Research

Positive interactions among plant species for pollinator service: assessing the 'magnet species' concept with invasive species

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Plants with poorly attractive flowers or with little floral rewards may have inadequate pollinator service, which in turn reduces seed output. However, pollinator service of less attractive species could be enhanced when they are associated with species with highly attractive flowers (so called 'magnet-species'). Although several studies have reported the magnet species effect, few of them have evaluated whether this positive interaction result in an enhancement of the seed output for the beneficiary species. Here, we compared pollinator visitation rates and seed output of the invasive annual species *Carduus pycnocephalus* when grow associated with shrubs of the invasive *Lupinus arboreus* and when grow alone, and hypothesized that *L. arboreus* acts as a magnet species for *C. pycnocephalus*. Results showed that *C. pycnocephalus* individuals associated with *L. arboreus* had higher pollinator visitation rates and higher seed output than individuals growing alone. The higher visitation rates of *C. pycnocephalus* associated to *L. arboreus* were maintained after accounting for flower density, which consistently supports our hypothesis on the magnet species effect of *L. arboreus*. Given that both species are invasives, the facilitated pollination and reproduction of *C. pycnocephalus* by *L. arboreus* could promote its naturalization in the community, suggesting a synergistic invasional process contributing to an 'invasional meltdown'. The magnet effect of *Lupinus* on *Carduus* found in this study seems to be one the first examples of indirect facilitative interactions via increased pollination among invasive species.

Since Darwin (1859), competition has been considered as one of the most important forces driving the evolution and dynamics of populations. However, Bruno et al. (2003) have recently proposed that positive interactions must be included into ecological theory as another important force influencing those processes. Positive interactions are non-consumptive interactions between two or more species, benefiting at least one of the participants (reviewed by Callaway 1995). Facilitation is the most commonly reported positive interaction among plants, where one species have greater fitness when growing in association with other species than when grow alone (Callaway 1995, Brooker et al. 2008). Amelioration of physical stress by one or more facilitator species is the most common facilitation mechanism reported for plants (Callaway and Pugnaire 1999, Pugnaire and Luque 2001, Callaway et al. 2002, Molina-Montenegro et al. 2005). Associations between plants can also influence the fitness of participants by altering their interactions with other organisms, such as herbivores (Hjältén et al. 1993, Callaway et al. 2000, 2005, Ibañez and Schupp 2001) and pollinators (Rathcke 1988, Laverty 1992, Roy 1996, Brown et al. 2002).

For instance, in herbivory it has been shown that palatable species associated with unpalatable neighbors may avoid herbivore attack and, consequently, increase their size and reproductive output (Callaway et al. 2000,

2005). For animal-pollinated plants, pollinator service is an important process influencing their reproductive success, where changes in the frequency and/or quality of this service affect the seed output (Fægri and Van der Pijl 1971). Plants with inconspicuous flowers, or with little floral rewards, may have inadequate pollinator service, limiting pollen transportation between conspecific individuals and, consequently, having a reduced seed output (Pellmyr 1986, Laverty 1992, Agren 1996, Brys et al. 2004, Molina-Montenegro and Cavieres 2006). However, pollinator visitation rates of these less attractive species could be enhanced when they grow spatially associated with species with highly attractive flowers (Thomson 1978, Laverty 1992, Geer et al. 1995, Roy 1996, Moeller 2004, Ghazoul 2006).

More than twenty years ago, Thomson (1978) coined the term 'magnet-species' to refer to those highly attractive species that increase pollinator service of other species. More recently, Feldman et al. (2004) have assessed the consequences of this facilitative process on the fitness and population dynamics of participants by using mathematical models in which the presence of one showy flower species increases pollinator visits to a second species. Although the magnet species effect occurs in natural communities (Thomson 1978, Feinsinger et al. 1986, Laverty 1992,

Geer et al. 1995, Johnson et al. 2003, Moeller 2004), few studies has evaluated whether this positive interaction results in an enhanced seed output of the facilitated species (Laverty 1992, Moeller 2004, Ghazoul 2006). Moreover, all these studies have evaluated the positive interaction via a magnet species among native species.

