



Using DNA profiling to investigate human-mediated translocations of an invasive species



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ABSTRACT

The reconstruction of invasion history is the goal or foundation of many investigations of biological invasions. This study applies DNA profiling to investigate the sources and vectors of new propagules, to detect illegal human-mediated translocations and to improve the management of invasions by identifying invasion pathways that can be targeted for more stringent control. We use the European invasion of the American Eastern grey squirrel as a focal example. Many human-mediated translocations of this species have occurred in Europe since the 19th century. We built a genotype database of 1421 individuals from 59 locations across Europe and one in the USA, with each individual genotyped at 12 highly polymorphic microsatellites. DNA from newly detected populations and individuals of unknown sources were compared with this database. Our results indicated illegal human-mediated translocations in Aberdeen, the Isle of Skye and Northumberland in the UK, and revealed precise details of illegal squirrel trade in Italy. We recommend that multi-locus genotype databases be set up for all major invasive species considered attractive or ornamental, as these are often subject to illegal translocations through human actions such as the pet trade.

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1. Introduction

Molecular diagnostic techniques provide a potentially useful but under-used tool for biosecurity. Biosecurity was defined by Pyšek and Richardson (2010) as “the management of risks posed by organisms to the economy, environment, and human health through exclusion, mitigation, adaptation, control, and eradication”. Molecular methods are potentially very valuable in reconstructing the history of invasion processes, a critical step in analysing biological invasions (Cristescu, 2015; Estoup and Guillemaud, 2010). The geographic pathways followed by the founders of the invading populations, the type of invasion vector, the number of introduced individuals and the pathways of spread are all components of the invasion history, and provide key information about the origin and genetic composition of the invading populations (Dlugosch and Parker, 2008a; Estoup and Guillemaud, 2010). This information can be useful for management of an invasion, and may be substantially illuminated through molecular diagnostic techniques.

Over the last few decades, the reconstruction of invasion history has become the foundation of many long-term investigations of biological

invasions (Dlugosch and Parker, 2008b; Estoup and Guillemaud, 2010; Ficetola et al., 2008; Walker et al., 2003). Humans are the main force facilitating the global spread of invasive species: geographic barriers to dispersal and gene flow are continually being removed by human trade and travel (Cristescu, 2015; Mooney and Cleland, 2001). The relatively recent history of many human-mediated invasions suggests that approaches that adopt DNA profiling can be very useful in serving the goal of reconstructing the most likely invasion scenarios (Cristescu, 2015).

DNA profiling is already an important tool for identifying illegal trades in protected species. Its application to detect crimes against protected species is becoming widespread, with examples including detection of the sources of ivory, tiger bone, mouflon carcasses, and other products (Lorenzini et al., 2011; Ogden et al., 2009; Wasser et al., 2008, 2015; Wetton et al., 2002). DNA profiling has also been successfully applied to the detection of illegal introductions and translocations of invasive or potentially invasive species that could threaten biodiversity (Richardson and Pyšek, 2006) or have huge economic impacts (Kettunen et al., 2008), though such applications have been less common than applications to protected species. It is a goal of this study to advocate expanded application of DNA profiling to the study and management of invasions.

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Applications of DNA profiling to invasions involve special difficulties not encountered in typical applications to protected species; the example applications of this study provide an illustration of how some difficulties can be overcome or circumvented. Human mediated invasions often involve complex routes with multiple sources of introduction and repeated introductions (Wilson et al., 2009). New propagules of invasive species are often noticed only once populations establish and densities become high, sometimes many years after the introductory event (Crooks and Soulé, 2001; Geller et al., 1997). Allelic frequencies of the new population may have started to differentiate from those of the source by that time, making it more challenging to find the source of the new invasive population and to reconstruct its history. Many difficulties associated with the reconstruction of the dispersal history of widespread invasive organisms are primarily related to the availability of an extensive reference database, to minimize errors in results caused by 'ghost populations' which have not been sampled but that acted as sources of new populations (Estoup and Guillemaud, 2010).

The example species used for this study is the American Eastern grey squirrel (*Sciurus carolinensis*), a highly invasive rodent that has been introduced and translocated multiple times in Europe and elsewhere (Bertolino, 2009; Martinoli et al., 2010; Middleton, 1931). In the UK and Ireland, grey squirrels were introduced for the first time in 1876 and 1911 respectively and have since expanded quickly. Through a combination of competition and a disease they carry but do not suffer mortality from, their presence in the UK has resulted in the almost complete replacement of red squirrels (*Sciurus vulgaris*) in much of the red squirrels' original distribution (Gurnell et al. 2004). Restrictions of grey squirrel movements are now the subject of legislation in Europe. The trade of this species among countries within Europe is now regulated by the inclusion of the species in Annex B of European Community Regulation no. 338/97, the European Union Wildlife Trade Regulation that enforces the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES); and by the Regulation 1143/2014 on invasive alien species, which came into effect on 1 January 2015. The species is further regulated by national laws such as the Italian Legislative decree 24/12/2012, aimed at forbidding the importation and trade of grey squirrels and their release into the wild. In the UK, the import, keeping and release of grey squirrels has been prohibited by several national laws since the 1930s (Bosch and Lurz, 2012): the 1932 Destructive Imported Animals Act; the 1937 grey squirrel Prohibition of Importation and Keeping Order; and Section 14 of the Wildlife and Countryside Act of 1981.

