Gene Flow in Volant Vertebrates: Species Biology, Ecology and Climate Change

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Abstract | Gene flow, the exchange of genetic material between populations is an important biological process, which shapes and maintains biodiversity. The successful movement of individuals between populations depends on multiple factors determined by species biology and the environment. One of the most important factors regulating gene flow is the ability to move, and flight allows individuals to easily move across geographical barriers. Volant vertebrates are found on some of the remotest islands and contribute significantly to the biodiversity and ecosystem. The availability of next-generation sequencing data for non-model animals has substantially improved our understanding of gene flow and its consequences, allowing us to look at fine-scale patterns. However, most of our understanding regarding gene flow comes from the temperate regions and the Neotropics. The lack of studies from species-rich Asia is striking. In this review, we outline the importance of gene flow and the factors affecting gene flow, especially for volant vertebrates. We especially discuss research studies from tropical biomes of South and Southeast Asia, highlight the lacuna in literature and provide an outline for future studies in this species-rich region.

Keywords: Bats, Birds, Gene flow, South Asia, Southeast Asia; Volant vertebrates

1 Introduction
Gene flow is the movement of individuals/genes between populations 74, 75. It allows for genetic exchange and connectedness between populations thereby countering the diversifying effects of genetic drift, mutation and selection 72, 74, 75. Gene flow is, therefore, necessary to maintain the potential for the evolution of a species by regulating its genetic diversity 21. Often considered as a restraining force, gene flow can on one hand nullify population differentiation or local adaption patterns, and on the other hand acts as an active evolutionary force leading to the spread of adaptive/novel genes between populations 22, 75. Genetic exchange is particularly critical for the survival of insular and endangered populations/species thereby making it one of the most important component for conservation programs 21. However, the lack of gene flow not only endangers survival but can also act as an active agent for speciation, both across an evolutionary time scale wherein a gradual decrease of genetic connectivity slowly segregates isolated populations which eventually forms new species, and also across ecological timescale wherein ecological adaptation can swiftly act upon isolated populations segregating them into distinct species 59, 75, for exceptions see 37, 38.

While allowing for the exchange of alleles, gene flow in natural populations increase genetic variability and connects not only geographically isolated populations but also evolutionary divergent species-level lineages 28, 44, 83. The process of successful reproduction between two species is known as hybridization and the process of introduction of novel genetic material from one species to another when fertile hybrids successfully mate with either one or both of the parent species is known as introgression 44, 69. Contingent upon species history and environment, divergent speciation, both across an evolutionary time scale wherein a gradual decrease of genetic connectivity slowly segregates isolated populations which eventually forms new species, and also across ecological timescale wherein ecological adaptation can swiftly act upon isolated populations segregating them into distinct species 59, 75, for exceptions see 37, 38.

Hybridization: successful reproduction and exchange of genetic material between two species.

Introgression: incorporation of genetic material of one species to another through the process of hybridization and backcrossing.
Hybrid zone: area of overlap between two species where both genetically pure, hybrids and introgressed individuals can be observed.

lineages can come in secondary contact thereby exchanging genetic material and forming hybrid zones. Hybrid zones play a significant role in speciation dynamics. They provide the only natural settings to test reproductive barriers between closely related sympatric lineages. At times, hybrids upon the effect of natural selection can also evolve into distinct species (hybrid species) thereby enhancing biodiversity. In general, hybridization and introgression in hybrid zones is generally a pervasive force leading to homogenization and loss of differences between species and blurring species boundaries. However, on the other hand, introgression can be also beneficial through the introduction of novel variation in a species, like cases of adaptive introgression of red wing pattern genes from Heliconius melpomene into H. cydno, introgression of pesticide resistance genes from Anopheles gambiae into A. coluzzii; and introgression of rodent poison resistance from Mus spretus to Mus musculus. In extreme circumstances, introgression from invasive species can also replace and deplete the genetic diversity of the native biota thereby endangering biodiversity. For example, in the North American hybrid zones where the closely related golden-winged and blue-winged warblers frequently mate and hybridize, the golden-winged warblers experience genomic invasion from the blue-winged warblers, concomitant range contractions, and endangerment. Although previously considered uncommon in animals, the past two decades have seen an enormous rise in the number of publications documenting introgression in all major branches of the tree of life, especially with the application of next-generation sequencing (NGS) data.

