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Holocene extinctions of a top predator – effects of time, habitat area and habitat subdivision

Short title: Extinctions of northern pike

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Summary:

1. Loss of habitat and changes in the spatial configuration of habitats are major drivers of species extinctions, but the responses to these drivers differ between organisms. To advance theory on how extinction risk from different types of habitat alteration relate to species-specific traits, there is a need for studies of the long-term extinction dynamic of individual species.
2. The goal of this study was to quantify how habitat area and the spatial configuration of habitats affect extinction rate of an aquatic top-predator, the northern pike *Esox lucius* L.
3. We recorded presence/absence of northern pike in 398 isolated habitat fragments, each one consisting of a number of interconnected lakes. Time since isolation of the habitat fragments, caused by cut-off from the main dispersal source in the Baltic Sea, varied between 0 and 10 000 years. Using survival regression, we analysed how pike population survival was affected by time since isolation, habitat size, and habitat subdivision. The approach builds on the assumptions that pike colonized all fragments before isolation and that current absences result from extinctions. We verified these assumptions by testing i) if pike was present in the region throughout the entire time period when the lakes formed, and ii) if pike typically colonize lakes that are formed today. We also addressed the likelihood that unrecorded anthropogenic introductions could bias our estimates of extinction rate.
4. Our results supported the interpretation that current patterns of presence/absence in our study system are shaped by extinctions. Further, we found that time since isolation and fragment area had strong effects on pike population survival. In contrast, spatial habitat subdivision (i.e., if a fragment contained few large lakes or many small lakes) and other environmental covariates describing climate and productivity, were unrelated to pike survival. Over all, extinction rate was high in young fragments and decreased sharply with increasing fragment age.

5. Our study demonstrates how the link between extinction rate and habitat size and spatial structure can be quantified. More similar studies may help us find generalizations that can guide management of habitat size and connectivity.

Introduction

Habitat loss and fragmentation are major drivers of species extinctions (Hanski 2005).

Although some extinctions occur soon after habitat modifications, it is well known that considerable time may pass until species with low abundances go extinct (Tilman *et al.* 1994).

This delay means that past or current environmental change will continue to cause many extinctions in the future. However, remedial actions may be taken if the conditions causing extinction debt can be predicted. It is therefore valuable to quantify how different changes to the spatial habitat structure affect extinction risks (Hylander & Ehrlén 2013).

A rich theoretical literature has demonstrated strong links between extinction risk and various aspects of spatial habitat structure, such as habitat size, degree of subdivision, patch size distribution and network structure (Hanski & Ovaskainen 2000; Fagan 2002; Ovaskainen 2002; Holland & Hastings 2008). There is strong empirical support for a general, negative relationship between habitat area and extinction risk (Hugueny 2017). In contrast, it has proved difficult to find useful generalisations about the effects of habitat subdivision and connectivity on extinction risks. This is illustrated by the longstanding “SLOSS” debate about reserve design, which focused on the relative merits of a single large habitat patch and several small patches for population persistence (Ovaskainen 2002), and more recently by the related debate about the role of fragmentation *per se* (Hanski 2015; Fahrig 2017; Fletcher *et al.* 2018). An important lesson from theoretical studies is that dispersal capacity is crucial for how organisms respond to changes in the spatial structure of the habitat (Keeling, Wilson & Pacala 2002; Sjödin *et al.* 2014). For example, species with either high or low dispersal capacities may experience the same landscape as consisting of a single large habitat or many small isolated habitats, respectively (Thomas 2000; Öckinger *et al.* 2009; MacDonald *et al.* 2018). Other species specific traits, including the degree of resource specialization, trophic position, and habitat preference can also modify responses to fragmentation (Ewers &

Didham 2006; Ramiadantsoa, Hanski & Ovaskainen 2018; Valente & Betts 2019). It has therefore been argued that fragmentation effects are best tested in studies of individual species rather than communities, as the latter may include species with dissimilar responses to fragmentation (Hanski 2015).

Studies that focus on extinctions of individual species may also allow management efforts to focus on species with particularly strong effects on the structure and function of ecosystems, such as top predators and invasive species (Englund *et al.* 2009; Henriksson *et al.* 2016). So far, studies of single species extinction dynamics in natural systems have concerned recent human impacts such as logging and dam construction (Morita & Yamamoto 2002; Stouffer, Strong & Naka 2009). Thus, there is a lack of studies of species' long-term extinction dynamics in natural populations. To address this issue, we make use of an extensive natural experiment, the generation of isolated lakes by isostatic post-glacial land-uplift in Northern Scandinavia. This ongoing process has generated thousands of lakes that cover a gradient in time since isolation from 0 to 10 000 years (Englund, Eriksson & Nilsson 2013). Upon formation, these lakes were colonized by freshwater fish species in the Baltic Sea (Olajos *et al.* 2018). After isolation the species richness has been reduced, suggesting that the present distribution of fish species is shaped by extinctions (Englund *et al.* 2009; Bellard, Englund & Hugueny 2019). In this study, we use presence/absence data from nearly 700 lakes in 398 isolated habitat fragments with known time since isolation to describe the extinction dynamics of an important top predator, the northern pike *Esox lucius* L. First, we test the theoretical predictions that pike occurrence decreases with habitat age, and increases with increasing habitat area. Second, we make use of the fact that the isolated habitat fragments typically include several well-connected lakes to examine how different measures of habitat size and habitat subdivision affects extinction risk.

Methods

Study area

The coast of the northern Baltic Sea is rising 6-8 mm per year, due to post-ice-age isostatic recovery (Berglund 2004). This land uplift is transforming bays to lakes, which are colonized by Baltic Sea fish species (Englund *et al.* 2009). The salinity of the northern Baltic Sea is only 2-4 ‰ and most (>90%) of the fish species living in freshwater are also present in the Baltic Sea. Hence, there are 35-40 species that can potentially colonize these lakes. Isolation is a gradual process due to water level fluctuations in the Baltic Sea, and it takes approximately 100 years from a situation where a lake is isolated 5% of the time until it is isolated 95% of the time (Salonsaari 2002).

This study includes 698 lakes in northern and central Sweden, between latitudes and longitudes of 59.09 °N – 66.38 °N and 11.88 °E – 23.94 °E, respectively (Table 1). Mean annual precipitation in the area amounts to 700 mm, mean temperatures range from around 15 °C in July to –10 °C in January. Most lakes are ice- and snow-covered for approximately six months per year.

