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LETTER

Walk, swim or fly? Locomotor mode predicts genetic differentiation in vertebrates

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Abstract

Limited dispersal is commonly used to explain differences in diversification rates. An obvious but unexplored factor affecting dispersal is the mode of locomotion used by animals. Whether individuals walk, swim or fly can dictate the type and severity of geographical barriers to dispersal, and determine the general range over which genetic differentiation might occur. We collated information on locomotion mode and genetic differentiation (F_{ST}) among vertebrate populations from over 400 published articles. Our results showed that vertebrate species that walk tend to have higher genetic differentiation among populations than species that swim or fly. Within species that swim, vertebrates in freshwater systems have higher genetic differentiation than those in marine systems, which is consistent with the higher number of species in freshwater environments. These results show that locomotion mode can impact gene flow among populations, supporting at a broad-scale what has previously been proposed at smaller taxonomical scales.

Keywords

Dispersal, F_{ST}, locomotion, reproductive isolation, speciation, vicariance.

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INTRODUCTION

The disparity in species richness and diversification rates between land and sea has been described as one of the largest biodiversity gradients in nature (Grosberg *et al*. 2012; Wiens 2015). For example, it was recently shown that diversification rates on land are roughly twice that of marine clades (Wiens 2015), and that around 80% of all living species are found on land, despite terrestrial environments comprising only 30% of Earth's surface (May & Godfrey 1994). A variety of hypotheses have been proposed to explain such disparity, including greater net primary productivity in terrestrial environments, greater opportunities for specialisation and decreased rates of extinction on land (Vermeij & Grosberg 2010; Grosberg *et al.* 2012; Wiens 2015). Possibly the most compelling and testable hypothesis relates to the putative difference in dispersal ability for organisms living on land compared to those in the sea (Wiens *et al*. 2011; Wiens 2015). This rests on the general assumption that there are more geological and ecological barriers to dispersal on land than in the sea and this creates more opportunity for reproductive isolation to occur among terrestrial populations (May & Godfrey 1994). Vicariance, coupled with progressive genetic differentiation in isolation, should in turn promote more instances of allopatric speciation (Jablonski 1986; Ikeda *et al*. 2012).

Indeed, restricted dispersal is typically invoked to explain empirical estimates of genetic divergence among populations (Slatkin 1987). For example, benthic species of reef fish disperse less than pelagic species and also show higher genetic structure (greater differentiation) in their populations (Riginos *et al*. 2014). More broadly, however, aquatic life histories and the fluid characteristics of the ocean are expected to create the opportunity for extreme long-distance dispersal in the sea (Palumbi 1994). One outcome of this may be a reduction in reproductive isolation and decreased potential for speciation. Conversely, in terrestrial environments, the decreased gene flow and reduced population connectivity of land animals could explain the higher species richness and diversification rates on land (Vermeij & Grosberg 2010; Wiens 2015).

Yet increased dispersal has also been suggested to promote speciation if speciation is predominantly the product of colonising new environments (Wessel *et al*. 2013; Weeks & Claramunt 2014). That is, the greater an animal's ability to disperse over a wide range, the more likely it will encounter and settle in a new environment where new ecological opportunities might prompt adaptation that instigates reproductive isolation and subsequent speciation (Shafer & Wolf 2013). The question, then, is to what extent populations differ in gene flow and does this differ between organisms living on land compared to the sea.

Gene flow among populations is not only a product of the likelihood of physical barriers impeding dispersal, but also dependent on the energetics of transport and the mode of locomotion more generally (Marko 2004; Dawson & Hamner 2008; Bonte *et al*. 2012). For example, in platypuses the cost

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of terrestrial locomotion is twice as high as the cost of swimming (Fish *et al.* 2001). Even in similar environments, different locomotor modes can create variation in population connectivity. For instance, not all marine animals have long dispersal distances, and many are sessile. There are also major differences in locomotor modes on land, even within clades such as mammals (e.g. flying bats vs. walking mammals). Locomotor modes, more than environments *per se*, may be fundamental in explaining differences in biodiversity patterns by generating variation in population connectivity. In birds and beetles, flightless species retain higher genetic differentiation among populations than flying species (Baker *et al.* 1995; Ikeda *et al.* 2012). In carrion beetles, locomotor mode (e.g. flight vs. walking) not only explains the higher genetic structure of flightless populations, but flightless lineages also have higher rates of speciation (Ikeda *et al.* 2012). Similarly, Amazonic ovenbirds with poor flight performance have higher speciation rates (Claramunt *et al.* 2012) and in Australasia, birds with shorter wings – and therefore poorer flying abilities – have higher speciation rates (Weeks & Claramunt 2014). Taken together, there appears to be a strong causal link between locomotive ability and diversification processes.

We used meta-analytical tools and macro-evolutionary analyses to assess at a broad-scale whether differences in locomotion mode have a predictive effect on the level of genetic divergence exhibited among populations. Specifically, we used genetic information in the form of F_{ST} values computed among populations for over 400 species of vertebrates. We expected F_{ST} values to differ as a function of locomotor mode because the type of locomotion used by an animal – walking, swimming, or flying – should have an impact on gene flow through its gross effect on dispersal range (Rousset 1997; Selkoe & Toonen 2011). We predicted that species with locomotor modes that facilitate long-range dispersal – swimming or flying – would have higher gene flow and decreased potential for differentiation among populations, compared to the more restricted locomotor mode of walking. To our knowledge, this is the first study to test the putative link between locomotion mode and genetic divergence across all vertebrates.

