Climate, host phylogeny and the connectivity of host communities govern regional parasite assembly

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Abstract

Aim: Identifying barriers that govern parasite community assembly and parasite invasion risk is critical to understand how shifting host ranges impact disease emergence. We studied regional variation in the phylogenetic compositions of bird species and their blood parasites (Plasmodium and Haemoproteus spp.) to identify barriers that shape parasite community assembly.

Location: Australasia and Oceania.

Methods: We used a data set of parasite infections from >10,000 host individuals sampled across 29 bioregions. Hierarchical models and matrix regressions were used to assess the relative influences of interspecies (host community connectivity and local phylogenetic distinctiveness), climate and geographic barriers on parasite local distinctiveness and composition.

Results: Parasites were more locally distinct (co-occurred with distantly related parasites) when infecting locally distinct hosts, but less distinct (co-occurred with closely related parasites) in areas with increased host diversity and community connectivity (a proxy for parasite dispersal potential). Turnover and the phylogenetic symmetry of parasite communities were jointly driven by host turnover, climate similarity and geographic distance.

Main conclusions: Interspecies barriers linked to host phylogeny and dispersal shape parasite assembly, perhaps by limiting parasite establishment or local diversification. Infecting hosts that co-occur with few related species decreases a parasite’s likelihood of encountering related competitors, perhaps increasing invasion potential but decreasing diversification opportunity. While climate partially constrains parasite distributions, future host range expansions that spread distinct parasites and diminish barriers to host shifting will likely be key drivers of parasite invasions.

Keywords
community assembly, host shifting, host specificity, interspecies barriers, parasite invasion, Plasmodium

1 | INTRODUCTION

Regional variation in community composition is a central property in nature (Kraft, Cornwell, Webb, & Ackerly, 2007; Wallace, 1876). With increasing environmental destabilization and biotic homogenization, predicting how ecosystems will function following disturbance relies on identifying processes that govern community assembly (Ricklefs, 1987; Barnagaud et al., 2014; see Table 1 for bold term definitions). Understanding parasite community assembly is crucial, as changes to parasite composition or the frequency of host–parasite interactions...

A strong incentive exists to identify barriers to species establishment and determine how these barriers modulate invasion risk (Hoberg, 2010; Kelly, Paterson, Townsend, Poulin, & Tompkins, 2009; Springborn et al., 2015). For parasites, geographic barriers (such as distance or mountain ranges) are known to constrain species’ distributions (Brooks & Ferrao, 2005; Krasnov, Shenbrot, Kokoikhlova, & Degen, 2016; Lafferty, 2009; Warburton, Kohler, & Vonhof, 2016). In addition, environmental barriers (such as temperature and precipitation) drive development or transmission rates for many parasites, especially vector-borne parasites such as those causing malaria and lyme disease (Epstein, 2001; Githeko, Lindsay, Confalonieri, & Patz, 2000; Patz, Campbell-Lendrum, Holloway, & Foley, 2005). However, parasite distributions are also linked to host life histories and distributions (Poulin, Krasnov, & Mouillot, 2011; Olsson-Pons, Clark, Ishliaq, & Clegg, 2015; Fecchio et al., 2017). Such interspecies barriers are increasingly recognized to govern local assembly (HilleRisLambers, Adler, Harpole, Levine, & Mayfield, 2012; Mayfield & Stouffer, 2017; Wisz et al., 2013). Predicting how parasite composition may change in the future relies on defining a consistent framework to identify patterns that improve knowledge of assembly and elucidate underlying mechanisms acting as barriers. Such patterns may be driven by a hierarchical process, where parasites must first break through geographic and/or environmental barriers to initially colonize a new range (Agosta et al., 2010; Brooks & Hoberg, 2007). Following colonization, assembly may be limited by interspecies barriers that govern parasite spread and diversification (Figure 1). This process, termed “ecological fitting” (Janz, 1985), suggests many parasites are capable of infecting a broader range of hosts than is currently realized, with changes to host and/or parasite distributions producing new associations that may be limited by host phylogenetic relationships (Araujo et al., 2015; Brooks & Ferrao, 2005; Radtke, McLennan, & Brooks, 2002).

