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Getting there and around: Host range oscillations during colonization of the Canary Islands by the parasitic nematode *Spauligodon*

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Abstract

Episodes of expansion and isolation in geographic range over space and time, during which parasites have the opportunity to expand their host range, are linked to the development of host–parasite mosaic assemblages and parasite diversification. In this study, we investigated whether island colonization events lead to host range oscillations in a taxon of host-specific parasitic nematodes of the genus *Spauligodon* in the Canary Islands. We further investigated whether range oscillations also resulted in shifts in host breadth (i.e., specialization), as expected for parasites on islands. Parasite phylogeny and divergence time estimates were inferred from molecular data with Bayesian methods. Host divergence times were set as calibration priors after a priori evaluation with a global-fit method of which individual host–parasite associations likely represent cospeciation links. Parasite colonization history was reconstructed, followed by an estimation of oscillation events and specificity level. The results indicate the presence of four *Spauligodon* clades in the Canary Islands, which originated from at least three different colonization events. We found evidence of host range oscillations to truly novel hosts, which in one case led to higher diversification. Contemporary host–parasite associations show strong host specificity, suggesting that changes in host breadth were limited to the shift period. Lineages with more frequent and wider taxonomic host range oscillations prior to the initial colonization event showed wider range oscillations during colonization and diversification within the archipelago. Our results suggest that a lineage's evolutionary past may be the best indicator of a parasite's potential for future range expansions.

KEYWORDS
host specificity, host switches, parasite island syndrome, phylogeography, range expansion

1 | INTRODUCTION

Whether and how organisms can survive in new environments lies at the core of important conservation questions, whether related to climate change (Charmantier et al., 2008; Valladares et al., 2014) or species invasion (Davidson, Jennions, & Nicotra, 2011; Knop & Reusser, 2012). When it comes to parasites, the ability to successfully explore new resources (hosts) has important consequences for the emergence of infectious diseases (Hoberg & Brooks, 2015) but is also key to understanding the complex interactions between hosts and parasites and their impacts on ecological communities (Hatcher, Dick, & Dunn, 2012). Such complexity has been widely recognized as a consequence of the ability of parasites to persist in other hosts, independent of their degree of host specialization (Araujo et al., 2015; Brooks, León-Règagnon, McLennan, & Zelmer, 2006; Duval et al., 2007; Ricklefs, Fallon, & Bermingham, 2004).

Cyclical episodes of expansion and isolation in host geographic range are linked to the development of mosaic assemblages where hosts can either lose or gain parasites, and parasites may expand their host range (Hoberg, Galbreath, Cook, Kutz, & Polley, 2012). Under the oscillation hypothesis (OH) (Janz, Braga, Wahlberg, & Nylin, 2016; Janz & Nylin, 2008; Janz, Nylin, & Wahlberg, 2006), the incorporation of new hosts is associated with lineage diversification. This hypothesis presumes changes on a microevolutionary scale leading to host range oscillations, and on a macroevolutionary scale where such events would lead to elevated diversification rates. Host range oscillations can be simply defined by the diversification of host use due to host shifts, where a parasite expands its range by incorporating a new host, but later specializes in the new host and loses the ancestral one (parasite prevalence in ancestral host is zero). The period of multiple hosts may or may not be brief, meaning that such shifts do not necessary lead to changes in the parasite's host breadth beyond the shift period (Janz et al., 2016). There are two types of oscillations: colonizations of truly new hosts (hosts that were not used in the parasite's evolutionary past) and recolonizations of hosts already explored in the past which should be more common (Janz et al., 2016). New shifts are constrained by a parasite's ability to persist in other hosts due to its degree of plasticity, or its inherited ability to explore a certain host due to its evolutionary history (host already used in the past) and phylogenetic conservatism related to host use (same host-like environment used in the past) (Brooks & Hoberg, 2013). From this hypothesis two questions arise: i) Are host range oscillations a determinant of parasite diversification occurring during episodes of expansion in geographic range? and ii) Are oscillations in host range restricted by boundaries related to evolutionary history, or do they occur independently with unrelated hosts reached by "stepping stones"? Unravelling the evolutionary history of past oscillations may allow us to determine parasite compatibility boundaries for future host expansions.

Oceanic islands are great model systems to study parasite host range oscillations, as each colonized island represents an episode of geographical expansion/isolation for both parasite and host. Successful island colonization requires the parasite to not "miss the boat" (i.e., parasite needs to be present in the host founder population) and persist in the new environment. Within islands, life history, abundance and distribution of species may provide opportunities for new host–parasite associations to emerge by promoting encounters between parasites and hosts. Nonetheless, reconstructing the evolutionary history of a parasite lineage requires a fine balance between correctly assessing both the colonization history (i.e., ancestral hosts), speciation/extinction dynamics and uncovering host–parasite associations, which is in turn influenced by parasite prevalence and abundance. Previous studies on islands have shown that parasites undergo a loss in host specificity and increase in host switch rates compared to the mainland, as they experience the "island syndrome" (Nieberding, Morand, Libois, & Michaux, 2006; Pérez-Rodríguez, Ramírez, Richardson, & Pérez-Tris, 2013). In this case, host range oscillations on islands would be characterized by longer periods of multihost use or even changes in a parasite's host breadth, that is, from specialized to generalist.

In this study, we investigate whether and when events of island colonization lead to host range oscillations, and whether oscillations are characterized by changes in host breadth beyond the period of switch. We studied the colonization pattern of the Canary Islands by the nematode *Spauligodon*, a taxon of obligate parasites of reptiles. *Spauligodon* nematodes have a direct oral–faecal life cycle and no free-living stages; they infect the intestine of reptiles and require a single host to complete the life cycle (Adamson, 1990; Jorge, Roca, Perera, Harris, & Carretero, 2011). One peculiarity is their haplodiploid form of reproduction (i.e., males derive from nonfertilized eggs and are haploid, whereas females derive from fertilized eggs and are diploid). A single female is sufficient to colonize a new host and initiate a new population by mating with its produced male progeny (Adamson, 1990, 1994). However, these nematodes have low dispersal potential due to high susceptibility of their eggs to desiccation (Adamson, 1990). *Spauligodon* parasites are generally highly host specific (at species or genus level), resulting in relatively high population differentiation, with direct implications for their diversification (Adamson, 1990; Falk & Perkins, 2013; Jorge et al., 2011). Previous studies have assessed *Spauligodon* genetic structure on islands, restricting their sampling strategy to a single host genus (Falk & Perkins, 2013; Jorge et al., 2011). As a consequence, it remains unclear whether in fact specificity is limiting the parasite from expanding its host range even when ecological opportunity arises, or whether the estimated level of specificity is a result from sampling bias.

The Canary Islands, an archipelago of seven main islands and several islets, were formed during the past 20 Mya in an east-to-west formation sequence by a volcanic hotspot in the Atlantic Ocean located approximately 100 km off the northwestern coast of Africa (Figure 1a,b; Guillou, Carracedo, Paris, & Torrado, 2004; Ancoechea, Hernán, Huertas, Brändle, & Herrera, 2006; Sanmartín, van der Mark, & Ronquist, 2008). All the islands arose from a single edifice with the exception of Tenerife Island, which resulted from the union of three independent and consecutive shield volcanoes (Guillou et al., 2004). There are 13 extant species of native reptiles in the Canary Islands, grouped into three distantly related genera: *Tarentola* geckos, *Chalcides* skinks and *Gallotia* lacertid lizards. The three reptile taxa exhibit different ecology: *Gallotia* lizards are diurnal and ground-dwelling, *Chalcides* skinks are also diurnal but semi-fossorial and *Tarentola* geckos are crepuscular/nocturnal and saxicolous (Mateo, Ayres, & López-Jurado, 2011). Interestingly, each taxon has colonized the archipelago following a distinct pathway (Figure 1c,d,e), and only *Gallotia* lizards appear to be the result of a single colonization event. Of the three genera, *Gallotia* is the only one endemic to the archipelago, with seven recognized living species. *Tarentola* geckos and *Chalcides* skinks are both represented by four species. Each genus is represented by one species per island, with the exception of Tenerife, La Gomera and El Hierro, where two *Gallotia* species coexist, and in La Palma where no *Chalcides* representative is found. With the exception of the four endangered species (lacertid lizards: *Chalcides simonyi*, *G. intermedia* and *G. bravoana*; and the skink: *C. simonyi*), which live in restricted areas, all other reptiles are generally widespread and attain high densities, often coexisting in

