

BRIEF COMMUNICATIONS

'Devil's gardens' bedevilled by ants

An ant species uses herbicidal weaponry to secure its own niche in the Amazonian rainforest.

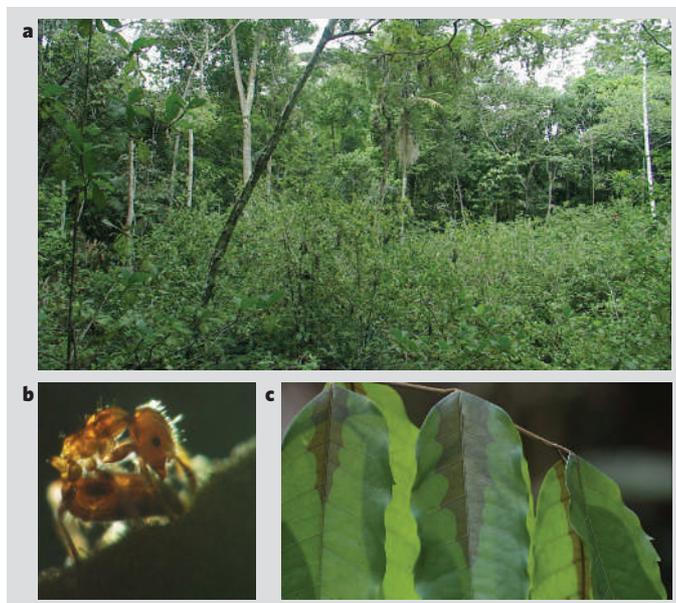
'Devil's gardens' are large stands of trees in the Amazonian rainforest that consist almost entirely of a single species, *Duroia hirsuta*^{1–5}, and, according to local legend, are cultivated by an evil forest spirit. Here we show that the ant *Myrmelachista schumanni*, which nests in *D. hirsuta* stems, creates devil's gardens by poisoning all plants except its host plants with formic acid. By killing these other plants, *M. schumanni* provides its colonies with abundant nest sites — a long-lasting benefit as colonies can live for 800 years.

M. schumanni lives in the hollow, swollen stems (domatia) of *D. hirsuta*, the tree species that dominates devil's gardens (Fig. 1a). Previous studies of the mutualism between *D. hirsuta* and *M. schumanni* indicated that devil's gardens result from allelopathy, which is the local inhibition of plant growth by another plant, by *D. hirsuta*^{2–5}. However, studies of a different ant–plant mutualism — between an unidentified species of *Myrmelachista* and the ant-plants *Tococa guianensis* and *Clidemia heterophylla* — indicated that *Myrmelachista* may create stands comprising only its host plants by using herbicide^{6,7}.

We did an ant-exclusion experiment to determine whether the selective killing of plants inside devil's gardens is due to the activity of *M. schumanni* workers or to allelopathy by *D. hirsuta*. We planted saplings of a common Amazonian tree, the cedar *Cedrela odorata*, inside and outside devil's gardens, and either excluded or did not exclude ants from the saplings (for methods, see supplementary information).

We found that the *M. schumanni* workers

Figure 1 | The ant *M. schumanni* creates devil's gardens by killing all plants other than its host tree, *D. hirsuta*. **a**, A devil's garden, or mono-specific stand of *D. hirsuta*, in the foreground contrasts with the species-rich rainforest in the background. **b**, A worker *M. schumanni* ant attacking a plant: the ant bites a small hole in the leaf tissue, inserts the tip of its abdomen into the hole and releases formic acid. **c**, Leaves develop necrosis along primary veins within hours of the attack.



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promptly attacked the saplings in devil's gardens from which ants had not been excluded, injecting a poison into their leaves (Fig. 1b), which developed necrosis within 24 hours (Fig. 1c). Most of the leaflets on these saplings were lost within five days, and the proportion lost was significantly higher than on saplings from which ants were excluded (Fig. 2). We also found that ant-free *C. odorata* inside devil's gardens fared as well as *C. odorata* planted outside devil's gardens. These results show that devil's gardens are produced by *M. schumanni* workers, rather than by *D. hirsuta* allelopathy.

