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COMMENTARY ON SIMBERLOFF (2006): MELTDOWNS, SNOWBALLS AND POSITIVE FEEDBACKS

Simberloff (2006) revisits the evidence for the hypothesis of invasional meltdowns (Simberloff & Von Holle 1999) with a narrative review of recent examples of facilitation between invasive species, as well as a discussion of whether this – or any – metaphor helps or hinders scientific progress. I argue here that progress on evaluating invasional meltdowns will be better served by focusing on positive feedbacks as an ecological phenomenon rather than on the more restricted issue of facilitation; that in addition to better primary studies we need to employ better means to summarize and evaluate those studies to answer the really interesting questions about the generality of meltdowns; and, lastly, that while this metaphor has been useful, scientists need to be held to a higher standard than the general public in using metaphors and concepts precisely.

The focus of both the original 1999 and the 2006 papers was on facilitation among invasives, and acceleration of invasion rates. Positive feedbacks are mentioned only in passing in the 1999 paper, and not at all in the 2006 paper. However, facilitation itself does not really lead to anything in particular, and accelerating rates of invasion can have many different causes. I argue that positive feedbacks are the most interesting and important aspect of the hypothesis of invasional meltdowns, and this is where the conceptual and empirical focus should be. Different systems from engineering to economics to ecology have positive feedbacks, but they have been greatly underemphasized in community ecology relative to negative feedbacks (particularly competition and predation). Negative feedbacks damp down system level changes, leading to stability. Runaway positive feedbacks in a system create 'snowball' effects in which a phenomenon builds on itself in an accelerating fashion, becoming unstoppable. Positive feedbacks are therefore both of fundamental interest in ecology, and potentially of enormous practical importance in conservation ecology. A 'meltdown' due to a positive feedback implies that after a certain point is reached, ordinary intercession is impossible, and a drastic state change is inevitable – whether it occurs in a toddler in the supermarket, a nuclear reactor, or an invaded ecological community. The elements of inevitability and irreversibility have important implications for conservation biology.

So, what is the evidence for invasional meltdowns in nature? How frequent are they relative to all invasions? Do facilitative interactions among invaders commonly alter one another's demographic parameters, leading to mutually accelerating population increases of the invaders? Are invasional meltdowns implicated in most cases of major invasions, a substantial fraction, or very few? Do positive feedbacks have, on average, large and persistent effects, or minor effects? Do they occur evenly across taxa and systems, or are they more prevalent for a few species or only under certain circumstances? How important are complex synergisms between positive feedbacks among invasives and other effects such as climate change and overharvesting, as proposed for the widespread system changes in the Gulf of Maine (Harris & Tyrrell 2001), or complex trophic cascades involving negative and positive interactions between native and invasive species (Inderjit, personal communication)?

Convincing evidence in support of full invasional meltdowns has been very limited, as Simberloff (2006) acknowledges. Invasions themselves certainly are strongly implicated as drivers of major state changes in many communities – but how often are positive feedbacks between invaders a major factor leading to increased populations of invaders and increased impacts on native communities? Despite a flood of publications on ecological invasions (over 1300 publications, with approximately 1100 in the past 10 years), Simberloff cites only two cases that have been published since the 1999 paper in which invasional meltdowns have been reasonably well demonstrated – invasive yellow crazy ants and scale insects on Christmas Island, and rats, rabbits and two introduced succulent plant species on islands off southern France. All of the other studies he discusses are examples of one-way facilitation. In those studies, no positive feedbacks are involved – one species helps another, but there is no snowball, no acceleration, no inevitability, and no evidence of irreversibility or major state changes as a result of the mutual facilitation of a group (or even pair) of invaders. Nor can the acceleration of introduced species in the Great Lakes that Simberloff cites be taken as strong evidence for an invasional meltdown, because other explanations for the accelerating rate of invasion are also plausible (e.g. Inderjit *et al.* 2005). With almost 150 citations of the Simberloff & Von Holle (1999) paper to date, the idea of invasional meltdowns has garnered considerable attention from both scientists and the public. I found 50 published studies in a search on 'invasion,' 'invader' or 'invasive' and 'meltdown'. The lack of evidence for its existence is certainly not for want of attention to the hypothesized phenomenon.

Why is the evidence for invasional meltdowns so scanty? The phenomenon may, in fact, be uncommon. Simberloff (2006) is also correct that it is difficult to demonstrate, and that few studies have been done at the right ecological level (e.g. demographic studies). But Simberloff (2006) also states that recognition that facilitative interactions sometimes occur among introduced species is more important than addressing their relative frequency and importance. I cannot disagree more strongly: assessing the relative magnitude and importance of positive feedbacks in invasion is essential if we are to hope to evaluate and understand mechanisms of invasion. The only way to do this is to both accumulate more good primary studies and to use appropriate methods for the quantitative synthesis of their results, including meta-analysis (e.g. Gurevitch & Hedges 1999). Attempts to summarize existing studies have relied on flawed vote counts (e.g. Simberloff & Von Holle 1999) or anecdotal reviews (Simberloff 2006), both of which are inadequate for assessing the relative or absolute magnitude of effects in ecology.

