The spatial distribution of termite activity in grazed and ungrazed Chihuahuan Desert grassland

Keena N. Tracy, David M. Golden & Thomas O. Crist★

Department of Zoology, Miami University, Oxford, OH 45056, U.S.A.

Termites are important in litter decomposition and nutrient cycling in desert grasslands but little is known about the spatial distribution of termites and how spatial patterns are affected by topography and grazing by livestock. We measured the distribution of surface activity by the subterranean termite *Gnathamitermes tubiformans* in grazed and ungrazed Chihuahuan Desert grassland along 900 m transects that spanned a topographic gradient. Numbers of termite casts on litter and plants were recorded in 900 contiguous 1 m² quadrats along a transect located in a grazed area and in an ungrazed control. Cover of plants and litter were also recorded in 1 m² quadrats every 10 m along each transect.

Over 6800 casts were recorded along the control transect and fewer than 3500 casts in the grazed transect. A greater percentage of casts was found on litter (64% control, 57% grazed) than on plants (36% control, 43% grazed). Termite casts were most numerous on threeawn (*Aristida* spp.) in the ungrazed control and on fluff grass (*Erioneuron pulchellum*) in the grazed area. Spatial autocorrelation in numbers of termite casts on litter showed a greater fine-scale patterning along the control transect than in the grazed transect. Spectral analysis of termite casts on litter in the control transect also indicated strong spatial patterning at fine scales (2–4 m and 10–20 m) as well as significant variation at broader scales (>100 m). On the grazed transect, however, the fine-scale peak (2–4 m) in spectral density was absent. Termite activity in desert grasslands is therefore strongly influenced by the fine-scale patchiness in litter around plants as well as broad-scale variation in litter availability due to grazing and topography. A loss of fine-scale spatial coupling of termite activity to litter and a decrease in overall termite activity occurs in response to grazing, which may suggest a diminished role of termites with continued livestock grazing and shrub encroachment in desert grasslands.

© 1998 Academic Press

★ Corresponding author.

Introduction

Subterranean termites (Isoptera: Termitidae) are considered keystone insects in arid ecosystems because they affect soil properties such as bulk density and porosity by constructing soil galleries on surface litter and plants (Whitford, 1996). Soils altered by termites may be enriched with nutrients (Nutting *et al.*, 1987) and support a greater plant biomass or a different plant species composition (Whitford *et al.*, 1995). Termites also reduce erosion by transporting stable subsoil aggregates to the surface and replacing the loose surface soil that is readily eroded (Whitford, 1996). Following significant rainfall, termites construct mud galleries around dead stems of several species of desert shrubs, forbs, and grasses (Ueckert *et al.*, 1976; MacKay *et al.*, 1985). Traveling through galleries, termites can consume over 50% of the net primary production, making them the prominent invertebrate in the cycling of carbon and other nutrients in desert grasslands (Silva *et al.*, 1985). Despite the important roles of subterranean termites in decomposition, little is known about the spatial distribution of termite activity in semi-arid grasslands (Haverty *et al.*, 1975; Nash & Whitford, 1995; Crist, 1998).

The distribution of soil invertebrates in desert grasslands may vary considerably with topography and livestock grazing (Whitford *et al.*, 1995). Sloping alluvial plains, or bajadas, are common topographic features of deserts. A continuous sorting of soil particle size occurs along bajadas from coarse-textured soils to fine-textured soils in the lower bajada (Wierenga *et al.*, 1987). The gradient in soil characteristics affects the spatial distribution and community structure of plants (Ludwig & Cornelius, 1987; Wierenga *et al.*, 1987) and animals (Turner *et al.*, 1991; Johnson, 1992). Few studies, however, have documented broad-scale spatial distribution patterns of termites in semi-arid grasslands (Haverty *et al.*, 1975), especially as they vary with topography (Nash & Whitford, 1995; Crist, 1998). Broad-scale termite distributions might also be affected by livestock grazing in desert grasslands, where plant community structure and ecosystem function are substantially altered by grazing (Schlesinger *et al.*, 1990; Bock & Bock, 1993; Holechek *et al.*, 1994). For example, the fine-scale patchiness of organic matter and nutrients associated with perennial bunchgrasses (Schlesinger *et al.*, 1996) gradually becomes redistributed by overgrazing and drought which favor shrub invasions of desert grasslands (Schlesinger *et al.*, 1990). Grazing may therefore affect the fine-scale patterns of termite distribution in response to litter redistribution as well as the broad-scale changes in termite abundance in response to overall changes in food availability.

