substrates depend on binding at this site, there are probably additional substrate recognition sites. Another contribution to substrate selection is made by scaffold proteins, e.g. AKAP79, which target the phosphatase to neuronal synapses or other cellular sites. Calcineurin also delegates work to protein phosphatase 1 (PP1) through a phosphatase cascade, in which dephosphorylation of the PP1 antagonists DARPP-32 or inhibitor-1 by calcineurin relieves their inhibitory effect on PP1, and allows PP1 to act on its own preferred substrates.

What are its inhibitors? Cyclosporin A (CsA) and FK506 bind tightly to the abundant intracellular proteins cyclophilin A and FKBP12, respectively, and the resulting ligand–protein complex binds to calcineurin and impedes access of protein substrates to the active site. Blockade of a biological process by CsA and independently by FK506 is diagnostic for calcineurin involvement. Other inhibitors that find frequent experimental use are the autoinhibitory peptide from calcineurin and fragments of the regulatory proteins DSCR1/MCIP/calcipressin/Rcn1p, Cabin1/cain, and AKAP79.

Does it have any medical relevance? Calcineurin signalling is prominent in transplant rejection and autoimmune disease, where the inhibitors CsA and FK506 are used clinically, and is being studied for its contribution to myocardial hypertrophy and to virulence in fungal pathogens.

Where can I find out more?

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Essay

How effective were mangroves as a defence against the recent tsunami?

Whether or not mangroves function as buffers against tsunamis is the subject of in-depth research, the importance of which has been neglected or underestimated before the recent killer tsunami struck. Our preliminary post-tsunami surveys of Sri Lankan mangrove sites with different degrees of degradation indicate that human activity exacerbated the damage inflicted on the coastal zone by the tsunami.

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Mangrove forests have iconic status as natural ecosystems that provide services to humans. They function as breeding, spawning, hatching and nursing grounds for marine and pelagic species, and are important in the daily livelihood of local human subsistence communities. Mangrove representatives such as *Rhizophora* spp. also function as a physical barrier against tidal and ocean influences by means of their large above-ground aerial root systems and standing crop. Like many habitats, mangrove forests have been degraded and destroyed by humans, and their loss is a source of global concern. In the second half of the 20th century, 50% of the world's mangrove forests have been destroyed, and current annual loss rates vary from 1 to 20% [1]. Ironically, the great human tragedy of the recent December 26th tsunami may provide the stimulus for a better understanding of what mangrove forests can and cannot do for human well-being.

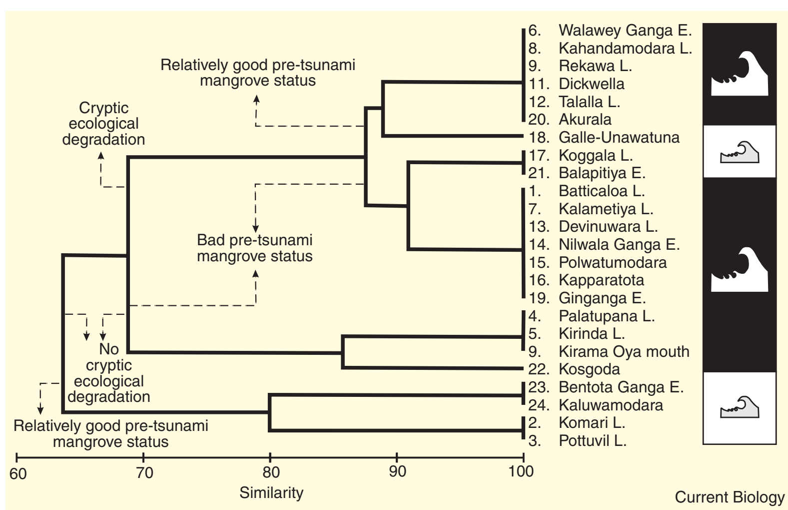

Figure 1. Dendrogram generated by a cluster analysis of the 24 mangrove sites investigated, indicating their characteristics and the impact of the tsunami (big wave, severely impacted; small wave, little impacted).

The 'mangrove status' is a combination of pre-tsunami aerial extent of the front mangrove and pre-tsunami mangrove destruction (see text). The tsunami had only a small impact on lagoons that show no cryptic ecological degradation (sites 2, 3, 23 and 24) or that are protected by the distance from the shore and by frontal *Rhizophora* spp. fringes (sites 17, 18 and 21). The lagoons are numbered clockwise from East to West, to emphasize that damage was not linked to geographic position in view of tsunami wave energy. A map overview of all lagoons can be found in Jayatissa *et al*. [18], with the exception of Batticaloa, Komari and Potuvil, which are located at the easternmost extremity of the island. L, Lagoon; E, Estuary.

