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Abstract

The frequency and severity of outbreaks by pestiferous insects is increasing globally, likely as a result of human-mediated introductions of non-native organisms. However, it is not always apparent whether an outbreak is the result of a recent introduction of an evolutionarily naive population, or of recent disturbance acting on an existing population that arrived previously during natural range expansion. Here we use approximate Bayesian computation to infer the colonization history of a pestiferous insect, the winter moth, *Operophtera brumata* L. (Lepidoptera: Geometridae), which has caused widespread defoliation in northern Fennoscandia. We generated genotypes using a suite of 24 microsatellite loci and find that populations of winter moth in northern Europe can be assigned to five genetically distinct clusters that correspond with 1) Iceland, 2) the British Isles, 3) Central Europe and southern Fennoscandia, 4) Eastern Europe, and 5) northern Fennoscandia. We find that the northern Fennoscandia winter moth cluster is most closely related to a population presently found in the British Isles, and that these populations likely diverged around 2,900 years ago. This result suggests that current outbreaks are not the result of a recent introduction, but rather that recent climate or habitat disturbance is acting on existing populations that may have arrived to northern Fennoscandia via pre-Roman traders from the British Isles, and/or by natural dispersal across the North Sea likely using the Orkney Islands of northern Scotland as a stepping-stone before dispersing up the Norwegian coast.

Highlights

- Using a combination of Bayesian assignment, genetic distance, and approximate Bayesian computation methods, we analyzed a dataset that included genotype scores from 24 microsatellite markers obtained from winter moth individuals collected across northern Europe to determine the geographic origins of an outbreaking population of winter moth in northern Fennoscandia.
- Genetic analyses revealed the presence of strong biogeographic structuring of populations in northern Europe.
- Contrary to most studies that examine genetic diversity of northern populations, we find that populations of winter moth in northern Europe are equally diverse as those in more southern latitudes.
- Approximate Bayesian computation analyses indicate that the northern Fennoscandia population was likely introduced from the British Isles, and that these populations diverged ~2,900 years ago.
- Our study highlights the role of natural dispersal across the North Sea for the introduction of organisms to Fennoscandia, and the potential role of pre-Roman traders in the spread of invasive forest pests.

Keywords: approximate bayesian computation, Quaternary climatic oscillations, Lepidoptera, population genetics

Introduction

Homogenization of ecological communities due to intensification of global trade can result in increases in the frequency and intensity of outbreaks of insect species (Samways 1999). For effective management strategies of these resulting outbreaks to be initiated, species-level identifications and the determination of its region of origin are required (Andersen and Wagner 2016). For insects, the most species-rich multicellular group of organisms, determining species identity and region of origin is complicated by the fact that the vast majority of species have yet to be described (Berenbaum 2017) and that it is often unclear whether outbreaks are the results of contemporary introductions facilitated by human dispersal (e.g., Kumschick et al. 2015) or natural shifts in species distributions as a result of the Quaternary Climatic Oscillations (Hewitt 1996, 2000, Kobayashi et al. 2011, Avtzis et al. 2019, Økland et al. 2019). One approach to disentangle the temporal nature of an insect outbreak is to utilize historical records and/or genetic data (e.g., Speer 2001, Peltonen et al. 2002, Samarasekera et al. 2012, Coleman et al. 2014, Sherwin et al. 2015, MacLean 2016, Robert et al. 2018, Słowiński et al. 2019). For genetic datasets, approximate Bayesian computation (ABC) has become a popular framework to determine both the region of origin of an outbreaking species and its timing of introduction (e.g., Havill et al. 2016, Kim et al. 2017, Wang et al. 2017, Song et al. 2018, Javal et al. 2019, Lesieur et al. 2019). Under this approach, dataset(s) are simulated based on scenarios that include several likely regions of origin, and summary statistics from the sample dataset are compared to those from the simulated datasets to determine the most likely scenario. The approach can be used to examine the evolutionary histories of native organisms that have become pests by exploring whether outbreaks are the result of natural range expansion or introductions of novel (and potentially more virulent) populations (e.g., Wei et al. 2015, Andersen et al. 2019). However, this approach is not without its limitations. For example, to be computationally efficient, summary statistics – which are chosen arbitrarily by the investigator (Aeschbacher et al. 2012; but see Raynal et al. 2019 for novel approaches to this problem) – are compared. For ABC analyses based on microsatellite genotypes, another important limitation is the expectation that loci are evolving under a simple-stepwise-mutation model, an expectation that is not always observed in nature (Bhargava and Fuentes 2010). Limitations aside, ABC has been used to generate credible reconstructions of extremely complex invasion histories (see Lombaert et al. 2010, Stone et al. 2017 for example), that might not have been possible to disentangle with other methods.

The winter moth, *Operopthera brumata* L. (Lepidoptera: Geometridae) is an impactful tree defoliator that has a detailed historical record documenting its range expansion and outbreak activity. In northern Fennoscandia, winter moth has expanded its distribution northward, presumably in response to warming climates, and has in recent decades reached outbreak status as far north as the low arctic timberline in northeastern Norway

(Jepsen et al. 2008, 2011). Winter moth is native to Europe, northern Africa, and eastern Asia, and occasionally reaches outbreak densities across much of its distribution (Ferguson 1978, Tenow et al. 2013, Young et al. 2014, Jepsen et al. 2016, Mannai et al. 2017). However, persistent cyclic population dynamics, with periods of 7–15 years, are mainly found in northern Fennoscandia and high elevation regions in south-central Norway (Vindstad et al. 2019). Winter moth population dynamics have been well studied with respect to spatial synchrony and heterogeneity (Hittenbeck et al. 2019, Vindstad et al. 2019), and the species is considered a model system for studying population ecology (Varley et al. 1973). However, little is known about the presence of winter moth in northern Fennoscandia before it reached population outbreak status. In addition, winter moth has been reported in Iceland, where the first records date back only to 1928 (Halldórsson et al. 2013), and the introduction of this species has been linked to the importing of non-native trees (Ottósson 1982). Whether this species was introduced to Iceland in the early 1920s, or was previously present but unrecorded, is unknown.

