

Should we further investigate the cascading effects of introduced fish on insectivorous birds?

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We investigated whether the introduction of fish (brown trout, *Salmo trutta*) in previously fishless boreal lakes could alter the aquatic insect subsidy and affect the nesting population of insectivorous migratory birds, with a particular focus on the pied flycatcher, *Ficedula hypoleuca*, which is the most represented species. According to our paleolimnological data and bioenergetic model, introduced trout increased the adult midge biomass output from 18.6 to 28.7 kg (+54.6%), which was energetically significant and could have theoretically supported an increase in insectivorous birds nesting around the lake. While the long-term series of insectivorous birds nesting around the lake seemed to increase according to the modeled fish effects, we could not establish a clear link with changes in food availability. Our control (pied flycatchers) showed similar patterns as our treatment, suggesting that this species' abundance was affected by factors other than fish presence in the lake. The demographic fluctuations and trends of the pied flycatcher at the regional scale seemed to override cascading effects linking introduced fish, emerging midges, and insectivorous birds. We conclude that further studies will be needed to investigate this topic and propose some areas for future research.

Introduction

Introduced species have been widely recognized as one of the most significant factors in ecosystem change and species decline (Leprieur *et al.* 2008, Milardi *et al.* 2018). Most research on this topic has been focused on the detrimental effects caused to the environment (e.g., Strayer 2010) or the biological communities (e.g., Hobbs and Huenneke 1992). However, species introduc-

tions can trigger a wide and complex spectrum of effects and may even occasionally produce beneficial effects on some native species (Rodriguez 2006).

Fish are one of the most commonly introduced taxa into aquatic ecosystems because stockings are routinely carried out as a means of managing fisheries (FAO 2016). It is well known that introduced fish can cause trophic cascades, inducing profound alterations of entire food

webs (Pace *et al.* 1999, Carpenter *et al.* 2001, Baxter *et al.* 2004, Knight *et al.* 2005). Several studies have extended this concept, focusing on the ability of fish to act as a link between the terrestrial and the aquatic domains by expanding or disrupting some of the least significant pathways of energy transfer from terrestrial to aquatic ecosystems (Likens and Bormann 1974, Nakano *et al.* 1999, Milardi *et al.* 2016c). Fewer studies have focused on estimating the magnitude of this effect, for instance on the global nutrient budget of lakes. As such, there remains a certain degree of uncertainty regarding its ecological relevance (Vanni and Layne 1997, Schindler *et al.* 2001, Milardi *et al.* 2016b). Even less studies have devoted efforts towards unraveling the reverse mechanism: the possibility that fish could alter biological energy fluxes from aquatic to terrestrial ecosystems (Baxter *et al.* 2004, Knight *et al.* 2005, Epanchin *et al.* 2010, Wesner 2010).

High-latitude habitats are an ideal setting to study these complex and indirect effects; they are located in areas of low anthropogenic impact and host simple food webs, thus presenting fewer confounding factors than low-latitude habitats. High-latitude lakes generally originate as fishless, but have become extensively stocked with non-native fish (Tammi *et al.* 2003, Miró and Ventura 2013). In boreal lakes, aquatic insect communities are largely dominated by the larval stages of midges (Chironomidae), which represent a substantial fraction of the diet of introduced fish (e.g., Skov *et al.* 2010). Hence, it can be expected that fish can cause significant reductions in the amount of midge larvae. On the other hand, studies have shown that fish presence can also positively affect midge larvae abundance, likely as a combined result of top-down control on their invertebrate predators and the increased availability of egested nutrients (see Goyke and Hershey 1992, Tiberti *et al.* 2014, Milardi *et al.* 2016d, Tiberti *et al.* 2016). By affecting the composition and abundance of aquatic invertebrates in the lake, it is possible that fish presence can influence the magnitude of aquatic subsidies to the terrestrial system (Eby *et al.* 2006, Finlay and Vredenburg 2007). These subsidies could be further influenced by fish predation on pupating larvae, which could reduce or even negate the effects of larvae abundance alterations.

