Seasonal changes in habitat preferences of two closely related millipede species

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Abstract

The habitat preferences of two closely related millipede species, *Centrobolus richardii* and *C. fulgidus*, were investigated on three different seral stages of a coastal dune forest successional sere north of Richards Bay, South Africa. Fixed-width transects were used to survey millipedes in three habitats of different ages. Habitat preference occurred on both inter- and intra-site levels and was influenced by season. A habitat shift was recorded for *C. richardii*, while *C. fulgidus* was dormant during the winter months, reflecting two different strategies used by these closely related species to meet their resource requirements. Successional changes previously reported are masked by these differential responses.

Key words: habitat, millipedes, seasonality, South Africa, succession

Résumé

On a étudié les préférences d'habitat de deux espèces très proches de mille-pattes, *Centrobolus richardii* et *C. fulgidus*, à trois niveaux différents d'une forêt de dune côtière au nord de Richards Bay, en Afrique du Sud. On s'est servi de transects de largeur fixe pour recenser les mille-pattes dans trois habitats d'âge différent. Il y avait des préférences en matière d'habitat tant à l'intérieur des sites qu'entre les sites et elles étaient influencées par les saisons. On a relevé un changement d'habitat chez *C. richardii*, tandis que *C. fulgidus* était dormant pendant les mois d'hiver, ce qui reflète deux stratégies différentes chez ces deux espèces proches pour répondre à leurs besoins. Les changements successifs reportés précédemment sont masqués par ces réponses différentielles.

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Introduction

Millipedes are detritivores and influence the decomposition of plant material through mechanical fragmentation and the moistening of litter (Lavelle, 1988). This results in increased microbial activity and the mineralization of nitrogen and cations (Anderson, Ineson & Huish, 1983; Anderson & Ineson, 1984; Visser, 1985). Millipedes also redistribute organic material throughout the soil profile and influence soil water relations and soil structure (Hopkin & Read, 1992). Millipedes are therefore important mineralizing and humifying agents within an ecosystem (Bano, 1992).

Since 1978 coastal dune rehabilitation undertaken by Richards Bay Minerals north of Richards Bay following dredge mining for heavy minerals has resulted in the development of dune forest successional seral stages of known age. These form the basis for investigations of factors that might influence the development of biological diversity in coastal dune forests (Van Aarde, Ferreira & Kritzinger, 1996a,b; Van Aarde *et al.*, 1996c). The seral stages of regenerating dunes are inhabited by at least thirteen millipede species and species richness increases with the age of regenerating dunes. Millipede succession during early seral stages (6–14 years old) is characterized by species replacement and during later

stages (more than 30 years old) by species replacement and addition (Van Aarde *et al.*, 1996a).

Lawrence (1967) described 23 species of *Centrobolus* occurring in the eastern half of southern Africa. Habitat differentiation is therefore expected for species in this genus, especially for those of whom the distribution overlaps. Some of the conspicuously coloured spirobolid millipedes that live in the coastal forests of Natal are known to be excellent tree climbers while others live on the forest floor (Lawrence, 1984). Two *Centrobolus* species, *C. richardii* (Lawrence, 1967) and *C. fulgidus* (Lawrence, 1967) dominate developing coastal dune forests older than ≈ 6 years in the region. The co-occurrence of these closely related juliformid species, similar in size (≈ 10 cm) and appearance (both red in colour), on coastal stands of known age and successional stage (Van Aarde *et al.*, 1996a), makes them ideal for investigating similarities and differences that may explain their apparent coexistence.

In this paper we investigate season-specific surface densities of *C. richardii* and *C. fulgidus* on different vegetation strata within specified seral stages of succession, in an attempt to explain their coexistence.

Materials and methods

The study area was situated on the coast of Kwazulu-Natal, approximately 15 km north-east of Richards Bay (28°43′S, 32°12′E). The area consisted of seral stages of rehabilitating coastal dune forests, dominated by *Acacia karroo* (Hayne), ranging from 1 to 16 years old at the time of the study, and patches of unmined forest, most of which are being continually disturbed by pastoralists. The study area has been described by Van Aarde *et al.* (1996b). Three regenerating sites of known age were selected for this study. Two of these were regenerating in response to post-mining rehabilitation and at the time of the study were 11–13 and 14–16 years old. The third site regenerated to indigenous vegetation following its clearing for afforestation 30 years prior to the study. Both *C. fulgidus* and *C. richardii* occur in abundance on these sites (Van Aarde *et al.*, 1996a–c), but no information is yet available on their life history characteristics. The primary morphological differences between these two species are in the colour of the ventral surface of the body and leg length. *Centrobolus richardii* has a red ventral surface and long legs, while the ventral surface of *C. fulgidus* is pink and has shorter

legs. Initial identification was from specimens collected in the field and compared to reference collections at the Natal Science Museum in Durban, South Africa.

