

## Research article

# Species richness and aggregation effects on the productivity of ruderal plant communities under drought perturbation

**Nodoka Nakamura\***

School of Agriculture, Policy and Development, University of Reading, Earley Gate, Reading, PO Box 237, RG6 6AR, UK.

\* **Corresponding author.** Oxford University Centre for the Environment, South Parks Road, Oxford, OX1 3PG, UK. Tel: 01865 283933  
Email: nodoka.nakamura@ouce.ox.ac.uk

**Supervisor:** Dr Andrew Wilby, School of Agriculture, Policy and Development, University of Reading, Reading, UK. Present address: Department of Biological Sciences, Lancaster University, Lancaster, UK.

The effect of species richness and spatial aggregation on the stability of community productivity in response to drought perturbation was investigated with experimental plant communities. Communities comprising all single- and three-species combinations of the ruderal species, *Capsella bursa-pastoris*, *Tripleurospermum inodorum*, *Poa annua*, and *Stellaria media*, were established in glasshouse. Habitat patchiness was manipulated by applying different seed-sowing patterns, either aggregated or random. After the establishment of communities, 8 days of drought treatment was imposed. Followed by a week of recovery with a regular watering regime, aboveground biomass was harvested. Community biomass was not affected by species richness or by aggregation, but was affected by perturbation. When multi-species community productivity was compared with monocultures in relative terms, species mixtures performed better in drought-induced conditions. This suggests that the positive effect of species richness may be enhanced under the perturbed condition. Sampling effects were evident under perturbation favouring the least productive species, *P. annua* and drought-tolerant *S. media*. All species except *C. bursa-pastoris* showed reduced productivity in species mixtures, but this may be mitigated under perturbed environments by species complementarity. Lack of clear responses to aggregation may suggest that the revealed diversity effect is not related to spatial structure. While competition predominates in communities in the resource-rich environment, drought perturbation enhance overall community productivity via a shift in relative significance of species interactions from competition to sampling and complementarity effects.

**Key words:** biodiversity effects, ecosystem stability, drought perturbation, relative yield total.

## Introduction

Ecosystem properties are regulated through interactions between abiotic factors, such as soil fertility and climate, and the functional traits of individual organisms that occur in a community.<sup>1–3</sup> Two important ecological questions have been the focus of research: how do ecosystems respond to changes in the environment, and which elements in the ecosystem are important determinants for maintaining the function of ecosystems? Disturbance (changes in the conditions of the environment) can occur over various spatial and temporal scales with different intensity and selectivity of impacts on ecosystems.<sup>4</sup> For instance, disturbance may

be climatic, such as drought, heavy rain, frost or lack of sunlight or may be biotic; outbreak of diseases, pests or intense grazing which limit production of biomass or the life cycle of individual species, plant communities and ecosystems.<sup>5</sup> Evidence supporting the view that different species express different response patterns to such changes in the environment suggests that an increase in diversity, species richness or functional diversity would lead to the extension of range of possible responses by an ecosystem. Hence, diversity would increase the stability of an ecosystem against environmental perturbation.<sup>1,6,7</sup> This idea is expressed in the ‘insurance hypothesis’ which proposes that a more diverse ecosystem has a higher potential of containing species

which are well adapted to a change in the environment and are able to compensate for the decline of the less adapted species.<sup>8,9</sup>