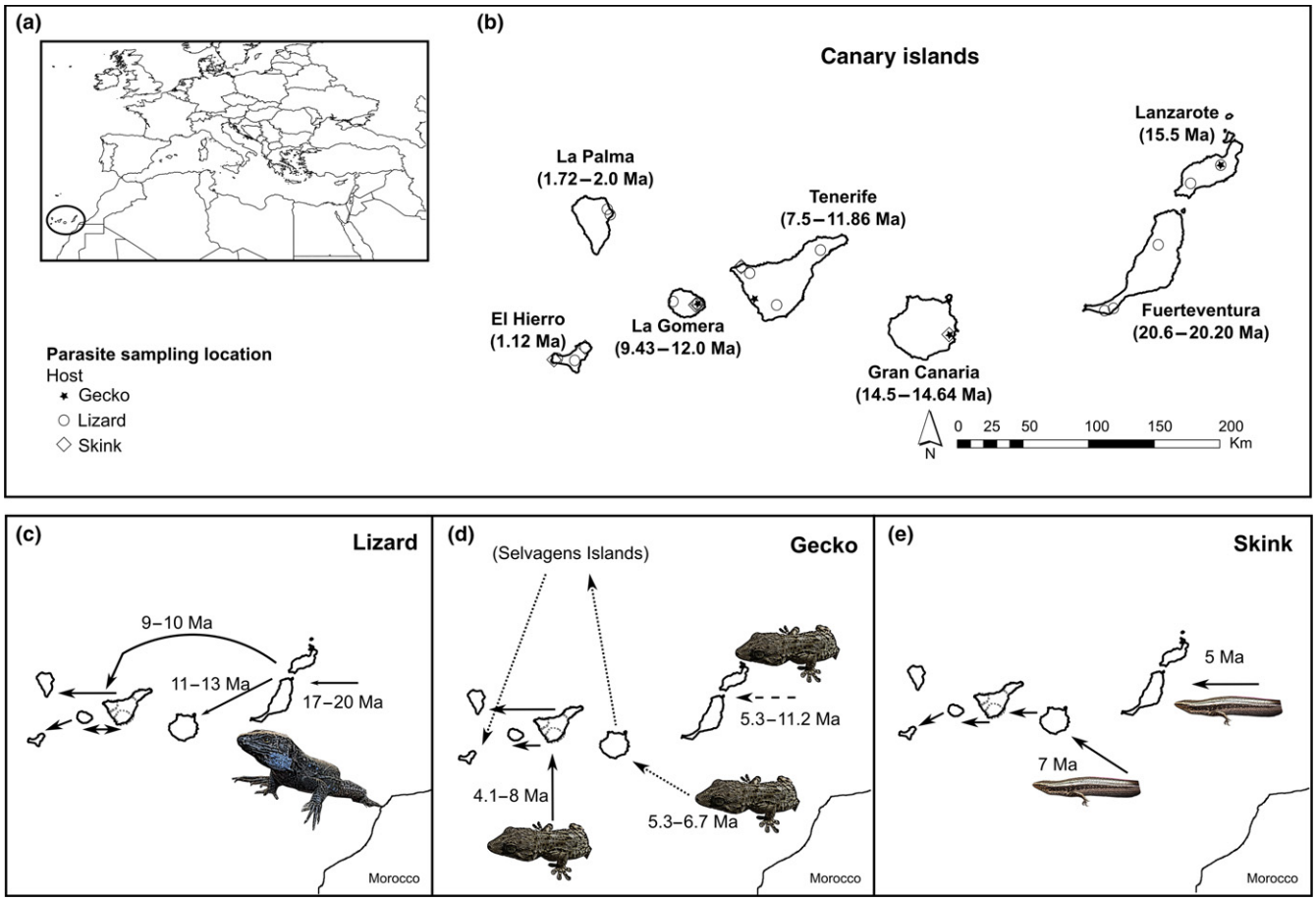

FIGURE 1 (a) Geographical location of the Canarian archipelago; (b) Canary Islands with the approximate ages of the islands (Carracedo et al. 1998; Guillou et al., 2004); Main colonization routes with estimated ages for (c) the *Gallotia* lizards (Cox, Carranza, & Brown, 2010), (d) *Tarentola* geckos (Carranza, Arnold, Mateo, & Geniez, 2002) and (e) *Chalcides* skinks (Carranza, Arnold, Geniez, Roca, & Mateo, 2008) [Colour figure can be viewed at wileyonlinelibrary.com]

sympatry. Regarding their helminth fauna, *Spauligodon* is one of the common reptile parasitic nematodes, with three described species in the Canary Islands: *Spauligodon tarentolae*, *Spauligodon atlanticus* and *Spauligodon occidentalis* (Jorge, Perera, Carretero, Harris, & Roca, 2013; Jorge et al., 2011; Spaul, 1926). While *S. atlanticus* and *S. occidentalis* have been found infecting *Gallotia* lizards in eastern and western islands, respectively (Jorge et al., 2011; Jorge & Perera et al., 2013), *S. tarentolae* has been only found in *Tarentola* geckos from the island of Tenerife.

In this study, we explore the diversification *of Spauligodon* parasites in the Canary Islands focusing on their host use. If parasite diversification is restricted by host use due to parasite specificity, oscillations to truly new hosts will not occur, and parasite diversification will be shaped by host tracking (cospeciation), without changes in host breadth (i.e., specificity). However, if host specificity decreases as predicted under the parasite island syndrome, the two types of oscillations should be equally likely, and there will also be changes in host breadth. We also predict higher lineage diversification in lineages where host range oscillations occurred. We considerably expanded a previous study on *Gallotia* lizards (Jorge et al., 2011) to include all other potential nonthreatened endemic reptile host species, namely *Tarentola* geckos and *Chalcides* skinks. The phylogeny of the parasites was inferred to assess the number of monophyletic groups that may represent independent colonization events and determine parasite specificity by identifying their extant hosts. We subsequently used an estimation of the time-calibrated phylogenetic trees to infer when they first colonized the islands, as well as their ancestral geographical distribution and host range. As accurate estimates of divergence times depend on adequate calibration data, we calibrated the parasite phylogeny with secondary calibration priors based on host divergence times only for individual host–parasite associations likely to represent cospeciation links determined a priori using a global-fit method. We then evaluated the level of host–parasite co-evolutionary congruence and determined host range oscillation events and changes to host breadth for each parasite lineage.

2 | MATERIAL AND METHODS

2.1 | Sampling

In an effort to sample all of the nonthreatened species and subspecies of the three potential host genera, a total of 217 *Gallotia*

spp. lacertid lizards comprising three species (hereafter *Gallotia* lizard), 138 *Chalcides* spp. skinks comprising three species (hereafter skink) and 331 *Tarentola* spp. geckos comprising four species (hereafter gecko) were sampled across the Canary Islands between 2012 and 2014 (Table 1). The reptile specimens were mostly collected from sympatric populations (Table 1). Samples consisted of faecal pellets (467) and intestine contents (219) and were collected and processed as described in Jorge et al. (2014). From the total of 686 sampled hosts, 143 were infected with *Spauligodon* parasites. From these, representatives from all infected host species and localities available were selected for molecular analyses. To provide a more robust framework for phylogenetic inference, 14 different *Spauligodon* putative species found infecting 20 different reptile host species from other geographic regions (Table S1) were also collected and selected for molecular analyses. Whenever possible, samples from respective hosts were also collected from tail tips and stored in 96% ethanol for genetic confirmation of species identity and for posterior cophylogenetic analysis.

2.2 | Molecular techniques

We analysed three gene fragments: two nuclear genes, the 18S ribosomal RNA (18S) and 28S ribosomal RNA (28S), and one mitochondrial gene, the cytochrome oxidase subunit I (COI). DNA extraction and polymerase chain reactions (PCR) were performed as described in Jorge et al. (2014). DNA from 48 parasitic nematodes from hosts that had not been studied previously was successfully amplified and sequenced. Parasite sequence chromatograms were trimmed and edited in GENEIOUS ver. 8.1.4 (http://www.geneious.com/, Kearse et al., 2012). Thirty-one previously unreported haplotypes were retrieved from these samples. *Parapharyngodon echinatus* and *Thelandros tinerfensis* were used as outgroups, as they belong to the same nematode family as *Spauligodon* and have proven useful in previous studies (Jorge et al., 2011, 2014). The data set for each gene was aligned using MAFFT (Katoh, Misawa, Kuma, & Miyata, 2002; see Appendix S1). Three relevant specimens lacked sequence information for some of the genes. However, given the importance of those samples and because missing data are expected to have minor impact on the accuracy of phylogenetic analysis and divergence dating (Wiens & Morrill, 2011; Zheng & Wiens, 2015; Streicher, Schulte, & Wiens, 2016), these sequences were included in the analyses but coded as "?". Possible substitution saturation in the codon partitions was evaluated in DAMBE ver. 5.3.48 (Xia, 2013; see Appendix S1).

For the sampled hosts, total genomic DNA was extracted from small pieces of tail using standard methods (Harris, Arnold, & Thomas, 1998). A partial gene fragment of the mitochondrial 12S rRNA (12S) was amplified and sequenced using the primers 12Sa and 12Sb (Kocher et al., 1989) as described in Harris et al. (1998). Polymerase chain reactions product purification and sequencing was performed by a commercial facility (Macrogen Corporation, http://www.macrogen.com/). The alignment of the host 12S sequences corresponding to each host–parasite link of the parasite data set was performed using MAFFT (Katoh et al., 2002). In cases where host DNA samples could not be collected, 12S sequences from the same host species, and whenever possible from the same geographic region, were downloaded from GenBank and included in the host data set (Table S2).