The indirect cascading effects of fish introductions on terrestrial insectivores (e.g., invertebrate predators such as spiders, amphibians, water shrews and birds) that draw on adult aquatic insects as subsidies could be hard to detect (Finlay and Vredenburg 2007, Epanchin *et al.* 2010, Benjamin *et al.* 2011). For example, a series of biomanipulation studies carried out in the North American Sierra Nevada Mountains (e.g., Pope *et al.* 2009, Pope and Hannelly 2013) have underlined a decreased flux of aquatic insects to the terrestrial system, which was suggested in order to explain a decline in the presence of insectivorous birds around the lakes (Epanchin *et al.* 2010). However, other studies on the same series could not detect such a clear effect on frog populations (Joseph *et al.* 2011). While these studies provide an important contribution to our knowledge on this topic, it remains unclear whether the direction and magnitude of these effects is equally present in other lentic ecosystems.

In this study, we investigated whether fish introductions in remote lakes could alter Chironomid emergence from boreal lakes. Furthermore, we investigated whether the fish-induced changes in midge emergence would also affect insectivorous birds that eat adult midges. As a model ecosystem, we selected a lake in a strict nature reserve located in northeastern Lapland, Finland, where brown trout (*Salmo trutta*) have been stocked (in 1980) and subsequently removed (in 2012) in the absence of other anthropogenic disturbances. We used paleolimnological reconstructions and a bioenergetic model to infer the lake insect output under the presence/absence of fish. We then used this information to estimate the net change in aquatic subsidy available to terrestrial predators and compared it with the long-term series of insectivorous birds nesting in the nature reserve and nearby the lake. In particular, we focused on the pied flycatcher (*Ficedula hypoleuca*), as it is the only primarily insectivorous species in the area (Lundberg and Alatalo 2010); adult Diptera were found to be its second most abundant prey item (Sanz 1998). We hypothesized that the introduced trout would induce a change in the net Chironomid output (either decrease or increase), and that this change would either be: 1) energetically significant, with

a clear effect on consumer (i.e., bird) numbers, or 2) energetically not significant, without clear effects on consumer numbers.

Methods

Model ecosystem and study setup

Lake Kuutsjärvi (67°44′49.13″N, 29°36′35.47″E) is a small northern boreal headwater lake in northeastern Finnish Lapland (area = 0.7 ha; maximum depth = 8.5 m), 341 m above mean sea level. Water temperatures (measured at a depth of 2 m during 2009–2012) vary from 1.5 °C in January to 11.8 °C in July. The ice-free period typically lasts from late May to early October. The lake is mesotrophic (total phosphorus (TP): 13–26 µg l⁻¹; total nitrogen (TN): 67–152 µg l⁻¹) and clear (Secchi depth usually to the bottom). Due to the surrounding steep slopes, Lake Kuutsjärvi has a very limited littoral area (minimum depth ~2 m), which is typical of boreal lakes at higher elevations. The catchment area is small (< 1.5 km²), covered by a northern boreal coniferous forest dominated by Scots pine (*Pinus sylvestris* L.) and Norway spruce (*Picea abies* (L.) Karst.). The upper part of the catchment area is dominated by mountain birch (*Betula pubescens* var. *pumila* L.), dwarf birch (*Betula nana* L.), or treeless tundra. The lake was originally fishless due to the presence of downstream dispersal barriers (waterfalls, rocks and steep rapids). However, in 1980 it was stocked with adult brown trout (hereafter trout) from nearby populations (E. Pulliainen, pers. communication) to create local recreational fisheries. The trout quickly established a self-sustaining population. In 1981, the Värriö Natural Reserve was officially established (Hari *et al.* 1994), which is a strict natural reserve (under the national Nature Conservation Act and Wilderness Act) that does not allow human activities besides research and reindeer herding (<https://www.atm.helsinki.fi/varrio/eng/?q=node/3>). The reserve covers 125 km² roughly centered on Lake Kuutsjärvi and the nearby research station, where research activities on birds have been ongoing since 1969. In order to restore the natural state of the lake, trout were removed by

angling and gillnetting between 2010 and 2012; most fish were removed in August 2011 and have not been detected since. For more details on this removal, see Milardi *et al.* (2016b).

We used Lake Kuutsjärvi as a model ecosystem and took advantage of the introduction and removal of fish to set up a field experiment comparing midge emergence before and after fish stocking and removal, in order to model fish-induced changes to the adult midge output from the lake. At the same time, we used long-term data series on insectivorous bird abundances from 1) the treatment area (the area surrounding Lake Kuutsjärvi) and 2) two control series at different spatial scales (a mountain area 1 km from Lake Kuutsjärvi, Fig 1, and the entire northeastern Lapland region), in order to compare the response of birds with the introduction of fish in the treatment area to local and regional trends in untreated areas.