In this paper spatial patterns of above-ground activity of the subterranean termite *Gnathamitermes tubiformans* Buckley were measured along a topographic gradient in two different grazing regimes within a Chihuahuan Desert grassland. The objectives of this study were to (1) determine the spatial distribution of termite activity along a topographic gradient in the presence and absence of livestock grazing, and (2) examine how the spatial pattern in termite activity varies with scale and how scale-dependent patterns change with plant species composition and litter availability in response to grazing.

Materials and methods

Study site

This study was conducted at the New Mexico State University Rangeland Research Center (College Ranch) of the Jornada Experimental Range. The Jornada is located in the Chihuahuan Desert in southern New Mexico, and is managed by the US

Department of Agriculture as a site for long-term grazing studies. Historically, the Jornada was mostly semi-arid grassland, but shrub invasion during the past century has transformed large areas of grassland into desert shrublands (Buffington & Herbel, 1965; Schlesinger *et al.*, 1990). The elevation of the Jornada Basin varies between 1100−1400 m. Mean monthly temperatures fluctuate between 13°C in January to 36°C in July and annual precipitation is highly variable with a mean of 247 mm. Over half of the annual precipitation occurs between July and September, with a small peak during winter (MacKay *et al.*, 1985). Topography consists of gently sloping alluvial fans (bajadas), closed drainage basins (playas), and shifting dune systems. Gravel-like soils are located near mountain bases, coarse sandy soils are found in mid-slope positions, and clays and silts occur in the playas.

The dominant grasses include several species of threeawn (mostly *Aristida purpurea* Nutt.), bush muhly (*Muhlenbergia porteri* Scribn.), fluff grass (*Erioneuron pulchellum* [H.B.K.] Tateoka), black grama (*Bouteloua eriopoda* Torr.), and mesa dropseed (*Sporobolus flexulosus* [Thurb.] Rydb.). In many areas of the Jornada Basin, perennial grasses have been replaced by creosote bush (*Larrea tridentata* [D.C.] Cov.) and honey mesquite (*Prosopis glandulosa* Torr.) (Buffington & Herbel, 1965). Common annual forbs include leather leaf croton (*Croton pottsii* [Klotzsch] Muell), nightshades (*Solanum* spp.), globemallow (*Sphaeralcea* spp.), and Russian thistle (*Salsola iberica* Sennen & Pau). Soaptree yucca (*Yucca elata* Engelm.) and sub-shrubs such as broom snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby) are also locally common.

Plant and termite sampling

In August 1997, two 900 m transects were established along a north-facing bajada, one in the grazed and one in the ungrazed (control) area. The ungrazed area was in a 0.5×3.0 km fenced exclosure constructed in 1982. To determine the effect of topography on termite density, our transects spanned 900 m from just above a playa upward to a mid-bajada position. Transects in both the grazed area and the ungrazed control were dominated by grasses and forbs with little shrub invasion by *L. tridentata* or *P. glandulosa*.

To assess the availability of plants and litter to termites, basal cover of each plant species and surface litter in 1 m × 1 m quadrats was estimated at 10-m intervals along each transect. Cover of surface litter and plants was estimated to the nearest 1%; plants with negligible cover were given a value of 1%.

Studies on subterranean termites often use baits of toilet paper or wood to estimate termite abundance or spatial distribution (Haverty *et al.*, 1975; Nutting & Jones, 1990; Whitford *et al.*, 1995; Crist, 1998). In this study, we sought to determine how the association of termite activity with surface litter and different plant species changed between grazed and ungrazed areas. Therefore counts of above-ground soil galleries (casts) were used as a measure of termite activity and it was assumed that measures of termite activity density (number of casts per unit area) reflected the spatial variation of termite abundance in soil.

Above-ground gallery construction by *Gnathamitermes tubiformans* occurs in wet soils following significant rainfall (MacKay *et al.*, 1985). Surface activity of termites was not evident until after the series of rainfall events in late July 1997, when casts became numerous on the surface. Summer rainfall data from the site showed 29.5 mm in June, 56.7 mm in July, and 8.2 mm in August. During 1−5 August 1997, termite cast density on plants and litter were measured by counting distinct casts in contiguous 1 m^2 quadrats along a 900 m transect in both grazed and ungrazed areas for a total of 1800 counts of termite cast density. There was no rainfall during this 5-day sampling period.