For parasites that rely on host dispersal to colonize new areas, regions comprising a diversity of host species whose ranges overlap with other potential hosts (i.e., high distributional connectivity to other regions; “host community connectivity”) should support broader parasite diversity due to increased niche space (Hector, Dobson, Minns, Bazeley-White, & Hartley Lawton, 2001, Viana, D. S., Santamaria, L., & Figuerola, J. (2016)) and a higher likelihood for parasites to break geographic and/or environmental barriers (Figure 1). However, biotic barriers could still limit parasite invasions in phylogenetically diverse systems, particularly if invasion success is positively related to the invader’s local phylogenetic distinctiveness (i.e., more locally distinct invaders are less likely to be limited by related competitors; HilleRisLambers et al., 2012). Yet, while host community connectivity can overcome geographic dispersal barriers, few studies recognize this aspect as a potential driver of parasite assembly (but see Buckee, Danon, & Gupta, 2007).

Parasites are often restricted to hosts with phylogenetically conserved ecological or physiological traits (Janzen, 1968; Rohde, 1980; Schulze-Lefert & Panstruga, 2011; Streicker et al., 2010), a phenomenon that has powerful consequences for species interactions and ecosystem functioning (Ehrlich & Raven, 1964; Hoberg & Brooks, 2008). As parasites with high host specificity may be unable to shift hosts, the local availability of suitable hosts can present an invasion barrier following initial dispersal, especially if parasites are adapted to hosts that do not commonly co-occur with closely related species (Brooks, 1979; Even et al., 2012; Clark & Clegg, 2015; Ellis et al., 2015; Mata, da Silva, Lopes, & Drozetski, 2015; Figure 1).

While ecological fitting (governed at least partly by parasite host-specificity and host evolutionary history) and host dispersal potential are clearly important mechanisms impacting parasite establishment and diversification, identifying their roles in natural host–parasite systems is challenging. We develop a framework to identify relative influences of barriers to regional parasite community assembly and apply this framework to naturally occurring parasite infections from Australasian bird communities. Haemopsemblidias (genera Plasmodium

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### TABLE 1 Glossary of definitions for proposed community assembly barriers and metrics used in analyses

<table>
<thead>
<tr>
<th>Assembly Barriers</th>
<th>Definitions</th>
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<tbody>
<tr>
<td>Community assembly</td>
<td>The establishment and maintenance of local communities through arrival of potential colonists from external species pools.</td>
</tr>
<tr>
<td>Environmental barriers</td>
<td>Environmental differences between regions that may govern species’ distributions, including variation in macroclimate, habitat and altitude.</td>
</tr>
<tr>
<td>Geographic barriers</td>
<td>Physical barriers to between-region parasite dispersal, including geographic distance, mountain ranges and water barriers.</td>
</tr>
<tr>
<td>Host community connectivity</td>
<td>The distributional overlap of host communities among regions, taking into account host species richness and host geographic range sizes. Here, Sampled.Con describes host community connectivity while considering only sampled avian host species, and Total.Con describes connectivity for all occurring avian species within a local assemblage.</td>
</tr>
<tr>
<td>Host specificity</td>
<td>The range and diversity of host species observed to be infected by a parasite. Here, ( d ) describes parasite host-specificity using host–parasite interaction networks, while ( STD^* ) describes phylogenetic host specificity using host phylogenetic distances.</td>
</tr>
<tr>
<td>Interspecies barriers</td>
<td>For parasites, interspecies barriers relate to variation in host species attributes that prevent parasite spread and diversification. These may include host phylogenetic relatedness and ecological similarity (e.g., microhabitat use, nesting behaviour and feeding behaviour).</td>
</tr>
<tr>
<td>Local phylogenetic distinctiveness</td>
<td>The average pairwise phylogenetic distance between a focal taxon and co-occurring taxa within a local assemblage. Here, ( Dis ) describes parasite species distinctiveness, ( Sampled.Dis ) describes host species distinctiveness with respect to co-occurring sampled host species, and Total.Dis describes host species distinctiveness with respect to all co-occurring sampled avian species.</td>
</tr>
<tr>
<td>Phylogenetic community skewness</td>
<td>A measure of the asymmetry of species’ pairwise phylogenetic distances, where a left skew indicates relatively more distantly than closely related species in a community, while a right skew indicates the opposite.</td>
</tr>
<tr>
<td>Phylogenetic turnover ( (\beta) )</td>
<td>The shifts in phylogenetic diversity between communities. Here, ( \beta ) describes parasite phylogenetic turnover, ( Sampled.\beta ) describes turnover of sampled host assemblages, and Total.( \beta ) describes turnover of total avian assemblages.</td>
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</table>
and Haemoproteus) are vector-borne blood parasites that display a range of host specificities (Križanauskienė et al., 2006). Due to limited vector dispersal (Ejiri et al., 2011), avian hosts are the primary vehicles by which these parasites disperse (Pérez-Tris & Bensch, 2005). Avian haemosporidians have been introduced to numerous bioregions, sometimes with devastating effects on native birds, raising questions about how interspecies and geographic barriers regulate parasite assembly and invasion potential (Hellgren et al., 2014; van Riper, van Riper, Goff, & Laird, 1986, Clark, Clegg & Lima 2014).

