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INVITED REVIEWS AND META-ANALYSES

The biogeography of mitochondrial and nuclear discordance in animals

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Abstract

Combining nuclear (nuDNA) and mitochondrial DNA (mtDNA) markers has improved the power of molecular data to test phylogenetic and phylogeographic hypotheses and has highlighted the limitations of studies using only mtDNA markers. In fact, in the past decade, many conflicting geographic patterns between mitochondrial and nuclear genetic markers have been identified (i.e. mito-nuclear discordance). Our goals in this synthesis are to: (i) review known cases of mito-nuclear discordance in animal systems, (ii) to summarize the biogeographic patterns in each instance and (iii) to identify common drivers of discordance in various groups. In total, we identified 126 cases in animal systems with strong evidence of discordance between the biogeographic patterns obtained from mitochondrial DNA and those observed in the nuclear genome. In most cases, these patterns are attributed to adaptive introgression of mtDNA, demographic disparities and sex-biased asymmetries, with some studies also implicating hybrid zone movement, human introductions and *Wolbachia* infection in insects. We also discuss situations where divergent mtDNA clades seem to have arisen in the absence of geographic isolation. For those cases where foreign mtDNA haplotypes are found deep within the range of a second taxon, data suggest that those mtDNA haplotypes are more likely to be at a high frequency and are commonly driven by sex-biased asymmetries and/or adaptive introgression. In addition, we discuss the problems with inferring the processes causing discordance from biogeographic patterns that are common in many studies. In many cases, authors presented more than one explanation for discordant patterns in a given system, which indicates that likely more data are required. Ideally, to resolve this issue, we see important future work shifting focus from documenting the prevalence of mito-nuclear discordance towards testing hypotheses regarding the drivers of discordance. Indeed, there is great potential for certain cases of mitochondrial introgression to become important natural systems within which to test the effect of different mitochondrial genotypes on whole-animal phenotypes.

Keywords: mitochondrial DNA, nuclear DNA, mito-nuclear discordance, cytonuclear discordance, hybridization, introgression

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Introduction

It is now commonplace for studies of molecular biogeography to employ a diverse suite of genetic markers, including loci both in the mitochondrial genome (mtDNA) and throughout the nuclear genome (nuDNA). This variety of genetic information is, in many cases, now complemented with broad taxon sampling encompassing a large geographic scope. In most studies that employ a diverse array of genetic markers and a robust sampling effort, the patterns observed between different genetic marker types generally align (Avise 1994). This is true for comparisons between species as well as phylogeographic structure that arises within species – the localities that harbour deep splits

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between mtDNA clades also have corresponding differences in the nuclear genome (Zink & Barrowclough 2008). This observation is one reason the 'barcoding of life' project has proved successful: clades identified in mtDNA are generally concordant with other phenotypic and genetic information (e.g. 94% of taxonomic bird species in North America have concordant mtDNA clusters; Kerr *et al.* 2007). However, concordant patterns between mtDNA and nuclear DNA are not always observed (Funk & Omland 2003; Chan & Levin 2005). In fact, the number of studies that report discordant patterns between mtDNA and nuclear markers, while not large, is increasing, especially within the last decade, as more researchers have been able to use both types of markers in combination.

Discordance between mtDNA and nuDNA can be most broadly defined as a significant difference in the patterns of differentiation between these two marker types. Most commonly, these conflicts can be in the overall amount of differentiation or in how these markers reconstruct relationships among groups. This type of discordance is expected because the mitochondrial genome is haploid and uniparentally inherited in most animals (but see Hoeh *et al.* 1991), and therefore has a fourfold smaller effective population size (Hudson & Turelli 2003; Zink & Barrowclough 2008). This means that mtDNA will complete the process of lineage sorting, where ancestral polymorphisms are lost over time, faster than nuDNA, as this rate is inversely proportional to the effective population size (Funk & Omland 2003). While the inheritance properties of mtDNA make it more likely than any single nuclear marker to accurately reflect recent divergence (Zink & Barrowclough 2008), studies that rely solely on mtDNA to infer phylogenetic relationships risk generating gene trees that do not represent the true relationships among taxa (Edwards & Bensch 2009). The prevalence of incomplete lineage sorting in contributing to discordant patterns between mtDNA and nuDNA has been discussed extensively (Funk & Omland 2003; Zink & Barrowclough 2008; McKay & Zink 2010), and the primary resolution is that, where feasible, researchers should include multiple independent loci to generate robust phylogenetic relationships (Edwards & Bensch 2009).

Even if numerous nuclear loci are employed, mitonuclear discordance can also arise if there are differences in how selection acts on the mitochondrial genome as compared to the nuclear genome or if there is biased movement of either marker type driven by demographic asymmetries, such as sex-biased dispersal (Rheindt & Edwards 2011). For instance, despite the long-held assumption that variation in mtDNA is primarily neutral, a number of studies have identified intra- and interspecific variation in the proteins encoded by genes in the mitochondrial genome that authors have attributed to natural selection (Bazin *et al.* 2006; Meiklejohn *et al.* 2007; Edwards 2009; Ballard & Rand 2005; Ballard & Melvin 2010; Scott *et al.* 2011). If selection for mtDNA variants varies geographically, then discordant patterns between mtDNA and nuDNA can arise (Irwin 2012). In addition to differences in the adaptive landscapes for nuDNA and mtDNA, demographic asymmetries can also create discordant patterns and distributions of these different marker types. For instance, female-biased dispersal or disparities in range size or abundance between hybridizing groups can promote the dispersal of mtDNA in the absence of concordant movement of nuDNA (Funk & Omland 2003).

Distinguishing between incomplete lineage sorting and these other types of discordance can be difficult (McKay & Zink 2010). One important distinction, however, is that discordance that arises from incomplete lineage sorting is not expected to leave any predictable biogeographic pattern (Fig. 1; Funk & Omland 2003). Therefore, in cases where there are strong geographic inconsistencies between patterns in mtDNA and

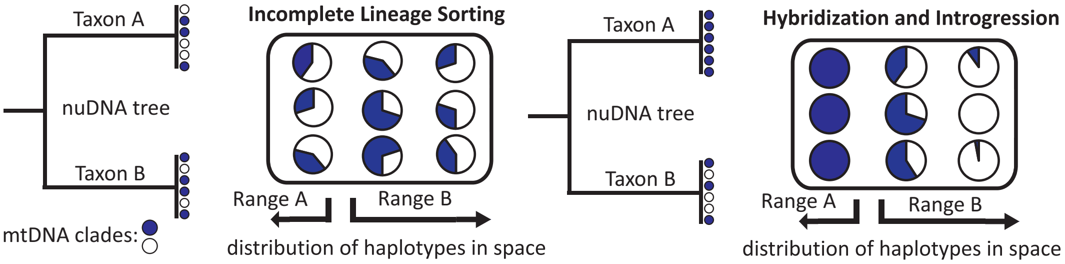

Fig. 1 A scenario illustrating different biogeographic patterns expected under incomplete lineage sorting versus hybridization and introgression. The left panel is consistent with a pattern of incomplete lineage sorting of mtDNA, where two mtDNA clades are distributed between two nuclear clusters (as illustrated with the phylogenetic tree), taxon A (blue) and taxon B (white), with no discernible geographic pattern in the distribution of mtDNA clades among the nuclear groups. While less likely, this pattern is also consistent with complete introgression of mtDNA that is maintained at low frequency across the range of both taxa. The right panel illustrates a pattern that is consistent with partial introgression of mtDNA from taxon A into taxon B (as distinguished by nuDNA markers), where individuals in the range of taxon B have mtDNA from taxon A at the range edge.

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nuDNA, incomplete lineage sorting can usually be ruled out. This type of discordance, referred to more generally as biogeographic discordance, can result from clines in mtDNA being displaced from nuclear DNA in both their location and/or their width (Fig. 2). Biogeographic discordance can be extensive, such as the complete replacement of mtDNA of one species by another (i.e. 'mitochondrial capture'), or more limited, where mtDNA haplotypes show a higher frequency in a given population than would be expected from nuDNA markers.

Two general situations can lead to biogeographic discordance between mtDNA and nuDNA: following isolation and hybridization or *in situ* (i.e. secondary versus primary contact). Most of the taxa that display patterns of biogeographic mito-nuclear discordance are groups that were isolated for long periods of time and are either currently in secondary contact or have experienced range contact at some point in their past. During this period of isolation, it is assumed that divergent groups accumulated mutations in both their mitochondrial and nuclear genomes, which increased to high frequency via selection, drift or some combination of the two (i.e. 'genetic draft'; Hudson & Turelli 2003). Upon secondary contact, these groups formed hybrid zones, interbreeding to varying extents, and mtDNA–nuDNA discordance was promoted by divergent patterns of gene flow between the two genomes.