Three potential outcomes of how the trout introduction affected insectivorous bird nesting were considered (Fig. 2b, c and d) depending on aquatic invertebrate abundance and trout predation and considering different types of responses by the bird population. Compared with baseline conditions (Fig. 2a), fish presence could be either significantly increase (Fig. 2b) or decrease (Fig. 2d) the output of adult aquatic insects from the lake, thus inducing a corresponding change in birds nesting around the lake. However, a third outcome is also possible: that fish presence does not significantly change the adult aquatic insect output or this change does not influence the nesting bird population (Fig. 2c).

Modeling the adult insect output from the lake

In order to model the changes in adult midge output from the lake, we compared the dynamics of insect emergence during the presence and absence of fish. Three distinct time periods were identified: before trout introduction (before 1979), during trout residency (1980–2012), and after trout removal (2012–present).

Before trout introduction, the output of adult insects from the lake was likely constituted by a variety of taxa (e.g., Trichop-



Fig. 1. Polar map showing the boreal forest global distribution (in grey, left panel) and the location of the Värriö Natural Reserve in Finland (center panel, square at approximately 67°44'49.13" N, 29°36'35.47" E). The right panel shows the topography of the study area and the location of nest boxes around Lake Kuutsjärvi (star symbol) and Kotovaara Mountain (triangle symbol).

tera, Ephemeroptera), which were subsequently greatly reduced by trout predation (Milardi *et al.* 2016d). However, Chironomidae are by far the most abundant taxon among aquatic insect larvae in the area (see the fishless lake Tippakurulampi, reported in Milardi *et al.* 2016d) and the only taxa whose abundance can be reconstructed through paleolimnological analysis. Using a paleolimnological approach, Milardi *et al.* (2016d) estimated that the average midge larvae accumulation rate ($\text{ind} \times \text{cm}^{-2} \times \text{year}^{-1}$) in Lake Kuutsjärvi was 1.86 before trout introduction. Accumulation rates refer to an assembly of individual larval remains (head capsules) integrated over the span of a few years (Milardi *et al.* 2016d). We therefore derived a monthly accumulation ($\text{ind} \times \text{m}^{-2} \times \text{month}^{-1}$) as a measure of average midge larvae density in the lake at hatching time. We used average midge larval density to estimate the total number of larvae and their biomass in the entire lake at a specific time, given the lake bottom surface (estimated at 10 500 m²) and the average wet weight of an individual larva derived from literature (2.28 mg; Moore 1979). According to literature, midges at this latitude usually take at least two years before hatching (Moore 1979, Ward and Stanford 1982). For practical purposes, in the model, we assumed that since trout predation was absent and invertebrate predation not significant, all of these larvae could escape undis-

turbed from the lake and transform into adult insects prior to 1980.

After trout introduction, Milardi *et al.* (2016d) estimated that the average midge larvae accumulation rate ($\text{ind} \times \text{cm}^{-2} \times \text{year}^{-1}$) in Lake Kuutsjärvi was 3.9 (2.1 times higher than before), based on subfossil head capsules counts. This rate should already account for direct predation of trout on larvae (i.e., the total number of midge larvae head capsules in the sediment refer to the population that survived predation). We used similar assumptions for the period prior to the fish introduction to derive from this number an estimate of the biomass of hatching midge larvae in a given year. We assumed that the output of adult insects from the lake during trout residency was equal to the biomass of hatching midge larvae, minus the consumption of midge pupae during the period of emergence. Assuming that trout predation in June 2010 (first sampling of the population) would provide the best estimate for the consumption of midge pupae prior to biomanipulation, we used previously published midge pupae predation rates during emergence (84% of the trout diet; Milardi *et al.* (2016a)) to estimate the midge pupae consumption by trout using a temperature-dependent bioenergetic model for cool-water species (Thornton and Lessem 1978, Hanson *et al.* 1997). The model estimated consumption rates for each cohort in the brown trout population prior to

biomanipulation (in 2009), based on species-specific metabolic levels. The model used water temperatures (measured with a resident logger), diet proportions (derived from published stomach content analyses), energy/nutrient content for each prey item (from published literature) and average measured growth rates. A thorough description of the model and its references is provided in Milardi *et al.* (2016b).

After trout removal, we hypothesized that the situation would eventually revert to levels equivalent to the period prior to fish introduction (Fig. 2a), but with a lag time for the system to shift its balance. We therefore assumed that, in the period after trout removal (2012–2016) the presence of midge larvae in the lake would be 60% of that estimated during trout residency (i.e., slightly higher than baseline values) and that adult midge emergence would not be reduced by the trout predation.