It is suggested that several explicit mechanisms, termed 'biodiversity effects', underlie diversity–ecosystem functioning relationships and it is likely that these mechanisms also mediate the response to environmental perturbation. These consist of three components: the sampling effect, functional complementarity and positive species interaction or facilitation.<sup>2, 10–12</sup> The sampling effect is the dominance of particular species. This component is suggested based on the theory that a highly diverse ecosystem is likely to contain some superior species, which have strong effects on ecosystem functioning.<sup>12,13</sup> Complementarity arises through niche partitioning between species, resulting in the alleviation of inter-specific competition over limiting resources.<sup>1, 2, 11, 14–16</sup> Ecosystem stability should be correlated with biodiversity if resources limit the growth of species in a community and if the resource partitioning allows for the increased efficiency in total resource use over temporal and spatial scales. Facilitation (positive interspecific interaction) occurs when a certain species has the ability to mitigate the harsh environmental conditions to which a community is exposed or when there is a supply flow of resources from one species to others which is beneficial to the survival of the recipients. Thus, productivity is enhanced with increased diversity if facilitative interactions increase.<sup>1, 17, 18</sup> If the effect of facilitation was predominant under perturbed conditions, it would lead to an increase in ecosystem stability.<sup>18</sup> Individual instances or combinations of these biodiversity effects have been shown in experimental work under controlled environments. It might be expected that these effects would also be observed in the perturbed environment.

There is still a lack of consistency among empirical studies over the expression of diversity–function mechanisms under perturbation. There is an evidence of complementarity in some studies, such as an increase in community water-use efficiency under drought conditions.<sup>15</sup> Another experiment in a species-rich, semi-natural grassland revealed there was an increase in belowground biomass production via shifts in resource allocation from aboveground to belowground in response to perturbation.<sup>19</sup> Negative sampling effects have also been found in some empirical studies that showed perturbation selected for the least productive species, such as grasses, by allowing faster resource uptake which exceeded their inherent low resource use efficiency and productivity.<sup>14, 15</sup> However, other studies have failed to show such effects.<sup>1, 20–22</sup> Several studies have indicated that there is a strong dependency of stability on the traits of dominant species present in a given ecosystem.<sup>23, 24</sup> In addition, the significance of species composition and identity has been highlighted in some experiments. The presence of a particular species, for instance, nitrogen-fixing legumes, seems to cause nutrient enrichment, leading to the expression

of complex responses by communities to perturbation.<sup>25–27</sup> To clarify the link between biodiversity effects and ecosystem stability, further empirical studies are needed to provide explicit evidence.

One area where experiments have failed to represent natural systems is spatial patchiness of communities. Distributional and colonization patterns of organisms are dependent upon the mobility and dispersability of species, thus individual species tend to create aggregated populations in some spatial scales.<sup>28</sup> This leads to patchiness in a habitat occupied by different species and provides some possibilities for the coexistence of species through spatial niche differentiation, i.e. resource partitioning. The heterogeneity in community structure has been given little attention in biodiversity experiments.<sup>29</sup> Aggregation increases intra-specific competition between individuals, resulting in the formation of monoculture-like patches in a habitat. In such circumstances, complementarity is expected to be reduced.<sup>29, 30</sup>

A model developed by De Boeck *et al.*<sup>29</sup> demonstrated that aggregation alters the relative significance of biodiversity effects. Under high levels of clumping, resource-use efficiency both aboveground and belowground was reduced due to a decrease in complementarity. The increase in intraspecific competition between neighbouring individuals of the same species results in a decrease in overall productivity. Stoll and Prati<sup>30</sup> found that the growth of a superior competitor was suppressed in an intraspecifically aggregated community, whereas the performance of inferior species was stimulated. This can be interpreted as a mechanism to promote coexistence of species, and hence to maintain species diversity. If interspecific interactions in aggregated communities under perturbation are altered to mitigate the dominance hierarchy in manner advantageous to weak competitors, it would lead to enhanced ecosystem stability.<sup>30–32</sup> While much work has highlighted the significance of incorporating the spatial structure of communities in examining the functional importance of biodiversity, empirical evidence to support those proposed consequences is still limited. Assuming that aggregation has impacts on competitive interactions, complementarity or other biodiversity effects and coexistence of species, it is also likely to affect the response of community biomass to perturbation. The effects of spatial aggregation on diversity–stability relationships should be taken into account.<sup>28, 33, 34</sup>

The aim of this study is to investigate three topics in relation to biodiversity, ecosystem functioning and ecosystem stability using experimental glasshouse plant communities. Three hypotheses are tested:

- (1) Multispecies communities have higher aboveground productivity than had the monocultures.
- (2) The relative performance of multi-species and monocultures is moderated by drought.

