

Shrub hummocks as foci for small animal disturbances in an encroached shrubland

S. Daryanto, D.J. Eldridge*

Evolution and Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

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ABSTRACT

Resources in semi-arid landscapes are concentrated around woody plants (trees and shrubs), and therefore attract soil-disturbing fauna. Globally the trend has been to remove encroaching shrubs from semi-arid shrublands to increase their value for pastoralism, potentially affecting shrub-resident biota. We examined the distribution of animal disturbances created by a range of organisms (e.g. ants, scorpion, cicada, reptiles, small mammals) under two ploughing treatments, with and without grazing, in a semi-arid shrubland. We hypothesized that 1) animal structures would be clustered around resource-rich shrub patches, and 2) the density and composition of animal structures would differ between undisturbed (ungrazed and unploughed) and disturbed (ploughed and/or grazed) plots. Overall, we found more animal disturbance within shrub patches than in the interspaces irrespective of grazing and/or ploughing treatments, and well-defined increases in density of animal disturbances with increasing shrub cover. Our study highlights the importance of shrub hummocks as habitat patches for animals, and the potential negative feedbacks processes arising from shrub removal.

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1. Introduction

The spatial distribution of resource patches is a strong driver of the distribution of faunal assemblages in arid and semi-arid environments (Steward et al., 2000). In semi-arid environments, resources such as nutrients and water are typically concentrated into patches such as shrubs and their hummocks ('islands of fertility' *sensu* Garner and Steinberger, 1989), and to a lesser extent, areas of coarse woody debris (debris mounds). Litter decomposition is generally greater under shrub canopies due to the greater abundance and diversity of soil invertebrates (Doblas-Miranda et al., 2009), and a number of abiotic and biotic attributes such as infiltration and temperature are mediated by the shrubs. Shrubs also act as nurse plants, increasing the diversity, biomass and stability of understorey populations and may protect palatable plant species from herbivory (Soliveres et al., 2011). Further, soil beneath debris mounds have been shown to contain relatively higher concentrations of carbon and nitrogen than interspace soils due to a combination of enhanced decomposition by termites (Tongway et al., 1989), and deposition of surface sediments and aeolian material (Okin et al., 2006).

Over the past century there have been substantial increases in the density, cover and biomass of shrubs over large areas of semi-arid woodland and grassland. This process, known variously as encroachment or woody thickening, has the capacity to alter habitat structure and connectivity (Eldridge et al., 2011) and potentially influence the diversity and abundance of a range of vertebrate and invertebrate taxa (e.g. Simonetti, 1989). Foraging, for example, within shrublands may be associated with a lower risk of predation than foraging in open areas (Brown et al., 1988).

Shrublands are not always viewed positively by land managers because of the perception that they suppress plant biomass and productivity (Eldridge et al., 2011) and exacerbate livestock management problems. Attempts to remove shrubs using a range of techniques including ploughing and destocking have led to mixed success, often stimulating shrub regrowth and leading to the eventual persistence and dominance by shrubs (Daryanto and Eldridge, 2010). The effects of shrubs on soil and ecological processes are relatively well-known (e.g. Eldridge et al., 2011). Less well-known, however, are their effects on specific biota, including those that disturb the soil surface.

We used long-term vegetation enclosure to examine the effects of ploughing, with and without grazing, on soil disturbance by a range of shrub-resident soil-disturbing biota. Our aim was to assess the extent to which soil-disturbing biota use shrub-encroached woodlands and the extent to which patches with different resources

* Corresponding author. Tel.: +61 2 9385 2194; fax: +61 2 9385 1558.

E-mail addresses: s.daryanto@student.unsw.edu.au (S. Daryanto), d.eldridge@unsw.edu.au (D.J. Eldridge).

(i.e. resource-poor vs resource-rich) might influence biotic communities. There are many advantages of using disturbances rather than measuring organisms *per se*. Firstly, disturbances such as foraging pits of vertebrates, or nests and emergence holes of invertebrates, indicate surface usage over a longer time period than would be reflected in a one-off assessment of animal activity because surface structures have relatively long half-lives (Borchard and Eldridge, 2011). Secondly, the magnitude of soil disturbances is indicative of the magnitude of ecosystem processes such as nutrient retention and soil removal, which would be influenced by surface-disturbing biota. A number of studies has shown that sites of animal disturbances have enhanced level of nutrients and greater plant germination (e.g. Eldridge and Mensinga, 2007). We predicted that the density of animal disturbances would be greater under resource-rich shrub patches than the relatively resource-poor interspaces and therefore that increasing shrub cover would be associated with higher density of animal disturbance. We expected that the least disturbed site (unploughed and ungrazed) would support the greatest density of animal disturbances, consistent with studies elsewhere (e.g. Eccard et al., 2000).

