Paper:

Clark, N., Clegg, S., Sam, K., Goulding, W., Koane, B. & Wells, K. (2018). Climate, host phylogeny and the connectivity of host communities govern regional parasite assembly. *Diversity and Distributions, 24*(1), 13-23.
http://dx.doi.org/10.1111/ddi.12661

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

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Running title: Barriers to regional parasite assembly

Abstract word length: 232

Word count (Introduction through Biosketch): 5144

Number of references: 92

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 dataset 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.

Key words: community assembly, host shifting, host specificity, interspecies barriers, parasite invasion, *Plasmodium*

INTRODUCTION

Regional variation in community composition is a central property in nature (Wallace, 1876; Kraft *et al.*, 2007). With increasing environmental destabilisation and biotic homogenisation, 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 can alter risks of parasite invasions and emerging disease (Brooks & Hoberg, 2007; Hoberg & Brooks, 2008; Lafferty, 2009; Agosta *et al.*, 2010; Adlard *et al.*, 2015).

A strong incentive exists to identify barriers to species establishment and determine how these barriers modulate invasion risk (Hoberg, 2010; Kelly *et al.*, 2009; Springborn *et al.*, 2015). For parasites, **geographic barriers** (such as distance or mountain ranges) are known to constrain species' distributions (Brooks & Ferrao, 2005; Lafferty, 2009; Warburton *et al.*, 2016; Krasnov *et al.*, 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 (Githeko *et al.*, 2000; Epstein, 2001; Patz *et al.*, 2005). However, parasite distributions are also linked to host life histories and distributions (Poulin *et al.*, 2011; Olsson-Pons *et al.*, 2015; Fecchio *et al.*, 2017). Such **interspecies barriers** are increasingly recognised to govern local assembly (HilleRisLambers *et al.*, 2012; Wisz *et al.*, 2013; Mayfield & Stouffer, 2017). 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 colonise a new range (Brooks & Hoberg, 2007; Agosta *et al.*, 2010). Following colonisation, assembly may be limited by interspecies barriers that govern parasite spread and diversification (Fig. 1). This process, termed 'ecological fitting' (Janzen, 1985), suggests many parasites are capable of infecting a broader range of hosts than is currently realised, with changes to host and/or parasite distributions producing new associations that may be limited by host phylogenetic relationships (Brooks & Ferrao, 2005; Radtke *et al.*, 2007; Araujo *et al.*, 2015).

For parasites that rely on host dispersal to colonise 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 *et al.*, 2001) and a higher likelihood for parasites to break geographic and/or environmental barriers (Fig. 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 recognise this aspect as a potential driver of parasite assembly (but see Buckee *et al.*, 2007).

Parasites are often restricted to hosts with phylogenetically conserved ecological or physiological traits (Janzen, 1968; Rohde, 1980; Streicker *et al.*, 2010; Schulze-Lefert & Panstruga, 2011), 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; Ewen *et al.*, 2012; Clark & Clegg, 2015; Ellis *et al.*, 2015; Mata *et al.*, 2015; Fig. 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. Haemosporidians (genera *Plasmodium* 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 (van Riper III *et al.*, 1986; Hellgren *et al.*, 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 homogenised 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.

METHODS

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 *et al.*, 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 (Fig. 2). In all cases, parasite lineages were identified using PCR targeting the cytochrome-*b* (cyt-*b*) gene (Hellgren *et al.*, 2004; Waldenström *et al.*, 2004). Evidence indicates lineages differing by as little as one base pair may be reproductively isolated (Bensch *et al.* 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 = 2500m; and lowlands, mean altitude = 60m). Island sites were either grouped by island (if at least three parasite species were recovered) or into regions representing nearby islands in an archipelago (Fig. 2; Supplementary Dataset 1).

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 1km^2 (island endemics) to 28,000km^2 (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.Con**$_H$*) and a second using total assemblages (all occurring avian species; ***$Total.Con_H$***). We included *$Total.Con_H$* 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 specialised parasites that are unlikely to occur in unsampled host species.