Most of our understanding about gene flow and its effects come from studies of natural populations from the temperate regions and the Neotropics. However, the highly heterogeneous landscape of tropical South and Southeast Asia comprising some of the most species-rich regions, multiple biodiversity hotspots, and home to major biogeographic barriers, form the perfect settings to discuss the evolutionary significance of gene flow in shaping biotic diversity. Hence a comprehensive review of the current status of the gene flow research in this region is necessary. South and Southeast Asia are also home to an intricate network of island systems which are engines of biotic diversification and provide a natural laboratory to test various evolutionary theories. In the following sections we will discuss the importance of gene flow in shaping the current biodiversity, and examine various factors that affect gene flow in the wild, with a greater emphasis on studies from island systems and complex habitats. Throughout the review, we attempt to highlight examples from South and Southeast Asia. However, such case studies are scant compared to studies from the Neotropics or from the Northern hemisphere. While lack of generous funding is a major hurdle in South and Southeast Asia, difficulty in obtaining necessary permits is another major limiting factor contributing to the lack of progress in gene flow research in this region. Only a few research groups have been able to establish long-term and dedicated monitoring projects, which are necessary to address evolutionary questions. Further, many areas are not accessible due to either difficult terrain or conflict. It is necessary to establish long-term collaborative projects, build capacity by training local researchers and implement successful technology transfers to establish long-term gene-flow-based research programs in this biodiverse region. For the purposes of the current review, owing to the paucity of available literature from South and Southeast Asia, case studies from the Neotropics and temperate regions are also discussed to highlight recent advancements in our overall understanding of the causes and consequences of gene flow.

2 Volant Vertebrates and Gene Flow

Owing to their capability to fly, volant vertebrates can traverse great distances, colonise distant islands, cross steep environmental gradients, and thus forms an important study system to understand the evolutionary contingents of gene flow across complex landscapes. Volant vertebrates are ubiquitous and present in virtually every habitat. They are species-rich groups with high biodiversity and are important bioindicators. For example, the number of birds in a breeding area can indicate the productivity and habitat quality of the region. Similarly, insect bat diversity and abundance are directly correlated to arthropod diversity. They are keystone species playing an important role in pollination, seed dispersal, and pest management. Both birds and bats are endotherms and face similar selection pressures on their morphology and physiological traits due to their ability to fly. Miniaturization of body size, prolonged lifespan, smaller but effective digestive tract, high metabolic rate and antioxidant capacity, smaller genomes are some of the common traits observed in both birds and bats.
However, some differences also exist, like birds tend to live longer for their body size, even compared to bats. Both birds and bats are significant carriers of viruses of zoonotic potential, however, birds tend to have lower viral loads. Birds also differ in their immune response in general compared to mammals, however, both birds and bats are generally tolerant to viruses and hence are able to co-exist with multiple potentially pathogenic viruses and references therein. Given the high load of viruses in both birds and bats, it is important to understand the patterns of gene flow in volant vertebrates due to their ability to move long distances and potential to spread viruses across remote landscapes. Bats are one of the most important mammalian reservoirs of RNA viruses and have been implicated in multiple zoonotic outbreaks like SARS (severe acute respiratory syndrome), MERS (Middle East respiratory syndrome), Nipah and Hendra to name a few. Similarly, birds are associated with zoonotic diseases like avian flu, psittacosis, salmonellosis among others. They can easily transfer viruses over large distances and potentially infect healthy populations. Hence a thorough understanding of the evolutionary contingents of gene flow in these animals can also help us to understand its role in host–pathogen coevolution. We will specifically review the volant vertebrate literature, present recent advances in our understanding of patterns of gene flow with the availability of large scale genomic data from non-model organisms, highlight the bias and lacunae in the current literature and propose future directions of the study of gene flow in volant vertebrates across complex landscapes.

3 Quantifying Gene Flow in Natural Populations

It should be noted that gene flow and dispersal are not the same and gene flow assumes that the individual that has dispersed to a new population successfully reproduces and is able to contribute to the gene pool of the next generation. Both protein and nucleic acids can be used as genetic markers to quantify gene flow. DNA based markers such as microsatellite, single nucleotide variation (SNPs), sequence data tend to work better than protein makers due to their high resolution. With the advent of NGS platform for non-model organisms, we have gained unprecedented power in quantifying gene flow levels in natural populations. Gene flow can be quantified using direct and indirect methods. Direct methods involve...
**Figure 1:** Differential pattern of gene flow based on life-history in many volant vertebrates. 

- **a** higher levels of gene flow can be observed in canopy birds compared to understory birds, and 
- **b** higher levels of gene flow can be observed in frugivores compared to insectivores. Black arrows depict higher levels of gene flow in comparison to grey arrows. Clipart were obtained from [http://clipart-library.com](http://clipart-library.com)