We assess barriers that may govern parasite local coexistence at the species level by estimating effects of host community connectivity and interspecies barriers (host phylogeny and parasite host-specificity) on parasite local phylogenetic distinctiveness. We then address barriers at the community level by (1) exploring effects of host phylogenetic turnover, environmental variation and geographic distance on parasite turnover, and (2) testing if host connectivity or environmental variation influence parasite phylogenetic community skewness. We expect that increased host community connectivity reduces barriers to parasite establishment, leading to phylogenetically homogenized parasite communities. If host phylogeny acts as a relatively strong interspecies barrier to parasite assembly, we expect that distinct hosts carry distinct parasites and that between-region host turnover predicts parasite turnover. We also expect host-specialist parasites to be more locally distinct than generalists, as specialists may have less opportunity to diversify through host range expansions. Alternatively, if higher diversities of host specialists are able to co-occur through extensive niche packing (Ricklefs, 2010), then we expect specialists to be less distinct than generalists.

2 | METHODS

2.1 | Host–parasite occurrence data and avian community connectivity

We surveyed published literature and queried the MalAvi database (http://mbio-serv2.mbioekol.lu.se/Malavi/; accessed September 2016; Bensch, Hellgren, & Pérez-Tris, 2009) to compile data from >10,000 sampled host individuals (from 297 avian species) across 83 sites, ranging across latitudes −50.77 to 14.27 and longitudes −159.78 to 178.07 (Figure 2). In all cases, parasite lineages were identified using PCR targeting the cytochrome-b (cyt-b) gene (Hellgren, Waldenström, & Bensch, 2004; Waldenström, Bensch, Hasselquist, & Östman, 2004). Evidence indicates lineages differing by as little as one base pair may be reproductively isolated (Bensch, Pérez-Tris, Waldenström, & Hellgren, 2004). We thus regard each unique sequence as a parasite “species”. Low numbers of recovered parasites at some sites meant we could not assess within-site composition. We thus grouped sites into 29 regions. Australian mainland sites were grouped by climate zone using the Bureau of Meteorology’s Köppen classification, which defines zones using temperature, precipitation and vegetation data (http://www.bom.gov.au/jsp/ncc/climate_averages/climate-classifications/; accessed November 2016). Papua New Guinea mainland sites were grouped based on elevation (highlands, mean altitude = 2,500 m; and lowlands, mean altitude = 60 m). Island sites were either grouped by island (if at least three parasite species were recovered) or into regions representing nearby islands in an archipelago (Figure 2; Data set S1).
We downloaded range maps for all avian species occurring in the study area (N = 3,024 species) from BirdLife International and NatureServe (http://www.birdlife.org/datazone; accessed October 2016). For each region, we obtained lists of occurring avian species (defined as the "total" assemblage) by recording all species whose ranges overlapped 111 km buffers (1° at the equator) around sites. Bird range sizes were calculated as the total area of range polygons. Range sizes varied from 1 km² (island endemics) to 28,000 km² (wide-ranging seabirds).