2.3 | Phylogenetic inferences

To determine how many different parasite lineages are present in the Canary Islands and infer the number of independent colonization events, we conducted a Bayesian inference (BI) analysis in MRBAYES ver. 3.2.2 (Ronquist et al., 2012). We first analysed each gene fragment separately, and later the concatenated data set including 28S and nonsaturated COI. The 18S was not included in the concatenated data set due to its low resolution at this taxonomic level. We used reversible-jump Markov chain Monte Carlo (MCMC) to integrate over the pool of all 203 possible reversible 4×4 nucleotide models (see Appendix S1). One hundred million MCMC generations were sampled every 1,000th step, and the first 25% were discarded as burn-in. Mixing and convergence of each run were monitored through the statistics provided in MRBAYES and in TRACER ver.1.6 (Rambaut, Suchard, Xie, & Drummond, 2014) (see Appendix S1).

To further explore the expectations that higher lineage diversification should be found in lineages where host range oscillations occurred, we analysed the genetic differentiation within main lineages. Due to the small sample sizes for some lineages, this analysis was only performed within the main Canary clade (clade A, see Results). We constructed a phylogenetic network using the Neighbor-Net (NNet) network method (Bryant & Moulton, 2004) as implemented in SPLITSTREE ver. 4.0 (Huson & Bryant, 2006), over all three COI codon positions, based on uncorrected distances. The data set included specimens with haplotypes not represented in previous data sets (five specimens from *S. occidentalis* from La Gomera island) given that they were not successfully amplified for the 28S. Estimates of evolutionary divergence for COI were calculated using pairwise uncorrected differences (*p*-distance) in MEGA ver. 6 (Tamura, Stecher, Peterson, Filipski, & Kumar, 2013).

2.4 | Divergence time estimates

Time calibration was performed through a Bayesian–MCMC joint estimation of phylogeny and divergence times in BEAST ver. 2.3.0 (Bouckaert et al., 2014), using the concatenated 28S and COI data set (1st and 2nd codon positions) without outgroups. Following previous model definitions implemented in MRBAYES, estimates of all three components of the site model were inferred during the MCMC analysis, using reversible jump (see Appendix S1). The method is implemented in the bModelTest package of BEAST (Bouckaert & Drummond, 2017). Two different clocks were assumed: one for the nuclear and the other for the mitochondrial data set, and an uncorrelated lognormal relaxed clock model was selected for both clocks (see Appendix S1). The birth–death constant speciation and extinction rates model (Nee, May, & Harvey, 1994; Gernhard, 2008) were set as tree prior. To establish an evolutionary timescale, we combined temporal constraints on

TABLE 1 Prevalence and mean intensity of Canarian *Spauligodon* clades at each locality and host species

					Clade A1		Clade A2		Clade B		Clade C		Clade D	
Island	**Loc.**	**Host species**	**S**	**N**	**I.H (P)**	**I**	**I.H. (P)**	**I**	**I.H. (P)**	**I**	**I.H. (P)**	**I**	**I.H. (P)**	**I**
Lanzarote	1	*G. atlantica*	F	19	0		0		12(63%)	20	0		0	
		T. angustimentalis	F	20	0		0		0		0		0	
		T. angustimentalis	I	10	0		0		0		0		0	
	2	*G. atlantica*	I[a]	13	0		0		3(23%)	6	0		0	
		G. atlantica	F	18	0		0		9(50%)	7.67	0		0	
		T. angustimentalis	F	18	0		0		1(6%)[b]	5	0		0	
	3	*G. atlantica*	I[a]	11	0		0		4(36%)	5.75	0		0	
		T. angustimentalis	I	10	0		0		0		0		0	
		G. atlantica	F	24	0		0		18(75%)	18.1	0		0	
		T. angustimentalis	F	21	0		0		0		0		0	
Fuerteventura	4	*G. atlantica*	I[a]	11	0		0		0		0		0	
		T. angustimentalis	I	10	0		0		0		0		0	
		G. atlantica	F	20	0		0		1(5%)	1	0		0	
		T. angustimentalis	F	20	0		0		0		0		0	
	5	*G. atlantica*	F	10	0		0		4(40%)	23	0		0	
		T. angustimentalis	F	22	0		0		0		0		0	
	6	*G. atlantica*	I	10	9(90%)	65	0		0		0		0	
		T. angustimentalis	I	10	0	0	0		0		0		0	
Gran Canaria	7	*G. stehlini*	I[a]	20	0		0		0		0		0	
		C. sexlineatusi	I[a]	15	0		0		0		0		0	
		G . stehlini	F	20	0		0		0		0		0	
		T. boettgeri	F	27	0		0		0		0		0	
		C. sexlineatusi	F	17	0		0		0		0		0	
	8	*G . stehlini*	I	1	0		0		0		0		0	
		T. boettgeri	I	10	0		0		0		0		6(60%)	108
		C. sexlineatusi	I	10	0		0		0		0		1(10%)[b]	10
	9	*G . stehlini*	F	1	0		0		0		0		0	
		T. boettgeri	F	3	0		0		0		0		0	
		C. sexlineatusi	F	19	0		0		0		0		0	
	10	*G . stehlini*	I	4	0		0		0		0		0	
		T. boettgeri	I	10	0		0		0		0		0	
		C. sexlineatusi	I	10	0		0		0		0		0	
Tenerife	11	*G . galloti*	I[a]	10	5(50%)	5.8	0		0		0		0	
		T. delalandii	I	10	0		0		0		0		0	
		C. viridanus	I	10	0		0		0		0		0	
	12	*G . galloti*	F	1	0		0		0		0		0	
		T. delalandii	F	3	0		0		0		0		0	
		C. viridanus	F	3	0		0		0		0		0	
	13	*G . galloti*	F	3	0		0		0		0		0	
		T. delalandii	F	21	1(5%)[b]	8	0		0		0		0	
	14	*G . galloti*	I	10	6(60%)	48.67	0		0		0		0	
		T. delalandii	I	10	0		0		0		0		0	
		C. viridanus	I	10	0		3(30%)	20.33	0		0		0	

(Continues)

TABLE 1 (Continued)

					Clade A1		Clade A2		Clade B		Clade C		Clade D	
Island	Loc.	Host species	S	N	I.H (P)	I	I.H. (P)	I	I.H. (P)	I	I.H. (P)	I	I.H. (P)	I
La Palma	15	G. galloti	I[a]	10	4(40%)	30.5	0		0		0		0	
		T. delalandii	I	10	0		0		0		0		0	
	16	*G . galloti*	F	2	1(50%)	83	0		0		0		0	
		T. delalandii	F	1	0		0		0		0		0	
	17	*G . galloti*	F	19	6(32%)	4.5	0		0		0		0	
		T. delalandii	F	27	0		0		0		0		0	
La Gomera	18	*G. caesaris*	F	3	0		0		0		0		0	
		T. gomerensis	F	26	0		0		0		0		0	
		C. coeruleopunctatus	F	1	0		1(100%)	24	0		0		0	
	19	*G. caesaris*	F	4	1(25%)	2	0		0		0		0	
		T. gomerensis	F	6	0		0		0		0		0	
		C. coeruleopunctatus	F	5	0		0		0		0		0	
	20	*G. caesaris*	I	10	2(20%)	1.5	0		0		0		0	
		T. gomerensis	I	11	0		0		0		0		1(9%)	3
		C. coeruleopunctatus	I	10	0		6(60%)	52.67	0		0		0	
El Hierro	21	*G. caesaris*	I[a]	10	3(30%)	69	0		0		0		0	
		T. boettgeri	I	3	0		0		0		0		0	
		C. coeruleopunctatus	I	10	0		6(60%)	30	0		2(20%)	164	0	
		G. caesaris	F	10	5(50%)	16.2	0		0		0		0	
		T. boettgeri	F	1	0		0		0		0		0	
		C. coeruleopunctatus	F	9	0		4(44%)	6.5	0		0		0	
	22	*G. caesaris*	I[a]	10	5(50%)	71	0		0		0		0	
		T. boettgeri	I	10	0		0		0		0		2(20%)[c]	6.5
		C. coeruleopunctatus	I	10	0		7	61.29	0		0		0	
		G. caesaris	F	29	7(24%)	1.14	1(3%)[b]	28	0		1(3%)	36	0	
		C. coeruleopunctatus	F	11	0	0	6(55%)	5	0		0		0	
	23	*C. coeruleopunctatus*	F	3	0		1(33%)	2	0		1(33%)	31	0	

N, number of hosts sampled; I.H., number of infected hosts and respective prevalence (in percentage); I, mean intensity; Loc., locality number (locality information is detailed in Table S1, Appendix). S., sample type: F, faeces and I, intestines. *G.*, *Gallotia*; *C.*, *Chalcides*; *T.*, *Tarentola*.

[a]Reference Jorge *et al.* (2011).

[b]occurrence classified as spillover rather than truly host use.

