Research Article

Specific Niche Characteristics Facilitate the Invasion of an Alien Fish Invader in Boreal Streams

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We studied the ecological niche relations of native stream fish and an alien invader, brook trout (*Salvelinus fontinalis*), to examine if brook trout had located an underused environmental niche in our boreal study system. In both study years (1994 versus 2004), we found brook trout to have the most marginal niche position of all the fish species examined. The most important environmental variable affecting the distribution of brook trout was pH, with acid headwater sites being dominated by this species. Brown trout, in contrast, had relatively nonmarginal niche, occurring in average conditions across the sampled sites. Other fish species had niche positions between the two salmonids. Our results show that fish invasions may be strongly facilitated by the presence of suboptimally occupied environmental niche space in the recipient river system.

1. Introduction

Introductions of species beyond their native ranges have been increasing throughout the world, and a plethora of separately evolved species now cooccur and interact in local communities. These interactions have often resulted in harmful effects on native species and, therefore, regional conservation efforts should include an effective management plan to restrict the invasion of alien species and control their potentially detrimental effects on native biodiversity. However, this is complicated by the fact that, in many cases, alien species may fail to establish viable populations in their novel environments [1]. Such variability in the ecological success of alien species highlights the unpredictability of invasion outcomes. Thus, there is clearly a need to clarify the roles of various factors influencing the invasion process and the subsequent success of alien organisms [2, 3]. Numerous hypotheses have been coined to account for the invasion success [4], some of which are related to species' niche characteristics. For example, it has been suggested that by comparing the niches of the alien and native species, and by projecting niche requirements of the invader in its region of origin to the recipient environment, one could predict the dynamics of invasions [3, 5].

Ecological communities vulnerable to invasions often have low species richness [6, 7]. This hypothesis has been questioned, however, because invaders frequently occur in species-rich communities [8–11]. Therefore, it may be that some of the habitat and food resources in recipient ecosystems are used suboptimally by the native species, providing opportunities for alien species to invade, if environmental conditions are suitable for the invader. This opportunity has been termed as alien species possessing "keys that fit the ecological locks of recipient communities" [12].

Invasion may also lead to interactions between native and alien species that compete for shared resources. If there are no ecologically similar species present, native species can exploit the environment extensively, thus being ecologically released. Conversely, after the introduction of an ecologically similar alien species, the niche space of the native species should narrow [13]. The ability of species to adjust their niches during the invasion process is one possibility for the native and invasive species to coexist in the long term [14].
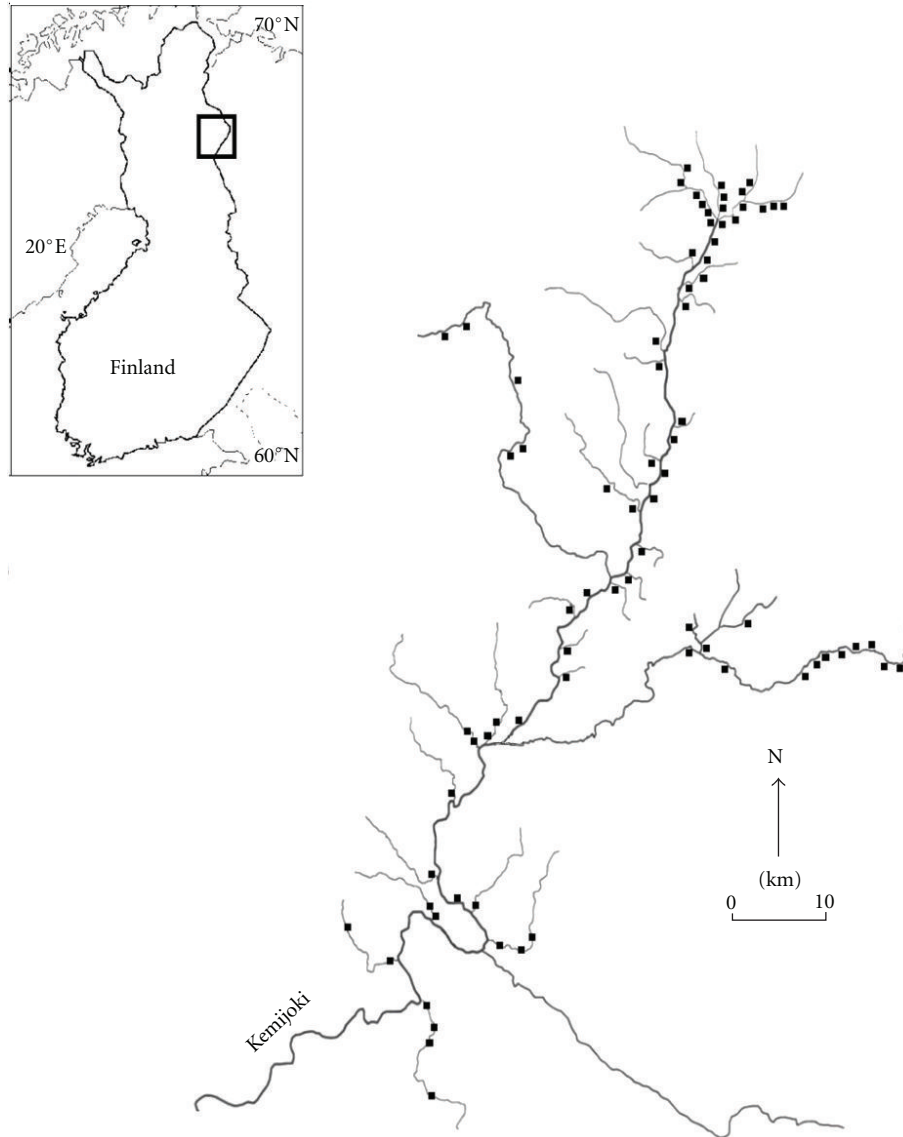
Figure 1: The study area in the upper river Kemijoki drainage basin in northeastern Finland. Black squares indicate sampling sites ($N = 78$) for both years (1994 and 2004).

