

Enigmatic northern plains of Mars

A network of ridges in this region opens a new tectonic window onto this planet.

Although the northern plains of Mars form the flattest known surface in the Solar System, they are crisscrossed by ridge features¹. Here we test the idea that they might once have been covered by an ocean² by examining the topographic profiles of possible shorelines. We conclude that these candidate shorelines were more likely to have been formed by tectonic rather than oceanic processes.

Linear slope changes in the northern plains have been identified as possible shorelines of an ancient ocean formed during the middle period of martian history². Figure 1 shows topographic profiles, generated from Mars Orbiter Laser Altimeter (MOLA) data¹, across two such groups of shorelines. Candidate shorelines near the Utopia impact basin are flat terraces, with a higher ridge bounding their landward, or upslope, side (Fig. 1a). Possible shorelines on the other side of the proposed ocean, near the Alba Patera volcano, are also flat terraces, with a raised ridge bounding their oceanward, or downslope, side (Fig. 1b).

We believe that this morphology is hard to explain in terms of a shoreline-formation process, as is the reversal of shoreline morphology from one side of the ocean to the other. We favour the idea that these candidate shorelines were created by tectonic activity, on the basis of recent MOLA digital terrain models of kilometre-scale horizontal resolution of the northern plains of Mars.

As seen from early images recorded by Viking (Fig. 1c), these plains are essentially flat and featureless, but MOLA data (Fig. 1d) reveal a network of ridges spanning the northern plains, some of which are the candidate shorelines of the proposed ancient ocean². Most ridges appear to be related to obvious stress centres, such as the volcanic Tharsis Rise, the Utopia impact basin and the Alba Patera volcano. These ridges are generally perpendicular to the predicted directions of maximum compressive stress, which indicates that the ridges have a tectonic origin³. They also have the characteristic profile of wrinkle ridges formed by compressive tectonism⁴. Some ridges are close to known wrinkle ridge provinces, such as Lunae Plenum, and have similar strikes; clearly, these formed with the known wrinkle ridges. Both groups of candidate shorelines have orientations consistent with their formation by compressive tectonism.

The causes of the youth and smoothness of the northern plains are still debated. This network of ridges is the only tectonic feature in this region and their discovery opens a new tectonic window onto Mars.

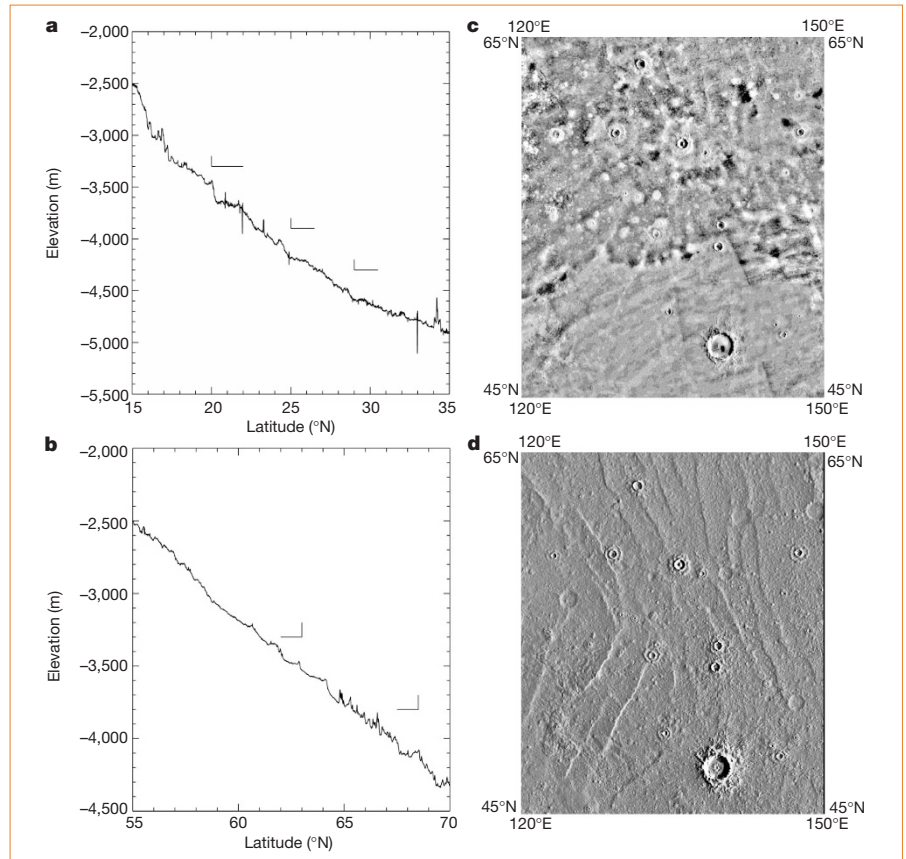


Figure 1 Martian topography. **a**, MOLA profile 10190 near the Utopia impact basin. Terraces and ridges are marked by horizontal and vertical lines, respectively. **b**, MOLA profile 10929 near the Alba Patera volcano. Terraces and ridges are marked by horizontal and vertical lines, respectively. Vertical exaggeration in **a** and **b** is by a factor of ~400. **c**, Viking photomosaic near the Utopia impact basin, Mercator projection. **d**, Shaded relief map generated from MOLA digital terrain model of the same region with the same projection. Many ridges are visible in the MOLA image that are not evident in the Viking image.