[c]lineage identification based only on morphological characteristics due to unsuccessful DNA amplification.

sequence divergence with the molecular data. Fossil calibrations are not available for these taxa. Usually for island systems without fossil record, studies rely on relative geological dating, based on island emergence as hard bounds (i.e., Cox et al., 2010). However, as we identified several lineages in the same islands, this approach was not followed. Instead, we selected different calibration priors based on host divergence time estimates following the assumption that those particular parasite lineages have diverged within the range of timescale of their hosts. While this assumption is unarguably bold, it was based on an a priori cophylogenetic analysis with the global-fit method Procrustean Approach to Cophylogeny (PACo, Balbuena, Míguez-Lozano, & Blasco-Costa, 2013; see below), where the respective host–parasite associations were found to likely represent cospeciation links (host–parasite links that contributed relatively little to the residual sum of squares; Figure 2). Three nodes were selected, and age constraints on parasite lineages were set according to the knowledge of divergence time estimates of the respective hosts. Specifically, we constrained the age of the most recent common ancestor (mrca) of: (i) the lineages infecting *T. mauritanica* and *T. desertii* with a prior reflecting the estimates of the mrca of *T. mauritanica* and *T. desertii* inferred by Rato, Carranza, and Harris (2012) (prior with a normal distribution with mean = 8.69, sigma = 1.3); (ii) the lineages infecting *Podarcis* spp. from the Balearic Islands and Sardinia not to be older than the estimated age of origin of the genus *Podarcis* (prior with a uniform distribution with lower bound = 3.79, upper bound = 10.42), as previously estimated (Arnold, Arribas, & Carranza, 2007; Mendes, Harris, Carranza, & Salvi, 2016); and (iii) the lineage from Addaia Petita and Dragonera islands infecting *P. lilfordi* with a prior set according to the divergence of the *P. lilfordi* host populations inhabiting Addaia Petita and Dragonera islands as estimated by Brown et al. (2008) (prior with a

lognormal distribution with mean = 0.5904079, standard deviation = 0.85, offset = 1.45), all constrained to be monophyletic. The four Canarian clades retrieved in BI analysis were also constrained to be monophyletic. Additionally, to evaluate the consistency of the set of calibrations used in this study, we performed (i) separate analysis of the individual time constraints and (ii) analysis after excluding one constraint in turn, after which we assessed whether the 95% credibility intervals estimates for each of the Canarian clades were congruent. This was not intended to be a cross-validation test to determine the quality of the set of calibrations, as the assumption of such an approach is violated in a Bayesian framework, where the effective priors for a given calibration vary depending on the presence or absence of other constraints (Warnock, Parham, Joyce, Lyson, & Donoghue, 2015). Instead, the consistency tests aimed at assessing whether the divergence estimates would significantly differ (i.e., in case any of the calibrated host–parasite links did not represent a true cospeciation link), and if so, whether they would influence the assumptions of the parasite colonization history. For each analysis, three independent MCMC analyses were run for 100 million generations with a sampling frequency of 10 thousand. The first 25% of generations were discarded after evaluation of convergence (see Appendix S1).

2.5 | Cophylogenetic analysis

To visualize host–parasite associations, a tanglegram was generated from the combined COI and 28S BI parasite tree and from the most complete available phylogeny for Squamata (Pyron, Burbrink, & Wiens, 2013) on the vector graphic software INKSCAPE (http://www.inkscape.org/). We evaluated the level of co-evolutionary congruence between host and parasite phylogeny using the global-fit statistic tool PACo (Balbuena et al., 2013) in R ver. 3.2.2 (R Core Team, 2015). While global-fit methods do not consider cophylogenetic events (cospeciation, switching, sorting and duplication), they have the advantage of not requiring resolved phylogenies and identify the associations contributing the most to the cophylogenetic structure. We used as input the 28S parasite and 12S host data sets and the respective binary matrix coding the host–parasite associations from which sequence information was available (Figure 2, Table S2). The congruence between the host and parasite phylogenies was measured with the residual sum of squares of the Procrustean fit, whose significance was established by 100,000 random permutations of the host–parasite association data. The contribution of each individual host–parasite association with the global fit was measured by means of jackknife estimation of their

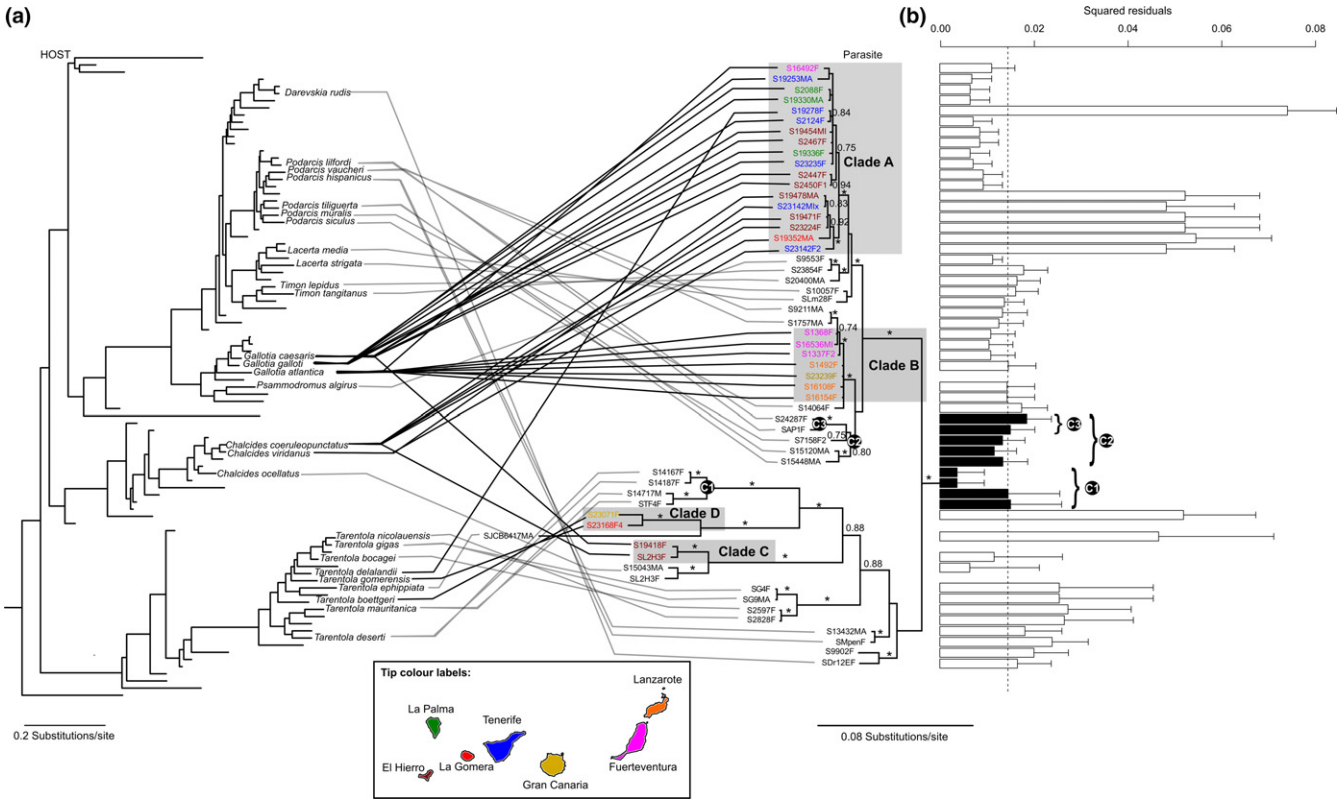

FIGURE 2 (a) Tanglegram of the cophylogenetic relationships between *Spauligodon* parasites and their respective reptile host. Host tree: adapted from Pyron et al.'s (2013) phylogeny of Squamata. Parasite tree: Bayesian 50% majority-rule inference tree for the concatenated 28S and cytochrome oxidase subunit I (COI) parasite data set. Shaded rectangles indicate Canarian parasite clades. Host–parasite associations from the Canary Islands indicated in black lines and associations from different geographic areas are in grey. Branch labels show posterior probabilities (values below 0.75 not shown), and star symbols correspond to Bayesian posterior probabilities higher than .95. Tip labels from each clade are coloured according to the islands of origin. Nodes used as calibrated priors in BEAST analysis are marked as C1, C2 and C3. (b) Jackknifed squared residuals (bars) and upper 95% confidence intervals (error bars) estimated for each host–parasite link. Dashed line represents the median squared residual value. Squared residuals of the host–parasite links considered for the age constrains of BEAST analysis are shaded in black [Colour figure can be viewed at wileyonlinelibrary.com]

respective squared residuals, together with a 95% confidence interval associated with each host–parasite link.

2.6 | Host specificity and host range oscillation estimates

To evaluate the level of specificity expressed at the host species level, we calculated the prevalence and mean intensity. Parasite prevalence was calculated as the ratio between the number of infected host individuals and the total number of sampled host individuals, and parasite mean intensity as the mean number of parasites per infected host. Given the differences in detectability and abundance of nematodes depending on the origin of the samples (see Jorge, Carretero, Roca, Poulin, & Perera, 2013), these parameters were calculated separately for each sample type (intestines or faeces). Because only a subset of parasite specimens were sequenced, estimates of prevalence and intensity are based strictly on morphological identification of the parasites recovered, meaning that in some cases the presence of other parasite species may have been overlooked. Single-case infections, where only one host individual from a reptile taxon not classified as a parasite's main host was found infected, were classified as possible cases of spillover.