To assess whether changes in the adult midge output from the lake would be ecologically significant, we also estimated the variation in biomass in terms of energy content. The caloric content of midge adults ranges from 19.1 to 25.3 kJ per gram of dry mass (where dry mass equals 9.5% of wet mass; Cummins and Wuycheck 1971, Wissing and Hasler 1971, De la Noüe and Choubert 1985). We then compared that estimate with bird energy requirements, to check whether the observed variations in our treatment series could be linked to changes in adult aquatic insect outputs. Female insectivorous passerine birds were reported to expend 60 kJ per day during incubation (Moreno and Sanz 1994) and 55 kJ per day during nestling care (Moreno *et al.* 2001).

Treatment and control of long-term bird series

Our treatment series consisted of a long-term record of bird nest boxes placed on the trees around Lake Kuutsjärvi, spanning over 40 years (1970–2016). We used this series to verify the response of insectivorous birds to the modeled variations of emerging midge subsidy. All Passeriformes nests were monitored routinely and consistently through time (the eight nest boxes

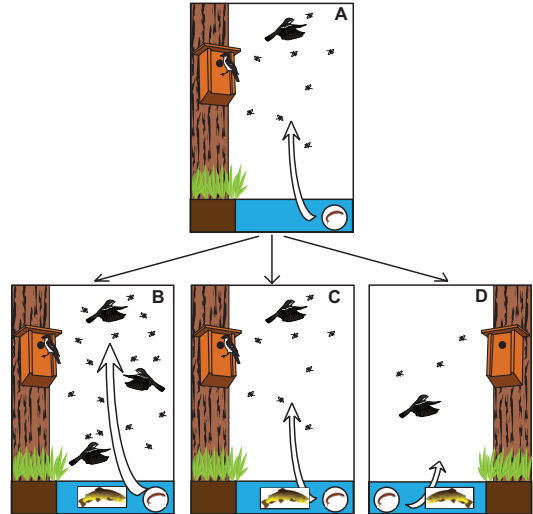


Fig. 2. A hypothetical model of the changes in the adult aquatic insect subsidy available to birds around a pristine fishless lake (a), with two opposing scenarios of effects related to fish introduction, depending on predation by introduced fish (b and c). Once the fish are removed, the system should eventually revert to the pristine state (a), albeit with a lag time. Edited from Milardi *et al.* (2015).

were checked 3–4 times per week during the nesting season); the nests of all species are readily noted and monitored. We focused on nesting numbers of migrating birds that are primarily insectivorous and that have low site-fidelity. Nest prospecting is a key process for these species to assess food availability, as low food resources can decrease reproductive success (Siikamäki 1998, Both *et al.* 2006, Burger *et al.* 2012). We focused on the pied flycatcher nesting numbers because this species is the most abundant primarily insectivorous bird in the area and was also recorded in our control series. Pied flycatchers have been observed preying on flying insects during their nesting phase around the lake (Milardi, pers. observation).

As a control for our treatment, we used two different long-term series of pied flycatchers: 1) a nest box series (from 1976–2016), located at the Kotovaara Mountain ca. 1 km from the lake, and close to a few fishless lakes, and 2) a regional estimate of the pied flycatcher population (from 1986–2016). The Kotovaara Mountain nest box series consists of a larger number of nest boxes (40 in total) and the monitoring methods were

the same as those used in the Lake Kuutsjärvi area. The regional (NE Finland) pied flycatcher population was monitored as a part of the Finnish Common Bird monitoring program (methodology described in Laaksonen and Lehikoinen 2013) between 1986 and 2016. Altogether, the data consisted of 151 line transects and point count routes situated between 65°47'–69°22'N and 25°54'–30°7'E. Among the 151 sites, on average, 21 sites were counted annually (from 8–49) and on average, 29 pied flycatcher pairs were seen annually (from 12–80). We calculated the annual pied flycatcher population abundance indices for the region using the TRIM (TRENds and Indices for Monitoring data; Pannekoek and van Strien (2005)) program. TRIM is a commonly used tool in bird monitoring in Europe that accounts for over-dispersion and serial correlation and interpolates missing observations using a Poisson general log-linear model (www.ebcc.info). TRIM produces annual abundance indices and their standard errors.