Avian community connectivity was calculated as an inverse Simpson diversity index (Simpson 1949) using species' range sizes as weights (instead of using species abundances). Here, increased species richness, larger species range sizes and more even range size distributions all lead to increased collective mobility of a local host assemblage. Two connectivity indices were created, one using sampled hosts (Sampled. ConH) and second using total assemblages (all occurring avian species; Total. ConH). We included Total. ConH because many haemosporidians infect a diversity of avian species (Ewen et al., 2012; Olsson-Pons et al., 2015), suggesting unsampled but present host species impact parasite assembly. This will be especially relevant for generalist parasites, whereas sampled hosts should be representative for specialized parasites that are unlikely to occur in unsampled host species.

2.2 | Parasite and host phylogenetic reconstructions

Parasite cyt-b sequences (205 Haemoproteus and 80 Plasmodium parasites) were used to reconstruct phylogenetic relationships in BEAST v1.8.1 (Drummond & Rambaut, 2007; See Fig. S1). We identified the best evolutionary model (HKR+G) using maximum likelihood in MEGA v7.0 (Tamura, Dudley, Nei, & Kumar, 2007). We specified a Yule speciation prior and ran two chains of 17,500,000 iterations, sampling every 100,000 and removing 2,500,000 samples as burn-in. Chains were examined visually for stationarity and convergence.

Avian phylogenies were gathered from Birdtree.org (http://birdtree.org; accessed September 2016), which contains a Bayesian posterior distribution of phylogenies for 9,993 avian species (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012). We gathered 100 trees from the “Ericsson All Species Trees” data set for the 297 sampled host species, and another 100 trees for the 3,024 avian species occurring in the sample area. For all trees, branch lengths represented substitutions per site and were scaled (dividing branch lengths by the maximum) prior to analyses.

2.3 | Species-level analyses

2.3.1 | Host and parasite phylogenetic distinctiveness

For sampled host species, local phylogenetic distinctiveness (Sampled. DisH) was calculated as mean pairwise phylogenetic distance between a focal species and all other sampled host species in a region. This distance was divided by the mean of all pairwise distances in the region, resulting in region-specific distinctiveness (higher values indicating
more distinct species). We calculated total host distinctiveness (Total. Dis_H) using mean phylogenetic distance between a sampled host and all occurring avian species (sampled and unsampled) in a region. Parasite distinctiveness (Dis_P) was calculated separately for each parasite genus.

2.3.2 | Parasite host-specificity

Two indices described parasite host-specificity. First, we built bipartite networks (using numbers of infected individuals for each host species) and calculated the d' specialization index using Kullback–Leibler distances (Blüthgen, Menzel, & Blüthgen, 2006). Ranging from zero (no specialization; i.e., using all available hosts) to one (perfect specialist), d' quantifies how strongly a parasite is "specialized" compared to other parasites in terms of host range and interaction frequencies. We calculated phylospecificity for each parasite (STD*: Poulin & Mouillot, 2005), which accounts for the number of infected host species and their phylogenetic distances. Because STD* ranges from one (specialist) to greater than one, we used inverse STD* so both metrics could be interpreted in the same scale and direction. Parasite STD* and d' were uncorrelated (Pearson correlation: t = −1.41, p = .16), suggesting they capture different aspects of parasite host-specificity (d' capturing the level of host sharing by parasites and STD* capturing phylogenetic relationships of infected hosts).

2.3.3 | Influences of host community connectivity, host phylogeny and host specificity on parasite distinctiveness

We tested whether interspecies barriers influenced parasite distinctiveness (Dis_p) with a hierarchical linear model, using 548 unique parasite-host-region combinations as data points (Data set S2). Because Dis_p indices were non-negative and positively skewed, we log-transformed values and specified a Gaussian error distribution. Continuous predictors were the two host distinctiveness metrics (Sampled.Dis_h, Total.Dis_h), the two host connectivity metrics (Sampled.Con_h, Total.Con_h), host geographic range and both parasite host-specificity metrics (d', STD*). Because parasite genera showed different phylogenetic patterns (see Results) and Total.Dis_h explained a significant proportion of variance in Dis_p in preliminary analyses, we tested a Total.Dis_p parasite genus interaction. To decompose variation among covariates and account for underlying phyleogeographic structure, host phylogeny and sample region were included as random grouping terms, allowing inferences for group-specific slopes whilst estimating between-group variation (Gelman & Hill, 2007).