MATERIALS AND METHODS

We extracted information on F_{ST} values and geographical distances from published studies. Genetic structure is expected to change across populations as a function of distance: populations that are more geographically distant from one another are expected to have greater genetic differentiation (Rousset 1997). Genetic analysis of population structure using Wright's F_{ST} (Wright 1931) is a common tool for estimating divergence across populations (Weersing & Toonen 2011; Puebla *et al.* 2012). Although there is some debate surrounding the accuracy of F_{ST} as a measure of genetic structure (Hedrick 2005; Jost 2008), it continues to be a valid measure that accounts for mutation processes better than its analogues, and it is also the most ubiquitous method in the genetic connectivity literature (Weersing & Toonen 2011; Whitlock 2011; Cooke *et al.* 2016).

Data collection

A systematic literature search was conducted in Web of Science. Titles, abstracts and keywords of all articles published over a 10 year period (from 2002 to 2012) were searched using the terms: 'phylogeography*', 'population genetic structure*', 'population genetic*' and 'landscape genetic*'. Of the 2206 articles found, 489 papers contained usable geographical information and measured pairwise F_{ST} in vertebrates. From these papers we extracted 1150 data entries, 248 belonging to birds, 426 to fish, 370 to mammals and 108 to reptiles (see PRISMA diagram Figure S1). Two data points were extracted per paper per species, which corresponded to the closest and furthest distances sampled. For each of these entries we collated information on the genetic marker used (mitochondrial DNA or microsatellites), the species studied, the average sample size per population, the F_{ST} value, the geographical distance associated with each F_{ST} calculated, the locomotion mode of each species (swim, fly or walk; the latter included terrestrial crawlers and snakes) and environmental system (terrestrial, marine or freshwater). Most birds were flying species but the flightless cormorant (*Phalacrocorax harrisi*) was classified as a walker and two species of penguin were classified as swimmers (*Megadyptes antipodes* and *Spheniscus humboldti*). All fish in the dataset were considered to be swimmers and classified as either freshwater or marine based on the dominant environment occupied. Mammals included swimmers (such as seals, whales and dolphins), flyers (bats and flying squirrels) and walkers (the majority of species). Reptiles were mostly terrestrial walking species but some were classified as marine or freshwater swimmers (e.g. turtles). All data are available in Figshare https://doi.org/10.6084/m9.figshare.5830887 and 10.6084/m9.figshare.5830878.

Statistical analysis

We began our analyses by assessing the data for potential publication bias. Details of this investigation are provided in full in the Supporting Information (Figure S2). We found no indication that our results were affected by any publication bias. In particular, there was no evidence that the sample size used by a study was associated with the magnitude of reported F_{ST} values, which might implicate potential bias in the likelihood of studies being published (see Supporting Information for details).

For our main analysis, we predicted that genetic differentiation between populations would be higher for those locomotor modes and environmental systems that have greater limits to dispersal, after accounting for covariation with geographical distance. To test this, we used a generalised linear mixed model (GLMM) with genetic differentiation (F_{ST}) as dependent variable, and with locomotor mode and geographical distance as fixed effects, along with their interaction. We also controlled for taxonomic identity by including additional fixed effects of taxonomic group (bird, mammal, reptile or fish; see also below for phylogenetically controlled analyses), as well as the type of genetic marker used in the study (mtDNA or microsatellite), given that the mode of evolution of both markers is different. We did not include information about the specific genes used for mitochondrial markers because the number of overlapping studies was too few to warrant such a focussed analysis. Species name was included as a random factor (since several studies examined the same species: 12 of 440 species corresponding to 23.4% of the data points) and the model was weighted using the average sample size (number of individuals) of populations sampled in each study following Fisher *et al.* 2017 (i.e. studies with larger average sample sizes were given more importance in the model). However, we also present the results of this general model without using this weighting scheme in Table S2 (NB: the general conclusions of our analyses were unchanged and this particular analysis is not discussed further).

As in previous studies (e.g. Emelianov *et al.* 2004), F_{ST} values that were negative were converted to zero (5.4% of the data points; F_{ST} values are expected to lie between 0 and 1, and negative values effectively indicate that population differentiation is negligible; Roesti *et al.* 2012). Given F_{ST} values were bounded between 0 and 1, we used a logit transformation, adding 0.001 to all values to avoid infinity values (Warton & Hui 2011). Models with no phylogenetic correction were implemented using the R package 'lme4' ver 1.1-12 (Bates *et al.* 2015). For all analyses, geographical distance was log-transformed and converted into a *z*-score to decrease heteroskedasticity and improve model convergence.

Phylogenetically controlled analyses

To explore the sensitivity of our results to the underlying phylogenetic relationships among species, we repeated the analysis described above for a subset of taxa for which phylogenetic information was available ($N = 327$ of 440 species, data points = 936 of 1150). Essentially, we built the same GLMM described above but this time it included phylogenetic relationships and species identity as random factors (and excluded taxonomic clade). Details on the methodology of these analyses are provided in the Supporting Information.

We also conducted a third set of analyses exclusively on mammals because this group was the only one to have representatives of all three locomotor modes (swim, fly, walk) and phylogenetic information for most of the species. That is, we expected that the patterns documented across all vertebrates would also be mirrored within mammals. For these analyses, we used the same procedure described above (again see Supporting Information for other details on the associated phylogenetic analyses).

