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The Influence of Pocket Gopher Disturbance on the Distribution and Diversity of Plants in Western Washington Prairies.

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Abstract

Local disturbances are known to influence patterns of plant species occurrences in a variety of habitats. To explore potential effects of pocket gopher disturbance on Puget Sound prairie plant communities, we recorded plant species present on and immediately surrounding gopher mounds as well as in non gopher-disturbed control plots at three different prairies. At all sites, overall plant species diversity was higher on the gopher mounds than in control plots; however greater diversities of non-native forbs ere found on the gopher mounds than in the control plots. Although more non-native than native species were generally present on the mounds, several important native species (i.e. Aster curtus) apparently preferred gopher mounds to controls. Differences between prairies suggested that background vegetation plays a key role in determining which species colonize gopher mounds.

INTRODUCTION

The Mazama pocket gopher, *Thomomys mazama*, is associated with glacial outwash prairies in western Washington, an ecosystem of conservation concern. Wherever they are found, pocket gophers create mounds of fresh dirt as a result of excavating their burrow systems. Small scale, predictable disturbances such as that created by gopher mounds often promote species diversity in communities by providing refuge to species that are inferior competitors but good colonizers (Paine 1969; Lubchenco 1978). Indeed, studies of pocket gophers in midwestern prairies suggest that gophers enhance plant diversity as suggested by the disturbance-diversity theory (Hobbs and Mooney 1985; Inouye et al. 1987; Martinsen 1990; Tilman 1983). However, all recent studies have ignored the distinction between native and non-native plant diversity (but see Platt 1975). In western Washington prairies a major focus of conservation efforts has been directed towards eradicating non-native plants, which are a major problem. Thus, from a conservation perspective the question is not simply what does gopher activity do to overall diversity, but also what does gopher activity do to native plant diversity versus the abundance of invasive non-native plants? We begin to answer this question by surveying the composition of vegetation found on established gopher mounds and in plots undisturbed by gopher activity. We examined our data with respect to total plant diversity, native plant diversity, and

abundance of especially significant plants, such as *Aster curtus* (a species of conservation concern). Our data indicate several hypotheses about gopher activity and its effects on plants that warrant experimental scrutiny.

METHODS

During the months of July and August of 1996, we recorded data on the plant species that occurred on and around old gopher mounds in three sites in western Washington: Marion Prairie and Upper Weir Prairie on the Fort Lewis Military reservation and the Scatter Creek wildlife area east of Rochester, WA. An established mound was considered to be one that had at least 10% of its surface area covered with vegetation. However, due to the variability between sites (soil type, rockiness) this was not always an accurate indicator of age and we biased our search towards selecting mounds that had a certain eroded or settled look. For each mound, information was gathered pertaining to what grew on the mound, immediately surrounding the mound and in a non gopher-disturbed "control" environment 10m away from the mound.

On each mound we recorded the species present and the relative numbers of each species on a scale of 1-10, >10, >20, >50, >100 and >500. We also estimated percent vegetation cover, percent moss coverage and the percentage of surface area made up of rocks. To control for variability that might arise from size differences we recorded of the size of each mound (greatest width x longest length). On average, mounds had an area of .149m^2 (SE = .007). Using the same procedure, we collected the data from selected paired "non-mound" control areas (matched in size) in a random radial direction 10 meters away from the mound. All control areas were selected to be at least 1 meter away from old mounds and at least 5 meters away from any fresh new gopher activity.

In addition to directly sampling mounds and paired control areas, we also sampled the vegetation surrounding these paired plots. Specifically, we made a list of all species found within the 1 meter annulus surrounding each mound or control plot. We quantified this information by taking five point counts at regular intervals along each of four 1 meter "transects" radiating from the central plot (mound or control area) pointing north, south, east and west (for a total of twenty point counts per mound or control). For each radial transect, we recorded the fraction of the transect that spanned bare ground or moss. In total we surveyed 137 mounds (37 in Marion, 50 at Scatter Creek and 50 at Upper Weir), each with a paired control.

RESULTS
Effects of gopher disturbance on plant species diversity.