Figure 2. *Nypa fruticans* at Talalla (A) and young mixed mangrove fringes at Rekawa (B) show damage caused by the tsunami, whereas interior mangrove zones and land areas were largely unaffected. Young *N. fruticans* shoots are now regenerating (LPJ).

In the aftermath of the Indian Ocean tsunami, which killed over a quarter million people and left millions homeless, experts and the media wondered how many lives might have been saved if only we had not destroyed our mangrove forests. Others, however, were more skeptical, countering: “fear of big waves is no reason to plant mangroves” [2]. What, then, is the role of mangroves, and how many lives might they have saved?

Despite the popular and widely accepted view that mangroves act as living dykes [3], there is surprisingly little data available to test that hypothesis. The important question is what future role should mangrove forests play in coastal zone management and protection? The answer will not be simple, as there are a lot of different types of mangrove forest in a wide variety of settings, and in some places mangroves are simply absent from the natural environment.

Apart from occasional observations and photographic evidence of uprooted terrestrial trees [4,5], the closest scientific evidence for the buffering function of mangroves comes from socio-economic and ethnobiological surveys that focus on the services of mangrove forests. Over the last several years, our teams have conducted interviews with local people in Mexico, Gambia, Cameroon, Tanzania, Kenya, India, Sri Lanka and Vietnam, and inquired about their relationships with mangrove forests, and about the services that these forests provide — for construction and fire wood, ethnomedicinal products, fishing habitat, coastal protection and so on.

In late 2001, we interviewed local inhabitants on the Indian subcontinent — the region second-hardest hit by last December’s tsunami — asking about the extent to which mangroves protected their homesteads against disastrous ‘water-related’ events: cyclones and wave action, but also tsunamis and sea level increases. They substantiated their view well; one interviewee noted: “during the recent devastation by tropical cyclone 07B (November 6th, 1996) areas where mangroves were in relatively good condition were saved from the fury of the cyclone and its associated flooding events as opposed to adjacent places where mangroves had been converted to shrimp farms”. Similarly, in the Philippines, such traditional ecological knowledge of fisherfolk indicated that mangroves have a protective buffering function [6,7].

In January 2005, we conducted preliminary post-tsunami surveys in 24 mangrove lagoons and estuaries in Sri Lanka’s coastal zones along the South-West, South and South-East coasts of the island. The districts visited were heavily hit and counted at least 23,558 deaths, more than

Box 1

Are all plants in the mangrove environment true mangrove species?

Mangrove plants are commonly subdivided into major components (true, strict or exclusive mangrove species), minor components (non-exclusive mangrove species) and mangrove associates. The major components feature a complete fidelity to the mangrove environment, pure stands, morphological and physiological adaptations and taxonomic isolation [19]. An additional distinction should be made between mangroves that are disturbance-resistant (for example *Excoecaria agallocha*), euryhaline (for example *Avicennia marina*) or fairly well adapted to freshwater (for example *Sonneratia caseolaris*), on the one hand, and those that are most ecologically vulnerable, most valuable and impacted from an ethnobotanical point of view, and those considered most characteristic of mature natural mangroves from an aesthetical point of view (for example Rhizophoraceae), on the other hand [9,18]. This distinction is required to help detect ‘cryptic ecological degradation’, in which introgressive mangrove-associated vegetation or minor mangrove species slowly start to dominate a forest of true mangrove species (qualitative degradation) without loss of spatial extent (no change or an increase in area) [9].

80% of the total Sri Lankan death toll [8]. Aided by previous field knowledge, we assessed the following five characteristics semi-quantitatively: (A) the pre-tsunami extent of the front mangrove (the first 500m fringe, taking into account that this is a conservative width able to provide protection against a tsunami); (B) the extent of mangroves already destroyed before the tsunami; (C) the 'naturalness' of the mangrove, in terms of the presence or absence of cutting activities and of cryptic ecological degradation [9]; (D) tsunami damage to the front mangrove; and (E) tsunami damage to lives and properties in the back mangrove and behind the mangrove. These characteristics were compiled into the pre-tsunami mangrove status (A+B), the presence of cryptic ecological degradation (C), and the destruction by the tsunami (D+E), and a cluster analysis (group average), using PRIMER version 5.2.8, was performed based on Bray-Curtis similarity (Figure 1).

