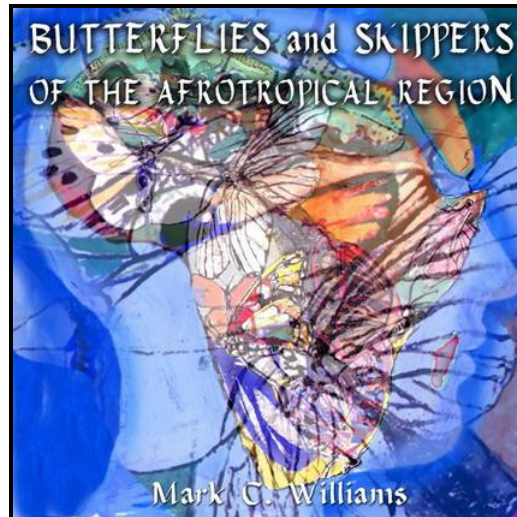


AFROTROPICAL BUTTERFLIES



BIBLIOGRAPHY OF GENERAL REFERENCES

(complete from 1973 to 2016)

E-mail: mark.williams@up.ac.za

This bibliography is a selection of publications dealing with general and technical aspects of the study of butterflies that may be of interest to those with a primary interest in the Afrotropical butterfly fauna.

* Indicates that a PDF is in my possession.

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populations largely comprising different components of genetic diversity reflecting contrasting evolutionary processes. We recommend that, under the general lineage (unified) species concept, the definition of subspecies be restricted to extant animal groups that comprise evolving populations representing partially isolated lineages of a species that are allopatric, phenotypically distinct, and have at least one fixed diagnosable character state, and that these character differences are (or are assumed to be) correlated with evolutionary independence according to population genetic structure. Phenotypic character types include colour pattern, morphology, and behaviour or ecology. Under these criteria, allopatric subspecies are a type of evolutionarily significant unit within species in that they show both neutral divergence through the effects of genetic drift and adaptive divergence under natural selection, and provide an historical context for identifying biodiversity units for conservation. Conservation of the adaptedness and adaptability of gene pools, however, may require additional approaches. Recent studies of Australian butterflies exemplify these points.

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Abstract: Aim: Swallowtail butterflies (Papilionidae) are a diverse and widespread group of insects that constitute a popular model system for ecological and evolutionary studies. We reconstruct the historical biogeography of Papilionidae to identify the dispersal or vicariance events that best explain their present-day distribution, and test several proposed biogeographical hypotheses about the processes that shape distribution patterns in cosmopolitan groups. Location: Worldwide, with disjunct elements. Methods: The phylogenetic relationships of 203 swallowtail species were determined by Bayesian inference using DNA data from mitochondrial (COI and COII) and nuclear (EF-1a) genes. Divergence time estimates were inferred using Bayesian relaxed clock approaches. To investigate competing biogeographical hypotheses, geographical range evolution was reconstructed using recently developed approaches: (1) a Bayesian empirical approach to dispersal/vicariance analysis that takes phylogenetic uncertainty into account, and (2) a likelihood approach implementing the dispersal/extinction/cladogenesis model that uses time-dependent stratified palaeogeographical matrices. Results: Our biogeographical results are congruent regardless of the biogeographical approaches or dating estimates used and support the importance of dispersal events in shaping swallowtail distributions. Contrary to common observations for other groups, the origins and diversification of northern taxa are better explained by range expansion through the Bering land bridge than by the Thulean or De Geer routes. We also stress that the seemingly Gondwanan biogeographical pattern in the Southern Hemisphere is more likely to have resulted from multiple, independent, long-distance dispersals than old vicariance events. The role of alternative colonization routes is also demonstrated for Madagascar, which facilitated multiple stepping-stone colonizations from India or Southeast Asia to Africa, and also for South America via the Caribbean land bridge. Main conclusions: Overall, the present geographical distributions of swallowtails can be better explained by dispersal events than by the long-held view of ancient vicariance events. This biogeographical study represents one of the most comprehensive phylogenetic and biogeographical studies on swallowtails. This work highlights the importance of using novel methodological approaches that provide the robust statistical frameworks needed to distinguish between competing biogeographical hypotheses. We emphasize the value of extensive taxonomic coverage for assessing the direction and frequency of supposedly rare events such as the multiple independent colonizations of Madagascar.
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Abstract: Recognizing how different species react to environmental changes provides fundamental information for conservation biology. Population and distribution trends in changing environments have been hypothesized to be highly dependent on the degree of generalism and dispersal capacity. However, different outcomes are expected for different situations. Assessing these is complicated by the paucity of reliable data over time and by the lack of continuous variables measuring the degree of species' generalism and dispersal capability. We demonstrate the value of applying two newly constructed indices, that measure the degree of species' generalism and dispersal ability, to recently published reliable data on distribution and population trends for British butterflies. We tested linear and non-linear relationships between distribution trends and species' characteristics and found that distribution cover (number of occupied squares) is highly, positively correlated with degree of generalism and dispersal ability. However, we found that distribution trends (fraction of area gained or lost over the last 10 years) has a non-linear, 'U' shaped, relationship with generalism and no relationship with dispersal ability. The non-linear relationship revealed that specialists have the highest positive trends and mid generalists the most negative trends. In accordance with a recent review, we concluded that specialists can monopolize restricted resources on fragmented habitats as long as these are large, and profit from local conservation measures, while extreme generalists can profit from any resource and can move easily among suitable patches. Intermediate species cannot competitively engage either of these alternative strategies and are thus most seriously affected by the recent environmental changes.