We tested the effect of gopher mounds on species diversity both prairie-by-prairie, and for all prairies lumped together. Using a one-way analysis of variance we asked whether diversity as quantified by Simpson's diversity index (Begon, et al. 1990) differed between gopher mounds and control plots (Table 1). Consistently (for each prairie separately and for all prairies lumped together), Simpson's diversity index was significantly higher on gopher mounds than on control plots. Moreover, the magnitude of these differences was strikingly large -- often threefold or more. However, these analyses do not differentiate between native and weedy exotic species. If exotic species are a major contributing factor for the higher

diversity ratings on mounds, then one should   probably not

Table 1 - A comparison of plant diversity for all prairies surveyed using Simpson's index.   M = mound, C = control.

SITE	All Species		Natives only		All Forbs		Native Forbs		Exotic Forbs	
	M	C	M	C	M	C	M	C	M	C
MARION Richness	37	35	15	14	26	24	13	10	13	13
Simpson's Index	8.74*	2.59*	1.91	1.23	7.36	5.89	4.3	4.06	5.83*	4.59*
SCATTER CREEK Richness	31	36	16	21	23	28	13	18	10	10
Simpson's Index	10.5 *	1.95*	4.55*	1.46*	6.71	8.77	2.73 *	4.97*	5.85 *	4.61*
WEIR Richness	34	33	19	20	26	27	16	17	10	10
Simpson's Index	4.51*	2.62*	2.2*	1.24*	5.4	8.97	4.02*	3.61*	3.95 *	5.68*
ALL SITES Richness	48	51	23	28	37	40	20	25	17	15
Simpson's Index	7.72 *	2.53*	2.89*	1.28*	10.13	12.3	4.55*	5.57*	5.95*	6.74*

* Denotes those values that differed significantly (p < .01).

consider these mounds favorable disturbances with respect to plant biodiversity. Consequently we repeated exactly the same analyses of variances, only broke the plant data up into native species only (forbs and grasses), and into all forbs, native forbs, and exotic forbs. This more refined analysis indicated that mounds still exhibited higher diversity than control plots when considering native species alone, but not when considering only native forbs, indicating the dominance of grass species in undisturbed prairie (see Table 1). It also appears that mounds contain higher diversities of exotic forbs than do control areas, an observation we return to later.