Finally, fish – the largest group of swimmers – were reported to be either freshwater or marine, which effectively corresponded to land-locked or open environments respectively. This provided the opportunity to test whether these habitat types (freshwater vs. marine) played a role in the genetic differentiation of fish, given geographical barriers to dispersal are likely to be higher for land-locked water bodies than open sea. These analyses were independent of locomotor mode (all fish were swimmers) and instead included fixed effects for environmental system (scored as freshwater 'F' or marine 'M'), geographical distance (log z-score), its interaction with environmental system and the genetic marker used (mtDNA or microsatellite). Species name was included as a random effect and weighting schemes by sample size were identical to other models described above with no phylogenetic control. The analysis was also repeated on a subset of taxa for which it was possible to include the phylogenetic relationships of species into the model. However, < 50% of fish species in our dataset were covered by the most comprehensive available phylogeny (Betancur-R *et al.* 2015, $N = 83$ of 172 species, 255 of 426 data points). We present the phylogenetically controlled analysis in the main text, and the analysis on the full dataset in the Supporting Information.

For each GLMM analysis with and without the incorporation of phylogeny, we extracted parameter estimates (slopes) and their associated *P*-values. For analyses with no phylogenetic correction we were also able to extract effect size estimates (*t*-values), and for those that included phylogenetic correction we computed the 95% confidence intervals for estimates and *P*-values across the range of alternate trees considered (see Supporting Information). To graph our results, we used the command 'predictSE' in the 'AICcmodavg' package (Mazerolle 2016) to extract and plot the F_{ST} parameter estimates and associated confidence intervals from each model.

As a last sensitivity test, we replicated some of our analyses using an entirely different approach of converting F_{ST} values into a metric that controls for geographical distance directly in the response variable (the approach developed by Cooke *et al.* 2016). The results of these analyses were consistent to those from the analyses outlined above and are presented in full in the Supporting Information. Given that this method generated an F_{ST} index that effectively removed the effect of geographical distance (β), we used the metric β to explore the extent to which genetic differentiation might be linked to speciation rates within mammals. To this end, we used the software BAMM (Rabosky *et al.* 2014) to calculate speciation rates only within mammals, because this group comprised the three different types of locomotion mode and had the most complete phylogeny. Species coverage is important in this type of analysis because the estimated rate of speciation is highly dependent on the number of species sampled for a group. For mammals, we used the entire Bininda-Emonds *et al.* (2007) phylogeny comprising 4510 extant species that equates to *c.* 83% of all mammalian species (Stadler 2011). We then extracted speciation rate estimates computed for 117 species in our dataset. We repeated the BAMM analysis three times varying the random solution of the polytomies. To explore whether diversification rates were correlated with genetic differentiation, we tested for correlation between log-transformed speciation rates and log-transformed β measure of genetic differentiation. We focussed only on species evaluated with microsatellite markers because this data set was larger than in the subset evaluated with mitochondrial markers. We used STRAPP, a test that accounts for covariance between species and implemented in BAMMtools (Rabosky *et al.* 2014). To complement this analysis we also averaged the speciation rates from the three BAMM analyses and entered this value into a phylogenetic generalised least squares regression [PGLS; (Orme *et al.* 2013)] to test whether higher speciation rates could be explained by locomotion mode and genetic differentiation β, since currently STRAPP cannot deal with categorical variables with more than one level. Other details of the

BAMM analysis are given in the Supporting Information [NB: this analysis should be considered as exploratory because we had to randomly resolve the polytomies in the Bininda-Emonds phylogeny (and assign zero branch lengths to these nodes). This is not trivial, given that the tree is only 46.7% resolved compared to a fully bifurcating tree. This can impact estimated speciation rates across the full tree. We also refer readers to recent discussions of the accuracy of this method for estimating diversification/speciation rates (Meyer & Wiens 2018)]

RESULTS

Geographical distance had a statistically significant, positive association with genetic differentiation in all analyses (Table 1; see also Tables S1–S5). Populations separated by larger geographical distances were those typically estimated to have higher F_{ST} values. Marker type was also a predictor of genetic differentiation, with studies using mitochondrial DNA reporting higher F_{ST} values than those using microsatellites DNA (Table 1 and S1–S5). Taxonomic clade (in the analysis that did not incorporate phylogeny, but had a greater sample size) had an effect on the degree of genetic differentiation across populations (GLMM, $X^2 = 8.67$, *P*-value = 0.035), with birds and fish having lower genetic differentiation than mammals or reptiles.

In addition to the effects of distance and marker type, locomotor mode was a predictor of F_{ST} values, and this was consistent for models applied to all vertebrates, regardless of model specification, sample size, whether phylogeny was incorporated or not and the response variable used (e.g. raw F_{ST} values vs. β) (Table 1a and b; see also Tables S1–S4). For any given distance, species that walk had significantly greater genetic divergence among populations than species that swim and greater divergence than species that fly, depending on the phylogeny (Fig. 1).

Similar patterns were recovered within mammals that had representatives of all three locomotor modes (Table 1c, Fig. 2), although the difference between flying and walking mammals specifically was not statistically significant. This is potentially a reflection of the low number of independent clades that fly within mammals (only bats and one species of flying squirrel), or low statistical power more generally (127 overall of a total of 440 species). In mammals, rates of speciation were higher for flying species than for walking (PGLS estimate = −0.65, $P = 0.03$; Figure S3) and swimming species (PGLS estimate = −1.06, $P = 0.012$; Figure S3), but there was no detectable association between speciation rates and the degree of genetic differentiation (PGLS estimate = 0.206, $P = 0.863$, STRAPP estimate = 0.38, $P = 0.078$).