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 in Supplementary Material). We identified the best evolutionary model (HKR+G) using maximum likelihood in MEGA v7.0 (Tamura *et al.*, 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 *et al.*, 2012). We gathered 100 trees from the 'Ericsson All Species Trees' dataset 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.

Species level analyses

Host and parasite phylogenetic distinctiveness

For sampled host species, local phylogenetic distinctiveness (***Sampled.Dis$_H$***) 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.

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'*** specialisation index using Kullback-Leibler distances (Blüthgen *et al.*, 2006). Ranging from zero (no specialisation; i.e. using all available hosts) to one (perfect specialist), *d'* quantifies how strongly a parasite is 'specialised' 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 = 0.16), 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).

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 (Supplementary Dataset 2). 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 $Total.Dis_H$*parasite genus interaction. To decompose variation among covariates and account for underlying phylogeographic 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 MCMCglmm (Hadfield, 2010). We used a flat prior for residual variance and parameter expansion (redundant multiplicative reparameterisation 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).

Community analyses

Interspecies and geographic barriers to parasite phylogenetic turnover

To describe shifts in diversity among regions, parasite phylogenetic turnover (**β_P**) 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_P 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.

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 *et al.*, 2008), suggesting future colonising 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 colonise. Skewness was calculated for regions where three or more parasites occurred.

We tested if parasite skewness was predicted by host connectivity ($Sampled.Con_H$, $Total.Con_H$) 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 MCMCglmm 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 & Schielzeth (2013). Data was 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: (doi: XXXXX XXXXX).

RESULTS

Host phylogeny, local distinctiveness and connectivity drive parasite distinctiveness

Parasite distinctiveness (Dis_P) was strongly related to host phylogeny (variance explained = 46.8 to 78.3%), with hosts from certain clades more likely to carry distinct parasites (Fig. 3). These included carriers of distinct *Haemoproteus* spp.

such as doves (Columbidae), kingfishers (Alcedinidae) and corvoids such as crows (Corvidae) and whistlers (Pachycephalidae; Fig. 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, Dis_P was also positively predicted by local host total distinctiveness ($Total.Dis_H$; coefficient 95%CI = 0.04 to 0.12; variance explained = 2.48 to 6.38%; Fig. 3), suggesting host relatedness to the local avian assemblage acts as an interspecies barrier to parasite assembly. This relationship varied between parasite genera, as increases in $Total.Dis_H$ lead to a 1.95 times higher increase in Dis_P for *Haemoproteus* than for *Plasmodium* parasites.

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

We observed considerable variation in host specificity for both parasite genera, though neither specificity metric influenced Dis_P (coefficients overlapped with zero). For both genera, *STD** (phylospecificity) 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, $Total.Con_{H,}$ $Sampled.Con_{H,}$ $Total.Dis_{H,}$ $Sampled.Dis_{H,}$) explained 5.7 to 13.2% of variance in Dis_P while the full model (including host phylogeny and region grouping terms) explained 69.8 to 88.9%.

Host phylogeny and climate shape parasite community structure

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

Mainland communities such as Papua New Guinea and eastern Australia showed low mean parasite turnover among paired regions (low average pairwise β_P after accounting for geographic distance; Fig. 2; Supplementary Dataset 3), 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 northwest Australia showed high turnover (Fig. 2). *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 (Fig. 2).

Parasite community skewness indices were predominantly negative (right-skewed; Fig. 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 to 2.98; variance explained = 0.2 to 10.6%), with colder regions harbouring more negatively skewed communities (Fig. 4). Parasite skewness also differed between genera (coefficient = -0.91 to -0.02; variance explained = 7.5 to 27.10%), with *Plasmodium* more negatively skewed than *Haemoproteus* communities (Fig. 4). Interestingly, *Haemoproteus* communities in Papua New Guinea were positively skewed, while those in eastern Australian were negatively skewed (Fig. 4), suggesting neighbouring parasite assemblages with low phylogenetic turnover (Fig. 2) can vary substantially in community structure.

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.