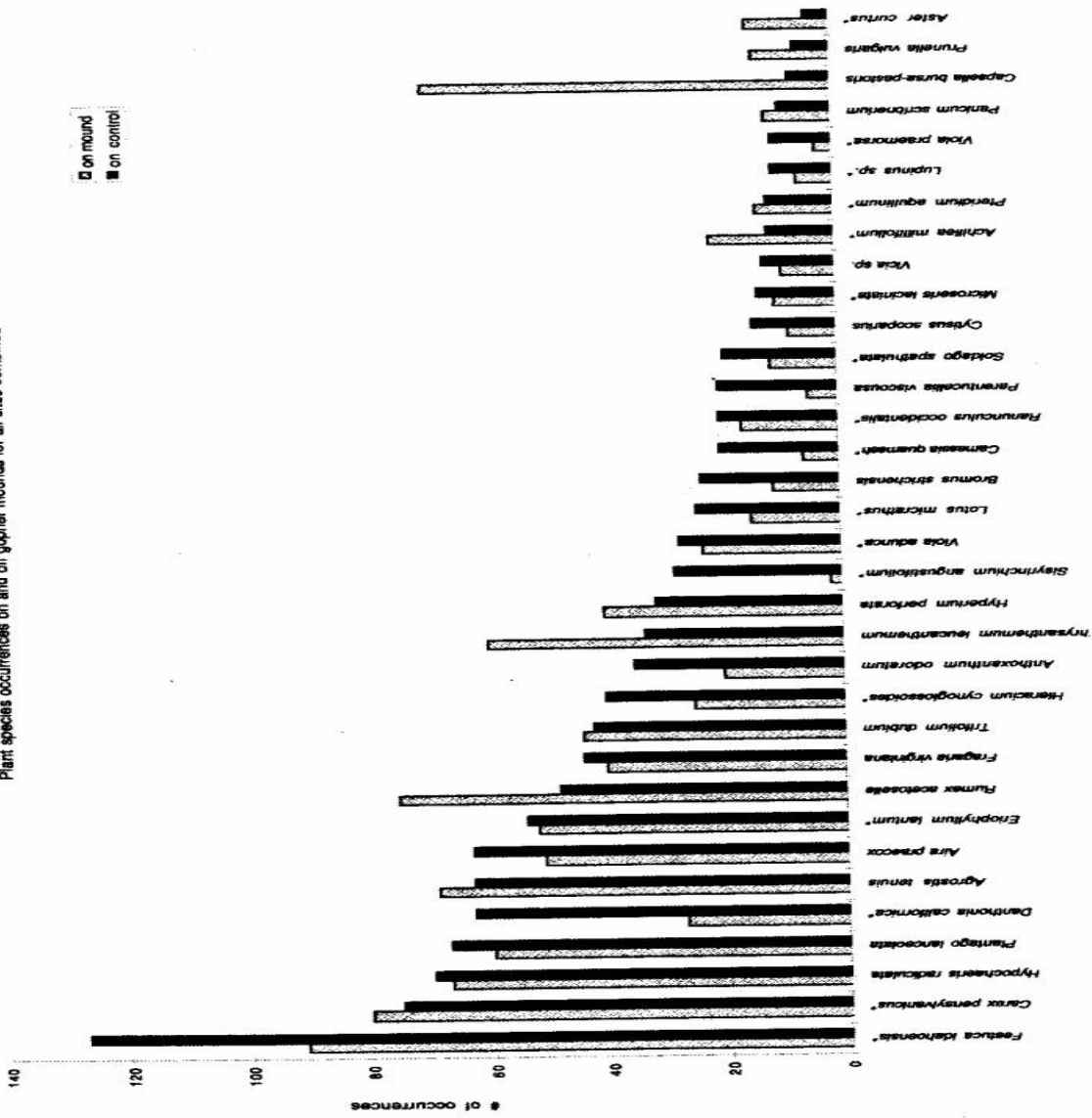Plant species occurrences on and off gopher mounds for all sites combined