2. Materials and methods

2.1. Study site

The study was conducted at two semi-arid woodland sites, Wapweelah, 35 km west of Enngonia (29° 16'S, 145° 26'E) and Bloodwood, 120 km north-west of Bourke (29° 30'S, 144° 45'E) in north-western New South Wales, Australia. Wapweelah falls within the Gumbalie Land System and it is characterised by sandy red earths with surface textures of loams to sandy loams. Bloodwood has calcareous red earths and sandy earths with sandy topsoils and it falls within Goonery Land System (Walker, 1991). Both sites have similar climates characterised by hot summers (mean maximum 36.4 °C) and mild winters (mean minimum 17.9 °C). Rainfall averages about 300 mm annually at both sites, with 45% more rain during the summer months. The landscape is level to slightly undulating (<1% slope) and is comprised of sandplains of Quaternary alluvium and aeolian sediment.

Similar shrub species occurred at both sites, though with slightly different composition. Both sites supported narrow-leaved hopbush (*Dodonaea viscosa*), turpentine (*Eremophila sturtii*), green turkey bush (*Eremophila gilesii*) and budda (*Eremophila mitchellii*). However, Bloodwood was dominated by narrow-leaved hopbush while Wapweelah supported denser stands of turpentine and green turkey bush. Scattered mulga (*Acacia aneura*) trees were also found at both sites. The groundstorey vegetation at Bloodwood and Wapweelah was dominated by a range of perennial grasses such as woollybutt (*Eragrostis eriopoda*) and wiregrasses (*Aristida* spp.), with assorted ephemeral forbs from the families Chenopodiaceae and Brassicaceae (Robson, 1995; Eldridge and Robson, 1997).

2.2. Shrub removal design

In 1990, one 200 m × 400 m block was established and divided into four linear plots 200 m long by 100 m wide. The two central plots were enclosed in a 6 m high, herbivore-proof fence, leaving the remaining two unfenced plots grazed. The grazed plots were grazed by camels, sheep, goats, cattle and kangaroos. One of the two central plots and one of the grazed plots was ploughed while the other two plots were unploughed. The ploughing treatment consisted of a single pass with a 4.2 m wide single-tyred 'Stationmaster' blade plough pulled by a 90 kW crawler tractor and only shrubs were removed during ploughing. This design resulted in two different degrees of ploughing (ploughed vs unploughed)

and two levels of grazing (grazed vs ungrazed). This experimental setup was repeated at three replicate blocks which were separated by distances of 1–5 km for each site.

