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RESEARCH ARTICLE

Interannual patterns of avian diseases in wild New Zealand avifauna near conservation areas

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Abstract

The past few years have seen a noticeable increase in the emergence of infectious diseases in wildlife, especially vector-borne diseases, presenting a challenge for the conservation of endangered species. One such vector-borne disease, avian malaria (*Plasmodium* spp.) is on the rise in New Zealand avifauna, threatening bird populations that are among the most extinction-prone in the world. Furthermore, recent reports have outlined an increase in deaths of native iconic bird species specifically due to this disease. In order to help manage breakouts of this pathogen at a local scale, we need a better understanding of potential drivers of the emergence of avian malaria in wild New Zealand avifauna. Here, we set to test the role of climatic drivers in synchronizing contacts between avian hosts and vectors, assess the temporal stability of transmission dynamics between years, and determine the role of introduced species in causing spill-over of this pathogen towards native species. Our study focused on three sites that were sampled regularly during two consecutive years in the austral summer, each site being adjacent to a breeding colony of Yellow-eyed penguins (*Megadyptes antipodes*). Our results reveal an overall temporal stability of avian malaria incidence patterns, with a decrease in infection throughout the austral summer for both sampled years. Moreover, we highlight a phylogenetic signal among sampled bird species, with introduced species being more heavily infected by avian malaria than their native counterparts. In contrast, we found no effect of the two climatic drivers investigated, temperature and rainfall, on mosquito abundance. Our results suggest a strong effect of alien species acting as reservoirs for diseases spilling-over towards immunologically naïve species, and provide conservation managers with a critical timeframe to control avian malaria breakouts.

KEYWORDS
avian malaria, disease ecology, emerging infectious disease, species conservation

INTRODUCTION

Emerging infectious diseases are a serious threat to naïve individuals that have not evolved with them (Tompkins et al., 2015). In the past few years, many diseases have been shown to drive abundant species to the brink of extinction and alter species composition at local scales (Smith et al., 2006; Young et al., 2017). For example, populations of bats in the United States have drastically declined and bat communities have been

significantly altered by the white-nose syndrome caused by the fungus *Pseudogymnoascus destructans*, clearly demonstrating that pathogens can have a widespread effect on naïve populations (Langwig et al., 2012). Additionally, anthropogenic modification to the landscape can further increase disease risk in wildlife by altering habitat niche breadth, allowing for new host species colonization and interactions (Gottdenker et al., 2014). Indeed, species colonization by translocation is one of the main drivers of emerging infectious diseases in wildlife (Daszak et al., 2000), as the pathogens of colonizing species often spill-over into native wildlife populations. Disease spill-over can have drastic effects on new host–pathogen interactions. With no co-evolutionary history leading to increased immunological efficiency in hosts, changes in pathogen virulence are likely, potentially leading to local extirpation of naïve wildlife (Lymbery et al., 2014). Moreover, colonizing species add to the total density and biomass of hosts in the area, maintaining the necessary threshold for constant spill-over and transmission towards naïve wildlife (Cunningham, 1996). With the accelerated rate of species extinction occurring worldwide, wildlife disease management thus remains one of the key issues for conservation efforts.

Vector-borne diseases, that is, vertebrate pathogens transmitted by biting or blood sucking insects, are a main cause of species extinction worldwide (Smith et al., 2006). This is particularly true for insular wildlife, which is prone to extirpation by vector-borne diseases. For instance, avian malaria (*Plasmodium* spp.) – a haemosporidian parasite of birds vectored by mosquitoes (Valkiūnas, 2005) – is one such disease, and its occurrence has been shown to be a cause of decline of wild birds in multiple island systems (LaPointe et al., 2012; Wood et al., 2007). For example, following the translocation of multiple alien bird species and an ornithophilic mosquito to the Hawaiian Islands, native bird species have been subject to a sharp decline in their abundance, even shifting their spatial gradient towards higher elevations, thus presumably avoiding mosquito vectors (Van Riper III et al., 1986). This is but an example of the catastrophic effect that avian malaria can have on wild ecosystems.