The number of host range oscillations (i.e., diversification of host use by host shifts) was estimated from the inferred parasite phylogeny, divergence times and current host–parasite associations. Specifically, a host range oscillation was considered to have occurred whenever two sister parasite lineages were found infecting two different hosts species (i.e., specialized in different hosts), and prevalence was zero or classified as a spillover in all other host species. Under the OH, host range oscillations are classified into two types: colonizations of truly new hosts and recolonizations (Janz et al., 2016). However, we classified host range oscillations, as shifts from one host species to another, into three types: i) switches to truly novel hosts (i.e., hosts from genera not used in the evolutionary past), ii) switches to new host species within the same host genus currently in use by the parasite lineage (as opposed to cospeciation) and iii) recolonizations (i.e., switches, after a previous oscillation to a novel host, to a host species from a genus used in the evolutionary past). We further assessed whether the host range oscillations were followed by changes in host breadth, that is, (i) from specialist exploring only one host genus to generalist exploring more than one genus or (ii) maintenance of high specialization with multihost use limited to the period of shift.

3 | RESULTS

Parasite data sets included in the phylogenetic analyses consisted of 47 sequences for 18S, 56 sequences for 28S and 57 sequences for COI, excluding outgroup sequences. Final sequence lengths for each marker were of 774 bp for 18S, 1,078 bp for 28S and 601 bp for COI. The 18S was the least informative marker with 4.5% (35) variable sites, against 35.3% (397) for the 28S and 43.4% (291) for the COI (in all cases excluding the respective outgroups). The concatenated COI and 28S data sets included 57 taxa, 29 of which represented the main parasite haplotypes found in the Canary Islands. Xia tests indicated substantial saturation at the level of third codon positions of COI either assuming a symmetrical topology (Iss < Iss.cSym, $p = .0727$ for $N = 16$), or an asymmetrical one ($N = 8$ Iss < Iss.cSym, $p = .2026$; while for $N = 16$ or 32 Iss > Iss.c, $p = .005$). This saturation was also evident in plots (Figure S1). However, no saturation was observed within each of the four Canarian clades. The data set for the phylogenetic network reconstruction for the main Canarian clade consisted of 30 specimens.

3.1 | Phylogenetic inference

In all the BI analyses, each separate run converged to an average deviation split of frequencies of<0.003. The BI from each marker produced trees that varied in the degree of resolution, with the 18S being the least informative. Overall, analysis of the concatenated data set generated a better-supported and resolved phylogeny than single gene data sets. The *Spauligodon* nematodes in the Canary Islands are divided into four well-supported clades that are polyphyletic (posterior probability>0.99) (Figure 2). However, in the phylogenetic inference from the slower evolving 18S, only three clades are recovered, with clades A and B grouping together within a larger clade. Clade A includes Canary nematodes ascribed to *S. occidentalis*, infecting *Gallotia* lizards from the western islands and *Spauligodon* sp. infecting skinks from the western islands (Table 1). Clade B includes specimens ascribed to *S. atlanticus* infecting *Gallotia* lizards from the eastern islands (Table 1). Clade C includes specimens infecting skinks and *Gallotia* lizards and is exclusively from the easternmost island (El Hierro) (Table 1). Clade D groups *Spauligodon* sp. specimens infecting geckos from Gran Canaria and La Gomera (Table 1). Clade A is associated with parasites from Morocco, Iberian Peninsula and Caucasus, infecting lacertid lizards of the genera *Psammodromus*, *Timon* and *Lacerta*, respectively. Clade B groups together with other *Spauligodon* nematodes infecting *Podarcis* lizards from Morocco and northeastern Iberia. Clade C clusters together with other parasites infecting skinks from Morocco and Italy, while clade D groups with *Spauligodon* infecting geckos from Mauritania. Unfortunately, the lack of a complete phylogeny for *Spauligodon* prevents an unambiguous phylogenetic placement for all four clades.

The NNet splits graph for clade A is shown in Figure 3 (clade A: fit value = 97.93). The NNet highlights a predominantly tree-like signal and shows some degree of reticulated structure, but also some level of ambiguity. The most prominent split separates the clade in two: A1 lineage infecting mainly *Gallotia* lizards (i.e., *S. occidentalis*) and A2 lineage infecting mainly skinks (Figure 3), similar to what was inferred in the concatenated BI tree. The lineage infecting *Gallotia* lizards appears to have higher structure complexity, and haplotype diversity, even if the two haplotypes present in La Palma (islands where skinks are absent) are not considered.

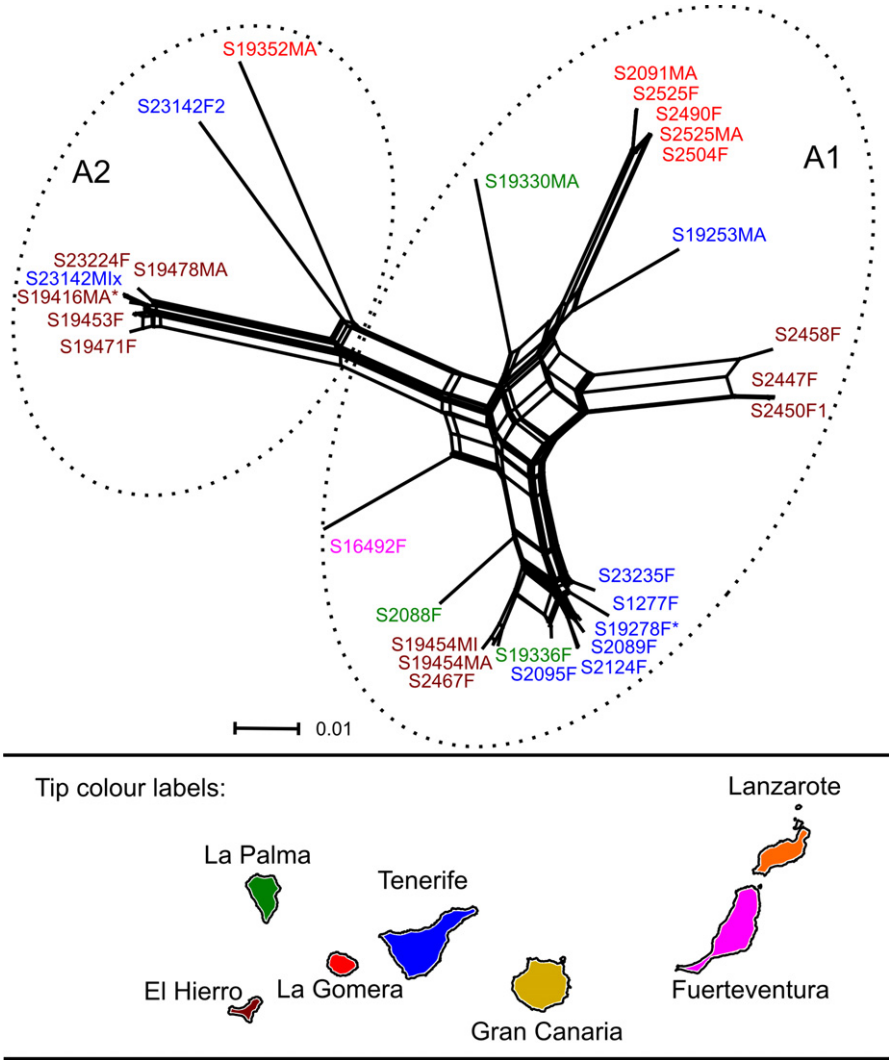

FIGURE 3 Split decomposition Neighbor-Net of the cytochrome oxidase subunit I (COI) *Spauligodon* parasite data set for clade A with pointed lines clustering the two different lineages A1 (found in *Gallotia* lizards) and A2 (found in *Chalcides* skinks). Tip labels from each clade coloured according to the island of origin, and asterisks denote a spillover rather than truly host use [Colour figure can be viewed at wileyonlinelibrary.com]

Clade D was only represented by two genetically very different specimens, showing the highest within clade genetic diversity (uncorrected *p*-distance of 11.6%), followed by clade A (7.7%). The estimate of molecular divergence between the two subclades of clade A was also very high (uncorrected *p*-distance of 10.5%). Between each of the four *Spauligodon* Canarian clades and their respective sister taxa, we found estimates of divergence ranging from 7.5% (for Canary clade B vs. Moroccan and French taxa) to 18% (for Canary clade D vs. one specimen from Mauritania).

3.2 | Divergence time estimates

Overall, the marginal densities for each run of the divergence time estimate analysis were nearly identical, indicating that the runs converged on the same stationary distributions. In all runs, the marginal densities for the standard deviation hyperparameter of the uncorrelated lognormal relaxed clock model were quite different from the prior, with no significant density at zero and with a coefficient of variation between 0.47 to 0.57 for COI and 0.99 to 1.01 for 28S. The estimated clock rate from the nuclear data set was 1.72×10^{-3} (95% highest posterior density (HPD) 8.79×10^{-4} - 2.63×10^{-3}) substitution per site per Ma, whereas from the mitochondrial it was 4.33×10^{-3} (95% HPD 2.05×10^{-3} - 7.16×10^{-3}) substitution per site per Ma. The time estimates for the mrca of each clade and in each analysis are given in Table 2 and in Figure 4. Analysis with only the calibrated prior 3 was the one presenting higher discrepancies in divergence time estimates, estimating older ages (Table 2). However, no significant difference was found between analyses, with all estimated values falling within the 95% HPD interval for divergence time estimates of each other.