2.3. Sampling design

In August 2008, 18 years after ploughing and fencing, we established a 100 m² transect through the centre of each plot in order to measure the density and size of all animal-created soil disturbances such as foraging pits, nests and emergence holes created by a range of vertebrates and invertebrates. Burrows and emergence holes are constructed by ants, ground-foraging spiders such as Lycosids (Main, 2001), scorpions (Hasiotis and Bourke, 2005), cicadas (Moulds, 1990) and skinks in both the shrub hummocks and interspaces. The above-ground cappings of termite (*Drepanotermes perniger*) mounds may also occur in the interspaces where soils clay content is higher (Noble et al., 1989). We also recorded pits excavated by Gould's sand goanna (*Varanus gouldii*) and the Short-beaked echidna (*Tachyglossus aculeatus*). Disturbances vary greatly in their morphology and would be expected therefore to have differential effects on resource capture and retention. Ground-foraging fossorial spiders (e.g. Lycosids) have permanent burrows (Main, 2001), that may sometimes reach 1 cm in diameter and often with an almost invisible trap door. The nests of many ant species have burrows with variable amounts of soil surrounding the entrance (Eldridge and Pickard, 1994). Scorpion burrows are common in sandy soils (Locket, 1993) and characterised by a crescent-shaped entrance, angled between 20° and 30° from the surface. The width and height of the burrow range from 5 to 25 mm and from 2 to 10 mm, respectively, and those dimensions are proportional to the size of the occupying scorpion (Rutin, 1996). Skink burrows are characterised by a single opening with a shallow dipping shaft. However, this shaft generally has one or more escape tunnels that switch back on one another to the surface (Hasiotis and Bourke, 2005). Termite pavements, the above-ground cappings of subterranean termites (*D. perniger*), are typically circular, with either concave or convex surfaces, surrounded by termite carton (i.e. a thin surface layer of decomposing soil mixed with organic matters (Noble et al., 1989)). The short-beaked echidna constructs shallow nose pokes, deep pits and extensive tracts of bull-dozing (Rismiller, 1999) as they forage for macro-invertebrates. Echidna foraging pits tend to be circular-shaped, about 15–25 cm in diameter, 5–15 cm deep, and are surrounded by poorly-aggregated material in sandy soils, but cloddy and highly aggregated material in loamy soils (Eldridge and Mensinga, 2007). Foraging pits constructed by Gould's sand goanna range from narrow, ellipsoid-shaped pits excavated at an angle of about 40° to the soil surface to wedge-shaped pits characterized by shallow, v-shaped grooves along either side of the base where the soil had been excavated by the reptiles' strong forelimbs (Eldridge and Kwok, 2008).

We recorded the dimensions (length, width, depth or height) of each disturbance found along the transect, as well as the animal that created it (ant, termite, spider, scorpion, cicada, skink, goanna, echidna) and the microsite within which the disturbance was located (shrub hummock, debris mound, interspace). Shrub hummocks are sites under shrubs and their accreting soils and litter, while debris mounds represent sites where shrubs have died and accumulate on the surface. Interspace areas represent the generally sparsely-vegetated areas between the shrubs and log mounds.

2.4. Statistical analyses

We used chi-squared tests to examine whether the density of disturbances varied significantly among microsities, given differences in relative proportion of the different microsities. A permutational multivariate analysis of variance (PERMANOVA; Anderson,

2001) was used to examine potential differences in the composition of animal disturbances with a split-plot design. The main plot considered block, ploughing and grazing effects, and the second plot microsite effects (i.e. shrub hummock vs debris mound vs interspace) and their interactions with grazing and ploughing. This combination of block, grazing, ploughing and microsite resulted in a dataset of 36 rows for both sites. The data were converted to a similarity matrix using $\log_{(x+1)}$ transformation and Euclidean distance coefficient within the PERMANOVA package. Regression analysis using various linear and non-linear models was used to examine potential relationships among shrub hummock cover and density of disturbances by different animals. The effects of ploughing and grazing were examined using a mixed-models ANOVA of the same structure as that used in the PERMANOVA analyses. Analyses were conducted separately for both sites.

3. Results

3.1. Effects of microsities

At Bloodwood, there was little difference in disturbance density between resource-accumulating (shrubs hummocks, debris mounds, 68.7 ± 10.5 disturbances 100 m^{-2} ; mean \pm SE) and resource-shedding (interspaces; 62.0 ± 4.6 disturbances 100 m^{-2}) microsities. Accounting for the relative proportion of the various microsities however, there were substantially more disturbances in resource-accumulating areas than would be expected by chance (Table 1), a trend that was more apparent at Wapweelah (Fig. 1). Indeed, shrub hummocks and debris mounds at Wapweelah supported more animal disturbances (94.3 ± 25.5 disturbances 100 m^{-2}) than the interspaces (35.4 ± 3.3 disturbances 100 m^{-2}). At Wapweelah, shrub hummocks consistently supported more ant nests ($\chi^2 = 397.4$, $P < 0.001$, $df = 2$) and disturbances by either all invertebrates ($\chi^2 = 693.4$, $P < 0.001$, $df = 2$) or all vertebrates (goannas, skinks, echidnas; $\chi^2 = 87.7$, $P < 0.001$, $df = 2$) than debris mounds or interspaces. At Bloodwood, we recorded more ant nests ($\chi^2 = 40.71$, $P < 0.001$, $df = 2$) and disturbances by all invertebrates ($\chi^2 = 32.82$, $P < 0.001$, $df = 2$) or vertebrates ($\chi^2 = 81.53$, $P < 0.001$, $df = 2$) in the shrub hummocks (Table 1). We also detected significant differences in composition of animal disturbances (based on density) among microsities at both Bloodwood (Pseudo $F_{2,16} = 8.20$, $P(\text{perm}) < 0.001$) and Wapweelah (Pseudo $F_{2,16} = 5.26$, $P(\text{perm}) < 0.001$). Pair-wise tests for Wapweelah indicated that the composition of disturbances differed between debris mound and either interspace or shrub hummock, but not interspace and shrub hummock ($t(\text{perm}) = 0.45$).

