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LETTER

Establishment of exotic parasites: the origins and characteristics of an avian malaria community in an isolated island avifauna

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Abstract

Knowledge of the processes favouring the establishment of exotic parasites is poor. Herein, we test the characteristics of successful exotic parasites that have co-established in the remote island archipelago of New Zealand, due to the introduction of numerous avian host species. Our results show that avian malaria parasites (AM; parasites of the genus *Plasmodium*) that successfully invaded are more globally generalist (both geographically widespread and with a broad taxonomic range of hosts) than AM parasites not co-introduced to New Zealand. Furthermore, the successful AM parasites are presently more prevalent in their native range than AM parasites found in the same native range but not co-introduced to New Zealand. This has resulted in an increased number and greater taxonomic diversity of AM parasites now in New Zealand.

Keywords

Avian malaria, introduced birds, introduction success, invasive parasites, New Zealand.

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INTRODUCTION

Parasites are increasingly being spread by human activities, and subsequently establishing exotic populations in locations beyond the limits of their native geographical ranges (Daszak *et al.* 2000; Cleaveland *et al.* 2002; Prenter *et al.* 2004). These exotic parasites and the diseases they potentially cause pose a serious threat to human and animal health (reviewed by Davis 2009; chapter 7), especially if they subsequently jump between hosts in the new localities to infect native species (Woolhouse *et al.* 2005). Catastrophic outcomes from the inadvertent establishment of parasites are well known, such as the spread of smallpox into the Americas with Europeans, causing high mortality in native Indians (Li *et al.* 2007) and the spread of co-introduced rinderpest into East Africa with introduced domestic cattle, causing mass mortality when spilling over into wild ruminant species (Plowright 1982). There is thus a strong incentive to identify characteristics related to invasion success in exotic parasite species.

Most studies of exotic parasites address the likelihood that a host species carries its parasites with it during the invasion process, and/or the consequences of losing or retaining parasites for host success. In the former context, parasites may be absent from the faunas of remote bioregions because they 'missed the boat' (were absent from the hosts introduced; Paterson & Gray 1997) or 'drowned on arrival' (were present in introduced hosts but either the hosts or the parasites failed to establish; MacLeod *et al.* 2010). If pathogen loss positively affects host traits such as reproduction and survival, then the likelihood that an exotic host population can become established may be increased: this is known as the Enemy Release Hypothesis (Keane & Crawley 2002; Colautti *et al.* 2004). Conversely, an exotic host species may benefit from the co-introduction of its parasites, if those parasites subsequently infect and cause population declines in native species that otherwise would compete with or predate upon the exotic host: this is known as the Novel Weapon Hypothesis (Daszak *et al.* 2000; Ricklefs 2010). The possible occurrence of such host switches and the characteristics that determine whether or not a parasite can make such a jump have also received attention (Woolhouse *et al.* 2005). However, we know of no studies that have considered the characteristics of parasites that determine whether or not they are successfully co-introduced to a new region with their hosts, even though many studies have assessed the traits possessed by successful exotic host species (reviewed by Kolar & Lodge 2001; Pyšek & Richardson 2008; Blackburn *et al.* 2009a,b; Davis 2009).

The processes that underpin the 'missing the boat' and 'drowning on arrival' hypotheses nevertheless lead to predictions regarding the likely characteristics that enable the successful establishment of exotic parasites at a new locality. First, these parasites are predicted to be generalists, as this should increase the probability that they will infect one of the host species chosen for introduction, and find sus-

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ceptible hosts to infect in the new location. Second, these parasites are predicted to have relatively high prevalence and low virulence in the natural host, as they must be present in the small number of hosts transported for release, but not cause host mortality during the invasion process. Third, these parasites should have suitable competent vectors in the new area. Parasites arriving through human-mediated introductions to isolated bioregions are also likely to be absent from the native parasite assemblage, as such systems are typified by low species richness and high faunal endemism (MacArthur & Wilson 1967). However, empirical data on the characteristics of exotic parasites with which to test these predictions remain scarce (Woolhouse *et al.* 2005).

Studies of avian malaria (AM; parasites of the genus *Plasmodium*, Valkiunas 2005) provide an excellent opportunity to develop a detailed picture of the traits favouring human-mediated invasion in a parasite taxon. There is now unprecedented knowledge of host identity and geographical distribution for hundreds of AM lineages (Bensch *et al.* 2009). Herein, we examine the origins of the AM community in the remote island archipelago of New Zealand, to determine what characteristics of these lineages helped them to be successfully co-introduced with their exotic hosts, and hence to become exotic species themselves. New Zealand has a rich exotic avifauna comprising more than 30 species from 14 families (Duncan *et al.* 2006), resulting largely from the efforts of Acclimatization Societies, founded in the Victorian period (mid-to-late 1800s), with the aim of 'enriching' the recipient countries fauna and flora. New Zealand has therefore had abundant opportunities for co-invasion by avian parasites. Using an extensive global database of AM parasites, we determine how the stocking of New Zealand with exotic bird species in colonial times has contributed to the current malaria parasite fauna. If AM parasites have been introduced to New Zealand we would expect the New Zealand parasite assemblage to show a low degree of host specialisation, a broad geographical range and for successful parasite invaders to occur at high prevalence in their native ranges.

Here, we test whether AM lineages found in New Zealand are more host generalist or geographically widespread than those AM lineages recorded globally but not found in New Zealand. We then test whether AM lineages found in New Zealand occur at higher prevalence in host species in their native range than other AM lineages recorded in the same area but not found in New Zealand. Finally, we document where these exotic AM have also jumped into new (native) hosts.