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Food-web dynamics

Animal nitrogen swap for plant carbon

Predatory plants are typically found in discrete groups living under conditions of extreme nutrient stress. But we show here how a common species of boreal tree can act indirectly as a predator of arthropods living in the soil by virtue of a fungal symbiont that supplies it with animal nitrogen in exchange for the plant's carbon. If the way in which this partnership operates proves to be widespread, ideas

about nutrient cycling^{1,2} and food-web dynamics³ in temperate forests may have to be modified.

Ectomycorrhizas are mutualisms between soil fungi and the roots of trees that improve plant nutrition, specifically by nitrogen, in exchange for carbohydrates⁴. Soil arthropods such as springtails and mites selectively feed on fungi, including mycorrhizal, decomposer and pathogenic groups⁵.

During a routine feeding study in microcosms, however, we found that less than 5% of springtails (*Folsomia candida*, a soil-dwelling arthropod) survived after two

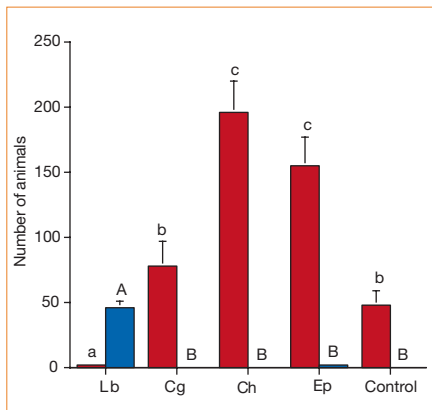


Figure 1 Predation on animals by an ectomycorrhizal fungus. Effect of different soil fungi on the survival of springtails is shown, where 'Lb' and 'Cg' represent the ectomycorrhizal fungi *Laccaria bicolor* and *Cenococcum geophilum*, respectively, which are both associated with the tree roots of *Pinus strobus*; Ch, *Cladosporium herbarum* and Ep, *Epicoccum purpurascens*, both fungal saprobes; control, no fungus. All organisms were collected from a forest dominated by *P. strobus* in Ontario, Canada. Experimental units consisted of a single fungus growing on nutrient agar in Petri dishes. Fifty springtails placed on the fungal cultures were incubated for two weeks at 20 °C and the number of living (red bars) and dead (blue bars) springtails then recorded. Animals were sectioned and analysed for internal hyphal infection. Lettering on bars represents differences at the significance level $P < 0.05$ following a Tukey *post-hoc* test; $n = 10$. Error bars represent 1 s.e.

weeks' exposure to the ectomycorrhizal fungus *Laccaria bicolor* (Fig. 1). All dead animals were internally infected by *L. bicolor*. In contrast, when grown with other test fungi, most animals survived and actively reproduced (Fig. 1; $F = 2.34$, $P = 0.00001$). No animals died after the other treatments, including in the fungus-free control (Fig. 1; $F = 1.97$, $P = 0.00001$).

This indicated that *L. bicolor* might be acting as a predator on these arthropods. Careful observation of the microcosms revealed that the ectomycorrhizal fungus immobilized the animals before infecting them. A similar strategy is used by a fungal saprobe, which produces the paralyzing toxin ostreatin⁶. We showed that a proportion of animals were still alive after being immobilized by *L. bicolor* by their positive reaction to a vital stain, fluorescein diacetate; springtails killed in ethanol were unstained. This result indicates that *L. bicolor* may also produce a toxin to paralyse its prey before hyphal invasion.

To determine the fate of the arthropod-derived nitrogen, we used ¹⁵N-labelled

springtails as prey in another microcosm study and determined the amount of ¹⁵N ending up in the foliage of young *Pinus strobus* seedlings reared in the presence of ectomycorrhizal fungi to test whether this animal-origin nitrogen taken up by *L. bicolor* could be transferred to the plant host.

Springtails (alive or already dead) labelled with ¹⁵N were added to the microcosms containing mycorrhizal or non-mycorrhizal plants. The experiment was set up so that only the fungus and not the roots made contact with the animals. The amount of nitrogen in plant tissues and extraradical fungal hyphae of animal origin were determined over a two-month period.