**Figure 2:** Map depicting the current coast line of South and Southeast Asia shown in dark grey and emergent landmass shown in light grey, when the sea level drops by 120 m during periods of global cooling. Formation of land bridges during the periods of glacial maxima and climate cooling facilitated movement of both terrestrial and volant vertebrates between isolated landmasses. Map was reproduced and modified with permission from Voris [86] from Field Museum, Chicago, USA. Clipart were obtained from [http://clipart-library.com](http://clipart-library.com)
inconsequential for larger bats, which were able to fly across oceanic barriers. Interestingly, the correlation between body size and dispersal ability in birds is low. Migratory behaviour in polar birds is strongly correlated with hand-wing index (HWI), an estimate of wing-tip pointedness. Tropical bird species tend to be sedentary in nature compared to the species in the polar regions, due to low variation in breeding territories and high resources. Mode of locomotion is also an important attribute that affects gene flow as it determines the dispersal distance, and thus the levels of genetic connectivity. For example, terrestrial species will be less mobile compared to species that can fly. Volant vertebrates may find it easier to cross certain barriers like rivers, bad habitat, roads etc. and a comparison of genetic differentiation across 400 vertebrates, confirmed this pattern that species with high vagility and mobility tend to have low levels of genetic differentiation. Due to their flight ability, bats are the only native land mammals from islands of New Zealand, Hawaii and other Pacific islands. However, even for volant vertebrates, species biology remains a strong determinant of the ability to move great distances and cross biogeographic barriers. Birds and bats often reveal this effect while travelling to distant landmasses, across environmental clines or crossing biogeographic barriers. For example, in a comparative study of genetic connectivity in bats and rodents from Philippines, the rodents showed high differentiation and low genetic connectivity similar to the forest-dependent bat species (habitat specialists), whereas bats living in disturbed habitats (generalists) were easily able to cross the oceanic barriers. Even when there are no physical barriers to gene flow, distance can become an important factor determining population subdivision and isolation. Genetic break in connectivity is observed over large distances as in the case of short-nosed fruit bat, with populations from Southern India being isolated from Eastern India.

At the microgeographic level, social structure and mating system determines the movement between social groups and populations. Sex-biased dispersal is observed in many animals and is driven by the mating system. For example, in monogamous birds, female-biased sex dispersal is observed whereas in polygynous territorial mammals (including volant mammals), generally males leave their natal sites to establish new breeding territories. Although, dispersal is a costly strategy, exposing the migrants to multiple risks like predation, starvation, aggression, etc., it is a common phenomenon across the tree of life. The cost associated with dispersal is offset by multiple benefits that can be acquired by the dispersing individuals. For example, sex-biased dispersal can help in countering the ill effects of genetic drift and avoid competition for resources. Dispersal distance in great tit was inversely related to inbreeding, with individuals dispersing short distance exhibiting higher levels of inbreeding. In bats, male-biased dispersal reduces the ill effects of inbreeding in Bechstein’s bat by allowing genetic exchange between populations. In many species of bats, females are philopatric and form large maternal colonies. Although, most females within these maternal colonies are related, overall population relatedness is close to zero, possibly due to male-biased dispersal.

Another important factor determining genetic connectivity is species ecology and niche preference. Generalist species are able to move across poor habitat, whereas this may be an impediment for niche specialists. In spite of their ability to fly, this pattern is also observed in volant vertebrates. For example, in Amazonian birds, floodplain and forest edge species populations were homogeneous compared to upland forest species. Low levels of gene flow and population divergence were observed in forest species. Similarly, canopy birds were easily able to cross across barriers, while forest species were restricted in their movement. Volant mammals too follow these general patterns of population subdivision. Low levels of population structure are expected in bats due to the ability to fly, especially in migratory species of bats low levels of population subdivision is observed in comparison to non-migratory species due to the ability to move long distances. For example, haplotype sharing was observed over 2800 km in the migratory southern long-nosed bat. Similarly, small cave roosting bats from Andaman islands exhibit population subdivision, however, the large frugivores bats were able to move across islands and display no population subdivision.

### 4.2 Climate and Habitat Fragmentation

At the macrogeographic level, gene flow between geographically isolated populations is determined by both habitat and earth climatic history. Paleo climate has played a key role in shaping the current biotic diversity. For the past 2.6 million years, earth has undergone multiple cooling and warming cycles. Known as the Quaternary, this period has led to episodic...
isolation and connectivity between natural populations leading to the gradual divergence of many taxa across the globe \[30, 31\]. In the temperate latitudes and high-altitude mountain ranges, glaciers and ice sheets expand during periods of climatic cooling covering continental landmasses in temperate regions with ice sheets, and leaving little pockets of suitable habitable environmental conditions for biotic survival \[30, 31\]. Distribution ranges of many animals shrink and are largely confined into refugia in the southern latitudes, leading to isolation and speciation in many cases \[30, 31\]. The number and quality of corridors largely characterizes the extent of connectivity between refugial populations contingent of species biology and ecology. For example, many species in Europe were restricted to few pockets of suitable habitat in the Iberian Peninsula, Italy, and the Balkans during the Last Glacial Period \[30\]. Only once the ice retreated, the rest of Europe was recolonized. General patterns of colonization can be drawn based on the area of glacial refugia. For example, the Balkans was an important refugia and contributed significantly to the current diversity of Eastern as well as Western Europe \[30\].

