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## Similar yet different: co-analysis of the genetic diversity and structure of an invasive nematode parasite and its invasive mammalian host

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### ABSTRACT

Animal parasitic nematodes can cause serious diseases and their emergence in new areas can be an issue of major concern for biodiversity conservation and human health. Their ability to adapt to new environments and hosts is likely to be affected by their degree of genetic diversity, with gene flow between distinct populations counteracting genetic drift and increasing effective population size. The raccoon roundworm (*Baylisascaris procyonis*), a gastrointestinal parasite of the raccoon (*Procyon lotor*), has increased its global geographic range after being translocated with its host. The raccoon has been introduced multiple times to Germany, but not all its populations are infected with the parasite. While fewer introduced individuals may have led to reduced diversity in the parasite, admixture between different founder populations may have counteracted genetic drift and bottlenecks. Here, we analyse the population genetic structure of the roundworm and its raccoon host at the intersection of distinct raccoon populations infected with *B. procyonis*. We found evidence for two parasite clusters resulting from independent introductions. Both clusters exhibited an extremely low genetic diversity, suggesting small founding populations subjected to inbreeding and genetic drift with no, or very limited, genetic influx from population admixture. Comparison of the population genetic structures of both host and parasite suggested that the parasite spread to an uninfected raccoon founder population. On the other hand, an almost perfect match between cluster boundaries also suggested that the population genetic structure of *B. procyonis* has remained stable since its introduction, mirroring that of its raccoon host.

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### 1. Introduction

The widespread introduction of non-native flora and fauna resulting from anthropogenic activities carries the risk of simultaneously introducing pathogens into new areas (Taraschewski, 2006; Kelehear et al., 2013). Indeed, parasite invasions can constitute a problem for biodiversity conservation, agriculture and human/animal health (Daszak et al., 2000; Walker et al., 2008). Parasitic nematodes are likely to be translocated with their hosts, as they are widespread and many animal and plant species have one or more associated species of roundworm (Taraschewski, 2006; Gilbert and Wasmuth, 2013; Demiaszkiewicz, 2014). Once introduced, non-indigenous nematodes can become highly inva-

sive – even reducing the occurrence of native parasites in their new hosts in some cases (Radwan et al., 2010) – and can be a major cause of destructive disease (Cheng et al., 2008; Plantard et al., 2008).

However, the ability of pathogens to adapt to new environments and hosts is likely to be affected by their overall degree of genetic diversity. Parasite populations experiencing frequent and severe bottlenecks are expected to be less diverse and, having less variation for natural selection, slower to adapt than large populations that maintain a constant size (McDonald and Linde, 2002). Alien species generally experience a genetic bottleneck at introduction and there are many examples of genetically depauperate invaders (Dlugosch and Parker, 2008), including parasitic nematodes (Wielgoss et al., 2008; Boucher et al., 2013). Conversely, some invasive nematodes have genetic diversity levels comparable to the source population, probably as a result of multiple

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introductions from different origins (Cheng et al., 2008; Valadas et al., 2012) or, in the case of animal parasites, large infra-population size. Understanding genetic diversity can provide an indication of the evolutionary potential of invasive nematodes and therefore may be relevant for predicting the potential success of control programmes.

Gene flow between geographically distinct populations counteracts genetic drift and increases effective population sizes. Pathogens that exhibit a high degree of genetic exchange are therefore likely to have a greater genetic diversity than those that are genetically isolated (McDonald and Linde, 2002). Gene flow will be facilitated in species whose life-history characteristics ensure population connectivity over large geographic scales (Gilleard and Beech, 2007). Dispersal of parasitic nematodes with direct life cycles is expected to be mediated by host dispersal and the population genetic structures of both host and nematode can be highly correlated (Mazé-Guilmo et al., 2016). Host and parasite gene flow might, however, not be equivalent and there may be large differences in the effective population sizes as some hosts are not infected and prevalence rates can differ across the landscape (Criscione et al., 2006). Analysis of the population genetic structures of parasites and comparison with those of their hosts will contribute to estimating parasite migration rates and assessing gene flow patterns (Mazé-Guilmo et al., 2016). While there have been several studies co-analysing the genetic structures of parasites and their hosts, especially at larger spatial scales and/or only using mitochondrial DNA (Mazé-Guilmo et al., 2016), the number of regional studies that analyse the landscape genetic structures of the parasite and its host are rarer (e.g., Nadler et al., 1990; Lavandero et al., 2011; Dharmarajan et al., 2016), especially in the case of invasive species (but see Prugnolle et al., 2005).