Statistical analysis

Spatial autocorrelations of termite cast densities were conducted along each transect. Spatial autocorrelation measures the degree of similarity between pairs of samples separated by increasing distances (lag distances) along a transect (Turner *et al.*, 1991). Lag lengths up to 100 m were analysed but only autocorrelations ranging from 0 to 50 m are presented. A 95% confidence interval (1·96 × SE) was calculated across lag length to determine which peaks in spatial autocorrelation were significant. Separate autocorrelations were calculated to determine the scales of spatial dependence of total termite cast abundance on surface litter and on plants. Autocorrelation of termite casts on the two plant species were also analysed where casts were most numerous. Autocorrelations were calculated using SYSTAT Series (SYSTAT, 1992).

Spectral analysis was conducted to partition the spatial variability across scales and to further identify scales of repeated patterns in termite cast abundance. Spectral analysis identifies patterns in a data sequence by comparing successive values to wave-form patterns of different sizes (spatial scale). The resulting spectral density partitions the spatial variation into components according to various wavelengths (m) which show the relative contributions of different spatial scales to the overall variation in the data (Davis, 1986). A plot of the relative variation and the frequency (m^{-1}) associated with each wavelength (periodogram) shows the proportion of the total spatial variation explained by spatial dependence at different scales. Large peaks indicate a wave-form that corresponds to significant spatial patterning, whereas smaller peaks in the graph represent noise in the data. Spectral analysis was conducted using a computer program based on the source code provided by Manly (1991), which uses the fast-Fourier transform algorithm to calculate spectral density. Values of spectral density were then normalized so that the spectral density across all periods summed to 1·0 (Manly, 1991). Separate spectral analyses were run for termite casts on the plants most frequently used by termites in grazed (*E. pulchellum*) and ungrazed areas (*Aristida* spp.), as well as for termite casts found on litter and on all plants in both transects. Spectral densities were smoothed using a 13-point running average prior to graphing to reduce the noise of small peaks and to highlight larger peaks in the periodogram (Diggle, 1990).

To identify statistically significant peaks in spectral density, the Kolmogorov−Smirnov test statistic (D_{max}) was used to calculate a 95% confidence interval around the cumulative distribution function of a periodogram for a random series with the same mean (Diggle, 1990). The value of D_{max} at a probability $p = 0.05$ and df. = 449 $(N/2 = 450)$ is 0·0906 (Sokal & Rohlf, 1981), which is added and subtracted from the expected cumulative distribution to form the upper and lower bounds, respectively (Diggle, 1990). The observed cumulative distribution of the normalized periodogram was then plotted along with the 95% confidence interval to assess significant departures in the spectral density across different periods. Statistical tests were conducted on unsmoothed periodograms.