Biological invasions have been recognized as one of the major threats to biodiversity and one of the greatest environmental problems (Sala et al. 2000). Despite the emphasis that negative interactions have received as one of the main drivers of invasions (Bruno et al. 2005), recent reviews have started to highlight that interactions among invaders may be positive (Simberloff and Von Holle 1999, Richardson et al. 2000, Simberloff 2006). Nevertheless, studies that experimentally evaluate positive interactions between invasive plants are scarce, particularly those where enhancement of the pollination service is the main mechanism of facilitation (Richardson et al. 2000).

Carduus pycnocephalus (Asteraceae) and *Lupinus arboreus* (Fabaceae) are invasive species in Chile, and they have been considered among the most aggressive and harmful weeds in the country (Matthei 1995). *Lupinus arboreus* (yellow bush lupine) is native to North America; it has large (8–10 cm length), yellow and fragrant flowers, displayed in large whorls along tall stems (Matthei 1995). *L. arboreus* is a nitrogen-fixing plant species and has a large floral display, with 15–30 floral stems per plant, and 24–40 yellow flowers per stem (Matthei 1995). *Carduus pycnocephalus* (Italian thistle) is an annual plant species, thus its life-cycle completely depend upon seed production for reproduction. This species is native to Europe, and it has 1–5 small capitula (up to 1.5 cm across) per flower stem, with small, pale-blue flowers which are visited by different insect species (Holm et al. 1997). Supplemental hand-pollination experiments in *C. pycnocephalus* have shown that the seed output is pollen-limited ($t_{1,38} = 28.69$, $p < 0.001$; Molina-Montenegro unpubl.). Considering that species with numerous and large brilliant color flowers have higher pollinator visitation rates than species with smaller and/or inconspicuous flowers (Sih and Baltus 1987, Krannitz and Maun 1991, Brown et al. 2002), we hypothesized that *L. arboreus* can act as a magnet-species for associated individuals of *C. pycnocephalus*, increasing pollinator service and seed output of the latter species. Nevertheless, because it is well known that facilitation may also occur because of direct effects of facilitators on availability of resources (Callaway et al. 1991, Shumway 2000), we also examined nitrogen and water availability in the soil beneath *C. pycnocephalus* growing with and without *L. arboreus* to assess possible 'bottom–up' reproductive effects (sensu Muñoz et al. 2005).

Material and methods

Study site and target species

This study was carried out in Peninsula Hualpen (36°45′S, 73°13′W), a protected area of 5 ha, located 15 km east from Concepción in central Chile. At this site, mean annual rainfall is 900 mm and mean annual temperature is 12.2°C (Di Castri and Hajek 1976). Vegetation is comprised of patches of coastal forest dominated by *Cryptocarya alba* (Lauraceae) and *Aextoxicon punctatum* (Aextoxicaceae). Forest patches are surrounded by extensive grassland areas where several shrubs and herbaceous plants can grow, including the target species of this study: *Carduus pycnocephalus* (hereafter *Carduus*) and *Lupinus arboreus* (hereafter *Lupinus*) (Fig. 1).

Pollinator visitation rates

To compare pollinator visitation rates between *Carduus* individuals growing alone and when growing in association with *Lupinus*, flower visitors of *Carduus* were recorded on three consecutive sunny days in January 2004. Each day four independent plots of 3×3 m each, and distanced by 12–15 m each where delimited. Each plot included four *Carduus* individuals. All these *Carduus* plants had one flower stem with 3–5 open floral heads (capitula). In two of these plots the *Carduus* individuals were growing alone (more than 13 m away of any *Lupinus*), while in the other two plots *Carduus* individuals were associated (within 0.2 m) with one *Lupinus* individual in bloom. Each day we delimited four different plots, hence, plots registered one day were different to those used on the other days. Thus, a

Figure 1. *Carduus pycnocephalus* (A) and *Lupinus arboreus* (B) individuals growing in the study site.

total of 12 plots were studied, six with *Carduus+Lupinus* and six with *Carduus* alone.

Although companion species were mainly small herbs and grasses, to avoid any possible interferences we removed all other species in bloom within a radius of 2 m around each target individual. Each observation day was divided in 21 15-min observation periods, beginning at 9:00 h and finishing at 19:15 h. During each observation period, two paired plots (one with and the other without *Lupinus*) were simultaneously observed, and the number of flower visitors on each *Carduus* individual was recorded. Therefore, 252 observation periods were carried out in total. Flower visitors were considered as pollinators only if they touched the inflorescence, making probable the contact with anthers or stigma. Visitors touching any other part of the capitula were not considered as pollinators. Pollinator visitation rates were calculated as the average number of pollinator visits per plant during each observation period, and were compared between *Carduus* growing with and without *Lupinus*, and between observation periods, with repeated-measures ANOVA.