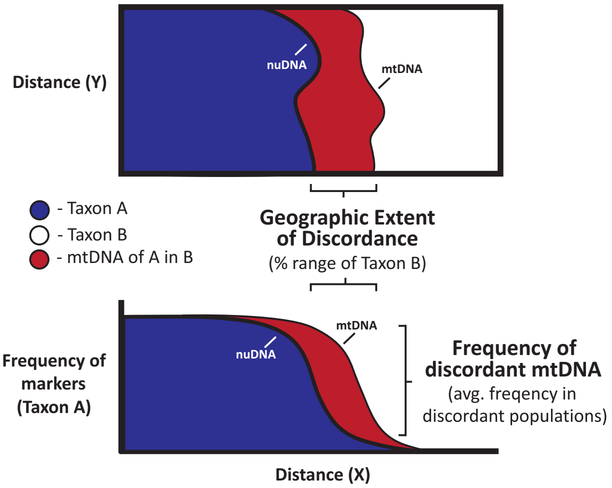

Fig. 2 A hypothetical scenario with a range map and geographic clines of alternative means to quantify biogeographic patterns of discordance. The top panel shows the ranges of two taxa, taxon A (blue) and taxon B (white), as distinguished by nuclear genetic markers, where the mtDNA of taxon A can be found within the range of taxon B (red area); this demonstrates the geographic extent of discordance. The bottom panel depicts this mito-nuclear discordance measured as relative to frequencies of nuclear markers (blue) and mtDNA (red) of taxon A.

It has also been suggested that mito-nuclear discordance can arise in the absence of geographic isolation, where mitochondrial types show strong frequency differences between localities that potentially arose in the face of gene flow (Irwin 2002; Ribeiro *et al.* 2011). In these cases, patterns in the nuclear genome, combined with the biogeographic history of the taxa, suggest a narrow mtDNA divide that may not be the product of geographic isolation followed by secondary contact. This pattern is consistent with a scenario where selection favours one mitochondrial variant over another in a given area; in some cases, these differences may be associated with important environmental characteristics (Cheviron & Brumfield 2009; Irwin 2012).

In many cases, discordant biogeographic patterns have been used to infer the potential drivers of discordance. For situations where the mtDNA of one taxon shows complete fixation in another or where a mtDNA cline centre is displaced and/or wider as compared to nuDNA, a number of processes have been inferred: (i) adaptive introgression of mtDNA; (ii) demographic disparities; (iii) sex-biased asymmetries; (iv) hybrid zone movement; (v) *Wolbachia* infection; and (vi) human introductions. Adaptive processes can create discordance if selection favours mutually beneficial mitochondrial variants and promotes introgression upon secondary contact. Demographic disparities can generate discordance if there are large differences in population or range size between two taxa, especially if there is the potential for very small population sizes to influence mtDNA frequency by sampling effects (i.e. genetic drift), promoting asymmetric introgression (i.e. Currat *et al.* 2008). A subset of more general demographic differences, systems with female-biased dispersal propensity, behavioural differences in mating likelihood and differential production of offspring can promote mtDNA introgression because of its matrilineal inheritance. Hybrid zone movement can also create discordance when the majority of nuclear markers (in addition to phenotypic traits) shift their geographic location, leaving a wake of mtDNA behind (Rohwer *et al.* 2001). In insects, *Wolbachia* infection is a potentially important driver of discordance, where mating incompatibilities can arise between individuals with and without this cytoplasmic endosymbiotic parasite and mtDNA hitchhikes (i.e. infected males mated with uninfected female are incompatible, whereas infected females mated with uninfected males suffer less fitness loss; Jiggins 2003). It has also been recognized that human actions can facilitate secondary contact and generate some of the demographic asymmetries outlined previously by moving individuals (i.e. Perry *et al.* 2001) or by facilitating interaction via habitat alteration, potentially generating discordance.

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Biogeographic discordance is also distinguished if secondary contact and hybridization generate more structuring in mtDNA and/or narrower geographic clines as compared to nuDNA. These are likely produced by either nuclear introgression and/or sex-biased asymmetries. Sex-biased asymmetries in this context can be driven by male-biased dispersal, mating behaviour or sex-biased offspring production. This latter scenario (sex-biased offspring production) has been the focus of theoretical and empirical investigations, as it is a specific prediction of 'Haldane's rule' (reviewed in Coyne & Orr 2004). This theory posits that, following secondary contact and interbreeding between divergent taxa, if one sex suffers a fitness loss, it will more often be the heterogametic sex. It follows that in those systems that where females are the heterogametic sex (i.e. ZW systems), as in Aves and Lepidoptera, mtDNA will be less likely to introgress between divergent groups as compared to other taxonomic groups with XY sex determination (such as mammals), and subsequently, mtDNA will have a narrow cline (Coyne & Orr 2004).

Given the increase in interest and the availability of molecular markers, biogeographic patterns of mito-nuclear discordance are being identified more readily in many systems (Edwards & Bensch 2009). However, in most cases, the processes driving such patterns are still unknown. Here we attempt to address some of these knowledge gaps by reviewing recent progress in our understanding of mito-nuclear discordance in animal taxa. Our goals in this synthesis are to: (i) review known cases of biogeographic mito-nuclear discordance in animal systems, (ii) to summarize the geographic patterns in each instance and (iii) to identify common drivers of discordance in various groups. Our treatment

Box 1. Previous Treatments of Mitochondrial Discordance and Introgression

Discordance between mtDNA, nuDNA and other taxonomic characters has been the focus of a number of previous reviews and discussions. In an early synthesis, Avise (1994) highlighted a number of systems that were among the first to report strong discordance between nuDNA markers and mtDNA, owing to hybridization and introgression. Funk & Omland (2003) extended this in a more general review by attempting to quantify the prevalence, causes and consequences of genealogical polyphyly at the species level. Patterns of biogeographic discordance and asymmetric introgression of mtDNA were considered along with a number of other processes contributing to discordant phylogenetic patterns, such as imperfect taxonomy, inadequate phylogenetic information and incomplete lineage sorting (Funk & Omland 2003).

McKay & Zink (2010) further explored Funk & Omland's (2003) analysis by trying to distinguish, in each case of polyphyly in avian systems, whether imperfect taxonomy, incomplete lineage sorting or gene flow was responsible for the discordance. While some authors suggest that taxonomy may not be the ideal guide for studies of mtDNA paraphyly (i.e. Rheindt & Edwards 2011), McKay & Zink (2010) reported that approximately 14% of 856 avian species examined showed evidence of paraphyly and that imperfect taxonomy was the most prevalent explanation for the discordances (55.7% of cases) as compared to incomplete lineage sorting (15.6%) or introgression (5.7%), although in many cases, they suggest that the latter two processes could not be distinguished (21.3%; McKay & Zink 2010).

By more specifically examining the correspondence between estimates of divergence in mtDNA and nuDNA in avian systems, Zink & Barrowclough (2008) suggested that, in most cases, there was little conflict between the estimates obtained from nuDNA and mtDNA. For instance, in most of the cases, they reported that mtDNA divergence was greater than estimates from nuDNA, as would be expected from the differences in effective population size. This result was interpreted as an affirmation of mtDNA, 'under siege' in phylogeography, to recover robust relationships (Zink & Barrowclough 2008). In their reply, Edwards & Bensch (2009) suggest that this conclusion may be true in many cases, but argue that there is much value at little cost if mtDNA data are supplemented by additional loci in the nuclear genome.

Models of mito-nuclear discordance have been derived analytically (Chan & Levin 2005) and from simulations (Currat *et al.* 2008). Chan & Levin (2005) modelled the propensity for incomplete premating barriers (i.e. strong mating preference) to promote mtDNA introgression between taxa as compared to postmating barriers (i.e. strong selection against hybrids). They found that postmating barriers to reproduction were better at preventing introgression, an observation that has generally been borne out in empirical systems (e.g. Lamb & Avise 1986), although in many cases, there is little information on the barriers acting in any given system. The simulations performed by Currat *et al.* (2008), which were supplemented by a review of empirical examples by Petit & Excoffier (2009), focused on mtDNA introgression following invasion and hybridization with a related taxon. They found that gene flow was consistently in the direction of the native taxon towards the colonizer, and, counter-intuitively, the genetic markers with *lower* intraspecific gene flow were more likely to introgress between taxa (Currat *et al.* 2008; Petit & Excoffier 2009). They suggest this is because these low-dispersing genetic markers are less likely to be swamped out by gene flow of from other populations of the colonizing taxon. From this result, they predicted that gene flow of mtDNA in systems with male-biased dispersal will be higher as compared to those systems with female-biased dispersal (Currat *et al.* 2008; Petit & Excoffier 2009). Unfortunately, in the cases reviewed by Petit & Excoffier (2009), the dispersing sex is confounded with taxonomy (i.e. birds versus mammals), sex-determining system and, combined with limited data on dispersal bias, it is currently difficult to determine how prevalent this process is in natural systems. However, these nonintuitive results were not predicted based on previous surveys of empirical systems, suggesting that such simulation studies present a promising line of enquiry into the drivers of discordance in the future (i.e. Irwin 2012).

differs from previous articles in both scope and inclusiveness, as the primary criterion for our survey is only that the systems display a strong biogeographic signal of mito-nuclear discordance (see Box 1 for a discussion of previous treatments of mito-nuclear discordance). We focus on biogeographic discordance because these cases are much more likely to be associated with other complementary historical, biological and ecological information that can be used to reveal the underlying processes driving discordance.