- (3) Aggregation affects the relative performance of multi-species compared with constituent monocultures.

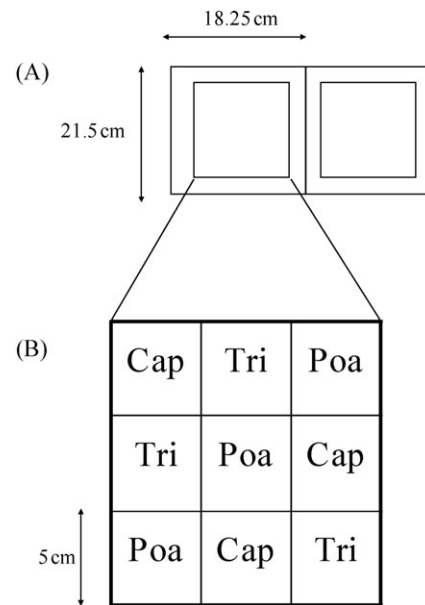
## Materials and methods

Four common ruderal plant species (three forbs and one grass) were used in the experiment: shepherd's purse *Capsella bursa-pastoris* (Brassicaceae) denoted Cap, scentless mayweed *Tripleurospermum inodorum* (Asteraceae) denoted Tri, annual meadow-grass *Poa annua* (Poaceae) denoted Poa and chickweed *Stellaria media* (Caryophyllaceae) denoted Ste. These species were chosen for their reliable germination and high growth rate. All four species can proliferate on poor, disturbed soil and are adapted to complete their life cycle by rapid growth to maximize seed production. These species often co-occur in disturbed habitats, such as agricultural fallows,<sup>35, 36</sup> though all seeds were purchased from Herbiseed (Twyford, UK).

The experiment was conducted in the glasshouse at the University of Reading in summer 2006 (from 5 July to 17 August). Plant communities were established on compost-filled plastic pots ( $37 \times 21.5 \times 5 \text{ cm}^3$ ) each divided by water-tight barriers into two sub-plots ( $18.25 \times 21.5 \times 5 \text{ cm}^3$ ). Each main pot contained the same plant treatment and one sub-plot was exposed to drought and the other adjacent sub-plot received regular watering (Fig. 1A). The density of seeds per pot was equalized, such that each plot contained a total of 900 seeds with equivalent proportion of three species for multi-species mixtures. Seeds were sown on 5–6 July 2006 over compost-filled pots. A regular watering regime was set at 400 ml once every 3 days. At 25 days after sowing (29 July), the drought perturbation treatment started. For the first 2 days and the 2 days before the cessation of drought, perturbed plots received half the amount of water controlled plots received (200 ml). Then, there was no watering on perturbed pots for 8 days (from 31 July to 7 August). The original watering regime was maintained on control plots over the experimental period. Following the drought treatment, regular watering of 400 ml water per pot once every 3 days was performed across the plots until the end of the experiment (15 August).

In addition to the drought treatment, two other treatments were applied to the plots: plant diversity and species aggregation treatments. For the diversity treatment, single- and multiple-species communities were compared. The total number of species combinations was eight; four single species (Cap–Cap–Cap, Tri–Tri–Tri, Poa–Poa–Poa and Ste–Ste–Ste) and all possible three-species mixtures (Cap–Tri–Poa, Cap–Poa–Ste, Cap–Tri–Ste and Tri–Poa–Ste).

