Reply from W.J. Sutherland, G.A. Parker and P.A. Stephens

We admire the fine primatological research[1] to which Harcourt rightly draws our attention, and which shows the relationships between rank, group size and feeding behaviour. There does, however, seem to be a difference in terminology between this work and our own. We considered interference in terms of a quantified relationship between population density and mean or individual intake rate[2] as used in innumerable entomological and some ornithological studies. Many primate studies, for sensible reasons, consider interference as a change in foraging efficiency, activity budgets, or feeding-bout durations with group size; however, these measures may have a complex relationship with intake rate. Some studies do relate intake to rank (e.g. Refs 2–5) and group size (e.g. Ref. 5).

Although in such examples the data are not presented in a manner that can be used to calculate the strength of interference, we suggest it would be extremely useful, and probably reasonably straightforward, to use such data to do so – both to incorporate within theoretical models and provide comparisons with other taxa.

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Assessing ecosystem health

I recognize the importance of much of the material in Rapport *et al.*'s recent *TREE* article[1], but criticize the basic theme around which it is organized. There are problems with the concept of ecosystem health, and in particular with the assumption that it is both analagous with and contributory to human health.

There are well known difficulties in producing a rigorous definition of human health, but the idea that all was well before civilization came along smacks too much of 'noble savage' mythology. Wild populations of animals are not normally free of parasites, and we must imagine 'primitive' humans as also living in a fluctuating equilibrium with disease organisms of all kinds. Also, a population living with endemic malaria would not be regarded as a healthy one in modern terms. We presumably wish to define 'healthy' in terms of what can be expected under modern conditions, rather than in some primitive state that could be described as more 'natural'. The ecosystems visited by the early European settlers in Africa were probably reasonably healthy in their own terms. That did not stop them being called the white man's grave.

This immediately raises problems when we talk about humans as part of a wider ecosystem. The health of that system includes the welfare of the malaria parasite, and there is logically a negative correlation between that and human health. This is the fallacy of supposedly holistic views that assume no fundamental conflicts of interest, and it is one of the basic problems of the Gaia hypothesis.

Even if we leave humans out of it, the health of an ecosystem is still not a variable that can be defined in value-free terms. Rapport *et al.*'s example of the Ponderosa pine ecosystem includes some very clear value judgements: for instance, parasites of trees are an indication of poor ecosystem health whereas saprophytes signify good health. This is obviously being seen purely from the standpoint of trees and their human consumers, rather than from any more objective view of overall ecosystem health. The second problem with the 'healthy ecosystem' approach to the 'services' provided for humans is that mention is rarely made of the biggest of them all – the production of food. Highly productive agriculture always seems to involve ecosystems that by any definition are degraded. The biggest conservation dilemma is whether our population can continue to be fed (and clothed, housed and warmed) without destroying most of what is left of even passably 'natural' ecosystems in the process. The present catastrophic destruction of the Amazon forest ecosystem described in another *TREE* article[2] cannot be condoned, but would our objections be as easy to defend if there were a convincing scheme to replace it with productive and sustainable agriculture? Discussion of the global ecosystem as a holistic unity ignores these dilemmas completely. If the prime determinant of human health is adequate nutrition, it is unlikely to correlate with the measures of ecosystem health being proposed.

None of this is to deny the importance of an ecological view of both agriculture and human illness, and much that is said by Rapport *et al.* is very valuable, but the ecology invoked needs to be focused and relevant to specific problems, and not encumbered by mystical 'holistic' terminology.

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Reply from D.J. Rapport, A.J. McMichael and R. Costanza

The letter of D.A. Wilkins raises several issues concerning the validity of the ecosystem-health concept. His critique centers on the question of whether ecosystem health is both analogous with and contributory to human health. We have argued for this view, citing a number of references to case studies where the health metaphor has been a primary motivation, as well as number of studies where the human health consequences of ecosystem health status are transparent.

Wilkins goes on to raise other issues, some of which appear to bear little reference to our article[1]. For example, he suggests that we are advocating or implying that 'all was well before civilization came along'. We find no reference to this point of view, and would take issue with it. We have argued, however, that human-dominated ecosystems have recently become highly degraded with considerable risks and costs to humans[2,3]. He goes on to argue that our example of healthy and unhealthy Ponderosa pine forests (Box 2 of our article[1]) is considered 'purely from the standpoint of trees and their human consumers'. We disagree. We have suggested and documented elsewhere[4] that, owing to both heavy grazing and fire suppression, these forests have become highly dysfunctional – evidenced, for example, by reduced species diversity, increased disease prevalence, reduced rates of decomposition and nutrient cycling. These indicators, to be sure, have implications for humans, as well as the species that comprise this ecosystem.

The fact is there are no convincing schemes, such as argued by Wilkins, to replace the Amazon forest ecosystem, which has now been destroyed to a point of no return by human acts. The global impacts (global warming, etc.) should be an eye opener for modern civilizations when they consider their dependence upon these systems for their own survival.

Wilken's point that 'discussion of the global ecosystem as a holistic unity' ignores certain issues, may be a valid point. However, our article did not discuss the global ecosystems as a holistic unity, rather we showed how analyses of particular systems, contextually based, can be carried out within an ecosystem-health framework. Finally, we think it unscholarly to brand the efforts of many investigators referred to in more than 50 selected references as being flawed by 'mystical, "holistic"' terminology. This would be news not

only to those scientists who have developed quantitative methods for assessing ecosystem health (e.g. Refs 27 and 51 in our article), but also to agencies around the world that are presently engaged in monitoring and assessment programs in ecosystem health.

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Resource sharing in plant–fungus communities: did the carbon move for you?

