

LETTER

Trophic compensation reinforces resistance: herbivory absorbs the increasing effects of multiple disturbances

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Abstract

Disturbance often results in small changes in community structure, but the probability of transitioning to contrasting states increases when multiple disturbances combine. Nevertheless, we have limited insights into the mechanisms that stabilise communities, particularly how perturbations can be absorbed without restructuring (i.e. resistance). Here, we expand the concept of compensatory dynamics to include countervailing mechanisms that absorb disturbances through trophic interactions. By definition, ‘compensation’ occurs if a specific disturbance stimulates a proportional countervailing response that eliminates its otherwise unchecked effect. We show that the compounding effects of disturbances from local to global scales (i.e. local canopy-loss, eutrophication, ocean acidification) increasingly promote the expansion of weedy species, but that this response is countered by a proportional increase in grazing. Finally, we explore the relatively unrecognised role of compensatory effects, which are likely to maintain the resistance of communities to disturbance more deeply than current thinking allows.

Keywords

climate change, compensatory, inertia, stressors, top-down.

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INTRODUCTION

Communities of organisms are anything but static, being continuously shaped by abiotic and biotic disturbance (Paine *et al.* 1998). Despite continuous disturbance, most communities are stable in that they dynamically persist in a certain state without switching to a contrasting state. Although disturbance often results in small changes in community structure, the stability of communities tends to decrease when multiple disturbances combine. Stability is one of the most nebulous terms in ecology, provoking constant reflection of its definition and measurement (see Grimm & Wissel 1997 for comprehensive review). The persistence of an ecosystem state (i.e. stability) can be, however, represented by the dominance of a species or suite of species and reflects both the ability of the system to recover from (i.e. resilience) and withstand disturbance (i.e. resistance). The concepts of resilience and resistance, two aspects of stability, attract considerable assessment. Nevertheless, we have limited insights into the mechanisms that stabilise communities, particularly how perturbations can be absorbed without restructuring (i.e. resistance) (Loreau & de Mazancourt 2013).

The ability of a community to absorb disturbance and reorganise while undergoing change, so as to retain essentially the same structure and function, has been the hallmark of resilience research (Scheffer *et al.* 2001; Folke *et al.* 2004). Yet, understanding how disturbance can be absorbed through compensation is necessary if resistance is to be better incorporated along with resilience into the conceptual framework of community ecology. We consider that compensatory dynamics, which have long been identified as a fundamental mechanism of stability through which communities

withstand species loss (MacArthur *et al.* 1972; Holling 1973; Patten 1975; McNaughton 1977), provide a useful conceptual mechanism for accounts of stability in the presence of disturbance.

Compensatory dynamics are expected to be an important stabilising mechanism through which communities respond to environmental change, but have been studied almost entirely through the perspective of species loss, i.e. biodiversity–ecosystem function or insurance hypothesis (Gonzalez & Loreau 2009; Loreau & de Mazancourt 2013). In this conceptual framework, compensatory dynamics have been primarily described as adjustment in densities of species (i.e. density compensation) (MacArthur *et al.* 1972; Ernest & Brown 2001; Houlihan *et al.* 2007). Whilst variation in species densities may be a straightforward measure of compensation, it only partially accounts for stability, thus providing limited insights into the mechanisms that stabilise communities (Loreau & de Mazancourt 2013).

We explored compensatory processes as a countervailing mechanism that absorbs environmental change through trophic interactions. Whilst both ‘trophic dynamics’ and ‘compensatory dynamics’ have a long history in ecology, they are yet to be considered together as an account for ecosystem stability. If trophic responses act in equal magnitude as the imprint of disturbance, they may compensate for that disturbance to stabilise community structure. A critical aspect of ‘compensation’, therefore, is that the specific disturbance (or multiple disturbances) stimulates a proportional countervailing response that eliminates the otherwise unchecked effect of disturbance. Such compensatory mechanisms are likely to go unexplored because the stability they create causes no outward change in the overall structure of a community.