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 (Scordato & Kardish, 2014; Fecchio *et al*., 2017). 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 *et al.* 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 *et al.*, 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 *et al*., 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 (Brooks & Hoberg, 2007; Hoberg & Brooks, 2008; Hoberg, 2010; Agosta *et al*., 2010; Araujo *et al*., 2015). 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 since 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 (Kutz *et al.*, 2014; Sehgal, 2015; Clark *et al.*, 2016a,b). Indeed, regional temperature similarity impacted shifts in diversity for both parasite genera, albeit with different directional relationships. One possible explanation could be that haemosporidians are subject to influences of external temperature changes on ectothermic vectors (Paaijmans *et al.*, 2010), and *Plasmodium* and *Haemoproteus* parasites are transmitted by different arthropods (mosquitoes from family Culicidae and midges from family Ceratopogonidae, respectively; Santiago-Alarcon *et al.*, 2012). However, little is known about the particular vector species transmitting avian haemosporidians in the South Pacific (but see Ishtiaq *et al*., 2008), and so drawing conclusions from these different patterns remains challenging. Intriguingly, regions with colder temperatures harboured more closely related communities for both parasite genera, perhaps indicating minimum temperatures act as a strong filter for haemosporidian diversity, a finding that warrants future study. Regardless of the biological mechanism, accounting for interspecies interactions and environmental conditions can improve predictions of species distributions following climate shifts (Choler *et al.*, 2001; Wells *et al.*, 2014; Mayfield & Stouffer, 2017).

Determining which species are likely to be introduced and become invasive are prominent ecological questions (Wiens, 2011; Springborn *et al.*, 2015). Our results suggest that parasites introduced to regions with low host community connectivity, high host turnover and low minimum temperatures may be more likely to invade the community. These patterns highlight that New Zealand, which showed high rates of host and parasite turnover and contained distantly related (phylogenetically left skewed) *Plasmodium* communities, may be particularly vulnerable to invasions. Distinct invaders can have key competitive advantages and a greater chance of becoming invasive (HilleRisLambers *et al.*, 2012), as has been the case in the Galapágos where the invasive fly, *Philornis downsi*, parasitizes a diversity of endemic bird species

(Fessl *et al.* 2006). Indeed, invasive avian malaria parasites have already been recorded infecting a diversity of native New Zealand birds, with evidence suggesting that introduced birds play key roles in driving parasite spread (Ewen *et al*., 2012; Schoener *et al*., 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 *et al.*, 2015), as these regions contain a relatively balanced phylogenetic diversity of parasites and experience high host community connectivity.

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 are 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).

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 was 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, since host abundance plays a role in host reservoir potential and cross-species parasite transmission (Kilpatrick *et al.*, 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 (Brooks & Ferrao, 2005; Agosta *et al.*, 2010; Wells *et al.*, 2015; Sehgal, 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.

ACKNOWLEDGEMENTS

We thank S. Olsson-Pons, D. Treby, K. Lowe, J. LeBreton, S. Oghino, F. Cugny, W. Waheoneme, T. Read, Association pour la Sauvegarde de la Biodiversité d'Ouvéa, and Société Calédonienne d'Ornithologie for field and/or logistical assistance in Australia and New Caledonia. Australian and Melanesian fieldwork was conducted under Griffith University ethics clearance ENV/01/12/AEC (SC). Papua New Guinea fieldwork was conducted under UQ animal ethics permit GPEM/172/13/ APA (WG). SC acknowledges financial support from a Griffith University New Researcher Grant, a National Geographic Society Committee for Research and Exploration Grant (#9383-13) and Birds Queensland. KS acknowledges financial support from Czech Science Foundation 14-36098G and staff of The New Guinea Binatang Research Centre. BK was funded by Darwin Initiative for the Survival of Species No. 22-00. Work of KS and BK was conducted under University of South Bohemia animal ethic clearance 515-20424/2012-30 and PNG NRI Research Permit No. 99902077829. We thank two anonymous reviewers for comments that improved the manuscript.

SUPPLEMENTARY MATERIAL

Fig. S1: Phylogenetic relationships of *Haemoproteus* and *Plasmodium* cytochrome-*b* sequences.

Fig. S2: Relationship between regional total host community connectivity ($Total.Con_H$) and parasite local phylogenetic distinctiveness (Dis_P).

Dataset 1: Sample locations, host species sample sizes and parasite infection prevalence across regions.