New Zealand bird species face a similar challenge. Indeed, avian malaria occurrence has been shown to be on the rise in New Zealand avifauna, potentially threatening indigenous bird species that are considered to be the most extinction-prone in the world (Tompkins & Poulin, 2006). For instance, Yellow-eyed Penguin (*Megadyptes antipodes*) is one of New Zealand's key species for wildlife tourism and a flagship of conservation; however, the Northern population of this species has been brought to near extinction despite massive conservations efforts. Some recent alarming reports have identified that the population is declining rapidly due to starvation and avian malaria among other impacts, the latter being responsible for several deaths over the past few years (Alley & Webster, 2019). In fact, recent studies have highlighted the potential role of avian malaria in the decline of native New Zealand bird species (Niebuhr et al., 2016). Therefore, it is vital to improve our understanding of the pressure exerted by this disease on this iconic species. Additionally, biotic interactions with populations of generalist introduced birds well suited for disturbed environments, such as Blackbird (*Turdus merula*), Song Thrush (*Turdus philomelos*) and House Sparrow (*Passer domesticus*) (Bosenbecker & Bugoni, 2020), might enhance the risk of infection in Yellow-eyed penguins. Indeed, populations of those species have been shown to have high prevalence of avian malaria, potentially acting as reservoirs for the disease and enabling spill-over towards penguin populations (Howe et al., 2012; Tompkins & Gleeson, 2006). In addition, multiple New Zealand conservation agencies and rescue centres have reported increased Yellow-eyed penguin deaths in recent years (Webster, 2021), hinting that there might be an underlying temporal factor

driving this disease. It is thus crucial to better understand the effects and dynamics of avian malaria in these already fragile populations.

While bird species play an important role in shaping avian malaria transmission patterns in New Zealand, mosquito vectors also play a predominant role in transmitting the pathogen responsible for causing avian malaria in wild birds. Indeed, detection of one of the most competent vectors of avian malaria on the South Island of New Zealand, the mosquito *Culex quinquefasciatus*, coincided with a massive die-off of recently translocated Yellowhead (*Mohoua ochrocephala*), an endemic New Zealand species (Reed, 1997; Tompkins & Gleeson, 2006). With the potential for this mosquito species, and many other New Zealand ornithophilic mosquito species, to accelerate the spread of the *Plasmodium* pathogen across bird populations, there is a critical need for a better understanding of the vector population dynamics around conservation areas.

Here, we aim to unravel avian malaria transmission dynamics in the reservoir passerine populations near Yellow-eyed penguin nesting areas. Our goals are to (1) identify the main drivers of avian malaria transmission near Yellow-eyed penguin colonies and (2) assess the interannual stability of avian malaria dynamics in wild ecosystems. We predict that climatic factors, mainly local temperature and rainfall, will control mosquito emergence rates (Gallardo et al., 2009) and synchronize the activity and encounter rates of mosquitoes and birds, thus driving temporal opportunities for avian malaria transmission. In addition, we predict that avian malaria prevalence will be higher during the avian breeding season and decrease subsequently during the austral summer, as seasonality in temperate areas limits exposure risks to vectors (Altizer et al., 2006). We test these predictions at a local scale across three spatially isolated sites, each adjacent to a Yellow-eyed penguin colony, along the Otago coastline in the South Island of New Zealand. Our findings reveal disturbing disease patterns that are potentially hindering conservation and recovery efforts.

METHODS

Study system

Our study system consists of three spatially isolated Yellow-eyed penguin colonies on the Otago coastline (see Figure 1). Over the past centuries, these areas have been subjected to intense human disturbance, such as burning and agriculture, creating opportunities for generalist invasive species to colonize and establish themselves around the penguin nesting sites. However, in recent years, these areas were turned into Yellow-eyed penguin conservation areas, and since then much effort has been put into restoring and maintaining small patches of native vegetation, such as Podocarp trees, around breeding colonies (up to ~150 m), effectively creating a buffer zone between farming lands and this endangered species. This system thus provides an ideal ecological framework to understand how anthropogenization and diseases affect declining species.

Mosquito sampling

For each visit at each site, we put two mosquito-CDC type traps filled to the brim with dry ice in the evening prior to the bird sampling. This allowed us to capture mosquitoes for a 12-h timeframe during a known activity period, for example, between dusk and dawn (Abella-Medrano et al., 2015). Each mosquito was then preserved in 70% ethanol, and later identified to the

