ECOLOGY

A Pardon for the Dingo

The extinction of the thylacine and devil on mainland Australia is best explained not by the arrival of the dingo but by human population growth and climate change.

Richard G. Roberts

The dingo (*Canis lupus dingo*) has grown accustomed to bad press. Dingoes first set paw in Australia a few millennia ago, possibly in association with the spread of Austronesians into the Pacific. They have since been blamed for snatching babies, killing sheep, and forcing the marsupial thylacine (*Thylacinus cynocephalus*) and the related devil (*Sarcophilus harrisii*) into extinction on the Australian mainland. The present-day ecological role of dingoes is still debated (see Ripple *et al*. on page 151 of this issue) (*1*), but in a recent article, Prowse *et al*. (*2*) propose that Australia's favorite scapegoat can be largely absolved of blame for driving the mainland thylacine and devil to extinction.

Dingoes never reached the island of Tasmania. The survival there of the thylacine until 1936—dubbed the Tasmanian "tiger" because of its striped back—and the devil to modern times is generally attributed to the absence of competition and predation from dingoes. However, Prowse *et al*. (*2*) use ecological models to show that the dingo did not play a key role in the extinction of these species on the mainland. Instead, they point the finger at humans, perhaps assisted by increasing aridity. The pivotal role played by humans in this recent extinction event, superimposed on a background of climate change, echoes the earlier extinction of the Australian megafauna and highlights the repeated impacts of hunter-gatherers on Australian ecosystems over the last 50,000 years (*3*).

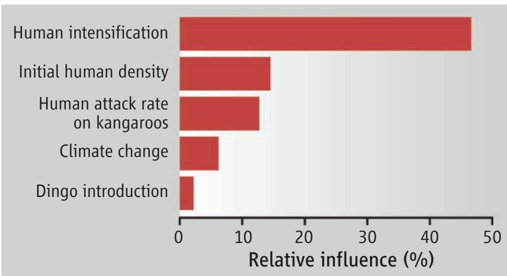
The Australian megafauna included marsupials, reptiles, and birds weighing more than 44 kg. Most had vanished by ~40,000 years ago (*4*–*6*), but differing views persist about the exact timing and mechanism of extinction. Some form of human impact is widely favored (*3*–*5*), possibly with climate deterioration as an added stressor (*6*). The disappearance of the megafauna left the thylacine and devil as the two largest terrestrial carnivores.

Thylacines were familiar to Aboriginal Australians and are depicted at numerous rock art sites in north and northwest Australia (see the first figure). A radiocarbon date of ~3500 years before present (yr B.P.) has been reported for a desiccated thylacine carcass found in a cave in southern Australia (*3*), but reliably dated sites with fossil remains of the thylacine and devil are scarce, frustrating attempts to establish exactly when and why they went extinct on the mainland.

Australian "tiger." Ancient rock paintings, drawings, and engravings of presumed thylacines have been recorded in north, northwest, and southeast Australia. This 50-cm-wide composition of a possible thylacine being speared or fended off by a person adorns a rock shelter in the far north of Western Australia (*12*).

Enter the dingo. Genetic estimates place its introduction at or before 4600 years ago (*7*), but no dingo fossils of such antiquity have been discovered. An almost complete dingo skeleton dated to ~3400 yr B.P. is one of the few remains older than 3000 years, with the sparse record hinting at dingo arrival shortly after 4000 yr B.P. (*3*).

Given the poorly resolved chronologies for entry of dingoes and exit of thylacines and devils on mainland Australia, Prowse *et al*. (*2*) took a modeling approach to evaluate the processes responsible for the extinction of these two marsupials. They first constructed a stochastic model to simulate the complex interactions among the hunters (humans, thylacines, devils, and dingoes) and the hunted (the herbivorous prey, represented in the model by kangaroos) in a grassland habitat. The goal was to determine which combination of factors was most effective at predicting the extinction of the two native carnivores. A simulation was judged to be successful if it predicted their dual extinction after the arrival of dingoes and before European landfall around 200 years ago.



Extinction drivers. Relative importance of the main model parameters for predicting thylacine and devil extinctions on mainland Australia, estimated from the best-performing boosted regression tree (*2*).

The model allows for competition between predators, the exponential growth in human populations on the mainland from ~5000 yr B.P. (*8*, *9*), and the effect on vegetation and prey populations of a climatic shift toward a drier regime at about the same time (*10*). A wide range of ethnographically, archaeologically, and ecologically plausible values are included in the model, such as predator and prey densities, population growth rates, predation rates, and factors to allow for competition for resources both within and between species. The authors modeled eight scenarios, representing the different permutations of dingo introduction (assumed to have

CREDIT: FIRST FIGURE, MIKE DONALDSON; SECOND FIGURE, ADAPTED FROM (2)

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occurred 4000 years ago), human intensification (modeled as population growth), and climate change. Ecological extinction was declared when populations dwindled to fewer than 500 individuals.