Within fish, the type of aquatic environment occupied had a detectable effect on genetic differentiation (Table 1d; see also Table S1d) with marine species exhibiting lower differentiation among populations for a given distance than freshwater species (Fig. 3). The same trend was found with the larger sample of the non-phylogenetically controlled analysis (Table S5, Figure S4).

DISCUSSION

Our results show that vertebrates that disperse on land by walking are more likely to diverge genetically over shorter geographical distances than species that fly or swim. This validates, at a major scale (across all vertebrates), what a handful of studies have found within narrow taxonomic groups [kiwi birds – (Baker *et al.* 1995); and beetles – (Ikeda *et al.* 2012)]. It also provides a direct link between the type of locomotion used in dispersal and the likelihood of genetic differentiation occurring among populations. This link implicitly underlies the assumption that a greater variety of geographical features can act as barriers to terrestrial dispersal, resulting in a higher incidence of reproductive isolation among populations on land. This idea has been used to explain why speciation rates are higher on land than in the sea (May & Godfrey 1994; Wiens 2015; see below for further discussion of this putative

Table 1 The effect of locomotor mode and type of environment on the reported genetic differentiation (logit F_{ST}) among populations in (A) all vertebrates with no phylogenetic control, (B) a subset of vertebrates with phylogenetic control, (C) within mammals and (D) within fish with phylogenetic control (only one tree). For models reported in B and C we provide 95% confidence intervals of estimates computed across 100 alternate phylogenetic trees. F: Fly, W: Walk, S: Swim.

	(A) All, no phylogenetic control (440 taxa, 1150 points)			(B) All, phylogenetic control. (327 species, 963 points)		(C) Mammals, phylogenetic control (117 species, 370 points)		(D) Fish, phylogenetic control (83 taxa, 255 points)	
Predictor	Slope GLMM	*t*-value	*P*-value	Slope MCMCglmm	*P*-value	Slope MCMCglmm	*P*-value	Slope MCMCglmm	*P*-value
Locomotion (F vs. W)	−0.827	−1.85	0.063	−1.047 to −0.704	0.042 to 0.162	−0.796 to −0.735	0.117 to −0.184	–	–
Locomotion (S vs. W)	−2.122	−6.31	< 0.0001	−2.067 to −1.919	< 0.001	−2.313 to −2.250	< 0.0001	–	–
Marker	−1.131	−8.26	< 0.0001	−1.094 to −1.067	< 0.001	−1.260 to −1.240	< 0.0001	−0.840	0.012
Distance	0.879	6.69	< 0.0001	0.909 to 0.965	< 0.001	0.811 to 0.826	< 0.0001	0.969	0.001
F * distance	0.033	0.17	0.171	0.093 to 0.142	0.473 to 0.655	0.362 to 0.394	0.111 to 0.180	–	–
S * distance	0.014	0.09	0.094	0.017 to 0.062	0.704 to 0.924	0.09 to 0.124	0.631 to 0.753	–	–
Environment	–	–	–	–	–	–	–	−1.406	0.016
Environment * distance	–	–	–	–	–	–	–	0.056	0.857

