions highly context-dependent. For example, brook trout is considered as a headwater specialist within its native range, but when introduced to Rocky Mountains, it has not colonized the uppermost headwaters which serve as a refuge for the native cutthroat trout and bull trout displaced from downstream reaches (De la Hoz Franco and Budy 2005, Rieman *et al.* 2006).

Impacts beyond congeners: alien salmonids induce trophic cascades

Although indirect effects have been largely overlooked in invasion biology (White *et al.* 2006), this is clearly not the case in streams salmonids. There is a large body of evidence on harmful impacts by alien trout on native stream ecosystems. For example, alien trout (mainly brown trout, but also rainbow and brook trout) impact in New Zealand streams comes in two forms: direct individual or population level effects on native fish (galaxiids) and indirect effects through modification of trophic interactions. Recent community- and ecosystem-level studies documented highly complicated effects of exotic trout on stream ecosystems in New Zealand (*see* reviews by McDowall 2003, Townsend 2003).

Brown trout is a highly effective predator of invertebrate grazers in New Zealand streams, thus releasing periphytic algae from grazing pressure. This cascading trophic interaction causes up to six-fold higher algal biomasses in trout streams as compared with those in streams lacking trout (Townsend 2003). This is an example of a behaviorally-induced trophic cascade: in the presence of trout, grazers tend to be more cryptic, spending less time feeding on periphyton on stone tops. This behavior, connected with depressed invertebrate densities in trout streams, reduces food intake and growth rate of galaxiids. Thus, the interaction between galaxiids and introduced trout species in New Zealand streams appears to be multidimensional: (1) direct predatory effect, (2) competitive displacement, (3) and food limitation (McDowall 2003, Townsend 2003).

Food web effects of introduced salmonids may traverse ecosystem boundaries, potentially altering the trophic status and nutrient flux across the aquatic–riparian interface. Recently, Baxter *et al.* (2004) reported such an expanded trophic cascade in Japanese streams where the adjacent riparian community was affected by the alteration in proportions of aquatic and terrestrial prey consumed by a native charr under competition by rainbow trout. Similarly, Koel *et al.* (2005) and Crait and Ben-David (2006) found that introduction of the nonnative lake trout (*Salvelinus naymaycush*) depressed populations of native salmonids, ultimately reducing the activity of mammals (bears and otters) that previously consumed native fish species. This probably results in a trophic cascade, modifying mammal distributions as these are forced to seek alternative energy sources. All these findings contribute to an emerging view that salmonid introductions may have wide-reaching impacts on trophic organization of stream communities and, further, on terrestrial organisms such as insects, spriders, amphibians, reptiles, birds, and mammals (Knapp and Matthews 2000, Dunham *et al.* 2004, Vredenburg 2004, Ortubay *et al.* 2006).

The magnitude of the trophic effect caused by invasive organisms is affected by the isolation of the recipient system and naiveté of prey toward the novel predator. Cox and Lima (2006) suggested that species in oceanic islands and freshwater ecosystems are the most vulnerable ones to introduced predators, owing to the lack of evolutionary experience with several predator archetypes that disperse freely in continental terrestrial systems. The remarkable ecosystem effects of introduced trout in New Zealand may thus be explained by the isolation of the island and vulnerability of freshwater prey to novel predators. It is thus not surprising that Zimmerman and Vondracek (2007) found no effects of brown trout on benthic invertebrates in eastern North America, where ecologically similar native predators (brook trout) are abundant.

When the key ecological traits and niche requirements of introduced species are poorly known, invasions may often look entirely unpredictable (Lodge 1993). This is not the case in stream salmonids, however. While there are only few well-designed studies on the effects of introduced salmonids in streams (Peterson and Fausch 2003), these species have a long history of extensive scientific documentation of various aspects of their ecology. Having such a large body of ecological information should facilitate future efforts to understanding and predicting the potentially harmful impacts these species may have on local biodiversity.

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