Such simulation studies will conceal regional and local responses to various parameters, as well as subtle interplay at fine spatial and temporal scales. But the main findings were clear-cut. Human intensification featured in 80% of the successful simulations, compared to the inclusion of climate change (44%) and dingo invasion (16%). Prowse *et al.* then analyzed a subset of these simulations using boosted regression trees (*11*) to assess the importance of different model parameters on the probability of successfully predicting the extinction of mainland thylacines and devils. This analysis confirmed humans as the main driver of the mainland extinctions. Human intensification was the most influential factor, followed by the initial human density and the rate of human predation on kangaroos (see the second figure). Climate change became important when the latter two parameters were at their lowest values, but dingoes had a negligible effect. Predictive success was affected more by human attack rates on kangaroos than on thylacines and devils; thus, human hunting of these native carnivores had less influence than did human predation on their common prey.

Vindication of the dingo for the extirpation of the thylacine and devil on mainland Australia puts people—and perhaps climate change—squarely in the frame. Humans are also implicated in the demise of the Australian megafauna (*3*–*6*). However, searching for prehistoric synergies among extinction drivers is made more difficult by the declines in quantity and quality of evidence further back in time, hampering efforts to resolve the causes of megafaunal extinction from dated fossils, artefacts, and proxy records of climatic and ecological change. Prowse *et al.*'s scenario-testing approach (*2*) offers a new lens through which to study the range of dynamic interactions and impacts responsible for this earlier mass extinction.

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Bacterial Vesicles in the Ocean

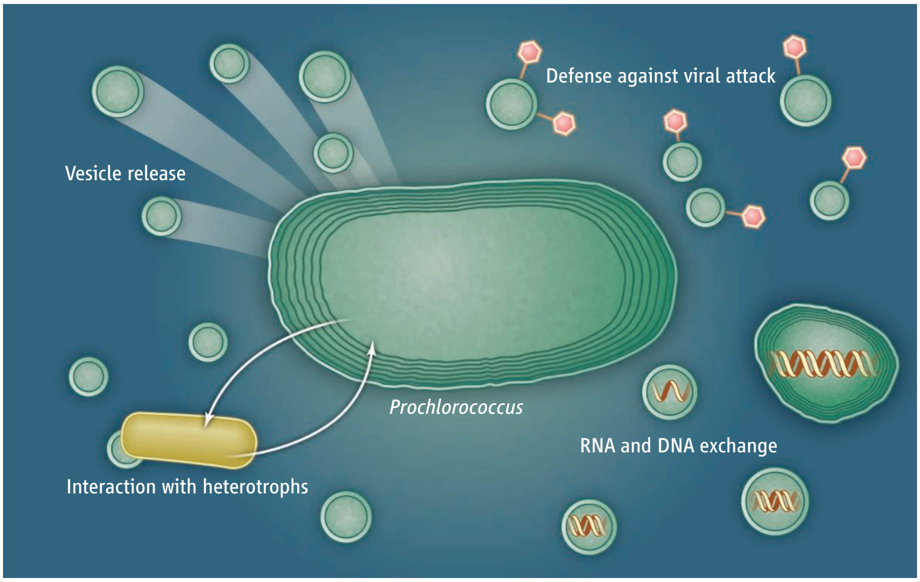
Vesicles released by phytoplankton may play key roles in carbon cycling, viral defense, and gene transfer.

David Scanlan

Marine microbes play a key role in global nutrient cycling (*1*). Phytoplankton account for less than 1% of the photosynthetic biomass on Earth, yet contribute almost half of the world's primary production (*2*). In open oceans between ~45°N and ~40°S, cyanobacteria of the genus *Prochlorococcus* dominate the phytoplankton (*3*). *Prochlorococcus* is the smallest free-living phototroph; its genome is subject to miniaturization (*4*), and distinct ecotypes are adapted to the strong gradients of light and nutrients in the surface ocean (*5*). On page 183 of this issue, Biller *et al.* (*6*) identify a further striking feature of *Prochlorococcus*: the production of extracellular vesicles that may play a role in carbon cycling, gene transfer, and viral defense.

Biological production of extracellular vesicles is widespread, with vesicles produced by species across all three branches of the tree of life (*7*). In Gram-negative bacteria, vesicles are produced when small regions of the outer membrane bulge away from the cell before pinching off and being released (*8*). Biller *et al.* carefully purified 70 to 100 nm-sized membrane-bound extracellular vesicles from exponentially growing *Prochlorococcus* cells. The vesicles contain not only periplasmic and outer-membrane proteins but also proteins characteristic of inner membrane and cytoplasmic compartments, although their relative abundance is unknown. They also contain DNA and RNA.

The authors show that vesicles are produced not only by *Prochlorococcus*, but also



Multipurpose vesicles. Biller *et al.* show that *Prochlorococcus* produce vesicles that may play functional roles in defending against viral attack, interactions between heterotrophs and *Prochlorococcus*, and horizontal gene transfer. This is a schematic presentation and is not to scale.

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