METHODS

Study site and sampling

In the austral summers between December 2003 and February 2006 we sampled exotic and native host bird species at a range of sites in northern New Zealand (820 individuals; see Appendix S1 in Supporting information for a breakdown of species sampled per site). Birds were mostly caught in mist nets with additional birds caught in feeding cage traps (*Notiomystis cincta*) or clap traps (*Petroica longipes*). The single kokako (*Callaeas cinerea*) was opportunistically sampled as a nestling during standard health screening. In all cases, a small blood sample (about 70 μL) was collected via brachial venipuncture and stored in 100% ethanol for later molecular analysis.

Native host sampling took place on two island reserves (Hauturu or Little Barrier and Tiritiri Matangi) in the Hauraki Gulf near Auckland, except for additional sampling of *Petroica longipes* which occurred near Benneydale, central north island (38°30′ S, 175° 24′ E). Hauturu (36°12′ S, 175°5′ E) is a 3083-ha island established as a reserve in 1894 and is one of the most pristine native ecosystems remaining in New Zealand including the most intact assemblage of native terrestrial avifauna. Tiritiri Matangi island is much smaller (220 ha; 36°36′ S, 174°53′ E) and was largely degraded to open farmland before an extensive revegetation programme, initiated in the early 1980s, returned the island to about 60% regenerating native forest cover. In addition, most extant native host bird species have been reintroduced to the island in the last few decades to recreate a diverse and near complete representation of northern New Zealand native terrestrial avifauna.

Exotic host species were sampled from all sites where native species were sampled and also other sites (farmland and urban areas) where many native species are absent. This included urban areas in Palmerston North (40°24′ S, 175°35′ E), orchards in Hawkes Bay (39°40′ S, 176°52′ E) and Benneydale, and pastoral farmland in Benneydale and Pukekohe (37°10′ S, 174°55′ E).

Laboratory analyses

We extracted DNA from blood, and detected parasite infections using the nested polymerase chain reaction (PCR) method described by Waldenström *et al.* (2004). This method amplifies a 479 bp segment of the parasite's cytochrome *b* gene. Parasite lineages were distinguished by their DNA sequences and any double infections were resolved following methods described in Pérez-Tris & Bensch (2005). Negative results were confirmed using repeat PCR and sample quality was confirmed by amplification of the bird's nuclear DNA (using universal sexing primers; Fridolfsson & Ellegren 1999). Negative controls (one after every 10 samples) always tested negative. The detection probability of AM lineages has not been directly assessed (see Lachish *et al.* 2012), and this was beyond our control for the large bulk of AM lineage data we analysed that has been generated from previous studies and deposited on the MalAvi database. While it is encouraging that Lachish *et al.* (2012) report high detection probabilities using PCR based approaches, we nevertheless note this potential source of uncertainty in our dataset.

Statistical analysis

Using the MalAvi database (Bensch *et al.* 2009), we studied the phylogenetic relationships, host range and geographical distribution outside of New Zealand of parasites found in New Zealand. We obtained host and geographical distributions of 294 *Plasmodium* parasite lineages that could be unambiguously identified by distinct cytochrome *b* sequence and contributed valid data for phylogenetic analyses (we discarded parasite lineages with sequences including many unresolved nucleotides). A maximum-likelihood phylogeny of these parasites was built using MEGA5 (Tamura *et al.* 2011). We used a Tamura-Nei (TN93) model of nucleotide substitution with gamma parameter $\alpha = 0.479$, and assumed proportion of invariable sites = 0.376. This was the best model according to the Akaike information criterion implemented in MEGA5 (Tamura *et al.* 2011). The best tree was obtained using a heuristic search with nearest neighbour interchange algorithm. We used a clade of four species

of mammal *Plasmodium* as the out-group. Support to internal branches of the tree was estimated using bootstrap analyses (1000 replicates).

We considered 898 confirmed associations between the above-mentioned 294 *Plasmodium* lineages and 637 host bird species. Geographical locations where host–parasite associations were observed were assigned to one of nine regions (Africa, South America, Central America, North America, Asia, Australasia, Europe and islands of the Indian Ocean and the Pacific Ocean; Bensch *et al.* 2009). The number of hosts a parasite is found to infect may not correctly represent the capability of the parasite to colonise new hosts if the parasite is introduced into a new region. Such capability will probably also be influenced by the ability of the parasite to thrive in hosts of diverse ancestry. This may be particularly true for New Zealand colonisers because host-taxonomically restricted parasites may be incapable of making host shifts if they derive from avifaunas that are relatively phylogenetically distinct from that in New Zealand. We therefore also computed an index of host taxonomic range (the standardised host range index S^*_{TD} index, see Hellgren *et al.* 2009), which takes into account not only the number of reported host species for the parasite but also the phylogenetic relationships among hosts. Hence, high values of S^*_{TD} reflect a greater host-taxonomic range.

One potential problem with our approach is that not all parasites included in MalAvi will have had the same chance of being introduced in New Zealand. Indeed, those parasites known to occur in bird species that were transported into New Zealand may better represent the true diversity of parasites potentially carried into New Zealand with their hosts. Therefore, we repeated our analyses of host taxonomic range using a smaller sample of 312 interactions involving 195 bird species and the 45 parasite lineages found outside New Zealand in the 25 bird species that were introduced in New Zealand from Europe.

We tested whether the parasites found in New Zealand occurred in more host species had higher S^*_{TD} indices and occurred in more geographical regions than expected by chance using Monte Carlo simulations of parasite assemblages. In each simulation, we randomly selected eight parasite lineages from the global pool ($n = 294$) to represent an assemblage with the same parasite richness found in New Zealand, and computed the difference between selected ($n = 8$) and not selected ($n = 286$) parasites in the average number of host species and geographical regions. The probability of randomly obtaining equal or greater host or geographical ranges than those observed in our study was computed from 10 000 simulations.