The model was fitted in a Bayesian framework using R package **mcclmm** (Hadfield, 2010). We used a flat prior for residual variance and parameter expansion (redundant multiplicative reparameterization of the linear model) for grouping terms, which reduces dependence among parameters and improves mixing (Gelman, 2006). To account for phylogenetic uncertainty, we ran separate models across 50 host trees (Guillerme & Healy, 2014). Models were run using two chains of 100,000 iterations with burn-in of 10,000 and thinning interval of 300. Chains were inspected for mixing/convergence both visually and with the Gelman–Rubin diagnostic (Gelman & Rubin, 1992). Autocorrelations were calculated to ensure independence of coefficient estimates (all autocorrelations < 0.1).

2.4 | Community analyses

2.4.1 | Interspecies and geographic barriers to parasite phylogenetic turnover

To describe shifts in diversity among regions, parasite phylogenetic turnover (β_H) was calculated (using binary occurrence data; Tsirogiannis & Sandel, 2015) between regions where three or more parasites occurred. Host turnover was calculated using either sampled hosts (Sampled.β_H) or total avian assemblages (Total.β_H). Distances between paired regions were calculated as beeline distance (km) between central points (mean latitude and longitude of regions). Regional climate dissimilarity was captured by three Gower’s distance matrices (Gower, 1971) to describe temperature and precipitation variation (both of which are thought to influence haemosporidian distributions; Sehgal et al., 2010; Sehgal, 2015). We used minimum temperature of the coldest month and mean temperature of the coldest quarter in a min. temp matrix, while a max.temp matrix included maximum temperature of the warmest month and mean temperature of the warmest quarter. Mean yearly precipitation and precipitations of the wettest and driest quarters were included in a precip matrix. For climate matrices, variables were sourced from (www.worldclim.org; accessed November 2016) and were continuous, unweighted and scaled by range (dividing by the maximum).

We tested if β_H was correlated with Sampled.β_H, Total.β_H geographic distance or climate dissimilarity matrices using multiple regressions on distance matrices (MRM; Goslee & Urban, 2007). Phylogenetic uncertainty was captured by repeating regressions over 1,000 iterations, where β values were re-calculated in each iteration using randomly sampled (with replacement) trees. To account for sampling variation that could bias turnover estimates (rare species may be more likely to be observed with larger sample sizes), we randomly removed subsets of species from well-sampled regions (>8 observed parasite species) prior to regression. We arbitrarily allowed the proportion of removed species to vary across a uniform distribution from zero to 30% in each iteration. Regression coefficients and R^2 values were gathered from the 1,000 iterations.

2.4.2 | Barriers to parasite phylogenetic community skewness

Host and parasite phylogenetic community skewness were calculated using pairwise phylogenetic distance distributions. A measure of symmetry, this index will be less than zero (right-skewed) if communities are made up of relatively more closely than distantly related species (Schweiger, Klotz, Durka, & Kühn, 2008), suggesting future colonizing parasites have a greater likelihood of being locally distinct. Thus, regions with right-skewed communities may be more vulnerable to
invasions by distantly related species if parasites are able to overcome environmental barriers and colonize. Skewness was calculated for regions where three or more parasites occurred.

We tested if parasite skewness was predicted by host connectivity (Sampled.ConH, Total.ConH) using linear regression with Gaussian error distribution. Mean annual precipitation and mean temperatures of the warmest and coldest quarters were included as continuous covariates to account for possible climate influences, while sampled and total host skewness were included to account for influences of host phylogenetic symmetry. parasite genus was included as a categorical covariate. The model was fitted using mcmglmm with a flat prior for residual variance. We ran two chains of 100,000 iterations with burn-in of 10,000 and thinning interval of 300, following procedures above to examine convergence and estimate autocorrelations.