In a second experiment, we investigated

whether *M. schumanni* attacks only plants that are not its host plants and whether the ant uses domatia to recognize its host. We planted *C. odorata* saplings with and without artificial domatia and *D. hirsuta* saplings with and without domatia in devil's gardens. After 24 h, there was significant leaf necrosis on all *C. odorata* plants (mean area on plants with artificial domatia: 39.7 cm²; s.e., 26.4–55.6 cm²; on plants without artificial domatia: 14.2 cm²; s.e., 9.2–20.3 cm²), whereas there was no leaf necrosis at all on any *D. hirsuta* plants, irrespective of the presence of domatia (analysis of variance, $F_{3,20} = 57.03$, $P < 0.0001$). We conclude that *M. schumanni* attacks only non-host plants such as *C. odorata* and that it does not rely on the presence of domatia to discriminate between its hosts and other plant species.

Chemical analysis revealed that the poison glands of *M. schumanni* contain formic acid ($0.43 \pm 0.12 \mu\text{l}$ per worker); no other compounds were detected. Treatment of leaves with formic acid induced leaf necrosis on all the plants we tested. (For details, see supplementary information.) Many formicine ants produce formic acid: to our knowledge, this is the first record of an ant using formic acid as a herbicide — although it is known to have bactericidal and fungicidal properties⁸.

Devil's gardens covered 4.5% of our study plot and grew by $0.7 \pm 0.3\%$ per year. Using this growth rate, we estimate that the largest

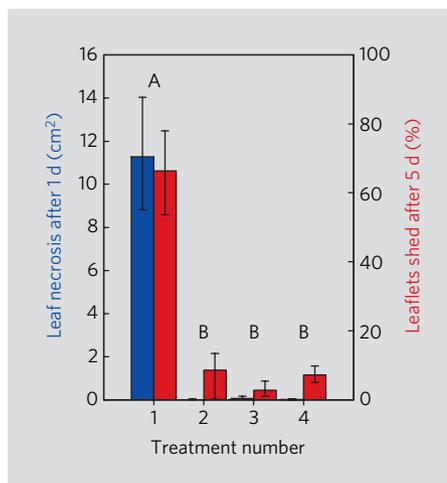


Figure 2 | *M. schumanni* ants, and not allelopathy, create devil's gardens. Saplings of the non-host plant *C. odorata* were subjected to different treatments: 1, planted inside a devil's garden, ants not excluded; 2, planted inside a devil's garden, ants excluded; 3, planted outside devil's gardens, ants not excluded; and 4, planted outside devil's gardens, ants excluded. Only saplings exposed to ants inside devil's gardens developed significant necrosis within one day (average \pm s.e.; blue bars) and shed a significant percentage of their leaflets within five days (average \pm s.e.; red bars). Multivariate analysis of variance results: Pillai trace, 0.88, $F_{6,72} = 9.41$, $P < 0.0001$. Analysis of variance (ANOVA) results (necrosis): $F_{3,36} = 52.78$, $P < 0.0001$. ANOVA results (leaflets shed): $F_{3,36} = 17.19$, $P < 0.0001$. Bars marked A are significantly different ($P < 0.001$) by Tukey post-hoc tests from bars marked B.

devil's garden in our plot, with 351 plants, is 807 years old (95% confidence interval, 446–4,234 years old). A devil's garden is tended by a single *M. schumanni* colony (our unpublished results) comprising as many as 3 million workers and 15,000 queens; the presence of many queens undoubtedly contributes to colony longevity.

The cultivation of devil's gardens by *M. schumanni* is an example of niche construction⁹. By killing plants of other species, the ant promotes the growth and establishment of *D. hirsuta*, thereby gaining more nest sites. A devil's garden begins when an *M. schumanni* queen colonizes a single *D. hirsuta* tree: over time, *D. hirsuta* saplings become estab-

lished within the vegetation-free area created by the ants, and the ant colony expands to occupy them. The devilry of *M. schumanni* today provides homes for ants in the future.