Air temperature trends and statistical analysis

It is well known that insect populations at high latitudes can fluctuate both over the years and through the summer months, following air temperature (Jepsen *et al.* 2008, Milardi *et al.* 2016a). To check for the possible impacts of air temperature trends, we calculated local average air temperatures during the bird residency season (mid-May–mid-August) from daily average temperatures measured at the Värriö Subarctic Research Station during the period from 1975–2010. Furthermore, to check for possible large-scale effects on the regional population and their insect subsidies, we also calculated regional average air temperatures over the same season (mid-May–mid-August) from daily average temperatures recorded at the Sodankylä climate station (~130 km west of the Nature Reserve) during the period from 1975–2010.

We used linear regressions to estimate the general trends of long-term local and regional temperature, as well as bird nesting numbers and regional population estimates. Linear regressions were also performed to test correlations

between temperatures and bird abundances. We also used the piecewise linear regression method in R software (Toms and Lesperance 2003, R Core Development Team 2017) to reveal turning points in both treatment and control series, without making assumptions about the expected change. Non-parametric tests (Mann-Whitney and Kolmogorov-Smirnov) were used to verify whether the mean and distribution, respectively, of nest numbers around Lake Kuutsjärvi would be significantly different before/after fish introduction (confronting nesting data in the baseline period, 1970–1980, with the trout residency period, 1981–2012), using PAST ver. 3.06 (Hammer *et al.* 2001). Non-parametric tests make no assumptions about the data distribution or shape and work better than parametric tests with smaller sample sizes.

Results

Changes in the adult insect output from the lake

Prior to the fish introduction, the estimated midge larvae density in Lake Kuutsjärvi was 1553 individuals m⁻² and the estimated total number of individuals was 16 310 000, with a biomass of 37.2 kg. According to our model, 8 155 000 individuals were hatching per year, with a total output of 18.6 kg of adult midges, all of which could escape from the lake.

During trout residency, the estimated total midge larvae density in Lake Kuutsjärvi was 3248 individuals m⁻² and the total modeled number of individuals was 34 107 500, with a biomass of 77.8 kg, half of which (38.9 kg) would be hatching per year. This time period was limited to a span of approximately 14 days each year, occurring between the end of May and the beginning of June (i.e., after the ice thaws). Overall, we estimated that the entire trout population consumed 10.1 kg of midge pupae during the two weeks of their emergence. Therefore, the net output of adult midges from the lake during trout residency equaled 28.7 kg. Although trout consumed a significant portion of the midge pupae, our model showed that the net output of adult midges from the lake in fact increased by

10.2 kg (+54.6%) after fish introduction, hence confirming the scenario in Fig. 2b.

After fish removal, we modeled a decrease in the output of adult insects from the lake to a level slightly higher (23.3 kg; +25.5%) than that at the baseline conditions prior to the trout introduction.

The modeled net output of adult midges from the lake was 969 g (dry biomass), corresponding to an energy transfer of 18 508–24 516 kJ. This energy could support a single insectivorous bird for 48–58 weeks, or four birds for 12–14.5 weeks.

Treatment response and control

On average, insectivorous birds around Lake Kuutsjärvi build their nest on day 152 of the year (± 10.12 days, standard deviation, corresponding to the last week of May to the first week of June). Therefore, the nesting period corresponded well with the period of adult midge emergence from the lake (i.e., around the end of May). A total of 132 nests were recorded in the treatment series, belonging to four species of insectivorous birds: the Siberian tit, *Poecile cinctus* (1 nest), the great tit, *Parus major* (4 nests), the common redstart, *Phoenicurus phoenicurus* (13 nests), and the pied flycatcher (114 nests) (Fig 3a). The treatment series showed a moderate overall rise in the number of nesting insectivorous birds around Lake Kuutsjärvi until around 2003, when the piecewise regression revealed a major turning point (95% CI 1987–2005, Fig. 3a). After this point, the local number of nests declined, reaching a minimum of approximately 50% lower than the original level. The mean and shape of the nesting number distributions around Lake Kuutsjärvi were significantly different before ($n = 11$) and after ($n = 36$) fish introduction (Mann-Whitney $p = 0.0061$; Kolmogorov-Smirnov $p = 0.0016$).

Pied flycatchers were the most common species in the treatment series and largely followed a similar trend and changes as the overall treatment series (Fig. 3b). On average, two more pied flycatcher nests were recorded after fish introduction (i.e., an average of four more pied flycatcher individuals nesting around the lake after 1980, Fig. 3b).