3.3 | Cophylogenetic analysis

The global-fit analysis provides evidence for overall significant congruence between the parasite and host phylogenies (m^2 global value = 0.9670347, $p < .0001$). The contribution of each individual host–parasite association with the global fit differs between clades, with subclade A1 having the lowest contribution with the exception of the link representing one specimen found in a gecko and classified as a spillover (Figure 2b). Other specimens classified as spillovers

TABLE 2 Divergence time estimates in million years (Ma), and node 95% highest posterior density (HPD) intervals for the *Spauligodon* Canary clades from each set of calibration priors. Letters represent the nodes in the maximum clade credibility tree (Figure 4)

Calibration strategy															
Clade/ Split	Node	1,2,3		1		2		3		2,3		1,3		1,2	
		Age	95% HPD	Age	95% HPD	Age	95% HPD	Age	95% HPD	Age	95% HPD	Age	95% HPD	Age	95% HPD
Clade A	a	4.2	1.95-6.78	2.86	0.86-5.32	3.82	1.37-6.93	15.41	2.23-38.27	5.18	2.28-8.48	4.65	1.91-7.92	3.19	1.39-5.36
Clade B	b	1.45	0.41-2.71	0.97	0.2-2.05	1.29	0.29-2.65	5.22	0.48-13.47	1.77	0.49-3.36	1.58	0.42-3.09	1.08	0.27-2.05
Clade C	c	1.04	0.01-2.95	0.67	0.01-1.99	0.91	0.2-2.62	3.62	0.01-11.33	1.24	3.38-23.57	1.15	0.01-3.22	0.75	0.01-2.1
Clade D	d	4.24	0.57-9.6	2.79	0.29-6.65	3.72	0.48-8.79	15.09	0.71-42.27	5.18	0.62-11.62	4.65	0.59-10.8	3.12	0.44-7.03

were not included in the analysis due to low sequence quality (Table S1). The contribution of the links used to set the age constraints contributed relatively little to the residual sum of squares, though some individual links have a higher squared residual than the median value (Figure 2b).

3.4 | Host specificity and host range oscillation estimates

Prevalence and intensity level of each *Spauligodon* clade from the Canary Islands are reported in Table 1. Each main lineage from each clade seems highly host specific, being found infecting mainly one host species/subspecies. Whenever found in another host (different from the main one), prevalences were always very low with usually only one individual host found infected, and consequently classified as a spillover (Table 1).

Several host-switching events (i.e., sister parasite lineages found infecting new hosts following association by colonization) were estimated to have occurred (Figure 5). Three switches to truly new hosts were inferred: one for clade A with a switch from skinks to *Gallotia* lizards soon after the mrca ancestor of clade A colonized the archipelago; one for clade B from an unknown host to *Gallotia* lizards around 2 Ma; and one for clade C from skinks to *Gallotia* lizards prior to the colonization of El Hierro. At least two switches to new species (as opposed to cospeciation) were inferred for clade A: i): switch in El Hierro between the two *Gallotia* species present in the island (possibly from *G. simonyi* to *G. caesaris*, Figure 5a labelled as 1), and ii) in Fuerteventura possibly between an introduced *Gallotia* species and *Gallotia atlantica* which is native on the island (Figure 5a labelled as 2). For clade D, one host-switching event to a new gecko species was inferred (from the ancestor of *T. gomerensis* to *T. boettgeri* or from *T. boettgeri* to *T. gomerensis*), which may have occurred in Gran Canaria or in La Gomera (Figure 5d labelled as 3). In all cases when a host-switching event was inferred, parasite lineages were always restricted to the new host species (Table 1) which indicates specialization. As a consequence, all host-switching events were also identified as cases of host range oscillations. Switches to a truly new host were classified as oscillations to truly new host (Figure 5a,b,c labelled as black stars) and switches to a new host species as oscillations to a new host species (Figure 5a,d labelled as white stars). No recolonization events were estimated for any of the clades.

4 | DISCUSSION

Ecological opportunities such as island colonization have been associated with decrease in host specificity and increase in host switch rates by exposing the parasite to other potential hosts (Nieberding et al., 2006; Pérez-Rodríguez et al., 2013). Increase in host switch rate can further lead to increase in diversification, even if no changes in host breadth have occurred (Hardy & Otto, 2014; Janz et al., 2016). In reality, the mechanisms of parasite

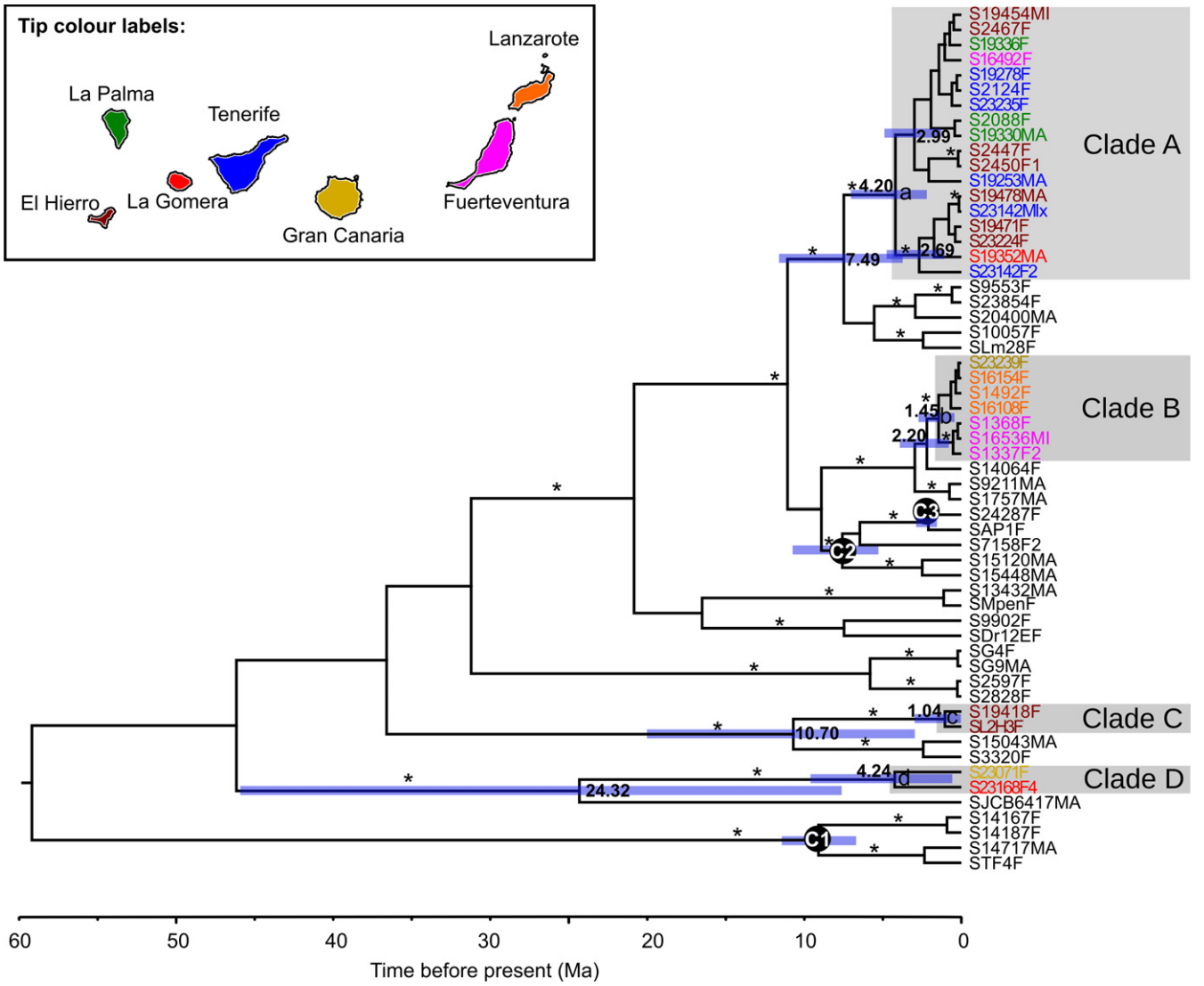

FIGURE 4 Maximum clade credibility ultrametric timescaled tree, generated under the birth–death model tree prior for the concatenated 28S and cytochrome oxidase subunit I (COI) parasite data set. Shaded rectangles indicate Canarian clades (labelled a-d). Node bars represent the 95% highest posterior density intervals for the key nodes. Node labels show mean divergence time estimates. Star symbol corresponds to Bayesian posterior probabilities higher than 95%. Tip labels from each clade coloured according to the islands of origin. Nodes used as calibrated priors in BEAST analysis are marked as C1, C2 and C3 [Colour figure can be viewed at wileyonlinelibrary.com]

diversification are still unclear, and other factors such as host density and host defence have also been linked with parasite diversification (Morand, 2015). Previous studies on *Spauligodon* nematodes have reported high population structure on islands, as a direct consequence of their specificity and diversification (Falk & Perkins, 2013). However, it remained unclear whether *Spauligodon* is in fact prevented by specificity barriers from expanding its host range, if it is somehow immune to the parasite island syndrome, or if sample bias had a strong influence on the observed patterns. In this study, we tested whether episodes of geographic expansion of *Spauligodon* nematodes, here represented as island colonizations, were associated with diversification of host use by host shifts, and consequently with higher lineage diversification in the context of the OH.