Study species

The northern pike (*Esox lucius* L.) has a circumpolar distribution and is widespread throughout Sweden except for the western mountain region. Pike is a dominant top predator that structures fish communities in Scandinavian lakes and streams through a range of direct and indirect mechanisms (Spens & Ball 2008; Hein, Öhlund & Englund 2012). It can invade existing fish communities, it often causes extinctions of resident species, it makes a strong contribution to biotic resistance, and it rarely goes extinct when other species invade (Henriksson *et al.* 2016). It has strong dispersal capacities and, although being primarily

associated with lakes, pike is frequently caught in both small and large streams (Ovidio & Philippart 2002; Hesthagen *et al.* 2015). Its distribution is limited by low pH (<5), which occurs in some small coastal lakes in our study area (Öhman *et al.* 2006), and low oxygen concentrations that occur in late winter in very shallow lakes (<2m) (Öhman *et al.* 2006; Englund *et al.* 2009). In the western mountains, which are not included in this study, it is also limited by low temperatures (Hein, Öhlund & Englund 2011). Thus, after excluding shallow and acidic lakes the only known limitations for pike occurrence in our study area are dispersal barriers and stochastic extinctions (Spens, Englund & Lundqvist 2007).

Fish data

Data on pike presence/absence and pike introductions were extracted from the data base PIKE (<https://gbif.vm.ntnu.no/ipt/resource?r=pike>, accessed in December 2018). The data base include information about the fish community and environmental conditions in ca 19000 Swedish lakes. The data have been assembled from a variety of sources, but most comes from a series of national surveys, the first being performed in the period 1880-1898 (Lundberg 1899). Additional data were collected for this study through telephone interviews with local fishers. The majority of the occurrence records in PIKE are based on interviews with fishery managers and local fishers, and a smaller fraction stems from gill net surveys. Interviews provide highly reliable presence/absence data for pike (Spens, Englund & Lundqvist 2007), since it is a large and charismatic predator that is easy to catch and often spotted when walking along the shore in warm weather. In contrast, pike is sometimes overlooked in gill net surveys (Rask *et al.* 2000). Thus we did not include absences based on a single gill net survey, unless the absence could be confirmed with interviews.

Three different data sets were extracted (Fig. 1). The main data set included presence/absence information for pike in 554 lakes that were isolated from downstream

dispersal sources (Fig. 1). We included lakes below the highest post-glacial coastline (present elevation 205-285 m a.s.l.) as it could be assumed that these lakes were open for colonization at the time when they were connected to the Baltic Sea. However, we also included lakes situated above the highest coast line if the isolating barrier was located below the highest coast line; the rationale being that these lakes could be colonized during the period from the ice melt to the emergence of the barrier. The small coastal lakes used in Englund et al. (2009) and Bellard et al. (2019) were also included. Some lakes in this data set were very shallow or acidic. Thus to avoid lakes where pike may not be able to persist due to low pH or low oxygen conditions (Öhman *et al.* 2006; Bellard, Englund & Hugueny 2019), we excluded lakes with depth < 2m or pH < 5.

To obtain more detailed data on short term extinction risk we compiled a second data set with lakes where pike was introduced in the period 1850-1980 (N=87). This set included lakes situated both below and above the highest post glacial coast line, but excluded lakes in the western mountain region where temperatures can be too low for pike (Hein, Öhlund & Englund 2011).

In the third data set we included 57 coastal lakes at elevations < 4 m that are well connected to the Baltic Sea. These lakes were used to test the assumption that pike were present in all lakes at the time of isolation.

Habitat isolation and age

Lakes were classified as isolated for pike if they lacked connecting streams or if the maximum slope along the river connecting to the nearest source population was > 7%, measured as the distance between the 5 m contour lines on the topographic map over Sweden (scale 1:50000). The 7% rule was used because Spens et al. (2007) and Hein et al. (2011) found that it

effectively identifies lakes that pike cannot colonize. For the set of small coastal lakes, isolation had been confirmed by site visits (Englund *et al.* 2009).

The rate of land uplift was nearly 10 cm per year immediately after the rapid ice melt ca 10 000 years ago. Since then the rate has steadily decreased and today it amounts to 6-8 mm per year (Berglund 2004). This means that the time since a lake became isolated from the Baltic Sea can be determined from the elevation of the isolating barrier. To find the relationship between elevation and age we used shore displacement data from three studies, which together cover the study area (Renberg & Segerström 1981; Berglund 2004; Linden *et al.* 2006). Because the total land uplift since the deglaciation vary with latitude and longitude (205-285 m) we modelled age as a function of elevation expressed as a proportion of the maximum post-glacial uplift (ELEV%). Combining data from all studies we fitted a fourth order polynomial to the data on age and ELEV% ($r^2=0.99$, Fig. S1 in the supplement):

$$\text{age} = -0.0000486 * \text{ELEV}\%^4 + 0.0229 * \text{ELEV}\%^3 - 3.781 * \text{ELEV}\%^2 + 301.94 * \text{ELEV}\% \quad (1).$$

To find the year of isolation for a specific lake, we calculated ELEV% by dividing the elevation of the isolating barrier with the maximum post-glacial uplift in the neighbourhood, and then applied eq. 1.

Habitat size and subdivision

When quantifying habitat size and spatial structure we defined three different habitat units (Fig. 2): (i) a single lake, (ii) a metapopulation, which is defined as a set of lakes with bidirectional connectivity, and (iii) a source population, which is the metapopulation plus upstream lakes situated above dispersal barriers, from which colonists could be recruited (Table 1). The distinction between metapopulation area and source-population area is relevant

since waterfalls and steep rapids are passable in downstream direction, but not in upstream direction. Lakes were characterized by their area, whereas metapopulations and source populations were characterized by the total area of all lakes, the number of lakes, and the coefficient of variation for lake area.

Environmental covariates

We extracted information about environmental covariates that could affect the distribution of pike (Table 1). As a measure of the temperature regime, we used the number of degree days with a base temperature of 6 °C. The number of degree days in a year was calculated as the sum of the differences between daily temperature readings and the base temperature as in Henriksson et al. (2015). Latitude, longitude, and elevation were extracted from the PIKE database (<https://gbif.vm.ntnu.no/ipt/resource?r=pike>, accessed in December 2018). Catchment area, and the proportions of the catchment that were covered by agricultural land and lakes were downloaded from <https://vattenwebb.smhi.se/modelarea/> (accessed in February 2019). The proportion of agricultural land in the catchment was included as a proxy of nutrient loading, whereas the proportion covered by lakes was used as a proxy for light conditions, which is known to control lake productivity in this region (Ask *et al.* 2009). Maximum depths were only available for 57% of the lakes and were therefore not included in the analyses.