Data on the prevalence of a subset of parasites in European hosts were obtained from Hellgren *et al.* (2009). This study reported data on average prevalence in Europe for 35 parasites, including five of the parasites found in New Zealand reported from European hosts. Hellgren *et al.*'s (2009) study uses prevalence data obtained from 26 different avian host species, for which the AM lineages were identified following the same methods as reported in our study. The prevalence of each AM lineage was calculated as the proportion of host individuals infected with the parasite. However, Hellgren *et al.* (2009) included no information on prevalence of Linn1 (a parasite found in New Zealand that occurs in Europe). We know of one study from Europe that reports prevalence of Linn1 (in *Cyanistes caeruleus*; Wood *et al.* 2007), so we used its prevalence estimate (0.6%) as the average prevalence of Linn1. We view the Hellgren *et al.* (2009) data set as suitable for our analysis as it is unbiased with respect to our goals and there have been very few studies published since then that are known to the authors (or appear in the MalAvi database); the one exception is the study by Wood *et al.* (2007), which we used to estimate the prevalence of Linn1.

RESULTS

We detected a variable prevalence of eight *Plasmodium* parasites in the 820 potential bird hosts screened in New Zealand, including samples from 10 exotic Passeriformes species and 15 native species (Passeriformes, Psittaciformes, Coraciiformes; Fig. 1).

Those parasite lineages found in New Zealand were recorded from more host species (GLZ model with Poisson error structure and log link function: $\chi^2 = 75.39$, df = 1, $P < 0.0001$) and were more widely distributed outside New Zealand ($\chi^2 = 55.46$, df = 1, $P < 0.0001$) than other known parasites not found in New Zealand (Figs. 2a and c). The sample of New Zealand parasites includes two putatively endemic lineages, which consequently had scores for the number of hosts and number of regions outside New Zealand equal to zero; this makes the result especially conservative. Furthermore, the parasites found in New Zealand had a broader taxonomic range of hosts (as shown by higher values of the standardised host range index S^*_{TD}; Hellgren *et al.* 2009) than the parasites not found in New Zealand ($\chi^2 = 35.88$, df = 1, $P < 0.0001$; Fig. 2b), indicating that these parasites are found not only in more host species but also in a wider taxonomic range of host species. The same results were obtained with reduced statistical power when these analyses were repeated using the 45 parasite lineages found outside New Zealand in bird species known to have been carried into New Zealand (all analyses with $P < 0.001$). We further tested whether the eight New Zealand parasite lineages occurred in more host species and in more geographical regions than expected by chance using Monte Carlo simulations of the parasite assembly process. None of the simulated assemblages produced greater differences between parasites present or not in New Zealand than those observed empirically (Figs. 3a and c). Similarly, the simulations revealed that it was very unlikely to select by chance six parasite lineages with equal or higher S^*_{TD} values than the observed values for the six lineages present both in New Zealand and elsewhere (Fig. 3b). The same results were found when the analysis was repeated using parasite lineages from bird species introduced in New Zealand (all analyses with $P < 0.002$).

Three of the four most globally widespread *Plasmodium* lineages, in the known diversity of the group (*P. relictum* GRW4 and SGS1, and *P. elongatum* GRW6), were found in New Zealand. Four of the globally widespread parasites found in New Zealand have not yet been recorded elsewhere in Australasia. New Zealand parasites absent from the Australasian region, such as *Plasmodium* sp. Linn1, *P. vaughani* Syat05 and *P. relictum* SGS1, were especially well represented in the exotic European avifauna.

The AM lineages found in New Zealand were not closely related to one another, but were widespread in the phylogeny of avian *Plasmodium* (Fig. 4). The six lineages that our data revealed were not endemic to New Zealand and have all been recorded from hosts in Europe, which is also the source region for their exotic bird hosts in New Zealand. Indeed, all six are present in the list of 45 parasite lineages that have been found outside New Zealand in the 25 bird species that may have carried parasites into New Zealand (because they were introduced in the past). These six parasite lineages showed a higher mean prevalence in European hosts than those parasites