3.2. Effects of shrub hummock density

At Bloodwood, the density of all animal disturbances increased with increasing cover of both shrub hummocks ($F_{1,10} = 9.14$,

Table 1
Results of χ^2 analyses for different microsities at Bloodwood and Wapweelah. Numbers in brackets represent the percentage cover of the three microsities.

Animal group	Shrub hummock	Debris mound	Interspace	χ^2 value	P-value
Bloodwood	(26.4)	(6.8)	(66.8)		
Ants	397	113	714	40.71	<0.001
All invertebrates	123	14	164	32.82	<0.001
All vertebrates	49	20	22	81.53	<0.001
Wapweelah	(20.8)	(7.2)	(72.0)		
Ants	342	12	302	397.36	<0.001
All invertebrates	232	3	35	693.38	<0.001
All vertebrates	40	9	11	87.73	<0.001

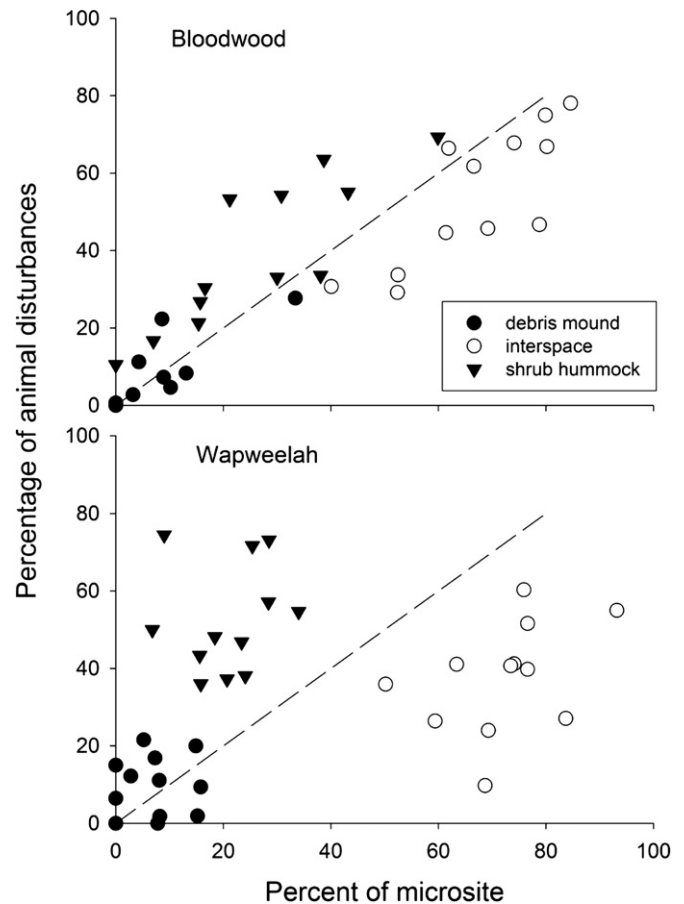


Fig. 1. Relationship between the percentage of animal disturbances found in a given microsite and the percentage of each microsite type available at a site. The broken line represents a 1:1 relationship.

$P = 0.013$, $R^2 = 0.43$) and debris mounds ($F_{1,10} = 47.78$, $P < 0.001$, $R^2 = 0.81$). In particular, the density of cicada emergence holes ($F_{1,10} = 11.93$, $P = 0.006$, $R^2 = 0.50$) and skink burrows ($F_{1,10} = 12.87$, $P = 0.005$, $R^2 = 0.52$) increased with increasing shrub hummock cover (Fig. 2). Similar correlations were apparent when we used data on the area of disturbances. However, we did not find any significant relationship between animal disturbance and the cover of shrubs at Wapweelah.