For all phylogenetic metrics (skewness, distinctiveness and STD*), we accounted for phylogenetic uncertainty by calculating median indices across 1,000 randomly sampled host and parasite trees. Significance of model effects was determined by examining if 95% quantiles (for MRM models) or 95% credible intervals (CI; for Bayesian models) of regression coefficients did not overlap zero. Continuous predictors were scaled (centred and divided by one standard deviation), and variances explained were calculated following Nakagawa predictors were scaled (centred and divided by one standard deviation) and variances explained were calculated following Nakagawa and Schielzeth (2013). Data were analysed in R v3.2.1 (R Core Team, 2016; R: A language and environment for statistical computing). Data and R code are presented in Supplementary Data and the Dryad Digital Repository: (https://doi.org/10.6084/m9.figshare.5432107).

3 | RESULTS

3.1 | Host phylogeny, local distinctiveness and connectivity drive parasite distinctiveness

Parasite distinctiveness (DisP) was strongly related to host phylogeny (variance explained = 46.8%–78.3%), with hosts from certain clades more likely to carry distinct parasites (Figure 3). These included carriers of distinct Haemoproteus spp. such as doves (Columbidae), kingfishers (Alcedinidae) and corvids such as crows (Corvidae) and whistlers (Pachycephalidae; Figure 3), all of which occupy a range of regions yet rarely co-occur with sympatric sister species (Dutson, 2012; Jønsson et al., 2014). After accounting for the strong influence of host phylogeny, DisP was also positively predicted by local host total distinctiveness (Total.DisH; coefficient 95% CI = 0.04–0.12; variance explained = 2.48%–6.38%; Figure 3), suggesting host relatedness to the local avian assemblage acts as an interspecific barrier to parasite assembly. This relationship varied between parasite genera, as increases in Total.DisH lead to a 1.95 times higher increase in DisP for Haemoproteus than for Plasmodium parasites.

DisP decreased with increasing total host connectivity (Total.ConH; coefficient = 0.01–0.09; variance explained = 0.04%–7.7%; See Fig. S2), indicating greater host diversity and collective mobility increase a parasite’s chance of encountering related parasites. Total.ConH was highest in Malaysia (509 avian species; Total.ConH = 83.60) and southeast Australia (468 avian species; Total.ConH = 80.42), moderate in Papua New Guinea where many endemic avian species occur (mean species = 520.5; mean Total.ConH = 42.62) and lowest in Vanuatu and New Caledonia (mean species = 115 and 110; mean Total.ConH = 32.3 and 31.6, respectively). DisP was not influenced by Sampled.ConH, Sampled.DisH or individual host range (coefficient CIs overlapped zero).

We observed considerable variation in host specificity for both parasite genera, though neither specificity metric influenced DisP (coefficients overlapped with zero). For both genera, STD* (phyllospecificity) ranged from 0.41 to 1 (mean = 0.79 and 0.87 for Plasmodium and Haemoproteus, respectively), while d’ (network specificity) ranged from 0 to 1 (means = 0.65 and 0.67). In total, fixed effects (d’, STD*), host range size, Total.ConH Sampled.ConH Total.DisH Sampled.DisH explained 5.7%–13.2% of variance in DisP while the full model (including host phylogeny and region grouping terms) explained 69.8%–88.9%.

3.2 | Host phylogeny and climate shape parasite community structure

We found evidence that both environmental and interspecies barriers influence parasite turnover. For Plasmodium, βp was positively correlated with Sample.βP (MRM coefficient = 1.01–1.86), indicating host phylogeny influences shifts in parasite diversity. Plasmodium βp also correlated positively with geographic distance (0.56–1.21), but negatively with max.temp (–0.09 to –0.18). For Haemoproteus, βp correlated positively with both host turnover metrics (Sampled.βP coefficient = 0.30–0.61; Total.βP = 0.58–1.13), and with geographic distance and max.temp (0.04–1.37; 0.16–0.45, respectively), but
negatively with \( \text{min. temp} \) (-0.11 to -0.28). Variance explained by predictors ranged from 47% to 57% for \( \text{Haemoproteus} \) and from 4% to 11% for \( \text{Plasmodium} \).