The Alps and Pyrenees mountain ranges continued to act as barriers to the movement of animals out of Italy to northern Europe even when suitable habitat became available during the warmer periods \[30, 31\]. Similarly, during periods of climatic cooling, in higher altitude mountain ranges ice caps form and ice sheets extend to lower altitudes, again pushing high altitude specialists into local pockets of refugia along the ice-free valleys, and shifting biotic communities to lower altitudes, allowing for genetic exchange between otherwise isolated montane populations \[30, 31\]. On one hand, such events of episodic isolation may eventually lead to speciation, on the other hand, secondary contacts of closely related species in glacial refugia often lead to hybridization while also playing a critical role in strengthening species barriers through reinforcement and character displacement. For example, in the case of the tyrant flycatchers in the Andes, population differentiation between lineages was reinforced during the last interglacial period, when isolated montane populations came in contact due to a shift in habitat \[10\].

Effect of the Quaternary glacial cycles are also observed in the species-rich tropics, wherein during the glacial periods, the sea level drops as most of the sea water gets locked up as ice, allowing for land connectivity (Fig. 2) \[3\]. The formation of land bridges enables the movement of individuals between populations across isolated landmasses leading to the homogenization of the gene pool \[23\]. Depending on the species biology these land bridges act as semipermeable conduits of gene flow \[22\]. For example, many bulbuls which can move across large distances in search for fruiting trees were able to utilize these Pleistocene land bridges but the same was not observed for insectivorous understory babblers which are comparatively sedentary in nature (Figs. 1b and 2) \[14\]. Similarly, in the satellite islands of Sulawesi, Peleng and Taliabu, forest-dependent bird species rarely utilized these land bridges to move between isolated island populations leading to genetic diversification and speciation, whereas edge tolerant species were able to move across the land bridges thereby retaining genetic connectivity and resisting genetic differentiation \[23\].

In addition to historical habitat changes, more recent alterations owing to human influences have proven to be a major barrier for animal movement thus hindering genetic connectivity between populations leading to inbreeding and heightened risk of extirpation. With the current climate crisis and the lightning speed of urbanization, species are now facing unprecedented habitat loss and genetic isolation that they have not faced in their evolutionary history. For example, highways prevent movement and gene flow between populations of desert bighorn sheep in the California and have led to around 15% decline in genetic diversity in only 40 years \[18\]. Similarly, simulation studies have suggested the importance of gene flow in maintaining current genetic diversity in tigers for the next 150 years \[2\]. In the absence of gene flow, within 25 years, even the large diverse populations of Tigers from Western Ghats will lose genetic diversity at an unprecedented rate due to genetic drift \[2\]. Even volant vertebrates are not immune to habitat destruction and lack of gene flow and loss of genetic diversity is observed. Genetic differentiation, due to habitat destruction was observed in insectivores birds in the island of Singapore \[15\]. Due to habitat destruction, forest-dependent understorey birds are unable to move between forest patches \[15\]. Similarly, in the Sholas of the Western Ghats, habitat loss has prevented the endemic White-bellied Shortwings from moving across recently fragmented habitats \[71\]. Even differences in song were observed between two patches, suggesting growing isolation and population differentiation \[71\]. Similar results were also observed in bats in disturbed landscapes in the neotropics \[30\]. However, we have only now started to understand the patterns of habitat fragmentation across
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Gene flow as an Agent of Spread of Infectious Diseases

The past two decades have witnessed a surge in the emergence of numerous infectious diseases in natural populations, which are further exacerbated with the threat of present climate change brought about by human activities. Emerging infectious diseases can have devastating effect on species demography, cause population fragmentation, population subdivision, isolation, and even extirpation. The effect of infectious diseases on gene flow is similar to habitat destruction and the spread of and co-evolution of host/pathogens are tightly linked with gene flow potential. Species with higher levels of gene flow tend to have higher genetic diversity and evolutionary potential to respond to changing selection pressures. An increase in levels of gene flow can bring in the necessary genetic variability required for selection to act upon and allow for emergence of pathogen resistance within the populations and references therein). However, high levels of gene flow can also lead to the spread of the infectious diseases across susceptible and uninfected populations. Introduction of *Pseudogymnoascus destructans*, a fungus that causes white-nose syndrome in bats from Eurasia to North America, led to one of the worst infectious disease outbreaks in recent times and decimated millions of bats in just a few years. While the European bats were resistant to the fungus, the North American bats were highly susceptible and high levels of gene flow allowed the fungus to spread across North America and Canada. Similarly, pathogenic strains of avian influenza can be carried across the globe by migratory birds. Highly pathogenic avian influenza subtype H5N8 outbreak occurred in South Korea in 2013–2014, which later spread to Japan, Europe, and North America most likely by long-distant migratory water birds. Thus high levels of gene flow can also be harmful to the species. South and Southeast Asia are a hot-bed for emerging infectious diseases, particularly zoonotic infections. However, work on the spread of infectious diseases in this region has only beginning to take shape and a major push in this area is necessary, especially given how the current pandemic has panned out.

