When belowground rumbles: a plant's interactions with antagonists are robust to earthquake-induced shifts in the below-ground environment

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Abstract: A major paradigm in plant ecology is the recognition of the profound consequences of the below-ground environment on the interactions between plants and other species above ground. It has recently been suggested that this perspective should be incorporated into plans to restore disturbed habitats. However, these efforts are undermined by our lack of knowledge on the consequences of naturally occurring below-ground disturbance. The 6.2 moment magnitude earthquake that struck near Christchurch, New Zealand, on 22 February 2011 provides a rare test case to identify the effects of profound below-ground disturbance on above-ground interactions. We study these effects by quantifying interactions between the weedy perennial *Malva sylvestris* and its above-ground antagonists. We show that across two spatial scales, the presence of earthquake-induced soil disturbance (liquefaction) has no significant effect on the abundance of antagonists on *M. sylvestris*. Our results demonstrate resilience of some above-ground interactions to profound, natural below-ground disturbance. This result is important both for understanding the limits of the above-ground – below-ground linkages paradigm and to help remediate the consequences of profound below-ground disturbances.

Keywords: above-ground – below-ground interaction; earthquake; *Malva sylvestris*; natural below-ground disturbance; *Puccinia malvacearum*

Introduction

Decades of work have now demonstrated that soil biology, chemistry, and microbial composition can have profound consequences for above-ground interactions between species (Bardgett & Wardle 2010). In spite of this work, we still do not know how natural disturbance below ground alters interactions between plants and their antagonists such as herbivores and pathogens. This represents a substantial conceptual gap in our knowledge and one that will become increasingly important as we seek to integrate the biology of below-ground interactions into efforts to restore sites that have been disturbed (Kardol & Wardle 2010). Here, we use an example of profound below-ground disturbance (earthquake damage) to test for the role of below-ground disturbance on easily quantified plant–antagonist interactions, specifically those between the weedy perennial *Malva sylvestris*, a rust pathogen *Puccinia malvacearum* and herbivores of *M. sylvestris*.

An extensive body of literature has shown that below-ground biology is important for above-ground species interactions (Van der Putten et al. 2001; Wardle et al. 2004; Bardgett & Wardle 2010). There are several mechanisms through which the below-ground environment can influence above-ground interactions between species. Numerous studies have documented how abiotic below-ground effects – here defined as changes in non-living soil properties –influence above-ground biotic interactions. For example, the production of plant defence chemicals that mediate above-ground plant–herbivore interactions can depend on below-ground nutrient uptake (Van Der Putten et al. 2009). The ability of plants to succeed in some environments can depend on the combined effects of soil type and herbivore pressure (Fine et al. 2004). Interactions between plants and the below-ground biotic environment can similarly have profound effects on above-ground plant–antagonist interactions. Soil biota can impact plant performance through nutrient acquisition, which in turn influences above-ground herbivores (Wardle et al. 2004). Below-ground biota can trigger direct and indirect production of defence compounds, which can affect above-ground herbivory (Bezemer & Van Dam 2005). Colonisation by mutualist mycorrhizal fungi can decrease above-ground herbivore growth and survival and so reduce damage to the leaves of plants (Rabin & Pacovsky 1985).

In spite of the profound consequences of the below-ground environment on above-ground interactions, we know little about the consequences of natural below-ground disturbance. There is some experimental work demonstrating that physical soil disturbance disrupts plant mycorrhizal interactions (Jasper et al. 1989) and plant-root nutrient uptake (Lucash et al. 2008). Fire is another form of disturbance that impacts on physical soil properties (Certini 2005) and has been shown to affect interactions between plants and soil biota (Carvalho et al. 2010). Another study showed that disturbance negatively affecting soil biota required the plant to have a superior competitive ability to establish (Fukano et al. 2013). Likewise, studies have documented some effects of artificial disturbance. For example, soils from sites that have been cultivated have different microbial communities than soils from uncultivated sites (Steenwerth et al. 2002). In contrast, there are compelling examples of natural above-ground disturbance altering plant–antagonist interactions. For example, hurricane-induced disturbance promoted leaf regeneration in the seashore shrub *Conocarpus erectus* that in turn increased the plant's susceptibility to herbivory (Spiller & Agrawal 2003).

