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Falklands: facts and fiction

A reply to McDowall, R.M. (2005) Falkland Islands biogeography: converging trajectories in the South Atlantic Ocean. *Journal of Biogeography*, **32**, 49–62.

A recent contribution (McDowall, 2005) analysed the biogeography of the Falkland Islands, an archipelago situated in the south-western Atlantic, known in Spanish as Islas Malvinas. After reviewing the

literature, McDowall (2005) concluded that the biotic and geological connections of the Falklands conflict with each other because the biota shows apparent relationships with Patagonia, whereas the geology suggests a historical relationship with South Africa. He considered that these results indicate that Croizat's dictum that 'earth and life evolve together' 'does not have general application in the way that some believe it has' (McDowall, 2005, p. 59), thus ruling out vicariance as an appropriate explanation for the evolution of the Falklands' biota.

We find that McDowall (2005) ignored several significant entomological papers that deal explicitly with panbiogeographical and cladistic biogeographical hypotheses on Falkland biogeography (Morrone, 1992a, 1993, 1994a, 1998, 2000; Morrone *et al.*, 1994; Posadas & Morrone, 2003, 2004). This is particularly disappointing as McDowall (2005, p. 52) stated: 'I have found exploring their [insects'] generalized affinities and biogeography rather more difficult than for some other groups'. Additionally, we concur with Knapp's (2005) comment on McDowall's paper that 'the dictum is self-evident and true across all timescales'.

For over a decade we have been studying the weevil fauna of the Falklands (Morrone, 1992a,b, 1993, 1994a,b, 1995, 1998, 2000; Morrone *et al.*, 1994; Morrone & Anderson, 1995; Morrone & Marvaldi, 1998; Posadas, 2002; Posadas & Morrone, 2003, 2004). In addition to revising several weevil genera distributed in the Falklands, we undertook phylogenetic analyses of their species and analysed their historical biogeography from the panbiogeographical and cladistic biogeographical viewpoints. We wish to comment here on our biogeographical contributions.

Morrone (1992a) undertook a panbiogeographical analysis of 50 plant and animal taxa, including species of ferns, angiosperms, Collembola, beetles (Carabidae, Staphylinidae and Curculionidae), Ephydridae, Delphacidae, Mallophaga, Crustacea (Ostracoda, Cladocera, Isopoda and Copepoda), Oligochaeta and Mollusca, distributed in several Subantarctic islands: the Falklands, Tierra del Fuego, South Georgia, Campbell and other New Zealand islands, Tristan da Cunha–Gough, Crozet, Marion, Prince Edward and Juan Fernández, as well as Patagonia and Magellan. This analysis allowed us to recognize five generalized tracks (Fig. 1a); four of these overlap in the Falklands, connecting them with Tierra del Fuego–Magellan–Patagonia, Tristan da Cunha–Gough, South Georgia, and Crozet-Marion–Prince Edward, thus identifying these islands as a node. A parsimony analysis of endemicity based on weevil species belonging to the families Anthribidae, Erirhinidae and Curculionidae (Morrone, 1998) led to the identification of four biotic components (Fig. 1b): New Zealand with the Snares, Auckland, Campbell and Chatham Islands; South America with the Falklands and Tierra del Fuego; Tristan da Cunha with Gough, Inaccessible and Nightingale Islands; and Kerguelen, Heard, Crozet, Marion and Prince Edward Islands. From both studies it can be concluded that the Falkland Islands have a complex biota, with some taxa exhibiting close relationships with the biota of southern South America, and other taxa showing biotic connections with other Subantarctic islands. All the weevils belong to the southern South American element, being distributed in the Maule, Valdivian Forest, Falkland Islands, Magellanic Moorland and Magellanic Forest provinces of the Subantarctic subregion (Morrone, 2000).

We undertook three cladistic biogeographical analyses, which included beetle taxa from the Falklands: one based on three genera of the weevil tribe Rhytirrhinini (Morrone, 1993); another based on seven genera of Carabidae, Cleridae and Curculionidae (Morrone *et al.*, 1994); and a third based on six genera and one generic group of weevils (Posadas & Morrone, 2003). The first analysis led to a general area cladogram (Fig. 1c), according to which the area fragmentation followed the sequence: (Magellanic Moorland (Valdivian Forest (Magellanic Forest, Falkland Islands))). In the general area cladogram from the second analysis (Fig. 1d), the sequence was: (Maule (Valdivian Forest (Falkland Islands (Magellanic Moorland, Magellanic Forest)))). The sequence of the general area cladogram from the third analysis (Fig. 1e) was: ((Central Chile (Maule, Valdivian Forest)), (Falkland Islands (Magellanic Forest, Magellanic Moorland))). All the cladistic biogeographic analyses basically agree in showing a close relationship of the Falklands with the Magellanic Forest or with the Magellanic Forest and the Magellanic Moorland.

