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Lack of genetic structure in pinworm populations from New World primates in forest fragments ☆

Brenda Solórzano-García [a,b], Jaime Gasca-Pineda [c], Robert Poulin [d], Gerardo Pérez-Ponce de León [a,*]

[a] *Departamento de Zoología, Instituto de Biología, Universidad Nacional Autónoma de México, A.P. 70-153, C.P. 04510 México D.F., Mexico*
[b] *Posgrado en Ciencias Biológicas, Instituto de Biología, Universidad Nacional Autónoma de México, Mexico*
[c] *Departamento de Biología de la Conservación, Centro de Investigación Científica y de Educación Superior de Ensenada, Baja California Sur 22860, Mexico*
[d] *Department of Zoology, University of Otago, P.O. Box 56, Dunedin 9054, New Zealand*

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ABSTRACT

Microevolutionary processes in parasites are driven by factors related to parasite biology, host abundance and dispersal, and environmental conditions. Here, we test the prediction that isolation of host populations results in reduced genetic diversity and high differentiation among parasite populations. We conducted a population genetic analysis of two pinworms, *Trypanoxyuris minutus* and *Trypanoxyuris atelis*, commonly found parasitizing howler and spider monkeys in tropical rainforests across south-eastern Mexico, whose populations are currently isolated due to anthropogenic habitat loss and fragmentation. Mitochondrial DNA was employed to assess parasite genetic patterns, as well as to analyse their demography and population history. Both pinworm species showed high haplotype diversity but, unexpectedly, lower nucleotide diversity than that reported for other parasites. No genetic differentiation or population structure was detected in either pinworm species despite habitat loss, fragmentation and host isolation. Several scenarios are discussed that could help to explain the genetic panmixia found in both pinworm species, including higher than expected primate inter-fragment dispersal movements, and passive dispersal facilitating gene flow between parasite populations. The results suggest that large population sizes of parasites could be helping them to cope with the isolation and fragmentation of populations, delaying the effects of genetic drift. The present study highlights the complexity of the drivers that intervene in the evolutionary processes of parasites. Detailed genetic studies are needed, both in host and parasite populations, to assess the effects that habitat perturbation and environmental changes could have on the evolutionary dynamics of pinworms and primates.

1. Introduction

Microevolution in parasites is mediated by many factors related to the biology of each parasite and that of its host, as well as to environmental conditions intervening in their subsistence. Parasite life history traits such as life cycle complexity, reproductive mode and population sizes, together with host abundance and dispersal, regulate some of the most important aspects of parasite population genetics (Nadler, 1995; Criscione et al., 2005; Blasco-Costa and Poulin, 2013; Lagrue et al., 2016). General patterns of parasite genetic structure have not been investigated in great detail (Blasco-Costa and Poulin, 2013), however, sexually reproducing parasites which are capable of infecting multiple host species, and with high dispersal capabilities and long-lived definitive hosts, are expected to be highly diverse and poorly differentiated. In contrast, strong host specificity, autogenic life cycles, and an aggregated distribution of host populations (either through behavioural, environmental or geographical factors) will most likely promote genetic structure among parasite populations (Nadler, 1995; Criscione and Blouin, 2004; Barrett et al., 2008; Blasco-Costa et al., 2012).

In addition, processes of parasite local adaptation, speciation and coevolutionary dynamics will be affected by host and parasite gene flow (Criscione et al., 2005; Lagrue et al., 2016). Genetic interchange among parasite populations is believed to be strongly correlated with host dispersal ability (Blouin et al., 1995; Prugnolle et al., 2005; Louhi et al., 2010); however, host vagility is mediated not only by its dispersal capability but also by landscape properties such as habitat extent and arrangement, connectivity and matrix configuration (Tischendorf et al., 2003). Habitat loss and fragmentation are considered among the most important threats for

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☆ Note: Nucleotide sequence data reported in this paper are available in the GenBank™ database under the accession numbers MF379058 to MF379260.

* Corresponding author.

E-mail address: ppdleon@ib.unam.mx (G. Pérez-Ponce de León).

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biodiversity (Fischer and Lindenmayer, 2007). The expansion of human settlements and the associated changes in landscape configuration have reduced native vegetation to patches within a matrix of anthropogenic vegetation, harbouring isolated wildlife populations. The severity of the effects that these processes could have on the persistence of any organism are species-specific and depend on the species' ecology and life history requirements (Betts et al., 2014).

Oxyurid nematodes of the genus *Trypanoxyuris* are commonly found in New World primates (Hugot et al., 1996). Pinworms of primates are highly host-specific and show interesting patterns of host-parasite coevolution (Hugot, 1999). These nematodes are characterized by having a direct life cycle with no free-living stages. They present a haplodiploid reproduction mode where males are haploid and derived from unfertilized eggs, while females are diploid and derived from fertilized eggs (Adamson, 1989). Transmission occurs by the ingestion of eggs which are passed to the external environment with host faeces and deposited in clusters; contact with infected conspecifics, autoinfection and retroinfection are thus common transmission modes (Cook, 1994; Felt and White, 2005; Gónzalez-Hernández et al., 2014).