Gene Flow and Islands as Drivers of Biodiversity

Island systems serve as the most interesting model to study gene flow. Although, islands tend to be species poor in comparison to continental land-masses, they are engines of diversification and...
contribute disproportionately to species biodiversity compared to the area they cover 70, 90. Species richness on islands is dependent on the size of the island, distance to mainland 43. Species composition on islands is a balance between immigration, extinction and speciation 40, 43, 90. Further, the Quaternary glacial cycles contribute disproportionately to the biodiversity of islands 88. Islands, acting as isolated landmasses surrounded by large mass of water impedes gene flow between not only terrestrial life forms but also between freshwater aquatic organisms.

Terrestrial animals find it difficult to cross the oceanic barriers in comparison to volant vertebrates. Thus rate of immigration and distance to the nearest mainland becomes an important factor determining species composition 43, 90. Further, land bridges formed during the Quaternary glacial maxima allow for terrestrial biota to occupy remote islands (Fig. 2) 23, 88. For example, the presence of large mammals like rhinoceros, orangutans, and elephants on the isolated island of Borneo, suggests that these land bridges may have played a role in the movement of these animals from continent to islands 19, 47, 57. However, it is easier for vagile animals to occupy remote islands 20, 29. Thus many remote islands are generally inhabited by volant vertebrates. The ability to fly, allows for genetic connectivity between isolated populations and reduces genetic differentiation across the barrier, especially during the cooling periods of the glacial cycle 72. Earth-historic factors play an important role in periodic connectivity and isolation between such isolated landmasses 30, 31. Within continental landmasses, climate change can expand or contract favourable habitats thereby controlling the extent of genetic connectivity between populations of habitat specialists 10. Over the course of time, these events increase population differentiation, ultimately leading to speciation or conversely wipe out any differentiation that may have built up over time, depending on the species requirements. In the Western Ghats, comparison of bird community across the sky islands in the Ghats, suggests that only a few species were affected by the Palghat Gap, a natural gap in the Western Ghats mountain ranges. More than half the species of birds showed no differentiation across the Palghat Gap, suggesting possible movement of montane birds across the barrier, especially during the cooling periods of the glacial cycle 72.

7 More Markers Bring Better Resolution: Genomic Revolution in Gene Flow of Volant Vertebrates

The ease of availability of the ever-growing repository of genomic data for non-model species obtained from NGS platforms has exponentially increased our knowledge about the effects of dispersal and gene flow 77. With the availability of thousands of genome-wide markers, it is now possible to acquire a complete picture of the genomic changes that occur due to gene flow. The power in detecting and quantifying levels and timing of gene flow has dramatically improved 77. For example, results based on a handful of genetic markers suggested gene flow between two species of fruit bats in Southern India, but an investigation with thousands of
genome-wide markers this signal disappeared highlighting the lack of power of fewer markers to correctly identify gene flow. Further, this same panel of genome-wide markers could also identify a cryptic species of fruit bat from Eastern India and discovered a hybrid zone between two species-level lineages with evidence of gene flow and introgression. NGS data has also helped in identifying various barriers to gene flow like physical features of the Earth (e.g. rivers and oceans) as well as species attributes (e.g. habitat preferences). For instance, unexpected fine-scale populations structure was revealed in forest-dependent birds within a small forested region of the island nation of Singapore when thousands of genomic markers were used. Although, we have made great progress in utilizing NGS data for volant vertebrates, our knowledge is still in its infancy especially for bats, where only a handful of studies exist. Future studies need to incorporate new technological advancements in addressing pertinent questions regarding speciation and gene flow.

8 Take-Home Message and Future Directions
Gene flow is a potent evolutionary force that improves genetic diversity, affects speciation, and plays a significant role in shaping biotic diversity. Gene flow is governed by the interplay of species history, biology, ecology as well as the environment. Volant vertebrates reveal similar trends as terrestrial animals, however owing to their ability to fly, the extent of gene flow may be higher in them thereby helping them to act as great dispersers and colonizers across remote and diverse landscapes. In this review, we have highlighted some of the important research on gene flow that has been carried out in South and Southeast Asia. Among volant vertebrates, most of our understanding of various evolutionary process and theories are based on extensive work on birds. However, bats being the only group of true volant mammals provide a unique system to understand selection, dispersal and adaptation. They are the second most specious group of mammals and are excellent bioindicators, but are comparatively less represented in research investigations targeting gene flow in natural populations. While few studies have utilized NGS data to understand gene flow and speciation in bats and birds, extensive efforts in the near future are necessary to develop general models of diversification and differentiation of volant vertebrates in the Indian subcontinent in general and bats in particular. In addition, most studies from the subcontinent report species-specific patterns of gene flow, necessitating future research programs targeting community-wide patterns of gene flow in this region. Going forward, such community-wide investigations would play a pivotal role in shaping our understanding of large-scale patterns of population structure and gene flow in natural populations of volant vertebrates.

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Conflict of Interest
On behalf of all authors, the corresponding author states that there is no conflict of interest.