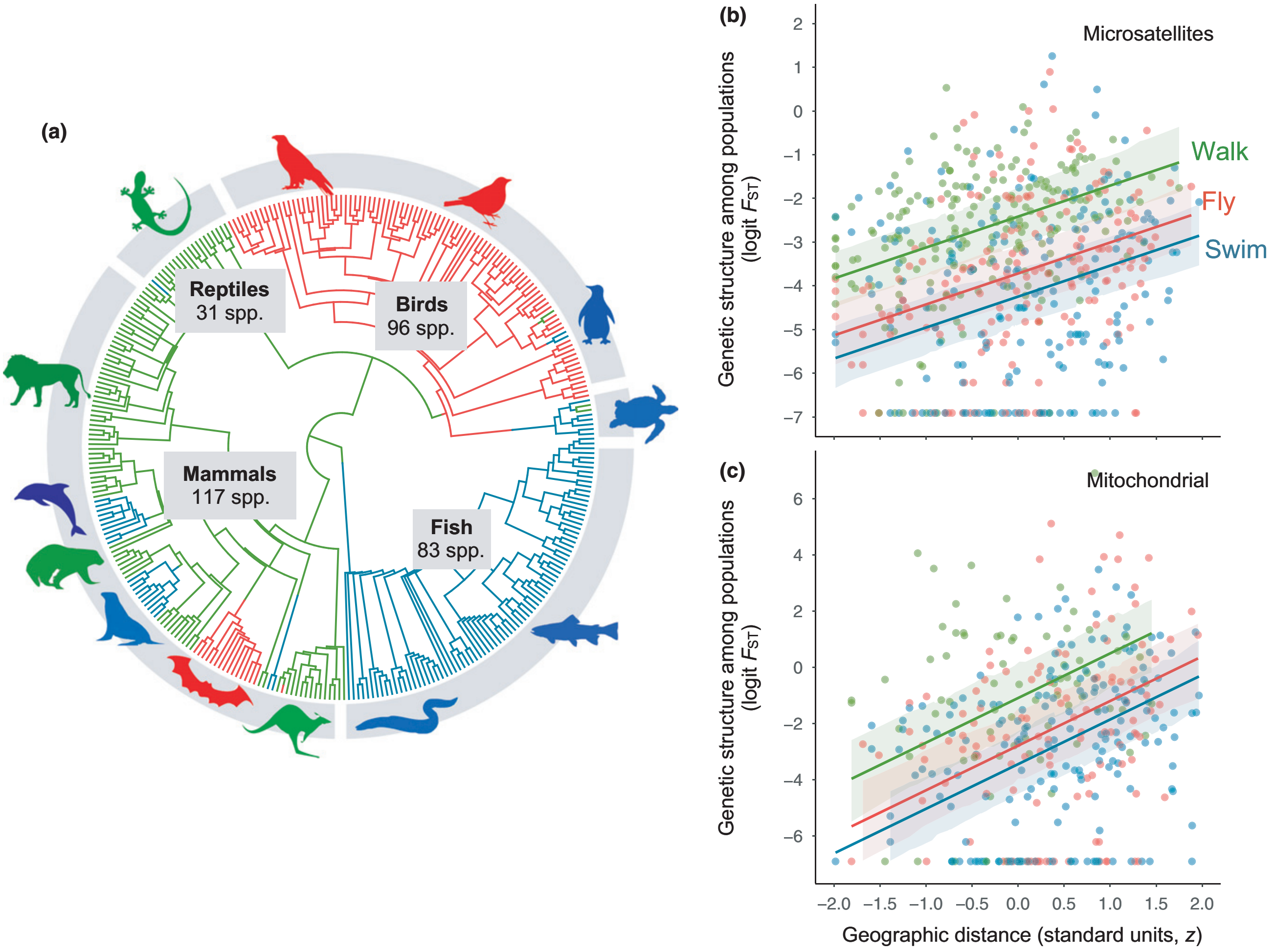

Figure 1 (a) The phylogeny of species included in our analyses ($N = 327$) with colour coding illustrating a representative stochastic mapping of locomotion mode using phytools ver 0.6 (Revell 2012) and a random tree (NB: this mapping was only used for this graphical illustration). Also shown are estimates of genetic differentiation among vertebrate populations as a function of geographical distance and locomotion mode based on (b) microsatellite and (c) mitochondrial markers. Points represent raw data and trend lines were predicted using the model reported in Table 1B, with the shaded bands illustrating upper and lower 95% confidence intervals. For geographical distance, a z-score of 0 corresponds to a distance of 200 km between populations, a value of 1 represents 2000 km and a value of −2 represents 2 km.

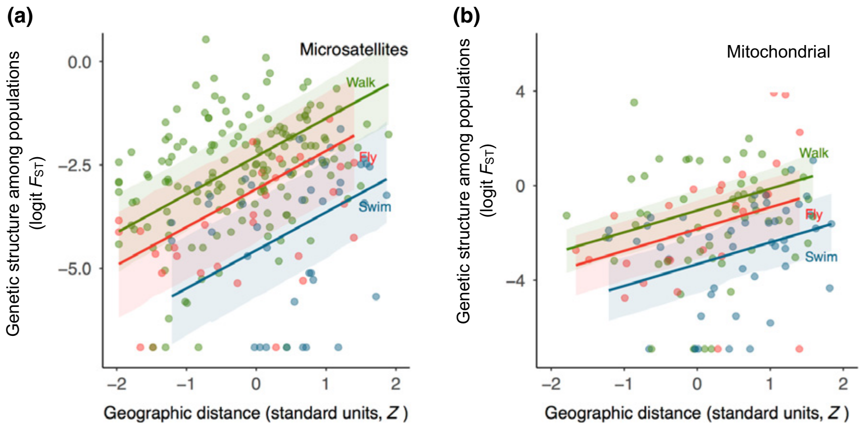

Figure 2 Genetic differentiation among mammal populations as a function of geographical distance and locomotion mode based on (a) microsatellites and (b) mitochondrial markers. Trend lines for locomotor modes were predicted using the model reported in Table 1C. Shaded bands represent upper and lower 95% confidence intervals of trend lines computed from that model. For geographical distance, a z-score of zero corresponds to a distance of 200 km between populations, a value of 1 represents 2000 km and a value of −2 represents 2 km.

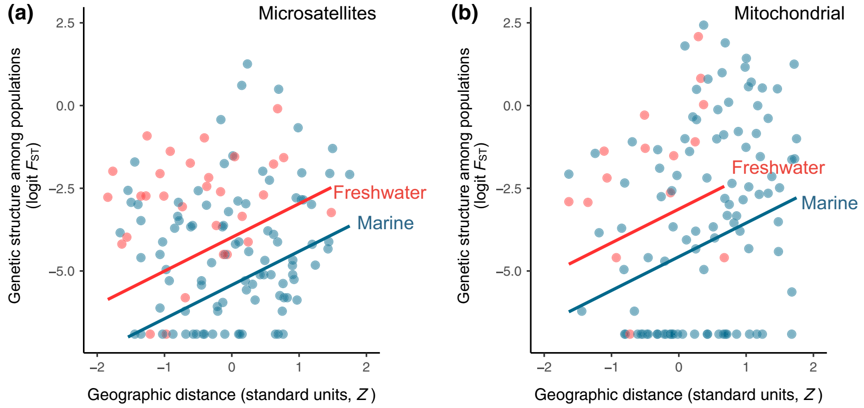

Figure 3 Genetic differentiation among fish populations as a function of geographical distance and environment based on (a) microsatellites and (b) mitochondrial markers. Trend lines for environments modes were predicted using the phylogenetically corrected analysis described in the main text and reported in Table 1D. For geographical distance, a z-score of zero corresponds to a distance of 200 km between populations, a value of 1 represents 2000 km and a value of −2 represents 2 km. 95% confidence intervals are not shown in this case because they are too wide (from −14 to 2 on the *Y*-axis).

link). Our study also clarifies the idea that it is not gross environment type *per se* – land vs. sea – that is key in affecting dispersal ability, rather it is the mode of locomotion used by species. For example flying terrestrial vertebrates have the obvious ability of circumventing many ground-based dispersal barriers (e.g. watercourses, canyons, some mountain ranges), and our analyses generally confirm that flying species tend to have lower levels of population genetic differentiation than those dispersing by walking. Interestingly, the effect of locomotion on genetic differentiation was comparable to the effect size (*t*-value) of geographical distance, highlighting its importance. According to our results, for two populations to reach a statistically significant level of genetic differentiation ($F_{ST} > 0.2$, Supporting Information Figure S5) they would have to be separated by at least 40 km, 500 km or 1500 km depending on whether they walk, fly or swim respectively.