Disturbances may drive change in ecosystems by acting as a constraint for some species (i.e. stressor), whilst providing opportunity for others (i.e. resource), depending on their life history (Paine *et al.* 1998). Disturbances that act to increase resource availability (e.g. substrate availability, eutrophication and carbon emissions) can alter the competitive balance between species, often driving community shifts by turning subordinates into dominants (Pickett & White 1985; Paine *et al.* 1998; Connell *et al.* 2013). For example, nutrient pollution has long been identified as a trigger of community shifts (Sarnelle 1992; Scheffer *et al.* 2001; Bertness *et al.* 2002), which is accompanied by a concomitant increase in herbivory (Sarnelle 1992; Cottingham & Schindler 2000; Kratina *et al.* 2012). Whilst such strengthening in trophic pressure is a common response to nutrient enrichment (Sarnelle 1992; Cottingham & Schindler 2000; Massad & Dyer 2010), there has been little to no assessment of the proportion to which it counterbalances disturbance *per se*. Importantly, we need to understand whether such proportional effects are not only a response to a single disturbance but also multiple disturbances that tend to be of predominant concern. If we find that multiple disturbances are compensated, then ecologists may only have a partial account for mechanisms that underpin ecosystem stability.

Our experimental assessment focuses on a model kelp system that has an intensive history of research, including the processes that drive shifts from one ecosystem state (i.e. kelp-dominated) to another (i.e. turf-dominated). The environmental conditions that bring major change to resource availability in kelp forests are local losses of canopies (light enhancement), middle-scale (nutrient enhancement) and global-scale (CO₂ enrichment) (Russell *et al.* 2009, 2011; Connell & Russell 2010). These resources drive subordinate turf-forming algae to displace the naturally dominant kelp forests by enabling turfs to dominate space through inhibition of kelp recruitment (Gorman & Connell 2009). Processes that oppose turf expansion, such as herbivory, enable kelp replenishment and persistence. For herbivory to compensate for resource-disturbance, rate of consumption by grazers must proportionally increase to match the rate of expansion of turfs (i.e. the rate at which canopies are lost), including accelerated rates of expansion by multiple disturbances (i.e. nutrient × CO₂: Russell *et al.* 2009). We hypothesised that gastropod grazers would increase *per capita* feeding rates proportionally to the effects of the individual and multiple disturbances of canopy loss (i.e. light enhancement), nutrient pollution and carbon enrichment. Hence, we predicted that grazers would be able to countervail increased turf growth, maintaining their covers to be equivalent to those in a non-disturbed kelp-dominated state.

We found that covers of turfs were held in check regardless of the identity, combination and resulting magnitude of disturbance. Such compensatory responses may underpin the general ability of kelp forests to resist resource-disturbance, accounting for why kelp forests are generally robust in the face of pollution and few succumb by switching to a turf-dominated state. We suggest that trophic compensation may not be unique to kelp systems and may represent an important additional, but largely unrecognised, compensatory process that underpins the stability of communities.

MATERIAL AND METHODS

Experimental design and setup

To determine the extent to which grazing compensates for an increasing number and magnitude of disturbances, we tested whether rates of *per capita* herbivory (i.e. percentage of turfs removed) would increase proportionally to the expansion by turfs caused by the individual effects of elevated CO₂ (current vs. future), nutrients (increasing levels, see below) and their combinations. As canopy loss initiates turf expansion via light enhancement (Connell 2005), canopy removal was included as a third factor (canopy vs. no-canopy) so that 'canopy' was fully crossed with all treatments, enabling all independent and interactive effects to be tested ($n = 5$ replicates in each treatment).

To assess the capacity of grazers to respond to varying magnitude of disturbance, nutrients were delivered in increasing amounts during four successive trials, with the final trial seeking and achieving concentrations of dissolved nitrogen in coastal urban catchments under moderate to heavy rainfall events (Gorman *et al.* 2009). The final trial allowed us to achieve the best interpretative value showing the compensatory response to the combination of global stressors (CO₂) with known levels of local stressors (nutrients), crossed with canopy removal.

Experiments were done in mesocosms (L 40 × W 30 × H 20 cm, 20 L) exposed to full sunlight and its natural day-night cycle at The University of Adelaide, South Australia. The target partial pressure of CO₂ (pCO₂) levels was based on the current ambient (contemporary, ~ 400 ppm of CO₂) and the prediction under the IS92a scenario for the year 2100 for atmospheric CO₂ (enriched, ~ 850 ppm) (IPCC 2007) (Table S1). Elevated CO₂ concentrations were maintained with enriched CO₂ into the appropriate mesocosms using a Pegas gas mass flow controller (Columbus Instruments, CO, USA). Water pH was measured daily and titration was performed during each trial to determine alkalinity using an automated titrator (888 Titando, Metrohm, USA). Partial pressure of CO₂ was calculated from measured pH, alkalinity, temperature and salinity using the CO2SYS program for Excel (Pierrot *et al.* 2006) with constants from Mehrbach *et al.* (1973) as adjusted by Dickson & Millero (1987).