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References
1. Anderson SH, Kelly D, Robertson AW, Ladley JJ (2016) Pollination by Birds: a functional analysis. In: Sekercioglu CJ (ed) Why birds matter: Avian ecological function and ecosystem services. University of Chicago Press, Chicago, pp 73–106
2. Bay RA, Ramakrishnan U, Hadly EA (2014) A call for tiger management using “reserves” of genetic diversity. J Hered 105(3):295–302
3. Bintanja R, Van De Wal RS, Oerlemans J (2005) Modelled atmospheric temperatures and global sea levels over the past million years. Nature 437(7055):125128
4. Bock CE, Jones ZF (2004) Avian habitat evaluation: should counting birds count? Front Ecol Environ 2(8):403–410
5. Bohonak AJ (1999) Dispersal, gene flow, and population structure. Q Rev Biol 74(1):21–45
6. Burger J, Gochfeld M (2004) Marine birds as sentinels of environmental pollution. EcoHealth 1(3):263–274
7. Burney CW, Brumfield RT (2009) Ecology predicts levels of genetic differentiation in Neotropical birds. Am Nat 174(3):358–368
8. Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. Proc Natl Acad Sci USA 114(30):E6089–E6096
9. Chakravarty R, Chattopadhyay B, Ramakrishnan U, Sivasundar A (2018) Comparative population structure in species of bats differing in ecology and morphology in the Andaman Islands India. Acta Chiropterol 20(1):85–98
10. Chattopadhyay B, Garg KM, Kumar AV, Doss DPS, Rheeindt FE, Kandula S et al (2016) Genome-wide data reveal cryptic diversity and genetic introgression in an Oriental cynopterine fruit bat radiation. BMC Evol Biol 16(1):1
11. Chuno Al (2014) Hybridization in a warmer world. Ecol Evol 4(10):2019–2031
12. Corlett RT (2015) The Anthropocene concept in ecology and conservation. Trends Ecol Evol 30(1):36–41
13. Cros E, Chattopadhyay B, Garg KM, Ng NS, Tomassi S, Benedick S et al (2020) Quaternary land bridges have not been universal conduits of gene flow. Mol Ecol 29(14):2692–2706
14. Diamond JM, Gilpin ME, Mayr E (1976) Species-distance relations in birds of the Solomon Archipelago, and the nature of species boundaries. J Hered 67(1):1–18
15. Epps CW, Palsbøll PJ, Wehausen JD, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecol Lett 8(10):1029–1038
16. Fernando P, Vidya TC, Payne J, Stuewe M, Davison G, Alfred RJ et al (2003) DNA analysis indicates that Asian elephants are native to Borneo and are therefore a high priority for conservation. PLoS Biol 1(1):e6
17. Fleming TH, Racey PA (2010) Island bats: evolution, ecology, and conservation. University of Chicago Press, Chicago
18. Frankham R (2015) Genetic rescue of small inbred populations: Meta-analysis reveals large and consistent benefits of gene flow. Mol Ecol 24(11):2610–2618
19. Garant D, Forde SE, Hendry AP (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. Funct Ecol 21:434–443
20. Garg KM, Chattopadhyay B, Wilton PR, Prawiradilaga DM, Rheeindt FE (2018) Pleistocene land bridges act as semipermeable agents of avian gene flow in Wallacea. Mol Phylogenet Evol 125:196–203
21. Gill FB (1980) Historical aspects of hybridization between Blue-winged and Golden-winged warblers. Auk 97(1):1–18
22. Greenwood PJ (1980) Mating systems, philopatry and dispersal in birds and mammals. Anim Behav 28(4):1140–1162
23. Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. Nature 470(7355):479–485
24. Hoyt JR, Kilpatrick AM, Langwig KE (2021) Ecology and impacts of white-nose syndrome on bats. Nat Rev Microbiol 19:1–15
25. Jones KE, Patel NG, Levy MA, Storeygard A, Balk D, Gittleman JL, Daszak P (2008) Global trends in emerging infectious diseases. Nature 451(7181):990–993
26. Jones G, Jacobs DS, Kunz TH, Willig MR, Racey PA (2009) Carpe noctem: the importance of bats as bioindicators. Endanger Species Res 8(1–2):93–115
27. Kerth G, Mayer F, Petit E (2002) Extreme sex-biased dispersal in the communally breeding, nonmigratory Bechstein’s bat (Myotis bechsteinii). Mol Ecol 11(8):1491–1498
28. Lamichhaney S, Han F, Webster MT, Andersson L, Grant BR, Grant PR (2018) Rapid hybrid speciation in Darwin’s finches. Science 359(6372):224–228
29. Larsen PA, Marchán-Rivadeneira MR, Baker RJ (2010) Natural hybridization generates mammalian lineage with species characteristics. Proc Natl Acad Sci USA 107(25):11447–11452
30. Lever SR, Lohman DJ, Racey PA, Molnar R (2015) Islandized birds: evolution, ecology, and conservation. University of Chicago Press, Chicago