Anthropogenic introductions

Humans have introduced pike in many lakes in northern Sweden. To account for this process we collected available data on published introductions (Lundberg 1899; Alm 1920; Brundin 1939; Filipsson 1994). We also performed extensive telephone interviews with fishery rights owners and local fishers. Nevertheless, it is likely that especially older introductions were unrecorded. Previous authors have noted that the likelihood of introductions correlates with

measures of human presence, such as population density or agricultural activities in the neighbourhood (Spens, Englund & Lundqvist 2007; Jakobs, Kueffer & Daehler 2010). Following these authors, we derived two metrics of human presence to be used as indicators of increased introduction probability: i) distance to the nearest farm, and ii) distance to the nearest village, defined as a cluster with >10 buildings (Table 1).

Archaeological records of pike

To examine if pike have had a continuous presence in the study area during Holocene we compiled archaeological findings of pike bones, scales and rock carvings. Archaeological records were extracted from the web service "Fornsök" (<http://www.fmis.raa.se/cocoon/fornsok/search.html>, accessed January 2019), a data base published by Ramqvist (2000), and older reports (Meschke 1967; Lepiksaar 1975; Ericson 1980; Ekman & Iregren 1984; Iregren 1989).

Modelling survival with censored observations

The data on the presence/absence of pike were analysed with survival models for interval-censored observations. Absences are considered as left censored observations as we know when the habitat was cut-off from the Baltic Sea, but not when pike went extinct. Presence observations are considered right censored, because we know that pike has survived since colonization, but not when it will go extinct. For a smaller number of lakes, we have uncensored observations, i.e., both the date of isolation/introduction and the date of extinction are known. To handle this mixture of data, we used the package *icenReg* (Anderson-Bergman 2017) in the R version 3.5.1 (R Core Team 2018) to analyse how the persistence of pike populations vary with time, habitat area, habitat subdivision, and other environmental covariates. We used a parametric proportional hazards model assuming that the baseline

distribution is loglogistic. This choice was based on a comparison of fitted baseline distributions for a semiparametric model and six different parametric models (Fig. S2).

Modelling strategy for the survival analysis

As a first step we tested if pike survival in a lake is best explain by the area of the focal lake or the area of all the lakes it is connected to, i.e., a metapopulation or source population. This analysis showed that pike survival is controlled by the total area of connected lakes rather than the area of the focal lake (Table 2). Thus we performed the following analyses using networks of connected lake as observation units. These habitat networks are henceforth called fragments and their size is characterized by the total lake area (metapopulation area or source-population area) and the number of interconnected lakes (metapopulation number or source-population number).

The first five models tested the effects of different measures of fragment size (model 1-5 in Table 3). The effect of fragmentation per se was then tested by including both metapopulation area and metapopulation number as predictors (model 6, Table 3), and the effect of lake size distribution in a fragment was tested by including metapopulation area and the coefficient of variation for lake area (model 7, Table 3). The following models were meant to examine how the survival estimates are affected by variables indicating habitat suitability or increased likelihood of pike introductions. These variables were added one at a time to a model including metapopulation area (model 8-16, Table 3). The best model included distance to farm. Finally, we added all remaining variables one at a time to a model including metapopulation area and distance to farm. Since none of the variables added in this round were significant (model 17-25, all p-values > 0.075), we stopped here. Several models had similar AIC values as the best model ($\Delta AIC < 2$) and we chose to interpret the one with fewest predictors.

Results

The interpretation that pike presence/absence patterns are shaped by extinctions relies on the assumption that all lakes had pike when they were isolated by land uplift. This assumption is supported by archaeological records showing that pike was present in the area throughout the last 10 000 years (Fig. 3), and the finding that all the 57 coastal lakes connected to the Baltic Sea have pike today. Moreover, we did not observe any gaps in the distribution of pike, i.e. lakes where pike was lacking despite being present in the other lakes of the fragment (N=292 lakes in fragments with >1 lake and pike presence). Thus, our data support the assumption that pike colonize all lakes they can reach and that the species has been present in the study area during Holocene.

Extinction patterns

Lake level analyses: All measurements of habitat area were positively related to pike persistence, but metapopulation area and source-population area were much better predictors of pike persistence than lake area (Table 2). Thus, we performed further analyses using fragments as observations.

Fragment level analyses: The probability of pike being present in a habitat fragment decreased with time since isolation (Fig. 4, Fig. S3), and the effect was highly significant (Table 3, the time effect is controlled by both α and β). The effects of our two measurements of fragment area, i.e., metapopulation area and source-population area, were strong and positive (Table 3, model 1-2). The model was not improved when including both predictors (Table 3, model 3), which reflects the high correlation between them ($r=0.986$). Since the

metapopulation area is a subset of the source-population area, we decided to use metapopulation area in further analyses. The magnitude of the effect of metapopulation area is illustrated in Fig. 4a. The effects of the number of lakes in a fragment were positive and significant, but considerably weaker than the effects of area (Table 3, model 4-5).

The effect of fragmentation per se was evaluated by including the number of lakes (metapopulation number) in a model with metapopulation area. A weak and insignificant effect of metapopulation number indicates that there is no effect of fragmentation per se (Table 3, model 6). To examine the effect on pike persistence of an unequal distribution of lakes sizes within a fragment, i.e., if there is both large and small lakes or if all lakes are of equal size, we included the coefficient of variation in lake area as predictor. This variable also had a weak and insignificant effect on persistence (Table 3, model 7).

To test if species introductions could have biased the observed patterns of persistence, we included two measures of human presence – the distances to the nearest farm and to the nearest village. A significant effect was found for the distance to nearest farm (Table 3, model 8). This effect was comparably weak, as shown in Fig. 4b. Including other covariates gave only minor improvements of the AIC value ($\Delta AIC < 2$). Thus we chose not to interpret more complex models (Table 3, model 9-25).

The extinction rate decreased with increasing fragment age (Fig. 5). The true effect is probably even stronger than shown in Fig. 5, as a semi-parametric model suggests that the initial decline in survival is not fully captured by the parametric model (Fig S2). The inclusion of introduction data could possibly explain the strong time effect, as the absence of pike at the time of introduction could indicate unsuitable habitat conditions. Alternatively, the time effect could be explained by the inclusion of young coastal lakes, which, as a crude generalization, are shallower and more acidic. However, excluding either the introduction data or the coastal lake data had a negligible effect on the modelled extinction rate (Fig. 5).