The study area has a warm temperate climate with a mean annual rainfall of 1292 mm (Schultze & McGee, 1978). The mean annual temperature is $21.5 \pm 7.4°C$ (Tinley, 1985). Summers are characteristically warm and wet, and are followed by intermediately wet autumns. Winters are characterized by a dry climate and are followed by a wet spring. Data obtained during summer (January to March) and winter (June to September) were analysed separately. These seasons were identified depending on the frequency of precipitation (see Ferreira, 1993).

Previous studies indicated that less than 5% of all surface millipedes were juveniles (Van Aarde *et al.*, 1996a) while soil samples revealed juveniles of other morphospecies (Van Aarde *et al.*, 1996b) as well as *C. fulgidus* specimens. For the purpose of this study only adult millipedes were surveyed during their maximal activity period (05.00–10.00 hours) on randomly selected transects of fixed width (35×6 m), as described by Van Aarde *et al.* (1996a). Three transects were intensively searched for surface-active millipedes on a specified day after random selection from 30 transects (10 per site) located in the study area. Surveys were conducted from January to March 1994 for a total of 16 days during the summer months and for 18 days from June to September 1994 during the winter period.

The vegetation stratum on which a millipede of a given species occurred was noted. The following vegetation strata were distinguished:
- Shrubs, defined as the shrub and herb layer (< 30 cm in height), including the ground surface which was usually covered with plant litter.
- *Acacia karroo* trees to a height of 3 m. Millipedes occurring out of reach (> 3 m) could not be collected and identified.
- Broad-leaved trees to a height of 3 m. This category included all trees other than *A. karroo*.

The distinction in the tree strata was made because *A. karroo* woodlands dominated the early seral stages but were gradually replaced by broad-leaved species in the older sites (Van Aarde *et al.*, 1996b).

The absolute (number of millipedes/transect) and relative densities (each species' density expressed as a fraction of the combined densities of both species) of each species within a particular site were determined

for a particular season. Higher absolute stratum-specific densities of a particular species were considered to indicate habitat preferences along the vertical axis of dispersion.

Analyses of variance and Tukey multiple range tests (Sokal & Rohlf, 1969) were used to determine differences in species-specific densities between sites as well as between vegetation strata. Absolute densities were used to indicate habitat preferences both on intra- and inter-site levels. Cochran's *C*-test was used to investigate homogeneity of variances. Data characterized by heterogeneous variances were log transformed after adding 0.1 to each data point (Caughley & Sinclair, 1994). To test for significant species-specific differences in the mean absolute densities between the two seasons, a *t*-test assuming unequal variances between the samples was used (Sokal & Rohlf, 1969). Significance was taken at a 95% level using a two-tailed test statistic to determine if these mean densities differed between seasons (Bethea, Duran & Boullion, 1975). All data are presented as mean values followed by one standard error of the mean.

Results

Absolute densities of *C.* richardii

Stand-specific densities of *C. richardii* did not differ significantly between vegetation strata during the summer or winter months. Although summer densities did not differ significantly between the vegetation strata of a given site, stratum-specific densities during winter did differ significantly (11–13-year-old site: $F_{3,52} = 16.24$; 14–16-year-old site: $F_{3,52} = 12.61$; 30-year-old-site: $F_{3,52} = 4.32$; $P < 0.05$; Tukey multiple range test), with higher absolute densities for the shrub stratum in all sites (Table 1).

Absolute densities of *C.* fulgidus

During summer, site-specific absolute densities differed significantly for the shrub stratum ($F_{2,43} = 5.97$; $P < 0.05$) and the *Acacia* tree stratum ($F_{2,43} = 8.38$; $P < 0.05$) but not for the broad-leaved tree stratum. As a result, total densities during summer also differed significantly between the sites ($F_{2,43} = 6.26$; $P < 0.05$).