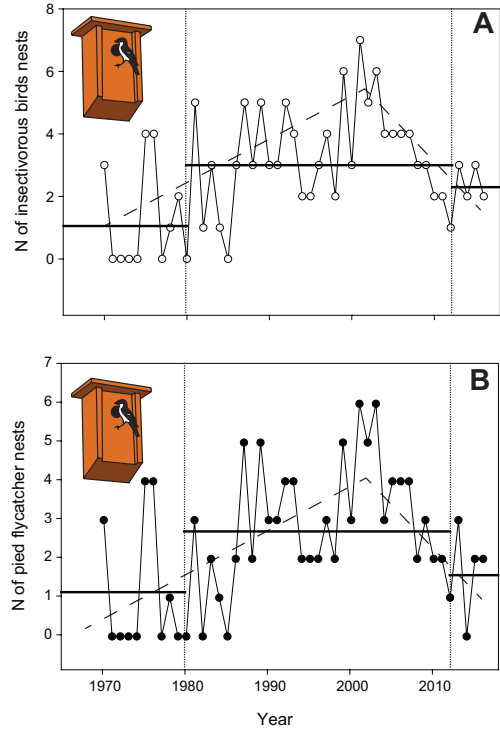


Fig. 3. Long-term trends in our treatment series of insectivorous birds nesting around Lake Kuutsjärvi (a, white circles), and pied flycatcher nest counts (b, black circles). Dashed broken lines represent the result of piecewise regressions. Vertical dashed lines indicate the dates of fish introduction (in 1980) and removal (in 2012). Solid black horizontal lines mark the average number of nests in the different periods.

The control series around Kotovaara Mountain recorded a total of 505 pied flycatcher nests and showed a similar trend as the treatment series, with increasing nest numbers until 2001 (95% CI 1990–2003, Fig. 4a) and a subsequent decline thereafter. The estimated regional pied flycatcher population index was fairly stable until around 2005 (95% CI 1996–2011, Fig. 4b), after which it declined.

Local average summer temperatures had a slight positive trend over the period of 1975–2010 ($n = 36$, slope 0.0365, $p = 0.023$, Fig. 5a). Regional average summer temperatures also had a slight positive trend over the period of 1975–2010 ($n = 36$, slope 0.052, $p < 0.0001$, Fig. 5b), closely mirroring the local conditions. The local temperature trend was not significantly correlated with the treatment series ($n = 36$, $R^2 = 0.14$, $p = 0.42$), with the pied flycatch-

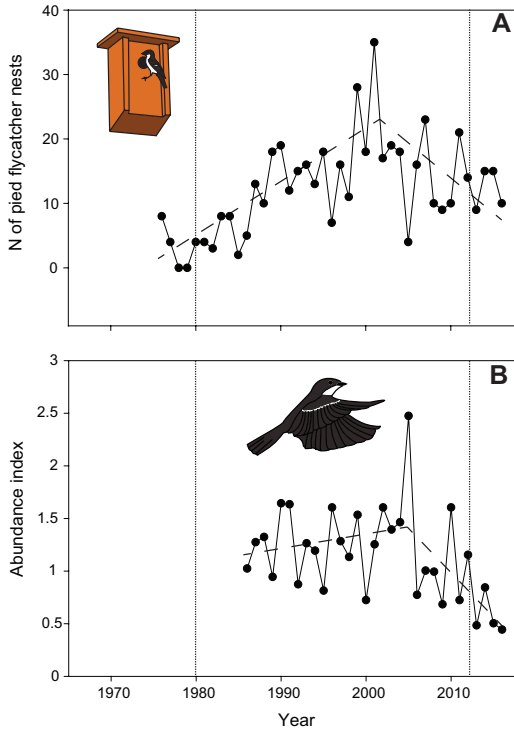


Fig. 4. Long-term control series of pied flycatcher nest numbers in Kotovaara Mountain (a) and their regional abundance index (b). Dashed broken lines represent the results of piecewise regressions. Vertical dashed lines indicate the dates of trout introduction (in 1980) and removal (in 2012) in Lake Kuutsjärvi, for reference.

ers in the treatment series ($n = 36$, $R^2 = 0.16$, $p = 0.34$), or with the Kotovaara Mountain control series ($n = 36$, $R^2 = 0.239$, $p = 0.17$). The regional temperature trend was not significantly correlated with the regional pied flycatcher control series ($n = 36$, $R^2 = 0.03$, $p = 0.35$).