Discussion

Much of our empirical knowledge about extinctions is based on natural experiments, such as the isolation of land bridge islands by rising sea levels (Foufopoulos & Ives 1999), and the formation of isolated habitats by human activities, such as logging and dam building (Morita & Yamamoto 2002; Stouffer, Strong & Naka 2009). Such studies typically have low temporal resolution or cover a relatively short time (Hugueny 2017). In this study we could gather data with both large temporal extent and high temporal resolution, by combining two types of data – the occurrence of pike in lakes that were isolated by land uplift during the last 10 000 years ago and the survival of pike populations introduced during the last 150 years. These data show that extinction rate increases with decreasing habitat size, and that fragmentation per se has little effect on extinction rate. The latter result adds support to the growing body of empirical evidence that fragmentation per se has weak effects on population persistence (Fahrig 2017). We could also establish that the relevant habitat unit for pike is not individual lakes, but a network of interconnected lakes between which pikes can move. However, the most important result is arguably that we could quantify the shape of the extinction curve. This curve provides crucial information about delayed extinctions, i.e., how many species or populations that are expected to go extinct following fragmentation and how long time it will take until these extinctions are realized.

Accumulating evidence suggests that delayed extinctions, often called extinction debt, is an important but often overlooked challenge for biodiversity conservation in a wide range of ecosystems (Tilman *et al.* 1994; Hylander & Ehrlén 2013). An important aspect of delayed extinctions is that there may be an opportunity to prevent not yet realized extinctions through habitat restoration and landscape management (Kuussaari *et al.* 2009). The shape of the extinction curve provide crucial information needed to guide such efforts. Our data show that

the extinction risk for pike populations decreased sharply with increasing population age, but did not reach zero even after 10 000 years. Thus, although logic suggests that there should be a relaxation time after which extinction rate stabilizes on a background level, it could not be detected in this study. Moreover, we found that the extinction debt is realized at a rather slow rate: After 100 years only 22% of the extinctions expected after 10 000 years had been realized (calculated for the median fragment size). This means that a majority of the expected extinctions happens over a time scale that is much longer than the typical time scale of management plans.

The approach used in this and other similar studies (Foufopoulos & Ives 1999; Englund *et al.* 2009; Hugueny 2017) requires careful consideration of alternative explanations for the observed patterns. We examined a wide range of environmental covariates and the only one besides fragment size that influenced pike persistence was the distance to nearest farm, suggesting that unrecorded introductions may have biased our estimates of extinction rate. This was not unexpected given that humans have introduced fish species in Scandinavia at least since the Viking Age, ca 1000 years B.P. (Huitfeldt-Kaas 1918). The expected effect of unrecorded introductions would be to make estimated extinction rates too low. Such an effect would, however, be small compared to the effects of time since isolation and fragment area, suggesting that this potential bias does not invalidate our interpretation.

Other types of data provided further support to the hypothesis that pike distribution can be interpreted as being primarily shaped by extinctions. The archaeological record suggests that pike were indeed present in the region during the entire Holocene. Although pike remains do not necessarily have a local origin - dried pike is a traditional trading commodity - we argue that the widespread occurrence of pike remains provide strong support for pike being present in the region. Other data show that pike readily colonize all lakes that can be reached. This was evident from our findings that pike was found in all lakes connected to the Baltic

Sea, and that the distribution of pike had no gaps in their within-fragment distribution. Still, we cannot rule out the possibility that pike were less prone to colonize newly formed lakes during some period in the past, perhaps because these lakes then were unsuitable for pike. If so, extinction rates would be overestimated for this period.

The strong colonization capacity of pike is also in agreement with the finding that fragment area, rather than lake area best explains pike persistence. Moreover, it suggests an explanation for why habitat subdivision within a fragment have no effect on persistence. This result is expected if a pike population experiences a set of lakes with bidirectional connectivity more or less as a single large patch. Thus, our data suggest that the relevant conservation unit for a pike population should include all lakes with bidirectional connectivity. Logic suggests that also upstream lakes with only downstream connectivity with the focal population should contribute to increased persistence through a rescue effect. However, this effect was not detected in this data set, probably because there were few large lakes upstream of barriers that could “rescue” downstream populations.

Extinction mechanisms

Pike, being a large growing and highly cannibalistic top predator, occurs in low numbers. Estimates of adult population density (>30 cm) in lakes from the study area vary between 1 and 4 individuals/ha (Persson *et al.* 1996). Given that the effective population size may range from 3-15 % of the adult population size (Miller & Kapuscinski 1997) it is obvious that populations in small fragments (<10 ha) are susceptible to demographic and environmental stochasticity. Moreover, pike is known to have low genetic variance in freshwater systems (Miller & Senanan 2003), suggesting that also low genetic variation and inbreeding contributes to high risks of extinction.

We found that extinction rates decrease sharply with increasing population age. A similar pattern was found for experimental populations of *Daphnia* (Drake 2006). This pattern is expected if there is among-population variation in extinction risk, such that populations with high extinction risk are rapidly lost, leaving more resistant populations. Decreasing extinction rates have also been found in studies where extinction rate is measured as species loss rate (Heaney 1986; Ferraz *et al.* 2003; Hugueny 2017). A similar explanation has been proposed, i.e., that species with high extinction risk are rapidly lost, leaving a community with more resistant species. Our data suggests that variation between populations also contributes to this pattern. Thus, it seems likely that this phenomenon is the result of selection both between species and between populations.

A related hypothesis is that the cost of adaptation to an isolated freshwater body contributes to increased initial extinction risk. Pike use bays and lakes that are in the process of being isolated for spawning in the spring, and a large fraction of the recruits migrates back to the Baltic Sea the first summer (Salonsaari 2002). When the lake becomes isolated, there should be strong selection against this migratory behaviour as individuals leaving the lake cannot return. These losses should have direct negative effects on population survival, as well as indirect negative effects resulting from reduced genetic variance and inbreeding. Populations that survive this initial critical phase may then have considerably lower extinction risk, either because population size is larger, or because the initial standing genetic variation is large enough to allow successful adaptation to the novel conditions.