4.1 | How many independent colonization events?

Our phylogenetic evidence suggests that *Spauligodon* nematodes in the Canary Islands evolved from at least four different lineages, but may only represent three independent colonization events, with skinks having perhaps simultaneously introduced two unrelated *Spauligodon* lineages (clades A and C; Figures 4 and 5). While it is estimated that reptile host diversity resulted from at least six independent colonization events (one in *Gallotia* lizards, three in *Tarentola* geckos and two in the *Chalcides* skinks; Carranza et al., 2002; Carranza et al., 2008; Cox et al., 2010), on any occasion they could have reached the islands "empty" of *Spauligodon*, or the latter became extinct. This pattern is also observed in other parasites of the archipelago, namely haemogregarines from the same reptile

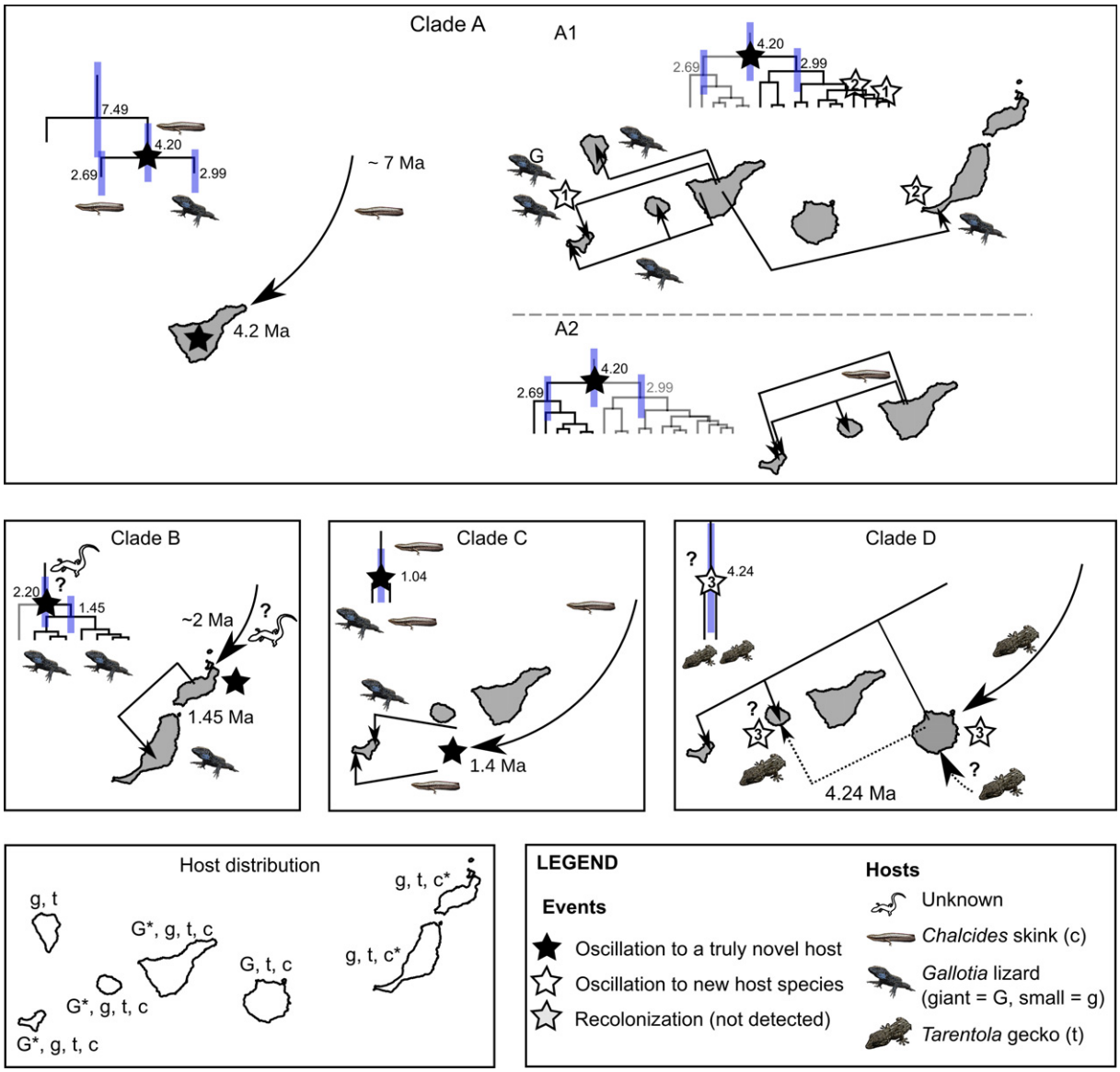

FIGURE 5 Inferred host switches and host range oscillation events during the colonization and diversification of each *Spauligodon* parasite clade in the Canary Islands with estimated divergence times: (a) clade A; (b) clade B; (c) clade C; and (d) clade D. (e) Host distribution, where asterisks denote the threatened status of the host. Whenever not indicated with a "G," all *Gallotia* representations in (a), (b) and (c) are from the small-type lizard species. Black stars represent host range oscillations to truly new hosts, white stars represent host range oscillations to new species and grey stars represent recolonizations (not detected, see Results for details of numbers). Trees represent the maximum clade credibility ultrametric timescaled tree. Subtrees are coloured in grey if not the focus of the associated schematic representation. Straight lines represent colonization routes and dashed line in D an alternative scenario for the location of the oscillation event (see Discussion for details) [Colour figure can be viewed at wileyonlinelibrary.com]

hosts which are inferred to have resulted from only three independent colonizations events (B. Tomé, A. Pereira, F. Jorge, M. A. Carretero, D. J. Harris and A. Perera, unpublished). However, we did not find *S. tarentolae* previously described by Spaul (1926) infecting *Tarentola delalandii* geckos in Tenerife. Unfortunately, this parasite taxon was only found in museum specimens, but no DNA could be successfully amplified (Jorge, Roca, Perera, Harris, & Carretero, 2012). At this stage, its phylogenetic placement and co-evolutionary history (i.e., whether it is part of clade D or it represents a different colonization event from this clade) remain unknown.

4.2 | Parasite specificity

As observed in previous studies (Falk & Perkins, 2013; Jorge et al., 2011), we found strong specificity for each main *Spauligodon* lineage. There was no evidence of a decrease in host specificity resulting in multiple host use as expected under the parasite island syndrome. Nevertheless, "occasional" infections (i.e., spillover) were detected, but prevalences were always very low with usually only one individual host found infected (Table 1). The presence of developed stages in those occasional hosts may result from phylogenetic

conservatism or general plasticity in traits related with resource use, whereas the lower prevalences may be related with a lower resource optimum. To what extent this is evident that *Spauligodon* parasites are generalists when it comes to their ability to infect host species (potential host range) but are actually host specific in terms of realized host use can only be unequivocally confirmed experimentally. This specificity seems to be the main factor currently shaping *Spauligodon* population structure in the Canary Islands, similar to what is observed in the Caribbean (Falk & Perkins, 2013), but it did not prevent the occurrence of host range oscillations to truly new host.

4.3 | When does a new colonization drive host range oscillation?

For all *Spauligodon* clades present in the Canary Islands, we found evidence of host range oscillations during the colonization of, and diversification within, the archipelago. These oscillations were first characterized by host switches, but later followed by parasite specialization as present-day associations, as inferred from prevalence values, are restricted to only one host species/subspecies. In three of the four clades, we found evidence of host range oscillations to truly new host, that is, new host genera (Figure 5). However, the lineages infecting geckos appeared to be more conservative or constrained regarding host range oscillations to hosts not sharing a closely related mrca. In fact, gecko parasites seem to be basal in the diversification of this parasitic group, not sharing mrca with parasites infecting other reptile groups. In contrast, clade A shares at a deeper evolutionary level a common ancestor with lineages infecting geckos, lacertid lizards and more recently skinks, and again lacertid lizards. This may suggest that parasitic lineages which originated from ancestors with more frequent and wider taxonomic host range oscillations (more colonizations of novel host taxa) across their evolutionary history have a higher chance of broadening their host range in future episodes of geographic expansion. This ability may be a direct result of their evolutionary past and phylogenetic conservatism of traits related to host use that are somehow maintained even after successful colonizations involving population bottlenecks. While sharp reductions in population size are expected to decrease the ability of a parasitic lineage to expand its host range (Araujo et al., 2015), host oscillations to truly new hosts occurred relatively soon after the *Spauligodon* colonization events. This pattern may be explained under Wright's shifting balance theory of evolution (Wright, 1932) where small effective population sizes would be the responsible factor enabling the parasite to adapt to new hosts by reducing the efficiency of selection. Nevertheless, the period of multiple hosts was limited to the switch period and afterwards parasites restrict their host use to a single host genus or species. However, it would be interesting to determine whether the rates of host switches are higher in islands than on the continent, as expected under the parasite island syndrome, something we cannot estimate with our data set.

4.4 | When, where and on which host did the parasites colonize the islands?