Discussion

According to our model, the presence of introduced trout increased the output of adult midges from the lake, despite their predation on midge larvae. The increased availability of adult midge resources around the lake was energetically significant and could have theoretically supported an increase in the number of insectivorous birds. While the number of insectivorous birds nesting around the lake seemed to respond to the fish introduction and removal events, a direct link

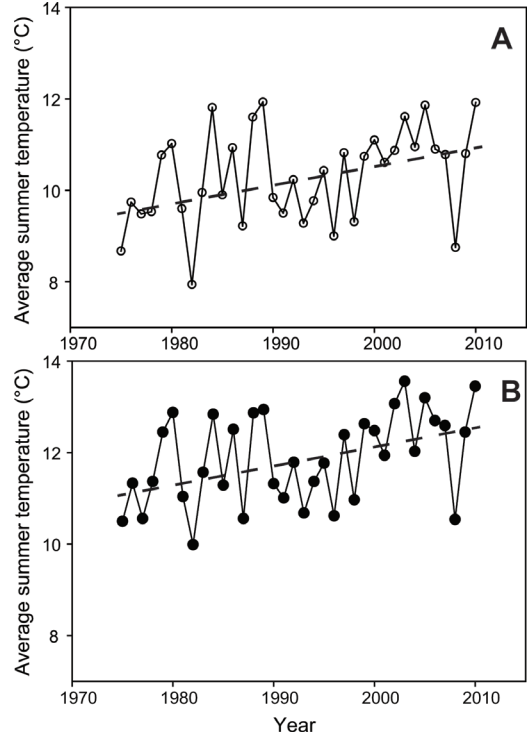


Fig. 5. Long-term trends in average summer temperatures during the migratory birds' residency season (mid-May–mid-August) recorded at the local (a) and regional (b) levels. Dashed lines represent the slopes of regression lines..

with the increased availability of food resources could not be established. Our control series focusing on pied flycatchers showed patterns of increase and decrease similar to those seen in our treatment series, suggesting that bird abundance was affected by factors other than fish presence in the lake. Temperature patterns over the last 35 years were similar at both local and regional levels, but were poorly correlated with bird abundances. Our results ultimately suggest that the influence of fish introductions on birds living near remote northern lakes could be less straightforward than previously reported. They also suggest that large-scale patterns of bird abundance might be more relevant than fish presence or food availability in shaping local patterns.

Fish that rely heavily on terrestrial prey can potentially increase the input of terrestrial carbon to a lake by feeding on terrestrial organisms (Mehner *et al.* 2005, Wurtsbaugh 2007, Milardi *et al.* 2016c, Rolla *et al.* 2017), although

this was shown to be not sufficient enough to tip the nutrient budget of Lake Kuutsjärvi (Milardi *et al.* 2016b). However, fluctuations in total primary production have been previously directly linked with differences in midge outputs (Welch *et al.* 1988). Therefore, a small increase in nutrients could significantly benefit some benthic organisms, such as diatoms or midges, even when pelagic primary production is not overly affected. Furthermore, trout-mediated nutrient transport from the pelagic or littoral areas to the benthic zones could affect benthic organisms without altering total primary production (Milardi *et al.* 2016b). This could be further emphasized by the very limited littoral zone of Lake Kuutsjärvi, which greatly reduces the importance of littoral aquatic insects (e.g., Odonata or Trichoptera) and emphasizes that of pelagic/profundal ones, such as midges. Our model results show that trout presence can increase the net output of midges to the terrestrial environment, despite the fact that trout consume a part of this increased flux (as observed by Tiberti *et al.* 2016). The increase in net output of emerging insects is a result opposite to what has been previously reported as the outcome of fish introductions (Epanchin *et al.* 2010, Joseph *et al.* 2011), perhaps because of the regional differences in dominant aquatic insect taxa. Moreover, this increase could have been significant enough to support an increase in nesting insectivorous birds around Lake Kuutsjärvi.

Indeed, emerging midges constitute one of the most important aquatic insect resources in the northern regions (Danks and Oliver 1972) and can support the life cycle of many terrestrial organisms that feed on insects. Terrestrial species are particularly adapted to exploit pulsed resources, with consumer organisms tuning their life cycles to respond to such pulses (Ostfeld and Keesing 2000). The timing and magnitude of this pulsed, seasonal resource can be one of the main factors affecting its final utilization by consumer species. However, the indirect effects and long-term implications of these subsidies remain uncertain (Nowlin *et al.* 2008, Bartels *et al.* 2012). As the timing of midge emergence is affected mainly by air temperature (Moore 1979), an interaction between trout-induced changes and long-term air temperature trends

is likely. However, the climate warming trend is unlikely to have shifted midge emergence during the study period, as the ice breakup time has not significantly changed in Lake Kuutsjärvi between 1992–2012 (always between the last week of May and the first week of June; Värriö Subarctic Research Station, unpublished data). Nevertheless, our results suggest that the magnitude of this pulsed subsidy to the terrestrial environment could have been significantly affected by the introduced trout population.