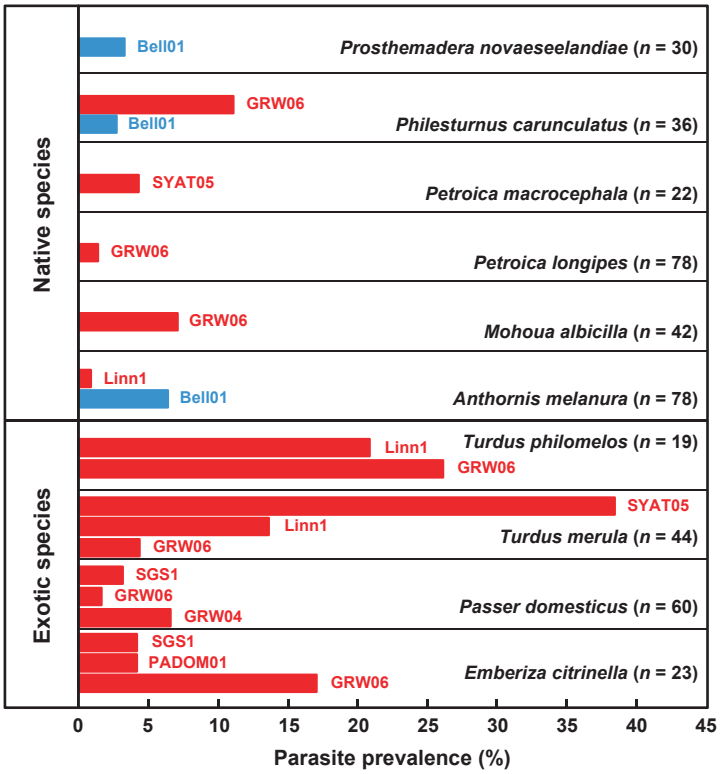

Figure 1 Prevalence of each parasite lineage (excluding KOKAKO1, which was found in an opportunistically sampled *Callaeas cinerea* individual) in native and exotic host species in New Zealand. Putative native parasites are represented with blue bars and putatively introduced parasites are represented with red bars. Host species with no parasite detections are, Native: *Cyanoramphus novaezelandiae* $n = 10$, *Gerygone igata* $n = 19$, *Hirundo tahitica* $n = 6$, *Nestor meridionalis* $n = 1$, *Ninox novaeseelandiae* $n = 1$, *Notiomystis cincta* $n = 261$, *Rhipidura fuliginosa* $n = 30$, *Todiramphus sanctus* $n = 6$, *Zosterops lateralis* $n = 16$; Exotic: *Carduelis cabaret* $n = 1$, *C. carduelis* $n = 5$, *C. chloris* $n = 10$, *Fringilla coelebs* $n = 5$, *Prunella modularis* $n = 1$, *Sturnus vulgaris* $n = 1$.

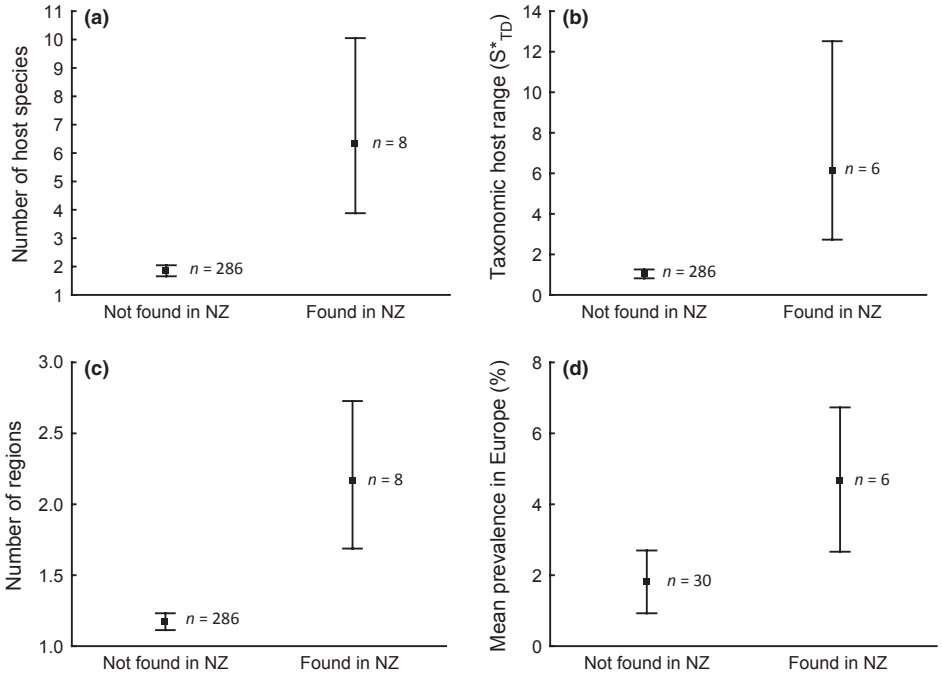

Figure 2 Variation in the number of host species (a), taxonomic host range S^*_{TD} (b), and the number of geographical regions (c) reported in the MalAvi database for *Plasmodium* parasites that were or were not found in New Zealand. Mean prevalence of the subset of parasites that occur in Europe and were or were not found in New Zealand (d), using data from Hellgren *et al.* (2009) and Wood *et al.* (2007). All data are reported as means with 95% confidence intervals.