Implications for the management of connectivity in stream networks

Restoring natural connectivity in stream networks by removing dams and building fish passes is an important activity for improving the ecological status of freshwater systems (Laitila & Paulrud 2008; Robbins & Lewis 2008). However, as such activities may facilitate the spread

of invasive species, managers must weigh the increased risk of invasions against the costs of fragmentation in terms of increased extinction risk (Morita & Yamamoto 2002; Fausch *et al.* 2009). The relationship between extinction risk and the size and age of the habitat is likely to be species-specific, because species differ widely in population size, mobility and ability to pass barriers (Fausch *et al.* 2009; Rahel & McLaughlin 2018). Thus, there is a need to extend our approach to a wider range of fish species. Only then can managers make informed decisions about the costs and benefits of restoring connectivity in invaded river networks. Pike is unusual in its ability to tolerate a wide range of environmental conditions, predators and competitors (Henriksson *et al.* 2016). Thus, we expect that quantifying extinction risks in many other fish species will also require that the effects of biotic interactions and environmental conditions are account for, as demonstrated in Bellard, Englund and Hugueny (2019).

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Author contributions

GE, GÖ and BH conceived the ideas. GE collected and analysed the data in collaboration with BH and GÖ and led the writing. All authors contributed to every draft and approved the final version for publication.

Data accessibility

The data will be made accessible from the DRYAD Digital Repository

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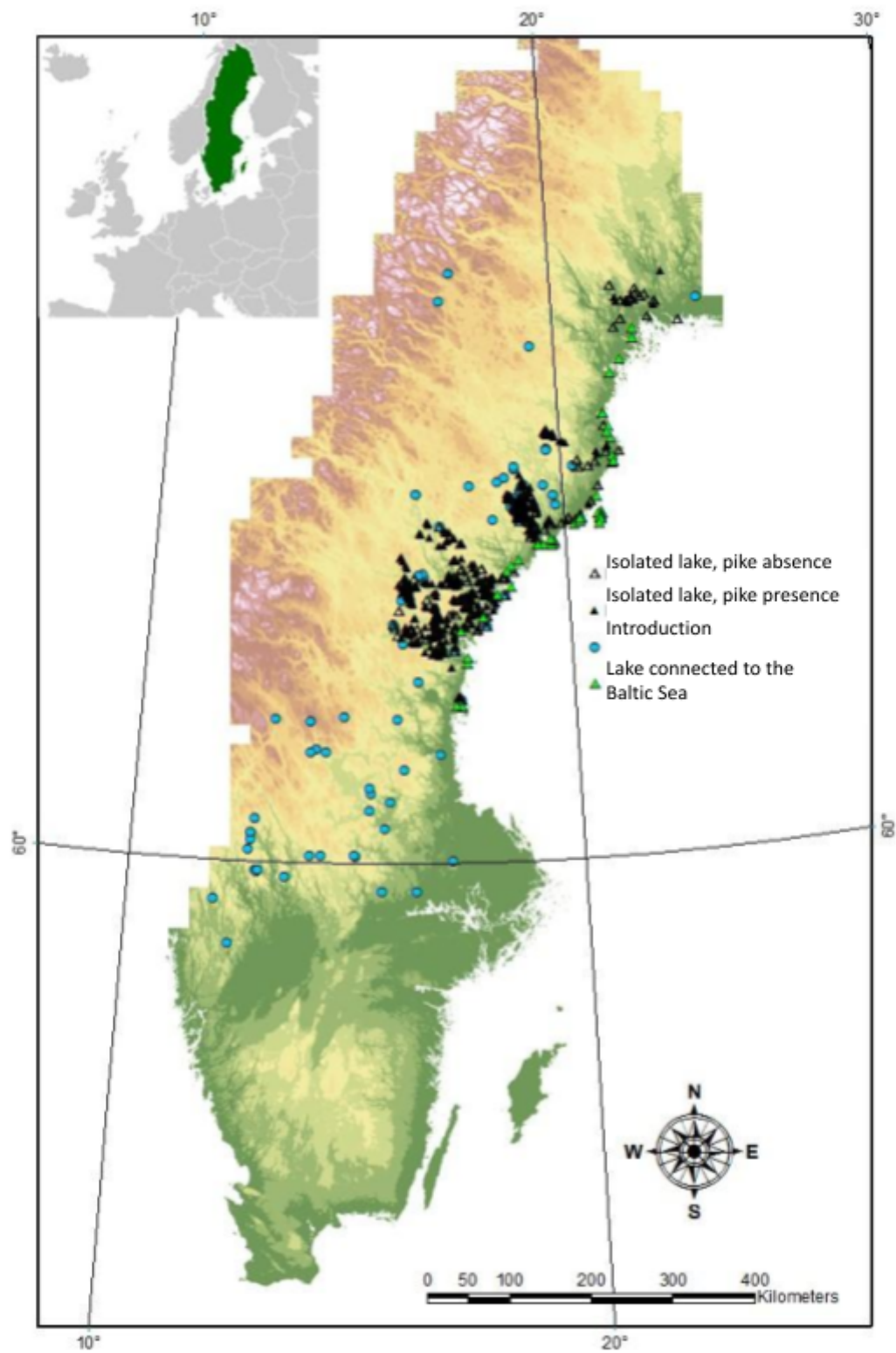
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Figures

Fig. 1. Map showing the location of the lakes included in the different data sets.



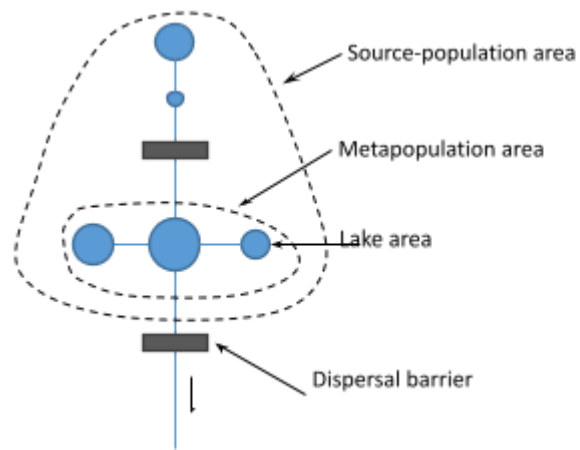


Fig. 2. Illustration of the measures used to quantify fragment area. Metapopulation area is the total lake area for the lakes with bidirectional connectivity, whereas source-population area also includes lakes upstream of barriers that than can provide colonizers but cannot be reached by the fish in the focal fragment.