Nutrients were enhanced using Osmocote Plus® (Scotts Australia PTY LTD, Bella Vista, NSW, Australia) controlled release fertiliser (6 months release: 15% N, 5% P, 10% K), which was placed in nylon mesh bags (1 mm mesh size) and attached to the bottom of mesocosm assigned to enriched nutrient treatments. Nutrients were added at increasing concentrations until reaching a final elevated concentration (5 g per mesocosm) which reproduced the concentrations of dissolved nitrogen in urban catchments under moderate to heavy rainfall events (Gorman *et al.* 2009) (Table S1). Ambient conditions were maintained using seawater on days of no runoff from land. Concentrations of supplied nutrients were quantified by collecting water samples using 25-mL sterile syringes, filtered with a 0.45-µm glass fibre filter and frozen before being analysed on a Lachat Quickchem 8200 Flow Injection Analyser (Hach Company, Loveland, CO, USA) for ammonia (NH₄⁺), nitrite + nitrate (NO_x) and phosphate (PO₄).

The 'canopy' treatment was added on each mesocosm by placing juvenile kelp [*Ecklonia radiata* (C. Agardh) J. Agardh] in combination with shading cloth to achieve the lower light intensity experienced by understory assemblages in kelp forests ('canopy' treatment) on half of each mesocosm, while light was not manipulated on the other half ('no canopy' treatment).

Grazers and algae

Grazers used in this experiment were *Turbo undulatus*, a species commonly found on subtidal rocky habitats across southern Australia and commonly inhabit kelp forests. Grazers were collected within a bed of *Ecklonia radiata* at a shallow site (0.5–1 m depth MLLW) at Granite Island (Victor Harbour, SA, Australia) and were acclimated to ambient mesocosm conditions for 1 month (April 2013) prior to exposing them to the experimental conditions. Grazers were then randomly reassigned to experimental units ($n = 1$ individual per cage) and maintained in the relevant treatments for the duration of the acclimation period (May 2013) and during feeding trials (June–September 2013). During the entire period, grazers were continuously fed with turf algae grown in the same treatment conditions. The sides of the cages were kept clean of turfs so that grazers could only feed from turf algae growing on panels placed at the bottom of each cage.

Turf-forming algae were recruited in the field on panels (10 × 10 cm) deployed on a shallow subtidal rocky reef. Panels were recovered from the field and randomly assigned to the experimental treatments, where turfs were grown for at least 1 month prior to feeding trials to allow changes in turf growth and composition as a response to experimental conditions. Each panel was placed within a cage and exposed to a single grazer. To quantify growth rates of turfs, control panels were treated in the same way but placed in cages without grazers.

Response variables and analyses

Rates of turf removal by grazers (i.e. feeding rates) were determined as the percentage cover of turf algae removed in 1-week feeding trials. Space availability is more informatively measured as percentage cover compared to biomass. Pilot trials revealed that the chosen length of time (i.e. 1 week) enabled an assessment of feeding rates without causing the entire removal of turfs, which can potentially cause an underestimate in treatments of elevated feeding rates. Percentage cover of turf on panels was recorded at the beginning and at the end of the feeding trial to quantify feeding rates, providing a measure of the potential compensatory response. Percentage cover was also assessed on control panels to quantify turf growth (i.e. the ecosystem state variable expected to change) under the different levels of disturbance. Feeding rates were then calculated taking into account differential rates of turf growth in each treatment as measured from control panels (i.e. without grazers). Percentage cover of algae was measured using a quadrat the same dimensions as the panel (10 × 10 cm), divided into 25 subquadrats and assigning between 1 and 4 points in percentage cover to each of the

25 subquadrats according to the cover of turf present, so that the total sum would be 100 in a panel completely covered by turfs. Feeding trials were repeated four times, at 1-month intervals, exposing the same grazers to new turf algae grown under the same experimental conditions.