The aggregation treatment was conducted only in multi-species communities by sowing seeds in aggregated cell patterns or randomly over the plot. In aggregated spatial pattern, these sub-plots of  $15 \times 15 \text{ cm}^2$  were further



**Figure 1.** The experimental design. (A) The Paired plot which was divided into two sub-plots with a plastic divider. One of the pairs was under control treatment and the other exposed to perturbation. (B) Plot with nine cells of  $5 \times 5 \text{ cm}^2$  which shows an example of aggregated seed sowing pattern of Cap–Tri–Poa. In the random and single pots, seeds were broadcasted over the  $15 \times 15 \text{ cm}^2$  plot.

divided into nine cells of  $5 \times 5 \text{ cm}^2$ ; each species occupied three cells in a Latin square pattern (Fig. 1B). For random treatment and for monocultures, seeds were sown randomly over the soil within  $15 \times 15 \text{ cm}^2$  (Fig. 1A).

In sum, there were a total of 24 combinations per experimental block; 12 diversity and aggregation treatments (4 monocultures + 4 aggregated three-species mixtures + 4 randomly sown three-species mixtures)  $\times$  2 perturbation treatments (perturbed or control). Four such randomized blocks were sown in the glasshouse.

Soil moisture content was monitored daily during and after the drought treatment period using *ThetaProbe* soil moisture sensor (type ML 2x). Maximum and minimum air temperatures were also monitored daily. Aboveground biomass was harvested on 17th August by clipping the shoots at ground level, and dried at  $60^\circ\text{C}$  for 48 h. After drying, the total aboveground shoot weights of each species in a pot were recorded.

## Data analysis

In order to investigate the relative difference in yield between monoculture and species mixtures, the extent of overyielding was calculated by comparing the productivity of monocultures with the expected productivity of the species mixtures based on the biomass of their constituent species in monoculture.<sup>13, 17, 37</sup> The proportion of biomass of species mixture relative to that of monoculture was used as a

measure of overyielding in this study which is called relative yield total (RYT)<sup>14</sup>;

$$\begin{aligned} \text{RYT} &= O/E = O_{ijk}/(Y_i/3 + Y_j/3 + Y_k/3) \\ &= \text{observed biomass/expected biomass} \end{aligned}$$

where  $Y_i$  is the biomass of component species  $i$  in monoculture and  $O_{ijk}$  the observed total yield of mixture including species  $i$ ,  $j$  and  $k$ . Expected biomass was calculated from the pot total weight of monoculture in the same block for observed biomass to take account of variation between blocks.

For individual species, biomass of each species in species mixture was compared with the one-third of biomass of the same species in monocultures;

$$\text{Species relative yield} = O_i/(Y_i/3)$$

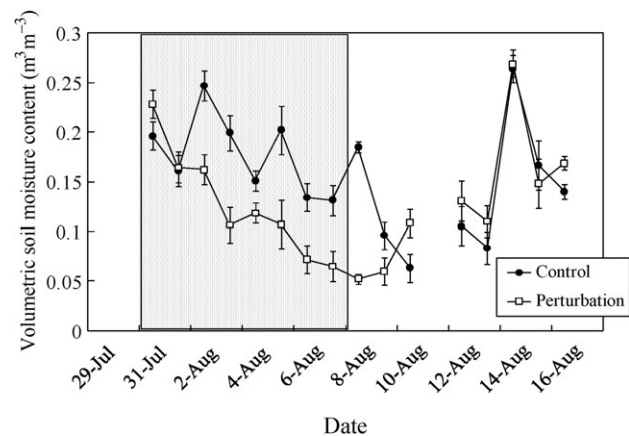
where  $O_i$  is the observed biomass of species  $i$  in species mixture and  $Y_i$  the biomass of species  $i$  monoculture.

The three response variables analysed were total above-ground biomass per pot, biomass of individual species, RYT and the relative yield (RY) of individual species in species mixtures. Data were analysed with general linear models (Type I Sum of Squares). The effects of perturbation treatment, aggregation and diversity (species richness) and their interactions on each response variable were tested. Though biomass data usually require log-transformation, distributions of residuals suggested that absolute above-ground biomass was more appropriate here for both pot total individual species weights. RYT and species RY were log-transformed to achieve normality.