The raccoon roundworm (*Baylisascaris procyonis*), a dioecious and obligate sexual nematode, is a common gastrointestinal parasite of the raccoon (*Procyon lotor*), its definitive host (Kazacos, 2001). The parasite is widespread in its native North American range (Hernandez et al., 2013) where prevalence of infection can be as high as 82% (Kazacos, 2001). Infected raccoons can shed millions of *B. procyonis* eggs in their faeces daily, which contaminate the environment and remain infective for years. *Baylisascaris procyonis* larvae are highly non-specific with regard to paratenic hosts: over 130 vertebrate species – including humans – have been reported to exhibit the clinical symptoms of larval migrans (Kazacos, 2001; Page, 2013). Transmission to paratenic hosts occurs at latrines when eggs are ingested (Sorvillo et al., 2002). While *B. procyonis* infections in the definitive host are normally benign, they can be fatal in paratenic hosts, including – rarely – in humans (Kazacos, 2001).

Translocations of raccoons have increased the global geographic range of *B. procyonis* (Beltrán-Beck et al., 2012; Page, 2013). Raccoons are particularly abundant and wide-spread in Germany, where the whole population descends from at least four separate introduction events (Frantz et al., 2013; Fischer et al., 2015). In comparison with its host, the geographic range of the parasite in Germany appears to be more restricted, with the parasite being absent from at least one of the four major founding populations (Schwarz et al., 2015). The number of introduced *B. procyonis* may therefore have been small(er), resulting in a severe(r) genetic bottleneck. Infected raccoons can, however, carry several hundred nematodes in their intestines (Kazacos, 2001). Depending on the inter-individual relatedness of such an infra-population, a small number of infected raccoons might suffice, however, for the parasite to maintain a high genetic diversity in its new range (Criscione et al., 2005).

If *B. procyonis* was introduced multiple times and if distinct introductions were followed by genetic admixture between clusters, genetic diversity levels of *B. procyonis* in Germany might be

comparable with the source population, or even higher (Kolbe et al., 2004). The pattern and degree of genetic admixture between geographically separated *B. procyonis* populations, however, is likely to depend on raccoon dispersal capabilities. Landscape barriers that separate raccoon populations are likely to have the same effect on *B. procyonis* populations. For example, Sarkissian et al. (2015) have recently shown a large river in Michigan, USA to be a gene flow barrier to *B. procyonis*. However, the proportion of trans-barrier-dispersing raccoons that fail to reproduce might be high (Riley et al., 2006). These hosts can nevertheless contribute to the spread and effective dispersal of parasites. In other words, populations of *B. procyonis* might conceivably be less genetically structured than those of its host (Mazé-Guilmo et al., 2016). Finally, prevalence rates of *B. procyonis* can differ substantially across the landscape (Gompper and Wright, 2005; Page et al., 2008), which might be an indication of large population fluctuations and colonisation events, leading to highly subdivided nematode populations.

Here, we analysed the population genetic structure of the raccoon roundworm and its host at the intersection of distinct raccoon founder populations that were known to be infected with *B. procyonis*. The overall objectives of this study were to estimate the number of colonisation events by the parasite, to understand its degree of genetic diversity and to jointly analyse the population genetic structure of the parasite and its host to make inferences about gene flow patterns in both species.

## 2. Materials and methods

### 2.1. Invasion history and sample collection

It was commonly assumed that all German raccoons stemmed from a small number of founders and two separate founding events in western (Hesse) and eastern (Brandenburg) Germany during the 1930s and 1940s, respectively (Lutz, 1995; Frantz et al., 2005). However, recent genetic work has shown the invasion history to be rather more complex (Fig. 1; Frantz et al., 2013; Fischer et al., 2015). In addition to two genetic populations centred around the known introduction sites, distinct raccoon populations were identified in Saxony (eastern-central Germany) and around the Harz Mountains in central Germany (Fig. 1). A fifth genetic population was identified in the city of Kassel, but Fischer et al. (2015) concluded that it probably did not stem from a distinct introduction event. A further two clusters were formed mainly by samples from Luxembourg and some outliers, respectively. The presence of *B. procyonis* has been reported from the western (Hesse) and central (Harz Mountains) German populations (Helbig, 2011; Michler and Michler, 2012), as well as from the city of Kassel, where 74% of latrines in inhabited houses have been shown to be contaminated with nematode eggs (Gunesch, E., 2003. Untersuchungen zur Populationsökologie urbaner Waschbärpopulationen. *Procyon lotor* L., 1758. am Beispiel der Stadt Kassel, Master's Thesis, Georg-August-Universität Göttingen, Germany). In contrast, there is no evidence for the presence of *B. procyonis* in the eastern, Brandenburg population (Schwarz et al., 2015) and, to the best of our knowledge, no information on the presence of the parasite in the eastern-central Saxony population.

During the years 2011–2015, we collected *B. procyonis* from 255 infected raccoons legally harvested in the southern parts of the German federal states of Lower Saxony and Saxony-Anhalt, as well as from the city of Kassel (Fig. 1). The study site was located at the intersection of two distinct raccoon founder populations (central and western) that were both known to be infected with *B. procyonis*. We genotyped all the raccoon hosts as well as one roundworm per host. We used the Germany-wide raccoon genotype

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