Previous studies have determined that the genetic structure of winter moth populations in Continental Europe was largely shaped by their use of glacial refugia during the last glacial maximum (LGM) (Andersen et al. 2017, 2019). One of these studies (Andersen et al. 2019) determined that outbreaking populations of winter moth in North Africa represented a native population that had likely been present in the region since at least the LGM. As such, the authors proposed that contemporary human-mediated disturbances and/or climate change might be responsible for the recent outbreak. Here, we explore the geographic origins and the timing of introduction of the European winter moth to northern Fennoscandia. Specifically, we utilize a combination of Bayesian clustering, genetic distance, and ABC simulations to examine the population genetic structure of winter moth in northern Europe, and comment on factors that might be influencing the outbreak of winter moth in this region.

Materials and Methods

Sampling

Sampling was conducted as a network effort by the authors and their contacts. Individual winter moths were collected using either pheromone-baited traps developed for adult males (Elkinton et al. 2010, Elkinton et al. 2011), or opportunistically (for adults and larvae). Following collection, adult moths were placed in glassine envelopes (Uline Corporation, USA), and stored at -20°C or -80°C prior to molecular analyses, and larval caterpillars were placed in 95% ethanol and stored at -80°C.

DNA extraction and microsatellite amplification

Following previously described methods (Andersen et al. 2017, Havill et al. 2017), DNA was extracted and 24 polymorphic microsatellite loci were amplified. Genotyping was performed at the DNA Analysis Facility on Science Hill at Yale University with the GeneScan

500 LIZ size standard (Thermo Fisher Scientific, Waltham, Massachusetts) using a 3730xl DNA Analyzer (Thermo Fisher Scientific), and fragment lengths were scored using the microsatellite plugin in the software program Geneious v. R11 (BioMatters, LTD). Genotype scores were then filtered to only include individuals from which ≥ 20 microsatellite loci were successfully amplified. To this dataset, genotype scores for additional individuals from England, Germany, Poland, Scotland, and Sweden (previously presented in Andersen et al. 2017) were added. Collection information for all individuals whose genotype scores were generated as part of this study are presented in Supplementary Table S1. Genotype scores for all individuals (including those individuals from Andersen et al. 2017) are available through the Dryad Digital Repository at <https://doi.org/10.5061/dryad.gf1vhhmnf>.

Population genetic statistics and genetic distances

For locations from which ≥ 10 individuals were genotyped during a single collection event, standard population genetic summary statistics including the average effective number of alleles (E_{eff}), the expected Heterozygosity (H_E), the observed Heterozygosity (H_O), the inbreeding coefficient (G_{IS}), and the average proportion of Null Alleles across microsatellite loci ($Null$), as well as the degree of genetic differentiation (F_{ST}) between populations were calculated using the software program GenoDive v.2.0b27 (Meirmans and Van Tienderen 2004). The distance matrix of F_{ST} values was then used to calculate a 'NeighborNet' network and visualized using the program SplitsTree v.4.14.2 (Huson and Bryant 2006). Average Maximum Likelihood estimates of the null-allele frequency across loci at each population were calculated using Dempsters EM method, and the presence of linkage disequilibrium among loci and between populations were both estimated as implemented in GenePop v. 4.7 (Raymond and Rousset 1995, Rousset 2008), respectively.

Bayesian genetic clustering

The probability of assignment (Q) of sampled individuals to distinct genetic clusters (K) was calculated using Structure v.2.3.2 (Pritchard et al. 2000, Falush et al. 2003) for values of $K=2$ through $K=10$. Ten independent analyses were run using the admixture model, correlated allele frequencies, and default settings, with random starting values, runtimes of 1,000,000 generations, and burn-in periods of 100,000 generations for each value of K . To determine the optimal number of clusters that best represented the genetic diversity present in the dataset, the ΔK statistic of Evanno et al. (2005) was calculated as implemented in StructureHarvester (Earl and vonHoldt 2012). Results were then summarized across runs to identify major and minor clusters using Clumpak (Kopelman et al. 2015).

Historical demography

To explore the post-glacial recolonization of northern Fennoscandia, we compared the evolutionary relatedness of individuals collected in northern

Fennoscandia to the genetic clusters determined in our Structure runs. Here, we used the proportional assignments of populations to different genetic clusters (as presented in the "PopFile" output from Clumpak) for $K=5$ to construct a hierarchical clustering diagram (Supplementary Fig. S1) using the *hclust* command in the statistical language R v 4.0.0 (R Core Team 2020). Thirty randomly selected individuals from each of the clusters were then used to represent the different populations for the DiyABC analyses. A complete list of all samples and to which genetic cluster they were assigned during the DiyABC analyses is presented in Supplementary Table S2. The dataset for DiyABC was organized so that the "British Isles" population included only individuals from the British Isles; the "Eastern European" population included individuals from Estonia, Russia, Poland, as well as one individual Siuntio, Finland; the "Central European" population included individuals from Denmark and Germany; and the "Northern Fennoscandia" population included individuals from northern Finland (Kevo Subarctic Research Station, Kilpisjärvi, Lemu, and Oulu) and northern Norway (Karlsøy, and Senja). In preliminary analyses, we also included individuals from Reykjavík, Iceland as a separate population, however models that included the Icelandic population failed to converge for nearly all examined scenarios (described below) being equally likely. Therefore, this population was not used in subsequent simulations.