We use four case studies to illustrate the potential of DNA profiling for reconstructing invasion histories and to examine how methods might be adapted from conservation applications to the peculiarities of this different context. We defined our tasks as building an extensive genetic database that can reduce the risks of errors from ghost populations, and answering the following questions: 1) What is the accuracy of the available assignment methods and software in the identification of sources of invasions, and what are the best available tools for determining source populations in the invasion context? 2) Can we detect the origins of the specific individuals and populations of interest in the aforementioned case studies, and do the results point to human-mediated releases or to natural expansion? And 3) Can we detect the origin of a population even if the population is sampled for the first time some years after its introduction? By addressing these questions, we assess the potential effectiveness of DNA profiling as a biosecurity tool for understanding and managing invasions.

2. Material and methods

2.1. Case studies

We present four case studies. Case study 1 involves the Isle of Skye (Scotland, UK; henceforth SKYE, all location abbreviations are given on Fig. 1 and Table A.1 in Supplementary material). SKYE is connected to

the mainland only by the A87 road bridge. There were no known squirrels, either the Scottish-native red or invasive grey, on the island prior to 2010. In October 2010 a grey squirrel was captured in the town of Breakish, on SKYE. The nearest known grey squirrel populations to Breakish are on the Scottish mainland at Fort William, and on the east side of Loch Ness, both approximately 130 km away. An anonymous resident informed authorities that a grey squirrel stowed away under the bonnet of a car from Glasgow and was released at Breakish. One of the authors (LS) was asked to assess the reliability of this report.

Case study 2 refers to a grey squirrel caught in 2010 in Northumberland (UK), near Wooler, in the Happy Valley (henceforth HAPPY) (Fig. 1), an area where grey squirrels were not previously known. Grey squirrels are now (2015) well established in Northumberland, having colonized the area from adjacent counties in Scotland to the north and from southern Northumberland and County Durham to the south (Signorile et al., 2014b, 2015). For conservation purposes it would have been important to know the origin of the isolated squirrel to control and minimize grey squirrel spread and to assess the relative likelihoods that the captured squirrel represented natural expansion or a human-mediated translocation.

Case Study 3 illustrates some of the potential differences between applications of DNA profiling methods to new populations, as opposed to isolated individuals. There is an established population of grey squirrels in Aberdeen, Scotland (henceforth AB) (Fig. 1), and the origin, time and mechanism of arrival of the founders of this population are poorly understood (Harris et al., 2006). Bryce (1997), examining Forestry Commission questionnaires assessing red/grey squirrel presence for the period 1980–1994, indicated that the animals arrived in that time range. However, records registered in the National Biodiversity Network's (NBN) Gateway database suggests that the squirrels arrived in the late 1960s. Furthermore, it is not known whether the population in AB was the result of a human-mediated introduction event or, as suggested by Staines (1986), a natural expansion from populations in Tayside, approximately 60 km away. Our aim was to determine the source of this population. In addition to providing a useful simple illustration of differences between conservation and invasion biosecurity, this case study also provides information about invasion history.

Case study 4 is the most complex and interesting of our case studies. In Italy the most important introduction occurred in 1948 when four grey squirrels were introduced near Turin and spread throughout the river Po plain, south of the city. In the last 10 years, 22 new grey squirrel populations have appeared in Lombardy, northern Italy, and one new population has appeared in the central part of the peninsula, in Umbria (Martinoli et al., 2010; Signorile et al., 2014a). The origin of the populations in Lombardy is unclear. The first nucleus was found in the Ticino Valley, in a regional park (Fig. A.2). The Valley is not far from the town of Trecate (Novara, Piedmont) where in 1994 six squirrels purchased from a known pet retailer were released for ornamental purposes. The pet retailer claimed he had bought the squirrels from a Dutch importer (Bertolino et al., 2000). The animals were thought to have been removed from Trecate, but some individuals could already have dispersed to the Ticino Valley before the removal (Bertolino et al., 2000). Other grey squirrel populations in Lombardy can therefore have one or more of the following origins: a natural expansion from the populations in the Ticino Valley; human-mediated introductions from that source; human-mediated introductions from Piedmont, the nearby region where the grey squirrel was first introduced into Italy; or introductions from the native range (North America) or from elsewhere outside Italy. The origin of the population in Umbria, in the peninsular part of Italy, is better known. In 1999 seven squirrels were purchased from an Italian pet trader by a private wildlife park and kept on display outdoors in Perugia (henceforth PG). The following year all the squirrels were declared to have escaped and the resulting population is now slowly spreading (Signorile et al., 2014a). In addition to the Lombardy and Umbria (PG) populations, a single grey squirrel was observed in 2009

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