Methods

Our survey consisted of two approaches. First, we collected all papers where authors explicitly reported mito-nuclear or cytonuclear discordance in animals. We used discordance that has occurred between divergent genera, species, subspecies and, in some cases, distinct genetic clusters within a taxon. We restricted our survey to animals to maintain reasonable bounds on the extent of our review and also because the mitochondrial genome can behave very differently in other taxonomic groups, such as plants (Galtier 2011). Second, to provide a more objective metric for the prevalence of biogeographic mito-nuclear discordance, we searched 100 randomly chosen studies published in *Molecular Ecology* for articles referring to mitochondrial markers and microsatellites, AFLPs or nuclear introns. For those studies that were relevant (i.e. empirical, in animal systems, not asexual hybrids and presented both marker types) and had sufficient sampling to identify potential discordance, we looked for congruence between the geographic patterns of mtDNA versus nuDNA makers. We did this to evaluate the extent of mito-nuclear discordance in the absence of an author's explicit discussion of discordance.

Biogeographic mito-nuclear discordance is best illustrated by studies that report geographic clines for mtDNA along with multiple nuclear markers and other phenotypic traits (Fig. 2). A number of studies do not report these clinal data, so for some cases in our literature survey we identified mtDNA–nuDNA discordance from maps, figures and supporting text. From these data we extracted two important characteristics for our synthesis: first, we estimated the geographic extent of mitochondrial and nuclear discordance, and second, we determined the average frequency of mtDNA haplotypes throughout the area of discordance. In the case of secondary contact, the geographic extent of discordance is defined as the percentage of the range for which the mtDNA of taxon 1 is observed within the range of taxon 2 (relative to the overall range of taxon 2) as defined by nuclear markers or, in a small number of cases, phenotypic characteristics (Figure 2). The frequency of mtDNA throughout the area of discordance is quantified as the average haplotype frequency of the foreign mtDNA in the region between the contact zone inferred from nuDNA and where the native mtDNA haplotype becomes fixed (in the cases where introgressed mtDNA is not at complete fixation; Fig. 2).

There are two points that should be noted in defining these groups based primarily on differences in the nuclear genome. First, most studies use only a small number of nuclear loci (i.e. <10) to assay the nuclear genome, especially studies employing intron sequencing or allozyme variation, and therefore may not be representative of the rest of the genome. Second, nuclear markers can be discordant among themselves, as a result of drift or of different patterns of dispersal, selection or demography. Only in cases where mtDNA was a clear outlier to the general pattern of other nuclear markers did we include it in our survey. Quantifying this type of discordance among nuclear markers was beyond the scope of the review; however, given the number of studies now employing numerous loci in a robust geographic framework, there is a need for future syntheses to quantify these patterns.

We used three bins to categorize both the geographic extent of discordance and the frequency of discordant haplotypes: <50%, 50–95% and >95%. These large bins allowed us to reliably quantify data reproduced in different forms in various papers. We use these biogeographic patterns to gain insight into some of the factors that may be promoting mito-nuclear discordance. In the case of mtDNA introgression following secondary contact, the extent and frequency of discordant haplotypes can indicate the relative importance of selection or neutral processes in driving discordant patterns (Rheindt & Edwards 2011). For instance, it is less likely that neutral genetic drift would explain the distribution of the mtDNA of taxon 1 at near fixation (>95% frequency) across more than half of the range of taxon 2, unless historical bottlenecks during or following introgression were frequent.

We supplement this coarse quantitative evaluation of inferred drivers of discordance with information provided by the authors in the text of each study. For the systems where mito-nuclear discordance is identified by less structuring of mtDNA and/or wider geographic clines compared with nuDNA, or where mtDNA and nuDNA were both structured, but the taxon boundaries differed between marker types, we classified each study (based on the interpretations of the authors of each study) as having evidence that supports one or more of the following scenarios (discussed in detail earlier): (i) adaptive introgression of mtDNA; (ii) demographic disparities (including genetic drift); (iii) sex-biased asymmetries; (iv) hybrid zone movement; (v) *Wolbachia*

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infection; and (vi) human introductions. Cases in which mtDNA was more structured and/or had narrower geographic clines compared with nuDNA were classified as being driven by either (i) nuclear introgression and/or (ii) sex-biased dispersal, mating or offspring production (discussed in detail earlier). Genetic drift is ubiquitous in finite populations and can interact with many of the aforementioned processes to increase discordance between mtDNA and nuDNA. While drift alone can also produce geographically discordant patterns (e.g. Petit & Excoffier 2009), authors of studies documenting mito-nuclear discordance typically propose other explanations. When authors did cite genetic drift as a likely explanation, there was usually complementary evidence of historical bottlenecks producing small population sizes, and therefore, we included these cases under the broad category of 'demographic disparities'.

We excluded studies based on a number of criteria, especially in cases where discordance was suspected, but was based on limited sampling. We also excluded studies where mtDNA–nuDNA discordance was generated by asexual offspring produced by sexual parental species. In this case, discordance is brought about when the female parental species always contributes its mtDNA to the asexual hybrid offspring (reviewed in Avise 1994). Dealing with potential cases of incomplete lineage sorting was more difficult. For instance, sharing of similar mtDNA haplotypes across the range of two taxa (i.e. >95% geographic extent and >95% haplotype frequency) can be the result of introgression and complete fixation of a foreign mtDNA or the result of incomplete lineage sorting. We excluded situations where morphology or traditional taxonomy was used to infer this type discordance. In fact, only in a few cases where phenotypic data showed a strong biogeographic signal, such as mtDNA discordance with morphology across a hybrid zone, were phenotypic characters included in our survey as proxy for patterns in the nuclear genome. This is because phenotypic convergence can create the impression of discordance where this is most likely the result of imperfect taxonomy (Funk & Omland 2003).

We included cases where there are strong differences in nuDNA markers, but much less differentiation in mtDNA if there was additional information supporting the discordance, such as evidence for current or past potential for hybridization. This is because it is expected that the mitochondrial genome will show either greater or comparable levels of divergence and structuring compared with markers in the nuclear genome (Zink & Barrowclough 2008). In these cases, significantly less mtDNA divergence compared with nuclear differentiation can implicate mitochondrial introgression between taxa (e.g. Cathey *et al.* 1998; Bachtrog *et al.* 2006; Irwin *et al.* 2009).

However, given the ability for high-resolution nuclear genetic markers such as AFLPs, microsatellites and full genome sequencing to detect very subtle and potentially very recent reductions in gene flow, it is becoming increasingly difficult to determine whether mtDNA homogeneity between groups divergent in nuclear DNA is a result of hybridization or of the high power of multi-locus nuclear data sets to detect differentiation (Edwards & Bensch 2009). These types of discordant patterns, where there is low but detectable amounts of nuDNA differentiation, were not included in our survey because incomplete lineage sorting of mtDNA could not be dismissed, even though many of these had excellent taxonomic and genetic sampling. Several examples of such discordant patterns can be found between sympatric colour morphs of the rockfish *Sebastes inermis* (Kai *et al.* 2002), in different host races of the leaf miner *Phytomyza glabricola* (Scheffer & Hawthorne 2007) and the grasshopper *Hesperotettix viridis* (Apple *et al.* 2010), between two subspecies of willow warbler *Phylloscopus trochilus* in Sweden (Bensch *et al.* 2009), and between various populations of the dispersal limited newt *Calotriton asper* (Milá *et al.* 2010). Other studies where biogeographic discordance is suggestive, but requires further confirmation with additional data, can be found annotated in Table S3, Supporting information.

Results and discussion

Prevalence of mito-nuclear discordance

The initial studies that identified mito-nuclear discordance were in systems where early genetic tools were more developed compared with other taxa: mitochondrial introgression between two species of fruit fly (*Drosophila pseudoobscura* and *D. persimilis*; Powell 1983) and between two species of the house mouse (*Mus domesticus* and *M. musculus* Ferris *et al.* 1983). Following these early discoveries, the number of cases slowly increased until, around 2001, methods for assaying numerous individuals for their nuclear genotype became more widely available to researchers and, subsequently, the number of cases increased dramatically (Fig. 3). For instance, between 2001 and 2011, on average, over eight studies have been published per year documenting mito-nuclear discordance in animals.