A series of earthquakes near Christchurch, New Zealand, provided a unique opportunity to study the impacts of naturally occurring below-ground disturbance on above-ground ecology. The most damaging of these earthquakes was a 6.2 moment magnitude earthquake that occurred within 10 km of Christchurch city centre on 22 February 2011 (Cubrinovski et al. 2011). Several other smaller or more distant earthquakes also produced damage.

One of the most pervasive effects of the earthquakes in Christchurch has been a profound change in the below-ground environment; liquefaction (Fig. 1), the transformation of solid, water-saturated soil into a medium that flows like a liquid. Liquefaction is caused by ground shaking in areas with a high water table and unconsolidated coarse silt and fine sandy sediments (Youd & Idriss 2001). Water held in soil pores was ejected onto the soil surface, bringing with it the fine sand and coarse silt particles characteristic of the subsoil. The point where water and soil particles were expelled often developed a raised profile, and was referred to as a sand volcano or blister. Liquefaction has had catastrophic effects on the inhabitants and infrastructure of Christchurch particularly over the eastern half of the city, where approximately 4000 ha were affected to varying degrees.

During the liquefaction process, the subsoil was ejected upwards onto the existing soil surface. The ejecta comprised 66% fine sand and 20% medium sand and had a maximum depth of 400 mm. The coarse texture of liquefaction-affected soil resulted in rapid water drainage and low water-holding capacity. Total available water by volume for liquefaction-affected soil was only 7.6%, whereas plant readily available water was only 7% (Morgenroth & Armstrong 2012). Liquefaction-affected soil also had low organic matter content (0.03%) and was nutrient deficient, having very low concentrations of macronutrients (N, P) and exchangeable bases (K, Ca, Mg, Na) (Almond et al. 2010). Liquefaction seems to have physically damaged tree roots in the city. As a result of this and other forms of earthquake damage there has been a 50% increase in tree removal in Christchurch (Morgenroth & Armstrong 2012).

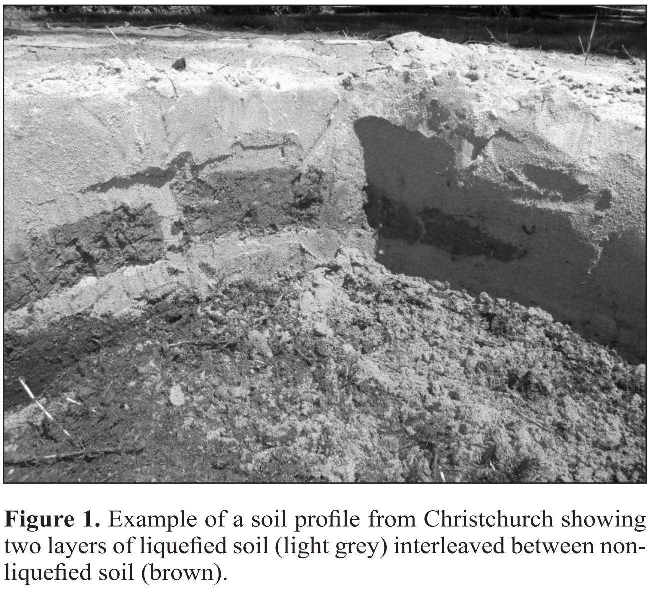

Figure 1. Example of a soil profile from Christchurch showing two layers of liquefied soil (light grey) interleaved between non-liquefied soil (brown).

We studied the effects of liquefaction in the large-flowered mallow (*Malva sylvestris* L.), a biennial or perennial herb, native to Europe, North Africa and south-west Asia (Webb et al. 1988). This species is widespread in the urban and peri-urban landscapes of Christchurch making it possible to locate plants on liquefied and non-liquefied ground. *Malva sylvestris* is also particularly amenable to study because the effects of its antagonists are readily quantified. This species commonly suffers from easily detected leaf herbivory, most likely from generalist insect herbivores. In addition it is frequently attacked by an easily quantified plant disease, hollyhock rust *Puccinia malvacearum* (Commonwealth Mycological Institute 1970). If below-ground disturbance such as liquefaction affects the interactions between *Malva sylvestris* and its antagonists, we expected to see a change in the success of antagonistic species at one or both of the following scales: when comparing (1) sites in parts of the city with liquefaction with parts of the city without liquefaction (hereafter our regional study) and (2) plants growing in liquefied and non-liquefied areas within a single study site (hereafter our local study).