Dataset 2: Raw data used to analyse parasite local phylogenetic distinctiveness (Dis_P)

Dataset 3: Turnover estimates and avian species richness metrics across regions.

DATA ACCESSIBILITY

Newly reported parasite sequences will be uploaded to GenBank and the MalAvi avian malaria database upon acceptance. R code and raw datasets will be uploaded as supplements and to the Dryad digital repository upon acceptance.

BIOSKETCH

Nicholas Clark is a disease ecologist interested in evolutionary ecology and the biogeography of wildlife pathogens. His research interests concern topics in computational phylogenetics, biodiversity and host-pathogen interactions, as well as large-scale patterns in community assembly.

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TABLES

Table 1: Glossary of definitions for proposed community assembly barriers and metrics used in analyses.

Community assembly: the establishment and maintenance of local communities through arrival of potential colonists from external species pools.

Environmental barriers: environmental differences between regions that may govern species' distributions, including variation in macroclimate, habitat and altitude.

Geographic barriers: physical barriers to between-region parasite dispersal, including geographic distance, mountain ranges, and water barriers.

Host community connectivity: the distributional overlap of host communities among regions, taking into account host species richness and host geographic range sizes. Here, $\mathit{Sampled.Con}_H$ describes host community connectivity while considering only sampled avian host species, and $\mathit{Total.Con}_H$ describes connectivity for all occurring avian species within a local assemblage.

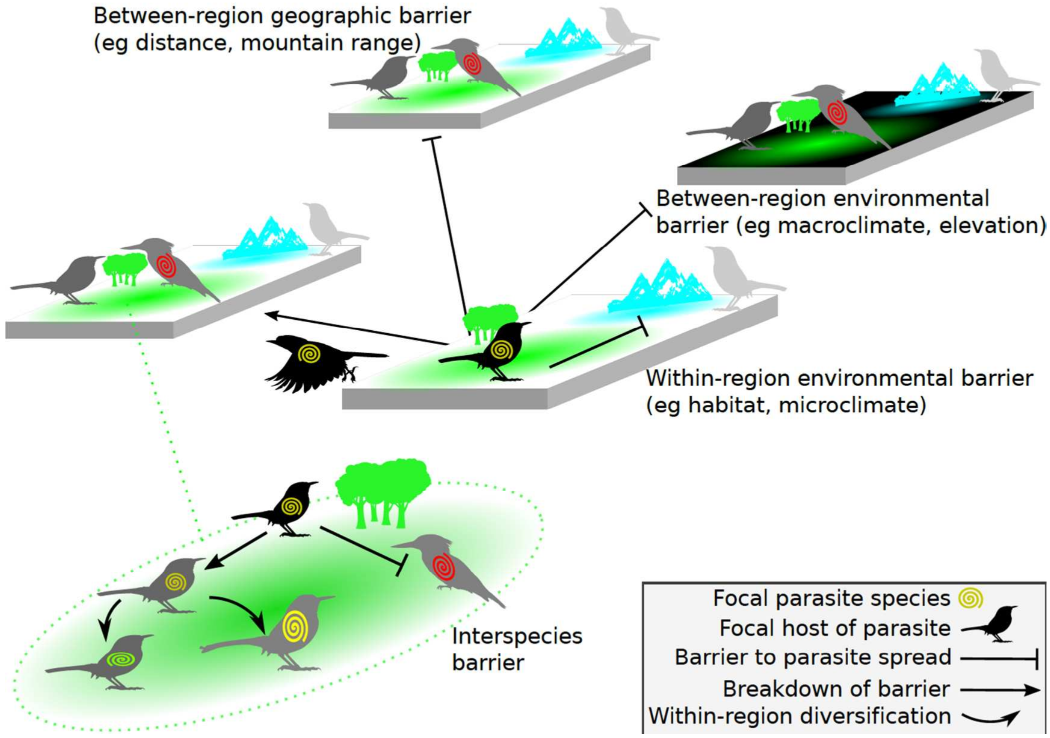
Host specificity: the range and diversity of hosts a parasite is observed to infect. Here, *d'* describes parasite host specificity using host-parasite interaction networks, while *STD** describes phylogenetic host specificity using host phylogenetic distances.