Significant fungus ($F = 1.15$, $P = 0.0003$), animal ($F = 2.00$, $P = 0.009$) and fungus \times animal ($F = 1.86$, $P = 0.016$) effects were found for ¹⁵N in plant tissues. Up to 25% of plant nitrogen was derived from springtails in the presence of *L. bicolor* (Fig. 2a; $F = 1.34$, $P = 0.00001$), which was able to acquire and transfer nitrogen to its host plant from either living or dead animals with comparable efficiency. At final harvest,

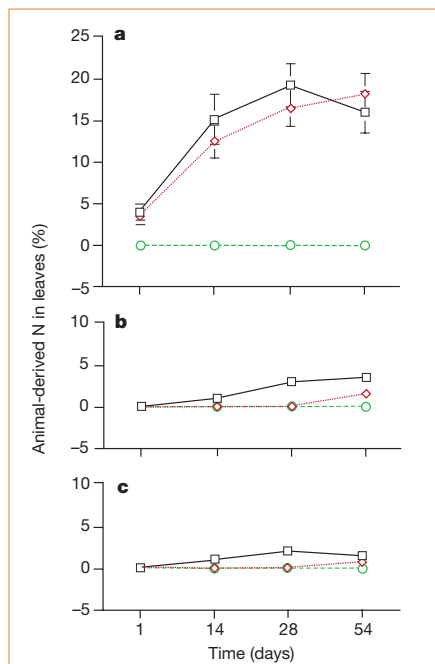


Figure 2 Percentage of plant nitrogen derived from springtails by an ectomycorrhizal fungus. Results obtained with **a**, *Laccaria bicolor*; **b**, *Cenococcum geophilum*; and **c**, without fungus. Nitrogen source: squares, live springtails; diamonds, dead springtails; and circles, no springtails. Each experimental unit consisted of a 30 \times 30 \times 1-cm glass microcosm containing silica sand, separated into two compartments by a 30- μ m mesh. One pre-germinated *P. strobus* seedling was planted in the left compartment, together with two 10-mm agar plugs of one of the two fungi added at 5 cm below the seedling. After one month of growth, 500 springtails labelled with ¹⁵N were added to the right compartment. Dead springtails were added after being killed by exposure to 50% ethanol for 30 min. Only the fungi were able to penetrate the mesh and move across both compartments. Plants were watered as needed and fertilized weekly with a low-nitrogen-containing solution. The amount of animal-origin nitrogen in the plant tissues was determined using a NOI-5 emissions spectrophotometer. Nitrogen utilization was calculated as $100 \times (\% \text{ } ^{15}\text{N in seedling leaves or fungal hyphae} / \% \text{ } ^{15}\text{N-labelled springtails})$. Plant biomass, ¹⁵N in fungal tissues, and the number of active animals remaining were determined on the final day. Results were analysed using a repeated measures factorial ANOVA; $n = 10$. Error bars represent 1 s.e. Further details are available from the authors.

plant biomass was stimulated in the *L. bicolor* + springtail treatments (mean, 1.34 g; s.e., 0.16) compared to all other treatments combined (0.81 g; s.e., 0.22) ($F = 2.02$, $P = 0.00001$). Animal extraction at the end of the experiment retrieved less than 10% of the number of animals at the start (mean, 47.2 individuals; s.e., 6.3).

In contrast, seedlings grown with a different ectomycorrhizal fungus (Fig. 2b; $F = 6.34$, $P = 0.003$) or in the absence of fungus (Fig. 2c; $F = 12.39$, $P = 0.34$) were only able to acquire nitrogen from dead springtails (less than 5% of plant N derived from springtails). Animals in these treatments had higher reproductive success and we extracted more animals than were added at the start (mean, 649.1 individuals; s.e., 98.2).

We conclude that ectomycorrhizal plants can indirectly depredate soil arthropods for a significant source of nitrogen through their fungal partners. Our results reveal a nitrogen cycle of far greater flexibility and efficiency than was previously assumed¹, where the fungal partner uses animal-origin nitrogen to 'barter' for carbon from the host tree. The host, in turn, supplies its fungal associate with carbon to synthesize proteolytic enzymes. Should this phenomenon prove to be widespread, forest-nutrient cycling may turn out to be more complicated and tightly linked than was previously believed.

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Power laws

Are hospital waiting lists self-regulating?

We have discovered that waiting lists to see hospital consultants are subject to the power laws of complexity theory, and so are likely to be an essential symptom of an efficient healthcare service. Like other complex networks, both privately and publicly funded healthcare systems probably organize themselves in such a way as to reduce the impact of any attempted intervention. They self-regulate to buffer against differing levels of demand, thereby creating bottomless pits that absorb all resources made available. It seems that we would be wiser to judge the system by measuring the overall quality of medical care, rather than by the length of hospital waiting lists.