Materials and methods

Sampling protocol

For the regional study, 19 field sites (11 on liquefied soil and 8 that had escaped liquefaction; Fig. 2) were surveyed from 6 to 20 December 2011 for antagonist damage on *Malva sylvestris*. Sites that had either experienced or escaped liquefaction were identified from preliminary maps of liquefaction-related land damage (Tonkin & Taylor 2011). The sites, many of which were urban waste areas or undeveloped housing sections, were spread across urban and suburban Christchurch (Table 1).

For our local study, *Malva sylvestris* plants were also surveyed (2 February 2012) at a single location of c. 1 ha containing both liquefied and non-liquefied soils. This local study site was at a grassland-dominated paddock at Travis Wetland Natural Heritage Park (S 43.492361, E 172.696638). This site experienced localised liquefaction consisting of several dozen patches of liquefied soil, each covering an area of approximately 1.0 m^2. Since 2006 the site has been in the process of restoration notably through the planting of indigenous plants such as cabbage tree (*Cordyline australis*) and New Zealand flax (*Phormium tenax*). Maintenance staff at Travis Wetland mowed this site roughly once a year to reduce the growth of weedy species. Before 2006, the site was a pasture. *Malva sylvestris* was a common weed growing among the young woody plants at this site.

Since liquefaction was highly localised, it was possible to identify neighbouring pairs of plants for comparison, one plant in liquefied soil and an adjacent plant in non-liquefied soil (typically less than 2.0 m apart). To accomplish this, we conducted an initial survey of the paddock, marking *Malva sylvestris* plants growing on liquefied soil, typically fewer than five plants per liquefaction patch. Each of these plants was then paired with the nearest plant growing in non-liquefied soil. There were 39 pairs of plants. We tested whether a plant was in liquefied soil or not by visually examining a soil sample at the base of the plant in question.

We sampled leaves from every plant by looking away, then picking the first leaf sighted that was 25–60 mm in diameter. Where possible we repeated this procedure five times per plant. Leaves smaller than 25–60 mm typically did not exhibit symptoms of infection with *Puccinia malvacearum*.