To assess the effect of floral density on pollinator visitation rates in *Carduus* with and without *Lupinus*, we recorded flower visitors on five sunny days in March 2008. Each day three independent plots of 15×15 m each and distanced by 40–50 m each where delimited. The plots delimited one day were different to those used on the other days, hence a total of 15 independent plots were used. The three plots delimited on each day were selected to account for high, medium and low density of *Carduus* flowers. On each plot there were *Carduus* individuals growing associated with *Lupinus* individuals in bloom (less than 0.2 m), while other *Carduus* were grouped with other con-specifics and distanced more than 13 m away from any *Lupinus*. Given that *Lupinus* individuals displayed between 20–30 floral stem per plant, some stems were cut in order to obtain flower densities similar to that of *Carduus*. Hence, after this manipulation, high density plots contained an average (± 2 SE) of 28.8 ± 1.48 and 27.9 ± 1.24 *Carduus* flowers growing with *Lupinus* and growing with conspecifics, respectively. Values for medium density plots were 13.7 ± 0.92 and 13.8 ± 0.75, while for low density were 5.6 ± 1.53 and 5.4 ± 1.22 for *Carduus* flowers growing with *Lupinus* and growing with conspecifics, respectively. Each observation day was divided in nineteen 15-min observation periods, beginning at 9:00 h and finishing at 18:00 h. Pollinator visitation rates were calculated as the average number of pollinator visits per plant and per hour, and were compared between *Carduus* growing with *Lupinus* and with conspecifics at different densities with ANCOVA, where flower density was the co-variable.

Seed output

To assess the effects of the association between *Carduus* and *Lupinus* on seed output, in late January 2004, 25 *Carduus* individuals growing with *Lupinus* and other 25 growing without it were chosen within the study site. We considered a *Carduus* individual as associated with *Lupinus* when the distance between both species was less than 0.2 m. *Carduus* individuals not associated with *Lupinus* were those where

the nearest *Lupinus* shrub was distanced more than 3 m away in any direction. All the selected *Carduus* individuals were 0.9–1.2 m tall to standardize possible plant size effects. Further, all *Lupinus* individuals had 25–30 branches with flowers and were 1.0–1.6 m tall to standardize the attractiveness effect. On each *Carduus* individual, three capitula were randomly selected and labeled with flags to evaluate seed output. In early March 2004, when labeled capitula were closed indicating that seed development had begun, they were bagged with nylon-mesh bags to prevent seed loss. Bagged capitula were collected in April, and seed output was calculated as the ratio between the number of filled seeds and the total number of seeds (i.e. including aborted and predated seeds) produced per capitula. Values of seed output per capitula were averaged for each *Carduus* individual, and this value was compared between *Carduus* individuals associated with *Lupinus* and growing alone with a student's t-test.

Microclimatic conditions of soil

To assess nitrogen availability in the root environment of *Carduus*, five *Carduus* individuals associated with *Lupinus* and other five individuals growing alone were selected in February 2004 and March 2008, before the onset of seed production in each year. A soil sample of 10 cm depth was taken beneath each individual. Soil samples were stored in hermetic plastic bags and sent for analyses to determine the concentration of nitrate (NO_3^-) and ammonium (NH_4^+) following the colorimetric techniques proposed by Robarge et al. (1983) and Longeri et al. (1979), respectively. Differences in total concentration of available nitrogen (NO_3^- plus NH_4^+) in soil beneath *Carduus* individuals growing with and without *Lupinus* were assessed with a two-way ANOVA.

To estimate differences in water availability, 10 *Carduus* individuals growing with *Lupinus* shrubs and another 10 individuals growing alone were selected in February 2004 and March 2008. Beneath each selected *Carduus*, soil matric water potential was measured with tensiometers. The tensiometers were dug at 20 cm depth, and matric potentials were recorded after 30 min of stabilization. These measures were taken in sunny days in late February 2004. Differences in soil matric potentials between *Carduus* associated with *Lupinus* and growing alone were assessed with a two-way ANOVA.

