Track analysis of agaricoid fungi of the Patagonian forests

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Abstract. Agaricoid fungi from Patagonia have been vastly studied taxonomically since 1887, and more recently ecologically. We found five generalised tracks and three nodes for a selection of nine ectomycorrhizal and nine saprophytic species. Two areas are supernodes, complex areas supported by many nodes. One of these supernodes could be a result of a lack of sampling in the Strait of Magellan area. The other could imply a biotic radiation and a differential tolerance to more arid climate conditions in the Andes mountain chain around 44.3°S, 71.5°W. Two important areas to focus future sampling of agaricoid fungi are suggested. Generalised tracks obtained match those found for weevils (Coleoptera: Curculionidae) and oribatid mites (Acari: Oribatida) distributed along the Magellanic Forest and Magellanic Moorland provinces of the Andean region. Overlap of generalised tracks among unrelated taxa supports the idea that common processes might have caused the observed patterns. The most significant and undeniable fact is that fungal species present ecological traits that can be vital for studying geological events that have marked the biotic development.

Introduction

Track analysis was developed originally by Léon Croizat (Croizat 1958, 1964), who pointed out that two types of periodic processes define the biotic history of any biogeographical area, namely dispersal and vicariance. In the former, biotas tend to expand their distribution area because of the lack of barriers (such as, e.g. geographical and climatical barriers). In the latter, distributional areas are limited by such barriers and may suffer fragmentation (Morrone 2015*a*). These processes explain why species that share the same biogeographical area may have different dispersal capacities and ecological requirements. Croizat's central idea was that the area occupied by a species is an attribute that gives the species an identity as such; two individuals belong to the same species if they share genetic information and if they occur in the same time and space (Espinosa Organista and Llorente Bousquets 1993).

To analyse disjunct distributions, namely, taxa distributed in two or more geographically isolated areas, pre-Darwinian scientists introduced the idea of 'multiple creation centres' (Morrone 2015*a*). Darwin (1859) and Wallace (1876) saw these patterns of disjunct distributions as a result of evolution of pre-existent species that randomly crossed barriers to colonise new locations, to which they adapted and evolved into new species. This model is known as Centres of Origin, Dispersal and Adaptation (CODA; Lomolino and Brown 2009; Heads 2014). Croizat (1958) analysed the geographic distribution of several taxa and found similar patterns of distributions across great distances among different organisms, such as birds, plants and wingless insects. Croizat concluded that it was unnecessary to propose different dispersal events for each taxon, and that vicariance was the main driving force causing the observed patterns.

Agaricoid fungi have been well studied in Patagonia since 1887 (Spegazzini 1887*a*, 1887*b*), with special focus on those in Tierra del Fuego (Singer 1969; Horak 1979) and in north-western Patagonia (Singer 1954, 1969). Gamundí and Amos (2007) recorded numerous mycological expeditions to Tierra del

Fuego from 1817 to 2006. Agaricoid fungi include most species forming gilled and fleshy basidiomata, and they include both saprophytic and ectomycorrhizal species (Rinaldi *et al*. 2008). The southern forests of Patagonia belong to the Maule, Valdivian Forest and Magellanic Forest provinces of the Subantarctic subregion of the Andean region (Morrone 2015*b*). The most diverse agaricoid fungi present in the Andean forests of Patagonia are associated with several species of the endemic genus *Nothofagus* (Fagales), which diversified in Gondwanaland (Manos 1997). *Nothofagus* includes native species of some interest to local industry, namely, *N. pumilio* (Poepp. & Endl.) Krasser., known as 'lenga'. This species covers the largest area of the southern Andean mountains in Patagonia, from 37°S to 55°S (Cabrera 1976; López Bernal *et al*. 2012). Some fungi are ecologically associated with *Nothofagus* species from different southern regions; among them, the parasitic *Cyttaria* (Ascomycota) stands out. The 11 species in this genus exclusively attack *Nothofagus* species, on which they produce cankers and produce their ascomata. They are distributed along the southern Andes, south-eastern Australia, Tasmania and New Zealand. More than one species of *Nothofagus* may be attacked by the same species of *Cyttaria*, and also the same species of *Nothofagus* may be attacked by more than one species of *Cyttaria*. Crisci *et al*. (1988) presented an analysis of morphological features that allowed them to produce two cladograms for *Cyttaria* species. With the development of new techniques, Peterson *et al*. (2010) reconstructed the cophylogeny of *Cyttaria* and *Nothofagus* and estimated the time of origin of the former at 148.4–112.2 million years ago; the separation of Australia and New Zealand took place 44.6–28.5 million years ago. This finding supports the existence of this association before the separation of South America and Australasia.