The evolutionary speculations of Perry[1], in his news & comment report on Wilkinson's paper[2] on resource sharing in plant–fungus communities are, perhaps, premature. The evidence that plants do share resources is at best equivocal[3]. Before such speculations can be useful the following three phenomena must be demonstrated, namely:

- Carbon movement from the fungus into the receiver plant.
- Bi-directional transfer.
- The involvement of hyphal links.

As yet, the evidence for all of these is uncertain or restricted.

The case for plant–fungal–plant carbon transfer has still to be directly proven in the arbuscular mycorrhizal (AM) symbiosis, which accounts for approximately 70% of all mycorrhizal symbiosis. Although several studies have found carbon movement from one plant to another, this carbon remained in the roots and was probably associated with fungal structures[4], thus failing a key criterion for recipient plant carbon transfer. Transport of carbon within the hyphal network makes physiological sense for a clonal organism such as a glomalean fungus, but it does not mean, nor is there currently evidence to suggest, that in AM associations the fungus then donates carbon to 'needy' plants. The fungal viewpoint is largely ignored in the literature.

In ectomycorrhizal (EM) systems the situation is different, with the innovative dual-labelling experiment of Simard *et al.*[5] demonstrating net carbon transport between plants. In this case, the label was detected in the *shoots*. True plant–fungal–plant transfer had therefore occurred, giving the potential to influence plant performance directly.

However, our second concern is that transport of ^{14}C from paper birch (*Betula papyrifera*) to Douglas-fir (*Pseudotsuga menziesii*; ≈6.6% of total fixed carbon) was ten times the reverse transport of ^{13}C from *P. menziesii* to *B. papyrifera* (≈0.6%, calculated as bi-directional transport minus twice net). It seems that Simard *et al.*[5] have demonstrated one-way, not bi-directional, transport, which would allow parasitism by one plant on another via mycorrhizal hyphal links. Perry[1] largely considers mutualistic interactions between connected plants.

Third, in the study by Simard *et al.*[5] large amounts of carbon must have been lost to soil from EM fungal hyphae and roots by rhizodeposition. This released carbon could have been recaptured by mycorrhizal fungi and even uninfected roots, leading to an overestimate of the amount of carbon moved via hyphal networks. We base this conclusion on the evidence that the AM western red cedar (*Thuja plicata*) control absorbed 18% as much carbon as was transferred between *B. papyrifera* and *P. menziesii*. This high figure indicates that carbon was moving between unlinked plants, which must have been via soil. Where carbon does move between plants, the form in which it does so is unknown. As EM can acquire nitrogen from organic sources, carbon movement might simply be a consequence of organic nitrogen transfer from fungus to plant.

We believe that Perry[1] and Wilkinson[2] have offered evolutionary explanations for a phenomenon whose existence and ecological importance remain unproven by the experimental evidence currently available.

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Reply from D.A. Perry

Contrary to what Fitter *et al.* state, transfer of labeled carbon into the shoots of arbuscular mycorrhizal (AM) plants has been shown in two studies of which I'm aware[1,2], and at least five others have shown transfer of phosphorus, nitrogen, or calcium from one AM plant into the shoots of nearby AM plants[3–7]. As of yet, no dual labeling studies have been published for AM plants, hence net transfer of elements has not been shown as it has for ectomycorrhizal (EM) plants[8]. However, a study in which Fitter and Robinson were co-authors used carbon-isotope natural abundances to evaluate the possibility of net carbon transfer between C_3 and C_4 plants[9]. They concluded there was evidence for transfer into the tops of one species but not the other. Although Fitter *et al.* maintain that transfer into the tops is the key criterion for interplant transfer; in terms of functional significance, I see no reason why that should be so. Even if transferred carbon remains within fungal tissues within the root, it can be viewed as a subsidy to the nutrient gathering system of the receiver plant[9]. If, as the evidence suggests, transfer is along gradients, one would not expect carbon to move to the tops unless the receiver is achlorophylous, in deep shade, or the carbon carries a nitrogen, phosphorus or sulfur along with it.

No one disputes that root exudation is one possible transfer pathway. However, most experiments in which the potential for mycorrhizal linkages is known to have been controlled show much greater transfer when mycorrhizal links are possible[1,2,7,8]. Walter *et al.*[6] attempted to control AM fungi in the field using a fungicide and found no effect on transfer, but were dubious they had successfully controlled the fungi. That mycorrhizal fungi facilitate transfer is not in itself proof that movement is through hyphae, but autoradiography shows that elements do move between plants through mycorrhizal hyphae[1,2]. However, some studies suggest direct transfer via mycorrhizal hyphae is not a major mechanism, and there may be large variability in the amounts transferred between any two plants, even when they potentially share mycorrhizal fungi. In this regard, I quite agree with Fitter *et al.* that we need to learn more about the details of this phenomenon.

Regarding the study by Simard *et al.*[8], by showing that carbon moved both ways between Douglas-fir (*Pseudotsuga menziesii*) and paper birch (*Betula papyrifera*) we established the potential for reciprocity, though during the second year's nine-day chase period Douglas-fir clearly got the better of it (especially when placed in deep shade). It is impossible to conclude in a short experiment what bi-directional gross and unidirectional net transfer means for the long-term relationship between the two species, because any effects on fitness must take into account direct and indirect consequences over a period of decades and perhaps centuries. As Read pointed out[2], carbon capture can be overrated as a determinant of fitness, particularly in protective systems where fast growth may have little to do with survival and reproduction.

Yes, more needs to be learned about the details of interconnection and transfer. But far from being premature, hypotheses on the functional significance of the transfer phenomenon are needed now to guide experiments. That is the engine that turns the wheels and moves us forward.

 0169-5347/99/$ – see front matter