Results

Pollinator visitation rates

Floral heads of *Carduus* and floral stems of *Lupinus* were visited by the same insects, mainly Hymenoptera (88%) and Lepidoptera (12%), where *Aucacoctei pales* (Nymphalidae), *Hylephila fasciolata* (Hesperidae) and *Bombus dahlbomii* (Apidae) were the most common pollinators. Pollinator visitation rates were significantly higher in *Carduus* associated with *Lupinus* than when growing alone ($F_{1,10} = 360.02$, $p < 0.01$). Pollinator visitation rates did not vary between observation periods ($F_{21,210} = 1.15$, $p = 0.29$), indicating that differences between *Carduus*
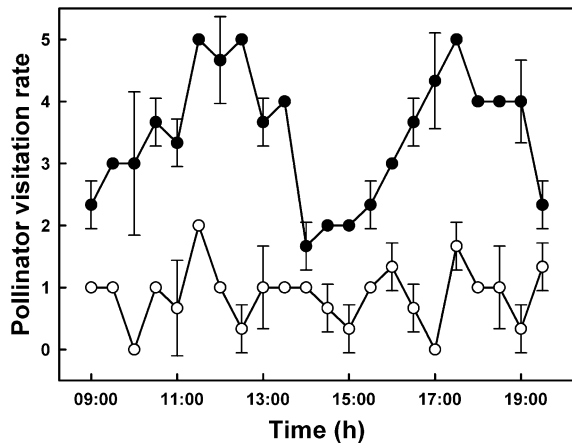
Figure 2. Pollinator visitation rates of *Carduus pycnocephalus* individuals associated with *Lupinus arboreus* (closed circles) and growing alone (open circles) at the different observation periods along day. Each value is the mean ($\pm$ 2 SE) number of pollinator visitations per *Carduus* in each 15-min observation period.

with and without *Lupinus* were maintained during the day (Fig. 2).

On plots with different flower densities, *Carduus* and *Lupinus* were visited by the same insects with all of them belonging to Hymenoptera. Pollinator visitation rates significantly increased with flower density ($F_{1,27} = 160.62$, $p < 0.0001$). However, the ANCOVA test showed that pollinator visitation rates were higher in *Carduus* growing in association with *Lupinus* than growing alone, even after correcting for flower density ($F_{1,27} = 198.91$, $p < 0.001$; Fig. 3).

Seed output

Production of viable seeds in *Carduus* individuals growing in association with *Lupinus* shrubs was 32% higher than in *Carduus* plants growing alone, with this difference being statistically significant ($t_{1,48} = 32.25$, $p < 0.01$; Fig. 4).
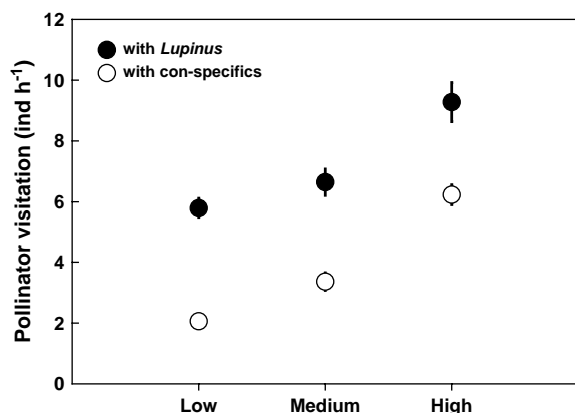

Figure 3. Pollinator visitation rates of *Carduus pycnocephalus* individuals growing associated with *Lupinus arboreus* and with con-specifics at low, medium and high density. Each value is the mean ($\pm$ 1 SD) number of pollinator visitations per *Carduus* individual and hour.
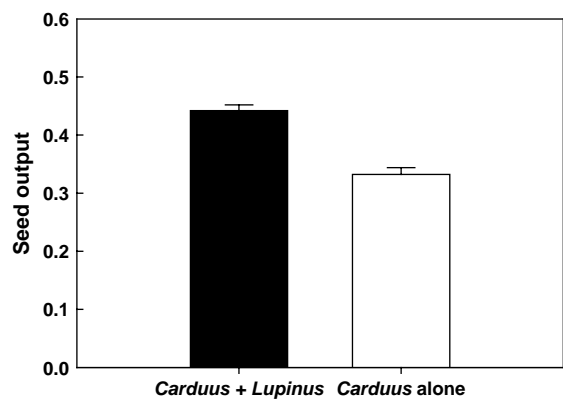

Figure 4. Seed output of *Carduus pycnocephalus* individuals growing within (solid bar) and without *Lupinus arboreus* (empty bar). Values are means ($\pm$ 2 SE) of the ratio between the number of viable seed and total seed production per capitula per *Carduus* individual.