The most significant fact is that fungal species present ecological traits (e.g. different nutritional modes, host specificity) that can be vital for studying different geological events that have marked the development of global biotas. Our objective was to find distributional patterns of agaricoid species in southern South America, using track analysis.

Materials and methods

The area analysed corresponds to southern South America, in Argentina and Chile, corresponding to the forests of the Subantarctic subregion of the Andean region (Morrone 2015*b*). This area is situated at 24–56°S, 57–76°W. An Andean region shapefile (G. M. Romano, unpubl. data) was used to study distributional patterns.

We used 18 agaricoid species selected by their biological and ecological relevance (Romano *et al*. 2017), nine of them being ectomycorrhizal (ECM) and nine saprophytic (SAP). Their occurrence was obtained from literature and herbaria as well as from material collected by the authors in *N. pumilio* forests. The herbaria of the Universidad de Buenos Aires (BAFC), Universidad Nacional de La Plata (LPS) and Centro de Investigación y Extensión Forestal Andino Patagónico (CIEFAP) were consulted. The ECM group is represented by *Austropaxillus statuum* (Speg.) Bresinsky & Jarosch (18 records), *Cortinarius austroduracinus* M.M.Moser (12 records), *C. magellanicus* Speg. (42 records), *C. permagnificus*

E.Horak (5 records)*, Descolea antarctica* Singer (18 records), *Inocybe geophyllomorpha* Singer (7 records), *Entoloma patagonicum* (Singer) Blanco-Dios (4 records), *Russula nothofaginea* Singer (13 records) and *Stephanopus stropharioides* E.Horak (5 records). The representatives of SAP species are *Clitocybe patagonica* (Speg.) Speg. (10 records), *Galerina gamundiae* Singer (6 records), *Gymnopus fuegianus* (Singer) Halling & J.L.Mata (9 records), *Hydropus dusenii* (Bres.) Singer (18 records), *Hypholoma frowardii* (Speg.) Garrido (22 records), *Mycena dendrocystis* E.Horak (4 records), *Pholiota baeosperma* Singer (16 records), *Pluteus spegazzinianus* Singer (23 records) and *Psathyrella falklandica* Cotton (28 records). Nomenclature follows Kirk *et al*. (2008). Nutrition information was obtained from Rinaldi *et al*. (2008).

Track analysis is based on three main concepts, namely, individual tracks, generalised or standard tracks and nodes (Morrone 2009). Once distribution points for each species were generated on a map, they were connected with a line representing the minimum distance between them, known as an individual track. Individual tracks represent the spatial coordinates of a species or a group of related species in a given area (Morrone 2015*a*). When individual tracks from different taxa match, they define a generalised track, which allows inference of the existence of an ancestral biota widely distributed and fragmented by vicariance events, suggesting a shared history (Torres-Miranda and Luna-Vega 2006). Individual tracks were considered part of a generalised track whenever they overlapped absolutely. When two or more generalised tracks overlap in an area, a panbiogeographic node (PN) is identified. It is considered a complex area, where different ancestral biotic and geological fragments interrelate in space–time as a consequence of terrain collision, docking or suturing (Morrone and Crisci 1995). Regarding the identification of nodes, it is important to note that not all species belonging to a generalised track are present in the nodes, because some individual tracks are not part of the entire extension of a generalised track. Nodes are represented by an 'x' enclosed by a circle (Fortino and Morrone 1997). All maps were generated using GlobalMapper, ver. 16.2 (Blue Marble Geographics, www.bluemarblegeo.com, accessed 20 August 2015), and Quantum GIS, ver. 2.12 Lisboa (QGIS Development Team, QGIS Geographic Information System, Open Source Geospatial Foundation Project, http://qgis.osgeo.org, accessed 5 November 2015).