We examined the environmental niche characteristics of native and introduced fish species during the invasion process in a boreal drainage system in northern Finland. Brook trout (*Salvelinus fontinalis,* Mitchill) originating from North America was first introduced to our study system more than three decades ago. These streams support populations of seven native species, including brown trout (*Salmo trutta* L.), our focal native species. Brook trout and brown trout are in many respects closely similar ecologically. However, brook trout is considered a headwater specialist that tolerates cold, acidic, and hydrologically variable environments. By contrast, brown trout is typically more common in larger streams, although it can also be found in headwaters [15–18]. If the niche-based approach to explain invasion outcome is correct, we should see the alien brook trout to colonize primarily headwater streams, where its niche characteristics are best met. Further, we examined temporal changes in niche positions and niche breadths that might result from species-specific responses to the abiotic environment, or from increased competition. We hypothesized that the low fish species richness, low biotic resistance, and the absence of headwater specialists in our study system should favour the establishment of the alien brook trout that should, in turn, occur in the habitat conditions matching its optimal niche characteristics.

2. Methods

2.1. Study System. The study area comprised the upper parts of the River Kemijoki basin, the largest river system in Finland (Figure 1). The scarcity of lakes in the drainage basin results in high snowmelt-induced floods in May. The

TABLE 1: Habitat characteristics of the sampling sites ($n = 78$).

Variable	Mean	Min	Max
Width (m)	13	2	60
Depth (cm)	35	11	66
Velocity (cm/s)	41	13	68
Substratum particle size*	4.5	0	7.4
Canopy shading (%)	11	0	56
Aquatic vegetation cover (%)	53	6	100
Conductivity (μS/cm)	51	18	290
pH	6.7	4.9	7.2

*Wenthworth scale: (0) <0.07 mm; (1) 0.07–2 mm; (2) 2.1–8 mm; (3) 8.1–16 mm; (4) 16.1–32 mm; (5) 32.1–64 mm; (6) 64.1–128 mm; (7) 128.1–256 mm; (8) >256.1 mm.

main stream channel is oligotrophic to mesotrophic (total phosphorous: mean across 1973–2004: 15 μg L^{-1}, range 2–57 μg L^{-1}) and circumneutral (mean pH 6.9, range 6.0–7.8; Regional Environmental Centre of Lapland, Finland). Smaller tributaries tend to be more acidic, with minimum pH below 5. The study sites are mainly low-gradient streams (mean slope: 0.7 m km^{-1}) with slowly flowing pool sections, interrupted by short riffle and run sections. Study sites were scattered across the upper River Kemijoki drainage basin, including various kinds of stream habitats from wide, open channels to narrow, and highly shaded headwater streams (see Table 1). There are no barriers for fish movement in this unregulated river that has no major waterfalls.

More than 1.5 million (mainly age 0+) brook trout were introduced to the middle and southern parts of the study area between 1972 and 1978 (Finnish Game and Fisheries Research Institute, Finland). The stocking of brook trout ceased in 1983, and the only fish stocked since then has been the native brown trout (annual mean of 14 000 individuals, age 1–5 years).

2.2. Sampling Protocol. The first electrofishing survey after brook trout introductions was conducted by the Finnish Game and Fisheries Research Institute in 1993 and 1994 (hereafter referred to as the 1994 survey) at autumn base-flow conditions [19]. In this survey, 78 sites in 34 streams were sampled and were included in the analysis, although some of the streams did not support either brown trout or brook trout. In 2004, the same sites were revisited, and fish were collected using the same methods as in the earlier survey [20]. The mean area electrofished at each site was 264 m^2 (range 51–1032 m^2). Densities of fish were estimated by the removal method (see [21]). All captured fish were measured and then returned to the stream. The fish were aged based on scale samples and length-frequency histograms. All fish were identified to the species level. A large majority of bullheads were *Cottus gobio* L., but also some *Cottus poecilopus* Heckel were identified in 2004. The latter species comprised a maximum of 5% of bullhead densities in our study streams, but could not be analysed separately due to the absence of species-level identification in 1994.