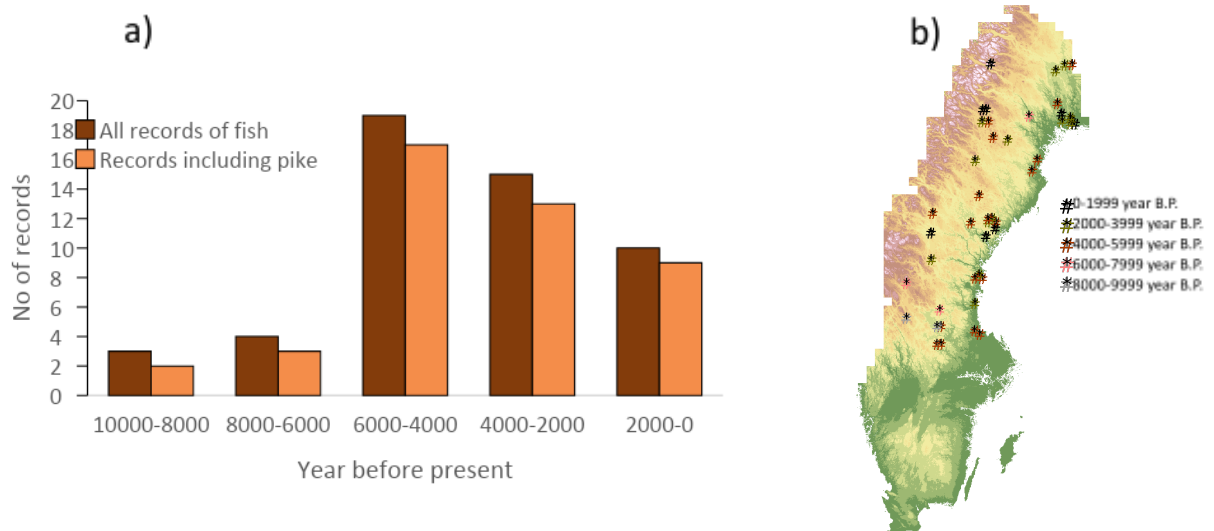


Fig. 3. a) Archeological records of fish remains identified to species level, and the number of those records that included remains of pike, in different time periods. b) The temporal and spatial distribution of pike records.

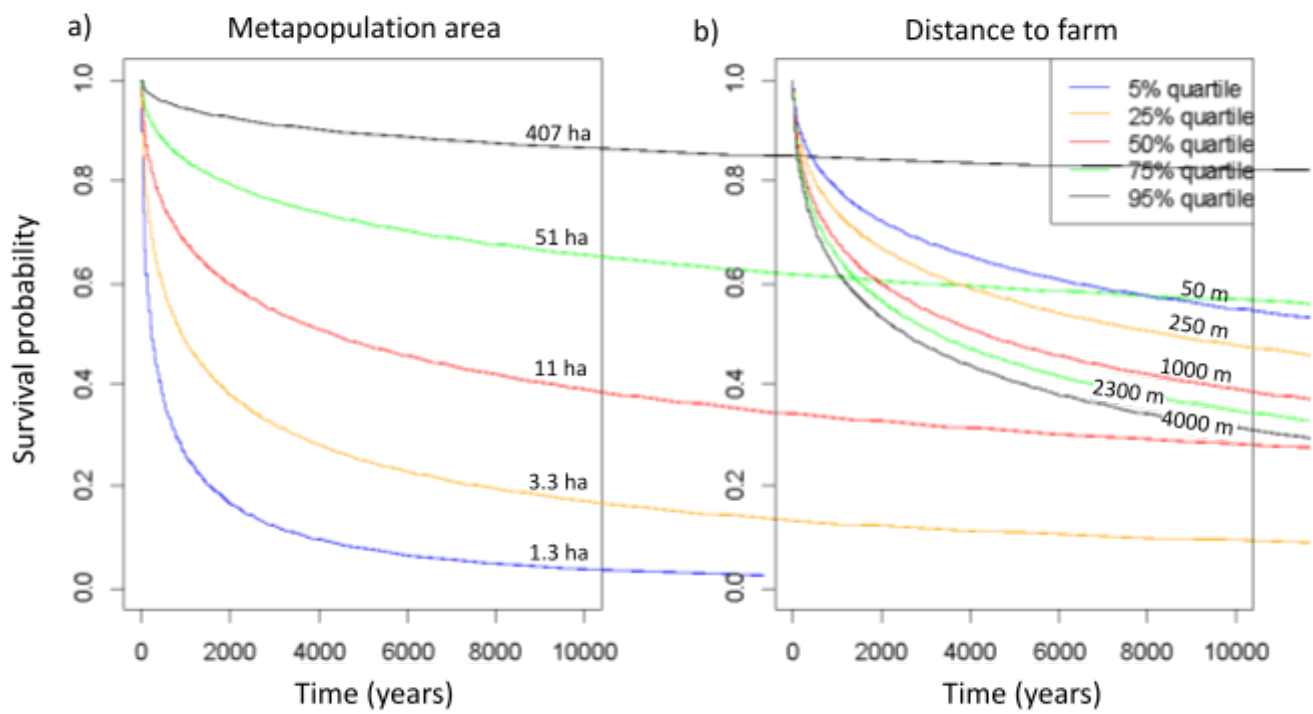


Fig. 4. a) Survival curves for different values of metapopulation area. Distance to farm is held at its median (1000 m). b) Survival curves for different values of distance to nearest farm when metapopulation area is held at its median (11 ha).