39. Letko M, Seifert SN, Olival KJ, Plowright RK, Munster VJ (2020) Bat-borne virus diversity, spillover and emergence. Nat Rev Microbiol 18:1–11
40. Lomolino MV (2000) A call for a new paradigm of island biogeography. Glob Ecol Biogeogr 9(1):1–6
41. Loureiro LO, Engstrom MD, Lim BK (2020) Comparative phylogeography of mainland and insular species of Neotropical molossid bats (Molossus). Ecol Evol 10(1):389–409
42. Lycett S, Bodewes R, Pohlmann A, Banks J, Ban yai K, Boni M, Bouwstra R, Breed A, Brown I, Chen H, GlobalConsortium for H5N8 and Related Influenza Viruses (2016) Role for migratory wild birds in the global spread of avian influenza H5N8. Science 354:213–217
43. MacArthur RH, Wilson EO (1967) The theory of island biogeography, vol 1. Princeton University Press, UK
44. Mallet J (2005) Hybridization as an invasion of the genome. Trends Ecol Evol 20(5):229–237
45. Marko PB, Hart MW (2011) The complex analytical landscape of gene flow inference. Trends Ecol Evol 26(9):448–456
46. Marshall JL, Arnold ML, Howard DJ (2002) Reinforcement: the road not taken. Trends Ecol Evol 17(12):558–563
47. Mays HL Jr, Hung C-M, Shaner P-J, Denvir J, Justice M, Yang S-F et al (2018) Genomic analysis of demographic history and ecological niche modeling in the endangered Sumatran rhinoceros Dicerorhinus sumatrensis. Curr Biol 28(1):70-76.e74
48. McKnight DT, Schwarzkopf L, Alford RA, Bower DS, Zenger KR (2017) Effects of emerging infectious diseases on host population genetics: a review. Conserv Genet 18(6):1235–1245
49. Medina I, Cooke GM, Ord TJ (2018) Walk, swim or fly? Locomotor mode predicts genetic differentiation in vertebrates. Ecol Lett 21(5):638–645
50. Meyer CF, Struebig MJ, Willig MR (2016) Responses of tropical bats to habitat fragmentation, logging, and deforestation. In: Voigt CC, Kingston T (eds) Bats in the anthropocene: conservation of bats in a changing world. Springer, pp 63–103
51. Moussy C, Hosken D, Mathews F, Smith G, Aegerter J, Bearhop S (2013) Migration and dispersal patterns of bats and their influence on genetic structure. Mammal Rev 43(3):183–195
52. Moyle RG, Filardi CE, Smith CE, Diamond J (2009) Explosive Pleistocene diversification and hemispheric expansion of a “great speciator.” Proc Natl Acad Sci USA 106(6):1863–1868
53. Myers N, Mittermeier RA, Mittermeier CG, Da Fonseca GA, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403(6772):853–858
54. Myhrvold NP, Baldridge E, Chan B, Sivam D, Freeman DL, Ernest SM (2015) An amniote life-history database to perform comparative analyses with birds, mammals, and reptiles: ecological archives E096–269. Ecology 96(11):3109–3109
55. Nabi G, Wang Y, Liu L, Jiang C, Ahmad S, Wu Y, Li D (2021) Bats and birds as viral reservoirs: a physiological and ecological perspective. Sci Total Environ 754:142372
56. Naka LN, Brunfield RT (2018) The dual role of Amazonian rivers in the generation and maintenance of avian diversity. Sci Adv 4(8):eaar8575
57. Nater A, Mattle-Greminger MP, Nurchaya A, Nowak MG, De Manuel M, Desai T et al (2017) Morphometric, behavioral, and genomic evidence for a new orangutan species. Curr Biol 27(22):3487-3498.e3410
58. Norris LC, Main BJ, Lee Y, Collier TC, Fofana A, Cornell AJ et al (2015) Adaptive introgression in an African malaria mosquito coincident with the increased usage of insecticide-treated bed nets. Proc Natl Acad Sci USA 112(3):815–820
59. Nosil P (2012) Ecological speciation. Oxford University Press, Oxford
60. O’Shea TJ, Cryan PM, Hayman DT, Plowright RK, Streicker DG (2016) Multiple mortality events in bats: a global review. Mammal Rev 46(3):175–190
61. Ottenburghs J, Kraus RH, van Hooft P, van Wieren SE, Ydenberg RC, Prins HH (2017) Avian introgression in the genomic era. Avian Res 8(1):30
62. Ouborg NJ, Piquot Y, Van Groenendael JM (1999) Population genetics, molecular markers and the study of dispersal in plants, J Ecol 87(4):351–368
63. Pabijan M, Wollenberg K, Vences M (2012) Small body size increases the regional differentiation of populations of tropical mantellid frogs (Anura: Mantellidae). J Evol Biol 25(11):2310–2324
64. Pardo-Diaz C, Salazar C, Baxter SW, Merot C, Figuereido-Ready W, Joron M et al (2012) Adaptive introgression across species boundaries in Heliconius butterflies. PLoS Genet 8(6):e1002752