Mesocosm experiments tend to be a simplification of the natural world, which enables the isolation and measurement of processes and development of theory. Nevertheless, their results cannot be disconnected from the scale at which ecological phenomena occur and need to be understood. Hence, while the nutrient effects measured here have been observed under field conditions (e.g. Russell & Connell 2005), the effects of CO₂ and canopy loss still need to be studied in nature, i.e. at CO₂ seeps.

RESULTS

Grazers increased their feeding rates in proportion to the increase in turf growth under increasing levels of disturbance (Fig. 1). In the absence of grazing, the rate of turf growth increased in the presence of each disturbance, i.e. canopy loss (ANOVA $F_{1,32} = 13.43$, $P < 0.001$), CO₂ (ANOVA $F_{1,32} = 9.99$, $P < 0.01$) and nutrient enhancement (ANOVA $F_{1,32} = 7.67$, $P < 0.01$), and tended to be greatest under increasing combinations of disturbances (Table S2), although not significantly. Concomitantly, feeding rates of grazers increased in the presence of these disturbances: canopy loss (ANOVA $F_{1,32} = 14.56$, $P < 0.001$), CO₂ (ANOVA $F_{1,32} = 25.52$, $P < 0.0001$) and nutrient enhancement (ANOVA $F_{1,32} = 29.88$, $P < 0.0001$) (Fig. 2, Table S2).

Where grazers were absent, the increased turf growth resulted in greater final turf cover in the presence of disturbances: canopy loss (ANOVA $F_{1, 32} = 7.80$, $P < 0.01$), CO₂ (ANOVA $F_{1, 32} = 24.45$, $P < 0.0001$) and nutrient enhancement (ANOVA $F_{1, 32} = 56.94$, $P < 0.0001$) (Fig. 3, Table S3). In contrast, despite the increased turf growth, the presence of grazers effectively maintained turf cover close to ambient conditions under all combination of disturbances, with the lowest cover found in the combined presence of both resource enhancements, i.e. CO₂ and nutrients (ANOVA $F_{1, 32} = 4.32$, $P < 0.05$) (Fig. 3, Table S3).

The grazers were caged so that they could not spend time on the sides of mesocosms. Herbivory was not swamped by fast growing algae; indeed, grazing maintained covers of turfs close to ambient conditions (Fig. 3, Table S3).

DISCUSSION

Grazing acted to counter disturbances that would otherwise drive expansion of turfs, such that the cover of turfs was maintained close to ambient levels in the presence of single through multiples of disturbances. The increase in *per capita* grazing rates was proportional to the increase in expansion of turfs, occurring independently of single or multiple combinations of resource enhancement across local (light), middle (nutrients) and global scales (CO₂). This compensatory effect represents a process that maintains open space against expansion of turfs that cause recruitment failure of kelp (Connell & Russell 2010). Where turf expansion occurs uncontrolled, it can shift community states from kelp-domi-