Interspecies barriers: 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).

Local phylogenetic distinctiveness: the average pairwise phylogenetic distance between a focal taxon and co-occurring taxa within a local assemblage. Here, Dis_P describes parasite species distinctiveness, $\mathit{Sampled.Dis}_H$ describes host species distinctiveness with respect to co-occurring sampled host species, and $\mathit{Total.Dis}_H$ describes host species distinctiveness with respect to all co-occurring sampled avian species.

Phylogenetic community skewness: 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.

Phylogenetic turnover (β): shifts in phylogenetic diversity between communities. Here, β_P describes parasite phylogenetic turnover, $\mathit{Sampled.}\beta_H$ describes turnover of sampled host assemblages, and $\mathit{Total.}\beta_H$ describes turnover of total avian assemblages.



FIGURES

Fig. 1: Schematic illustrating potential barriers to regional spread and diversification for parasites that rely on host movement for dispersal. Plates represent different bioregions, while zones (forest, mountain) within plates represent different habitat types. At the bottom left is a sectional zoom of the forested habitat in the left-hand plate, illustrating within-region parasite diversification where closely related host species enable the breakdown of interspecies barriers. Shown in black is the focal host of a given parasite species, with ecologically or phylogenetically similar host species depicted as similar shapes in varying shades of grey. A distantly related host species is depicted as a different body shape. Concentric oval shapes represent parasites, with different shapes and colours representing different parasite species.

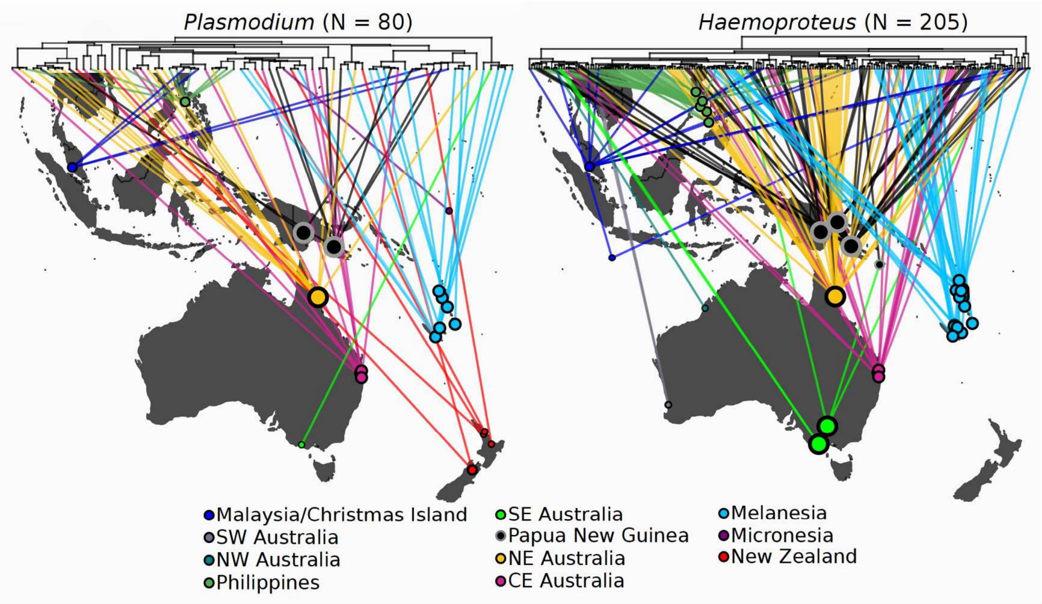


Fig. 2: Distribution of parasites across the study area. Lines connect phylogenetic parasite lineages to the region where they were most frequently observed. Circle sizes are inversely proportional to mean phylogenetic turnover (β_P) between the region and remaining regions, accounting for geographic distance. Hence, larger circles show communities with lower mean turnover to surrounding regions, which can be thought of as having more 'connected' parasite communities. Lines and circles are coloured according to region, with closely situated regions grouped to improve clarity.