Results

Litter cover was greater in the control than in the grazed transect, especially in the low to mid-portion of the transect (0−500 m) (Fig. 1(a)). In general, there was a greater plant cover in the grazed transect than in the control (Fig. 1(b)), primarily due to a greater cover of annuals in the grazed area. We found a higher mean per cent cover (1 SE) of *E. pulchellum* in the grazed transect (1·3 ± 0·06) compared to the control (0·7 ± 0·05), but a higher mean per cent cover of *Aristida* spp. in the control (2·4 ± 0·30) compared to the grazed transect (0·6 ± 0·05).
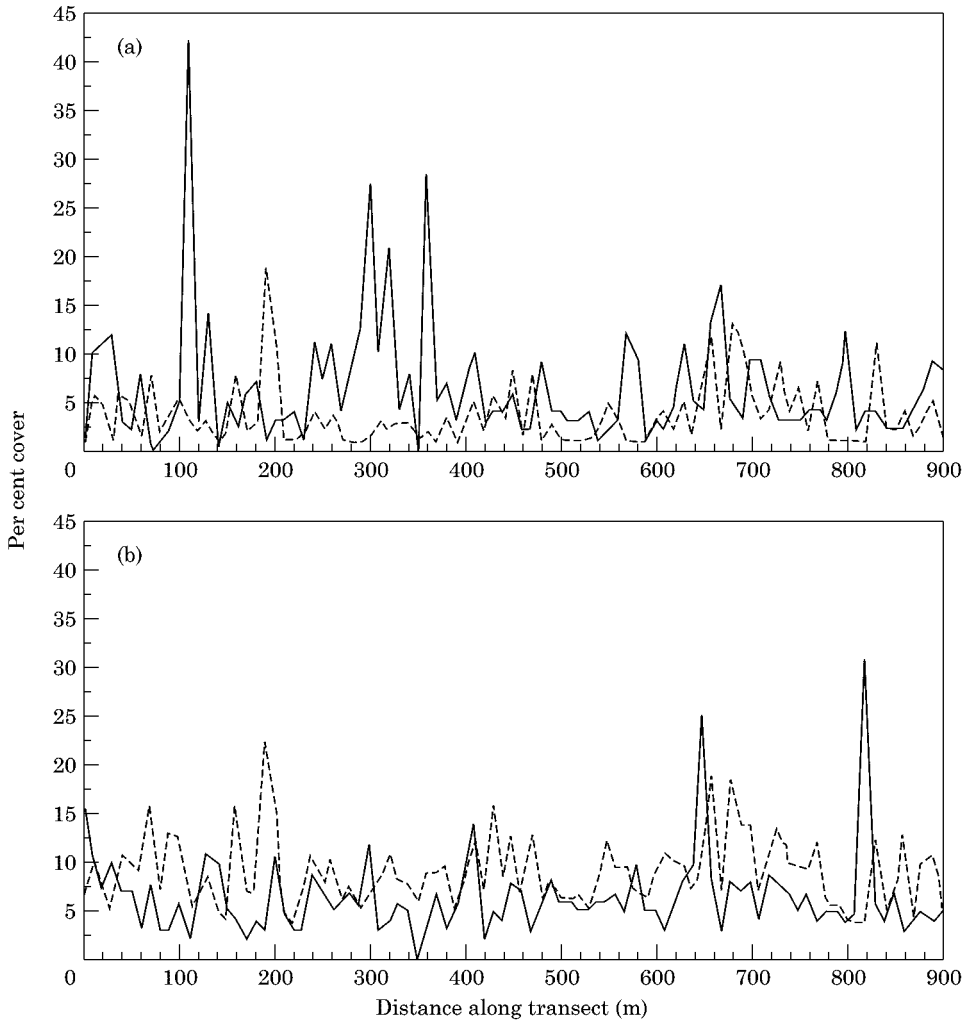
Figure 1. Per cent cover of (a) litter and (b) total plants (basal cover) in 1 m^2 quadrats at 10-m intervals along the control (———) and grazed (– – –) transects. Transects were located along a north-facing bajada and span a distance from a toeslope position just above a playa (distance = 0 m) to a mid-slope position (distance = 900 m).

A total of 10,314 termite casts were counted in the two transects: 6865 casts occurred along the control transect and 3449 casts were found along the grazed transect. In both transects, a greater percentage of casts were found on litter (64% control, 57% grazed) than on plants (36% control, 43% grazed) (Figs 2(a) and 3(a)). Casts were more numerous in the low to mid-portions of both transects (Figs 2(a) and 3(a)).

In both grazing regimes, autocorrelations reflected a strong spatial dependence in termite casts on surface litter (Fig. 2(b)). Spatial dependence in termite cast density on litter was spread over greater distances along the grazed transect (1–35 m, 39 m, 43–45 m, and 49 m) than on the control transect, where it was confined to few peaks at fine scales (1–4 m, 10 m, and 13 m).