Our model results rely not only on the well-known bioenergetics of trout, but also on the biology of midges, which is rather complex and relatively less studied. For example, the duration of midge emergence is highly variable and was not directly recorded during this study. Based on the literature, the timing and duration of emergence can fluctuate even within a spatially limited area (Danks and Oliver 1972), thus presenting a challenge for specifically-aimed sampling. Due to the difficulties in quantitatively sampling benthic invertebrates in a lake, where little fine-grained substrate is present but internally coherent, our model of midge output relied on reconstructed abundances of Chironomidae. However, one of its shortcomings was the fact that it was impossible to model a full time series of midge emergence with the same annual resolution as the bird nesting time series, which could have been used to perform correlation analyses. Specifically, it was impossible to continuously estimate a sensible midge output because paleo strata carried an intrinsic dating error and because we could not reconstruct the fish population structure for the whole time series. However, it is also possible that other aquatic insects have recolonized the lake after trout removal, thus dampening the modeled change in adult insect output and confounding the effects of biomanipulation. Future studies that apply mechanical traps to capture emerging Diptera and sediment grabs to estimate larval densities could improve our model, but would still face the challenge of linking present and past abundances. This challenge could potentially be surpassed by using biomanipulation as a tool for reconstructing the situation prior to the fish introduction.

While our model provided clear results on the fish-induced shifts in midge output, these

were only apparently linked to the number of insectivorous birds nesting around the lake. Overall, our treatment series seemed to shift according to our model predictions, increasing with the increased resource availability, independent of climate trends. However, a comparison with our control series revealed that the pied flycatcher population (i.e., the most abundant insectivorous birds nesting in the area) fluctuated similarly at all spatial scales, suggesting that the patterns observed around Lake Kuutsjärvi could be the result of larger population dynamics (e.g., migration survival or population decrease in overwintering territories) rather than of the modeled increase in the midge food resource. Food availability has been recognized as one of the main factors affecting pied flycatcher nesting choices and success (Siikamäki 1998). It would therefore be plausible that the increased availability of flying prey at the local level could result in higher nesting rates. The pied flycatcher has been observed to forage both on terrestrial and aquatic arthropods (including their larvae); in some comparative studies, Diptera were the second most abundant prey item (Sanz 1998) while Lepidoptera larvae seem to be a less important prey item outside of oak forests (Burger *et al.* 2012). Hunter *et al.* (2014) showed that the per capita rates of change of several moths were frequently negatively associated with climate change variables in the subarctic region, suggesting that the abundance of caterpillars might have decreased over our study period. Climate change might alter the timing of food resource pulses and its match with pied flycatcher nesting time (Both *et al.* 2006), such that earlier peaks in food availability can result in more drastic population declines. Nest scouting could play a role in reducing climate effects, at least in some habitats (Burger *et al.* 2012). This might partly explain why warming temperature trends did not appear to play a major role in our study, neither at the local nor the regional level.

Conclusions

Our results suggest two main conclusions: 1) that the ultimate effects of fish introductions on birds living near lakes could be opposite to what has

been previously reported, possibly depending on modulation at different levels; and 2) that local factors (i.e., the increased availability of a food resource around the lake) might not be relevant enough to counteract large trends at a larger spatial scale. In summary, our results show that the consequences of fish introductions to remote fishless lakes could be very complex and underline the need for further studies in this topic. Biomaniipulation approaches could be useful tools for these kind of studies, although they often suffer from the lack of rigorous (and extended) pre-post assessments of manipulation effects, such that other confounding factors can be significant. Future studies should also take into account more invertebrate taxa than was analyzed in this study and use many replicates to reduce noise. The lack of clear effects on terrestrial consumers in our results should not be interpreted as an endorsement of fish stocking practices, but rather as an example that further investigations into the consequences of human intervention are needed. Ultimately, more specific studies should be carried out before concluding whether the direction and magnitude of fish cascading effects are relevant to terrestrial consumers.

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