In total, we identified 126 cases in animal systems where there is strong evidence of discordance between the biogeographic patterns identified in mitochondrial DNA and those observed in the nuclear genome. The majority of cases (97%) are those where discordance likely arose following geographic isolation and second-

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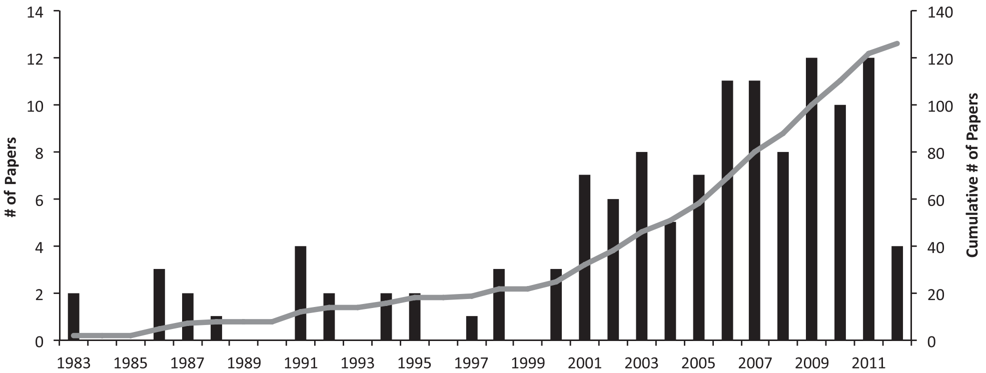

Fig. 3 The number of papers that report mito-nuclear discordance between 1983 and 2012 (filled bars). The cumulative number of papers (secondary axis) from 1983 is also shown (grey line).

ary contact (Table 1 and Table S1, Supporting information). Of those, 109 (89%) found evidence that mtDNA was an outlier, showing little affinity to boundaries identified by nuclear DNA. In the thirteen remaining cases, mtDNA showed a general geographic concordance with the nuclear genome, but had a narrower cline and/or more geographic structure (Table 2 and Table S2, Supporting information). In seven studies, there is evidence for extensive introgression of mtDNA between numerous pairs of closely related taxa (see Box 2). Interestingly, in four systems, there is evidence of strong mtDNA structuring that has likely arisen *in situ* in the absence of geographic isolation and maintained in the face of nuclear gene flow (see Box 3).

Our random survey of 100 articles in *Molecular Ecology* found 75 relevant studies and 61 of those that included both mitochondrial and multi-locus nuclear data that were presented in a way that would show major discrepancies between the marker types (see Table S3, Supporting information for additional information on each study). Of the 61 systems, 11 had discordant biogeographic patterns between mitochondrial and nuclear DNA (18%). While in all cases the authors noted discordance, most mentioned it in passing and did not make it a focus of the study. While this survey method does not avoid publication bias, it does try to control for author bias, and the finding of 18% of studies employing both marker types identifying mito-nuclear discordance is interesting. This is a large figure, especially when combined with the number of systems with discordance documented in the last two decades (Table 1), the suggestive cases requiring further confirmation (Table S3, Supporting information) and those likely caused by incomplete lineage sorting not included in our survey (e.g. McKay & Zink 2010). This suggests that discordance between the mitochondrial and nuclear genomes is a prevalent and important phenomenon.

In general, the prevalence of discordance was not disproportionate among any taxonomic group, although mammals and fish have a higher frequency of reported discordance compared with other groups (Fig. 4). This may represent a propensity for these taxonomic groups to exchange mtDNA and/or a publication bias for studies investigating these species. It has been suggested that birds, which have a ZW sex determination system, would be less likely to exchange maternally inherited mtDNA upon secondary contact owing to Haldane's rule (Chan & Levin 2005). We find limited support for this prediction: while almost half of the cases of narrow mtDNA compared with nuDNA clines were in avian systems (Fig. 4; Table 2), there are also a number of cases showing strong evidence of mtDNA introgression in birds (Table 1), a pattern not appreciated in previous treatments (e.g. Petit & Excoffier 2009).

Extent and type of discordance following secondary contact

When populations experience periods of geographic isolation and subsequent secondary contact, patterns of genetic variation in mtDNA and the nuclear genome can become dissociated. The most common form of mito-nuclear discordance is asymmetric movement of mtDNA, with our survey finding only four papers reporting bidirectional movement of mtDNA (Table S1, Supporting information; see also Chan & Levin 2005; Currat *et al.* 2008). In those cases where there was no directionality in the movement of mtDNA, this was because clines in mtDNA were wider than nuDNA (e.g. *Tamiasciurus* squirrels; Chavez *et al.* 2011). Some authors suggest that this pattern may be due to the fact that, in those cases, mtDNA harbours fewer genetic incompatibilities as compared to the nuclear genome, and thus, there are fewer barriers to introgression (Colliard *et al.* 2010).

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Table 1. Cases of mitochondrial–nuclear discordance following secondary contact where clines in mtDNA are wider than nuDNA. In cases of asymmetric discordance, taxon 1 is the 'foreign mtDNA', whereas taxon 2 is the 'native mtDNA'. For additional details on genetic patterns and inferred processes, see the Table S1 (Supporting information)

Taxon 1 ('foreign') Taxon 2 ('native')	Common Name	Inferred Process(s)	Geographic Extent			Haplotype Frequency			Reference
			0–50%	50–95%	>95%	0–50%	50–95%	>95%	
Amphibians									
Bombina variegata *B. bombina*	Yellow-bellied and fire-bellied toad	Adaptive, sex-biased, demographic	•				•		Hofman & Szymura (2007)
Bufo woodhousii *B. microscaphus*	Woodhouse's and Arizona toad	Sex-biased, demographic		•		•			Malmos *et al.* (2001)
Chioglossa lusitanica 'south lineage' *C. lusitanica* 'north lineage'	Gold-striped salamander	Adaptive, demographic	•					•	Sequeira *et al.* (2005)
Hyla eximia *H. arenicolor*	Tree frog	Adaptive, sex-biased	•			•			Bryson *et al.* 2010
Hyla gratiosa *H. cinerea*	Barking and American green tree frog	Sex-biased	•				•		Lamb & Avise (1986)
Hyla wrightorum *H. arenicolor*	Arizona and canyon tree frog	Adaptive, sex-biased	•			•			Bryson *et al.* (2010)
Plethodon glutinosus *P. shermani*	Northern slimy and red-legged salamander	Sex-biased		•				•	Weisrock *et al.* (2005)
Bufo siculus *B. balearicus*	Green toads	Demographic	•			•			Colliard *et al.* (2010)
Rana cascadae 'Oregon' *R. cascadae* 'Washington'	Cascades frog	Demographic		•				•	Monsen & Blouin (2003)
Rana kukunoris *Rana chensinensis*	Brown frogs	Sex-biased	•					•	Zhou *et al.* (2012)
Rana lessonae *R. ridibunda*	Pool and marsh frog	Adaptive	•					•	Plötner *et al.* (2008)
Rana plancyi *R. nigromaculatus*	Green pond frogs	Sex-biased		•				•	Liu *et al.* (2010)
Triturus cristatus *T. marmoratus*	Great-crested and marbled newt	Sex-biased	•					•	Arntzen *et al.* (2009)
Triturus montandoni *T. vulgaris*	Montandon's and smooth newt	Adaptive, demographic	•			•			Babik *et al.* (2003)
Birds									
Anas falcata *A. strepera*	Falcated duck and Gadwall	Sex-biased, demographic	•			•			Peters *et al.* (2007)
Aquila clanga *A. pomarina*	Greater and lesser spotted eagles	Sex-biased	•			•			Helbig *et al.* (2005)
Catharus ustulatus ustulatus *C. u. swainsoni*	Swainson's thrush	Sex-biased	•				•		Ruegg (2008)

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Table 1. *Continued*

			Geographic Extent			Haplotype Frequency			
Birds con't	Common Name	Inferred Process(s)	0–50%	50–95%	>95%	0–50%	50–95%	>95%	Reference
Emberiza citrinella *E. leucocephalos*	Yellowhammer and pine bunting	Adaptive			•			•	Irwin *et al.* (2009)
Falco rusticolus *F. cherrug*	Gyrfalcon and saker falcon	Demographic		•			•		Nittinger *et al.* (2007)
Foudia omissa *F. madagascariensis*	Forest and red fody	Sex-biased			•			•	Warren *et al.* (2012)
Icterus galbula *I. abeillei*	Baltimore and black-backed oriole	None given			•			•	Jacobsen *et al.* (2010)
Setophaga coronata *S. auduboni*	Myrtle and Audubon's warbler	Adaptive		•				•	Brelsford *et al.* (2011)
Setophaga townsendii *S. occidentalis*	Townsend's and hermit warbler	HZ movement		•		•			Krosby & Rohwer (2009)
Streptopelia capicola *S. vinacea*	Ring-necked and vinaceous dove	Demographic	•			•			den Hartog *et al.* (2010)
Zonotrichia leucophrys *Z. atricapilla*	White-crowned and golden-crowned sparrow	Demographic			•			•	Weckstein *et al.* (2001)
Zosterops lateralis *Z. lutea*	Yellow white-eyes and silvereye	Demographic	•					•	Degnan & Moritz (1992)
Fish									
Acipenser gueldenstaedtii *A. naccarii*	Russian and Adriatic sturgeon	Demographic		•		•			Ludwig *et al.* (2003)
Cottus gobio 'western clade' *C. gobio* 'eastern clade'	European bullhead	Sex-biased	•				•		Kontula & Vainola (2004)
Cyprinodon atrorus *C. bifasciatus*	Pupfish	Sex-biased			•			•	Carson & Dowling (2006)
Etheostoma caeruleum *E. uniporum*	Current and rainbow darters	Sex-biased, demographic			•			•	Ray *et al.* (2008)
Fundulus diaphanus diaphanus *F. d. menona*	Banded killifish	Adaptive, sex-biased	•					•	April & Turgeon (2006)
Gasterosteus aculeatus 'Pacific clade' *G. aculeatus* 'Sea of Japan clade'	Three-spined stickleback	Demographic			•			•	Yamada *et al.* (2001)
Lamprologus callipterus *Neolamprologus fasciatus*	Lake Tanganyika cichlid	Adaptive			•			•	Nevado *et al.* (2009)
Lepomis gibbosus *L. macrochirus*	Pumpkinseed and bluegill sunfish	Sex-biased	•					•	Konkle & Philipp (1992)
Luxilus cornutus *L. chrysocephalus*	Cyprinids	Sex-biased, HZ movement	•				•		Dowling & Hoeh (1991)