## Results

During the drought treatment, soil moisture content of the perturbed pots declined day by day (Fig. 2). When the treatment finished, soil moisture content decreased approximately to  $0.05 \text{ m}^3 \text{ m}^{-3}$ . Control plots showed moderately fluctuating patterns, but the soil moisture content was maintained on an average of  $0.2 \text{ m}^3 \text{ m}^{-3}$ . The soil moisture content was kept equivalent during the week of recovery period.

Block effects ( $F_{3,89} = 17.07$ ;  $P < 0.001$ ) and perturbation ( $F_{1,89} = 52.89$ ;  $P < 0.001$ ) had a statistically significant impact on total aboveground biomass; however, there was no significant effect of species richness, aggregation treatment or the interactions of these factors with perturbation (Fig. 3A and B). Variation in perturbed plots across the blocks was greater than control ones on average: 2.59 g (44.5% reduction) difference between maximum and minimum biomasses in perturbed treatment, 1.43 g (21.9%) in control. Compared with the aboveground biomass of the controls, productivity was decreased by the



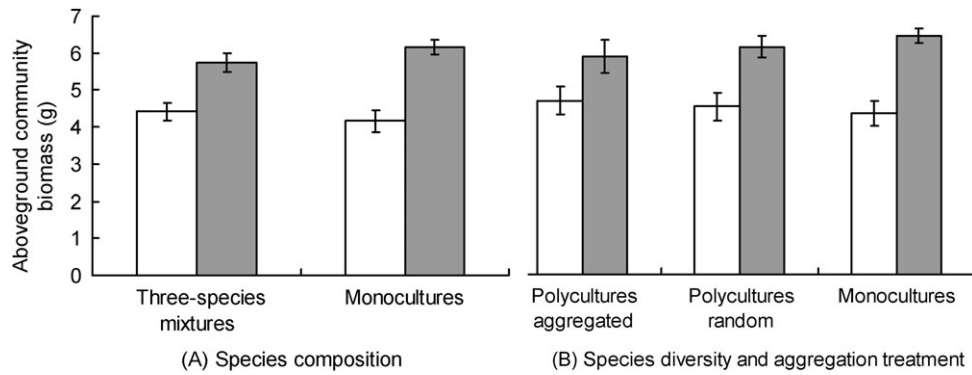
**Figure 2.** Changes in mean soil moisture content during the experiment ( $\pm$  SE). Mean of each time point is derived from four randomly selected measurements from each block of either treatment, i.e. 4 measurements  $\times$  4 blocks = 16 measurements for each treatment at one time point. The shaded period from 31 July to 8 August indicates the period of drought. The control watering treatment is denoted by solid circles, and the droughted by open squares. The gaps are when the data were not obtained.

perturbation treatment at the greatest by 48.80% in *C. bursa-pastoris* monoculture, and at the least by 1.66% in three-species mixture of *Tri-Poa-Ste*, average reduction of aboveground productivity was 24.53%.

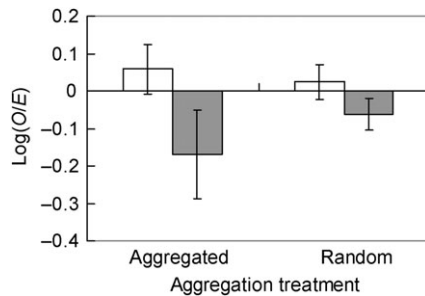
Perturbation exhibited significant effects on RYT ( $F_{1,57} = 4.50$ ;  $P = 0.038$ ). The observed biomass of species-mixture under the perturbation treatment was slightly greater than the expected biomass (on average by 7%). There was an overall reduction of productivity of the observed biomass of controls by 7% on average. Hence, in terms of RY, perturbed communities performed better than control ones by 14% on average. The response of multi-species communities depended on the occurrence of perturbation, relative biomass increased in perturbed, but decreased in the control treatment. This result shows that negative interspecific interactions predominated in the control environment, whereas positive interactions predominated under drought stress. Aggregation did not induce changes in RY (Fig. 4), indicating that the productivity of multi-species communities was not affected by spatial structural differences in any combination of species composition.