Termite casts were more abundant on *E. pulchellum* and spatial dependence occurred over greater distances (1–33 m) in the grazed transect than in the control (1–5 m) (Fig. 4). In contrast, casts on *Aristida* spp. were more abundant (Fig. 5(a)) and had a
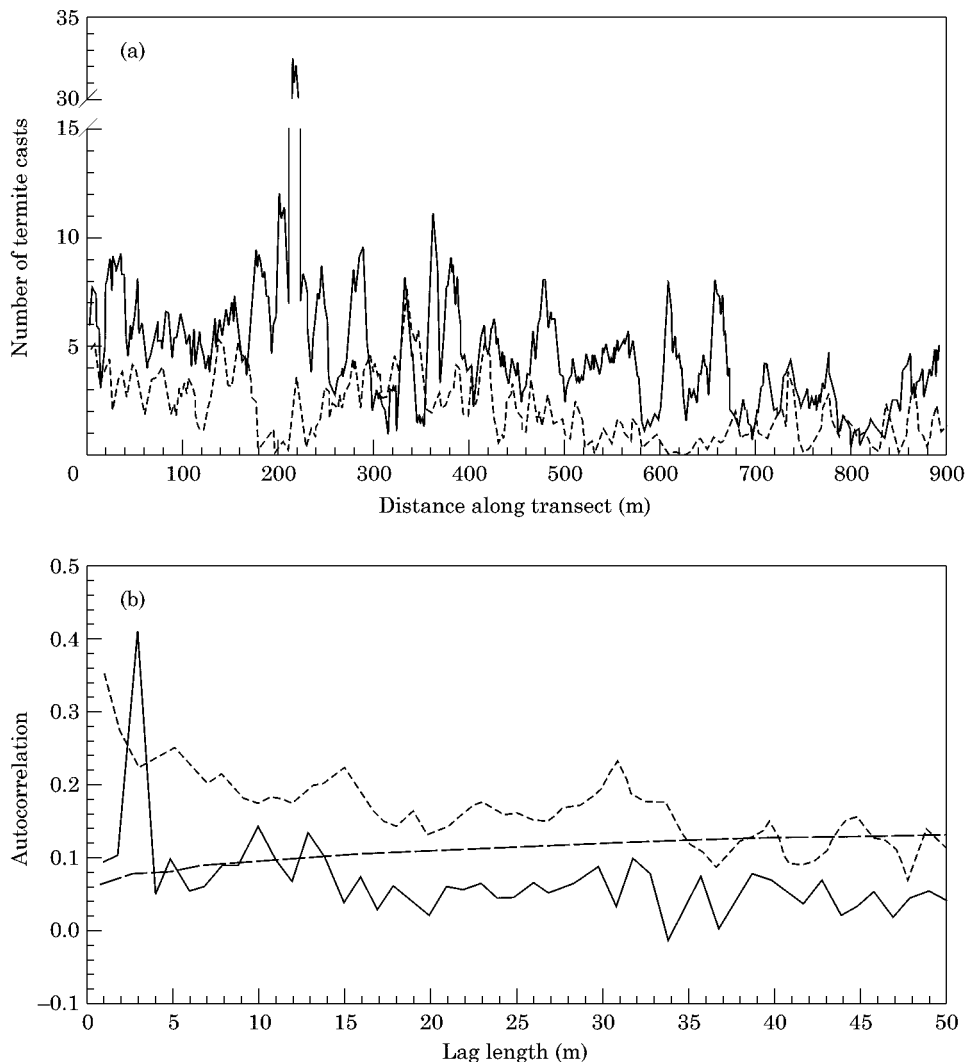
Figure 2. (a) Numbers of termite casts on surface litter in contiguous 1 m^2 quadrats along control (———) and grazed (– – –) transects, and (b) spatial autocorrelation of termite casts on surface litter along control (———) and grazed (— —) transects (the upper 95% confidence interval (- - -) is shown to indicate significant peaks).

stronger spatial dependence in the control (1–15 m) than in the grazed transect (Fig. 5(b)). Termite casts on *E. pulchellum* comprised 42% of the total casts on plants in the grazed transect, and casts on *Aristida* spp. accounted for 64% of the plant total in the control transect.