Morrone (1993) combined a panbiogeographical analysis with a cladistic biogeographical analysis. He obtained a Subantarctic generalized track, based on the species of nine genera of Rhytirrhinini, connecting the Valdivian Forest, Magellanic Forest, Magellanic Moorland and the Falklands (Fig. 1f). He then hypothesized the sequence of fragmentation of the widespread Subantarctic biota, based on the sequence of the general area cladogram (Fig. 1g–i). From this analysis we can see that some of the complexities of the Falkland biota may be explained by a double connection with both the Magellanic Forest and the Magellanic Moorland, and their isolation from them at two different times.

The weevil fauna of the Falklands is highly endemic, with 18 species and three genera endemic to the islands, and only four species of the islands also distributed in the Subantarctic provinces of the continent, namely Magellanic Forest, Magellanic Moorland and Valdivian Forest (Posadas & Morrone, 2004). The Subantarctic generalized track (Morrone, 1993, 1995) may indicate an ancestral biota which was fragmented by geological events. How did this Subantarctic biota come to the Falklands? We hypothesize that, during the glaciations of Tertiary and Quaternary times in the Southern Hemisphere, the geographical isolation of the Falkland Islands from southern South America was broken, thus allowing geodispersal. Additionally, sea-level variations induced by glacial–eustatic agents provided the vicariant events to fragment this biota.

McDowall (2005, p. 58) discussed the possibility of land connections between the Falklands and South America during the Pleistocene, however he underestimated their importance as determinant events for the biogeography of the islands. There is, however, strong geological evidence that most of the continental shelf of southern South America, where the Falklands are located, was an emergent land mass during the Pleistocene glaciations (Posadas & Morrone, 2004 and literature cited therein). Assuming the Falklands reached their actual position 130 Ma (following the literature cited by McDowall), and considering that only sea levels 200 m lower than present-day levels would allow their connection with Patagonia (a generous speculation, since it is possible that with only a fall of 100–150 m in sea level a land connection could be established between these areas, or at least the ocean gap was really substantially narrower than today), allows us to infer that the islands were land-connected to Patagonia more than once during the past 130 Myr. Sea-level curves of Haq *et al.* (1988) for Mesozoic and Tertiary times indicate that, at least from 115 Ma (Early Cretaceous) to 30 Ma (Late Oligocene), the sea level was 200 m lower than today, even with peaks of > 400 m, and for the past