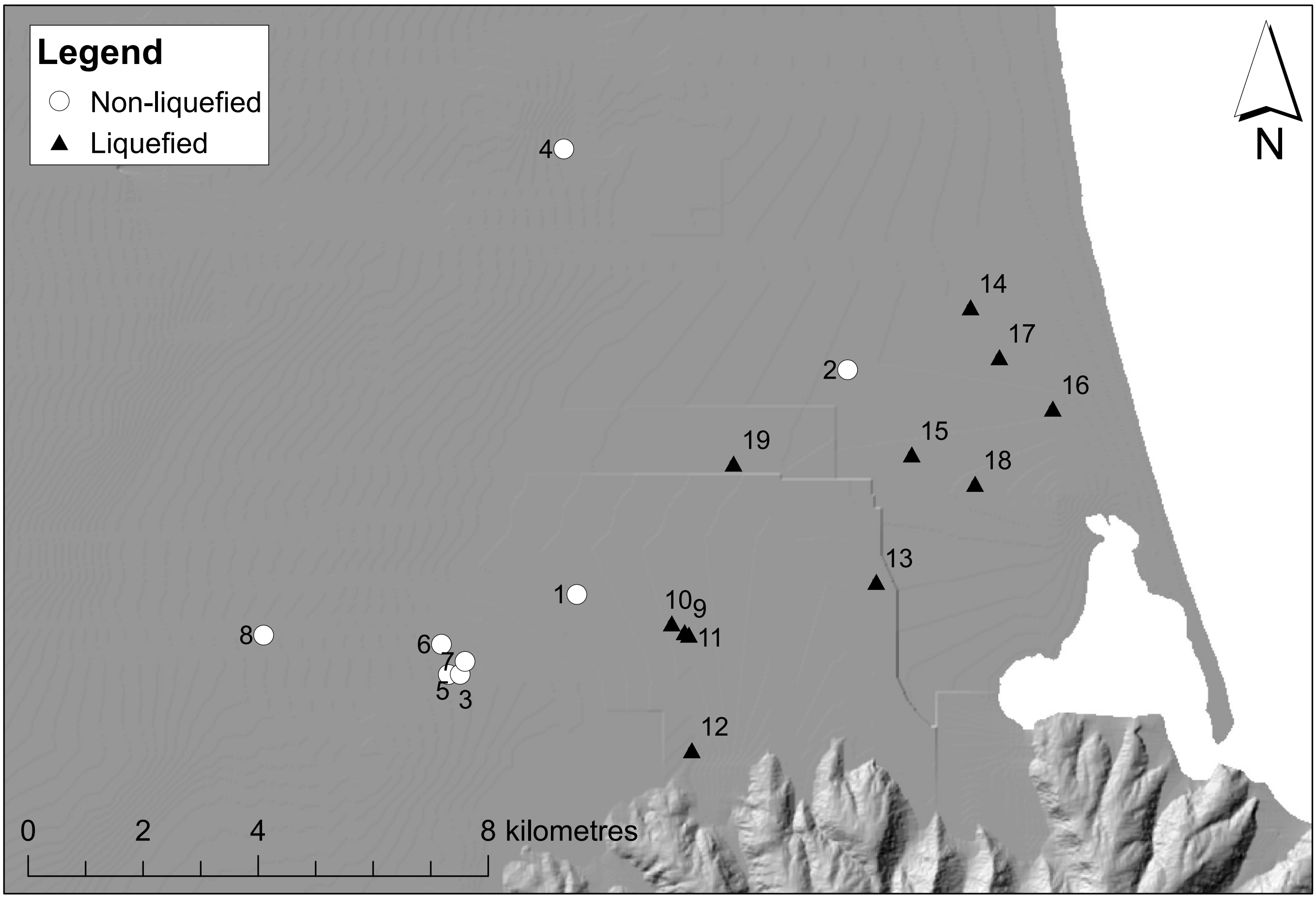

Figure 2. Map of urban Christchurch showing our sampling locations; the basemap is a hillshade layer in ArcMap 10. Refer to Table 1 for study site information.

Table 1. Description of study sites. Soil properties are from Webb et al. (1990).

Site no.	Latitude (S)	Longitude (E)	Liquefaction	Soil texture	Soil drainage
1	−43.5371	172.612	No	Silt loam	Poorly drained
2	−43.5021	172.67	No	Loamy sand	Well drained
3	−43.5495	172.584	No	Fine sandy loam	Imperfectly drained
4	−43.4673	172.609	No	Stony sandy loam	Poorly drained
5	−43.5495	172.586	No	Silt loam	Poorly drained
6	−43.5448	172.583	No	Silt loam	Poorly drained
7	−43.5475	172.588	No	Silt loam	Poorly drained
8	−43.5432	172.544	No	Silt loam	Imperfectly drained
9	−43.543	172.635	Yes	Silt loam	Poorly drained
10	−43.5416	172.632	Yes	Silt loam	Poorly drained
11	−43.5434	172.636	Yes	Fine sandy loam	Imperfectly drained
12	−43.5615	172.636	Yes	Fine sandy loam	Imperfectly drained
13	−43.5353	172.676	Yes	Loamy sand	Well drained
14	−43.4924	172.697	Yes	Complex	Poorly drained
15	−43.5154	172.684	Yes	Silt loam	Poorly drained
16	−43.5083	172.714	Yes	Silt loam	Poorly drained
17	−43.5002	172.703	Yes	Silt loam	Poorly drained
18	−43.52	172.697	Yes	Sand	Well drained
19	−43.5167	172.645	Yes	Peaty loam	Very poorly drained

Where possible, five plants were sampled per site. The same sampling protocol was used for both regional- and local-scale studies (488 and 388 leaves in total for each scale of sampling, respectively).

We used standardised photographs to measure the total area of each leaf, the total area of all pustules on each leaf, and the amount of herbivore damage. Photographs of each leaf were taken on a light board beside a black 100-mm^2 marker. Automated image processing was then used to compute summary statistics to determine the leaf area, the proportion of each leaf occupied by *Puccinia malvacearum* pustules, as well as the area of herbivore damage. For some leaves with severe insect damage the original leaf shape was estimated according to symmetric properties of the opposing leaf margin. Details of image processing can be found in the online Appendix S1.

For both regional and local studies the percentage pustule area and percentage herbivore damage were computed as the total area covered by pustules divided by the total area of all leaves × 100.

Data analysis

At a regional scale a linear mixed-effects model was used to account for uncertainty at two levels: sites with or without liquefaction; plants within sites. We considered the difference among sites to be a random effect and the difference between liquefied and non-liquefied sites to be a fixed effect. To produce a normally distributed response variable, the percentage of pustule area was log-transformed. The appropriateness of this assumption was confirmed with a quantile plot of the residuals. We tested whether knowing a site was liquefied improved model fit. To do this we computed a likelihood ratio test. Likelihood ratio tests represent a flexible method to assess whether a complex model is significantly better than a simpler null model. In our case, we tested whether a complex model including both differences among sites and differences between liquefied and non-liquefied sites was significantly better than a null model that only includes differences among sites. We fitted this model by maximum likelihood using the lmer package in R and assessed the significance using simulations (Faraway 2006).