Our results show that, where mangroves occur in the districts visited, they did in fact offer protection. Apart from some isolated trees of *Excoecaria agallocha* L., there were no records of uprooted adult mangrove trees. At most, mangrove fringes near the water edge took all the energy and were damaged (Figure 2). Creek-fringing *Nypa fruticans* (Mangrove palm) had its leaves bent or torn off, but anchoring protection of this plant by its rhizomatous stem allowed new young leaves to emerge less than a month after the tsunami impact. Other true mangrove representatives (Box 1) such as *Sonneratia* spp., the stem of which can measure several meters in circumference, or *Rhizophora* spp. or *Bruguiera* spp., which has wide prop or knee roots, also stood firm against the ocean surge.

Forests dominated by less typical mangrove associates (Box 1), however, were severely damaged (Figure 3A,B). This is also evident from the dendrogram, where the major splits indicate whether 'cryptic ecological degradation' occurred (Figure 1). Mangrove sites with no cryptic ecological degradation, or those well protected by distance inland and by *Rhizophora* spp. fringes, all experienced a low destructive impact from the tsunami. The key feature of those forests that were damaged appears to be a prominence of vegetative associates not typical of natural mangrove forests (Box 1). The important lesson is that, even though a coastal area might superficially seem to be protected by a mangrove forest, that habitat could be cryptically degraded and not offer the desired storm protection (see also [9,10]).

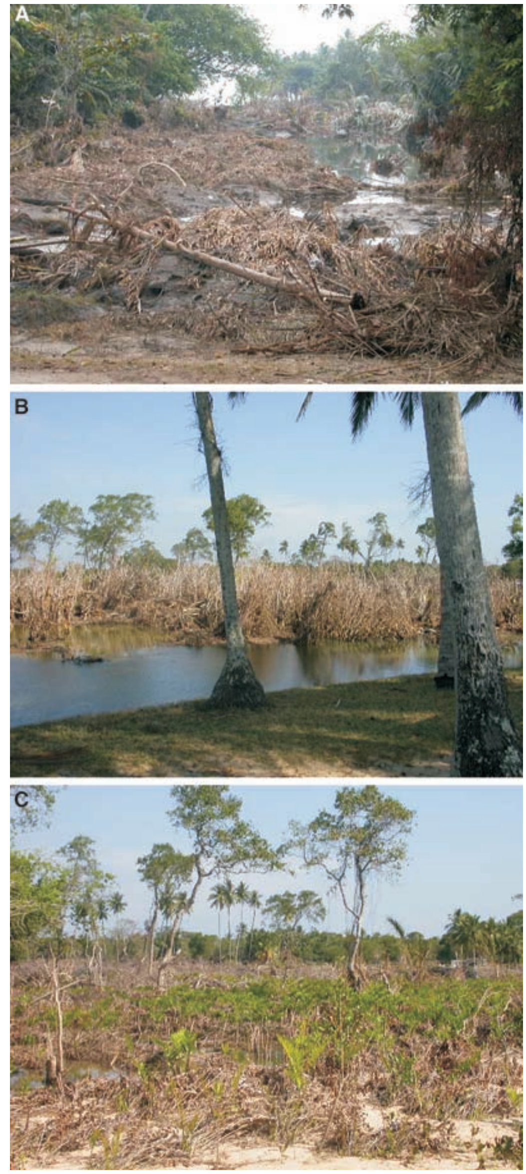

Figure 3. Two forest areas near Talalla (A) and Kahandamodara (B), which had become largely dominated by mangrove associates — cryptic ecological degradation — have been destroyed by the tsunami. It is very unlikely that these areas have the potential to be recolonized by original true mangrove representatives, because less than a month after the tsunami, *Acrostichum aureum* was showing signs of strong regeneration (C) (LPJ).

A more in-depth 'crime-scene investigation' is urgently needed, but at present our conclusions are that three factors can undermine the ability of mangroves to protect coastal villages: first, complete clearance; second, insufficient regrowth following a previous clearing; and third, infusion of adult mangroves (where present) with excess of non-mangrove vegetation components.

It is important to recognize that any compromising of mangrove 'protective function' is relevant to a wide variety of storm events, and not just tsunamis. Whereas the Indian Ocean area counted 'only' 63 tsunami events between 1750 and 2004, there were more

Figure 4. Sand dune vegetation and *Casuarina equisetifolia* plantations may contribute to a reduced impact by ocean surges.

However, it should also be investigated to which extent negative ecological influences occur from such artificially planted barriers. (A) Hambantota, (B) Tissamarahama, S. Sri Lanka coast (LPJ).

than three tropical cyclones per year in roughly the same area (Source: National Geophysical Data Centre, National Environmental Satellite, Data and Information Service, National Oceanic and Atmospheric Administration).