Table 1 The absolute densities (number of millipedes/transect ± standard error) for *C. richardii* and *C. fulgidus* for each of the stands across vegetation strata during summer and winter months

Site age in years	Species	Vegetation strata				
		Shrubs	Trees[1]	*Acacia* trees	Broad-leaved trees	Totals of all strata
Summer						
11–13	*C. richardii*	2.69 ± 1.18	3.90 ± 0.93	2.25 ± 0.64	1.63 ± 0.68	6.56 ± 0.03
n = 16	*C. fulgidus*	80.44 ± 25.75	7.38 ± 1.68	5.44 ± 1.51	1.94 ± 0.66	87.81 ± 26.89
14–16	*C. richardii*	4.13 ± 2.00	8.63 ± 2.74	6.81 ± 2.31	1.81 ± 0.58	12.75 ± 3.50
n = 16	*C. fulgidus*	15.38 ± 4.40	2.63 ± 0.77	0.81 ± 0.29	1.81 ± 0.59	18.00 ± 5.09
30	*C. richardii*	2.50 ± 1.20	10.29 ± 5.22	3.21 ± 1.55	7.07 ± 3.89	12.79 ± 5.56
n = 14	*C. fulgidus*	20.00 ± 9.60	1.93 ± 0.78	0.79 ± 0.40	1.14 ± 0.57	21.93 ± 10.27
Winter						
11–13	*C. richardii*	8.14 ± 2.53	2.64 ± 0.86	2.29 ± 0.66	0.36 ± 0.23	10.79 ± 3.00
n = 16	*C. fulgidus*	4.93 ± 2.23	1.36 ± 0.63	1.14 ± 0.51	0.24 ± 0.16	6.29 ± 2.86
14–16	*C. richardii*	8.43 ± 2.79	2.57 ± 0.56	2.00 ± 0.43	0.57 ± 0.43	11.00 ± 3.01
n = 16	*C. fulgidus*	3.50 ± 1.60	3.00 ± 1.34	2.57 ± 1.32	0.43 ± 0.25	6.50 ± 2.90
30	*C. richardii*	9.86 ± 3.27	3.43 ± 1.39	2.79 ± 1.25	0.64 ± 0.27	13.26 ± 4.13
n = 14	*C. fulgidus*	8.36 ± 2.71	2.50 ± 0.78	2.07 ± 0.65	0.43 ± 0.20	10.86 ± 3.18

[1]The tree strata is represented by the combined *Acacia* and broad-leaved strata (*n* = the number of transects surveyed in each stand).

Absolute densities were highest on the 11–13-year-old site for both the shrub stratum (80.44 ± 25.75 millipedes/transect) and the *Acacia* tree stratum (5.44 ± 1.51 millipedes/transect), resulting in a cumulative total density of 87.81 ± 26.87 millipedes/transect (Table 1). These values were significantly higher than those recorded on the other two sites. During winter, site-specific absolute densities for the vegetation strata were similar.

The absolute densities of *C. fulgidus* on the 11–13-year-old site differed significantly between summer and winter for the shrub strata ($t'_{15,0.05} = 2.92$; $P < 0.05$), the *Acacia* tree strata ($t'_{18,0.05} = 2.69$; $P < 0.05$), the broad-leaved tree strata ($t'_{17,0.05} = 2,54$; $P < 0.05$) and the total of all the strata ($t'_{15,0.05} = 3.01$; $P < 0.05$). On the 14–16-year-old site, absolute mean densities differed significantly between summer and winter only for the shrub strata ($t'_{19,0.05} = 2.53$; $P < 0.05$) and the broad-leaved tree strata ($t'_{20,0.05} = 2.17$; $P < 0.05$). For all these differences, summer absolute densities were higher than winter values. There were no significant differences between summer and winter stratum-specific, absolute densities on the 30-year-old site (Table 1).

Centrobolus fulgidus showed a significant preference for the shrub strata on all sites during summer (11–13-year-old site: $F_{3,60} = 15.10$; $P < 0.05$; 14–16-year-old site: $F_{3,60} = 5.24$; $P < 0.05$; 30-year-old site: $F_{3,60} = 4.19$; $P < 0.05$; Tukey multiple range tests). Densities were lowest on the broad-leaved tree strata and the other strata were no different to each other during winter in the 30-year-old forest ($F_{3,52} = 3.11$; $P < 0.05$; Tukey multiple range test).