Fig. 1 - The distribution of species occurrences on mounds as compared to paired controls. An occurrence is the presence of a species either on a mound or on its paired control. If mounds represent a random sample of the plant community, the number of occurrences on mounds is expected to be equal t the number on controls. * denotes native species.
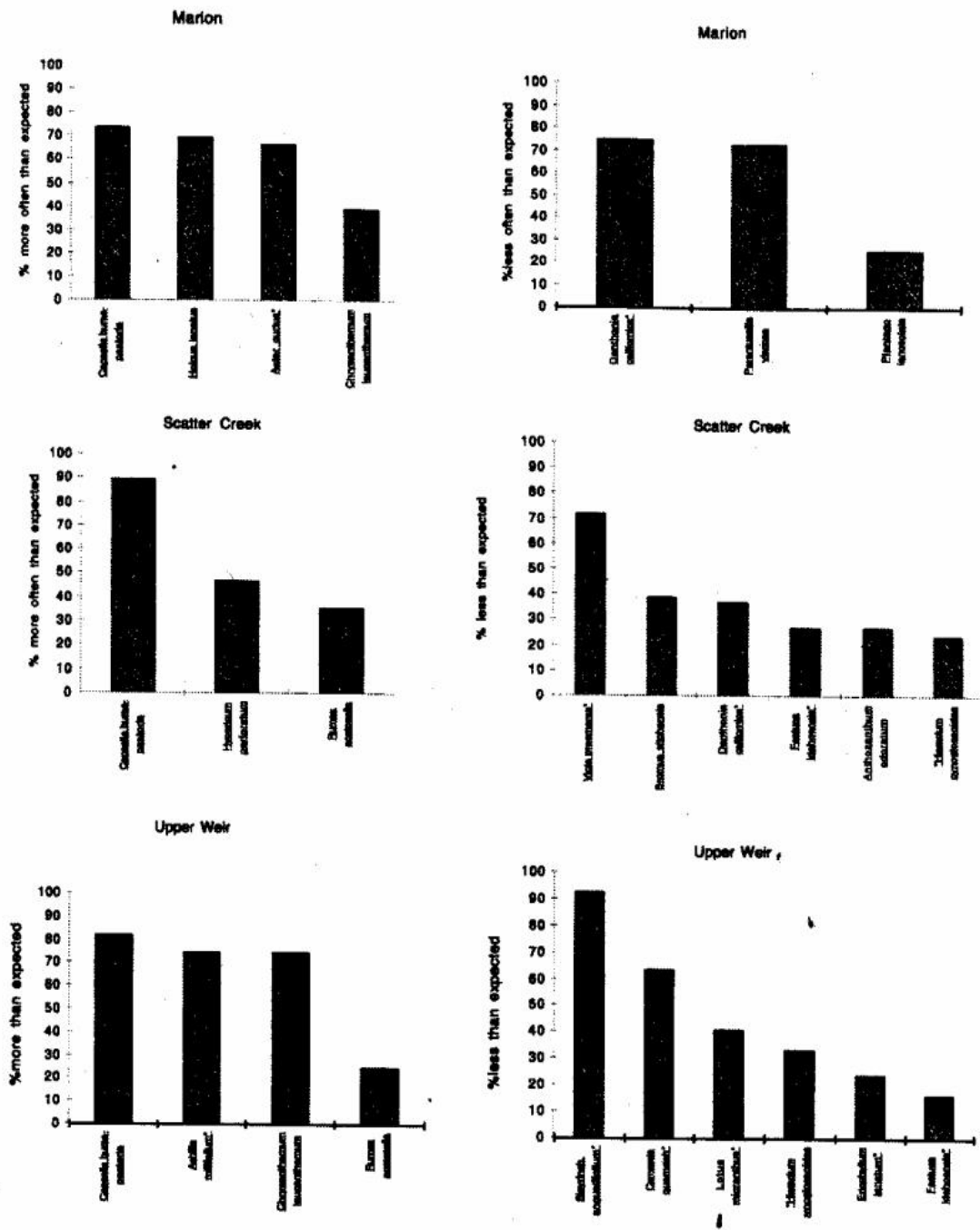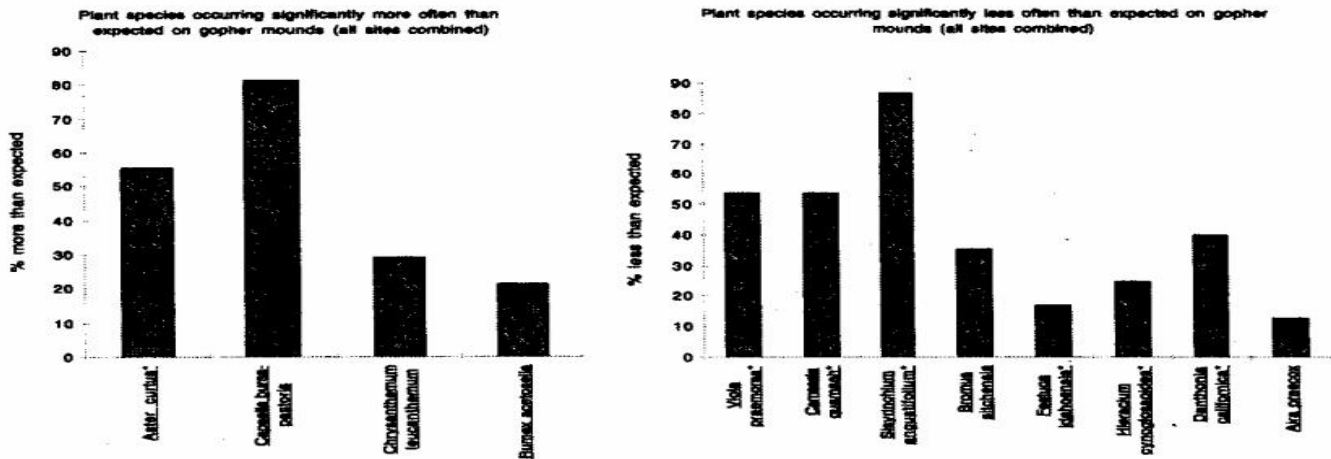
Figure 2 - Results of likelihood ratio Chi-square tests for all species at each site. Figures on the left show only those plant species present significantly more often on mounds than on paired controls at each site (p < .05). Figures on the right show only those species present on mounds significantly less often than on controls for that site. * Denotes native species.