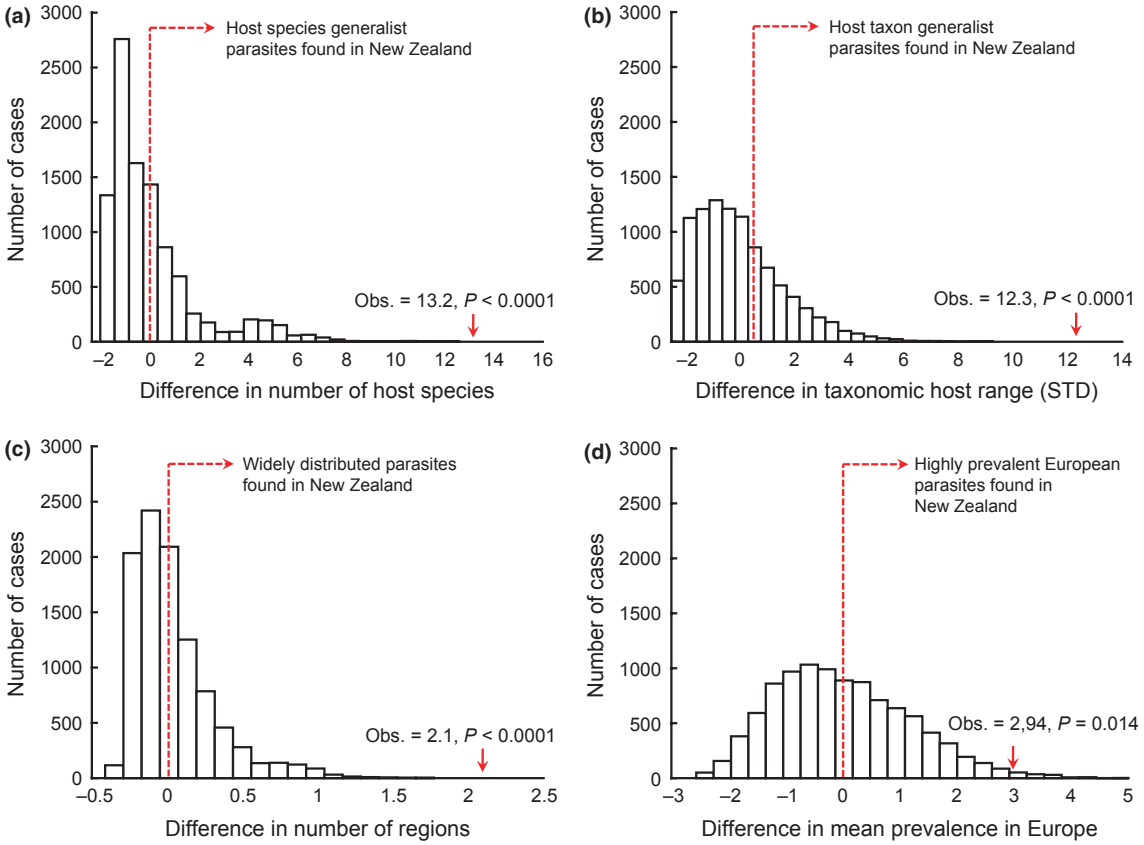

Figure 3 Distribution of differences in the average number of host species (a), taxonomic host range S^*_{TD} (b) and geographical regions occupied outside New Zealand (c) for randomly selected groups of eight parasites from MalAvi (representing randomly assembled parasite faunas with lineage richness as observed in New Zealand) and the remainder of the parasite lineages in the database. The distribution of differences in the mean prevalence of parasites in Europe (d) uses randomly selected groups of six parasites similarly representing randomly assembled parasite faunas which may have originated in Europe. Positive values show greater values for randomly assembled New Zealand parasites than for other parasites. Observed values are indicated by solid arrows, together with their probabilities of occurrence.

(n = 30) found in European hosts that were not also found in New Zealand (χ^2 = 6.94, df = 1, P = 0.008; Fig. 2d; we were unable to repeat the test considering only host species which have been introduced to New Zealand because few had prevalence data available). Again, Monte Carlo simulations showed that the probability of randomly selecting six European parasite lineages with equal or higher mean prevalence in Europe than these was low (Fig. 3d).

DISCUSSION

Given that AM parasites found in New Zealand were positioned widely through the *Plasmodium* phylogeny we can discount the idea that the New Zealand parasite assemblage resulted from a single endemic parasite radiation. The lack of close phylogenetic affinity, plus the fact that they are mostly found in exotic host species of European origin (Fig. 1), supports the view that different lineages arrived in New Zealand in multiple independent events. Most of the AM parasites we recorded in New Zealand are, in fact, common in other regions of the world, indicating a recent arrival.

We argue that the most parsimonious explanation is that the globally widespread AM parasites found in New Zealand 'caught the boats' which transported exotic host species during colonial times (Thomson 1922). Our argument is supported by the fact that all six of these lineages are recorded as infecting the exotic bird species transported to New Zealand. In addition, lineages such as *Plasmodium* sp. Linn1, *P. vaughani* Syat05 and *P. relictum* SGS1 have not been reported elsewhere in Australasia but are well represented in the European avifauna. Another recent study has also investigated the (successful) co-introduction of European AM lineages, in this case with European house sparrow *Passer domesticus* hosts (Marzal *et al.* 2011). Most exotic house sparrow populations seem to have lost the AM lineages infecting them in their native range, however, and acquired novel AM lineages from their exotic range. It may be that the invasion success of parasites is mediated by the parasite communities encountered, which raises interesting questions about the resistance to co-invasion by AM set by variable recipient communities (an idea discussed in Woolhouse *et al.* 2005) and the increased risks to more naïve host communities which may also be more open to AM colonisation (e.g. as seen in Hawaii, van Riper *et al.* 1986).

Our results directly support predictions about the traits of successful parasite invaders. First, we provide clear evidence that successful AM lineages have wide host ranges and geographical distributions. Moreover, AM lineages introduced to New Zealand occur in a wider phylogenetic breadth of host species than expected by chance. Second, AM lineages introduced to New Zealand are more prevalent in their native range in Europe than are AM lineages found in Europe but not in New Zealand. The positive