Previously, Andersen et al. (2017), examined the post-glacial recolonization of winter moth in Europe using ABC as implemented in the software program DiyABC v.2.1.0 (Cornuet et al. 2008, 2014), and found based on patterns of genetic diversity and estimates of divergence times, that populations of winter moth utilized distinct glacial refugia during the LGM. The authors also found that contemporary genetic diversity on the European continent could be summarized by the presence of three distinct genetic clusters, a "Western" European cluster that likely utilized the Iberian Peninsula during the LGM, a "Eastern" European cluster that likely utilized the Aegean Peninsula during the LGM, and a "Central" European cluster that is the result of admixture between the Eastern and Western clusters during post-glacial recolonization after the LGM. Therefore, to determine the origins of the Northern Fennoscandian population, we examined three scenarios (Fig. 1) that represent the most likely origins of this population based on geographic proximity. These include one from the Western cluster (here represented by samples from the British Isles; Fig. 1, Scenario 1), one from Central Europe (Fig. 1, Scenario 2), and one from Eastern Europe (Fig. 1, Scenario 3). Scenarios were compared and a reference table of 1,000,000 generations per scenario was generated. In preliminary analyses, we also included three additional scenarios wherein the northern Fennoscandia population was the result of admixture between pairs of European clusters recovered in Andersen et al. (2017). In these comparisons, an unmixed British Isles origin was supported by the "direct" comparison method ($P=0.76$), as implemented in DiyABC, but the "logistic

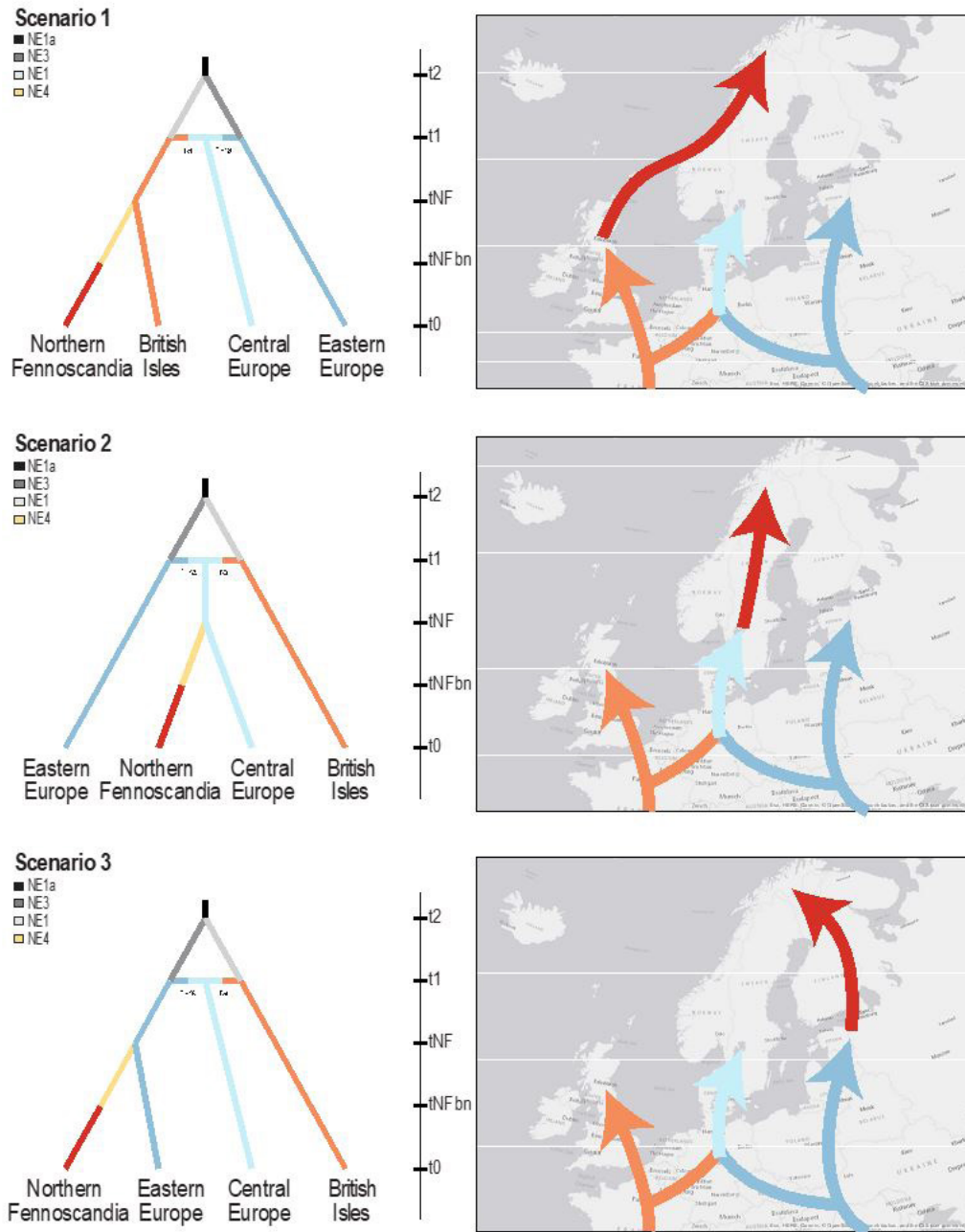


Figure 1. Graphical depictions of DiyABC scenarios depicting potential colonization scenarios by winter moth (*Operophtera brumata* L.) of northern Fennoscandia with branching patterns presented on the left and a map on the right. The map was drawn in ArcGIS v.10.3.1 (ESRI, Inc.) using the European Equal Area Projection. In each DiyABC scenario, colored lines represent different populations through time, with the Red, Dark Blue, Light Blue, and Orange lines representing the contemporary Northern Fennoscandia, Eastern Europe, Central Europe and British Isles populations, respectively. The Yellow line represents a historical pre-bottleneck Northern Fennoscandia population, while the Grey and Black lines represent ancestral populations prior to the admixture of the Eastern and Western European lineages. A time bar (not to scale) is drawn for each scenario to represent the order of merging and splitting events.

regression” method provided support for the scenarios that included admixture between the British Isles cluster and the other two European clusters, as well as an unmixed British Isles origin (P=0.52, P=0.27, and P=0.20 for the British Isles x Eastern Europe, British Isles x Central Europe, and British Isles only, respectively). We interpret this result to indicate that the expanded

suite of scenarios may include estimations for more parameters than can be effectively analyzed given the number of microsatellite loci in our dataset. We therefore report the results of the analyses without these admixture scenarios below.

For each scenario, we included multiple parameters to allow for changes in population sizes following

splitting/merging events and included the potential for a genetic bottleneck. We utilized the default mutation model parameters, except that the minimum mean mutation rate was set to 1×10^{-5} , and maximum values for the mean and individual locus coefficient P 's were both set to 1.0. We removed four loci with especially large allelic ranges (02339, 00925, 02191, and 12042) to improve the shape of the cloud of simulated datasets. We then calculated one sample (mean number of alleles, mean genetic diversity, mean size variance) and two sample (F_{ST} , classification index, and $(d\mu)^2$ distance) summary statistics. Priors and parameter ranges are presented in Supplementary Table S3.