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Table 1. *Continued*

Fish con't	Common Name	Inferred Process(s)	Geographic Extent 0–50%	Geographic Extent 50–95%	Geographic Extent >95%	Haplotype Frequency 0–50%	Haplotype Frequency 50–95%	Haplotype Frequency >95%	Reference
Neolamprologus spp. *N. marunguensis*	Lake Tanganyika cichlid				•		•		Salzburger *et al.* (2002)
Nothonotus camurus and *N. chlorobranchius* *N. rufilineatus*	Darters	Adaptive, sex-biased	•				•		Keck & Near (2009)
Oncorhynchus clarkii lewisi *O. c. bouvieri*	Westslope and Yellowstone cutthroat trout	Sex-biased	•			•			Forbes & Allendorf (1991)
Oncorhynchus mykiss *O. clarkii*	Rainbow and cutthroat trout	Adaptive, sex-biased, human	•				•		Metcalf *et al.* (2008)
Ophthalmotilapia boops *O. nasuta*	Lake Tanganyika cichlid	Sex-biased	•			•			Nevado *et al.* (2011)
Oreochromis aureus *O. niloticus*	Cichlid	Adaptive, sex-biased, demographic	•					•	Rognon & Guyomard (2003)
Oreochromis leucostictus *O. niloticus*	Cichlid	Human	•			•			Nyingi & Agnèse (2007)
Phoxinus neogaeus *P. eos*	Finescale and northern redbelly dace	Adaptive		•				•	Mee & Taylor (2012)
Pseudochondrostoma duriense *Achondrostoma oligolepis*	Iberian cyprinids	Adaptive	•				•		Aboim *et al.* (2010)
Salvelinus alpinus *S. fontinalis*	Arctic charr and brook charr	Adaptive	•					•	Glemet *et al.* (1998)
Salvelinus alpinus *S. namaycush*	Arctic charr and lake trout	Adaptive	•					•	Wilson & Bernatchez (1998)
Salvelinus confluentus *S. malma*	Bull trout and dolly varden	Sex-biased	•				•		Redenbach & Taylor (2002)
Salvelinus leucomaenis *S. malma*	White-spotted charr and dolly varden	Sex-biased	•				•		Yamamoto *et al.* (2006)
Tanganicodus cf. irsacae *Eretmodus cyanostictus*	Tanganyika cichlid	Adaptive, demographic	•					•	Rüber *et al.* (2001)
Thunnus alalunga *T. thynnus orientalis*	Albacore and bluefin tuna	Adaptive, demographic			•			•	Chow & Kishino (1995)
Insects									
Anopheles dirus 'species D' *A. dirus* 'species A'	Mosquitos	Adaptive, demographic			•			•	Walton *et al.* (2001)
Caledia captiva 'Moreton type' *Caledia captiva* 'Torresian type'	Grasshopper	HZ movement	•					•	Marchant (1988)

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Table 1. *Continued*

			Geographic Extent			Haplotype Frequency			
Insects con't	Common Name	Inferred Process(s)	0–50%	50–95%	>95%	0–50%	50–95%	>95%	Reference
Carabus lewisianus *C. albrechti*	Ground beetles	Adaptive, sex-biased	•				•		Takami & Suzuki (2005)
Chrysochus cobaltinus *C. auratus*	Chrysomelid beetles	Sex-biased	•				•		Monsen *et al.* (2007)
Dendroctonus rufipennis 'Rocky mountain clade' *D. rufipennis* 'Northern clade'	Spruce bark beetle	None given	•				•		Maroja *et al.* (2007)
Drosophila pseudoobscura *D. persimilis*	Fruit flies	Adaptive, sex-biased	•				•		Powell (1983)
Drosophila santomea *D. yakuba*	Fruit flies	Adaptive, *Wolbachia*			•			•	Bachtrog *et al.* (2006)
Drosophila simulans *D. mauritiana*	Fruit flies	Adaptive, *Wolbachia*		•				•	Aubert & Solignac (1990)
Eurema hecabe 'Brown type' *Eurema hecabe* 'Yellow type'	Common yellow butterfly	*Wolbachia*		•				•	Narita *et al.* (2006)
Gryllus pennsylvanicus *G. firmus*	Field cricket	Adaptive, sex-biased, *Wolbachia*	•					•	Ross & Harrison (2002)
Hemideina thoracica 'n=15 karyotype' *H. thoracica* 'n=17 karyotype'	Weta	Sex-biased, HZ movement	•				•		Morgan-Richards & Wallis (2003)
Lycaeides melissa melissa *L. m. samuelis*	Karner blue butterfly	Adaptive	•					•	Gompert *et al.* (2006)
Pissodes nemorensis *P. strobi*	Bark weevils	Sex-biased	•					•	Boyce *et al.* (1994)
Spodoptera frugiperda 'rice strain' *Spodoptera frugiperda* 'corn strain'	Armyworms	Adaptive, sex-biased	•			•			Prowell *et al.* (2004)
Mammals									
Alouatta pigra *A. palliata*	Howler monkeys	Sex-biased	•			•			Cortes-Ortiz *et al.* (2007)
Canis latrans *C. rufus*	Cyotes and wolves	Sex-biased, human	•				•		Lehman *et al.* (1991)
Capra spp. 'bezoar type' *Capra* spp. 'ibex type'	European goats	Sex-biased, demographic		•				•	Pidancier *et al.* (2006)
Cervus elaphus *C. nippon*	Red deer and Japanese sika deer	Sex-biased	•					•	Senn & Pemberton (2009)
Hemitragus jemlahicus *Capra* spp.	European goats	Adaptive, sex-biased			•			•	Ropiquet & Hassanin (2006)
Lepus timidus *L. granatensis*	Mountain and Granada hare	Adaptive, sex-biased		•			•		Melo-Ferreira *et al.* (2009)

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Table 1. *Continued*

Mammals con't	Common Name	Inferred Process(s)	Geographic Extent			Haplotype Frequency			Reference
			0–50%	50–95%	>95%	0–50%	50–95%	>95%	
Lepus timidus *L. europaeus*	Mountain and European hare	Sex-biased			•		•		Melo-Ferreira *et al.* (2009)
Lepus timidus *L. castroviejoi*	Mountain and broom hare	Sex-biased	•			•			Melo-Ferreira *et al.* (2009)
Loxodonta cyclotis *L. africana*	African forest and savannah elephant	Sex-biased	•				•		Roca *et al.* (2004)
Microcebus murinus *M. griseorufus*	Grey and reddish-grey mouse lemur	HZ movement	•					•	Gligor *et al.* (2009)
Microtus agrestis 'northern clade' *M. agrestis* 'southern clade'	Field voles	Sex-biased, demographic	•				•		Beysard *et al.* (2011)
Mus domesticus *M. musculus*	House mouse	Adaptive, demographic	•					•	Ferris *et al.* (1983)
Mustela lutreola *M. putorius*	European mink and polecat	Sex-biased	•			•			Cabria *et al.* (2011)
Myodes rutilus *M. glareolus*	Northern red-backed and bank vole	Adaptive, sex-biased	•					•	Tegelstrom (1987)
Myotis myotis *M. blythii*	Greater and lesser mouse-eared bat	Sex-biased, demographic	•					•	Berthier *et al.* (2006)
Odocoileus virginianus *O. hemionus*	White-tailed and mule deer	Sex-biased			•			•	Cathey *et al.* (1998)
Phocoenoides dalli *Phocoena phocoena*	Porpoise	Sex-biased	•					•	Willis *et al.* (2004)
Pipistrellus pipistrellus *P. pygmaeus*	Common and soprano pipistrelles	Sex-biased, demographic	•			•			Hulva *et al.* (2010)
Praomys daltoni 'Clade A' *P. daltoni* 'Clade C2'	Dalton's mouse	Sex-biased, demographic	•				•		Bryja *et al.* (2010)
Sorex araneus *S. granarius*	European common shrew	Adaptive, sex-biased, demographic			•			•	Yannic *et al.* (2010)
Spermophilus erythrogenys *S. major*	Red-cheeked and russet ground squirrel	None given	•					•	Spiridonova *et al.* (2006)
Tamias ruficaudus *T. amoenus*	Red-tailed and yellowpine chipmunk	Adaptive, demographic	•					•	Reid *et al.* (2010)
Tamiasciurus douglasii *T. hudsonicus*	Douglas and American red squirrels	Sex-biased, demographic	•			•			Chavez *et al.* (2011)
Thomomys bottae ruidosae *T. b. actuosus*	Pocket gophers	Demographic, HZ movement	•				•		Ruedi *et al.* (1997)
Ursus arctos *U. maritimus*	Brown bear and polar bear	Sex-biased			•			•	Edwards *et al.* (2011)