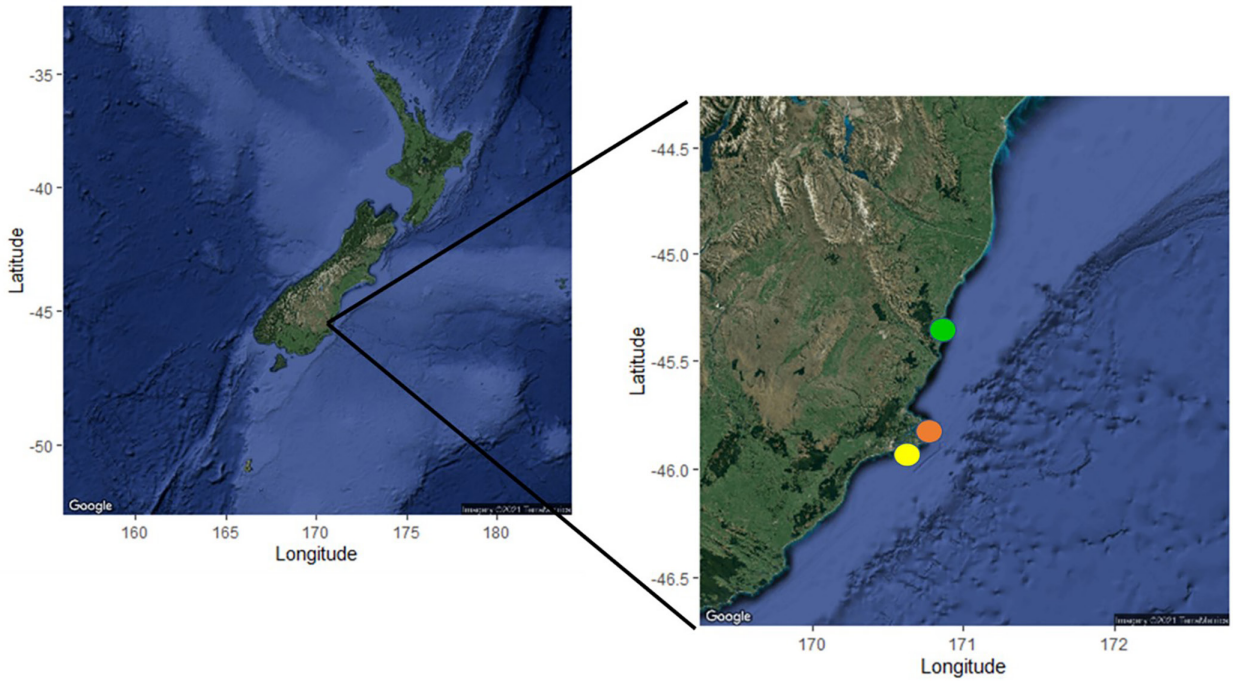

FIGURE 1 Map of the three sampled sites. Green represents the Tavora penguin reserve, Yellow the Okia penguin reserve and Orange the Otapahi penguin reserve.

finest taxonomical resolution under a 10× dissecting microscope using the mosquito identification key of Sneel (2005).

Bird sampling

Sampling was conducted over two consecutive austral summers (November 2019 to March 2020, and November 2020 to March 2021). For the first year, we sampled each site twice a month, and for the second year only once a month, for a total of 24 visits the first year (weather conditions prevented some sampling visits) and 15 visits the second year. At each site, passerine sampling was conducted on each one-day visit using three mist-nets set up at around 5:00 and taken down around 14:00. Each net was set near Yellow-eyed penguin nests (~30–50 m) to ensure a good representation of avian malaria infection and transmission at nest sites. All captured passerines were identified to species level and numbered with metal bands. Each individual that was resampled between sampling activities ($n = 2$) was counted as a new datapoint since infection could have happened between site visits. After swabbing with 70% ethanol, we used a 27 g needle to puncture the brachial vein of each captured individual and collected ~0.1 mL of blood, which was then placed unfrozen in a 1.5 mL Eppendorf tube containing 0.5 mL of Queen's Lysis buffer (Seutin et al., 1991). All sampling was undertaken under New Zealand Department of Conservation Wildlife Authorization Act # 87796-FAU and University of Otago Animal Ethics permit # AUP-20-90 with the permission of the Yellow-eyed Penguin Trust as the landowner.

Parasite detection

We used a Qiagen DNeasy Blood and Tissue kit (QIAGEN) to extract DNA from unfrozen avian blood in buffer. We then screened samples for *Plasmodium* spp. presence using a nested PCR protocol to amplify a

478 bp sequence on the cytochrome *b* gene following the general guidelines of Niebuhr et al. (2016). All samples were compared with a known *Plasmodium* positive sample.

Sequencing

All positive samples were sent to Genetic Analysis Service (Anatomy Dept, University of Otago) for sequencing with the forward primer of the nested PCR following gel purification. We then pruned our sequences with Geneious prime 2022.2 and compared them with known sequences from GenBank.