To determine the scenario(s) that most closely modeled the evolutionary history of winter moth in northern Fennoscandia, we used the *Logistic Regression* test implemented in *DiyABC* based on comparisons of 1% of simulated datasets closest to the observed data (Cornuet et al., 2008, 2014). To determine the goodness-of-fit of simulated scenarios, first a principle components analysis (PCA) was conducted, using the posterior distributions of summary statistics in comparison to the observed dataset (Supplementary Fig. S2) using the *Perform Model Checking* analysis. Then, error-rates were estimated using the *Evaluate Confidence in Scenario Choice* analysis globally and individually for the supported scenarios, both analyses were carried out as implemented in *DiyABC*.

Results

Sampling strategy, DNA extraction, and microsatellite amplification

Five-hundred and fifty-two individual winter moths were included after removing individuals from which fewer than 20 of 24 polymorphic microsatellites were

amplified as part of this study. To that dataset, 249 individuals genotyped in Andersen et al. (2017, 2019) were added to increase the geographic sampling of winter moth populations.

Population genetic statistics and genetic distances

For each population with ≥ 10 genotyped individuals, population genetic statistics are presented in Supplementary Table S4. The population displaying the highest number of effective alleles was Bialostocka, Poland ($Eff_Na = 5.116$), and the population with the highest level of observed heterozygosity was Reinhardshagen, Germany ($H_o = 0.668$). In contrast, the Reykjavik, Iceland population had both the lowest number of effective alleles ($Eff_Na = 1.964$) and the lowest level of observed heterozygosity ($H_o = 0.359$). As per previous studies (Andersen et al., 2017; Andersen et al., 2019), all sampled localities displayed significant deviations from Hardy-Weinberg Equilibrium ($P < 0.05$ for all). The average proportion \pm standard error (SE) of null alleles across sites and loci was 0.07 ± 0.01 . The average value \pm SE for F_{ST} among population pairs was 0.1513 ± 0.0037 . Values for all pairwise F_{ST} comparisons are presented in Supplementary Table S5. The NeighborNet analyses (Fig. 2) indicated that populations of winter moth were grouped similar to patterns observed in the Bayesian clustering analyses (Supplementary Fig. S1). This analysis indicated that the populations from northern Fennoscandia are most closely related to the populations from England, Northern Ireland, and Scotland, and not to the populations from southern Fennoscandia or eastern Europe as would be expected if they were the result of contiguous northward range expansion. The population from Reykjavik, Iceland, was placed on the end of a long branch related to both the British Isles and northern

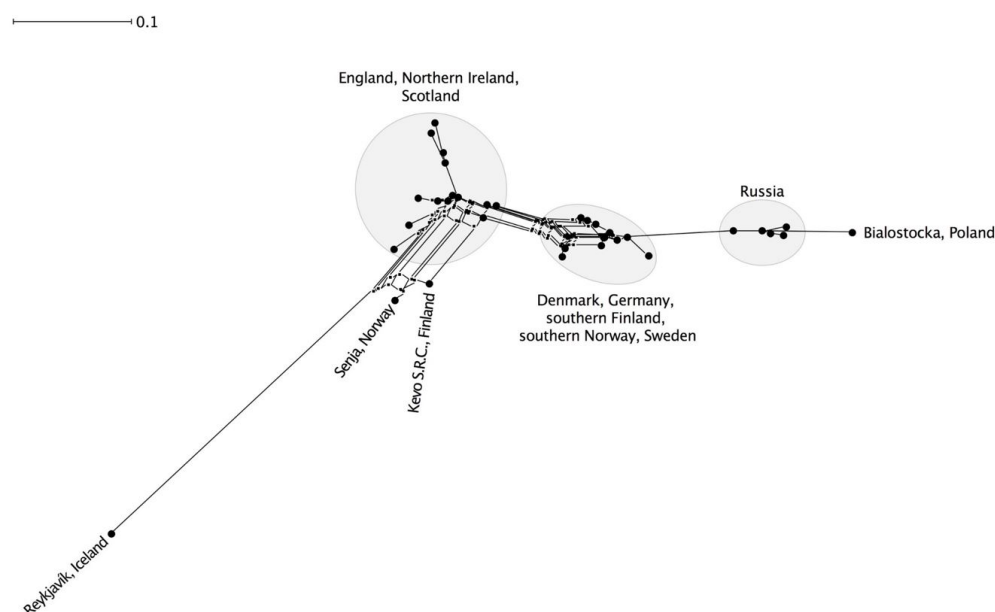


Figure 2. Neighbor-Net distance tree based on pairwise F_{ST} estimates for winter moth (*Operophtera brumata* L.) populations collected from across northern Europe. Individual sample localities are represented by bold circles. Shading is used to group samples into geographic regions, and individual populations are labeled when possible.

Fennoscandia populations. Globally, no locus-pairs showed evidence of LD ($\alpha = 0.05$), however; within populations an average of $8.32 (\pm 0.94)$ locus-pairs showed evidence of LD (Supplementary Table S4).

Bayesian genetic clustering

The mean negative log-likelihood scores increased with increasing numbers for K before reaching a plateau around $K= 6$ (Supplementary Fig. S3). Based on the ΔK statistic calculated in StructureHarvester,

$K=3$ represented the optimal number of genetic clusters present in the dataset, though a second peak indicating additional population sub-structure was also observed at $K=5$. At $K=3$, clusters broadly represented individuals from eastern Europe, western Europe, and Iceland, while at $K=5$, clusters broadly represented individuals from eastern Europe, the British Isles, central Europe, northern Fennoscandia, and Iceland (Fig. 3 and Fig. 4). Specifically, one cluster included the population from Reykjavík, Iceland; one cluster

