Reply from M.L. Arnold and S.A. Hodges

Day and Schluter highlight two important points concerning estimates of hybrid fitness. However, we believe that their conclusions do not reflect the tone of hybrid zone literature on the one hand nor our findings concerning hybrid fitness on the other[1].

The first caveat[1] concerns a potential sampling bias in the studies that report hybrid fitness. Day and Schluter suggest that analyses of hybrid fitness involve cases where natural hybrids are common; indicating that hybrids did 'not suffer any major reduction in fitness'. Thus, they state that a lack of any significant reduction in fitness for some hybrid classes 'is perhaps not surprising'. However, the most commonly used conceptual framework to explain the maintenance of hybrid zones, particularly in animals, is the 'tension zone'[2] model. This model has an explicit assumption that hybrids are less fit than their parents in *all* habitats[2,3]. Thus, it *is* surprising to many workers that hybrids can be equivalent in fitness, or even more fit, relative to their parents[1].

Day and Schluter discuss a second caveat to our conclusions related to those hybrids that demonstrate intermediate fitness. In this case, the hybrid class is less fit than a parent in that parent's habitat, but is more fit than the alternate progenitor. They conclude that the hybrid class would thus not be able to occupy either parental habitat. We agree with their conclusion. However, the findings from our analysis[1] indicate that hybrid 'intermediacy' in fitness is relatively infrequent and thus may not be a major factor in determining the evolutionary trajectory of most hybrids.

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Terpenoids: a plant language

There is an increasing recognition of the ecological importance of terpenoids as reflected by the several recent reviews, in *TREE* and elsewhere, of their ecological chemistry and role[1–3]. Moreover, the debate on the ecological and evolutionary significance of plant communication is currently active[3–5]. Indeed, we might regard terpenoids as a chemical 'language' of plants.

Like in any language, terpenoids are induced and emitted in response to internal (genetic and biochemical) and external (ecological) factors, both abiotic and biotic. Their information or effect is received and responded by other parts of the plant, and by other plants, animals and microorganisms. We can think the same way for other biochemical groups of secondary metabolites, but these have neither the diversity nor the multiple significance that give the terpenoids their enormous potential for mediating significant ecological interactions.

Terpenoids are compounds containing an integral number of five-carbon (5C) units, the 'syllables'. There is an astonishing array of structures, the 'words', resulting from the sequential combination of these basic 5C units in the familiar categories of C10 (mono-), C15 (sesqui-), C20 (di-), C30 (tri-), C40 (tetra-) and C > 40 (poly-) terpenoids. Diverse terpenoids blends, the 'messages', are emitted into the environment either through volatilization (mono- and sesquiterpenes), leaching or decomposition of plant debris.

Part of such terpenoid 'words' are common to all plants. For example, carotenoids, chlorophylls or hormones, such as cytokinins, gibberellins or abscisic acid, are terpenoid derivatives. But there are also 'dialects' of the terpenoid 'language' that are qualitatively or quantitatively characteristic of each family and each species, or even each cultivar and each organ of the plant[6]. This allows a specific 'language' among organs whereby, for example, damaged portions of the plant relay information to undamaged portions[7]. Terpenoids have even been proposed as an equivalent to an immune system by plants[8,9]. Terpenoid 'language' also communicates plants with other species of plants, animals, fungi and microorganisms. Terpenoids may (1) act as alarm signals to deter herbivores or to inform other plants, (2) simulate animal alarm pheromones or animal growth and sex regulators such as juvocimones (potent juvenile hormone mimics)[9], and (3) act as attractors of herbivore predators[10], or of other animals useful to the plant, such as pollinators[11].

Terpenoids are, thus, one of the most versatile chemical languages in the network of communication between plants and other organisms. They even seem to be kept in 'memory'. Plants 'remember' previous exposures and produce terpenoids (and compounds of other chemical languages such as phenolics or alkaloids) when they are needed. In general, after an interaction with another organism, there is a disproportionately high and fast increase in those chemicals that have the most intense effects on it[12]. Thus, plants are not much different from animals in their communication among themselves and with other organisms; they also have languages (with words and messages). Terpenoids are one of them.

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A protist writes...

Having learned a little about cladistic naming, I was not too surprised to discover that I am not only a bony fish, but a lobed-finned bony fish whose adults and juveniles are four-legged and terrestrial (Box 1 in Ref. 1). The next step will be to demonstrate that I am a *cartilaginous* bony lobed-finned bony fish... The inevitable end of cladistic analysis will come with the announcement that all life is in the Kingdom Monera.

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Letters to *TREE*

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