Mainland communities such as Papua New Guinea and eastern Australia showed low mean parasite turnover among paired regions (low average pairwise \( \beta_p \) after accounting for geographic distance; Figure 2; Data set S3), suggesting these assemblages were less phylogenetically unique within the study area. Parasite assemblages on Melanesian islands (New Caledonia and Vanuatu) showed moderate mean turnover, while relatively isolated and less well-sampled communities such as Christmas Island and north-west Australia showed high turnover (Figure 2). \( \text{Plasmodium} \) communities in New Zealand and Micronesia, where many occurring parasites are known to be introduced (Beadell et al., 2006; Ewen et al., 2012), showed high mean turnover (Figure 2).

Parasite community skewness indices were predominantly negative (right-skewed; Figure 4), with assemblages generally made up of more closely than distantly related parasites. Parasite skewness was not influenced by host community connectivity or host skewness but was driven by mean temperature of the coldest quarter (coefficient = 0.02–2.98; variance explained = 0.2%-10.6%), with colder regions harbouring more negatively skewed communities (Figure 4). Parasite skewness also differed between genera (coefficient = -0.91 to -0.02; variance explained = 7.5%-27.10%), with \( \text{Plasmodium} \) more negatively skewed than \( \text{Haemoproteus} \) communities (Figure 4). Interestingly, \( \text{Haemoproteus} \) communities in Papua New Guinea were positively skewed, while those in eastern Australian were negatively skewed (Figure 4), suggesting neighbouring parasite assemblages with low phylogenetic turnover (Figure 2) can vary substantially in community structure.

4 | DISCUSSION

We illustrate a framework for identifying relative influences of interspecies, environmental and geographic barriers to parasite community assembly. Using this framework, we show that host phylogeny is a key driver of local parasite assembly, while climate and the regional connectivity of host assemblages play lesser but nonetheless important roles. Moreover, host phylogeny and geographic distance were more important than environmental barriers in shaping parasite turnover, indicating alterations to host movement and community composition may strongly affect parasite dispersal and invasion potential across biogeographic scales.

4.1 | Barriers to parasite community assembly and their roles in parasite spread

Host phylogeny was an important driver of parasite distinctiveness and species turnover, supporting suggestions that host identity drives shifts in haemosporidian diversity and implicating host evolutionary history as a determinant of regional parasite assembly (Fecchio et al., 2017; Scordato & Kardish, 2014). Phylogenetic signals are a proxy for physical (i.e., physiological, morphological, biochemical) and ecological traits, where closely related species resemble each other more than random pairs, indicating conserved attributes likely play a role in modulating interspecies barriers to regional parasite assembly (Huang, Bininda-Emonds, Stephens, Gittleman, & Altizer, 2014). Yet, an important consideration here is that we do not know which shared host traits influence blood parasite assembly patterns. Determining underlying interspecies barriers to parasite composition will require additional interdisciplinary work, combining data on host traits with
methods that can decompose phylogenetic and ecological similarity to improve inference (Cadotte, Albert, & Walker, 2013; Clark & Clegg, 2017).

Future host range shifts may considerably impact parasite spread and disease emergence, both by breaking down existing barriers to host shifting and by increasing parasite dispersal (Atkinson & LaPointe, 2009; Young, Parker, Gilbert, Guerra, & Nunn, 2017). Here, a positive relationship between host and parasite distinctiveness indicates that diminishing phylogeographic barriers (where host range shifts may alter local host distinctiveness) could present more opportunities for parasites to shift between related hosts. Yet, a strong host phylogenetic signal, where distinct parasites are more strongly associated with certain host clades, suggests alterations to host species’ distributions may have different effects on parasite spread depending on host evolutionary history. For instance, we identified multiple host clades as prominent carriers of distinct parasites, including non- passerines (kingfishers and doves) as well as certain passerine groups (crows and whistlers), indicating that future range shifts for these host groups could lead to novel parasite introductions. Our work therefore corroborates a large body of literature to show that interactions between ecological fitting and shifting geographic distributions will have powerful influences on parasite assembly and emergence potential (Agosta et al., 2010; Araujo et al., 2015; Brooks & Hoberg, 2007; Hoberg, 2010; Hoberg & Brooks, 2008). However, a significant influence of host community connectivity suggests that parasite distinctiveness is not only driven by host phylogeny, but also by forces that limit host diversity and distributional overlap (i.e., competitive exclusion or dispersal barriers; Ricklefs, 2010; Ewen et al., 2012). This finding generates exciting new avenues for studying parasite assembly, particularly as few studies relate the connectivity of host communities to parasite dispersal opportunity (but see Buckee et al., 2007).