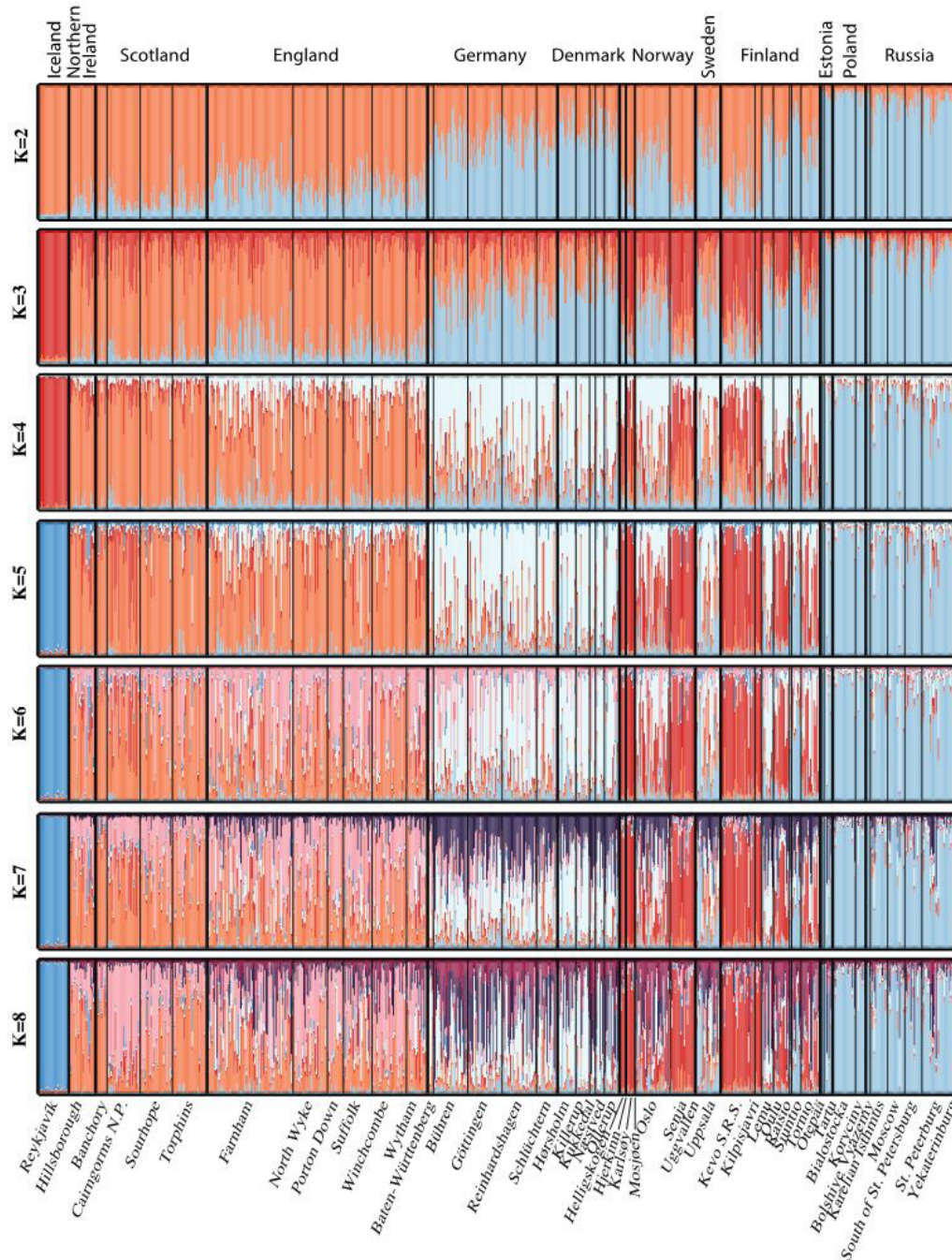


Figure 3. Proportional assignment (Q) of individual winter moth (*Operophtera brumata* L.) to genetic clusters (K) for values of $K=2$ through $K=8$, as summarized from ten independent Structure analyses using CLUMPAK. Each column represents a unique individual. Thick lines are drawn to differentiate samples from different countries, and narrow lines to differentiate different populations.