In 2004, we measured several habitat variables at each study site after fish sampling. Measurements were made along randomly placed cross-sectional transects covering the whole study section. The number of measurements for each variable varied between 18 and 25, depending on stream width and area sampled. At each measurement point, we recorded % cover of in-stream vegetation, % canopy shading, dominant substrate size (Wenthworth scale, see Table 1), current velocity (at 0.6 × depth; Schiltknecht MiniAir 20), depth, and width. We also measured pH and conductivity (μS cm^{-1}) at each stream, using a portable recorder (WTW pH/cond 340i). We assume that the habitat structure of our sampling sites remained stable between the sampling years, because no clear-cut logging or other extensive land use practices were conducted in the area between 1994 and 2004 (T. Rautiainen, Regional Environmental Centre of Lapland, Finland; personal communication). Had there been some climate-induced changes in stream characteristics (e.g., current velocity and depth), they should have affected the streams in a similar way, thus leaving the relative site-to-site habitat differences unmodified. Furthermore, the environmental measurements and fish sampling in 2004 were done at similar discharge levels as fish sampling in 1994.

2.3. Data Analysis. Niche position and niche breadth for each species were determined via OMI (outlying mean index) analysis [22]. This method measures the marginality of species habitat distribution, that is, the distance between the mean habitat conditions used by a species and the mean habitat conditions across the study area. The position of a species depends on its deviation from the distribution of a hypothetical species that tolerates "average" habitat conditions and is uniformly distributed across all habitat conditions. This index (OMI) thus measures the *niche position* of each species, and species that get high values of OMI have marginal niches, and those that get low values have nonmarginal niches. An additional variance term provided by this method is called species tolerance (T1) that measures the amplitude in the distribution of each species along environmental gradients, that is, *niche breadth*. Species that have high values of tolerance occur across widely varying environmental conditions (generalists; broad habitat niches), and those that get low values occur only across a limited range of conditions (specialists; narrow habitat niches). This method has been found to perform well in describing both unimodal and linear responses of species to environmental gradients [22], and it was successfully applied in studies on the distribution-abundance relationship of riverine fishes [23] and stream insects [24]. We calculated niche position (OMI) and niche breadth (T1) for each fish species (density data) in both 1994 and 2004 using the OMI analysis in ADE-4 [25, 26]. There were 13 explanatory variables in the analysis, five of which were coefficients of variation of the original variables (Table 1). We used permutation test (1000 permutations) to examine the null hypothesis that a species' OMI value is not different from that expected by chance.

Furthermore, we examined the habitat occurrence (presence-absence) of the two main focal species, brown trout and brook trout, using logistic regression with forward selection

TABLE 2: The number of sites occupied by the native species and the alien brook trout (*Salvelinus fontinalis*). Total number of sites was 78 in both years.

Species	Number of sites (1994)	Number of sites (2004)	Difference
Salmo trutta 1+	56	64	8
Salmo trutta 0+	32	23	−9
Salvelinus fontinalis 1+	21	28	7
Salvelinus fontinalis 0+	15	27	12
Lampetra planeri	32	22	−10
Phoxinus phoxinus	37	54	17
Lota lota	32	7	−25
Cottus gobio	69	70	1
Thymallus thymallus	8	12	4
Pungitius pungitius	16	20	4

of explanatory variables. Separate analyses were performed for 0+ and 1+ fish of both species. We also used logistic regression to analyse the habitat occurrence of bullhead, because its significant result in the OMI analysis in both years suggested specific responses to environmental conditions and because it was common in the study area.

Finally, to examine more directly variation in the density of brook trout, we used Spearman's rank correlation and multivariate analysis of variance (MANOVA). Correlations were used to test for a significant (negative) relationship between the densities of brook trout and brown trout in two groups of streams: (1) small (≤ 7 m wide; $n = 32$) and (2) large (> 7 m; $n = 46$) streams. One outlier in 1994 and two in 2004 were omitted from the correlation analysis due to exceptionally high densities of both focal species at these sites. However, we show correlations with both all sites included and the outlying sites excluded. MANOVA was used to test for the overall environmental differences between sites occupied versus not occupied by brook trout. All analyses were done separately for the 1994 and 2004 data. Analyses were conducted using SPSS for windows version 11.5 (SPSS Inc., 2002).