Relative densities during summer

During summer, *C. fulgidus* dominated the shrub strata: relative density decreased with stand age to a minimum of 0.64 ± 0.12 in the 30-year-old site. The relative density of *C. richardii* on the shrub stratum increased with stand age but never reached values higher than those of *C. fulgidus* (Table 2).

On the 11–13-year-old site, the tree stratum was dominated by *C. fulgidus*, while *C. richardii* dominated this stratum on the 14–16 and 30-year-old sites. The differences between the shrub and tree strata resulted in the patterns observed for total relative densities: *C.*

Table 2 The relative densities (± standard error) for *C. richardii* and *C. fulgidus* for each of the stands across vegetation strata during summer and winter months

Site age in years	Species	Shrubs	Trees[1]	*Acacia* trees	Broad-leaved trees	Totals of all strata
Summer						
11–13	C. richardii	0.05 ± 0.02	0.35 ± 0.06	0.34 ± 0.08	0.36 ± 0.10	0.10 ± 0.03
n = 16	C. fulgidus	0.95 ± 0.02	0.65 ± 0.06	0.66 ± 0.08	0.64 ± 0.10	0.90 ± 0.03
14–16	C. richardii	0.21 ± 0.07	0.72 ± 0.09	0.84 ± 0.07	0.51 ± 0.12	0.52 ± 0.09
n = 16	C. fulgidus	0.79 ± 0.07	0.28 ± 0.09	0.16 ± 0.07	0.49 ± 0.12	0.48 ± 0.09
30	C. richardii	0.36 ± 0.12	0.76 ± 0.09	0.74 ± 0.11	0.79 ± 0.10	0.46 ± 0.12
n = 14	C. fulgidus	0.64 ± 0.12	0.24 ± 0.09	0.26 ± 0.11	0.21 ± 0.10	0.54 ± 0.12
Winter						
11–13	C. richardii	0.86 ± 0.06	0.84 ± 0.07	0.84 ± 0.07	0.70 ± 0.15	0.87 ± 0.06
n = 16	C. fulgidus	0.14 ± 0.06	0.16 ± 0.07	0.16 ± 0.07	0.30 ± 0.15	0.13 ± 0.06
14–16	C. richardii	0.87 ± 0.05	0.70 ± 0.11	0.67 ± 0.12	0.50 ± 0.22	0.85 ± 0.06
n = 16	C. fulgidus	0.13 ± 0.05	0.30 ± 0.11	0.33 ± 0.12	0.50 ± 0.22	0.15 ± 0.06
30	C. richardii	0.62 ± 0.07	0.50 ± 0.12	0.49 ± 0.12	0.61 ± 0.17	0.50 ± 0.08
n = 14	C. fulgidus	0.38 ± 0.07	0.50 ± 0.12	0.51 ± 0.12	0.39 ± 0.17	0.50 ± 0.08

[1]The tree strata is represented by the combined *Acacia* and broad-leaved strata (*n* = the number of transects surveyed in each stand).

fulgidus dominated on the 11–13-year-old site, while the relative densities of *C. fulgidus* and *C. richardii* were similar on the 14–16 and the 30-year-old sites (Table 2).

Relative densities during winter

A different pattern emerged during winter: *C. richardii* dominated the shrub stratum on all stands, reaching its lowest relative density (0.62 ± 0.07) in the 30-year-old site. On the tree stratum, *C. richardii* featured as the most dominant species on all sites, although the relative densities of *C. fulgidus* and *C. richardii* differed very little on the 30-year-old site. This resulted in the total relative densities of *C. richardii* decreasing with site age, while that of *C. fulgidus* increased with site age to reach near equal values on the 30-year-old site during winter (Table 2).

Discussion

Three species of *Centrobolus* occurred in our study area, with the two reported on in this paper dominating older rehabilitating coastal dune forests north of Richards Bay. They have been recorded to be diurnally surface active on litter, shrubs and trees (Van Aarde *et al.*, 1996a). The third species, *C. sanguinipes* (Lawrence, 1967) was only recorded in unmined areas (Van Aarde *et al.*, 1996a). Although millipedes primarily consume decayed leaf litter of poor nutrient quality, surface mobility may be the most common feeding tactic to acquire higher quality food sources (Dangerfield & Telford, 1991; Dangerfield, Milner & Matthews, 1992). The two major sets of surface activity for juliform millipedes in savannah environments of southern Africa have been defined by Dangerfield *et al.* (1992) as: (1) movements within a habitat and (2) feeding behaviour. In this paper we provide possible explanations for the observed species-specific differences in activity for each of these sets of behaviour.