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CLIMATE MODELLING

Northern Hemisphere circulation

Air pressure at sea level during winter has decreased over the Arctic and increased in the Northern Hemisphere subtropics in recent decades, a change that has been associated with 50% of the Eurasian winter warming observed over the past 30 years, with 60%

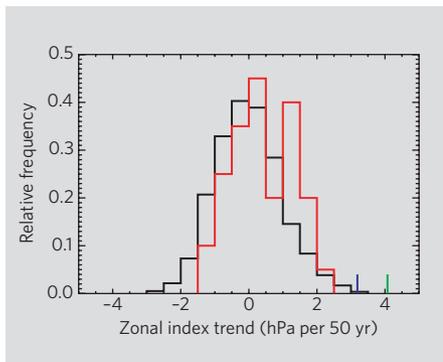


Figure 1 | Simulated and observed zonal index trends. The green line represents the 1955–2005 trend in the mean sea-level pressure in the Northern Hemisphere over December–February southwards of 45° N minus the mean sea-level pressure northwards of 45° N taken from the NCEP reanalysis⁴ and the blue line represents the same from the HadSLP2r data set (R. J. Allan and T. J. Ansell, manuscript submitted). The black line is a normalized histogram of 50-year zonal index trends in 3,903 overlapping segments of control simulations from nine coupled climate models obtained from the Intergovernmental Panel on Climate Change data archive of the Program for Climate Model Diagnosis and Intercomparison, Lawrence Livermore National Laboratory. The red line is a normalized histogram of 1955–2005 zonal index trends from 40 historical simulations of the nine models with anthropogenic and natural forcings. In cases where the historical simulations ended before February 2005, output from twenty-first century scenario integrations with only anthropogenic forcings was used for the missing years.

of the rainfall increase in Scotland and with 60% of the rainfall decrease in Spain¹. This trend is inconsistent with the simulated response to greenhouse-gas and sulphate-aerosol changes^{2,3}, but it has been proposed that other climate influences — such as ozone depletion — could account for the discrepancy³. Here I compare observed Northern Hemisphere sea-level pressure trends with those simulated in response to all the major human and natural climate influences in nine state-of-the-art coupled climate models over the past 50 years. I find that these models all underestimate the circulation trend. This inconsistency suggests that we cannot yet simulate changes in this important property of the climate system or accurately predict regional climate changes.

I derived a zonal index by subtracting the December–February mean sea-level pressure northwards of 45° N from the mean sea-level pressure between the Equator and 45° N using two data sets: the NCEP reanalysis⁴ and a newly completed data set of gridded observations known as HadSLP2r (R. J. Allan and T. J. Ansell, manuscript submitted). The trend in this zonal index over the period 1955–2005 is shown in Fig. 1 for both data sets. I compared the observed trend with output from nine coupled climate models from the Intergovernmental Panel on Climate Change data archive (UKMO-HadCM3, CCSM3, PCM, GFDL-CM2.0, GFDL-CM2.1, MIROC3.2(medres), MIROC3.2(hires), GISS-EH and GISS-ER).

To assess whether the observed trend could result from internal climate variability, I calculated equivalent zonal index trends in 3,903 overlapping 50-year segments of the models' control integrations (Fig. 1, black histogram). The NCEP zonal index trend exceeds all 50-year zonal index trends from the control simulations, and the HadSLP2r zonal index trend

exceeds all but one, indicating that the observed trend is inconsistent with simulated internal variability at the 5% significance level.

I assessed the possible role of external forcing by calculating zonal indices for the period 1955–2005 in historical simulations from the same climate models, which include greenhouse-gas, sulphate-aerosol, stratospheric-ozone, volcanic-aerosol and solar-irradiance changes. The resulting zonal index trends in each of the 40 ensemble members are shown by the red histogram in Fig. 1. Although the mean trend in these simulations is significantly positive (0.40 hectopascal per 50 yr), all the simulated trends are less than the observed trend, indicating that the simulated and observed trends are inconsistent at the 5% level, in contrast to previous findings based on the North Atlantic Oscillation index⁵.

Overall, I find that the observed Northern Hemisphere circulation trend is inconsistent both with simulated internal variability and with the simulated response to human and natural climate influences, although the mean simulated zonal index trend is consistent in sign with that observed. This is therefore an important aspect of large-scale climate change that these state-of-the-art climate models are unable to simulate; if we could understand and correct this bias, predictions of future regional climate change would be improved.

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