3. Results

Brown trout was the only native trout species in the study area, comprising 18% and 15% of the total fish density in 1994 and 2004, respectively. Other common native species were the two species of bullhead (47% in 1994 versus 50% in 2004) and European minnow (*Phoxinus phoxinus* L., 18% versus 20%). Brook lamprey (*Lampetra planeri* Bloch), burbot (*Lota lota* L.), nine-spined stickleback (*Pungitius pungitius* L.), and European grayling (*Thymallus thymallus* L.) occurred in low densities and less frequently (Table 2). The alien brook trout has established naturally reproducing populations, constituting 12% and 15% of the total fish density in 1994 and 2004, respectively. Fish species' distributions were not stable over time. For example, brook trout extended its distribution, while burbot showed the opposite

trend (Table 2). The mean number of fish species per study site was approximately three in both years (mean ± SE: 1994: 3.46 ± 0.14; 2004: 3.31 ± 0.14).

In 1994, brook trout 0+ had the most marginal niche position (high OMI value) of all fish species, followed closely by brook trout 1+ (Table 3). OMI values for both age classes of brook trout were significant. The most important environmental variable affecting the distribution of both 0+ and 1+ brook trout was pH, with a tendency for brook trout to occupy acid sites (Figure 2). Brown trout, in contrast, had a nonmarginal niche (low OMI value), occurring in average conditions across the sampled sites (Table 3). Niche breadths (T1 values) were relatively similar for brook trout and brown trout. Other fish species had, in general, niche positions (OMI values) between the two salmonids, while niche breadth varied from almost the same values with the two salmonids to a clearly higher one for European minnow (Table 3).

In 2004, brook trout 1+ had the most marginal niche position, followed by brook trout 0+ (Table 4). Similar to 1994, pH was again the most important variable related to the distribution of brook trout (Figure 3). OMI value for brook trout 1+ was significant. Brown trout had again less marginal niche position than brook trout. OMI value for brown trout 1+ was significantly different from that expected by chance. Brown trout 0+ had a broader niche than brook trout 0+, but brook trout 1+ had a slightly broader niche than brown trout 1+. Other fish species had generally less marginal niche positions than brook trout, but overlapped with the niche position of brown trout (Table 4). Niche breadth varied widely among the other fish species, being either lower or higher than those of brook trout and brown trout (Table 4).

Logistic regressions predicting the occurrence of brown trout and brook trout generally concurred with the results of OMI analysis (Tables 5 and 6; environmental and species vectors in Figures 2 and 3). Thus, in 1994, both brook trout 0+ and 1+ were significantly and negatively related to pH. Brown trout 0+ was positively and significantly related to CV of depth, while 1+ fish were positively related to CV of current velocity. Bullhead showed a positive response to pH and a negative one to canopy cover (Table 5). In 2004, brook trout 0+ and 1+ were again negatively related to pH, with 0+ fish being also positively related to current velocity. Brown trout 0+ were negatively related to macrophyte cover, while 1+ fish were positively related to substratum particle size. Bullhead was positively related to pH and depth (Table 6).

The densities of brook trout and brown trout were not significantly correlated in 1994, irrespective of whether the one outlying data point was included or not (all $r_s < 0.242$, $P > 0.100$). In 2004, however, brook trout and brown trout were negatively correlated in small streams, but only when the two outliers were excluded ($r_s = -0.365$, $P = 0.047$). When the outliers were included, the correlation was nonsignificant ($r_s = -0.134$, $P = 0.463$). The two species showed no correlation in larger streams ($r_s = -0.111$, $P = 0.464$). It was also apparent in a graphical comparison that brook trout had higher densities than brown trout in small acidic streams (Figures 4 and 1).

Table 3: Niche characteristics of the fish species in the 1994 survey. Brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) were divided into young-of-the-year (0+) and older fish (1+). Inertia: variability of species niche; OMI: outlying mean index or niche position; T1: species tolerance or niche breadth; and T2: residual tolerance. Percentages are from inertia for each species. Significances are from permutation test of the null hypothesis that a species' OMI value is not different from that expected by chance (1000 permutations).

Species	Inertia	OMI	T1	T2	OMI%	T1%	T2%	*P*
Salmo trutta 1+	12.47	0.44	1.37	10.66	3.5	11.0	85.5	0.075
Salmo trutta 0+	10.79	0.92	1.73	8.14	8.5	16.0	75.5	0.347
Salvelinus fontinalis 1+	18.57	4.88	0.67	13.30	26.3	3.6	70.1	**0.004**
Salvelinus fontinalis 0+	15.80	5.77	1.73	8.30	36.5	10.9	52.6	**0.012**
Lampetra planeri	10.00	0.71	1.21	8.10	7.1	12.0	80.9	0.808
Phoxinus phoxinus	12.99	1.73	3.72	7.55	13.3	28.6	58.1	**0.049**
Lota lota	10.68	1.66	2.54	6.47	15.6	23.8	60.6	0.518
Cottus gobio	12.12	0.61	1.49	10.03	5.0	12.3	82.7	**0.000**
Thymallus thymallus	10.86	1.49	2.05	7.32	13.8	18.9	67.4	0.833
Pungitius pungitius	14.51	1.67	2.05	10.79	11.5	14.1	74.3	0.402