According to Dangerfield & Kaunda (1994) it is rarely possible to study the foraging behaviour of litter-feeding detritivores. Dangerfield *et al.* (1992) did however, make observations on the feeding behaviour of juliform millipedes in savannah environments of southern Africa, in which they found that a range of food types were selected and high quality food sources such as *Acacia* seeds were located as part of the feeding strategy. Dietary specialization is often considered an effect of competitor avoidance, thus enabling biotic interactions to primarily influence the assemblages of different species (Dangerfield & Telford, 1992). Dangerfield & Kaunda (1994) also noted that plasticity of food selection in response to current availability of foods might be important for macro-arthropods that have a restricted foraging period.

Our analyses demonstrate habitat differentiation between *C. richardii* and *C. fulgidus*. However, the patterns recorded during the summer and winter differed considerably. During summer, intra-site habitat differentiation was clearly defined, with these two species separating on a vertical scale according to vegetation strata. *Centrobolus richardii* occurred predominantly on trees and *C. fulgidus* on the shrub layer.

Centrobolus richardii has longer legs than *C. fulgidus*. This could be an adaptation to an arboreal life style during the adult phase as Lewis (1971a) found that soil-dwelling polydesmoids had relatively shorter legs than surface- and litter-dwelling species. Analysis of the faeces of arboreal millipede species revealed that such species do feed on soft bark and leaves. If *C. richardii* was influencing canopy processes through herbivory during summer months, this in turn could influence litter micro-arthropods (Schowalter & Sabin, 1991).

Schowalter *et al.* (1991) found that defoliation of the canopy significantly increased light and water penetration and N, K and Ca flow to the litter. Qualitative changes in micro-arthropod communities could affect decomposition processes during defoliation periods so that the taxa that respond to defoliation may become less abundant or disappear when defoliation is prevented or suppressed (Schowalter & Sabin, 1991). Maruam & Scheu (1996) showed that digestion and pellet formation of beech leaf litter by *Glomeris marginata* (Villers) resulted in an increase in nutrients (phosphorus, nitrogen) available to microorganisms. These microorganisms could only be used for microbial growth if the fragmented litter in faecal pellets also contained decomposed carbon resources, which was not found in winter and spring. Likewise, *C. fulgidus* may be dependent on the arboreal activities of *C. richardii* during summer months because of the indirect qualitative changes that *C. richardii*'s feeding habits may have on the food resources of *C. fulgidus*.

Site-specific differences in the trees preferred by *C. richardii* probably reflect site-specific differences in the density of different tree species. *Acacia karroo* is the most abundant tree species on the 11–13-year-old site, while broad-leaved trees outnumber *A. karroo* in the 30-year-old site (Van Aarde *et al.*, 1996b,c). *Acacia* spp. dominate earlier stands where low levels of nitrogen are known to occur, as they are able to fix nitrogen on these stands (Van Aarde, Smit & Claassens, 1998).

Centrobolus richardii changed its habitat preference during winter when it occurred predominantly on the shrub stratum. This change in preference is not associated with a change in absolute densities for this species and thus reflects on a seasonal shift and broadening of its spatial niche. Relative densities revealed possible patterns of species replacement over time in terms of progressing habitat age. Svardson (1949) predicted that when resources become scarce or of low quality, species expand their niches as they are forced to exploit a wider range of sub-optimal resources. It is therefore conceivable that the availability and quality of resources on trees declines during winter, resulting in the recorded shift in habitat preference and widening of the spatial niche of *C. richardii*.

In contrast, *C. fulgidus* was recorded predominantly on the shrub strata during winter and summer. However, absolute density for this species during winter was significantly lower than during summer in two of the sites. This decline in density results in *C. richardii* dominating during winter. The seasonal change in the absolute densities of *C. fulgidus* may be ascribed to seasonality in breeding and activity as in other millipedes (Lawrence, 1967). However, this decline in density of *C. fulgidus* may account for the shift in the spatial niche of *C. richardii*, where the absence of a closely related and morphologically similar species results in a relaxation of potential interspecific competitive interactions, either for food resources or space.