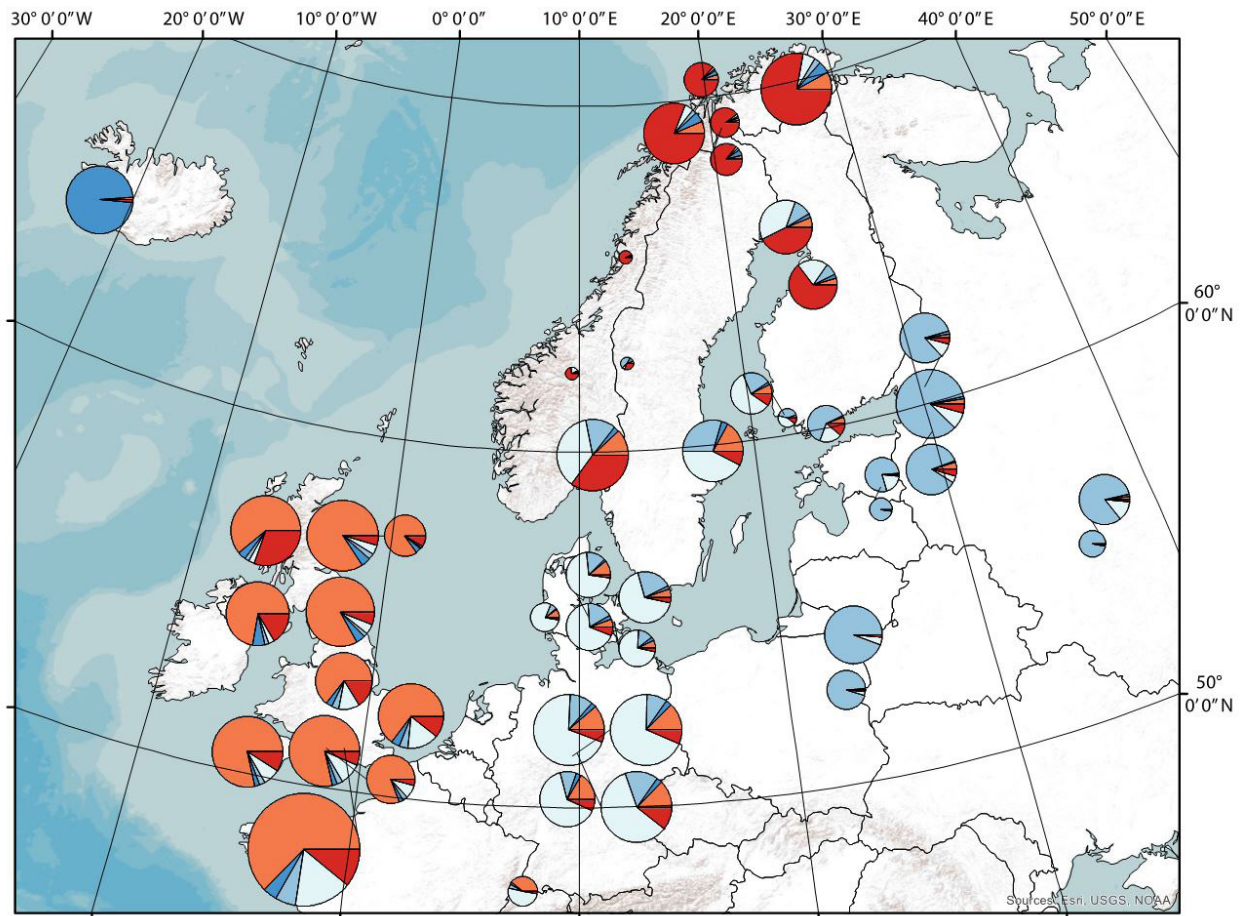


Figure 4. Geographical representation of the Bayesian clustering results for populations of winter moth (*Operophtera brumata* L.) collected in northern Europe. The shading of each chart represents the proportional assignment (Q) of individuals in that population based on the Structure results for $K=5$ genetic clusters, and the relative size of each chart indicates the number of samples. The map was drawn as per Figure 1.

included all populations from Estonia, Poland, and Russia, as well as the population from Siuntio, Finland; one cluster included all populations from England, Northern Ireland, and Scotland; one cluster included all populations from Denmark, Germany, and Sweden, as well as the Finnish populations from Lemu, Raisio, and Tornio, and the Oslo, Norway population; and the final cluster (representing Northern Fennoscandia) included the Finnish populations from the Kevo Subarctic Research Station, Kilpisjärvi, and from Oulu, and the Norwegian populations from Helligskogen, Hjerkin, Karlsøy, Mosjøen, and from Senja (Supplementary Fig. S1). For partitions of $K=2$ through $K=7$ and $K=9$, all ten independent Structure runs were congruent to one major cluster each using Clumpak (Supplementary Fig. S4). Two patterns of clustering were found for $K=8$ and $K=10$. At $K=8$, six runs were assigned to the major cluster and four to the minor cluster, and at $K=10$, nine runs were assigned to the major cluster and one to the minor cluster (Supplementary Fig. S5).

Historical demography

Results from simulations conducted during our DiyABC analyses indicated that the northern Fennoscandia

population was most closely related to the British Isles population (Fig. 5) and this association received approximately 100% support from the 'Logistic Regression' test (Supplementary Table S6). Model-checking analyses for the posterior distributions for summary statistics indicated that simulated datasets formed a distinct cloud around the observed dataset (Supplementary Fig. S2). The confidence in the scenario choice indicated an accuracy of 96.7% for the British Isles scenario. Posterior parameter estimates from simulations for the British Isles scenario indicated that the northern Fennoscandia population diverged from the population that settled in the British Isles $\sim 2,900$ years ago (ya), and that a possible bottleneck likely occurred around ~ 560 ya. All estimates for demographic parameters are presented in Supplementary Table S7.

Discussion

Insect outbreaks as a result of contemporary introduction of novel organisms have been well documented in response to increases in global trade and biotic homogenization (Samways 1999). However, in regions of the world where human mediated