Table 4: Niche characteristics of the fish species in the 2004 surveys. For other explanations, see Table 3.

| Species	Inertia	OMI	T1	T2	OMI%	T1%	T2%	*P*
Salmo trutta 1+	12.30	0.70	2.45	9.15	5.7	19.9	74.4	**0.020**
Salmo trutta 0+	17.32	2.23	4.44	10.64	12.9	25.7	61.4	0.377
Salvelinus fontinalis 1+	21.98	6.23	2.86	12.90	28.3	13.0	58.7	**0.001**
Salvelinus fontinalis 0+	15.66	4.04	1.49	10.12	25.8	9.6	64.7	0.097
Lampetra planeri	11.78	2.72	2.30	6.76	23.1	19.5	57.4	0.163
Phoxinus phoxinus	12.68	0.20	0.88	11.60	1.6	6.9	91.5	0.792
Lota lota	15.90	3.20	6.89	5.81	20.1	43.3	36.5	0.112
Cottus gobio	12.34	0.71	1.84	9.78	5.8	14.9	79.3	**0.006**
Thymallus thymallus	12.93	1.87	1.08	9.97	14.5	8.3	77.2	0.090
Pungitius pungitius	18.30	2.60	2.34	13.36	14.2	12.8	73.0	**0.005**
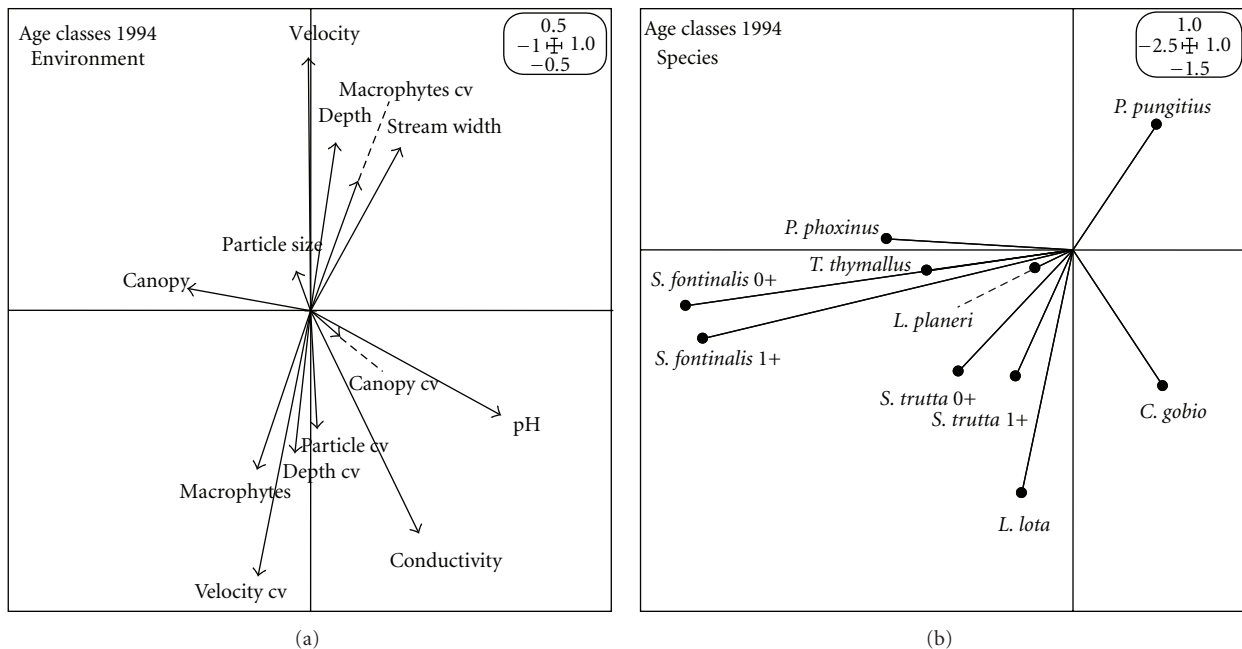
Figure 2: Environmental (a) and species (b) vectors on the first factorial plane of the OMI analysis. Analysis was based on the 1994 data, with the age classes of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) shown separately.
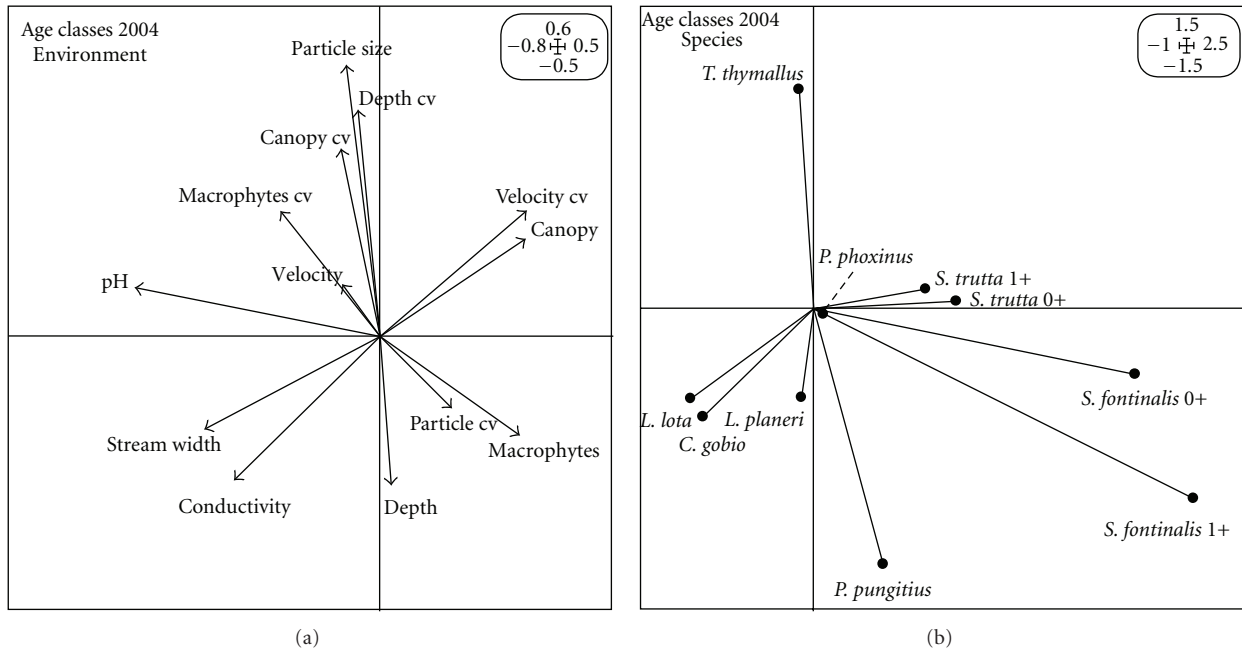
(a)