Perturbation caused a decrease in biomass production of three species; *C. bursa-pastoris* ( $F_{1,49} = 10.31$ ;  $P = 0.002$ ), *T. inodorum* ( $F_{1,49} = 7.66$ ;  $P = 0.008$ ) and *P. annua* ( $F_{1,49} = 4.27$ ;  $P = 0.044$ ); however, there was no significant effect of species richness or its interaction with perturbation treatment.

Under perturbation, there was a reduction in biomass on average of 37.5% in *C. bursa-pastoris* (34.7% in species mixtures, 48.0% in monocultures), 25.2% in *T. inodorum* (23.9% and 28.2% in mixtures and monocultures, respectively) 17.2% in *P. annua* (11.3% in mixtures, 32.8% in



**Figure 3.** Differences in mean ( $\pm$  SE) aboveground community biomass between perturbed and control pots in relation to plot-level treatments of (A) species richness (three or one); (B) aggregation treatment of polyculture-aggregated, polyculture-random, monocultures. Coloured bars, control; open bars, droughted.

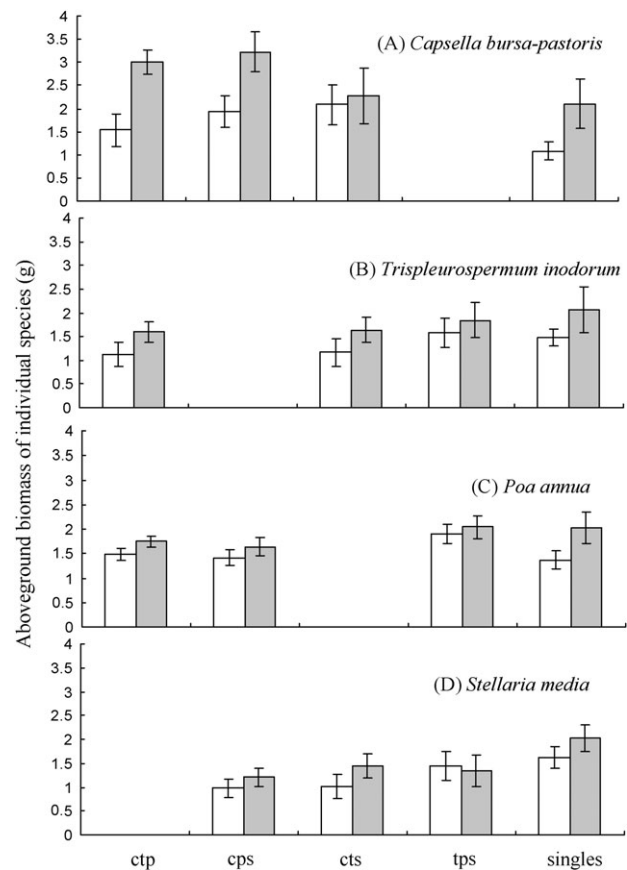


**Figure 4.** Differences in mean ( $\pm$  SE) relative yield total of aboveground community biomass between perturbed and control pots in relation to aggregation treatment. Coloured bars, control; open bars, droughted.

monocultures) (Fig. 5). In general, monocultures were more affected by drought, but also showed a greater variability.