Microclimatic conditions of soil

Neither nitrogen availability ($F_{1,16} = 3.05$, $p = 0.10$; Fig. 5A) nor soil matric potential ($F_{1,36} = 3.38$, $p = 0.80$; Fig. 5B) differed between *Carduus* individuals associated with and without *Lupinus*. Additionally, not differences were found between years ($F_{1,16} = 0.41$, $p = 0.53$ and ($F_{1,36} = 0.01$, $p = 0.93$) both for nitrogen availability and soil matric potential, respectively (Fig. 5A–B).

Discussion

Our results support the hypothesis that the pollinator service of a less attractive species such as *Carduus pycnocephalus* is enhanced when growing in association with a species with large showy flowers and greater floral display such as *Lupinus arboreus*. Thus, the higher pollinator visitation rates detected on *Carduus* individuals associated with shrubs of *Lupinus* in bloom compared to those *Carduus* individuals growing alone suggests that *Lupinus* acts as a magnet species for *Carduus*. Although, the higher pollinator visitation rates on *Carduus* individuals could be related with increases in flower density, we found that for similar flower density *Carduus* individuals always received higher insect visitations when grow associated with *Lupinus*. Therefore, our data support the hypothesis that *Lupinus* act as a magnet species even controlling for flower density.

Moreover, our results indicate that the enhanced pollinator service results in increases in the seed output of *Carduus*. Thus, the fitness of *C. pycnocephalus* is enhanced when grow in association with the magnet species *L. arboreus*, indicating that one invasive species can indirectly facilitate other invasive species through increasing pollination service.

Increases in pollinator visitation rates due to the presence of a magnet species have been reported in several other studies (reviewed by Feinsinger 1987). For instance, Thomson (1978) showed that the number of insects visiting the yellow-flower *Hieracium florentinum* was higher when it
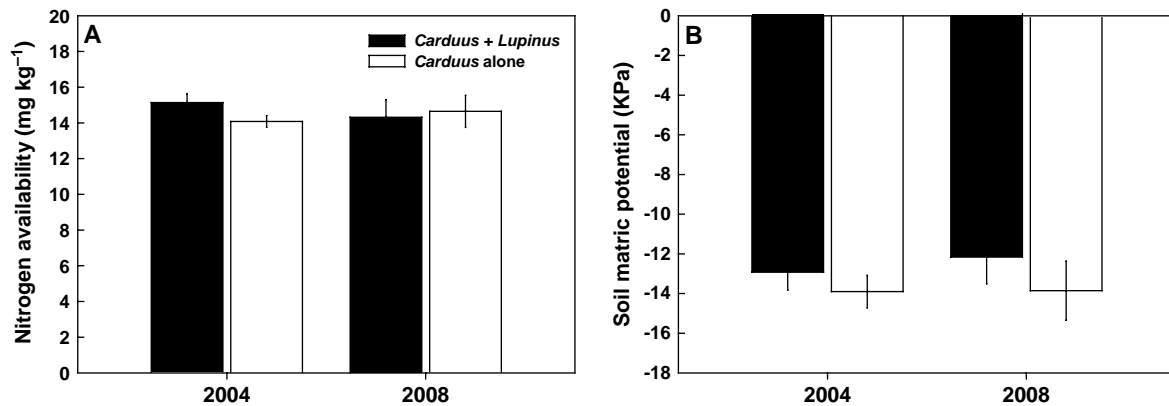
Figure 5. Available nitrogen (A) and matric water potential (B) in soil beneath *Carduus pycnocephalus* individuals associated with *Lupinus arboreus* (solid bar) and growing alone (empty bar). Values are means ($\pm$ 2 SE) are shown.