Results

Individual tracks for each of the ECM and SAP species analysed are presented in Figs 1 and 2 respectively. Individual tracks showed two main patterns of distribution, with the first one exhibiting a north–south orientation almost parallel to the Andes mountain chain and meridian 71°W across Subantarctic forests to finally rotating to the east beyond parallel 51°S (Figs 1A–D, 2A, B, D, E, G, H), and the second pattern running across the Patagonian steppe, always crossing 50°S, 70°W (Figs 1E–I, 2C, F, I). Another characteristic of the individual tracks obtained is that if one extends to the north beyond 40°S, it jumps to the Chilean side of the Andes mountain chain, being further west than 72°W. Among all species studied,
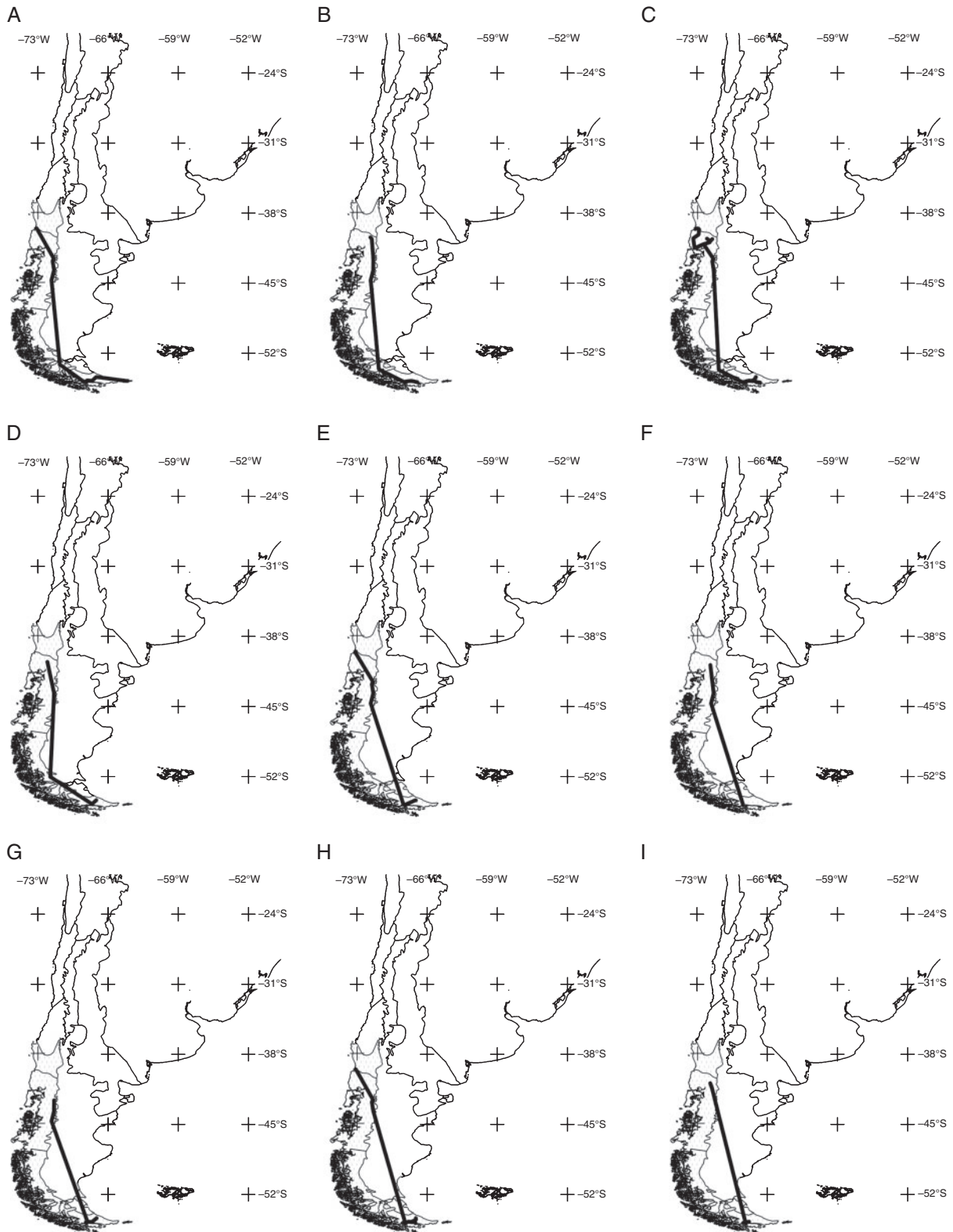