More generally, has the use of metaphor helped or hindered our understanding of the phenomenon of species invasions, particularly in the case of invasional meltdown? There has been some hand-wringing that the general public uses the term sloppily, generically, and imprecisely. Thinking like a scientist depends on years of intensive training. It is unlikely that the general public will evaluate scientific issues with the same precision and nuance one expects from scientists. The meltdown metaphor helped increase public awareness of the urgency and importance of biotic invasions. Glitzy terms can attract attention for an idea; obscurity and blandness are neither virtues nor essential to good science. Invasional meltdown is a rich and powerful metaphor because it provides useful, testable implications at several levels. It is alarmist, but is it unrealistically so? We cannot know that until we answer the scientific questions of its generality and magnitude.

On the other hand, expecting scientists to think precisely and clearly about scientific metaphors, and in general about testing scientific hypotheses, is both realistic and necessary. 'Meltdown' has been used to describe snowball-free major system changes without any positive feedbacks or acceleration (e.g. Roy *et al.* 1999; Terborgh *et al.* 2001), as well as where unidirectional facilitation without positive feedbacks occur. Emphasizing the importance of precise and careful evaluation of the evidence regarding specific impacts of invasive species (e.g. Gurevitch & Padilla 2004) is not 'a rearguard action to convince biologists and the lay public that the ecological threat from introduced species is overblown' (Simberloff 2006). Nor are inaccuracies and loss of scientific credibility due to employing metaphors. They are the result of scientists' use of unclear and vague use of concepts and terminology, over-generalization and overstatement, and use of inadequate or inappropriate methodology to address scientific questions. The consequences are hindered understanding and impediments to effective action.

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REJOINDER TO SIMBERLOFF (2006): DON'T CALCULATE EFFECT SIZES; STUDY ECOLOGICAL EFFECTS

Certainly positive feedbacks beyond facilitation may precipitate an invasional meltdown, although the interactions of non-indigenous species, native species, and various processes in feedbacks that characterize some meltdowns are likely to entail facilitation. For instance, Simberloff & Von Holle (1999) cited the increased frequency and severity of fires upon invasion by flammable weeds as leading to a positive feedback, but even here, facilitation may be important. In the US West, introduced livestock facilitated replacement of native bunchgrasses by Eurasian grasses, which in turn fostered fires that further damaged native plants (Mack 1989; D'Antonio & Vitousek 1992). And, as I stressed (Simberloff 2006), the population impacts of many published examples of facilitation claimed to contribute to meltdown remain to be confirmed (just as the population impacts of many other interspecific interactions of potential ecological and conservation significance remain to be confirmed). So I agree that a search for positive feedbacks is likely to aid in understanding the importance of invasional meltdown.

I am unconvinced, however, that progress on evaluating invasional meltdown will be better served today by searching for positive feedbacks than by searching for facilitative interactions and studying the population and community-level consequences of those that are identified. I noted that there has traditionally been little attention paid to facilitative interactions relative to competitive and predatory ones (Simberloff 2006), and a rectification of that imbalance will likely 'challenge some of our most cherished paradigms' (Bruno *et al.* 2003, p. 119). The number of intriguing examples of facilitation recently reported in the invasion literature (e.g. Klironomos 2002; Ridenour & Callaway 2003) suggests this is a very fertile field of inquiry.

Gurevitch (2006) cannot disagree more strongly with my assertion that recognizing that facilitative interactions sometimes occur among non-indigenous species is more important than addressing their relative frequency and importance. She advocates a two-pronged approach: (i) more good primary studies; and (ii) different methods, including meta-analysis, for quantitatively synthesizing results of such studies. I agree completely that we need more good primary studies, as would most ecologists and invasion biologists. In fact, Simberloff (2006) advocated exactly this approach and ended by contending that improved prediction of invasion impact (with concomitant improvement in regulatory and management procedures) 'will increase only apace with a growing number of empirically studied cases'. However, on Gurevitch's second point, and particularly on the need for meta-analysis in determining the frequency and magnitude of facilitation and meltdown in invasions, I cannot disagree more strongly.

In my view, ecology, especially at the level of communities where most attention of invasion biologists has been focused, is a highly idiographic science best served by amassing a catalogue of case studies (Shrader-Frechette & McCoy 1993; Simberloff 2004). In invasion biology, broad patterns exist (e.g. many introduced mammals but few introduced birds have major impacts), but each case is largely *sui generis*. It is important to know much more than we do about how often facilitation and meltdown occur and what the consequences for recipient communities might be (as it is for competition between invaders), but determining a mean effect size is unlikely to be very useful for invasion policies or management. Ultimately, of course, a large catalogue of case studies designed so that the relevant statistics can be extracted to do a meta-analysis will answer the interesting but largely academic question of whether facilitation, when it occurs, has a bigger impact than competition, when it occurs. But what would be most useful right now, in understanding