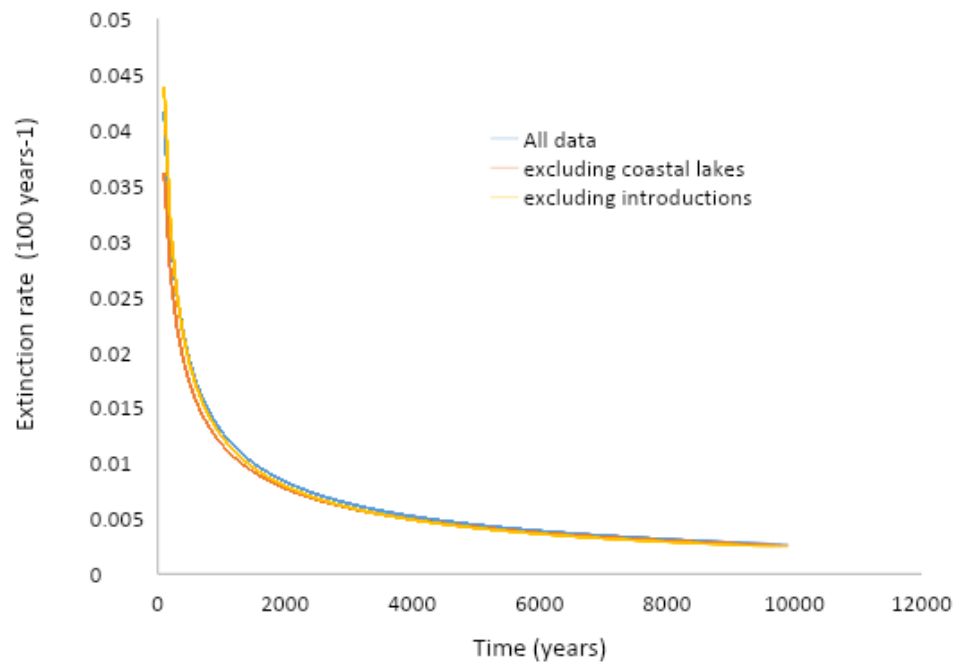


Fig. 5. Estimated extinction rates for pike in fragments of different age. Analyses were made for all data, and when excluding either the coastal lake data set or the introduction data set.

Tables

Table 1. Summary statistics describing the lakes and fragments included in the analyses of pike presence/absence.

	Median	Min	Max	N
Age (years)	7780	10	9585	398
Metapopulation area (ha)	11	0.167	3233	398
Source-population area (ha)	11.5	0.167	3233	398
Metapopulation number	1	1	29	398
Source-population number	1	1	29	398
Distance to farm (m)	1000	10	6100	398
Distance to village (m)	2500	10	16000	398
Elevation (m a.s.l.)	205	1	523	398
Degree days	928	514	1345	398
Max depth in fragment (m)	11.4	2.1	63.3	246
Latitude	63.1118	59.0916	66.4671	398
Longitude	17.8410	11.8842	23.9392	398
% agricultural land	0	0	18.6	398
% lake area	8.0	0.046	52.1	398
Catchment area (ha)	752	1.1	50128	398
CV lake area	0	0	3.87	398
Lake max depth (m)	9.5	2	63.3	366
Lake area (ha)	10	0.17	1790	642

Table 2. Models used to examine the association between habitat area and the persistence of pike populations in individual lakes (N= 642).

Model	Parameter	Est.	SE	Z	p-value	AIC	Δ AIC	AICw
Source-population area	log alpha	10.9	0.39	27.9	<0.00001	557.3	0	0.61
	log beta	-0.73	0.13	-5.39	<0.00001			
	log source-pop. area	-0.62	0.046	-13.6	<0.00001			
Metapopulation area	log alpha	11.0	0.40	27.3	<0.00001	558.1	-0.9	0.39
	log beta	-0.73	0.14	-5.34	<0.00001			
	log metapop. area	-0.64	0.047	-13.4	<0.00001			
Lake area	log alpha	11.0	0.51	21.5	<0.00001	726.7	-169.4	0
	log beta	-1.04	0.18	-5.91	<0.00001			
	log lake area	-0.48	0.048	-10.0	<0.00001			

Table 3. Models used to examine the association between the survival of pike populations and habitat area, habitat spatial structure, and other environmental variables. Each observation is an isolated fragment that consists of either a single lake or several interconnected lakes (N=398 fragments).

No	Model	Parameter	Est.	SE	Z	p-value	AIC	ΔAIC	AICw
1						<0.0000			0.014
	Source-population area	log alpha	8.88	0.26	33.6	1	419.7	4.3	
						<0.0000			
		log beta	-0.68	0.13	-5.04	1			
						<0.0000			
		log source-pop. area	-0.53	0.06	-9.36	1			
2						<0.0000			0.019
	Metapopulation area	log alpha	8.91	0.27	33.2	1	419.2	3.7	
						<0.0000			
		log beta	-0.69	0.14	-5.05	1			
						<0.0000			
		log metapop. area	-0.56	0.06	9.34	1			
3						<0.0000			0.010
	Metapopulation area+	log alpha	9.06	0.27	33.3	1	420.4	4.9	
						<0.0000			
	Source-population area	log beta	-0.68	0.14	-5.04	1			
		log metapop. area	-0.35	0.27	-1.29	0.20			
		log source-pop. area	-0.21	0.26	-0.82	0.42			
4						<0.0000			0
	Source-population number	log alpha	9.16	0.32	29.0	1	474.3	59	
						<0.0000			
		log beta	0.68	0.13	-5.22	1			
						<0.0000			
		source-pop. number	-0.39	0.07	-5.36	1			

5					<0.0000		0
	Metapopulation number	log alpha	9.09	0.30	30.2	1	481.8 66
					<0.0000		
		log beta	-0.67	0.13	-5.16	1	
					<0.0000		
		metapop. number	-0.53	0.10	-5.21	1	
6					<0.0000		0.017
	Metapopulation area+	log alpha	9.00	0.29	30.9	1	419.4 3.9
					<0.0000		
	metapopulation number	log beta	-0.68	0.14	-5.05	1	
					<0.0000		
		log metapop. area	-0.51	0.07	-7.14	1	
		metapop. number	-0.12	0.09	-1.22	0.22	
7					<0.0000		0.023
	Metapopulation area+	log alpha	8.93	0.27	32.9	1	418.8 3.3
					<0.0000		
	CV area	log beta	-0.67	0.13	-5.02	1	
					<0.0000		
		log metapop. area	-0.51	0.07	-7.67	1	
		CV lake area	-0.50	0.34	-1.45	0.15	
8					<0.0000		0.066
	Metapopulation area+	log alpha	8.96	0.28	31.9	1	416.7 1.3
					<0.0000		
	distance to farm	log beta	-0.71	0.14	-5.16	1	
					<0.0000		
		log metapop. area	-0.53	0.06	-8.35	1	
		log distance to farm	-0.15	0.07	2.07	0.038	
9					<0.0000		0.017
	Metapopulation area+	log alpha	8.93	0.28	32.4	1	419.4 3.9