Figure 3 - Results of likelihood ratio Chi-square tests for each species across all sites. Figure on left shows only those species occurring significantly more often on mounds than on the paired controls. Figure on left shows only those species occurring significantly less often on mounds than on controls for all sites combined. * Denotes native species.

How are the distributions and abundance of particular species influenced by gopher activity?

There are many ways of assessing the impacts of gopher activity on a species-by-species basis that reveal more biologically interesting results than are possible with diversity indices. For our analyses we focused on frequency of occurrences -- or how often species were present in gopher plots versus their paired control plots. In all of these analyses we included only those species that occurred at least five times either on a mound or in a control plot. First we asked a community-wide question: did the patterns of occurrences for species on

mounds match the expected distribution if we interpret the expected distribution to be that of the control plots? For each species, we thus obtained an expected occurrence frequency on mounds which can then be compared to the observed; in this way each species provides a single term in a large chi-square test statistic that is summed over all species. Examining the data in this way, it was obvious that plant occurrences on gopher mounds deviate extremely significantly from the occurrence patterns on control plots (Figure 1, $X^2 = 799$, $34 = df$, $p < .00001$). To gain a more detailed perspective, we statistically analyzed each species separately for each prairie separately (Figure 2), and for all the prairies lumped together (Figure 3). When performing this analysis, instead of saying the control plots
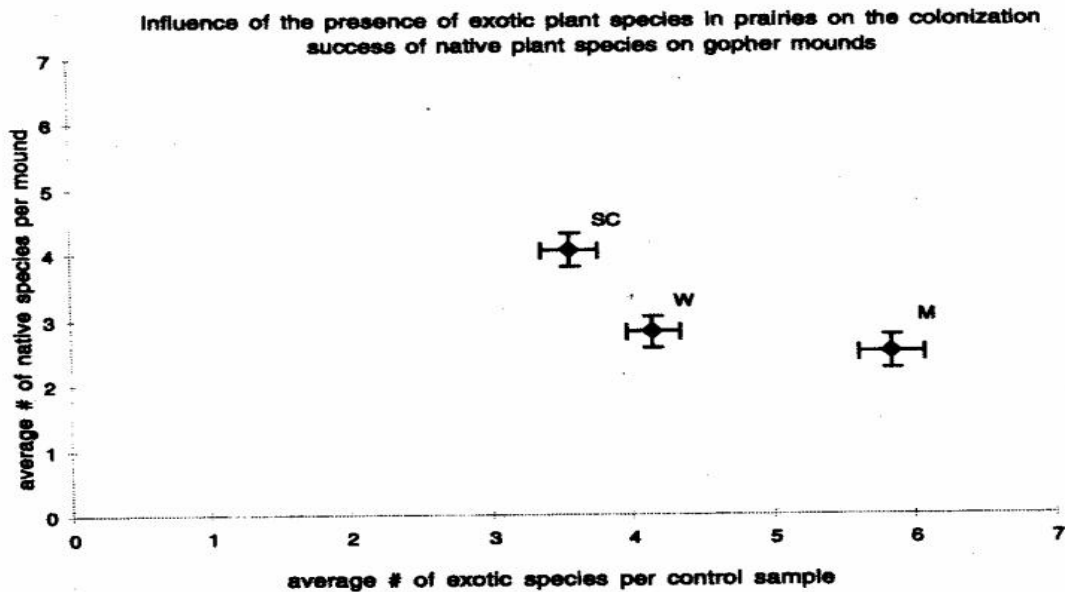
represented the expected frequency. We adopted an even more conservative approach -- we assumed the null model was that patterns of presence/absence were equivalent on mounds and off mounds, so that the expected in a two-by-two chi square table is given from the marginal frequencies in the standard way (see Steinberg 1996 for a sample calculation). When this analysis was performed for each prairie separately, the number of species significantly deviating from the null hypothesis ranged from seven (Marion prairie) to eleven species (Upper Weir prairie). For all the prairies lumped together, 12 out of 35 species exhibited significantly nonrandom patterns of occurrences (i.e., were found on mounds substantially more or less often than expected if mounds were equivalent to control plots). Figures 2 and 3 display these results in terms of percentage more or less than expected, so that the magnitude of these significant departures can be quickly viewed. Here, the % "more than expected" or "less than expected" is obtained by the equation: 100 x (observed-expected)/expected.