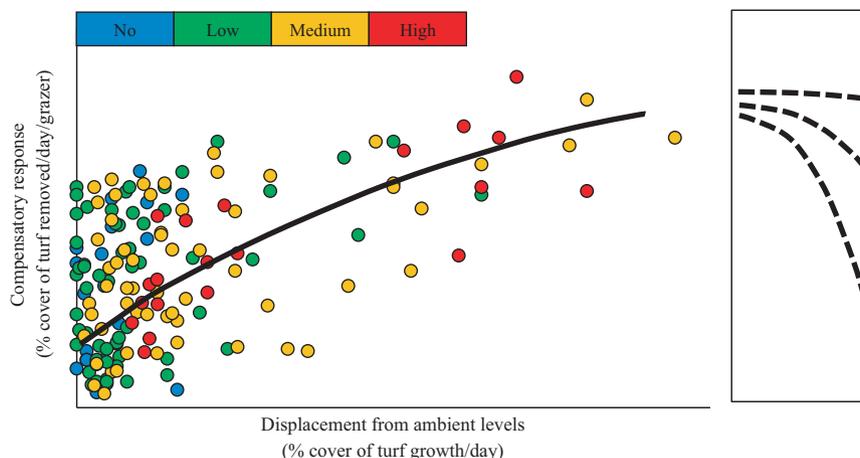


Figure 1 Compensatory response by grazers (measured as percentage cover of turf removed/day/gastropod) plotted against change in ecosystem state variable (percentage cover of turf growth/day) as levels of disturbance increase. Colours indicate progressively increasing levels of disturbance in all combinations of factors: blue = no disturbance (0 stressors: ambient levels of CO₂ and N under canopy); green = low disturbance (1 stressor: + CO₂ or + N under canopy; ambient no canopy); orange = medium disturbance (2 stressors: + CO₂ × N under canopy; + CO₂ or +N and no canopy); red = high disturbance (3 stressors: + CO₂ × N and no canopy). The box next to the figure considers how the compensatory response could be expected to decline under progressively increasing levels of disturbance past a compensatory threshold.

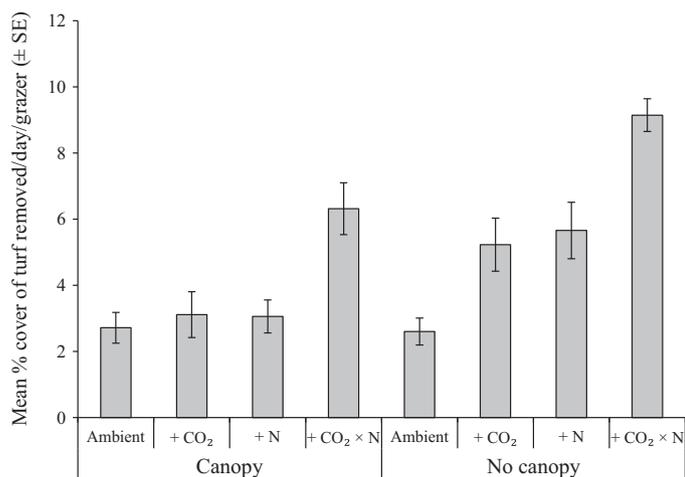


Figure 2 Rates of turf removal by grazers ($n = 5$) increased with increasing levels of disturbance (canopy removal, CO₂ and nutrients, alone or in combination), allowing grazers to compensate for the increased turf growth.

nated to turf-dominated (Connell *et al.* 2008). Well before such change occurs, however, trophic responses may act as countervailing mechanisms that absorb the effects of disturbances to stabilise community structure and reduce the size of community change.

Trophic sensitivity may not only account for the stimulation of countervailing processes but also why their strength may increase in proportion to the strength of disturbance. Primary producers, including turf algae, often respond to an increase in availability of such resources by increasing productivity, with concomitant change to their quality as food (e.g. C : N ratio) which stimulates feeding (Stiling & Cornelissen 2007; Tylianakis *et al.* 2008; Falkenberg *et al.* 2013). Hence, the mechanisms that increase gross primary production do not necessarily occur without increasing rates of consumption; an

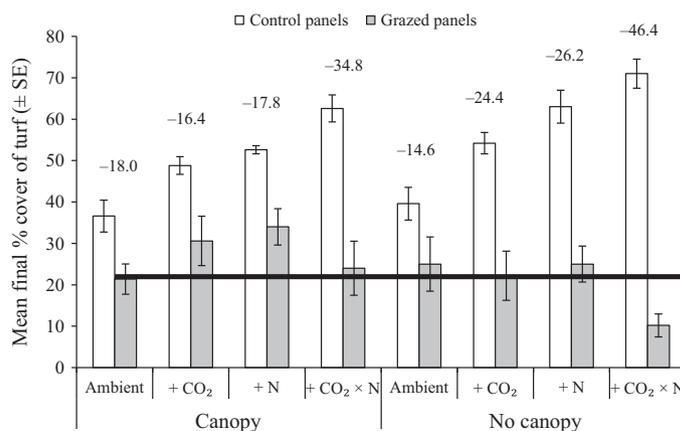


Figure 3 In the absence of grazers (white bars, $n = 5$), turf cover increased in the presence of disturbance (canopy loss, CO₂ and nutrients, alone or in combination). The presence of grazers (grey bars, $n = 5$), however, compensated for the increased cover of turf maintaining their cover close to ambient levels (black horizontal bar) in all treatments. The greatest compensatory response occurred in the presence of combined elevated levels of CO₂ and N, where turf cover was greatest. Numbers on top of the bars represent total percentage turf removed during the feeding trial by grazers in each treatment.

inherent countervailing mechanism to increases in net production. Whatever the mechanism, countervailing responses to environmental changes are not restricted to nutrient enrichment. We show that trophic compensation may represent a general mechanism through which communities absorb the effects of resource-disturbance, thus stabilising overall community structure.