For many years limited dispersal and genetic isolation have been considered an engine of diversification (Wiens *et al.* 2011). Several lineages of flightless insects and birds with poor flying abilities have higher divergence rates among populations, and higher speciation rates (Smith & Farrell 2006; Claramunt *et al.* 2012; Ikeda *et al.* 2012; Weeks & Claramunt 2014). There is also a positive association between genetic differentiation and diversification in some bird groups (Harvey *et al.* 2017). Taken together, we would expect then that species with locomotion modes that are more restrictive to long-range dispersal, and subsequently have higher levels of genetic isolation among populations, should also have higher speciation rates. This is a central assumption of one of the main hypotheses attempting to explain the massive disparity in species richness between sea and land (May & Godfrey 1994; Vermeij & Grosberg 2010). Our results are broadly consistent with this idea: terrestrial walking species exhibited higher genetic differentiation among populations than swimming species. Furthermore, fish occurring in land-locked freshwater systems tended to have higher genetic differentiation than their marine counterparts. Speciation rates of freshwater fish are also higher than in marine fish (Bloom *et al.* 2013). Indeed, *c.* 40% of all fishes in the world occur in freshwater ecosystems despite these environments comprising only 0.01% of Earth (Bloom *et al.* 2013; Mitterboeck *et al.* 2016). In the specific case of freshwater fishes, the apparent effect of dispersal limitation on reproductive isolation could be further accentuated by ecological differences between freshwater and marine environments. For example, freshwater systems might have a greater diversity of ecosystems associated with them (lakes, ponds, rivers, etc.) that may trigger specialisation and further genetic differentiation.

Furthermore, our analyses hinted at similar, additional mechanisms to vicariance potentially prompting population genetic differentiation within other systems as well. Flying (terrestrial) species had lower levels of genetic divergence among populations than species that disperse by walking, which presumably reflects greater connectivity among populations of flying vertebrates. Yet there is compelling evidence that flying vertebrates have high (not low) diversification rates (Alfaro *et al.* 2009; Stadler 2011; Rolland *et al.* 2014a; Rolland & Salamin 2016) and our exploratory analysis within mammals supports this trend. Diversification rates in birds (especially in modern birds, Neoaves) are several orders of magnitude higher than their sister clade, Crocodylians (Alfaro *et al.* 2009). Similarly, bats are the second most diverse order of mammals after rodents and comprise 20% of all mammalian species (Jones *et al.* 2005; Stadler 2011). Therefore, the lower propensity of flying vertebrate populations to genetically diverge from one another (this study) has not evidently decreased speciation rates (apparently to the contrary; see also Alfaro *et al.* 2009; Stadler 2011; Rolland *et al.* 2014a; Rolland & Salamin 2016).

Several studies have shown that long-distance dispersal can actually facilitate diversification (Owens *et al.* 1999; Phillimore *et al.* 2006). Dispersal through flying might increase gene flow among populations (as shown here), but this is potentially counteracted by the increased likelihood of colonising new environments that could promote adaptive divergence among populations of species that fly. On the other hand, increased dispersal ability might also decrease extinction rates by allowing flying species to escape stochastic events or adverse fluctuations in environmental conditions that occur in some areas but not others (Owens *et al.* 1999).

There are other reasons why flying vertebrates might exhibit high rates of speciation, which are not directly linked to dispersal. In bats, coevolution with flowering plants and frugivory have been suggested as important factors leading to high diversification rates (Fauvelot *et al*. 2007). In birds, vocal evolution and its reinforcement of reproductive isolation among populations, the link between strong sexual selection and reproductive isolation more generally, or the evolution of sedentary habits in species that were historically migratory (Rolland *et al*. 2014b; Mason *et al*. 2017) might have all led to increased speciation rates, on average, for the group as a whole. That is, rather than vicariance, broad ecological differences between flying and non-flying species could play a central role in subsequently driving large differences in speciation rates.

Overall, we show that locomotor mode specifically, and environmental system to some extent (freshwater vs. marine systems, not land vs. sea more generally), have important consequences for the genetic connectivity of populations. Our findings support the hypothesis that geographical barriers may increase the likelihood of genetic divergence on land, but this is specific to walking locomotor modes, which helps clarify the mechanistic basis of higher rates of speciation on land than in the sea (Vermeij & Grosberg 2010; Grosberg *et al*. 2012; Wiens 2015). Flying vertebrates on land and fish, however, have lower levels of gene flow among populations, and this presumably reflects an increased ability for long-range dispersal through flying and swimming. Given that flying vertebrates include some of the most speciose groups on the planet (Jones *et al*. 2005; Alfaro *et al*. 2009), this implies ecological speciation via the colonisation of novel environments or speciation through other mechanisms (e.g. sexual selection) could prove to be more important drivers of diversity in flying vertebrates than vicariance alone.