Climatic variable sampling

To record air temperature at each site, a HOBO MX2302A temperature sensor (ONSET) was placed under the cover of the canopy so that no direct sunlight could bias the instrument. Each sensor was set for 1 measurement/h over the whole duration of the sampling period. We also downloaded local rainfall data from NIWA's National Climate Database (https://cliflo.niwa.co.nz/), located at ~50 km from the farthest sampling site. Since the daily temperature and rainfall values would probably be poor indicators of mosquito emergence on the sampling day, we averaged the temporal lag of temperature and precipitation data for the 7 and 14 days period prior to the sampling date, as mosquito development from larvae to emergence as adults usually takes from 4 to 14 days (EPA, 2021).

Data analysis

All analyses were performed in R version 4.0.0 (R Core Team, 2020). We downloaded 1000 avian phylogenetic trees from BirdTree.org using the backbone tree from Hackett et al. (2008) and used a seeded random sample of 100 trees, pruned to include only the species in our dataset, in order to account for phylogenetic uncertainty (see R code in Appendix S1 and Barrow et al., 2019 for further details). A covariance matrix was then constructed (MCMCglmm package; Hadfield, 2010) to be used in the phylogenetically corrected models using the 'brms' package (Bürkner, 2017). To determine if malaria prevalence exhibits phylogenetic structure among bird species, we calculated the phylogenetic signal using the hypothesis method in 'brms' (*vignette: Estimating Phylogenetic Multilevel Models with brms*), with the notable exception of replacing the gaussian 'sigma' parameter with the 'shape' parameter of the negative binomial distribution. A strong phylogenetic signal would indicate that closely related bird species tend to have more similar malaria prevalence than expected by chance; in other words, it may indicate that certain clades of related birds are the main reservoir of malaria.

All models were performed using the 'brms' package. Firstly, to determine the role of climatic drivers in regulating mosquito abundance/emergence throughout the austral summer, we pooled all sampled mosquitoes regardless of species, since there is little information available on which species can act as malaria vectors and which cannot. We used multilevel models with the total number of mosquitoes collected per site as a response variable (negative binomial distribution) and both lagged temperature and rainfall data as population-level effects (scaled values), while always accounting for sampling location as a group-level effect. We then created two sets of models, in the first one each variable was independently predicting

the abundance of mosquitoes, and in the second we included an interaction term between temperature and rainfall for each temporal lag (e.g. 7 and 14 days analysed separately).

Secondly, to test the stability of temporal patterns in avian malaria infections throughout the two sampling years, we used a Bayesian generalized additive model (BGAM). We used the number of individuals found infected with avian malaria by species among the total number of sampled individuals as a response variable (negative binomial distribution), and used a basic spline with three knots to include the temporal series (Julian days) as a population-level effect while accounting for the sampling size of each species in the population-level effect. Knots parameter refers to the number of local regressions among the non-linear effects investigated. Site, year and species were used as group-level effects. Furthermore, we controlled for species phylogenetic relatedness by including a species co-variance matrix in the group-level effects. We used informative priors adjusted on the sample mean for intercept and population-level effects. For all models, we made sure each parameter converged by checking the potential scale reduction factor on split chains (Rhat) indicator (at convergence, Rhat is equal to one). Lastly, we checked the validity of the models using leave-one-out cross validation and *k*-fold validation (package loo; Vehtari et al., 2017).

RESULTS

Overall, we collected 160 birds of 14 species (10 introduced species, four native species) during the first season and 58 birds from 12 species (11 introduced species, one native species) in the second season. The overall avian malaria prevalence for each year was relatively low, 5.6% ($n = 9/160$) the first year and 5% ($n = 3/58$) the second year (see Table 1 and Table S1 for samples breakdown). Infections were mostly clustered in the phylogenetic tree, with only five species found with infections, as supported by a moderate phylogenetic signal (Pagel's lambda, $\lambda = 0.20$; see Figure 2).

The climatic variables included in the analysis had little or no influence on mosquito abundance during both sampling years. Indeed, we failed to find any relevant effect of lagged temperature (1 week: Estimate = 0.08, lower CI = −0.16, upper CI = 0.32; 2 weeks: Estimate = 0.16, lower CI = −0.18, upper CI = 0.49) or lagged rainfall (1 week: Estimate = −0.07, lower CI = −0.18, upper CI = 0.05; 2 weeks: Estimate = −0.16, lower CI = −0.36, upper CI = 0.05). The models including an interaction term did not yield any relevant results either.