General considerations of how environmental change could provoke ecological responses that stabilise ecosystems were recognised decades ago (Odum 1971). Conceptual accounts for such ideas, i.e. ‘stability landscapes’, depict basins of

attraction where positive feedbacks can maintain stable equilibria (Holling 1973). Biotic feedbacks are sometimes considered to be stabilising the community in a certain state and that shifts to a contrasting state are triggered merely by physical events (Scheffer *et al.* 2001). Here, we propose trophic compensation as a biotic feedback that stabilises communities against physical events.

From ecological to evolutionary time scales, changes in environmental conditions from short (e.g. pollution) to long term (e.g. ocean acidification) can be viewed as shifts and shocks (Hughes *et al.* 2013). Many of such changes, however, occur slowly relative to the lifespan of organisms. Whether environmental change is abrupt or gradual, we propose that trophic compensation may play a major role in stabilising ecological communities. Nevertheless, where communities undergo profound change, compensatory responses may have been weak relative to the disturbance. Communities, therefore, remain stable where compensation absorbs varying levels of disturbance, but change occurs where disturbance is larger than the capacity of compensatory mechanisms (Fig. 1, right panel). Indeed, variation in type and strength of compensatory mechanisms could explain why some systems change, or even shift, while others do not, despite the ubiquitous presence of multiple disturbances.

Despite disturbance being nearly continuous in nature, communities do not constantly shift from one state to another. Change is often minimal. The capacity for absorption of disturbance without change is one of the less understood mechanisms by which communities adjust to disturbance, possibly because change is more readily observable and tractable to study and report than no change. While compensatory dynamics have been identified as a central mechanism of ecosystem stability, they have been investigated within the context of the diversity–stability debate and species loss (e.g. insurance hypothesis; Yachi & Loreau 1999; Pfisterer & Schmid 2002; Bai *et al.* 2004; Zhang *et al.* 2014). In this framework, compensation to species loss occurs when there is no overall change to community biomass of species (i.e. density compensation) or the lost species are replaced by functional equivalents (i.e. functional compensation) (Lawton & Brown 1993; Yachi & Loreau 1999; Gonzalez & Loreau 2009). McNaughton (1977) was one of the first authors to recognise functional compensation, considering the importance of species functional responses to environmental changes as mechanisms underpinning stability rather than adjustments in densities. Yet, four decades later, compensatory dynamics remain focussed on fluctuations in species abundance as a mechanism of ecosystem resistance to species loss due to disturbance (see Loreau & de Mazancourt 2013 for a review).

We consider compensatory mechanisms, such as trophic compensation, as processes that may act well before species loss occurs. Such compensatory mechanisms are likely to go unexplored because they produce no outward change in community structure or function. Trophic sensitivity to environmental disturbance operates as an unseen but important organising force that underpins stability (McAllister *et al.* 1972). We show that trophic compensation counters the effects of single through multiple disturbances, potentially representing an important additional, but relatively unexplored, mechanism of resistance that complements density and

functional compensation by stabilising community structure and function.

The stability of communities and their resistance to change remains a central and open question in ecology. Given the importance of resource (bottom-up) and consumption (top-down) processes in structuring communities (McNaughton *et al.* 1988; Pace *et al.* 1999; Duffy 2002), we suggest that trophic compensation, as a process that promotes community stability, may strengthen resistance more heavily than current thinking allows. We contrast this notion of stability to resilience, which defines the ability of a system to absorb disturbance and reorganise while undergoing change so as to retain the same function and structure (Folke *et al.* 2004). To more fully understand stability, therefore, we also need deeper insights into resistance and mechanisms that absorb disturbance without causing the system to undergo change. The capacity for adjustment in strength of trophic interactions, whilst acting as a relatively imperceptible mechanism to absorb global and local disturbances, may enhance community stability well before significant loss of species occurs.

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AUTHORSHIP

GG and SDC wrote the manuscript, SDC originated the idea and design, GG undertook the experiments and BDR assisted with interpretation, design and manuscript feedback.

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