For our local study we analysed pairs of plants, one in liquefied soil and the nearest plant in non-liquefied soil (usually within 2 m). Quantile–quantile plots on the residuals of a paired *t*-test revealed that our data on pustule area and herbivory were non-normally distributed. As a result we tested for difference between liquefied and non-liquefied plants using a paired Wilcoxon rank sum test. This is a non-parametric test equivalent to a paired *t*-test, which we used to test for a difference in either pustule area or herbivore attack rate between each plant on liquefied soil and a predetermined adjacent plant on non-liquefied soil.

We created a map of our sampling locations in ArcMap 10 (Fig. 2) using University of Canterbury geospatial data and additional information from koordinates.com.

Results

Across the city the percentage of leaf area with pustules varied between 0.02% and 5.38%. There was no significant difference between sites with liquefaction and without. In other words the addition of a fixed-effect term to distinguish liquefied and non-liquefied sites did not significantly improve our model ($P = 0.07$). The percentage of herbivore damage varied from 0.006% to 6.63%. The difference in herbivory between liquefied and non-liquefied locations was non-significant ($P = 0.61$). Likewise, there was no significant difference in leaf area between sites with and without liquefaction ($P = 0.133$).

For the local study at Travis Wetland, the leaf area covered by pustules varied from 0 to 4.96% with a mean of 0.38% (Fig. 3). The Wilcoxon rank sum test was non-significant ($P = 0.25$) with a 95% confidence interval for the difference between liquefied and non-liquefied plants of −0.02% to 0.14%. Herbivore damage varied from 0.005% to 9.5%. The Wilcoxon rank sum test was non-significant ($P = 0.15$) with a 95% confidence interval for a difference between liquefied and non-liquefied plants of −0.68% to 0.15%. There was no difference in average leaf area between liquefied and non-liquefied plants (*t*-test $P = 0.4622$) with a 95% confidence interval from −470 mm to 217 mm.

Discussion

Changes in the below-ground environment can have strong effects on above-ground interactions (Bardgett & Wardle 2010). Earthquakes represent a strong candidate for a study system to identify the consequences of below-ground disturbance.

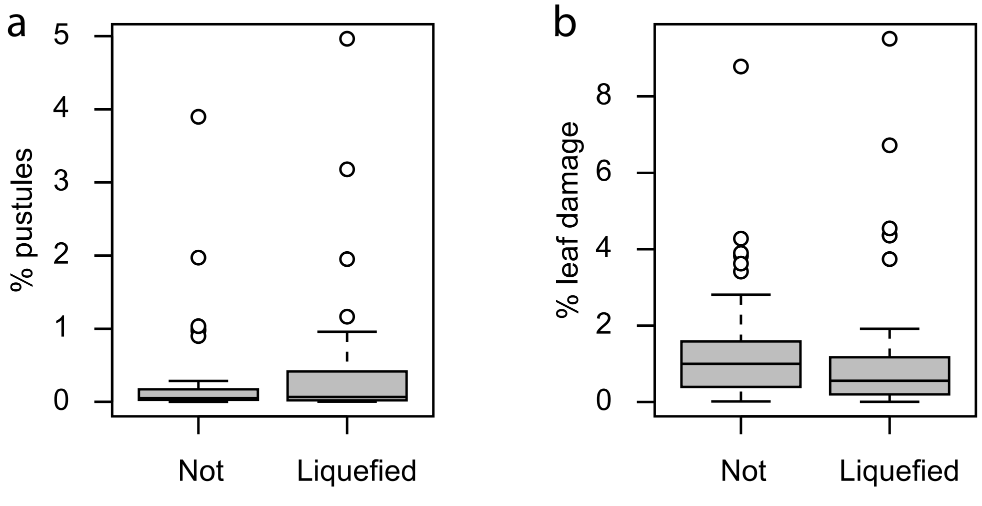

Figure 3. Box-plot comparison of (a) percentage pustule area and (b) percentage leaf damage for plants in not-liquefied and liquefied soils from the local study at Travis Wetland.