3.3. Effects of grazing and ploughing

We detected some effects of both grazing and ploughing on the cover of shrub hummocks, but only at Bloodwood where the cover of shrub hummocks on the ploughed plots (17.9%) was half that of the unploughed plots (34.9%; $F_{1,6} = 18.24$, $P = 0.005$). Grazing increased the cover of shrub hummocks by 1.5-times from 20.3% to 32.5% ($F_{1,6} = 9.33$, $P = 0.02$). Despite the effects of ploughing and grazing on hummock cover, neither treatment affected the composition of animal disturbances (grazing: Pseudo $F_{1,6} = 2.73$, $P(\text{perm}) = 0.071$; ploughing Pseudo $F_{1,6} = 0.63$, $P(\text{perm}) = 0.639$).

4. Discussion

Many studies have described the marked differences in abiotic conditions between resource-rich shrub hummocks and their resource-poor interspaces (e.g. Garner and Steinberger, 1989). Because shrubs modify environmental conditions around their

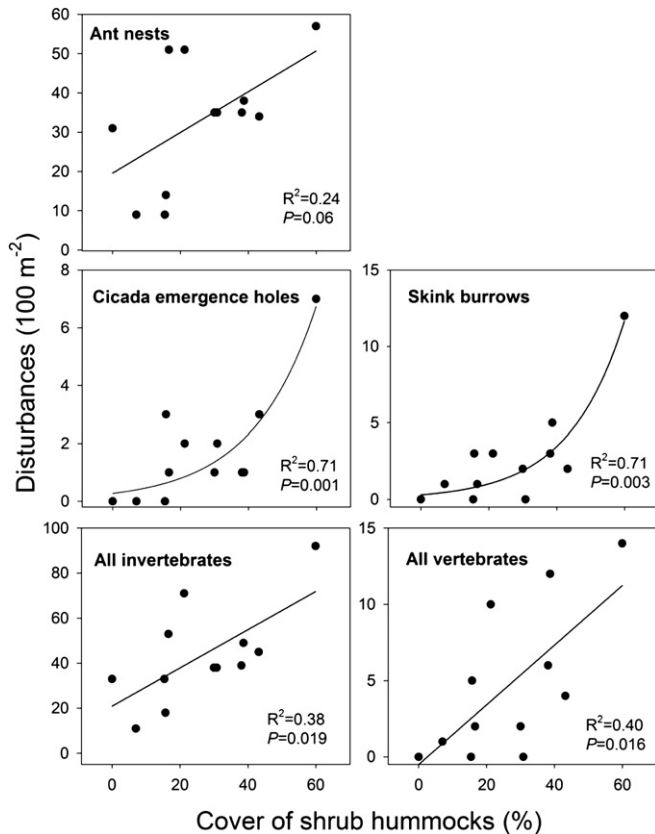


Fig. 2. Relationship between the density of cicada emergence holes, skink burrows and all invertebrates and vertebrates and the cover of shrub hummocks at Bloodwood. Note the different scales of the y-axes.

hummocks, they are favoured sites for plant germination and establishment (Soliveres et al., 2011), provide nesting, perching and foraging sites for a range of biota (e.g. the ‘perch effect’; Pausas et al., 2006) and act as refugia against predation. Part of the ‘fertile island’ affect associated with shrubs probably results from the activity of hummock-resident biota.

Shrub hummocks in our study were preferred sites of vertebrate and invertebrate disturbances, and increasing cover of hummocks corresponded with increasing densities of cicada emergence holes, skink burrows, and to a lesser extent, ant nests. The hummocks of arid area shrubs provide habitat not only for arthropods (e.g. Whitehouse et al., 2003) but also their reptilian predators (Whitford, 2002). Reptiles use shrubs and their hummocks as refugia from predation (Castellano and Valone, 2006), and sites for foraging and thermal regulation (Diaz, 1992). Soil-disturbing reptiles such as the desert skink (*Egernia inornata*), broad-banded sand swimmer (*Eremiascincus richardsonii*) and the burrowing skink (*Lerista labialis*) inhabit encroached shrubland in our study area (Ayers et al., 2001). Burrowing skinks, in particular, use compacted crusted sand for burrow sites, as sands are easily excavated (Greenville and Dickman, 2009), and the typically thin biological crust provides a structurally stable burrow entrance (Zaady and Bouskilla, 2002). The close association between skink burrows and shrub hummocks may also provide access to shrub-resident prey such as arboreal invertebrates in the shrub canopies or subterranean termites, which occur in galleries around the roots (Letnic et al., 2004). Surprisingly, debris mounds were not preferred sites of animal disturbance, even though they are substantially resource-rich and support a moderate density of invertebrates (Tongway et al., 1989).