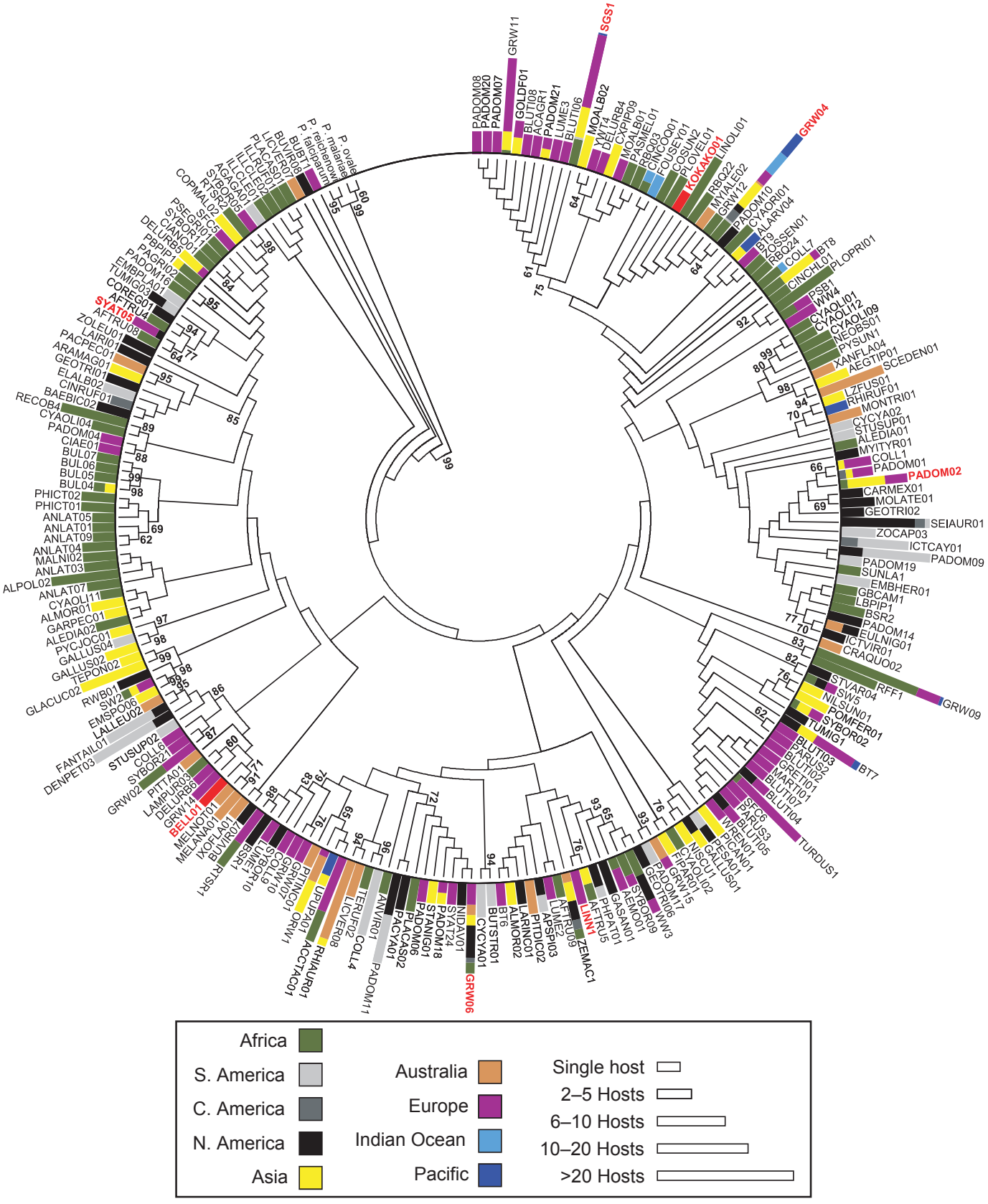

Figure 4 Maximum-likelihood phylogenetic tree of 294 avian *Plasmodium* lineages, with four mammal *Plasmodium* species as out-groups. Bootstrap support for branches is indicated (only values $\geq$ 60). Bars of different size represent variable number of reported hosts among parasites, and the colours represent parasites' geographical ranges (both outside New Zealand). The eight parasites found in New Zealand are highlighted with red text (putative endemic parasites are shown with red bars too).

relationships between generalism, prevalence and invasion success are important and untested associations in exotic parasite faunas.

Our results concord with associations demonstrated for the bird hosts of the AM parasites, for which wide geographical distributions and habitat and dietary generalism have been shown to be predictors of success in establishment in exotic locations (Blackburn & Duncan 2001; Duncan *et al.* 2006; Blackburn *et al.* 2009a). The association between geographical range size and establishment success in birds probably arises because species with large range sizes tend to be introduced in larger numbers (Cassey *et al.* 2004), the number of individuals introduced being the primary driver of establishment success (Lockwood *et al.* 2005). The association between geographical range size and successful co-introduction for the AM parasites of birds may well have a similar ultimate explanation. Nevertheless, the exact mechanism by which widespread, generalist AM parasites come to be present in New Zealand needs further investigation, as our results do not distinguish whether it is because they are more likely to be introduced, more likely to establish once introduced or both.

One potential issue in interpreting our results is that the co-introduction of AM lineages probably happened over a century ago, when exotic birds were introduced to New Zealand (Duncan *et al.* 2006), and when the geographical distributions or prevalences of AM lineages might have been very different. Thus, there may have been no positive relationship between geographical distribution at the time of introduction and the likelihood of co-introduction. However, this requires that those AM lineages co-introduced to New Zealand in the nineteenth century were not then more widespread or prevalent in their native range than other AM lineages, but subsequently and independently became so. This seems unlikely. If any such changes did occur, they were certainly not as a result of range size increases in co-introduced host species in their native ranges. Those bird species that were widespread in the late 19th century were also widespread in the late 20th century (Holloway 1995), so that the Spearman rank correlation in number of counties in the UK occupied by species introduced from the UK to New Zealand in these two periods was 0.94 ($n = 25$, $P < 0.001$, data from Holloway 1995; Duncan *et al.* 2006).

Our final prediction was that New Zealand should be home to a suitable vector for AM. It has been suggested that the transmission of AM in New Zealand has been greatly facilitated by establishment of the exotic mosquito *C. quinquefasciatus* only a few decades ago (Tompkins & Gleeson 2006; Massey *et al.* 2007), raising the spectre of a disease-driven extinction event there comparable to that caused by AM in Hawaii (van Riper *et al.* 1986). However, we have shown evidence for the presence of *Plasmodium* lineages which may have a relationship independent of exotic host introductions (also recently reported in Baillie & Brunton 2011). Also, New Zealand does have native mosquito species which are known to be a suitable vector for at least one *Plasmodium* lineage (Massey *et al.* 2007). Together, this suggests that the New Zealand avifauna has a history of association with AM that pre-dates human colonisation of the islands. Whereas this has not prevented co-introductions of exotic AM, it remains important to determine whether or not an evolutionary history between AM and New Zealand avifauna offers them some resistance to infection and disease.