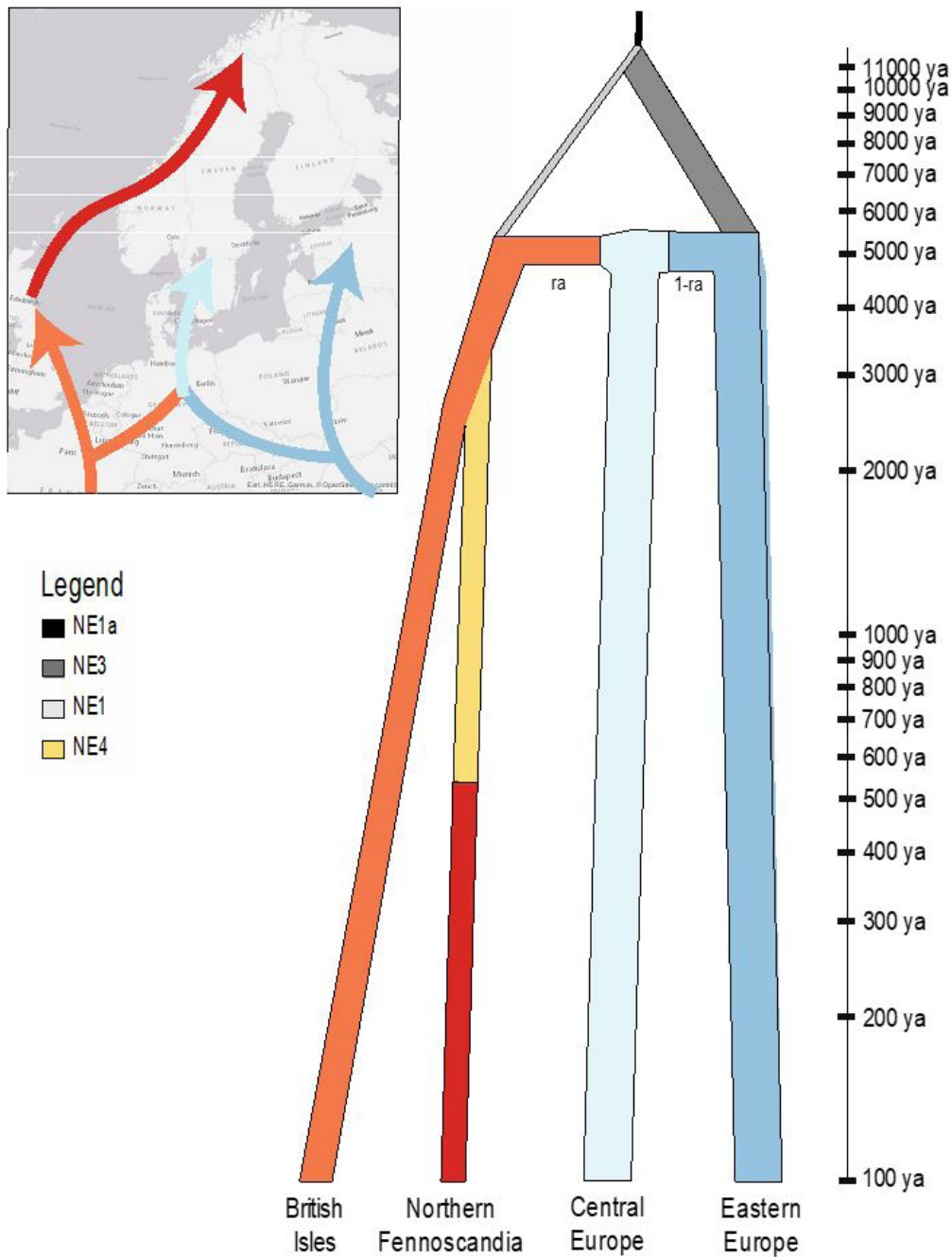


Figure 5. Graphical representation of the most supported Approximate Bayesian computation (ABC) scenario for the origins of the outbreaking winter moth (*Operophtera brumata* L.) population in northern Fennoscandia. Mean values for population sizes are signified by the width of bars and branching times (in years) are drawn on the y-axis using a Log10 scale. Shading used to represent ancestral populations (NE1, NE1a, NE3, and NE4) are presented in the legend, and the proportion admixture (ra) is presented with the width of the bars relative to the amount of admixture. See Supplementary Table S5 for mean estimates and confidence intervals. The map was drawn as per Figure 1.

disturbances and trade have been occurring for thousands of years, it is quite possible that some of the historical movements of pests might be the source of outbreaks observed today. In these regions, recent human-mediated changes to local ecosystems (e.g., Teste et al. 2011, De Prins et al. 2013, Hammond et al. 2018, Joseph et al. 2018) might also play an important role in the contemporary outbreaks of historically

introduced species. Here, we find evidence that outbreaking populations of winter moth in northern Fennoscandia are neither related to populations to the south of the region nor to populations to the east in western Russia and Poland. Rather, this population is most closely related to the population found in the British Isles from which it diverged ~2,900 ya (95% confidence interval = 958 to 5,610 ya). These

results suggest that winter moth invaded northern Fennoscandia by dispersal across the North Sea. Two possible modes of introduction, are plausible given the timing of this divergence: 1) natural dispersal, possibly using the Orkney Islands, and/or Shetland Islands as stepping-stones; or 2) human transport via early pre-Roman era trade between Scandinavian, Gaelic, or Pict merchants. We discuss these two possibilities below. In addition, we find that contrary to the commonly observed pattern that the introduction of a species to novel habitats results in genetic bottlenecks that reduce genetic diversity (Dlugosch and Parker 2008), the northern Fennoscandian winter moth population is just as diverse as populations in more southern localities (Supplementary Table S4). Whether this is due to the fact that the population was genetically diverse at the time of introduction, or that genetic diversity has rapidly been re-established within this population is unclear. Recent studies in the region have shown that some insect species have the ability to rapidly regain genetic diversity following introduction (e.g., Kaňuch et al. In Press). Similarly, multiple introductions have been found to increase the genetic diversity of introduced populations (e.g., Dlugosch and Parker 2008). More detailed analyses, particularly those utilizing genome wide single nucleotide polymorphisms (SNPs) could shed light on the drivers of the genetic diversity of winter moth populations in northern Fennoscandia, and these analyses might also help unravel why winter moth populations in this region are so adaptable in regards to changes in the local climate.

Human-mediated introduction of winter moth by Pre-Roman traders?

Archaeological records indicate that sea-faring peoples began the recolonization of the Scandinavian coastlines around 11,500 ya (Wickler 2019), and that extensive trade was occurring between peoples in both Scandinavia and southeastern Europe as early as 3,000 ya (Görman 1990). During Roman times, trade likely increased between these regions (Hornstrup et al. 2012), and even after the fall of the Roman Empire, historical records suggest that early Gaelic and Pict traders may have been in contact with Scandinavian traders for several centuries prior to the onset of the Viking raids (Noble et al. 2013). Recently, analyses of ancient DNA have shown that during this period, early traders moved food items such as Arctic Cod (*Gadus morhua*) between locations spanning from northern Norway to Germany (Star et al. 2017). As such, it is easy to imagine that these human-mediated movements resulted in the transportation of forest materials or fruit-trees from Scotland back to Scandinavia, and along with these goods, it is quite possible that winter moth was accidentally transported. Once established, this population could then have spread northward following warming climate periods and/or additional human-mediated dispersals finally reaching northern Fennoscandia approximately 100 ya, when it began to occur at outbreak densities (Jepsen et al. 2008). If this is the case, then the movement of winter moth from the British Isles to Fennoscandia might represent

one of the oldest identified examples of the accidental introduction of a forest pest by European traders.

Conversely, our results can not preclude the possibility that winter moth individuals could have dispersed from northern Scotland, across the North Sea to the Norwegian coast using the Orkney Islands and/or Shetland Islands as stepping stones. Recent winter moth studies have shown that wind direction influences the level of population synchrony between sites, presumably via wind dispersal of either larvae or adults (Vindstad et al. 2019). Larval ballooning (i.e., when larvae secrete silken threads and are dispersed through the wind) has also played an important role in the long-distance dispersal of winter moth across the Orkney Islands in the North Sea (Leggett et al. 2011).