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Table 1. *Continued*

	Common Name	Inferred Process(s)	Geographic Extent			Haplotype Frequency			Reference
			0–50%	50–95%	>95%	0–50%	50–95%	>95%	
Reptiles									
Anolis distichus ravitergum *A. d. ignigularis*	*Anolis* lizards	Sex-biased	•				•		Ng & Glor (2011)
Crotaphytus collaris *C. bicinctores*	Common and Great Basin collared lizard	Adaptive, demographic	•					•	McGuire *et al.* (2007)
Crotaphytus collaris *C. reticulatus*	Common and reticulate collared lizard	Adaptive		•				•	McGuire *et al.* (2007)
Ctenosaura pectinata 'Colima–Balsas clade' *C. pectinata* 'north C & D clade'	Mexican black iguana	Demographic	•				•		Zarza *et al.* (2011)
Emys orbicularis *E. o. fritzjuergenobsti, E. o. galloitalica*	European pond turtle	Sex-biased, demographic	•				•		Pedall *et al.* (2010)
Podarcis spp. (not sampled) *P. hispanicus, P. liolepis*	Iberian wall lizard	Adaptive	•					•	Renoult *et al.* (2009)
Sceloporus tristichus 'northern clade' *S. tristichus* 'southern clade'	Fence lizard	HZ movement	•				•		Leache & Cole (2007)
Others									
Carcinus maenas *C. aestuarii*	Green crabs	Sex-biased	•			•			Darling (2011)
Mesobuthus gibbosus 'Anatolian type' *M. gibbosus* 'greek type'	Scorpion	Adaptive, sex-biased	•					•	Gantenbein & Largiader (2002)
Mytilus edulis *M. galloprovincialis*	Blue and Mediterranean mussel	Adaptive		•				•	Rawson & Hilbish (1998)
Mytilus edulis *M. trossulus*	Blue and bay mussel	Adaptive, demographic		•				•	Quesada *et al.* (1999)
Orconectes rusticus *O. propinquus*	Rusty northern and clearwater crayfish	Sex-biased, human	•				•		Perry *et al.* (2001)
Strongylocentrotus pallidus *S. droebachiensis*	Sea urchins	Sex-biased, demographic	•			•			Addison & Hart (2005)

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Table 2. Cases of mitochondrial–nuclear discordance following secondary contact where clines in mtDNA are narrower than nuDNA. For additional details on genetic patterns and inferred processes, see the Table S2 (Supporting information)

Taxa	Animal Group	Common Name	nuDNA Introgression	Sex-biased	Reference
Rana blairi *R. pipiens*	Amphibian	Plains and northern leopard frog	•	•	Di Candia & Routman (2007)
Hippolais icterina *H. polyglotta*	Bird	Icterine and melodious warbler	•		Secondi *et al.* (2006)
Larus spp.	Bird	*Larus* Gulls	•	•	Crochet *et al.* (2003)
Parus minor *P. major*	Bird	Japanese and great tit		•	Kvist & Rytkoenen (2006)
Passerina cyanea *P. amoena*	Bird	Indigo and lazuli bunting		•	Carling & Brumfield (2008)
Phylloscopus collybita collybita *P. c. brehmii*	Bird	Iberian and common chiffchaff		•	Bensch *et al.* (2006)
Setophaga petechia 'west' *S. petechia* 'east'	Bird	Yellow warbler		•	Gibbs *et al.* (2000)
Coregonus clupeaformis	Fish	Lake whitefish	•		Lu *et al.* (2001)
Limenitis arthemis astyanax *L. a. arthemis*	Insect	Admiral butterflies	•		Mullen *et al.* (2008)
Macaca mulatta *M. fascicularis*	Mammal	Rhesus and long-tailed macaque	•	•	Bonhomme *et al.* (2008)
Microtus arvalis	Mammal	Common vole		•	Braaker & Heckel (2009)
Pongo pygmaeus	Mammal	Orang-utan		•	Nietlisbach *et al.* (2012)
Sorex antinorii	Mammal	Valais shrew		•	Yannic *et al.* (2012)

Box 2. Extensive Discordance in Various Groups

A number of studies evaluating mtDNA and nuclear variation in many taxa have reported rampant discordance between marker types, where there is evidence for extensive introgression of mtDNA between numerous pairs of taxa within a single taxon complex. Such patterns have been reported in: *Laupala* crickets (Shaw 2002), *Neodiprion* sawflies (Linnen & Farrell 2007), *Bufo* Toads (Fontenot *et al.* 2011), *Brienomyrus* electric fishes (Sullivan *et al.* 2004), *Ohomopterus* carabid beetles (Sota 2002), *Lycaeides* butterflies (Gompert *et al.* 2008) and Tibetan megophryid frogs (Chen *et al.* 2009). Most studies show numerous cases of discordance between phylogenies generated from mtDNA and nuDNA in the absence of specific cases of hybridization (i.e. Shaw 2002). In a particularly well-developed case, Linnen & Farrell (2007) report that mitochondrial gene flow was consistently higher than nuclear gene flow across 120 pairwise species comparisons in *Neodiprion* sawflies. They suggest that shared hosts and/or pheromones facilitate hybridization between species and that differences in abundance between pairs could promote mitochondrial introgression (Linnen & Farrell 2007).

In another interesting case, Gompert *et al.* (2008) identified a single mitochondrial haplotype ('h01') that is distributed among various taxonomic groups of *Lycaeides* butterflies. This pattern is not concordant with other mtDNA clades or nuclear DNA, but was positively associated with the presence of the endosymbiotic bacterium *Wolbachia*. In general, however, it is not clear why these taxonomic groups tend to show a propensity to introgress mtDNA compared with others, aside from incomplete reproductive barriers facilitating hybridization. Indeed, identifying any unifying characteristics across these disparate taxonomic groups displaying extensive discordance will be important for future studies.

However, in the majority of studies, sampling suggests that asymmetric discordance does not extend far beyond the current area of sympatry – most studies found that foreign mtDNA did not extend beyond 50% of the range of the native taxon (Fig. 5). For example, in a hybrid zone between the Guatemalan black howler monkey, *Alouatta pigra*, and the Mantled howler, *A. palliata*, hybrids are rare, but the majority have *A. pigra* mtDNA (Cortes-Ortiz *et al.* 2007). In this case, the authors suggest that this is caused by a combination of biased mating and postzygotic selection on offspring, where hybrids between female *A. palliata* and male *A. pigra* do not develop. In some cases where human-mediated introgression has been implicated, discordance also does not appear to be extensive. For instance, in lakes where rainbow trout (*Oncorhynchus mykiss*) have been introduced and allowed to hybridize with native cutthroat trout (*O. clarkii*), mtDNA shows a bias towards *O. mykiss* haplotypes, beyond what would be expected based on nuclear genotypes, but not to complete fixation (Metcalf *et al.* 2008).

In those cases where foreign mtDNA haplotypes are found deep within the range of a second taxon, they are

Box 3. Mitochondrial Structure in the Absence of Geographic Isolation

The vast majority of studies that identify mitochondrial DNA structure and/or divergence also have complementary historical and biogeographic evidence that imply divergent mitochondrial haplotypes evolved during periods of geographic isolation (Tables 1 and 2). Interestingly, four recent studies have identified mtDNA divergence where long periods of allopatry are less likely, all of which are in avian systems. This pattern has been observed between highland and lowland mtDNA clades of the rufous-collared sparrow (*Zonotrichia capensis*; Cheviron & Brumfield 2009), arid and mesic clades of the karoo scrub-robin (*Cercotrichas coryphaeus*; Ribeiro *et al.* 2011), eastern and western clades of the greenish warbler (*Phylloscopus trochiloides*; Irwin *et al.* 2005), and between tree-nesting and ground-nesting host parasites of the greater honeyguide (*Indicator indicator*; Spottiswoode *et al.* 2011). While empirical examples of such phenomena are rare, simulation studies suggest that such phylogenetic breaks can arise in the absence of barriers to gene flow if dispersal and population sizes are low (Irwin 2002) or if selection favours different mtDNA haplotypes in different environments (Irwin 2012). In three of these four cases, the molecular markers used to assay the nuclear genome were microsatellites. It is important to note that because of their complex mutational patterns, microsatellites may imply higher gene flow than might otherwise be estimated from other nuclear markers with a simpler mutation mechanisms, such as SNPs (Brito & Edwards 2008). While differences in the biogeographic patterns between microsatellites and mtDNA are not necessarily expected, it would be valuable in the future for some of these cases to be confirmed with additional multi-locus nuclear markers.

Of the four cases, some period of allopatry is possible in the greenish warblers, but is not implied by phenotype or nuclear AFLPs (Irwin *et al.* 2001). In this case, it is thought that an ancestral population, which occurred near India, expanded its range northward as a 'ring' around the Tibetan plateau (Irwin *et al.* 2005). During this time, reproductive isolation evolved between northern ends of eastern and western groups and, in parallel, mtDNA structure around the southern side of the ring arose in the face of nuclear gene flow. The southern break between the two clades currently occurs in the Lāhul Valley, in the Himachal Pradesh province of India, in populations that are otherwise similar in phenotype and in their nuclear genome (Irwin *et al.* 2005). Future genomic studies employing many more nuclear genetic markers will be able to determine the role that geographic isolation did or did not play in generating the genetic patterns in this system.