Interestingly, only three of the globally widespread AM lineages (*P. elongatum* GRW6, *P. vaughani* Syat05 and *Plasmodium* sp. Linn1) were found in both exotic and native host species in New Zealand. These lineages were those detected in the two exotic host species that are widely acknowledged to successfully penetrate the native forest habitats of New Zealand (European song thrush, *Turdus philomelos* and European blackbird, *T. merula*; Holdaway 1990; Williams 2006). Of these, *P. elongatum* GRW6 has the widest host range within New Zealand (across three exotic families Emberizidae, Passeridae, Turdinae and three native families Callaeidae, Pachycephalidae, Petroicidae, Fig. 1). In contrast, *Plasmodium* sp. Linn1 and *P. vaughani* Syat05 were detected in very low prevalence in native host species (one infection detected in each case) and we suggest that these are uncommon infections of unsuitable hosts likely promoted by the ecological overlap of native bird species with their abundant *Turdus* hosts.

There is a growing consensus that most exotic AM lineages in New Zealand only occasionally infect free living native hosts in New Zealand, with the exception of *P. elongatum* GRW6 (Baillie & Brunton 2011; Castro *et al.* 2011; Howe *et al.* 2011). It may be that remnant populations of native hosts that are confined to native forest are partially protected from infection due to the lack of exotic hosts in that environment. Further support for this comes from cases of disease emergence often being associated with captive animals in urban environments (Tompkins & Gleeson 2006). Together these findings suggest a variable risk to native hosts from exotic AM, in some cases infection results in disease emergence and death, whereas in others the native hosts appear to tolerate chronic infections with little noticeable cost (Castro *et al.* 2011). Assessing the risk and negative impacts of exotic AM will be an important area for further study.

In summary, we have provided a rare quantitative test of hypotheses regarding the characteristics of parasites successfully co-established in exotic ranges with introductions of host species, confirming predictions about generalism, prevalence and invasion success. Importantly, our study adds further detail to our understanding of parasite introductions to new environments and may be invaluable for managing their impact. Others have shown that successful parasite co-introduction is linked to processes determining host introduction success (MacLeod *et al.* 2010), but we demonstrate that processes operating at the level of the parasite are equally important.

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AUTHORSHIP

JGE, CB and JP initiated study; JGE, TMB, PC and RC undertook fieldwork; SB, CB, RB and JP conducted molecular work; JP analysed data, JGE wrote first draft and all authors contributed substantially to revisions.

REFERENCES

Baillie, S.M. & Brunton, D.H. (2011). Diversity, distribution and biogeographical origins of *Plasmodium* parasites from the New Zealand bellbird (*Anthornis melanura*). *Parasitology*, 138, 1843–1851.

Bensch, S., Hellgren, O. & Perez-Tris, J. (2009). MalAvi: a public database of malaria parasites and related haemosporidians in avian hosts based on mitochondrial cytochrome *b* lineages. *Mol. Ecol. Res.*, 9, 1353–1358.

Blackburn, T.M. & Duncan, R.P. (2001). Determinants of establishment success in introduced birds. *Nature*, 414, 195–197.

Blackburn, T.M., Lockwood, J.L. & Cassey, P. (2009a). *Avian Invasions: The Ecology and Evolution of Exotic Birds*. Oxford University Press, Oxford.

Blackburn, T.M., Cassey, P. & Lockwood, J.L. (2009b). The role of species traits in the establishment success of exotic birds. *Glob. Change Biol.*, 15, 2852–2860.

Cassey, P., Blackburn, T.M., Sol, D., Duncan, R.P. & Lockwood, J. (2004). Introduction effort and establishment success in birds. *Proc. R. Soc. Lond. B*, 271, S405–S408.

Castro, I., Howe, L., Tompkins, D.M., Barraclough, R.K. & Slaney, D. (2011). Presence and seasonal prevalence of *Plasmodium* spp. in a rare endemic New Zealand passerine (tieke or saddleback, *Philesturnus carunculatus*). *J. Wildl. Dis.*, 47, 860–867.

Cleaveland, G.R., Hess, G.R., Dobson, A.P., Laurenson, M.K., McCallum, H.I., Roberts, M.G. et al. (2002). The role of pathogens in biological conservation. In: *The Ecology of Wildlife Diseases* (edsHudson, P.J., Rizzoli, A., Grenfell, B.T., Heesterbeek, H. & Dobson, A.P.). Oxford University Press, Oxford, pp. 139–150.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A. & MacIsaac, H.J. (2004). Is invasion success explained by the enemy release hypothesis? *Ecol. Lett.*, 7, 721–733.

Daszak, P., Cunningham, A. & Hyatt, A.D. (2000). Emerging infectious diseases of wildlife – threats to biodiversity and human health. *Science*, 287, 443–449.

Davis, M.A. (2009). *Invasion Biology*. Oxford University Press, Oxford.

Duncan, R.P., Blackburn, T.M. & Cassey, P. (2006). Factors affecting the release, establishment and spread of introduced birds in New Zealand. In: *Biological Invasions in New Zealand* (eds Allen, R.B. & Lee, W.G.). Springer-Verlag, Berlin, pp. 137–154.

Fridolfsson, A.K. & Ellegren, H. (1999). A simple and universal method for molecular sexing of non-ratite birds. *J. Avian Biol.*, 30, 116–121.