					<0.0000		
	distance to village	log beta	-0.70	0.14	-5.14	1	
					<0.0000		
		log metapop. area	-0.55	0.06	-8.90	1	
		log distance to village	-0.12	0.09	1.31	0.19	
10					<0.0000		0.011
	Metapopulation area+	log alpha	8.91	0.27	32.8	1	420.3 4.8
					<0.0000		
	degree days	log beta	-0.70	0.13	-5.17	1	
					<0.0000		
		log metapop. area	-0.56	0.06	-9.40	1	
		degree days	0.00	0.00	-0.98	0.32	
11					<0.0000		0.007
	Metapopulation area+	log alpha	8.90	0.27	32.9	1	421.1 5.7
					<0.0000		
	elevation	log beta	-0.69	0.14	-5.08	1	
					<0.0000		
		log metapop. area	-0.56	0.06	-9.25	1	
		Elevation	0.00	0.00	0.36	0.72	
12					<0.0000		0.030
	Metapopulation area+	log alpha	8.95	0.28	32.5	1	418.3 2.8
					<0.0000		
	latitude	log beta	-0.70	0.14	-5.08	1	
					<0.0000		
		log metapop. area	-0.55	0.06	-9.13	1	
		Latitude	-0.09	0.09	1.07	0.28	
13					<0.0000		0.030
	Metapopulation area+	log alpha	8.96	0.27	32.9	1	418.3 2.8
					<0.0000		
	longitude	log beta	-0.69	0.14	-4.98	1	

					<0.0000			
		log metapop. area	-0.54	0.06	-8.89	1		
		longitude	0.09	0.05	1.70	0.10		
14					<0.0000			0.011
	Metapopulation area+	log alpha	8.89	0.26	33.9	1	420.3	4.9
					<0.0000			
	% agricultural land	log beta	-0.66	0.14	-4.87	1		
					<0.0000			
		log metapop. area	-0.57	0.06	-9.30	1		
		% agricultural land	0.04	0.04	0.95	0.34		
15					<0.0000		414.4	0.021
	Metapopulation area+	log alpha	8.90	0.27	33.5	1	2	3.5
					<0.0000			
	% lake area	log beta	-0.67	0.13	4.98	1		
					<0.0000			
		log metapop. area	-0.57	0.061	-9.36	1		
			0.01					
		% lake area	4	0.010	1.51	0.13		
16					<0.0000			0.039
	Metapopulation area+	log alpha	8.89	0.27	33.5	1	419.0	2.3
					<0.0000			
	catchment area	log beta	-0.67	0.14	-4.97	1		
					<0.0000			
		log metapop. area	-0.44	0.090	-4.86	1		
		log catchment area	0.13	0.073	1.83	0.068		
17					<0.0000			0.061
	Metapopulation area+	log alpha	9.05	0.30	29.9	1	417.7	1.4
					<0.0000			
	distance to farm+	log beta	-0.71	0.14	-5.16	1		

					<0.0000			
	metapopulation number	log metapop. area	-0.48	0.072	-6.65	1		
		log distance to farm	0.14	0.073	1.97	0.049		
		metapop no	-0.10	0.094	-1.07	0.28		
18					<0.0000			0.056
	Metapopulation area+	log alpha	8.98	0.28	31.7	1	417.0	1.6
					<0.0000			
	distance to farm+	log beta	-0.70	0.14	-5.12	1		
					<0.0000			
	CV area	log metapop. area	-0.49	0.068	-7.20	1		
		log distance to farm	0.14	0.074	1.90	0.058		
		CV area	-0.42	0.34	-1.23	0.22		
19					<0.0000			0.023
	Metapopulation area+	log alpha	8.96	0.28	31.8	1	418.8	3.3
					<0.0000			
	distance to farm+	log beta	-0.71	0.14	-5.19	1		
					<0.0000			
	degree days	log metapop. area	-0.53	0.063	-8.35	1		
		log distance to farm	0.14	0.077	1.86	0.062		
			-0.00					
		degree days	0.41	0.001	-0.39	0.70		
20					<0.0000			0.025
	Metapopulation area+	log alpha	8.98	0.28	31.6	1	418.6	3.2
					<0.0000			
	distance to farm+	log beta	-0.71	0.14	-5.12	1		
					<0.0000			
	elevation	log metapop. area	-0.52	0.065	-8.01	1		
		log distance to farm	0.16	0.076	2.07	0.038		
			0.00					
		Elevation	0.32	0.001	-0.29	0.77		

21					<0.0000		0.034
	Metapopulation area+	log alpha	8.99	0.29	31.4	1 418.0	2.5
					<0.0000		
	distance to farm+	log beta	-0.72	0.14	-5.17	1	
					<0.0000		
	latitude	log metapop. area	-0.52	0.063	-8.36	1	
		log distance to farm	0.14	0.074	1.96	0.050	
			0.06				
		Latitude	9	0.087	0.80	0.42	
22					<0.0000		0.063
	Metapopulation area+	log alpha	9.00	0.28	31.7	1 416.8	1.3
					<0.0000		
	distance to farm+	log beta	-0.71	0.14	-5.10	1	
					<0.0000		
	longitude	log metapop. area	-0.51	0.063	-8.02	1	
		log distance to farm	0.14	0.074	1.86	0.063	
			0.07				
		Longitude	2	0.052	1.41	0.16	
23					<0.0000		0.090
	Metapopulation area+	log alpha	8.94	0.27	32.9	1 416.1	0.6
					<0.0000		
	distance to farm+	log beta	-0.67	0.14	-4.95	1	
					<0.0000		
	% agricultural land	log metapop. area	-0.53	0.064	-8.35	1	
		log distance to farm	0.19	0.078	2.44	0.015	
			0.07				
		% agricultural land	6	0.044	1.73	0.083	
24					<0.0000		0.067
	Metapopulation area+	log alpha	8.96	0.28	32.2	1 416.7	1.2

					<0.0000		
	distance to farm+	log beta	-0.69	0.14	-5.09	1	
						<0.0000	
	% lake area	log metapop. area	-0.53	0.063	-8.43	1	
		log distance to farm	0.15	0.073	2.04	0.042	
			0.01				
		% lake area	4	0.001	1.46	0.14	
25						415.5	0.12
					<0.0000		
	Metapopulation area+	log alpha	8.95	0.28	31.1	1	0
						<0.0000	
	distance to farm+	log beta	-0.69	0.14	-5.02	1	
						<0.0000	
	catchment area	log metapop. area	-0.41	0.091	-4.50	1	
		log distance to farm	0.15	0.073	2.02	0.043	
		log catchment area	0.14	0.074	1.78	0.076	