Spectral analysis provided a different perspective on the spatial patterning of termite casts by partitioning the spatial variation across a range of spatial scales. All six of the spectral analyses showed strong spatial patterning and were significantly non-random when the overall cumulative distributions (see insets, Fig. 6) were compared to those expected from a random series (range of $D_{max} = 0.1568$–0.2984; all $p < 0.01$). Termite casts on litter in the control transect showed peaks in spectral density at periods of 2·5–4 m, 10–20 m, and > 60 m (Fig. 6(a)). A relatively large component of the spatial
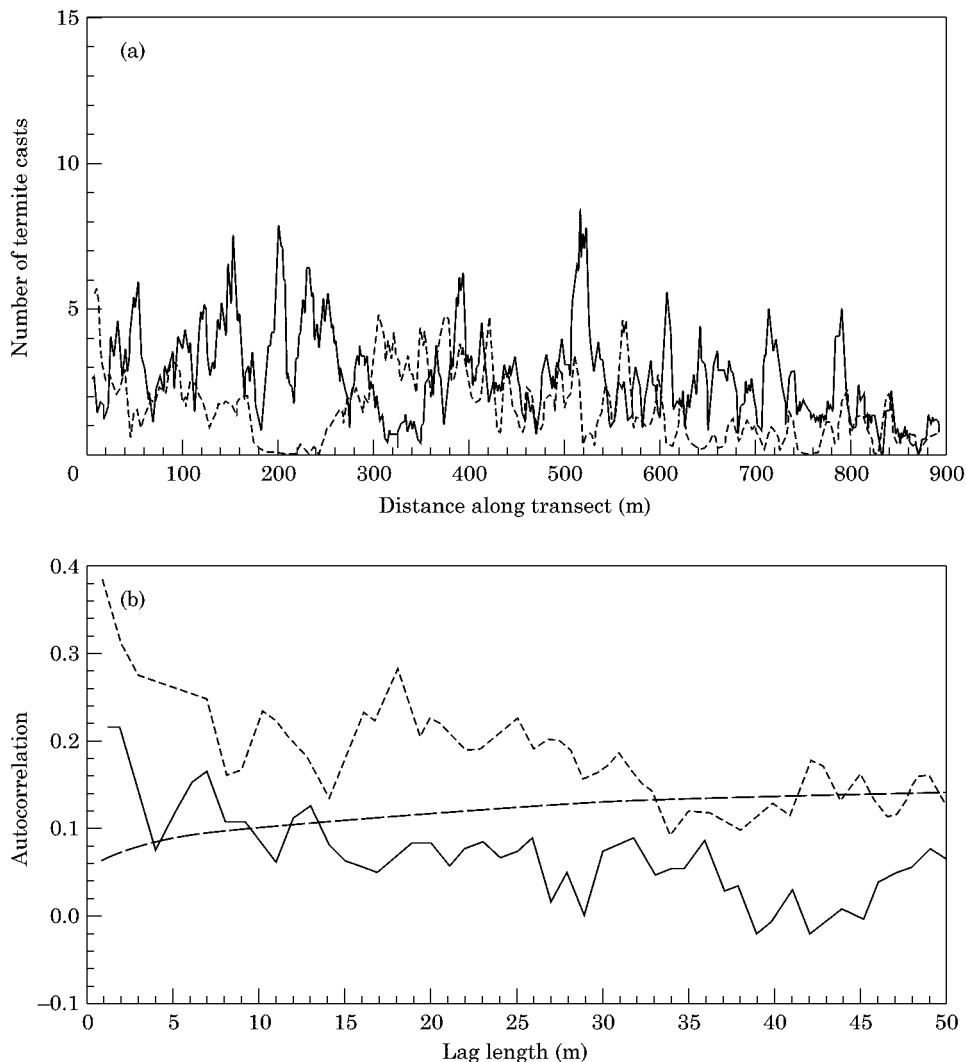
Figure 3. (a) Numbers of termite casts on all plants along control (———) and grazed (– – –) transects, and (b) spatial autocorrelation of termite casts on plants along control (———) and grazed (— —) transects (the upper 95% confidence interval (- - -) is shown to indicate significant peaks).

variation occurred at fine scales (2·5−4 m). In contrast, termite casts on litter in the grazed transect showed a weak signal at periods of 6−9 m with the strongest component of the variation at periods of 20−30 m and > 60 m (Fig. 6(a)). A loss of fine-scale patchiness in termite activity on surface litter clearly occurred in the grazed area.