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variables explained 27.60% of variation in richness for all groups and 13.43% of variation in abundance and diversity in dung beetles and birds. Bioregional and environmental variables explained 43.58% of the variation in the dissimilarity matrix between transects for all groups. Main conclusions: NeoMaps provides reliable estimates of richness, composition and relative abundance, required for rigorous monitoring and spatial prediction. NeoMaps requires a substantial investment, but is highly efficient, achieving survey goals for each group with 1-month fieldwork and about US\$ 18 per km². Future work should focus on other advantages of this type of survey, including the ability to monitor the changes in relative abundance and turnover in species composition, and thus overall diversity patterns.

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ABSTRACT: Aposematic passion-vine butterflies from the genus *Heliconius* form communal roosts on a nightly basis. This behaviour has been hypothesized to be beneficial in terms of information sharing and/or anti-predator defence. To better understand the adaptive value of communal roosting, we tested these two hypotheses in field studies. The information-sharing hypothesis was addressed by examining following behaviour of butterflies departing from natural roosts. We found no evidence of roost mates following one another to resources, thus providing no support for this hypothesis. The anti-predator defence hypothesis was tested using avian-indiscriminable *Heliconius erato* models placed singly and in aggregations at field sites. A significantly higher number of predation attempts were observed on solitary models versus aggregations of models. This relationship between aggregation size and attack rate suggests that communally roosting butterflies enjoy the benefits of both overall decreased attack frequency as well as a prey dilution effect. Communal roosts probably deter predators through collective aposematism in which aggregations of conspicuous, unpalatable prey communicate a more effective repel signal to predators. On the basis of our results, we propose that predation by birds is a key selective pressure maintaining *Heliconius* communal roosting behaviour.

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Abstract: Butterfly wing color patterns consist of many color-pattern elements such as eyespots. It is believed that eyespot patterns are determined by a concentration gradient of a single morphogen species released by diffusion from the prospective eyespot focus in conjunction with multiple thresholds in signal-receiving cells. As alternatives to this single-morphogen model, more flexible multiple-morphogen model and induction model can be proposed. However, the relevance of these conceptual models to actual eyespots has not been examined systematically. Here, representative eyespots from nymphalid butterflies were analyzed morphologically to determine if they are consistent with these models. Measurement of ring widths of serial eyespots from a single wing surface showed that the proportion of each ring in an eyespot is quite different among homologous rings of serial eyespots of different sizes. In asymmetric eyespots, each ring is distorted to varying degrees. In extreme cases, only a portion of rings is expressed remotely from the focus. Similarly, there are many eyespots where only certain rings are deleted, added, or expanded. In an unusual case, the central area of an eyespot is composed of multiple "miniature eyespots", but the overall macroscopic eyespot structure is maintained. These results indicate that each eyespot ring has independence and flexibility to a certain degree, which is less consistent with the single-morphogen model. Considering a "periodic eyespot", which has repeats of a set of rings, damage-induced eyespots in mutants, and a scale-size distribution pattern in an eyespot, the induction model is the least incompatible with the actual eyespot diversity.