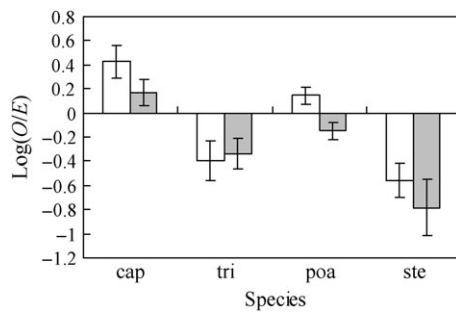
Productivity responses of *S. media* were different from the other species (Fig. 5D), although perturbation had no significant effect, aboveground biomass production was significantly lower in species mixture compared with monoculture ( $F_{1,49} = 6.65$ ;  $P = 0.013$ ). *S. media* was the least affected by perturbation with average reduction of biomass production by 16.1% (14.1% and 19.9% in mixtures and monocultures, respectively).

When aboveground biomass of each species was compared with the monoculture productivity, responses of species differed considerably (Fig. 6). *C. bursa-pastoris* increased productivity in three species mixtures (71.4% increase in the perturbed treatment, 34.9% increase in control compared to biomass of monocultures), but there was general decline of productivity in *T. inodorum* in mixture (12.9% decrease in perturbed, 17.7% decrease in control compared with monocultures, but for *P. annua* there was 17.7% increase in the perturbed treatment and



**Figure 5.** Differences in mean ( $\pm$  SE) aboveground biomass of individual species between perturbed and control pots and how biomass differed depending on species composition. (A) *Capsella bursa-pastoris*; (B) *Trispleurospermum inodorum*; (C) *Poa annua*; (D) *Stellaria media*. Species composition: ctp, Cap-Tri-Poa; cps, Cap-Poa-Ste; cts, Cap-Tri-Ste; tps, Tri-Poa-Ste; singles are monocultures of each species. Coloured bars, control; open bars, droughted.





**Figure 6.** Differences in mean ( $\pm$  SE) relative aboveground biomass yield in multi-species communities of each species under perturbed and control conditions. Species code: cap, *Capsella bursa-pastoris*; tri, *Tripleurospermum inodorum*; poa, *Poa annua*; ste, *Stellaria media*. Coloured bars, control; open bars, droughted.

10.9% decrease in the control. *P. annua* was the only species to show a response to the multispecies treatment that varied with perturbation.

## Discussion

### Absolute aboveground biomass

The effect of species richness was exhibited on the absolute aboveground biomass of *S. media* as an individual species. Aboveground community biomass and biomass of all individual species other than *S. media* were not affected by species richness. The selection of ruderal species may have led to functional similarity among species that might have blurred the biodiversity effect. High potential growth rate is one of the strategies of ruderal species to survive in environments with limited supply of resources and nutrients.<sup>5</sup> This allows individuals to alter the length of life cycle according to the availability of resources found in any environment. In this study, species response to the limitation in water may be similar, to encourage fast development to change generations in short period of time. This may have resulted in the overall similarity in community productivity irrespective of differences in species richness. Such response was also found in experiments on the soil food web.<sup>10, 20</sup> These studies showed that although there was high species diversity, processes driven by each species were similar or partly compensatory to each other due to low specialization of functioning in decomposer ecosystems. Therefore in this study, it appears that all four ruderal species respond to drought in the same way, shortening life cycles, and the similarity of functionality does not lead to biodiversity effects.

The great variability in response pattern, depending on the community, species or species composition observed, leads to some difficulty in proposing explicit explanations regarding the interaction of perturbation with diversity-functioning mechanisms. Although there is a lack of evidence for biodiversity effects in this study, responses of individual species

showed clear differences reflecting the effects of species identity. Several pieces of empirical work highlighted the idiosyncratic nature of species response to perturbation, which suggests that the underlying mechanisms of the diversity–stability relationship in real communities are more complex than those predicted by theory.<sup>1,15,19,26</sup> The experiment here provided one week with adequate watering after perturbation to investigate the recovery of communities. Quick recovery by ruderal species was observed with inflorescences produced in some plants of *C. bursa-pastoris* and *T. inodorum*, and from the emergence of new seedlings shown in *S. media*. Hence, the lack of diversity effects appears to be a consequence of over-riding species/community composition effects, consistent with other previous experiments. Diversity response may therefore originate from a combination of factors, some of which remain hidden.<sup>1, 20, 23, 24</sup>