Fig. 1. Individual tracks for each ectomycorrhizal species studied. A. *Austropaxillus statuum*. B. *Cortinarius austroduracinus*. C. *C. magellanicus*. D. *C. permagnificus*. E. *Descolea antarctica*. F. *Entoloma patagonicum*. G. *Inocybe geophyllomorpha*. H. *Russula nothofaginea*. I. *Stephanopus stropharioides*. White background with grey lines indicates Subantarctic subregion.
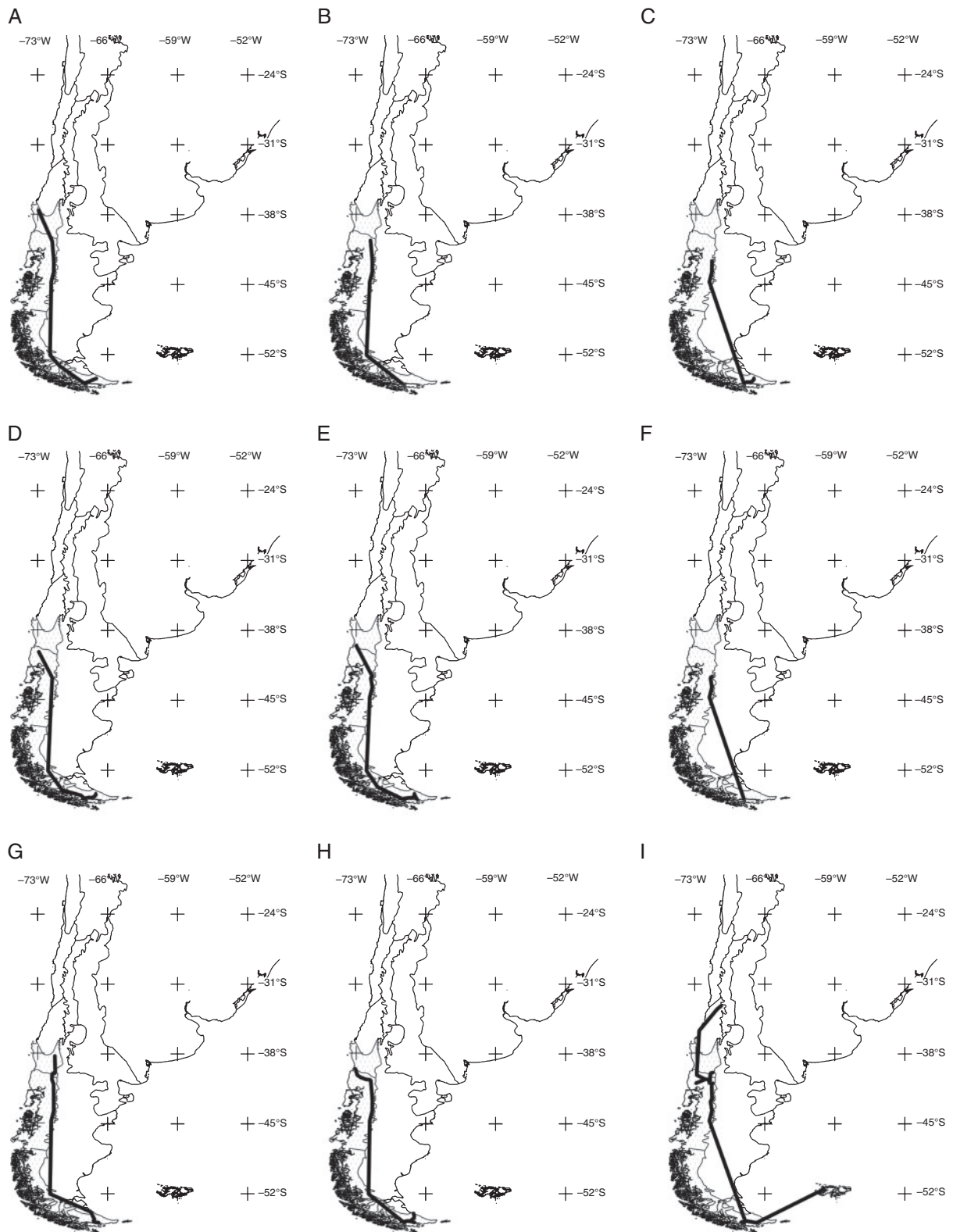
Fig. 2. Individual tracks for each saprophytic species studied. A. *Clitocybe patagonica*. B. *Galerina gamundiae*. C. *Gymnopus fuegianus*. D. *Hydropus dusenii*. E. *Hypholoma frowardii*. F. *Mycena dendrocystis*. G. *Pholiota baeosperma*. H. *Pluteus spegazzinianus*. I. *Psathyrella falklandica*. White background with grey lines indicates Subantarctic subregion.