(b)

FIGURE 3: Environmental (a) and species (b) vectors on the first factorial plane of the OMI analysis. Analysis was based on the 2004 data, with the age classes of brown trout (*Salmo trutta*) and brook trout (*Salvelinus fontinalis*) shown separately.
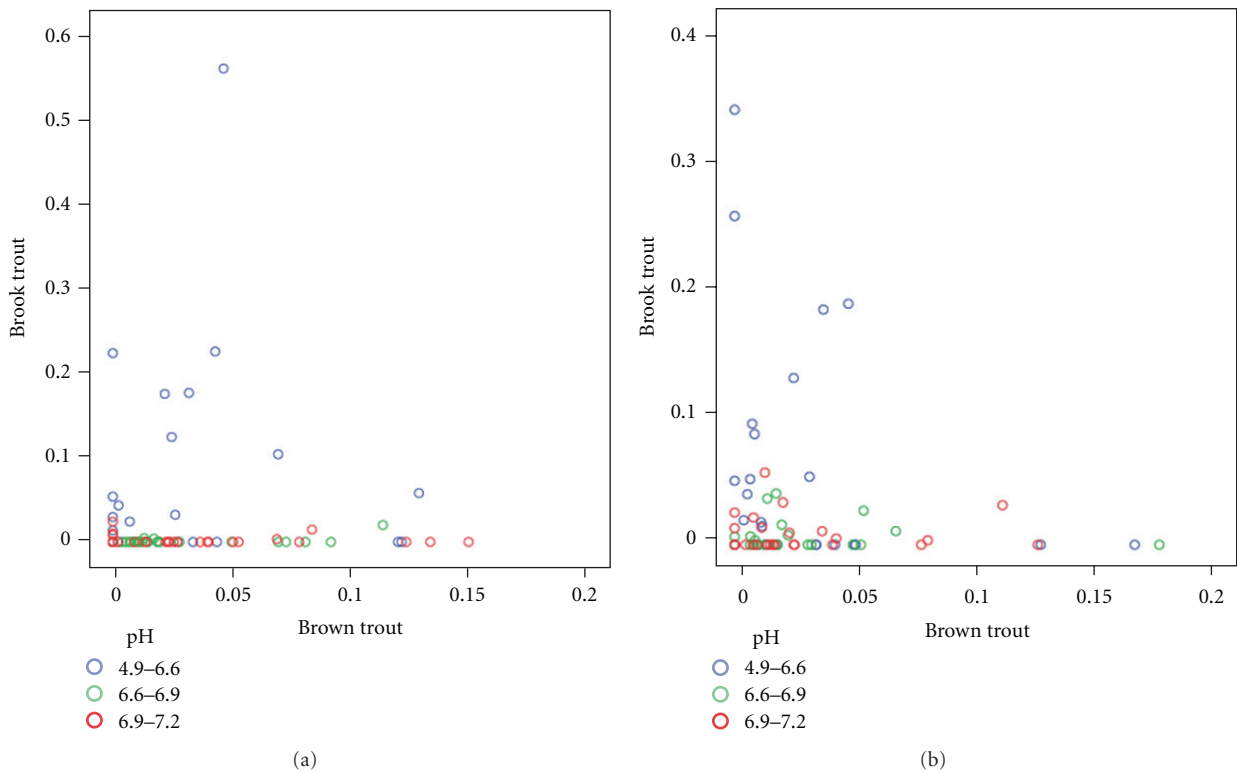