### Relative yield

When productivity of multi-species mixtures was compared with expectation based on the monoculture performance (RYT), it was clear that the positive effect of species-richness was enhanced under drought perturbation. Indeed the species mixtures under-yielded in the control treatment but over-yielded in perturbed conditions<sup>14,15</sup> (Fig. 4). This shows that diversity effect was negative in control, but positive in perturbed. This suggests that the emergence of diversity effects is dependent on resource availability. This is a key finding, which proposes that the relationship between ecosystem functioning and species diversity may be context dependent, e.g. it may vary in sign depending on the availability of abiotic resources. It is suggested that under the perturbed condition, functional complementarity or facilitation occurred, promoting the greater relative resource uptake by the least productive species (*P. annua*),<sup>15, 37, 38</sup> whereas the drought-tolerant species *S. media* maintained its productivity. A combination of these effects would have led to the enhanced relative community biomass. In the case of *S. media*, relative biomass in species mixture did not outweigh the performance of monocultures in spite of its tolerance to perturbation, indicating the limited magnitude of effects of dominance (selection) and complementarity in this experiment.<sup>15,19</sup> Relative productivity of individual species did not increase in multi-species communities, but that of community biomass increased under the perturbed environment. This suggests that complementary resource use or facilitation effectively mitigated the negative effects of diversity and perturbation of the component species, resulting in the overall increase in community biomass.

### Aggregation

Aggregation did not induce changes in response patterns of multi-species communities in either watering treatment. In terms of interaction of spatial structure with perturbation,

random communities did not increase productivity in response to perturbation. It was hypothesized that drought-tolerant species would increase productivity in the randomly distributed treatment.<sup>22, 30, 32</sup> However, such response was not observed in this experiment, which was probably due to a great reduction of productivity in all species except *S. media* under perturbed conditions. *C. bursa-pastoris* and *T. inodorum* reached reproductive development even in perturbed conditions, while *P. annua* in mixtures performed better, in relative terms, under perturbation. Such differences in strategies to overcome drought stress among species indicate that the component species are not spatially complementary to each other.

There were some probable limitations in manipulating spatial clumping patterns in this experiment such as differences in the timing of germination and the growth rate, and limitation in spatial scales of the experimental plant communities. The time taken for germination after the sowing of seeds differed among the four species which could have pre-set the hierarchy in resource uptake efficiency in favour of fast germinating or fast growing species.<sup>5</sup> Although explicit biomass measurements were not undertaken during the experimental period, the growth rate was variable. Hence, variability in the growing condition due to the timing of germination may have been beneficial or detrimental for resource uptake.<sup>5, 7, 39</sup> The experimental community had limited space ( $15 \times 15 \times 5 \text{ cm}^3$ ). The pot depth may have led to intense belowground competition which was inadequate to promote complementarity or other effects.<sup>40</sup> Belowground productivity was not analysed in this study partly due to the practical difficulties in extracting intensively entangled fine root biomass from the soil without losing a substantial amount of fine roots. Whether the root system was created as a result of intense competition due to limited spatial scale is unclear; however, the size of pots may have been unrealistic to manipulate responses of plant communities in relation to spatial structure. Improvement on these experimental limitations is recommended for further study.

## Conclusion

Except for the relative productivity (Hypothesis 2), hypotheses were all rejected mainly due to the idiosyncratic features of the component species in response to perturbation and due to the potential experimental biases. RYT<sub>s</sub> implied that the expression of diversity effects is dependent on resource supply. This study showed that a positive diversity effect would emerge when there is a limitation in resource in the environment. Such a beneficial result of multi-species communities is not found in the resource-rich environment potentially due to the stronger effect of competition between the component species, resulting in the reduction of relative community biomass.

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