In contrast, the BGAM analysis uncovered a clear decline in avian malaria infection throughout the sampling period, consistent across both years, and decreasing steadily through the austral summer (K1: Estimate = 0.79, lower CI = −50.78, upper CI = 57.26; K2: Estimate = 18.22, lower CI = 4.67, upper CI = 45.10; K3: Estimate = −11.41, lower CI = 1.63, upper CI = 37.55), and with the overall spline showcasing the same pattern (Estimate = 6.53, lower CI = 0.03, upper CI = 20.99; see Figure 3).

Sequencing results detected two main genotypes among the positive individuals, with *Plasmodium metutinum* LINN1 being the more prevalent (10 of 12 samples). The remaining samples were identified as belonging to *Plasmodium* spp. LINN2 lineage (2 of 12 samples).

DISCUSSION

Our results show increased avian malaria prevalence during the early months of the austral summer (November–December), with higher infection rates at the beginning of the summer followed by a constant decline

TABLE 1 Summary of all bird species captured in mist-nets at each site during the two sampling seasons along the Otago coastline in the South Island of New Zealand.

	November			December			January			February			March					
Site/species	**Tavora**	**Okia**	**Otapahi**	**Tavora**	**Okia**	**Otapahi**	**Tavora**	**Okia**	**Otapahi**	**Tavora**	**Okia**	**Otapahi**	**Tavora**	**Okia**	**Otapahi**	**# Pos**	**% Pos**	**Total**
Carduelis carduelis	–	1	–	1	1	–	–	4	1	3	–	–	1	–	–	0	0	12
Carduelis flammea	1	2	2	2	1	1	2	3	2	–	–	–	–	–	–	0	0	16
Prunella modularis	4	2	4	–	4	–	4	2	–	–	–	–	3	–	1	0	0	24
Turdus merula	–	–	2*	–	1	2	–	––	–	–	–	–	–	–	–	1	20	5
Zosterops lateralis	2	4*	2	3	6**	2*	1	12	5	2	4	2	3	3	–	4	8	51
Emberiza citrinella	–	2*	–	–	–	–	9	–	1	–	–	–	–	–	–	1	8	12
Gerygone igata	–	1	–	–	–	–	–	–	1	–	1	–	1	–	1	0	0	5
Hirundo neoxena	–	–	–	–	–	1	–	–	3	–	2	–	–	5	3	0	0	14
Anthornis melanura	–	–	–	–	–	–	–	1	–	2	–	–	–	–	–	0	0	3
Rhipidura fulginosa	–	–	–	–	–	–	–	1	–	2	–	–	–	–	–	0	0	3
Alauda arvensis	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	0	0	1
Passer domesticus	2*	–	–	–	–	–	–	–	2	–	–	–	–	–	–	1	25	4
Turdus philomelos	3**	–	–	–	–	–	–	–	4	–	–	–	–	–	–	2	29	7
Fringilla coelebs	1	–	–	1	–	–	–	–	–	1	–	–	–	–	–	0	0	3
Total 2019–2020	13	12	10	7	13	6	16	23	20	10	7	2	8	8	5	9	6.8	160
Carduelis carduelis	–	2	–	–	–	–	–	–	–	–	–	–	–	–	–	0	0	2
Carduelis flammea	–	–	–	–	1	–	2	–	1	–	–	–	–	–	–	0	0	4
Prunella modularis	1	–	1	1	–	2	1	2	1	–	1	–	–	–	–	0	0	10
Turdus merula	–	–	1	–	1	1	–	–	–	1	–	–	–	1	–	0	0	5
Zosterops lateralis	–	–	1	1	–	2	2	3	3	–	–	2	–	–	1	0	0	15
Emberiza citrinella	–	–	–	1	–	–	1	–	–	–	–	–	–	–	–	0	0	2
Hirundo neoxena	–	–	–	–	–	–	–	–	2	–	–	2	–	–	–	0	0	4
Anthornis melanura	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	0	0	1
Alauda arvensis	–	–	–	–	1	1	–	–	–	–	–	–	–	–	–	0	0	2
Passer domesticus	1	–	–	–	–	–	–	–	–	–	–	1	–	–	–	0	0	2
Turdus philomelos	1*	–	2*	–	–	2*	1	–	1	–	–	–	–	–	–	3	71	7
Fringilla coelebs	1	–	–	2	–	–	–	–	–	1	–	–	–	–	–	0	0	4
Total 2020–2021	4	2	5	5	3	9	7	5	8	2	1	5	0	1	1	3	8.6	58

Note: Each asterisk (*) represents a positive sample (infection) found for this species on any given sampling event.