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- Abstract:** Despite the monarch butterfly (*Danaus plexippus*) being famous for its adaptations to the defensive traits of its milkweed host plants, little is known about the macroevolution of these traits. Unlike most other animal species, monarchs are largely insensitive to cardenolides, because their target site, the sodium pump (Na⁺/K⁺-ATPase), has evolved amino acid substitutions that reduce cardenolide binding (so-called target site insensitivity, TSI). Because many, but not all, species of milkweed butterflies (Danaini) are associated with cardenolide-containing host plants, we analyzed 16 species, representing all phylogenetic lineages of milkweed butterflies, for the occurrence of TSI by sequence analyses of the Na⁺/K⁺-ATPase gene and by enzymatic assays with extracted Na⁺/K⁺-ATPase. Here we report that sensitivity to cardenolides was reduced in a stepwise manner during the macroevolution of milkweed butterflies. Strikingly, not all Danaini typically consuming cardenolides showed TSI, but rather TSI was more strongly associated with sequestration of toxic cardenolides. Thus, the interplay between bottom-up selection by plant compounds and top-down selection by natural enemies can explain the evolutionary sequence of adaptations to these toxins.
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- Abstract: 1. Dispersal ability of a species is a key ecological characteristic, affecting a range of processes from adaptation, community dynamics and genetic structure, to distribution and range size. It is determined by both intrinsic species traits and extrinsic landscape-related properties. 2. Using butterflies as a model system, the following questions were addressed: (i) given similar extrinsic factors, which intrinsic species trait(s) explain dispersal ability? (ii) can one of these traits be used as a proxy for dispersal ability? (iii) the effect of interactions between the traits, and phylogenetic relatedness, on dispersal ability. 3. Four data sets, using different measures of dispersal, were compiled from published literature. The first data set uses mean dispersal distances from capture-mark-recapture studies, and the other three use mobility indices. Data for six traits that can potentially affect dispersal ability were collected: wingspan, larval host plant specificity, adult habitat specificity, mate location strategy, voltinism and flight period duration. Each data set was subjected to both unifactorial, and multifactorial, phylogenetically controlled analyses. 4. Among the factors considered, wingspan was the most important determinant of dispersal ability, although the predictive powers of regression models were low. Voltinism and flight period duration also affect dispersal ability, especially in case of temperate species. Interactions between the factors did not affect

dispersal ability, and phylogenetic relatedness was significant in one data set. 5. While using wingspan as the only proxy for dispersal ability maybe problematic, it is usually the only easily accessible species-specific trait for a large number of species. It can thus be a satisfactory proxy when carefully interpreted, especially for analyses involving many species from all across the world.

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- Abstract:** Over the past four decades, many researchers have applied the theory of island biogeography (IBT) to predict and understand species loss and distribution in fragmented landscapes. Recent studies found that specialist species were more affected by fragment size and isolation than generalists. However, the mechanisms underlying different effects of area and isolation among specialists and generalists are unknown. We tested the predictions of IBT on butterfly assemblages in Tokyo, Japan, and hypothesized that the effects of fragment size and isolation would be stronger for specialists than for generalists. We classified butterfly species into specialists and generalists for each of two dimensions (food range and voltinism) and according to tolerance to the matrix. We recorded 26 feeding specialists and 27 generalists, 24 seasonal

specialists and 29 generalists, 32 low matrix-tolerant species and 21 high matrix-tolerant species in 20 forest fragments. We used generalized linear models to relate the number of species in a fragment to fragment size and isolation (distance to the mainland). The averaged models based on AICc showed that fragment size had positive and significant effects on both specialist and generalist and high matrix-tolerant butterfly species richness. However, the negative effects of isolation on species richness were only found in specialist and low matrix-tolerant species. Our results demonstrate that patch isolation only affects specialist species. This suggests that when applying IBT to terrestrial fragmented landscapes, researchers should be careful not to overlook patch area and isolation effects on specialists.

SOHN, J.-C., LABANDEIRA, C., DAVIS, D. & MITTER, C. 2012. An annotated catalog of fossil and subfossil Lepidoptera (Insecta: Holometabola) of the world. *Zootaxa* 2012, 30 Apr: 1-132.