In the karoo scrub-robin, genetic patterns in mtDNA and microsatellites are quite discordant – over its range in Southern Africa, the species shows little to no variation in nuclear DNA, but displays a strong east–west genetic break in mitochondrial DNA (Ribeiro *et al.* 2011). The authors report that mtDNA variation is explained best by environmental data, such as annual precipitation, as opposed to geographic distance. Whether mitochondrial variation can be attributed to adaptation to different climactic regimes, or whether other historical explanations can explain the observed patterns, will require further confirmation.

One of the most striking cases of discordance in the absence of geographic isolation can be found in mtDNA haplotype variation in the rufous-collared sparrow along an elevational gradient in South America (Cheviron & Brumfield 2009). Cheviron & Brumfield (2009) sampled individuals in populations at varying elevations in addition to populations at similar elevations at varying distances. Surprisingly, they report that the frequency of a mtDNA clade that is primarily found at high elevation, showing more genetic structure than implied by geographic variation in microsatellites along control transects. The authors hypothesize that this high-elevation haplotype may be adaptive for lower temperatures and oxygen levels in these populations, but have not yet tested these predictions.

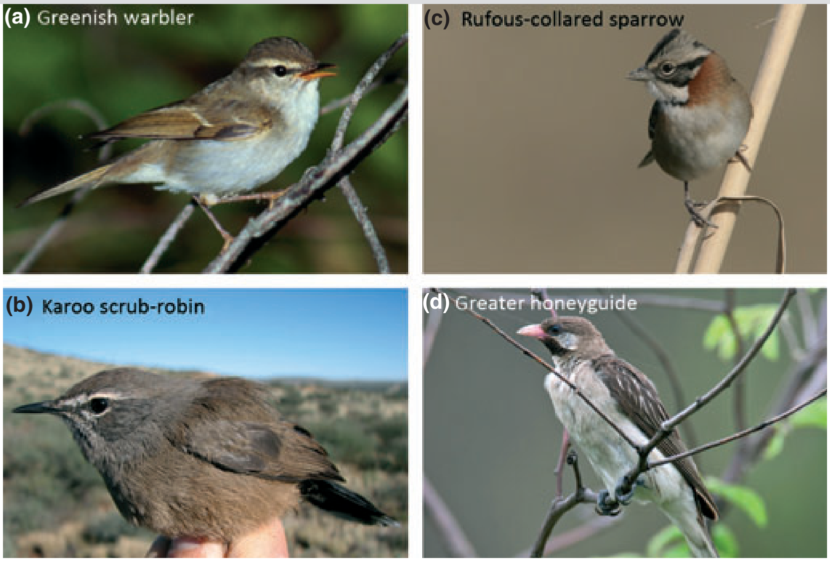

Fig. Box 3 Examples of systems where mitochondrial structure is inferred to have arisen in the absence of geographic isolation a) greenish warbler (*Phylloscopus trochiloides*) b) karoo scrub-robin (*Cercotrichas coryphaeus*) c) rufous-collared sparrow (*Zonotrichia capensis*) and d) greater honeyguide (*Indicator indicator*). Photographs reproduced with permission from Darren Irwin (a), Angela Ribeiro (b), James Lowen (c) and Warwick Tarboton (d).

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Box 3. *Continued*

Finally, a recent study of the greater honeyguide, an avian brood parasite in Africa, demonstrates strong mtDNA structure between individuals with ecologically distinct host species (ground-nesting birds versus tree nesters) with little to no structure in microsatellites (Spottiswoode *et al.* 2011). By comparison, other taxa closely related to the greater honeyguide show much more nuclear divergence for the same mtDNA distance. The authors suggest this is because of an ancient switch and subsequent adaptation to a new host species, which is faithfully parasitized by females (a behaviour that the authors suggest may be encoded by genes on the W chromosome), but where there is random mating by males between the types, facilitating nuclear gene flow. The current phylogeographic distribution of the mitochondrial clades suggests that these patterns likely arose in sympatry without a long period of geographic isolation.

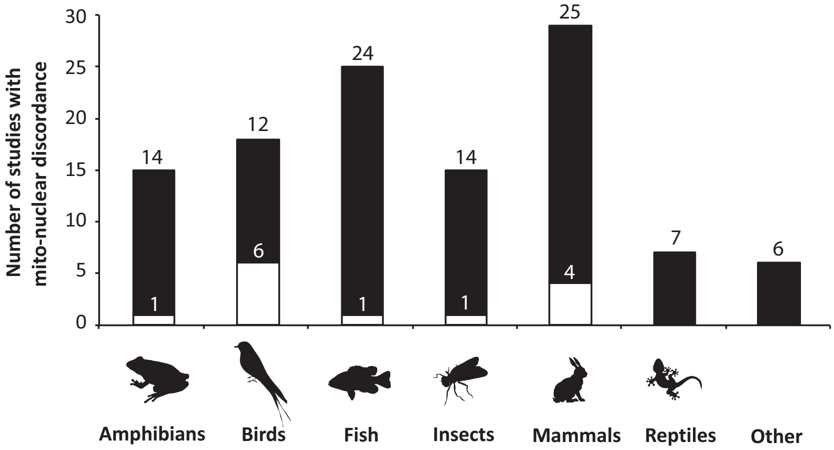

Fig. 4 The number of papers reporting mito-nuclear discordance following secondary contact distinguished by taxon group. The filled portion of the bars represent number of cases where mtDNA was less structured than nuDNA. Cases where mtDNA cline was more structured than nuDNA are indicated by the open portion of the bars.

likely to be at a high frequency (Fig. 5). For instance, we did not find any studies that identified a foreign mtDNA present at <50% frequency throughout the entire range of another taxon. In those cases where low-frequency mtDNA haplotypes (i.e. 0–50%) did extend over a large area (50–95% geographic extent), it was inferred to be caused either by hybrid zone movement (e.g. phenotypic Townsend's warblers, *Setophaga townsendii*, moving into the range of hermit warblers, *S. occidentalis*; Krosby & Rohwer 2009), large asymmetries in range size (e.g. introgression of the Woodhouse toad's mtDNA, *Bufo woodhousii*, into the Arizona toad, *B. microscaphus*, which has a nested range within *B. woodhousii*; Malmos *et al.* 2001) or differences in population sizes (e.g. the Russian sturgeon, *Acipenser gueldenstaedtii*, introgressing mtDNA into the critically endangered Adriatic sturgeon, *A. naccarii*; Ludwig *et al.* 2003). In many cases, authors could neither confirm nor rule out demographic explanations for observed discordance, where mtDNA introgression occurred because of variation in range sizes or preceding a population bottleneck and range expansion; however, most offered more specific explanations, such as adaptive introgression or sex-biased asymmetries.

Most studies identifying a large geographic extent of discordance found that, throughout the area of discordance, foreign mtDNA was either at or near fixation, completely replacing the mtDNA of the native taxon. In many of these cases, authors ascribed this to a hypothesized selective advantage of the introgressed mitochondrial type (Fig. 6a). For example, the replacement of the northern redbelly dace's (*Phoxinus eos*) mtDNA with that of the finescale dace (*P. neogaeus*) across most of its range is thought to be promoted by *P. neogaus*, with a more northerly distribution, having a mitochondria being better adapted to cold temperatures (Mee and Taylor 2012). The finding of myrtle warbler (*Setophaga coronata*) mtDNA throughout the majority of the range of the Audubon's warbler (*S. auduboni*), with considerably less nuclear introgression, also presents the potential for adaptive introgression, which authors presents may be correlated to a shift in migratory strategy (Brelsford *et al.* 2011; Milá *et al.* 2011). The repeated waves of introgression of common collared lizard (*Crotaphytus collaris*) mtDNA into populations of the Great Basin collared lizard (*C. bicinctores*) is a pattern that would not be expected under a neutral scenario and, as the authors suggest, is consistent with *C. collaris* mtDNA having a selective advantage (McGuire *et al.* 2007). In one of the few studies to test for the selective advantage of mtDNA, Aubert & Solignac (1990) found that experimental labora-

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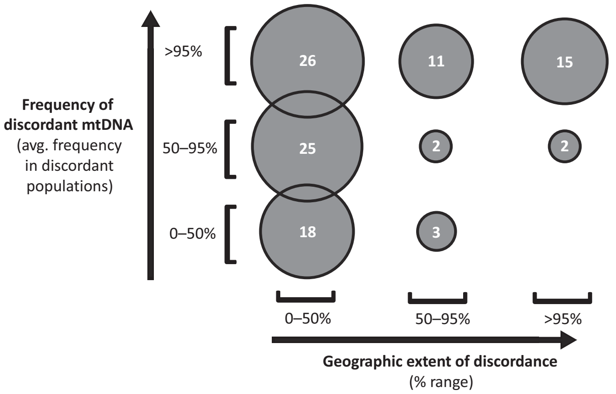

Fig. 5 The number of cases of mito-nuclear discordance following secondary contact (where mtDNA is less structured than nuDNA) distinguished by the geographic extent of discordance and the frequency of discordant haplotypes. The area of the circles is proportional to the number of cases observed in each bin, displayed in the centre of the circle.

tory conditions favoured the *Drosophila simulans* mtDNA over *D. mauritiana* haplotypes, consistent with the pattern of introgression documented in natural populations.