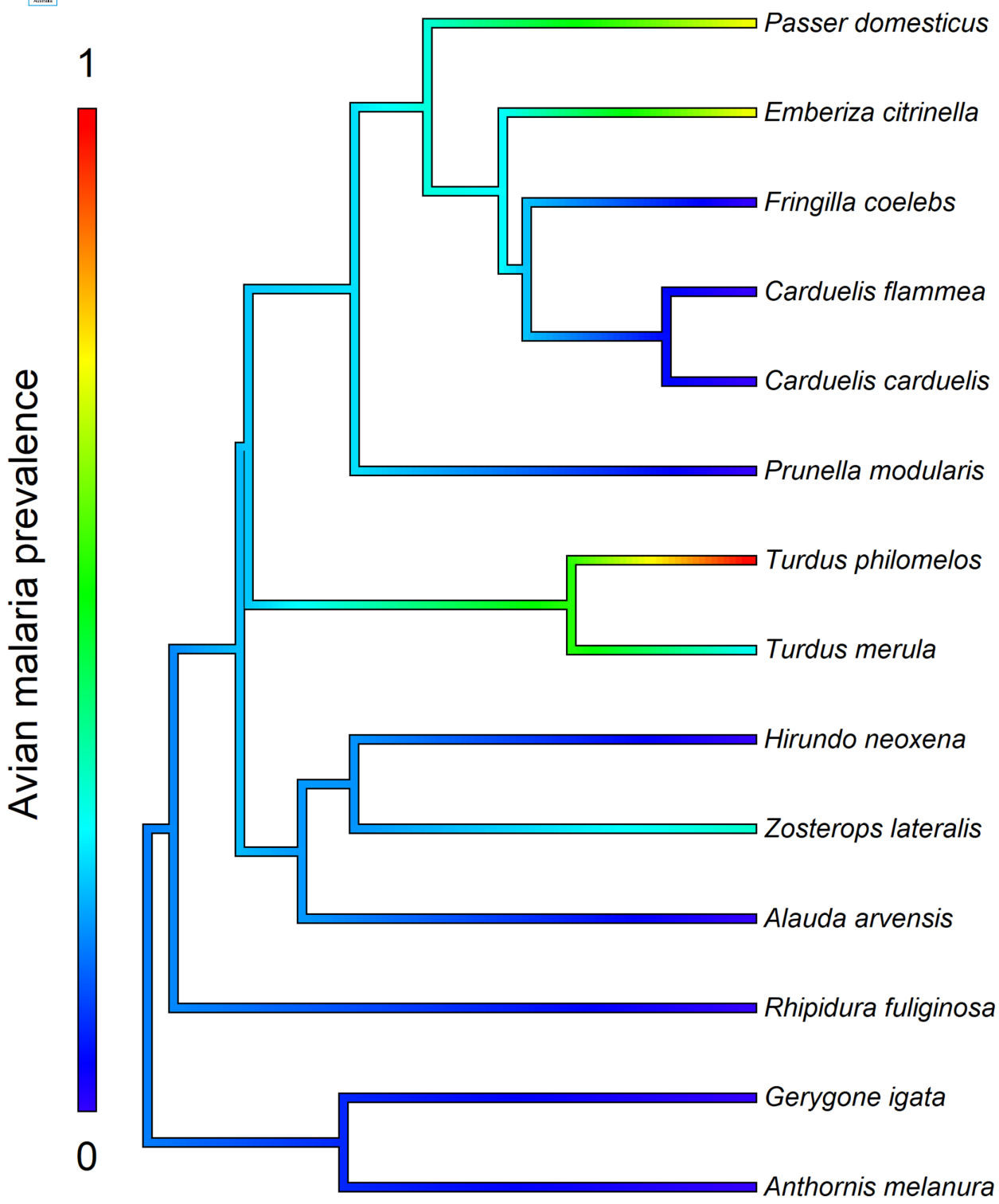

FIGURE 2 Phylogenetic distribution of avian malaria prevalence across all the sampled avian species. Pagel's lambda of this phylogram is 0.2.

later in the season. In addition, we show that rainfall and temperature in these cases appeared to be poor predictors of the potential for avian malaria transmission at a local scale, as neither variable had an influence on mosquito emergence and activity (measured by captures) during the two sampling years.