We know that earthquakes can have strong direct effects on vegetation through seismic shaking. Examples include forest destruction signalled by tree cohort recruitment following earthquakes along a 375-km length of the Alpine Fault in the South Island of New Zealand (Wells et al. 1999). Other studies have documented long-term effects of earthquake damage such as the slow decline in mangroves following ground uplift in the Andaman Islands (Ray & Acharyya 2011) and the death of trees over 4 years following an earthquake at Humboldt Bay, California (Jacoby et al. 1995). In Christchurch we know that the earthquakes have had profound impacts on the human and natural world, particularly through liquefaction (Cubrinovski et al. 2011; Morgenroth & Armstrong 2012). This makes our primary result surprising, that leaf size and the interactions between *Malvia sylvestris* and its antagonists were resilient to this disturbance. Below we discuss the robustness, biological significance and potential extensions of our results.

When designing our study, one of our primary goals was to develop a snapshot of the immediate effects of earthquake-induced disturbance on plant–antagonist interactions. Given the difficulty of experimentally replicating earthquakes, this necessitated studying plants that were already established in the ruderal habitats available in Christchurch. In short, this meant observing naturally occurring weeds. This design enforced several constraints on our work. We believe that each of these constraints must be considered when interpreting our results, but that our conclusions are still reliable.

The first ambiguity is due to the observational nature of our study. It is of course theoretically possible liquefaction does have an effect but that this effect is obscured by some other unmeasured environmental gradient. We believe that this is unlikely in our case primarily because we observe the same pattern across two different spatial scales. We would be hard-pressed to envision an unmeasured environmental gradient that could cancel out the effect of liquefaction across distances of either a metre or so and distances of tens of kilometres. Moreover, Christchurch is a reasonably homogeneous region, with elevations varying from 0 to c. 20 m above sea level and soil of similar parentage throughout our study sites (Table 1).

It is also possible that the biology of our focal interaction makes it particularly resilient to above-ground/below-ground effects. *Malva sylvestris* is a herbaceous weedy species, and as such is adapted to growing in a range of disturbed habitats (Webb et al. 1988). In the wild it is also known to be an effective scavenger/accumulator of mineral elements relative to other common species (Qasem 1992; Guerrero et al. 1999). Thus, while documenting the robustness of the interactions between *Malva sylvestris* and its antagonists is valuable, we must be cautious when extrapolating this observation to other systems.

Another potential issue was our limited ability to obtain new replicates. We made every effort to find abundant populations of *Malva sylvestris*. However, we faced constraints due to the urban nature of our study region and safety considerations due to earthquake damage in the central portions of Christchurch. As a result, it is still possible that earthquakes had an effect that was biologically significant albeit one that is difficult to detect with our design. We doubt that there is a strong, undetected effect of liquefaction, particularly in our local study, where the 95% confidence intervals were quite narrow (percentage pustule area: −0.02% to 0.14%, percentage herbivore damage: −0.68% to 0.15%) indicating that we have sufficient power to detect moderately large differences between liquefied and non-liquefied plants.

Finally, it is possible that some of the leaves in our study were older than the earthquake on February 2011. If this was the case, leaves might have completed development too early to show a significant difference due to liquefaction. This is unlikely to be the case in our local study in Travis Wetland because our study site was mown roughly once a year (J. Skilton, pers. comm.), and we conducted our research about a year after the earthquakes. Given the weedy growth form of *Malva sylvestris* we believe that most of the leaves we encountered in the regional study were also more recent than the earthquakes, though we cannot unambiguously confirm this. There is of course still room to test for longer-term effects of earthquake damage.

We have anchored this research on a conceptual question, ‘what are the linkages between the below-ground environment and above-ground species interactions’, a question whose answer may help restoration ecology (Kardol & Wardle 2010). We believe that we have a useful answer for this question. In the short term at least, the above-ground plant–antagonist interactions we have studied have remained relatively unchanged, even after changes in soil properties due to the major earthquake of February 2011. There are of course many facets of plant performance and ecology that we did not measure, but our hope is that this work will help to further the understanding of the role of below-ground disturbance.

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Supplementary Material

Additional supporting information may be found in the online version of this article:

Appendix S1. Image processing

The *New Zealand Journal of Ecology* provides online supporting information supplied by the authors where this may assist readers. Such materials are peer-reviewed and copy-edited but any issues relating to this information (other than missing files) should be addressed to the authors.