was associated with the orange-flower *Hieracium aurantium* than when it grew in monospecific stands. Similarly, Johnson et al. (2003) indicated that the orchid *Anacamptis morio*, whose flowers do not produce nectar, had higher visitation Fes of bumblebees when grow associated with nectar-producer plants than when grow alone. However, despite the widely reported positive effect of magnet species on pollinator service, empirical studies evaluating the consequences of such facilitated pollination on seed production are scarce. For instance, Laverty (1992) showed that both pollinator visitation rate and seed output of *Podophyllum peltatum* increases when grow close to the magnet species *Pedicularis canadensis*. More recently, Moeller (2004) showed that both inter and intraspecific interactions of co-occurring *Clarkia* spp. that share pollinators are positive, with increased seed outputs when two or more species co-occur.

Although, the higher seed output of *Carduus* when grow associated with *Lupinus* appears to be a consequence of facilitated pollination processes, similar increases in seed output could be produced if the facilitator species produce local increases in the availability of resources (Zimmerman and Pyke 1988, Mattila and Kuitunen 2000). We did not detect significant differences in soil nitrogen content in the rooting zone of *Carduus* with and without *Lupinus*. Although *Lupinus* is a nitrogen-fixing species, much of the fixed nitrogen is transported to its leaves and is released to the environment only after the plant dies (Maron and Connors 1996). Thus, given that neither nitrogen availability nor water availability differed between the root environment of *Carduus* individuals growing with and without *Lupinus*, we suggest that the higher seed output of *Carduus* associated with *Lupinus* was mostly due to increases in pollinator visitation rates rather than to differences in bottom–up effects. Nonetheless, the high levels of ammonium and nitrate fixed by *Lupinus* that can be available after the bush is dead can have important consequences for the establishment of other species. Indeed, Maron and Connors (1996) showed that in California coastal prairies *Lupinus arboreus* is a facilitator of exotic weed and annual grass invasions, which establish after the dense canopies of the short-lived *Lupinus* are opened by fire or insects.

The increase in seed output of *Carduus* when growing in association with the magnet species may have important implications for the persistence and grow of its populations. Feldman et al. (2004), following the initial propositions of Rathcke (1988), proposed a mathematical model to assess the net-outcome of facilitated pollination on the population dynamics of a magnet and a facilitated species, considering that these species compete for space when they co-occur. The model predicts that facilitated pollination may increase the population growth rate of facilitated species until a threshold at which competitive effects between species become stronger than facilitative effects (Feldman et al. 2004). Here, we did not assess the population dynamics of the target species, but our results support the suggestion that the enhancement of seed output due to facilitated pollination may increase the propagule pressure of *Carduus*, increasing its population growth. This is particularly important given the non-native nature of both the benefactor and beneficiary species considered in this study. Thus, the facilitated pollination of *Carduus pycnocephalus* by *Lupinus arboreus* could promote its naturalization and spread in the studied community, suggesting a synergistic invasional process. Simberloff and Von Holle (1999) called this process 'invasional meltdown', proposing that two or more alien species may increase their likelihood of survival and ecological impact when acting together than when acting separately. These authors highlighted the importance that positive interactions can have on the invasion process (Bruno et al. 2003, Bulleri et al. 2008), despite the primacy of evaluations of the importance of negative interactions in the invasion literature.

The invasional-meltdown is a community-level phenomenon (Simberloff 2006), and although pure and simple facilitative interactions do not itself constitute a meltdown, they certainly aid to this process to occur. So far, the most commonly reported mechanisms whereby facilitative interactions determine invasion processes are direct interactions among plants either between invasive species or between native and invasive species (Maron and Connors 1996, Carino and Daehler 2002, Lenz and Facelli 2003, Cavieres et al. 2005, 2008, Reinhart et al. 2006, Tecco et al. 2006, Badano et al. 2007). Among indirect interactions, non-native animals pollinating and dispersing invasive plants,

and non-native animals and plants modifying the environment in ways that favor the recruitment of other non-native species are the most frequently reported (Simberloff and Von Holle 1999, Richardson et al. 2000, Crooks 2002). Thus, the magnet effect of *Lupinus* on *Carduus* found in this study seems to be one the first examples of indirect facilitative interactions via increased pollination among invasive species. However, further studies considering more species would shed lights about the importance of this magnet effect of *Lupinus* on *Carduus* on the invasional meltdown.

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