Multiple post-glacial colonizations of Fennoscandia

In addition to the possibility of human-mediated dispersal, our results show that winter moth has colonized parts of Fennoscandia from different geographic regions as evident by the presence of multiple distinct genetic lineages in this region (Fig. 5). Populations in southern Finland, for example, appear to be of the “eastern” European genetic lineage, and suggest that this population of winter moth colonized the region following the retreat of glaciers along the eastern coast of the Baltic Sea. At the same time, a different genetic lineage that corresponds with the “admixed” lineage that inhabits parts of France, Germany and Switzerland reported in Andersen et al. (2017), followed the retreat of the glacial ice sheets and the reforestation of Fennoscandia by crossing the Jutland Peninsula and the Danish Archipelago into southern Sweden and southern Norway. Similar to Andersen et al. (2017), our results suggest the presence of several distinct populations within Europe (Jepsen et al. 2016), and that the presence of geographically structured populations may be a more parsimonious hypothesis for the decadal outbreaks observed across Europe compared to outbreak waves moving in an east-west direction across Europe proposed by Tenow et al. (2013).

In addition, we examined the post-glacial colonization of Iceland. However, our ABC analyses were unable to reconstruct the timing or source of the colonization of Iceland, potentially due to the fact that we only were able to sample moths from a single locality. While we hope to add additional moths from Iceland for future analyses, it is interesting to note that although this species has been reported to cause severe defoliation of various broad-leaved shrubs and trees (Ottósson 1982), there are no reported outbreaks of winter moth on birch woodlands in Iceland. In contrast, insect outbreaks in native birch forests by other introduced arthropods (Levanič and Eggertsson 2008) have been known in Iceland for centuries, which have become increasingly intense in recent decades (Halldórsson et al. 2013).

Conclusions

Here we find that an outbreaking population of winter moth in northern Fennoscandia likely originated from the British Isles, either via human transport or

natural stepping-stone dispersal. Studies in the region have shown that this outbreaking population has been spreading northward in response to climate change. It is therefore likely that populations were introduced to more southern parts of coastal Norway and have spread northward following their establishment. Further sampling of the region, including additional coastal locations, might provide a more detailed picture of the spread of winter moth in response to climate change in Northern Europe.

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Author Contributions

JCA, NPH, and JSE, conceived the ideas; BPH conducted laboratory work; JUJ, SH, TK, ICB, SAK, TTH, JM, YNB, AVS, and OPLV, conducted the fieldwork and collected samples; JCA, NPH, AC, and BPH analyzed the data; all authors contributed to the writing of the manuscript.

Data Accessibility

Genotype data for all samples are available through the Dryad Digital Repository at <https://doi.org/10.5061/dryad.gf1vhhmfn>

Supplementary Material

The following supplementary materials are available as part of the online article from <https://escholarship.org/uc/fb>

Table S1. Locality information for all sampled winter moth (*Operophtera brumata* L.) individuals collected in northern Europe including whether or not samples from the population were previously reported in Andersen et al. (2017) (noted as “A’17”).

Table S2. Information about which winter moth (*Operophtera brumata* L.) samples were used during DiyABC analyses examining the geographic origins of the outbreaking population in northern Fennoscandia and to which genetic cluster (“Cluster”) each sample was assigned.

Table S3. Parameter priors for all DiyABC scenarios simulating possible origins of the winter moth (*Operophtera brumata* L.) population in northern Fennoscandia. Parameter names are presented following the notations in Figure 5.

Table S4. Population genetic summary statistics for localities with $n \geq 10$ individual winter moths (*Operophtera brumata* L.) genotyped: including the average effective number of alleles (Eff), the expected Heterozygosity (H_E), the observed Heterozygosity (H_O), the inbreeding coefficient (G_{IS}), the average proportion of Null Alleles across microsatellite loci (Null), and the number of locus-pairs showing the presence of linkage disequilibrium (LD).

Table S5. The degree of genetic differentiation (F_{ST}) between populations of winter moth (*Operophtera brumata* L.) calculated using the software program GenoDive v.2.0b27

Table S6. Logistic regression results for the scenarios estimating the geographic origins of the winter moth (*Operophtera brumata* L.) population in northern Fennoscandia based on DiyABC simulations (Scenario 1 = British Isles origin, Scenario 2 = Central European origin, and Scenario 3 = Eastern European origin). Results are presented as the mean value with 95% confidence intervals in brackets for the inclusion of 36 summary statistics from different numbers of simulated datasets (n) closest to those from the observed dataset.

Table S7. Parameter posterior estimates for the best supported DiyABC scenario that estimated the northern Fennoscandia winter moth (*Operophtera brumata* L.) population to have originated from the British Isles. Estimates are presented using the notations in Figure 5. **Figure S1:** Hierarchical clustering diagram based on the population assignment coefficients (Q) estimated in STRUCTURE for populations of winter moth (*Operophtera brumata* L.) collected from northern Europe.

Figure S2: Principal component analysis (PCA) representing the goodness of fit of posterior estimates (solid circles) compared to prior estimates (open circles) for the DiyABC scenario that indicates that the northern Fennoscandia population of winter moth (*Operophtera brumata* L.) originated in the British Isles (Scenario 1) in relationship to the observed dataset (yellow circle).

Figure S3: The mean (circle) and standard deviation (lines) of the negative log-likelihood scores for Structure runs for values of $K=2$ through $K=10$, as summarized using STRUCTUREHARVESTER.

Figure S4: Clumpak summary of major modes for the proportional assignments (Q) of winter moth (*Operophtera brumata* L.) individuals collected from northern Europe to $K=2$ through $K=10$ distinct genetic clusters. Numbers represent the population assignments presented in the single-line format Structure file available through the Dryad Digital Repository at <https://doi.org/10.5061/dryad.gf1vhhmfn>

Figure S5: Clumpak summary of minor modes for the proportional assignments (Q) of winter moth (*Operophtera brumata* L.) individuals collected from northern Europe for $K=8$ and $K=10$ distinct genetic clusters. Numbers represent the population assignments presented in the

single-line format structure file available through the Dryad Digital Repository at <https://doi.org/10.5061/dryad.gf1vhhmnf>

Figure S6: StructureHarvester results representing the ΔK (rate of change) statistic presented in Evanno et al. (2005) as estimated based on the summary of 10 independent structure runs for each value of K from winter moth (*Operophtera brumata* L.) individuals collected from northern Europe.

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