Although the density of ant nests in our study increased with increasing hummock cover, the results were variable and site-specific. Ant biomass is often greater in ecotonal habitats (Dugas, 2001), so one might expect to record more nest entrances at the margins of the shrub hummocks and interspaces. The marked differences in nest size (range: 0.1–8 cm diameter) suggest that many taxa inhabited our study sites. Some species such as *Myrmecocystus*, *Melophorus*, and *Monoporium* prefer open habitats (Hoffmann and Andersen, 2003), and their small nest entrance size (<2 mm) corresponds with the small volumes of soil deposited on the surface. Other species such as *Aphaenogaster barbigula* prefer more vegetated sites, and deposit relatively large volumes of soil (up to 3.4 t ha⁻¹ yr⁻¹) around their large (~20 mm diameter) nests (Eldridge and Pickard, 1994). We are unable to determine species-level ant effects because we did not record individual species associated with the burrows and nests. We would expect, however, a stronger relationship between hummock cover and ant nest density if we were able to discriminate between different types of ants.

We failed to detect any differences in scorpion burrow density with changing hummock cover. Scorpions generally prefer coarser-textured soils such as those within hummocks because physically crusted soils restrict their ability to burrow (Bradley, 1986). Locket (1993) showed that most burrows of the scorpion *Urodacus armatus* occurred at the base of the sand dunes in areas occupied by *Senna* and *Eremophila* spp. shrubs. The concentration of scorpion burrows in sandy soils such as those characterised by shrub hummocks (Shorthouse and Marples, 1980) may be a mechanism for avoiding disturbances in frequently trampled areas. Burrowing behaviour may, however, be age-related, and while the burrows of young *Paruroctonus mesaensis* scorpions are associated with sites of dense vegetation cover, those of adults show a more random distribution (Polis et al., 1986), and adults may prefer open microsites. Finally, higher densities of the Desert screamer cicada (*Macrotristria hillier*) in shrub hummocks is related to their preference for the roots of *Acacia cambagei* and *Acacia excelsa*, which are important food plants for the nymphal stage (Moulds, 1990).

The preceding section indicates that there were generally more disturbances associated with shrub hummocks. However, contrary to expectation, we detected no significant differences in either the density or composition of animal disturbances between sites that were ploughed and unploughed, or grazed and ungrazed areas. This result should not be interpreted, however, as the absence of an effect on ecosystem processes. Rather, it suggests a consistent microsite effect across all treatments. The high rates of soil mixing and creation of macropores by ants, and their tendency to alter soil particle size through burrowing (Richards, 2009) suggest that they will likely enhance the infiltration of water (James et al., 2008) in the interspaces. Thus the preponderance of ant nests in the interspaces would be expected to influence the redistribution of water, which is generally localised under the shrubs (Segoli et al., 2008). Ants are also central-place foragers, and are likely to forage in the shrub hummocks. Therefore ant nests may provide a mechanism for reversing flows of water, litter and sediment (which is typically towards the hummocks) to the interspaces. The accumulation of finer material around the nests of ants may improve soil nutrients (James et al., 2008), enhance the diversity of soil microfauna (Zaragoza et al., 2007), and be importance for accretion of soil for colonisation by annual plants (Eldridge et al., 2009).

We only detected some grazing effects on the cover of shrub hummocks and no ploughing effects almost two decades after ploughing. However, our results indicate that management practices that reduce hummock cover are likely to have marked effects on the density of some soil disturbances. Removal of shrubs therefore might come at a long-term cost associated with loss of

habitat for shrub-resident and shrub-foraging taxa. It could also have potentially large, but unknown effects on ecosystem processes as broad as infiltration and nutrient processes.

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