Our surveys of villages and post-tsunami observations make it clear that mangroves play a critical role in storm protection, but with the subtle point that this all depends on the quality of the mangrove forest. We also found that there can be contributions to protection against ocean surges from other coastal vegetation types: salt marshes, seashores sand dunes and their vegetation (Figure 4). The more general message is that how humans use, plan and manage their habitats and landscapes can have profound and undesirable consequences.

The conversion of mangrove land into shrimp farms, tourist resorts, agricultural or urban land over the past decades [11], as well as destruction of coral reefs off the coast, have likely contributed significantly to the catastrophic loss of human lives and settlements during the recent tsunami event. While it may be a good investment to establish early warning systems for the next tsunami, it could be far more effective to restore and protect mangrove forests and other natural defenses in parallel. In fact, if we had early warning systems that cautioned us about mangrove degradation [12,13], and if we then acted to correct the mangrove degradation, not only would we save lives, but we would also minimize property damage and loss of subsistence livelihoods.

Fortunately, mangroves are resilient and may be restored. In Malaysia and East-Africa, mangroves have successfully been planted and/or managed for an extended period of time [14,15], and these could serve as model case-studies. So should areas that have been drastically cleared of mangroves [16], and then worst hit by the recent tsunami, such as Banda Aceh in Indonesia.

The story of mangroves and tsunamis is but one example of a broader story. Natural ecosystems throughout the world provide tremendous ecosystem services, including protection against extreme weather events and natural catastrophes [17]. When we fail to raise awareness about these functions, and we destroy or degrade the world's natural ecosystems too much, we do so at our own peril.

Acknowledgments

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A new mode of information transfer in foraging bumblebees?

Ellouise Leadbeater and Lars Chittka

Pollinating insects have provided one of the most enlightening systems for understanding how natural selection shapes animal foraging behavior, but their movements from one plant species to another are not thoroughly understood. Bumblebees forage in highly unpredictable habitats where the flower choices of conspecifics may provide exploitable up-to-date information about current reward levels. Nonetheless, interactions between foragers in the field have been largely viewed in an antagonistic context, where scent marks left by foragers on flowers act as a deterrent to other bees [1]. Here we show, conversely, that foraging conspecifics can not only increase the attractiveness of an inflorescence, but also entice bees to switch from a familiar species to sample a new flower type.

We examined the behavior of 17 'observer' and 'demonstrator' bees from three *Bombus terrestris* colonies in a flight arena (Figure 1). Individual observer bees chose between a yellow and a blue flower species, each represented by four artificial inflorescences (see Supplemental experimental procedures in the supplemental data available with this article online), all providing equally high amounts of 2 M sucrose solution *ad libitum.*

At the start of a trial, a demonstrator bee was allowed to forage upon one inflorescence, randomly chosen to be either yellow or blue and placed at a random location. Once the demonstrator had settled we introduced the seven alternative 'unoccupied' alternatives into the arena. The naïve observer bee was then released and allowed to choose one inflorescence to forage upon.

In this first trial, when observers were entirely unfamiliar with both species, bees strongly preferred the occupied inflorescence (Figure 2A; binomial test $p < 0.01$) over the seven unoccupied options. As demonstrators had not chosen the inflorescence that they foraged upon themselves, or

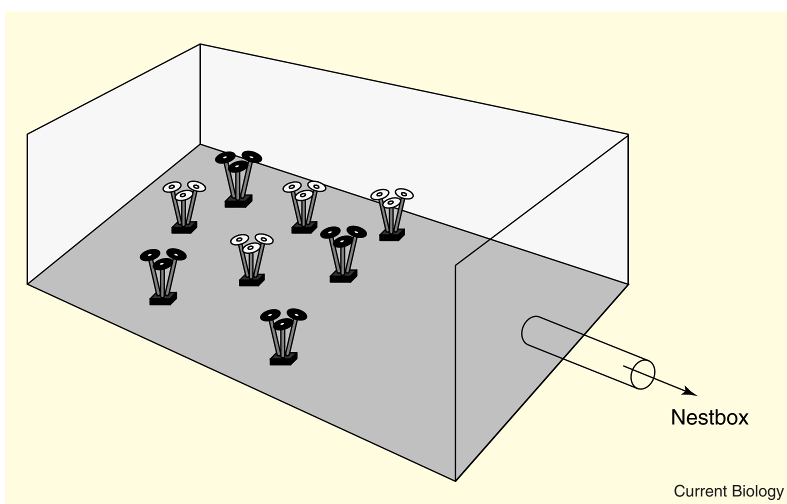

Figure 1. Choice array.

Eight equally and highly rewarding inflorescences, each containing three flowers, were presented to the observer bee in a 105 x 70 x 30 cm flight arena connected to the nestbox.