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COMPETING INTERESTS

The authors declare no competing interests.

AUTHORSHIP

T.J.O. and G.C. conceived and designed the study. G.C. collected the data. I.M. analysed the data. I.M. and T.J.O wrote the paper with editorial input from G.C. All authors gave final approval for publication.

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REFERENCES

Alfaro, M.E., Santini, F., Brock, C., Alamillo, H., Dornburg, A., Rabosky, D.L. *et al.* (2009). Nine exceptional radiations plus high turnover explain species diversity in jawed vertebrates. *Proc. Natl Acad. Sci. USA*, 106, 13410–13414.

Baker, A.J., Daugherty, C.H., Colbourne, R. & McLennan, J.L. (1995). Flightless brown kiwis of New Zealand possess extremely subdivided population structure and cryptic species like small mammals. *Proc. Natl Acad. Sci. USA*, 92, 8254–8258.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, 6, 1–48.

Betancur-R, R., Ortí, G. & Pyron, R.A. (2015). Fossil-based comparative analyses reveal ancient marine ancestry erased by extinction in ray-finned fishes. *Ecol. Lett.*, 18, 441–450.

Bininda-Emonds, O.R.P., Cardillo, M., Jones, K.E., MacPhee, R.D.E., Beck, R.M.D., Grenyer, R. *et al.* (2007). The delayed rise of present-day mammals. *Nature*, 446, 507–512.

Bloom, D.D., Weir, J.T., Piller, K.R. & Lovejoy, N.R. (2013). Do freshwater fishes diversify faster than marine fishes? A test using state-dependent diversification analyses and molecular phylogenetics of new world silversides (Atherinopsidae). *Evolution*, 67, 2040–2057.

Bonte, D., Van Dyck, H., Bullock, J.M., Coulon, A., Delgado, M., Gibbs, M. *et al.* (2012). Costs of dispersal. *Biol. Rev.*, 87, 290–312.

Claramunt, S., Derryberry, E.P., Remsen, J.V. & Brumfield, R.T. (2012). High dispersal ability inhibits speciation in a continental radiation of passerine birds. *Proc. Biol. Sci.*, 279, 1567–1574.

Cooke, G.M., Schlub, T.E., Sherwin, W.B. & Ord, T.J. (2016). Understanding the spatial scale of genetic connectivity at sea: unique insights from a land fish and a meta-analysis. *PLoS ONE*, 11, e0150991.

Dawson, M.N. & Hamner, W.M. (2008). A biophysical perspective on dispersal and the geography of evolution in marine and terrestrial systems. *J. R. Soc. Interface*, 5, 135–150.

Emelianov, I., Marec, F. & Mallet, J. (2004). Genomic evidence for divergence with gene flow in host races of the larch budmoth. *Proc. R. Soc. B*, 271, 97–105.

Fauvelot, C., Lemaire, C., Planes, S. & Bonhomme, F. (2007). Inferring gene flow in coral reef fishes from different molecular markers: which loci to trust? *Heredity (Edinb)*, 99, 331–339.

Fish, F.E., Frappell, P.B., Baudinette, R.V. & MacFarlane, P.M. (2001). Energetics of terrestrial locomotion of the platypus Ornithorhynchus anatinus. *J. Exp. Biol.*, 204, 797–803.

Fisher, R.M., Henry, L.M., Cornwallis, C.K., Kiers, E.T. & West, S.T. (2017). The evolution of host-symbiont dependence. *Nat. Commun.*, 8, 1–8.

Grosberg, R.K., Vermeij, G.J. & Wainwright, P.C. (2012). Biodiversity in water and on land. *Curr. Biol.*, 22, R900–R903.

Harvey, M.G., Seeholzer, G.F., Smith, B.T., Rabosky, D.L., Cuervo, A.M. & Brumfield, R.T. (2017). Positive association between population genetic differentiation and speciation rates in New World birds. *Proceedings of the National Academy of Sciences*, 114(24), pp.6328–6333.

Hedrick, P.W. (2005). A standardized genetic differentiation measure. *Evolution*, 59, 1633–1638.

Ikeda, H., Nishikawa, M. & Sota, T. (2012). Loss of flight promotes beetle diversification. *Nat. Commun.*, 3, 1–7.

Jablonski, D. (1986). Larval ecology and macroevolution in marine vertebrates. *Marine Sci.*, 39, 565–587.

Jones, K.E., Bininda-Emonds, O.R.P. & Gittleman, J.L. (2005). Bats, clocks, and rocks: diversification patterns in the chiroptera. *Evolution*, 59, 2243–2255.

Jost, L. (2008). G(ST) and its relatives do not measure differentiation. *Mol. Ecol.*, 17, 4015–4026.

Marko, P.B. (2004). What's larvae got to do with it? Disparate patterns of post-glacial population structure in two benthic marine gastropods with identical dispersal potentia. *Mol. Ecol.*, 13, 597–611.

Mason, N.A., Burns, K.J., Tobias, J.A., Claramunt, S., Seddon, J.M. & Derryberry, E.P. (2017). Song evolution, speciation, and vocal learning in passerine birds. *Evolution*, 71, 786–796.

May, R.M. & Godfrey, J. (1994). Biological diversity: differences between land and sea [and discussion]. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 343, 105–111.

Mazerolle, M.J. (2016). AICcmodavg: Model selection and multimodel inference based on (Q) AIC(c). (ed. 2.1-0, Rav).