Termite casts on plants also showed shifts in peaks between the control and the grazed transects, although shifts are not as strong as with litter. The largest peaks occurred between 7−10 m, 20−30 m, and 100−130 m for termite casts on plants in the control transect. Peaks were offset slightly for the grazed transect and were between 5−7 m, 60−90 m, and > 200 m (Fig. 6(b)). The most commonly used plants on control and grazed transects, *Aristida* spp. and *E. pulchellum*, respectively, also had slightly different patterns of spatial variation (Fig. 6(c)). Significant peaks for termites on
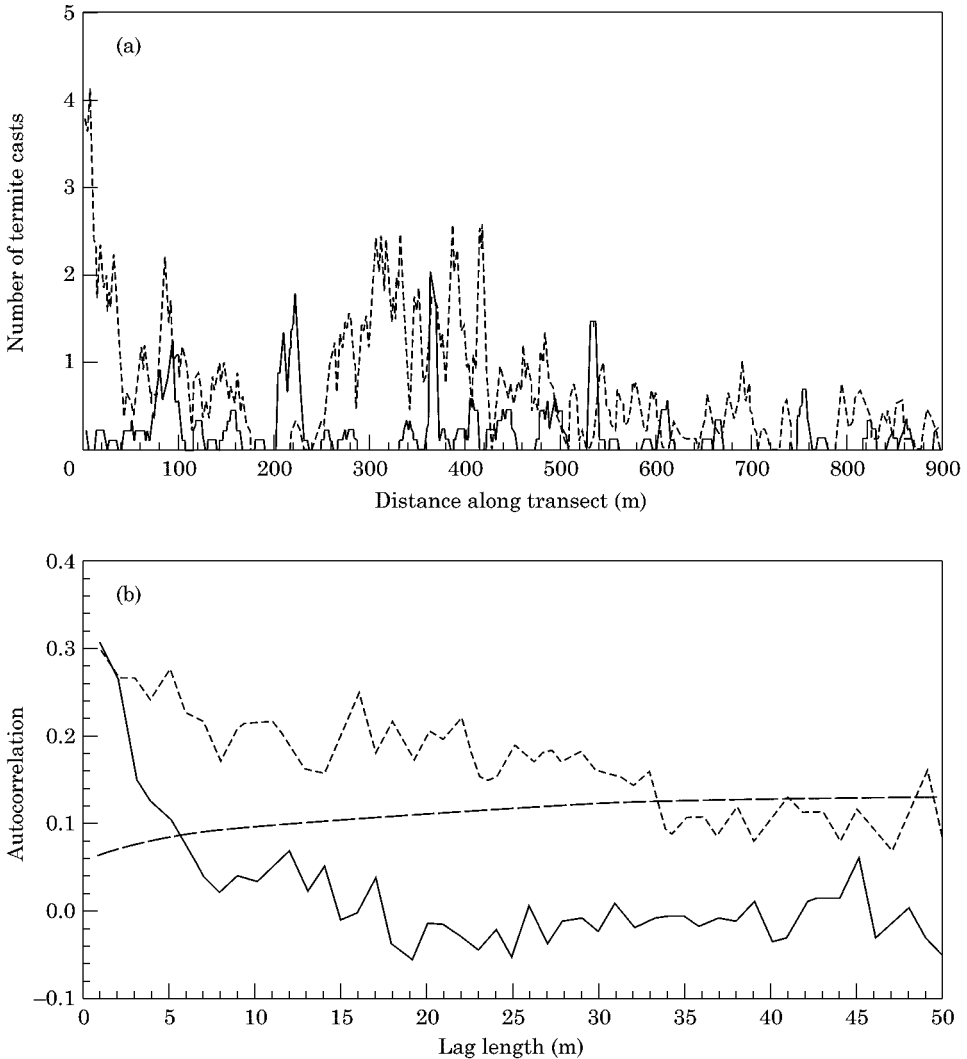
Figure 4. (a) Numbers of termite casts on fluff grass (*E. pulchellum*) along control (———) and grazed (– – –) transects, and (b) spatial autocorrelation of termite casts on *E. pulchellum* along control (———) and grazed (— —) transects (the upper 95% confidence interval is shown (- - -) to indicate significant peaks).

Aristida spp. were 6–7 m, 30–50 m, and 110–130 m; peaks for termites on *E. pulchellum* were 5–6 m, 70–90 m, and > 150 m. Thus, the overall differences in the spatial pattern of termite casts on plants in control and grazed transects are largely reflected by the spatial patterns of occurrence on the most commonly used plants in the two areas, *Aristida* spp. and *E. pulchellum*, respectively.