only *Austropaxillus statuum* (Fig. 1A) and *Psathyrella falklandica* (Fig. 2I) extend beyond Tierra del Fuego Island; *A. statuum* extends to Isla de los Estados, whereas *Ps. falklandica* extends also to Malvinas Islands (Falklands). The latter represents the most extended distribution among all species studied, with occurrences above 34°S. In contrast, *Gymnopus fuegianus* (Fig. 2C) and *Mycena dendrocystis* (Fig. 2F) have the most restricted distributions and exhibit very similar individual tracks. *Cortinarius magellanicus* (Fig. 1C), *Pholiota baeosperma* (Fig. 2G), *Pluteus spegazzinianus* (Fig. 2H) and *Psathyrella falklandica* (Fig. 2I) share a high number of occurrences around 41°S, 72°W.

The general tracks and nodes obtained (Fig. 3) reflect the main patterns observed for the individual tracks, as follows:

- Generalised track A (GtA) is supported by the individual tracks of *Russula nothofaginea* and *Stephanopus stropharioides*.
- Generalised track B (GtB) is supported by the individual tracks of *Cortinarius austroduracinus* and *C. magellanicus*, and it is the most extended among all generalised tracks obtained.
- Generalised track C (GtC) is supported by the individual tracks of *Gymnopus fuegianus*, *Inocybe geophyllomorpha* and *Mycena dendrocystis*.
- Generalised track D (GtD) is supported by the individual tracks of *Cortinarius permagnificus*, *Galerina gamundiae*, *Hydropus dusenii*, *Hypholoma frowardii*, *Pholiota baeosperma* and *Pluteus spegazzinianus*.
- Generalised track E (GtE) is supported by the individual tracks of *Descolea antarctica* and *Psathyrella falklandica*.

The individual tracks of *Austropaxillus statuum*, *Clitocybe patagonica* and *Entoloma patagonicum* did not match any of the generalised tracks found.

All generalised tracks found reflect two main patterns observed for individual tracks of the selected species, with one running parallel to the Andean forests (GtB and GtD) and another crossing the Patagonian steppe (GtA, GtC and GtE).

We found 13 nodes, most of which can be understood as supernodes, which comprise several nodes in an extremely complex area (Miguel-Talonia and Escalante 2013):

Panbiogeographical supernode 1 (SN1) is located around 44.3°S, 71.5°W, and it is based on the overlap of GtA, GtB, GtC, GtD and GtE. This supernode includes eight nodes (PN1–PN8), giving SN1 an outstretched aspect in a north–south orientation.

Panbiogeographical node 9 (PN9) is located at 52.7°S, 71°W, and is based on the overlap of GtB and GtD.

Panbiogeographical supernode 2 (SN2) is located around 54.6°S, 68.2°W, and is based on the overlap of GtA, GtB, GtC, GtD and GtE. This is also a supernode, supported by four nodes (PN10–PN13); unlike those supporting SN1, these give SN2 an 'L-shaped' aspect.

Discussion

Records of fungal species occurrences in the Subantarctic subregion of the Andean region are well documented as a whole, but are scant when analysed at a species level. The selection of nine species of agaricoid ECM species and nine SAP species allowed identification of tracks and nodes at an ecoregional level.
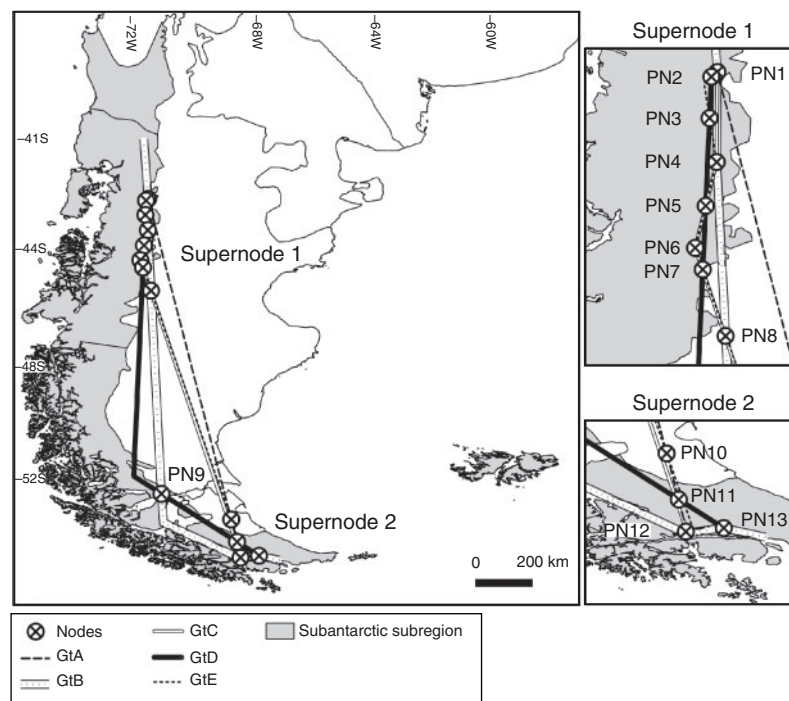