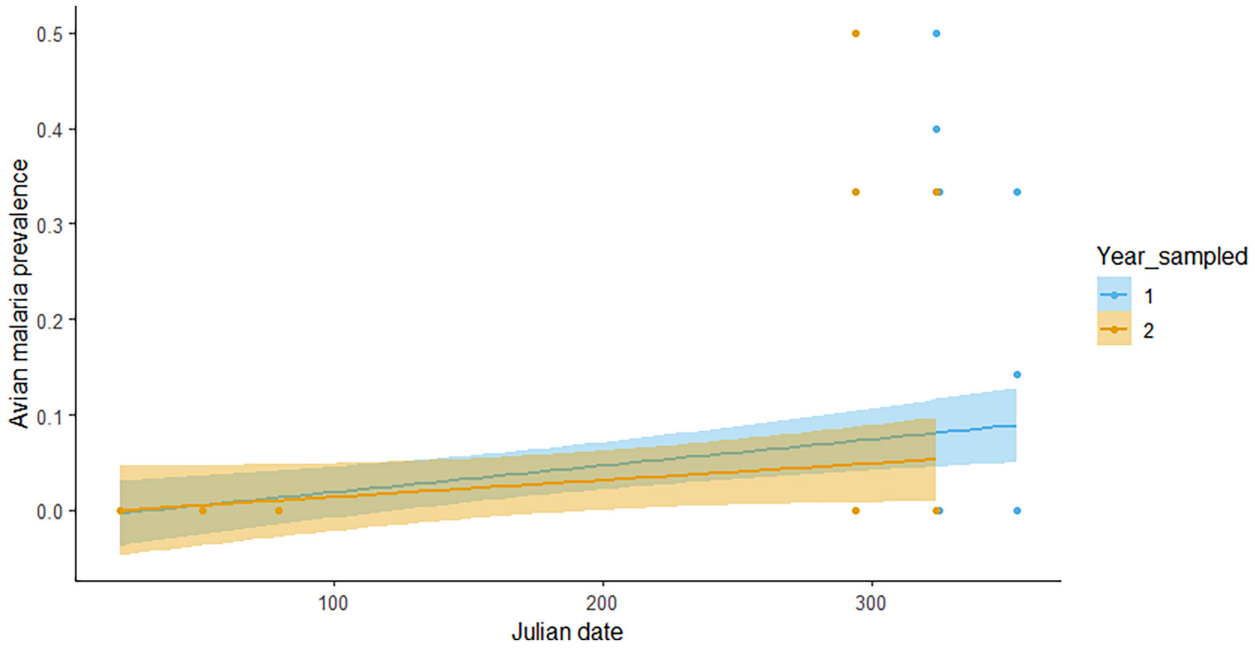

FIGURE 3 Graphical representation of the temporal pattern of avian malaria in the passerines reservoir populations for two consecutive sample years. The *x*-axis is in Julian days, ranging from 0 (January) to 365 (December). Each point represents the raw avian malaria prevalence across all species for a sampling event, and the lines represent fitted splines. Colours represent sampling year.

The phylogenetic signal in malaria prevalence across bird species observed in our data is consistent with other large-scale systems (Barrow et al., 2019; Filion et al., 2020), in which Pagel's Lambda values of ~0.24–0.35 have been observed. This may be due to the overrepresentation of infected non-native species in our study. Indeed, generalist host species, such as *Turdus* spp. and *Passer* spp. species (Bosenbecker & Bugoni, 2020) are known reservoirs of avian malaria in New Zealand (Filion et al., 2022; Howe et al., 2012; Tompkins & Gleeson, 2006). By constantly altering the landscape towards agricultural lands around conservation areas, humans have contributed to increased colonization by these species in those localities. As generalist species tend to have better resilience in disturbed environments (Jones et al., 2020), usually at the expense of native species, anthropogenization of the landscape could open the ecological niche, promoting a shift in species pool towards generalist susceptible species, in turn maintaining the biomass thresholds for avian malaria to persist in New Zealand conservation lands, thus providing a plausible explanation for the avian malaria phylogenetic range observed in this study. The phylogenetic pattern observed could also be explained by increased virulence of avian malaria in new hosts, which can lead to extirpation of native wildlife (Cressler et al., 2016) and also lower detectability of infections within a species as infected individuals die rapidly. For instance, the lineages that we found in the passerines were directly related to a mortality event in little blue penguin (*Eudyptula minor*) in New Zealand (Sijbranda et al., 2017), raising concern for future spillover events. As many New Zealand bird species are known to die off from infection by this disease (Howe et al., 2012; Schoener et al., 2014), increase in avian malaria virulence, leading to death of native hosts, seems an equally plausible explanation for the infection patterns observed in this study.