ABSTRACT: In this catalog, we attempt to assemble all fossil records of Lepidoptera described formally or informally in the world literature. A total of 667 records dealing with at least 4,568 specimens have been compiled. They include descriptions of 131 fossil genera and 229 fossil species, as well as 72 extant genera and 21 extant species to which some of these fossils supposedly belong or show superficial similarity. Replacement names of two fossil genera are proposed to avoid homonymy: *Baltopsyche* Sohn, gen. nov. for *Palaeopsyche* Sobczyk and Kobbert, 2009 and *Netoxena* Sohn, gen. nov. for *Xena* Martins-Neto, 1999. New generic combinations are proposed for: *Tortrix? destructus* Cockerell, 1916, *Tortrix florissantanus* Cockerell, 1907, and *Tortrix* sp. sensu Gravenhorst (1835), all three to *Torticites* Kozlov, 1988; *Pterophorus oligocenicus* Bigot, Nel and Nel, 1986, to *Merrifieldia* Tutt, 1905; *Aporia* sp. sensu Branscheid (1969) to *Pierites* Heer, 1849; *Noctua* spp. sensu Hope (1836) and Lomnicki (1894), both to *Noctuites* Heer, 1849. Eleven names improperly proposed for lepidopteran fossils are invalidated: *Baltonides roeselliformis* Skalski in Kosmowska-Ceranowicz and Popielek, 1981; *Baltodines* Kupryjanowicz, 2001; *Barbarothesa* Scudder, 1890; *Lepidopterites* Piton, 1936; *Palaeozygaena* Reiss, 1936; *Psamateia calipsa* Martins-Neto, 2002; *Saxibatinca meyi* Skalski in Kristensen and Skalski, 1998; *Spatalistiforma submerga* Skalski, 1976; *Thanattites juvenalis* Scudder, 1875; *Torticibaltia diakonoffi* Skalski, 1976; and *Zygaenites* Reiss, 1936. An unnecessary subsequent type designation for *Pierites* Heer, 1849, is discussed. A total of 129 records include lepidopteran fossils which cannot be placed in any taxonomic rank. There also exist at least 25 fossil records which lack any evidence of the supposed lepidopteran association. Misidentified specimens, including 18 fossil genera, 29 fossil species and 12 unnamed fossils, are excluded from Lepidoptera. All the known lepidopteran fossils are annotated by fossil type, specimen deposition, excavation locality, association with plants when present, and geological age. A bibliographic list of lepidopteran fossils is provided.

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Abstract: Due to its impact on local adaptation, population functioning or range shifts, dispersal is considered a central process for population persistence and species evolution. However, measuring dispersal is complicated, which justifies the use of dispersal proxies. Although appealing, and despite its general relationship with dispersal, body size has however proven unsatisfactory as a dispersal proxy. Our hypothesis here is that, given the existence of dispersal syndromes, suites of life-history traits may be alternative, more appropriate proxies for dispersal. We tested this idea by using butterflies as a model system. We demonstrate that different elements of the dispersal process (i.e., individual movement rates, distances, and gene flow) are correlated with different suites of life-history traits: these various elements of dispersal form separate

syndromes and must be considered real axes of a species' niche. We then showed that these syndromes allowed accurate predictions of dispersal. The use of life-history traits improved the precision of the inferences made from wing size alone by up to five times. Such trait-based predictions thus provided reliable dispersal inferences that can feed simulation models aiming at investigating the dynamics and evolution of butterfly populations, and possibly of other organisms, under environmental changes, to help their conservation.

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Abstract: As dispersal plays a key role in gene flow among populations, its evolutionary dynamics under environmental changes is particularly important. The inter-dependency of dispersal with other life history traits may constrain dispersal evolution, and lead to the indirect selection of other traits as a by-product of this inter-dependency. Identifying the dispersal's relationships to other life-history traits will help to better understand the evolutionary dynamics of dispersal, and the consequences for species persistence and ecosystem functioning under global changes. Dispersal may be linked to other life-history traits as their respective evolutionary dynamics may be inter-dependent, or, because they are mechanistically related to each other. We identify traits that are predicted to covary with dispersal, and investigated the correlations that may constrain dispersal using published information on butterflies. Our quantitative analysis revealed that (1) dispersal directly correlated with demographic traits, mostly fecundity, whereas phylogenetic relationships among species had a negligible influence on this pattern, (2) gene flow and individual movements are correlated with ecological specialisation and body size, respectively and (3) routine movements only affected short-distance dispersal. Together, these results provide important insights into evolutionary dynamics under global environmental changes, and are directly applicable to biodiversity conservation.

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