Trypanoxyuris minutus and *Trypanoxyuris atelis* parasitize howler monkeys (*Alouatta* spp.) and spider monkeys (*Ateles geoffroyi*), respectively (Solórzano-García et al., 2015, Solórzano-García et al., 2016). In Mexico, these primates are considered endangered, mainly due to habitat loss and fragmentation (Rodríguez-Luna et al., 2009; SEMARNAT, 2010), leaving isolated primate populations in what used to be a continuous tropical rainforest (Rodríguez-Luna et al., 2009; Solórzano-García et al., 2012). Both primate species can be considered as specialist dispersers since the probability of dispersal between forest fragments declines with increasing habitat loss; specifically by imposing a higher risk of mortality while crossing the matrix (Estrada and Coates-Estrada, 1996; Mandujano et al., 2004; Pozo-Montuy and Serio-Silva, 2007).

In this study, we evaluated the population genetic patterns of *T. minutus* and *T. atelis* occurring in isolated howler and spider monkey populations in south-eastern Mexico. First, we assessed the amount and geographic distribution of genetic diversity among parasitic pinworms in fragmented tropical forests. Second, we tested whether the processes of habitat loss and fragmentation, and the consequent isolation of host populations, have resulted in the genetic isolation and genetic structure of pinworm populations. Third, we investigated the demographic history of parasites based on the genetic data to reveal the genetic consequences of habitat fragmentation for the pinworm populations. In order to make regional and local inferences for both pinworm species, several primate populations were sampled across their distribution range in Mexico. Mitochondrial DNA (mtDNA) was used to assess parasite genetic patterns among and within fragments and geographic regions, as well as to analyse their demographic and population history. The life history properties of pinworms, the fragmented condition of the habitat, the limited ability of primates to cross the matrix and move across forest patches (Mandujano and Estrada, 2005), and the tight parasite-host association between pinworms and primates, fit the conditions for low diversity and strong genetic structure in parasite populations. Our unexpected results are discussed in light of their implications for primate ecology and conservation, in addition to contributing to our growing understanding of parasite evolution.

2. Materials and methods

2.1. Collection of pinworm specimens

Trypanoxyuris minutus specimens were collected from free-ranging howler monkey troops inhabiting 16 isolated forest fragments assigned to four geographic regions across their distribution range in south-eastern Mexico (Fig. 1). Distances between

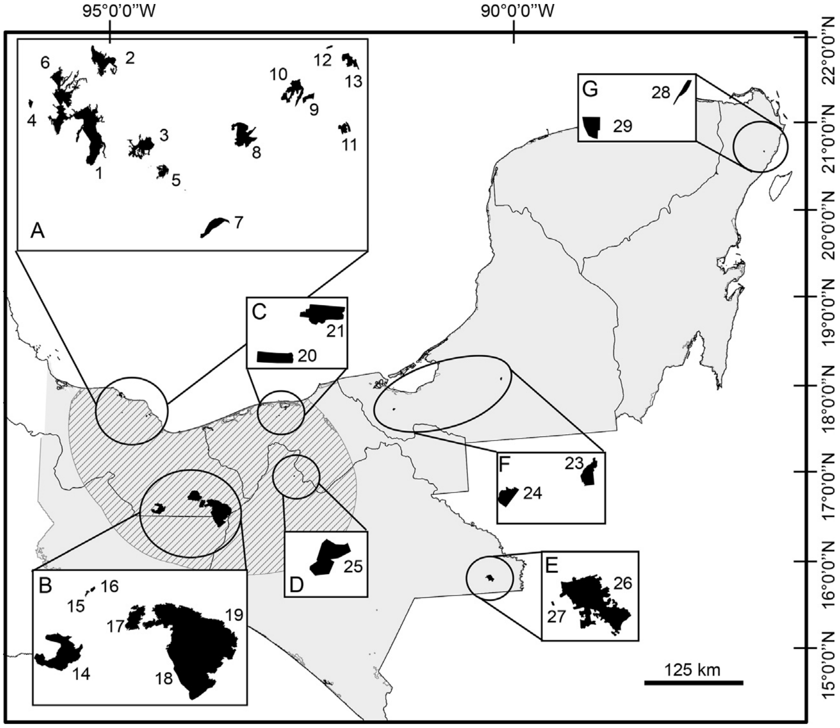

Fig. 1. Collection sites for pinworms across the distributional ranges of mantled howler monkeys (dashed area) and spider monkeys (grey area) in Mexico. Circles and ellipses correspond to geographic regions: (A) Los Tuxtlas, (B) Uxpanapa, (C) Tabasco, (D) Chiapas for mantled howler monkeys, (E) Chiapas for spider monkeys, (F) Campeche, (G) Quintana Roo. Black polygons are the tropical forest fragments where sampling was performed; numbers correspond to forest fragment IDs in Tables 1 and 2.

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