The temporal patterns we detected in avian malaria prevalence in wild passerines has been previously demonstrated in a different system on the North Island of New Zealand (Castro et al., 2011), and could be related to host life-history traits. For instance, most of the captured passerines in our

study breed during austral spring in New Zealand (Borgmann et al., 2013). This offers two potential explanations. Firstly, wild populations of bird hosts could face a trade-off with immunocompetence (i.e. ability to minimize fitness costs of an infection; Owens & Wilson, 1999) in regulating their susceptibility towards avian malaria. As reproduction costs can impinge on the immunocompetence of the host towards a disease (Sheldon & Verhulst, 1996), bird species may have to allocate more resources towards reproduction at the expense of increased infection risk, resulting in higher levels of infection during the breeding season. Second, breeding seasonality could enhance the rate of contact between vectors and hosts. Indeed, Fecchio et al. (2019) hypothesized that temporal concordance between pulses of resources due to seasonality and breeding activities of birds could concentrate all organisms needed for the avian malaria life cycle in the same area. This can enhance the potential for avian malaria transmission between its hosts for a brief period of time but with high intensity, effectively increasing infection rates during this short period. In addition, data from Yellow-eyed penguin colonies (Alley et al., 2019) showed a similar temporal pattern suggesting that deaths due to avian malaria were concentrated at highly stressful periods of the breeding cycle (i.e. fledge and moult), suggesting that this phenomenon is widespread among pathogens in New Zealand.

In contrast, we found no effects of climatic variables (temperature and rainfall) on mosquito abundance throughout the two sampling years. While this result is unexpected, as both these variables are known to be major synchronizing drivers of mosquito emergence (Day, 2001; Day et al., 1990), it is possible that their overall stability throughout the year in the Otago region makes them poor predictors of emergence. Indeed, Chaves et al. (2012) demonstrated that mosquito emergence may not be triggered by stable climatic conditions, but rather by pronounced changes in the weather acting as strong catalysts, providing a plausible explanation for the present result. The lack of effect from climatic variables could also be due to the presence of permanent natural ponds near the sampled sites. Presence of stagnant water throughout the year would provide enough available habitat for female mosquitoes to lay their eggs (Schneider et al., 2004; Scott et al., 2000), independently of climatic conditions, hence providing an alternative explanation. Interestingly, we managed to sample mosquitoes at a roughly equivalent rate during both years (see Table S1), suggesting that the potential for avian malaria transmission persists throughout the whole austral summer. This reinforces the possibility of a trade-off between host immunocompetence and reproduction during the breeding season.

In conclusion, our study shows a strong temporal pattern and inter-annual stability throughout the sampled years. Even if we did not find any relevant effect of climatic variables on mosquito emergence in our system, monitoring these variables remains useful as many other studies found them to be synchronizing agents between vectors and hosts. Of course, there are some limitations to the conclusions that can be drawn from this study. Firstly, the relatively small temporal scale at which this study was conducted might not represent long-term temporal conditions, especially with global warming increasing inter-annual variance. Second, the overall low prevalence of avian malaria found in wild passerines might have impeded our ability to detect any influence of natural drivers of avian malaria. Lastly, we must acknowledge that avian malaria infections are chronic, and are more difficult to detect via PCR outside of the passerines' breeding season (Valkiūnas, 2005), potentially biasing the temporal signal we observed. Nevertheless, we were able to extract evidence of temporal patterns of avian malaria in wild New Zealand birds. In addition, the phylogenetic signal observed is informative for conservation managers regarding the risks

posed by various introduced species. In particular, reducing the available habitat niche breadth would be a crucial step to lower the abundance of potential reservoir species, such as *Turdus* spp., around critically endangered wildlife. With the rise of emerging infectious diseases worldwide representing a growing challenge for conservation of wildlife, our study brings to light the critical timeframe during which already endangered wildlife become even more vulnerable to fast decline.

AUTHOR CONTRIBUTIONS

Antoine Filion: Conceptualization (lead); data curation (lead); formal analysis (lead); funding acquisition (supporting); investigation (lead); methodology (lead); resources (lead); software (lead); supervision (supporting); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (lead). **Trudi Webster:** Conceptualization (supporting); funding acquisition (lead); project administration (supporting); resources (supporting); supervision (supporting); validation (supporting); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Robert Poulin:** Conceptualization (supporting); funding acquisition (supporting); project administration (supporting); resources (supporting); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting). **Stephanie S. Godfrey:** Project administration (lead); supervision (equal); writing – original draft (supporting); writing – review and editing (supporting).

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study will be made openly available upon acceptance of this manuscript.

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