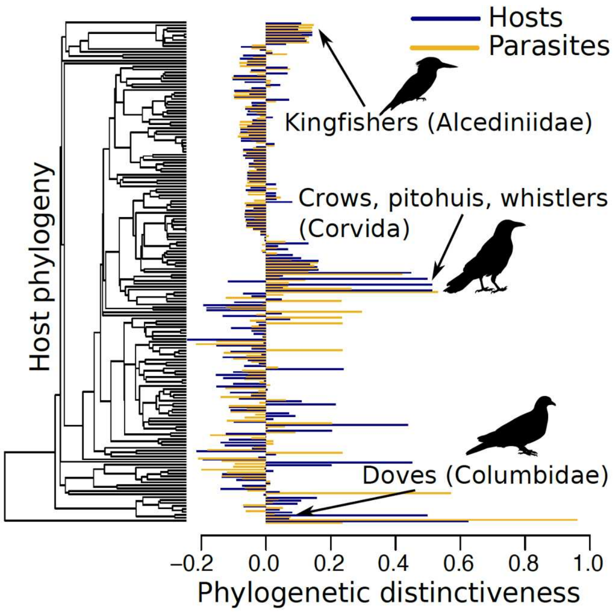


Fig. 3: Distribution of local phylogenetic distinctiveness for hosts ($Total.Dis_H$) and their parasites (Dis_P) across the host phylogeny. Distinctiveness represents mean phylogenetic distance between the focal species and all co-occurring species within a region. Values are scaled so values > zero indicate taxa that are more distinct, while those < zero indicate less distinct taxa.

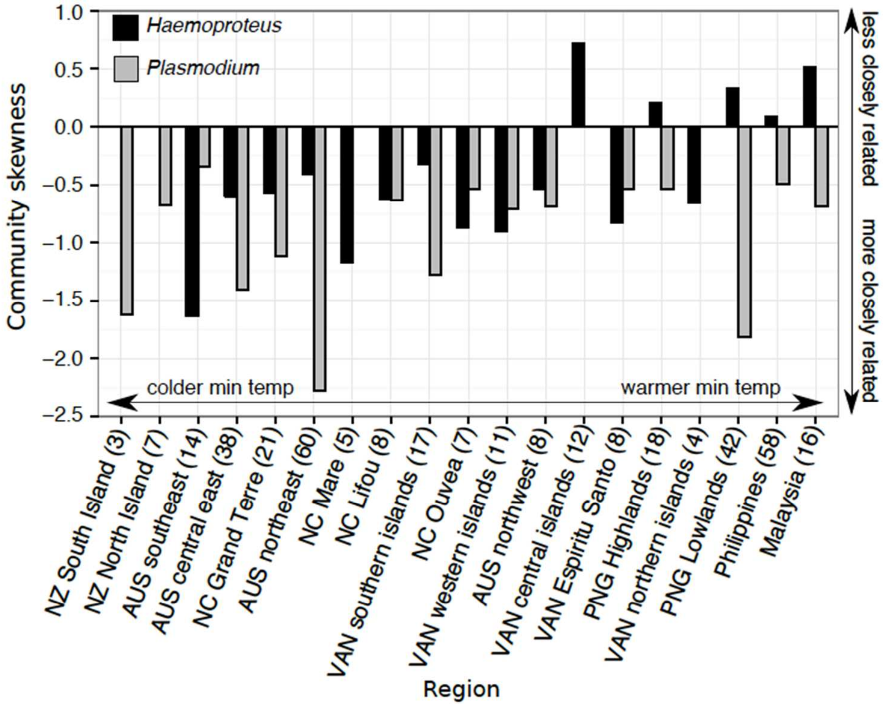


Fig. 4: Parasite phylogenetic community skewness across regions. Skewness > zero indicates co-occurring parasites are relatively distantly related (left skewed pairwise distance distribution), while < zero indicates parasites are relatively closely related (right skewed distance distribution). Regions are ordered based on mean temperature of the coldest quarter, with numbers in parentheses indicating the number of parasites recovered in each region. NZ, New Zealand; AUS, Australia; NC, New Caledonia; VAN, Vanuatu; PNG, Papua New Guinea.