65. Parreira BR, Chikhi L (2015) On some genetic consequences of social structure, mating systems, dispersal, and sampling. Proc Natl Acad Sci USA 112(26):E3318–E3326
66. Pauls SU, Nowak C, Bálint M, Pfenninger M (2013) The impact of global climate change on genetic diversity within populations and species. Mol Ecol 22(11):2310–2324
67. Pusey AE (1987) Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends Ecol Evol 2(10):295–299
68. Quintela M, Thulin CG, Höglund J (2017) Avian introgression in the global spread of avian influenza H5N8. Science 96(11):3109–3109
69. Rheindt FE, Edwards SV (2011) Genetic introgression: an genetic introgression in the global spread of avian influenza H5N8. Science 96(11):3109–3109
70. Rheindt FE, Prawiradilaga DM, Ashari H, Gwee CY, Lee GW, Wu MY et al (2020) A lost world in Wallacea:
description of a montane archipelagic avifauna. Science 367(6474):167–170
71. Robin V, Gupta P, Thatte P, Ramakrishnan U (2015) Islands within islands: two montane palaeo-endemic birds impacted by recent anthropogenic fragmentation. Mol Ecol 24(14):3572–3584
72. Robin V, Vishnudas C, Gupta P, Ramakrishnan U (2015) Deep and wide valleys drive nested phylogeographic patterns across a montane bird community. Proc R Soc B Biol Sci 282(1810):20150861
73. Sheard C, Neate-Clegg MH, Alioravainen N, Jones SE, Vincent C, MacGregor HE, Bregman TP, Claramunt S, Tobias JA (2020) Ecological drivers of global gradients in avian dispersal inferred from wing morphology. Nat Commun 11(1):1–9
74. Slatkin M (1985) Gene flow in natural populations. Annu Rev Ecol Syst 16(1):393–430
75. Slatkin M (1987) Gene flow and the geographic structure of natural populations. Science 236(4803):787–792
76. Song Y, Endepols S, Klemann N, Richter D, Matuschka F-R, Shih C-H et al (2011) Adaptive introgression of anticoagulant rodent poison resistance by hybridization between old world mice. Curr Biol 21(15):1296–1301
77. Sousa V, Hey J (2013) Understanding the origin of species with genome-scale data: modelling gene flow. Nat Rev Genet 14(6):404–414
78. Struwebig MJ, Kingston T, Petit EJ, Le Comber SC, Zubaib A, Mohd-Adnan A et al (2011) Parallel declines in species and genetic diversity in tropical forest fragments. Ecol Lett 14(6):582–590
79. Sutherland GD, Harestad AS, Price K, Lertzman KP (2000) Scaling of natal dispersal distances in terrestrial birds and mammals. Conserv Ecol 4(1), http://www.consecol.org/vol4/iss1/art16
80. Szulkin M, Sheldon BC (2008) Dispersal as a means of inbreeding avoidance in a wild bird population. Proc R Soc B Biol Sci 275(1653):703–711
81. Tamma K, Ramakrishnan U (2015) Higher speciation and lower extinction rates influence mammal diversity gradients in Asia. BMC Evol Biol 15(1):11
82. Thatte P, Chandramouli A, Tyagi A, Patel K, Baro P, Chhattani H et al (2020) Human footprint differentially impacts genetic connectivity of four wide-ranging mammals in a fragmented landscape. Divers Distrib 26(3):299–314
83. Todesco M, Pascual MA, Owens GL, Ostevik KL, Moyers BT, Hübner S et al (2016) Hybridization and extinction. Evol Appl 9(7):892–908
84. Toews DP, Taylor SA, Vallender R, Brelsford A, Butcher BG, Messer PW et al (2016) Plumage genes and little else distinguish the genomes of hybridizing warblers. Curr Biol 26(17):2313–2318
85. Tsang SM, Wiantoro S, Veluz MI, Sugita N, Nguyen YL, Simmons NB et al (2020) Dispersal out of Wallacea spurs diversification of Pteropus flying foxes, the world’s largest bats (Mammalia: Chiroptera). J Biogeogr 47(2):527–537
86. Voris HK (2000) Maps of Pleistocene sea levels in Southeast Asia: shorelines, river systems and time durations. J Biogeogr 27(5):1153–1167
87. Weeks BC, Claramunt S (2014) Dispersal has inhibited avian diversification in Australasian archipelagoes. Proc R Soc B Biol Sci 281(1791):20141257
88. Weigelt P, Steinbauer MJ, Cabral JS, Kreft H (2016) Late Quaternary climate change shapes island biodiversity. Nature 532(7597):99–102
89. Whitlock MC, Mccauley DE (1999) Indirect measures of gene flow and migration: FST ≠ 1/(4Nm+ 1). Heredity 82(2):117–125
90. Whittaker RJ, Fernández-Palacios JM (2007) Island biogeography: ecology, evolution, and conservation. Oxford University Press, Oxford
91. Wilkinson G, Fleming T (1996) Migration and evolution of lesser long-nosed bats Leptonycteris curasoae, inferred from mitochondrial DNA. Mol Ecol 5(3):329–339

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