Our findings that environmental effects influence parasite turnover and community skewness agree with previous studies to suggest that even if dispersal barriers break down, climate and perhaps other environmental conditions may constrain parasite distributions (Clark, Clegg, & Klaassen, 2016; Clark, Wells, Dimitrov, & Clegg, 2016; Kutz, Hoberg, Molnár, Dobson, & Verocai, 2014; Sehgal, 2015). Indeed, regional temperature similarity impacted shifts in diversity for both parasites and hosts (Ricklefs, 2010; Schoener, Banda, Howe, Castro, & Alley, 2013). Parasites introduced to highly connected host regions, on the other hand, may be more likely to experience competition with closely related parasites, perhaps curbing invasion potential. Under this consideration, areas such as eastern Australia and mainland Papua New Guinea may be less vulnerable to parasite invasions (though not immune; see Clark, Olsson-Pons, Ishtiaq, & Clegg, 2015), as these regions contain a relatively balanced phylogenetic diversity of parasites and experience high host community connectivity.

4.2 Accounting for unsampled host species in parasite assembly studies

Our study raises a critical point for assessing parasite composition, as measures of host relationships were more important in driving parasite assembly when considering the total host assemblage rather than only sampled hosts. A host’s distinctiveness with respect to the entire avian community positively predicted parasite distinctiveness, while considering only sampled hosts had no influence on parasite distinctiveness. Phylogenetic turnover of the total avian assemblage was also a stronger predictor of *Haemoproteus* turnover than was sampled host turnover. These findings imply that variation in unsampled but locally present host species is important for driving parasite establishment. Inferences beyond those obtained from sampled hosts are clearly needed, a process which is rarely considered in host–parasite interactions (but see Wells et al., 2012), despite being a well-known problem in the sample survey literature (Little, 2004).

4.3 Caveats and conclusions

There are several ways in which our study framework can be improved. First, we did not consider individual sites in our study as our data were limited by small sample sizes for many sites. Inclusion of site-specific species and climate data could be used as an additional
source of information to examine possible impacts of sampling bias on regional community inferences. Second, consideration of sampling distribution across regions may have an impact on community turnover estimates, as regions such as Christmas Island and Micronesia had a relatively high turnover that could have been influenced by low overall sample sizes and large geographic distances to many other study regions. Future studies that sample smaller and more regular geographic intervals could help to address this drawback. Finally, our phylogenetic metrics relied only on binary species occurrences (present or absent) and may be improved with better consideration of species’ relative abundances, as host abundance plays a role in host reservoir potential and cross-species parasite transmission (Kilpatrick, Kramer, Jones, Marra, & Daszak, 2006). Unfortunately, such data for host abundance were not available and would require additional field survey efforts.

In summary, our study agrees with previous work to suggest that in addition to identifying environmental barriers, considering host phylogenetic relationships and dispersal abilities is key to understanding regional parasite assembly (Agosta et al., 2010; Brooks & Ferrao, 2005; Sehgal, 2015; Wells, O’Hara, Morand, Lessard, & Ribas, 2015). Moreover, we show that accounting for the overall connectivity of the host community, rather than solely focussing on individual host species’ dispersal potentials, may be crucial to predicting future parasite invasions. With the pervasive need to understand how interspecies interactions shape species distributions (Wisz et al., 2013), our study represents an important step towards predicting how parasite assemblages will be shaped following future global change.

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DATA ACCESSIBILITY

Newly reported parasite sequences will be uploaded to GenBank and the MalAvi avian malaria database upon acceptance. R code and raw data sets are uploaded to figshare https://doi.org/10.6084/m9.figshare.5432107

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