In contrast to adaptive introgression, sex-biased mating or offspring production (the most common explanation for discordance; Fig. 7), while in some cases is implicated in large-scale discordances, is more often associated with cases of less extensive discrepancies (Fig. 6b). For example, a classic study by Lamb & Avise (1986) found that the mtDNA of the barking tree frog, *Hyla gratiosa*, was disproportionately found in hybrids with the American green tree frog, *H. cinerea*. This was supported by behavioural observations, which suggested that *H. cinerea* males were more likely to act as satellites and tended to intercept *H. gratiosa* females, facilitating the movement of mtDNA from the latter to the former. Recently, Ng & Glor (2011) identified strong discordance between Bayesian clustering assignments from nuclear markers, mtDNA haplotypes and dewlap coloration between two subspecies of *Anolis* lizards in the Caribbean. In one of their transects, they found the mtDNA of *Anolis distichus ravitergum* throughout populations that were otherwise *A. d. ignigularis* in their nuclear genome, which they attributed to asymmetric mating and/or survival of offspring (Ng & Glor 2011).

Untangling processes driving discordance from biogeographic patterns

One difficulty in interpreting the differences in the extent and frequency between sex-biased gene flow versus adaptive introgression is that, in many cases, authors base their interpretation of the drivers of discordance on biogeographic patterns themselves. Indeed, the fact that many authors presented more than one explanation for discordant patterns in a given system (i.e. areas of overlap in Fig. 7) suggests that more data are required. Ideally, experimental manipulations or other types of complementary data could elucidate the evolutionary processes generating discordant genetic patterns. For instance, sex-biased dispersal, mating and offspring production is a common explanation for mito-nuclear discordance, but behavioural and crossing data have only been collected for a handful of systems. For example, in a genetic survey of the dark-spotted frog (*Rana nigromaculata*), Liu *et al*. (2010) found that many populations are fixed for the eastern golden frog's (*R. plancyi*) mtDNA. Data combined from the field and laboratory suggest that all F1 males were sterile, but that females were partially fertile, consistent with Haldane's rule and with patterns of mito-nuclear discordance in natural populations (Liu *et al*. 2010). Unfortunately, these data are difficult to collect in many systems, and researchers instead rely on more general patterns.

Explanations invoking adaptive introgression between related species present another paradox: the conservation of mitochondrial genes, the interplay between mitochondrial and nuclear gene products, and the

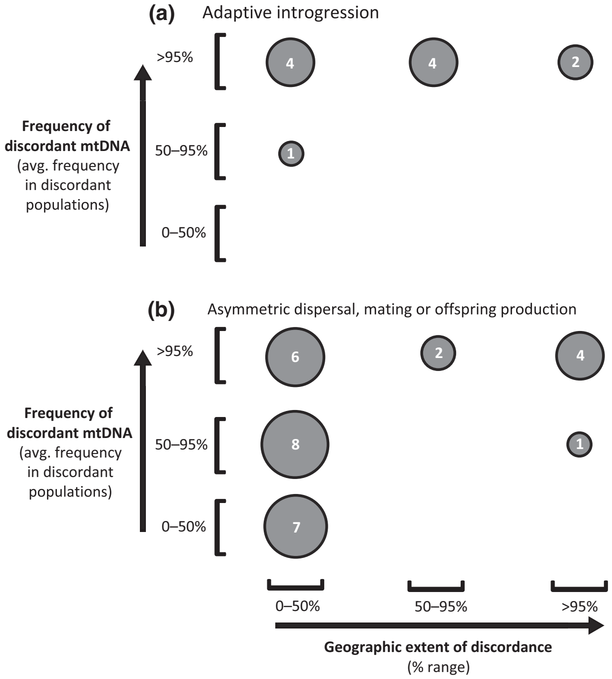

Fig. 6 The number of cases of mito-nuclear discordance following secondary contact (where mtDNA is less structured than nuDNA) distinguished by the geographic extent of discordance and the frequency of discordant haplotypes, for those cases that report only (a) adaptive introgression or (b) asymmetric dispersal, mating or offspring production. The area of the circles is proportional to the number of cases observed in each bin, displayed in the centre.

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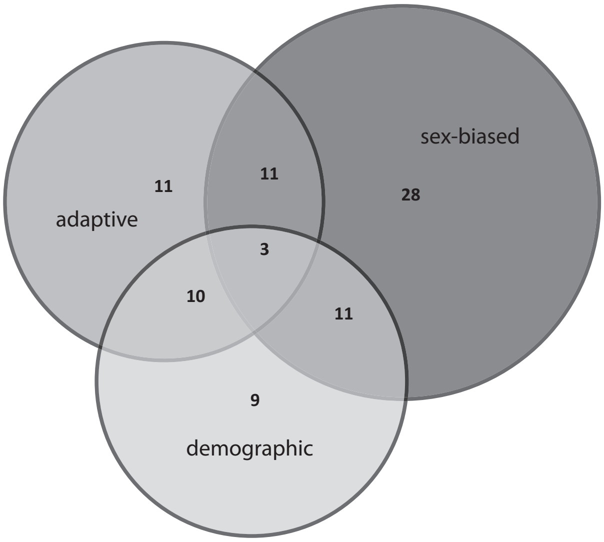

Fig. 7 A Venn diagram illustrating the prevalence of and overlap between different explanations for observed patterns of mito-nuclear discordance. The size of the circle is proportional to the number of cases within each category. It should be emphasized that overlap between the circles illustrates cases where authors offered more than one explanation for the observed discordance and is usually based on speculation as few studies have measured adaptation, dispersal or mating frequency driving discordant patterns.

central role of the electron transport chain in oxidative phosphorylation and basic metabolic functioning suggest that (i) functional mutations would only rarely have a selective advantage, and (ii) introgression between taxa with divergent mitochondrial clades would be unlikely. In fact our survey, in addition to previous work (Ballard & Whitlock 2004; Ballard & Melvin 2010) suggests that selection on the mitochondrial genome may commonly drive introgression, although few studies have tested for it. Surprisingly, of the few studies to assay potential functional differences between mitochondrial types that could influence introgression, most have found only limited support (e.g. *Salvelinus* by Blier *et al.* 2006; *Myodes* by Boratynski *et al.* 2011). For example, testing for differences in metabolic rate between sympatric individuals of the bank vole (*Myodes glareolus*), some with northern red-backed vole (*M. rutilus*) mitochondria, Boratynski *et al.* (2011) found that mitochondrial type explained very little variation in basal metabolic rate. Blier *et al.* (2006) also found little evidence to suggest that functional differences in enzyme activity could explain the introgression of Arctic charr (*Salvelinus alpinus*) mtDNA into brook charr (*S. fontinalis*). Combining these types of approach with more sensitive techniques assaying mitochondrial function directly, such as respiration in isolated mitochondrial preparations (Scott *et al.* 2009), will be valuable in determining whether introgressed mitochondria differ phenotypically from the native type and, ideally, how this might affect whole-animal fitness (reviewed by Dalziel *et al.* 2009 and Ballard & Melvin 2010). In this way, cases of mitochondrial introgression could potentially be used to link the effects of specific mtDNA mutations in introgressed genetic variants to phenotypic differences (Dalziel *et al.* 2009; Scott *et al.* 2011).

Conclusions and future research

Our survey extends previous reviews of mito-nuclear discordance by focusing on the biogeographic differences that can be recovered between these divergent genomes. The prevalence of this type of discordance confirms that this is a prevalent and important phenomenon shaping genetic variation in natural populations. While some have lamented the fact that such processes may muddy the phylogenetic waters, it is clear that most authors now recognize the potential pitfalls from inferring relationships from only a small portion of the genome (Edwards & Bensch 2009). We suggest the next generation of multi-locus studies should focus on the drivers of discordance rather than simply documenting discordance in and of itself. While improved sequencing technologies will greatly aid in identifying mito-nuclear and nuclear–nuclear discordances, testing various alternative explanations (including a null model of simple genetic drift) for observed patterns will be one of the biggest challenges. Gathering phenotypic and environmental data from natural populations will be a first step, with subsequent experimental and genetic crosses ideal where feasible. Therefore, these natural systems provide a number of unique research opportunities, which include quantifying the relative importance of introgression from independent evolutionary lineages in providing genetic variation for adaptive evolution, linking genotype to phenotype in introgressed populations and individuals and, more generally, addressing fundamental questions about how natural selection and demographics act and interact in nature.

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Supporting information

Additional supporting information may be found in the online version of this article.

Table S1 Excel file of Table 1 with additional annotations of the patterns and processes producing discordance.

Table S2 Excel file of Table 2 with additional annotations of the patterns and processes producing discordance.

Table S3 Excel file of a random survey of 100 articles in Molecular Ecology and studies where biogeographic discordance is suggestive, but require further confirmation with additional data.

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