There are several important biological details to be gleaned from figures 2 and 3. Most notably, when all three sites are summed together, the species *Aster curtus* occurs over 50% more often than expected on mounds. *Aster curtus* was more abundant on mounds in all prairies, but the small number of occurrences both on and off mounds meant that it could only be calculated with confidence at Marion Prairie. There it is found almost 70% more often on mounds than expected. *Aster curtus* is a species of special conservation concern, and it would thus appear that gopher disturbance is good for this sensitive species. On the other hand, at Marion prairie, the other species over-represented on gopher mounds are all exotic species. While each prairie shows a different pattern, in general it can be seen that grasses, in particular the native grasses *Festuca idahoensis* and *Danthonia californica*, are under represented on mounds, while the exotic forbs *Capsella bursa-pastoris*, *Rumex acetosella* and *Chrysanthemum leucanthemum* are repeatedly over represented. It appears that gopher disturbance markedly favors some species, and exclude other species, but which species get favored or excluded depends on local conditions -- specifically on the surrounding

plant community. We hypothesized that the influence of surrounding vegetation on mound occurrences was primarily through the presence and abundance of exotic species in the vicinity. Specifically, we hypothesized that prairies with many different exotic species would have fewer native species on mounds because the exotics could exclude the natives. This was exactly the pattern we observed (Figure 4). Scatter Creek prairie is distinguished by the richest diversity of native plants on gopher mounds, and the fewest exotic species and lowest abundance of exotic individuals. While this indicates it is impossible to make a general statement about gopher mounds and native diversity (because "it all depends"), at least it appears that the dependence of plant responses to gopher disturbance can be explained by simple hypotheses relating to competition with exotic species.

Influence of the presence of exotic plant species in prairies on the colonization success of native plant species on gopher mounds

Figure 4 - The average number of exotic species on control samples relative to the average number of native species on mounds. An increased abundance of exotics corresponds to a decrease in the number of native species found on mounds. Error bars calculated using standard errors. M = Marion Prairie, SC = Scatter Creek, W = Upper Weir.

IMPLICATIONS FOR MANAGEMENT AND FUTURE WORK

In general it appears that in western Washington prairies gopher disturbance promotes plant biodiversity, even native plant biodiversity. However, gopher disturbance also promotes several weedy exotic species, which end up being extremely common on established gopher mounds compared to the surrounding undisturbed prairie vegetation. Only by doing experiments can we learn whether the net effects of gopher mounds are favorable for restoring or maintaining native prairie communities. It may be that while weedy exotics are over represented on gopher mounds, their presence in undisturbed vegetation remains unaffected. Or alternatively, perhaps the populations of exotic forbs on gopher mounds serve as foci from which these exotics will also come to invade the undisturbed vegetation. Certainly, disturbance is not all bad, as seen from the enhanced abundance of *Aster curtus* on gopher mounds -- it could be that without such soil disturbance, *Aster curtus* would disappear from prairies.
One unequivocal conclusion that does emerge concerns the importance of exotic plants in the surrounding area on determining the effect of gopher mounds. Clearly, any management plan for prairie restoration and preservation must consider the "context" (what natives and exotics are already present), and cannot be applied across all prairies. We believe the second conclusion is especially important, that is the need for manipulative experimentation. Our study is purely correlative, but it would be straightforward to experimentally test our ideas. Further studies are planned to explore the processes underlying the patterns and interactions we have observed.

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