The contrasting behavioural response of these two millipede species to changing environmental conditions during winter probably results from species-specific resource requirements. Although tree leaf litter from *Acacia* spp. is often of high nutrient status and palatability to detritivores, it is rapidly decomposed, which limits its availability (Dangerfield *et al.*, 1992). In rain forests leaf fall reaches a peak at the height of the dry season after which time the accumulated litter dis-

appears rapidly during the rainy season (Madge, 1965). Litter dwelling species would thus be most active when litter is abundant and environmental conditions are favourable, that is at the beginning of the rainy season (Lewis, 1974).

It is likely that species-specific resource requirements are equally satisfied on the ground and shrub stratum during winter for *C. richardii* and on the tree stratum during summer, whereas species-specific resource requirements are not satisfied on any stratum for *C. fulgidus* during winter. While *C. richardii* widens its spatial niche to overcome the problems associated with resource limitations, *C. fulgidus* apparently becomes seasonally inactive to overcome this problem. This leads to inter- and intra-site differences in densities between the species. The summer density of *C. fulgidus* was highest in the youngest site investigated, while no real differences existed between sites during winter. Site-specific densities of *C. richardii* were the same during winter and summer.

The seasonal reduction in the density of *C. fulgidus* may thus be due to either a combination of reduced resource quality and availability during winter or unfavourable climatic conditions. Millipedes are known to aestivate which allows flexibility in the time to maturity, longevity and a general slowing down of the life cycle (Hopkin & Read, 1992). It is most likely that *C. fulgidus* has adapted in a similar way to survive unfavourable conditions. Presumably *C. fulgidus* was largely soil dwelling during winter months but it was not possible to confirm this as soil samples were not collected on a consistent basis and very few adult specimens were obtained from the soil samples. Juveniles could not be identified to species level. Lewis (1974) found that adult millipedes are the most desiccation-resistant active stage because of their large body size and are therefore the first to appear at the beginning of the rainy season. Although this study only focused on interspecific differences in activity patterns, several investigators have commented on sexual dimorphism in activity patterns of adult juliform millipedes (Blower, 1970; Lewis, 1971a; Dangerfield *et al.*, 1992). In most cases males were found to be most active. David & Vannier (1996) noted that starvation in the field affects male millipedes more severely than females. Studies on the supercooling point of *Polysonium germanicum* (Brandt), a widespread temperate species, revealed that a substantial part of the male population showed spontaneous fast-

ing during cold months in contrast with females which did not fast. Dry and cold surface conditions from May to October are generally overcome by the burrowing ability of many southern African species, while field observations of tropical millipede species suggested a hierarchy in the duration of surface mobility between species (Dangerfield & Milner, 1993). According to studies conducted by Dangerfield & Telford (1991) the duration of surface activity appeared to depend on the time of emergence rather than the duration of the rainy season with moisture being the most likely cue to induce activity. Millipedes are able to control their time of emergence by varying the depth at which they passed the dry season (Lewis, 1974). Bandyopadhyaya & Mukhopadhyaya (1988) also found that aggregations of millipedes occur within a more uniform habitat, such as leaf litter or tree strata, but may vary with depth of soil and are often related to humidity (Peitsalmi, 1974). Barlow (1957) suggested that humidity exerts the greatest influence on the distribution of millipedes. Lewis (1971b) noted that many temperate polydesmoids over-wintered partially or entirely as adults while adults in tropical regions die shortly after the rainy season and the larvae diapause in spherical moulting chambers during the dry season. The moulting chambers of diapausing larva were thought to be important in water conservation.

These changing habitat preferences mask successional patterns in millipede communities previously reported. Van Aarde *et al.* (1996a) suggested that *C. richardii* replaces *C. fulgidus* during succession. Their sampling was conducted during summer months and indicated, as in the present study, a decrease in relative density of *C. fulgidus* with a subsequent increase in relative density of *C. richardii* with an increase in stand age. Winter months during the present study were characterized by relative densities of *C. richardii* decreasing, while relative densities of *C. fulgidus* increased with habitat age. This results in successional patterns of change in millipede communities being masked by habitat preference of these two species. Interspecific studies on food preferences, life history characteristics as well as tolerance levels on the basis of physiological and morphological differences of these two closely related millipede species, would be necessary to determine whether biotic or abiotic factors are having the strongest influence on the observed species-specific differences in activity.

Acknowledgements

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