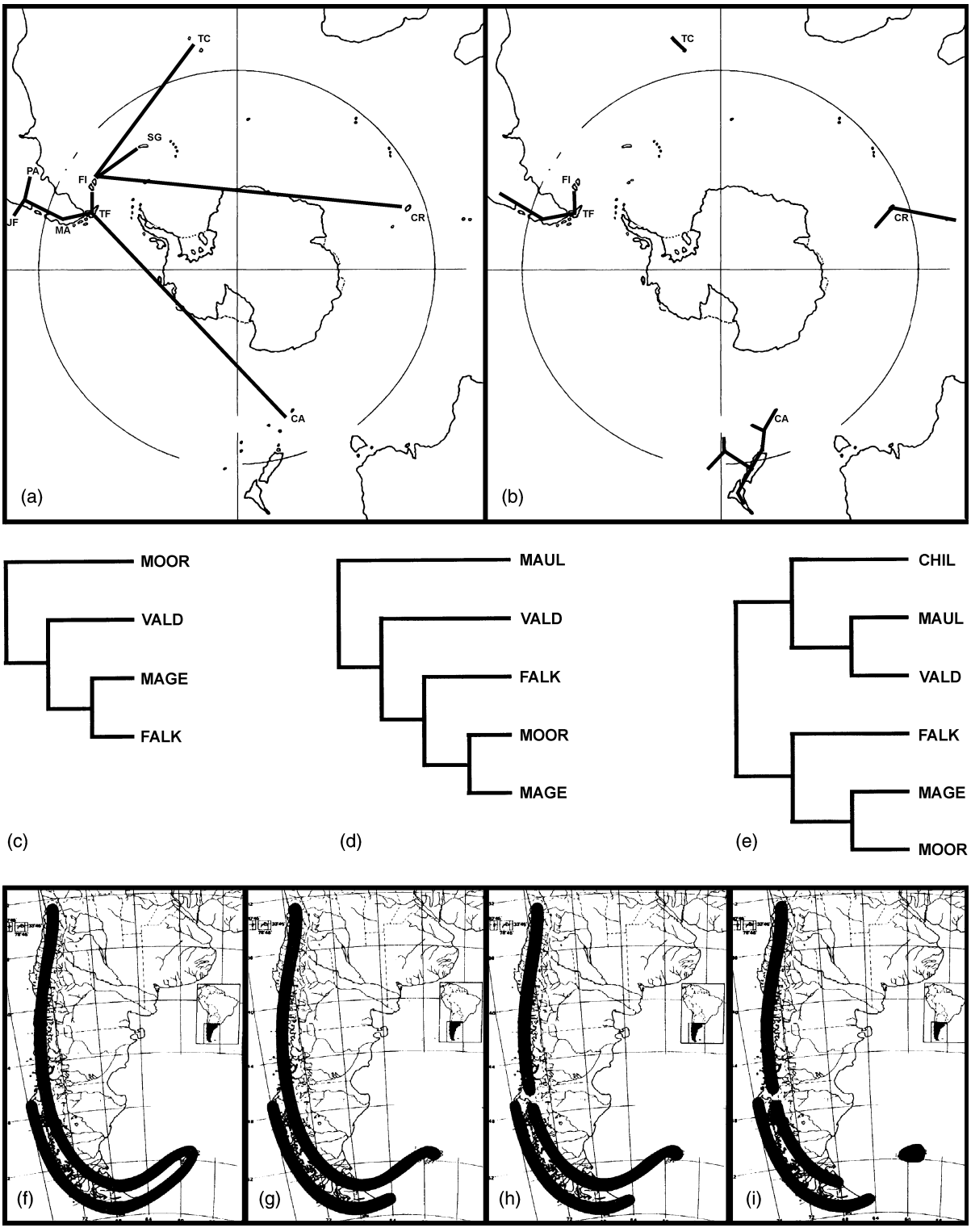

Figure 1 (a) Polar view of the southern hemisphere showing the generalized tracks obtained by Morrone's (1992a) analysis of 50 plant and animal taxa; (b) polar view of the southern hemisphere showing the biotic components identified by Morrone's (1998) parsimony analysis of endemicity based on weevil species; (c) general area cladogram from Morrone (1993) based on three genera of the weevil tribe Rhytirrhinini; (d) general area cladogram from Morrone *et al.* (1994) based on seven genera of Carabidae, Cleridae and Curculionidae; (e) general area cladogram from Posadas & Morrone (2003) based on six genera and one generic group of weevils; (f–i) sequence of area fragmentation based on a panbiogeographical and cladistic biogeographical analysis by Morrone (1993) of species of the weevil tribe Rhytirrhinini. CA, Campbell and other New Zealand Islands; CR, Crozet, Marion and Prince Edward Islands; FI, Falkland Islands; JF, Juan Fernández Islands; MA, Magellan area; PA, Patagonia; SG, South Georgia; TC, Tristan da Cunha–Gough Islands; TF, Tierra del Fuego.

11 Myr there have been at least five events when the sea level was around 100 m lower than the present. This means that, during most of the 130 Myr when the Falklands were placed in their actual position near Patagonia, they were land-connected.

McDowall (2005) emphasized the geological connection of the Falklands with Africa. This connection is confirmed in recent geological studies for pre-breakup times (late Permian; Trewin *et al.*, 2002). During pre-breakup times, however, South America, the Falklands and Africa were all part of a unique land mass, the Gondwana supercontinent. Fossil evidence supports the historical relationship of South America, Africa and the Falklands through the presence of Neopalaeozoic strata containing the typical *Glossopteris* flora (Ramos, 1999). Furthermore, Gondwanaland reconstructions for 100 Ma show the Falklands land-connected to South America, and with a strong ocean gap related to southern Africa (Pascual, 1998). Unfortunately, the scarce Mesozoic fossil evidence from the Falklands does not allow precise inference of when the biotic links of the islands became Patagonian rather than African (N.R. Cúneo, pers. comm.). But is it reasonable to trace a biotic Falkland–African connection, when these areas had broken apart at least 130 Ma, and to suppose that all Patagonian elements dispersed to the Falklands in the aforementioned context of sea-level variation? We think the answer is no. *Glossopteris* evidence for an ancient connection, and the geological evidence of eustatic changes, are enough to sustain the claim that Croizat's dictum is still valid for the Falkland biota.

There is a point in McDowall's (2005, p. 59) conclusions that we cannot leave aside. He suggests that one of the causes of the extinction of the African elements from the Falklands could be related to 'climatic fluctuations, perhaps especially Pleistocene to Recent, inflicting a severe sorting of the Falklands biota'. Could anybody be empirically justified in assuming that during the past 130 Myr – when the Falklands become completely separated from Africa and connected to the Patagonian continental shelf – that the most important events in their biotic history were related to the last few million years?