As we did not find significant differences between the 95% HPD interval for the divergence time estimates between analyses, the following discussion is based on the mean values estimated in the analysis with all three calibration priors.

Clade A: The mrca of clade A seems to have originated around 4.2 Ma, and soon after diversified in two lineages: one now present in the western *Gallotia* lizards (*S. occidentalis*) and the other in western skinks (Figure 4), sharing a mrca with non-Canarian *Spauligodon* lineages 7 Ma. These estimations exclude *Gallotia* lizards as a possible ancestral host as they seem to have colonized the Canary islands 17 to 20 Ma, reaching the westernmost islands around 9 to 10 Ma (Cox et al., 2010), while the ancestor of western skinks arrived to the central and western islands around 7 Ma (Carranza et al., 2008) (Figure 1c,e). The current parasite distribution also corroborates this hypothesis, as parasites from this lineage are absent from the easternmost islands. There is one exception, the lineage found in Fuerteventura, but its phylogenetic position suggests a recent colonization event, probably by host switch from introduced *Gallotia* lizards from Tenerife during the 1980s (Mateo, 2015). The diversification of clade A was driven initially by a range oscillation to a truly novel host, but later lineages of both skinks and *Gallotia* lizards have followed an overall congruent cophylogenetic pattern with their respective hosts. We observed differences in genetic diversity between these two lineages (Figure 3), with the lineage infecting *Gallotia* lizards (i.e., *S. occidentalis*) presenting higher intraspecific diversity. This result supports the OH, as the oscillation event leads to higher diversification.

Clade B: The evolutionary history of this clade, that is, *S. atlanticus*, is very intriguing. According to our data, this species only occurs in the oldest islands of the archipelago, but it represents one of the youngest colonizations. It diverged approximately 2 Ma ago from its closest relatives present in Morocco, postponing the timing of colonization of the reptile taxa currently inhabiting these islands [gecko, 3.63 to 6.30 Ma (Rato et al., 2012); *Gallotia* lizard, 17 to 20 Ma (Cox et al., 2010), and skink, 5 Ma (Carranza et al., 2008)]. Later, at about 1.45 Ma, the clade diverged into two lineages, one now present in Lanzarote and the other in Fuerteventura, which roughly coincides with the divergence between their current host subspecies (Cox et al., 2010). While it remains unclear which was the ancestral host of this clade, the occurrence in *Gallotia* lizards can only be explained by a host range oscillation event as their colonizations have a lag of more than 15 Ma. Recently, this parasite successfully colonized Gran Canaria together with an introduced population of *G. atlantica*.

Clade C: This clade was only found in the youngest island of the archipelago, El Hierro, infecting skinks and *Gallotia* lizards at a very low prevalence. In other clades, such low prevalence values (i.e., only 1 infected individual per locality) lead us to classify the use of the host as a spillover. However, both hosts presented the same low prevalence values so they were considered as main hosts. Whether the parasite went extinct in the other islands or its apparently low

prevalence resulted in false absences remains to be determined. The closest related taxa of this parasite clade are other *Spauligodon* nematodes infecting skinks from Morocco and Italy (estimated COI divergence of 13.3%, uncorrected *p*-distance), suggesting that its colonizing ancestor host was a skink as inferred for clade A. The estimated divergence between the two lineages within the clade, one present in skinks and the other in *Gallotia* lizards, is slightly younger than the emergence of El Hierro island (1.04 Ma and 1.12 Ma, respectively), providing further evidence of diversification by host range oscillation to a novel host (Figure 5c). However, due to the sample size, we were unable to test for differences in genetic differentiation between the two lineages.

Clade D: This clade was found in geckos from Gran Canaria, La Gomera and El Hierro (although identification of the latter was based only on morphological characteristics). While it is clear that the mrca of clade D colonized the archipelago together with the geckos ancestor that occupy these islands, the monophyly of these lineages is incongruent with host colonization history that has resulted from two separate colonization events [one 5.3 to 6.7 Ma by the ancestor of *T. boettgeri* to Gran Canaria, Selvages and El Hierro; and another, 4.1 to 8 Ma by the ancestor of *T. delalandii* and *T. gomerensis* to the western islands of Tenerife, La Gomera and La Palma, with their mrca dating to 7.2 to 11 Ma (Carranza et al., 2002); Figure 1d]. In any case, this was the only clade where we did not detect a host range oscillation to a truly new host, only a switch to a related host species (same genus).

4.5 | Estimates of divergence times

While estimates of absolute times are not essential to detect host range oscillations, it was an important tool to determine the temporal context of parasite colonization and diversification, and better support inferences regarding ancestor host identity. While mean divergence time estimates varied between calibration strategies, the 95% HPD intervals did not significantly differ. Nevertheless, the precision of age estimates was influenced by uncertainties of host age estimations, use of a secondary calibration as unique source of calibration and the placement of calibration information (Schenk, 2016). The selection of the calibration nodes in our study was based on the level of cophylogenetic congruence of the respective host–parasite links. Previous studies have also used host information as prior to calibrate parasite phylogeny, either to fix the molecular clock or to calibrate parasite nodes (Hamilton, Cruickshank, Stevens, Teixeira, & Mathews, 2012; McTaggart et al., 2016; Nieberding, Morand, Libois, & Michaux, 2004; Olson et al., 2010; Pettersen, Mo, Hansen, & Vøllestad, 2015; Ricklefs & Outlaw, 2010). While assumptions in the first case (i.e., a strict clock model) are not usually fulfilled due to rate heterogeneity between lineages, calibrating parasite nodes is based upon the assumption of host–parasite codivergence or host tracking at the node of placement of the calibration information. However, the assumption of codivergence or host tracking is not always clearly tested through the use of co-evolutionary methods (Olson et al., 2010; McTaggart et al., 2016; but see Nieberding et al., 2004). By combining a priori assessment of the degree of host–parasite cophylogenetic congruence with a global-fit method, our framework provides a more precise and clear assessment of the nodes on the parasite phylogeny suitable for the use of host divergence time. Alternatively, age estimates from fossils could be an option, but nematode fossils are rare and their correct placement in the phylogeny can be challenging. Biogeographic events are another possibility (i.e., Barratt et al., 2017) and have been used for host divergence time estimates. However, they were found unsuitable in our study due to the time intervals between island formation and host colonization.

The resulting mean clock rates obtained from our analysis are one order of magnitude lower than previous estimates for other nematodes [i.e., *Spauligodon* mitochondrial $\sim 1.08 \times 10^{-9}$ substitution per site per generation if assuming four generations per year based on Bursey and Goldberg (1992) vs. mitochondrial in nematodes from laboratory mutation-accumulating lines 1.7×10^{-8} - $9.7\ 10^{-8}$ (Denver, Morris, Lynch, Vassilieva, & Thomas, 2000; Howe, Baer, & Denver, 2010; Molnar, Bartelmes, Dinkelacker, Witte, & Sommer, 2011)]. However, this discrepancy can be explained by time-dependent effects on rates, as studies of overall substitution rates over a small number of generations may overestimate rates by one order of magnitude or more (Ho et al., 2011).

5 | CONCLUDING REMARKS

In this study, we found that host range oscillations have been a prominent feature of the evolutionary history of *Spauligodon* parasites in the Canary Islands. The colonization of the Canary archipelago was associated with the occurrence of host range oscillations in all parasitic clades. Host range diversification seems to be restricted by a parasite's evolutionary past and to the initial stages of the colonization period. As for the questions regarding *Spauligodon*, the parasite island syndrome and host specificity due to restricted sampling effort (one taxon): we did not find support for the island syndrome as host range oscillations did not lead to changes in host breadth. In fact, after sampling all potential hosts, there was still evidence of strong host specificity in contemporary host–parasite associations. This level of specificity may be responsible for the significant global cophylogenetic structure. However, host specificity does not pose insurmountable barriers to host switches, as we found ample evidence of incongruence between host–parasite cophylogenetic histories. The potential for host range oscillations seems to be shaped by the parasites' ability to retain ancestral traits related to host use. We suggest that parasite lineages with more frequent and more taxonomically diverse host range oscillations in their evolutionary past are more prone to future range expansions to distantly related hosts. However, our inferences rely on present-day host–parasite associations and distribution, and some of our historical reconstructions are based on few specimens due to low prevalence values. Comparative studies are needed to reveal whether this pattern also applies to other host–parasite systems. While it may seem difficult to predict

future host range oscillations, reconstructing the evolutionary past of parasites may be the best indicator of their potential for future shifts.

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DATA ACCESSIBILITY

All nematode and reptile specimens are deposited in the Herpetological and Parasitological collection of CIBIO-InBIO, University of Porto, Portugal. DNA sequences are deposited in GenBank under Accessions numbers MG573449 to MG573573. Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad (xml input file for the divergence time estimates in BEAST with the three calibration priors, and all input data used in the cophylogenetic analysis using the global-fit statistic tool PACo).

AUTHOR CONTRIBUTIONS

F.J., A.P., V.R. and M.A.C. carried out fieldwork. F.J. did the laboratorial work and data analyses. F.J. wrote the manuscript with contributions and editing from A.P., R.P., V.R. and M.A.C. All authors read and approved the final manuscript.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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