Hellgren, O., Pérez-Tris, J. & Bensch, S. (2009). A jack-of-all-trades and still a master of some: prevalence and host range in avian malaria and related blood parasites. *Ecology*, 90, 2840–2849.

Holdaway, R.N. (1990). Changes in the diversity of New Zealand forest birds. *NZ J. Zool.*, 17, 309–321.

Holloway, S. (1995). *Historical Atlas of Breeding Birds in Britain and Ireland: 1875–1900*. T & AD Poyser Ltd, London.

Howe, L., Castro, I.C., Schoener, E.R., Hunter, S., Barraclough, R.K. & Alley, M.R. (2011). Malaria parasites (*Plasmodium* spp.) infecting introduced, native and endemic New Zealand birds. *Parasitol. Res.*, 110, 913–923.

Kolar, C.S. & Lodge, D.M. (2001). Progress in invasion biology: predicting invaders. *Trends Ecol. Evol.*, 16, 199–204.

Keane, R.M. & Crawley, M.J. (2002). Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology & Evolution*, 17, 164–170.

Lachish, S, Gopalaswamy, A.M., Knowles, S.C.L. & Sheldon, B.C. (2012). Site-occupancy modelling as a novel framework for assessing test sensitivity and estimating wildlife disease prevalence from imperfect diagnostic tests. *Meth. Ecol. Evol.*, 3, 339–348.

Li, Y, Carroll, D.S., Gardner, S.N., Walsh, M.C., Vitalis, E.A. & Damon, I.K. (2007). On the origin of smallpox: correlating variola phylogenics with historical smallpox records. *Proc. Nat. Acad. Sci. U.S.A.*, 104, 15787–15792.

Lockwood, J.L., Cassey, P. & Blackburn, T.M. (2005). The role of propagule pressure in explaining species invasion. *Trends Ecol. Evol.*, 20, 223–228.

MacArthur, R.H. & Wilson, E.O. (1967). *The Theory of Island Biogeography*. Princeton University Press, Princeton, NJ.

MacLeod, C.J., Paterson, A.M., Tompkins, D.M. & Duncan, R.P. (2010). Parasites lost – do invaders miss the boat or drown on arrival? *Ecol. Let.*, 13, 516–527.

Marzal, A., Ricklefs, R.E., Valkiūnas, G., Albayrak, T., Arriero, E., Bonneaud, C. *et al.* (2011). Diversity, loss, and gain of malaria parasites in a globally invasive bird. *PLoS One*, 6, e21905.

Massey, B., Gleeson, D.M., Slaney, D. & Tompkins, D.M. (2007). PCR detection of *Plasmodium* and blood meal identification in a native New Zealand mosquito. *J. Vector Ecol.*, 32, 154–156.

Paterson, A.M. & Gray, R.D. (1997). Host–parasite co-speciation, host switching and missing the boat. In: *Host–Parasite Evolution: General Principles and Avian Models* (eds Clayton, D.H. & Moore, J.). Oxford University Press, Oxford, pp. 236–250.

Pérez-Tris, J. & Bensch, S. (2005). Diagnosing genetically diverse avian malarial infections using mixed-sequence analysis and TA-cloning. *Parasitology*, 131, 15–23.

Plowright, W. (1982). The effects of rinderpest and rinderpest control on wildlife in Africa. *Symp. Zool. Soc. Lond.*, 50, 1–28.

Prenter, J., MacNeil, C., Dick, J.T.A. & Dunn, A.M. (2004). Roles of parasites in animal invasions. *Trends Ecol. Evol.*, 19, 385–390.

Pyšek, P. & Richardson, D.M. (2008). Traits associated with invasiveness in exotic plants: where do we stand? In: *Biological Invasions* (ed. Nentwig, W.). Springer-Verlag, Berlin, pp. 97–125.

Ricklefs, R.E. (2010). Host–pathogen coevolution, secondary sympatry and species diversification. *Phil. Trans. R. Soc. Lond. B*, 365, 1139–1147.

van Riper, C., van Riper, S.G., Goff, M.L. & Laird, M. (1986). The epizootiology and ecological significante of malaria in Hawaiian land birds. *Ecol. Mon.*, 56, 327–344.

Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011). MEGA5: molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Mol. Biol. Evol.*, 28, 2731–2739.

Thomson, G.M. (1922). *The Naturalisation of Animals and Plants in New Zealand*. Cambridge University Press, Cambridge.

Tompkins, D.M. & Gleeson, D.M. (2006). Relationship between avian malaria distribution and an exotic invasive mosquito in New Zealand. *J. Roy Soc. N.Z.*, 36, 51–62.

Valkiunas, G (2005). *Avian Malaria Parasites and Other Haemosporidia*. 1st edn, CRC, Boca Raton, Florida.

Waldenström, J., Bensch, S., Hasselquist, D. & Ostman, O. (2004). A new nested polymerase chain reaction method very efficient in detecting *Plasmodium* and *Haemoproteus* infections from avian blood. *J. Parasitol.*, 90, 191–194.

Williams, P.A. (2006). The role of blackbirds (*Turdus merula*) in weed invasion in New Zealand. *NZ J. Ecol.*, 30, 285–291.

Wood, M.J., Cosgrove, C.L., Wilkin, T.A., Knowles, S.C.L., Day, K.P. & Sheldon, B.C. (2007). Within-population variation in prevalence and lineage distribution of avian malaria in blue tits, *Cyanistes caeruleus*. *Mol. Ecol.*, 16, 3263–3273.

Woolhouse, M.E.J., Haydon, D.T. & Antia, R. (2005). Emerging pathogens: the epidemiology and evolution of species jumps. *Trends in Ecology & Evolution*, 20, 238–244.

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