(a)

(b)

FIGURE 4: Scatter plots of the relationships between the densities of brook trout and brown trout across the study sites. Study sites are divided in three equal-sized groups of acidity classes. In 1994 (a), one outlier with high densities of both species was excluded. In 2004 (b), two outliers with high densities of both species were excluded.

Table 5: Results of logistic regression with forward selection for the occurrence of brown trout, brook trout, and bullhead in relation to environmental factors in 1994. Separate analyses were performed for 0+ and 1+ trout.

Variable	b	S.E.	Wald	P	Nagelkerke R^2
Brown trout 0+					0.117
Depth CV	7.402	2.987	6.141	0.013	
Constant	−3.409	1.270	7.209	0.007	
Brown trout 1+					0.267
Velocity CV	6.693	1.925	12.089	0.001	
Constant	−3.196	1.169	7.481	0.006	
Brook trout 0+					0.599
pH	−5.745	1.400	16.845	<0.001	
Constant	36.195	9.095	15.836	<0.001	
Brook trout 1+					0.461
pH	−4.431	1.104	16.101	<0.001	
Constant	28.377	7.315	15.048	<0.001	
Bullhead					0.441
pH	3.055	1.040	8.636	0.011	
Canopy cover	−0.082	0.032	6.557	0.003	
Constant	16.424	6.422	6.541	0.010	

Table 6: Results of logistic regression with forward selection for the occurrence of brown trout, brook trout, and bullhead in relation to environmental factors in 2004. Separate analyses were performed for 0+ and 1+ fish.

Variable	b	S.E.	Wald	P	Nagelkerke R^2
Brown trout 0+					0.082
Macrophytes	−0.029	0.014	4.283	0.039	
Constant	0.576	0.720	0.640	0.424	
Brown trout 1+					0.136
Particle size	0.556	0.226	6.043	0.014	
Constant	−0.774	0.926	0.699	0.403	
Brook trout 0+					0.219
pH	−1.802	0.676	7.100	0.008	
Velocity	3.260	1.586	4.223	0.040	
Constant	9.193	4.570	4.047	0.044	
Brook trout 1+					0.189
pH	−2.137	0.723	8.733	0.003	
Constant	13.688	4.838	8.006	0.005	
Bullhead					0.383
pH	2.994	1.092	7.513	0.006	
Depth	0.136	0.062	4.772	0.029	
Constant	−21.717	8.127	7.140	0.008	

MANOVA showed that streams with versus without brook trout differed significantly in environmental conditions in 1994 (Pillai's trace = 4.545, $P < 0.001$) but not in 2004 (Pillai's trace = 1.757, $P = 0.070$). In both years, however, some individual environmental variables exhibited significant differences. In 1994, pH ($P < 0.001$) and conductivity ($P = 0.001$) varied significantly between the two sets of streams, and the same was true for pH ($P = 0.001$) and stream width ($P = 0.004$) in 2004.

4. Discussion

Our results showed that the invasive brook trout had a highly marginal habitat niche position compared to all native fish species. This marginality persisted, although brook trout exhibited range expansion during the ten-year study period, showing that brook trout is a habitat specialist seeking for suitable habitats during the invasion process. The habitats of brook trout were best characterized by low-stream water pH, whereas the distribution of brown trout was related to in-stream habitat variables in both study years. Our findings thus suggest that brook trout had located suboptimally occupied habitat niche space in our study system, as evidenced by the highly differing niche positions and environmental relationships of all native species compared to those of brook trout. For example, based on a visual examination of the ordination plots, no native species occurred consistently in acid headwater streams that appeared to be highly suitable habitats for brook trout. Bullhead, for example, showed an opposite bias for large, nonacid streams.

Even though the range expansion of brook trout was directed towards the upmost headwaters, these do not represent a "vacant niche" for brook trout colonization, because brown trout was present, although in low numbers, in some of the headwater sites prior to brook trout invasion. In an experimental study, we showed previously that the field distributions of the two species reflect their differential habitat preferences rather than direct interspecific interactions, brook trout preferring slowly flowing pools, irrespective of the presence of brown trout [27]. Interestingly, the distributions of the two species in this study were significantly negatively correlated only in 2004, reflecting the expansion of the invasion frontier towards the headwaters during the ten intervening years (see also [20]). Sites occupied versus nonoccupied by brook trout differed in environmental conditions in 1994 but not in 2004, again suggesting that brook trout was moving towards the upmost headwaters during our study period. Even in 2004, however, many headwater sites that should provide suitable habitats for brook trout still remained unoccupied by the invader. It is probable that, given enough time, these sites will also be colonized by this headwater specialist, as there are no physical barriers to dispersal, and connectivity to source habitats is therefore unconstrained. Nevertheless, at least one North American study has shown that brook trout may not invade every accessible stream within a drainage basin, although the factors limiting their range expansion in some streams remain unknown [28]. In yet another study, distribution limits of another invasive salmonid, rainbow trout (*Oncorhynchus mykiss*), fluctuated upstream and downstream over the years [29]. Thus, only long-term monitoring will tell whether brook trout is indeed continuing its range expansion to invade the whole study