Fig. 3. Generalised tracks A, B, C, D, E; Panbiogeographical nodes PN1–13 and supernodes SN1, SN2.

Generalised tracks A, C and E show the trend of some species to disperse across two different subregions, namely, the Subantarctic and Patagonian subregions. Both represent very different habitats for fungal species because the first one comprises different layers of forest, whereas the latter is a steppe (Morrone 2015*b*). Individual tracks that contribute to GtA, GtC and GtE share a disjunct distribution, with no records to the south-west of 50°S, 70°W. The absence of such occurrences may possibly reflect poor sampling in that area rather than an actual pattern of distribution. If this were the case and all species found shared records south-west of 50°S, 70°W, such generalised tracks would not exist, leaving us with only GtB and GtD. Although the former is only supported by two species, it exhibits about the same pattern as the latter, supported by six species; that is, to run across the Andes mountain chain.

The lack of sampling could also be affecting individual tracks of *Austropaxillus statuum*, *Clitocybe patagonica* and *Entoloma patagonicum*, which did not match any of the generalised tracks found. It is also important to mention that no generalised track grouped agaricoid species by nutrition type, which could imply that such a condition is not acting as a biogeographical driving force, not at least among the species studied. In other words, if ECM species depended only on their host presence, they could be present in more locations of the Subantarctic subregion. More sampling in the region would help test this hypothesis.

Panbiogeographical supernode 1 consists of a group of nodes located in the Valdivian Forest province of the Subantarctic subregion. The area surrounding SN1 could be a bridge between biotas dispersing from north and south directions of the Andes mountain chain or a differential tolerance of the selected species to more arid climate conditions to the north of SN1.

Panbiogeographical node 9 and supernode 2 are located at both sides of the Strait of Magellan area, this may be an artefact of the lack of sampling in the area. To help determine the extent of the distribution of agaricoid fungal species in the Andean region, we denote the importance of focusing sampling in the area south-west of 50°S, 70°W, and Isla de los Estados. The latter represents the ultimate patch of the Magellanic Moorland province of the Subantarctic subregion (Morrone 2015*b*) and we have only records of *A. statuum* there (Spegazzini 1887*b*). *Psathyrella falklandica*, which had the most widespread distribution, was found not only in the continental portion of South America, but also in Malvinas Islands, where there is no Subantarctic forest (Broughton and McAdam 2005; Romano *et al.* 2017).The area around 40.9°S, 71.62°W could also be important to extend the known distribution of agaricoid fungi, because it represents an area beyond the limits of all generalised tracks found, except GtB. This generalised track could be supported by more species if they were found there.

For all species studied, more records would undoubtedly improve the accuracy of generalised tracks and nodes found in the Subantartic subregion. However, it is important to set a precedent for fungal panbiogeography in Patagonia, since fungal species present ecological traits that can be vital for studying different geological events that have marked the development of global biotas, as seen with *Cyttaria* species (Crisci *et al.* 1988; Peterson *et al.* 2010).

Generalised track B and GtD match the generalised tracks found by Morrone (2011) for weevils (Coleoptera: Curculionidae) distributed along the Magellanic Forest and Magellanic Moorland biogeographic provinces. Moreover, supernode SN2 found for agaricoid species is in close proximity to the node found by Morrone (2011) for weevils. Nodes found are also coincidental with those found by Ruiz *et al.* (2016) for oribatid mites (Acari: Oribatida).

Convergence of generalised tracks between unrelated taxa supports Croizat's idea that shared vicariance is causing the observed patterns (Croizat 1958).

Acknowledgements

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