Meyer, A.L.S. & Wiens, J.J. (2018). Estimating diversification rates for higher taxa: BAMM can give problematic estimates of rates and rate shifts. *Evolution*, 72, 39–53.

Mitterboeck, T.F., Chen, A.Y., Zaheer, O.A. & Ma, E.Y.T. (2016). Do saline taxa evolve faster? Comparing relative rates of molecular evolution between freshwater and marine eukaryotes. *Evolution*, 70, 1960–1978.

Orme, D., Freckleton, R., Thomas, G.H., Petzoldt, T., Fritz, S., Isaac, N. *et al*. (2013). caper: Comparative analyses of phylogenetics and evolution in R. (ed. https://cran.r-project.org/package=caper, Rpv).

Owens, I.P.F., Bennet, P.M. & Harvey, P.H. (1999). Species richness among birds: body size, life history, sexual selection and ecology? *Proc. R. Soc. B*, 266, 933–939.

Palumbi, S.R. (1994). Genetic divergence, reproductive isolation, and marine speciation. *Annu. Rev. Ecol. Syst*., 25, 547–572.

Phillimore, A.B., Freckleton, R.P., Orme, C.D.L. & Owens, I.P.F. (2006). Ecology predicts large-scale patterns of phylogenetic diversification in birds. *Am. Nat*., 168, 220–229.

Puebla, O., Bermingham, E. & McMillan, W.O. (2012). On the spatial scale of dispersal in coral reef. *Mol. Ecol*., 21, 5675–5688.

Rabosky, D.L., Grundler, M., Anderson, C., Title, P., Shi, J.J., Brown, J.W. *et al*. (2014). BAMMtools: an R package for the analysis of evolutionary dynamics on phylogenetic trees. *Methods Ecol. Evol*., 5, 701–707.

Revell, L.J. (2012). phytools: an R package for phylogenetic comparative biology (and other things). *Methods Ecol. Evol*., 3, 217–223.

Riginos, C., Buckley, Y.M., Blomberg, S.P. & Treml, E.A. (2014). Dispersal capacity predicts both population genetic structure and species richness in reef fishes. *Am. Nat*., 184, 52–64.

Roesti, M., Salzburger, W. & Berner, D. (2012). Uninformative polymorphisms bias genome scans for signatures of selection. *BMC Evol. Biol*., 12, 1–7.

Rolland, J. & Salamin, N. (2016). Niche width impacts vertebrate diversification. *Glob. Ecol. Biogeogr*., 25, 1252–1263.

Rolland, J., Condamine, F.L., Jiguet, F. & Morlon, H. (2014a). Faster speciation and reduced extinction in the tropics contribute to the mammalian latidudinal diversity gradient. *PLoS Biol*., 12, e1001775.

Rolland, J., Jiguet, F., Jonsson, K.A., Condamine, F.L. & Morlon, H. (2014b). Settling down of seasonal migrants promotes bird diversification. *Proc. R. Soc. B*, 281, 1–9.

Rousset, F. (1997). Genetic differentiation and estimation of gene flow from F-statistics under isolation by distance. *Genetics*, 145, 1219–1228.

Selkoe, K.A. & Toonen, R.J. (2011). Marine connectivity: a new look at pelagic larval duration and genetic metrics of dispersal. *Mar. Ecol. Prog. Ser*., 436, 291–305.

Shafer, A.B.A. & Wolf, J.B.W. (2013). Widespread evidence for incipient ecological speciation: a meta-analysis of isolation-by-ecology. *Ecol. Lett*., 16, 940–950.

Slatkin, M. (1987). Gene flow and the geographic structure of natural populations. *Science*, 236, 787–792.

Smith, C.I. & Farrell, B.D. (2006). Evolutionary consequences of dispersal ability in cactus-feeding insects. *Genetica*, 126, 323–334.

Stadler, T. (2011). Mammalian phylogeny reveals recent diversification rate shifts. *Proc. Natl Acad. Sci. USA*, 108, 6187–6192.

Vermeij, G.J. & Grosberg, R.K. (2010). The great divergence: when did diversity on land exceed that in the sea? *Integr. Comp. Biol*., 50, 675–682.

Warton, D.I. & Hui, F.K. (2011). The arcsine is asinine: the analysis of proportions in ecology. *Ecology*, 92, 3–10.

Weeks, B.C. & Claramunt, S. (2014). Dispersal has inhibited avian diversification in Australasian achipelagoes. *Proc. Biol. Sci*., 281, 20141257.

Weersing, K. & Toonen, R.J. (2011). Population genetics, larval dispersal, and connectivity in marine systems. *Mar. Ecol. Prog. Ser*., 436, 291–305.

Wessel, A., Hoch, H., Asche, M., von Rintelen, T., Stelbrink, B., Heck, V. *et al*. (2013). Founder effects initiated rapid species radiation in Hawaiian cave planthoppers. *Proc. Natl Acad. Sci. USA*, 110, 9391–9396.

Whitlock, M.C. (2011). Gst and D do not replace Fst. *Mol. Ecol*., 20, 1083–1091.

Wiens, J.J. (2015). Faster diversification on land than sea helps explain global biodiversity patterns among habitats and animal phyla. *Ecol. Lett*., 18, 1234–1241.

Wiens, J., Xa, J. & Dykhuizen, D. (2011). The causes of species richness patterns across space, time, and clades and the role of ecological limits. *Q. Rev. Biol*., 86, 75–96.

Wright, S. (1931). Evolution in Mendelian populations. *Genetics*, 16, 97–159.

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