system, possible at a cost to the native salmonid, brown trout.

The most important variable explaining the distribution and niche characteristics of brook trout was water pH. In their native range, brook trout are known to prefer cold and variable headwater environments with low pH [16–18, 30]. Brook trout has established in similar species-specific habitats also in our northern Finnish study system, and similar observations have been made in Swedish streams [31]. Headwater streams are known to provide challenging conditions for fish reproduction and, although all salmonids are relatively sensitive to acidity, brook trout is more tolerant to low pH than is brown trout [32, 33]. These observations underline the importance of studying species niche characteristics to explain and predict the outcome of invasion processes ("niche matching"; [3]). This method has been previously used to explain the variable establishment success of alien stream salmonids at the global scale. For example, Fausch et al. [34] found that in areas where rainbow trout has established permanent populations, the flood disturbance regime matches that of its native range in western North America.

Brook trout has been introduced throughout the world, with serious consequences on native stream biota [20, 35–37]. For example, certain subspecies of the native cutthroat trout (*Oncorhynchus clarkii*) are on the brink of extinction due to the extensive spread of the alien brook trout in western North America [36, 37]. It should be possible, through niche matching, to predict the invasion success of brook trout, and thus to better assess the risks involved in introducing this species to various stream systems. However, there is often only limited information on the ecological characteristics of most species in their native range, and the fundamental niches of species can be much wider than the realized niches in their native environments [38]. Therefore, the use of niche matching always entails a certain degree of uncertainty. Yet, in the case of stream salmonids, species-level ecological information is typically available, making the prediction of invasion success through niche matching more feasible (see [20]).

High native species richness in a recipient community creates biotic resistance that may hinder establishment of the invasive species [6, 8, 39]. This classical idea has been questioned in recent ecological literature; however, because many communities with high native richness also harbour numerous invaders [8, 11]. In our study system, the average number of fish species per site was as low as three (total pool of seven native species), which could have facilitated the invasion of brook trout due to low biotic resistance. Northern European streams are species-poor compared to eastern North American streams, mirroring the legacy of the last ice age [40]. Thus, it is perhaps not surprising that streams in northern Europe lack a headwater specialist fish. This offers opportunities for alien invaders tolerant of headwater conditions, such as brook trout, to establish breeding populations. It seems likely that the invasion of brook trout in our study streams can be partly explained by the low native species number, combined with the species-specific niche characteristics of brook trout. Brook trout

exhibited habitat niche marginality undetected in any of the native species present. Our results are thus in line with the early findings underlining the importance of under-utilized niches and low native species richness in explaining invasion success ([6, 7], see also [41]).

The relative competitive abilities of species during an invasion process may also contribute to invasion success. Brown trout is known to be an effective competitor that often dominates over brook trout in streams [42–44]. However, competitive ability as such may be of little relevance if direct interactions are likely to be infrequent due to the kind of habitat niche segregation we observed between brown trout and brook trout. Competitive abilities should be important in only those stream areas, where these morphologically and ecologically relatively similar species occur sympatrically and are directly competing for limited resources, such as feeding positions and food. Agonistic interactions are known to affect the population dynamics of stream salmonids that are territorial drift feeders, holding hierarchical and energetically optimal feeding positions; such interactions are especially frequent amongst young fish [45–47]. Because competitive abilities are also mediated by abiotic forces, such as acidity, the acid-tolerant brook trout may dominate over brown trout in many parts of a drainage system [17, 20, 27, 48]. However, we believe that competitive interactions are clearly secondary to environmental niche segregation in affecting the distributions of brook trout and brown trout in our study system [27, 49].

The finding that brook trout is an efficient colonizer of headwater streams outside its native range suggests some practical considerations for the management of stream invaders. For example, land use practices that lower stream pH are likely to affect negatively brown trout populations [50], while brook trout may tolerate better such environmental changes. Natural and anthropogenic environmental disturbances are generally known to facilitate invasion success [14, 51, 52]. Small headwaters with naturally fluctuating environmental conditions [53] are often the first ones to face environmental disturbances that may, in turn, create niche space for alien invaders to colonize [54]. These sites may then act as stepping stones, facilitating the spread of alien species, with potentially serious consequences on native biodiversity.

Acknowledgments

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