McDowall (2005) provided some generalizations on the distribution of Falkland plant and animal taxa, but failed to recognize eustatic changes, which result in geodispersal and vicariance, as determinant factors for biogeography. He provided minimal biotic evidence for a former African connection, and vague statements about the present biota being derived from Patagonia either over the sea, or land, or both (McDowall, 2005, p. 59). We feel his conclusions have more to do with his dispersalist faith than actual biogeographical and geological evidence.

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Falklands: fact, fiction or fiddlesticks?

A reply to J.J. Morrone & P. Posadas (2006) Falklands: facts and fiction. *Journal of Biogeography*, **32**, 2183–2187.

I appreciate the opportunity to respond to Morrone and Posadas's criticism of my paper on Falklands biogeography (McDowall, 2005).

At the outset let me state quite plainly that, despite their title, Morrone and Posadas persuade me of no fiction of any sort. They complain that my paper did not cite enough of their work, despite my reference to two papers by Morrone, both of which are in their list of those that they accused me of ignoring. Most of Morrone's papers are on weevils: they concern one family, in one order, of several classes, of many phyla, present on the Falklands. Yet, don't we all know how they feel? I sometimes think that authors could have cited different, or additional, papers of mine on galaxiid fishes. To some extent, for both of us, this may reflect the poor dissemination of some of the journals we have published in. Had I been aware of all of the additional papers these authors list, I would likely have examined them, but whether or not I would have cited them is my choice. My reference data base includes seven papers by Morrone, and so clearly, at some point, I made judgements that only two of them justified explicit mention in my paper, among more than 100 papers that I did cite.

Morrone and Posadas ask ''Could anybody be empirically justified in assuming that during the past 130 Myr…the most important events in their [the Falklands] biotic history were related to the last few million years?'' Apart from their requirement for empirical justification being unclear, my response is ''Why not?'' given the African origin of Falklands geology and the geological and climatic history of the Pleistocene. I find nothing in their critique to change my stance, but this seems scarcely the point.

Morrone and Posadas list references that indicate one or more former land connections between the Falklands and Pagatonia. I accepted Pugh's (2004) summary of the literature that reached a different conclusion, but this does not seem the place to deal with this in detail for, again, it misses the point.

What, then, is the point? It is this: the Falkland Islands' biota consists largely of elements shared with Patagonia (as Morrone and Posadas affirm); many species are in common (although, perhaps not amongst the weevils!). However, the islands themselves were formerly connected to southern Africa, so that geology and biology exhibit different historical connections. Croizat (1964) and his followers use 'generalised tracks' to predict former land connections, and this approach would fail to indicate Falkland connections to Africa (even for weevils, it seems). To that extent, earth and life have not evolved together. How did this come to pass? It seems to me that, in the present context, it matters little whether (1) there was never any land connection, and Patagonian elements in the Falklands biota reached these islands by dispersing across ocean gaps, or (2) there was one land connection, or even more than one, during periods of lowered sea levels and dispersal was across a land bridge.

The fundamental points are (a) that the Falklands biota contains little or no evidence of a known former African land connection, and (b) that the present biota reached the islands by dispersal, whether across the sea or across one or more intermittent land connections. Most likely both dispersal mechanisms were involved. It really makes little difference whether there were Patagonian land connections or not – although it is clearly simplistic to argue that everything took a land route, as recent history shows. What, then, of the 'information content' of generalised tracks? They seem to me to provide nothing much more than obfuscation; a seemingly simple answer to a complicated question. Croizat's mantra that earth and life evolve together, along with his dictum of primitive cosmopolitanism, are clearly, at best, half truths and, as I saw once on a church notice board, ''Beware of half truths, you may have the wrong half!'' Given that the Falklands biota could have been derived substantially by dispersal, whether across land, or across sea, or both, panbiogeography seems to have done little to determine either the mechanism or timing involved in the phylogenetic relationships of the Falklands and Patagonian biotas.

Morrone and Posadas are dismissive about what they call my ''faith in dispersalism''. I would not put it that way but, then, I suppose plenty of biogeographers have similar thoughts about the belief held by panbiogeographers of the connections between pattern and process, which is largely assumption driven, viz. that common patterns have common causes, and that those causes are always related to earth history. I think that these assumptions are unwarranted. Molecular studies may be informative in clarifying both phylogenetic relationships and the timing of arrival of the disparate elements in the Falklands biota.

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