Discussion

Our findings show that termite activity in desert grasslands is strongly influenced by the fine-scale patchiness in litter around plants, as well as broad-scale variation in litter
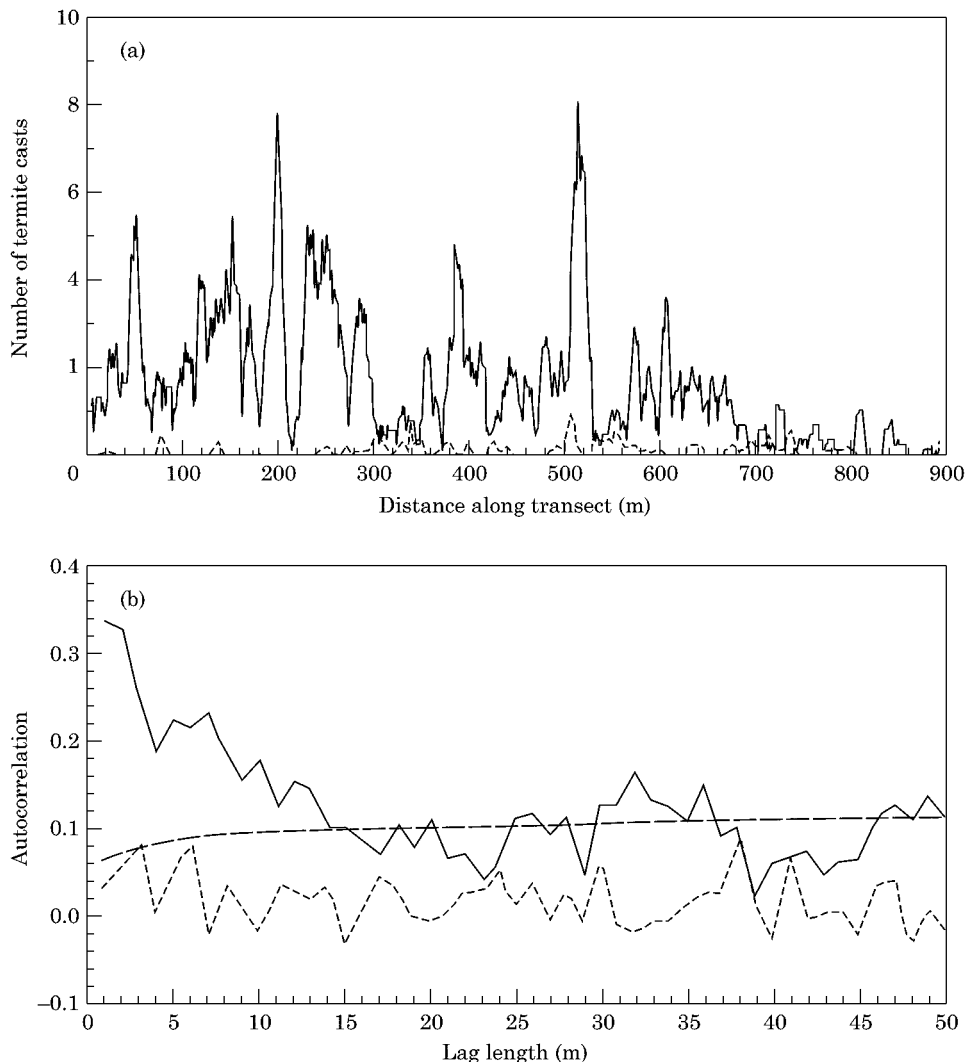
Figure 5. (a) Numbers of termite casts on threeawn (*Aristida* spp.) along control (———) and grazed (– – –) transects, and (b) spatial autocorrelation of termite casts on *Aristida* spp. along control (———) and grazed (— —) transects (the upper 95% confidence interval is shown (- - -) to indicate significant peaks).

availability due to grazing and topography. A greater number of casts were found in the ungrazed than in the grazed area, and in the lower bajada portion of the transects. Both autocorrelation and spectral analysis showed that activity in the control has greater fine-scale spatial dependence along the bajada, whereas fine-scale patterning in termite distribution was lost in the grazed transect where termites were primarily affected by changes in soils and plant cover at broader scales.

Nash & Whitford (1995) conducted a more extensive study of the relationship between termite distribution and soil organic matter along a 2700 m transect within the ungrazed exclosure at the same site. They found no spatial autocorrelation in soil organic matter among 89 samples taken 30 m apart. The lack of spatial dependence in organic matter shown by Nash & Whitford (1995) is consistent with our findings that
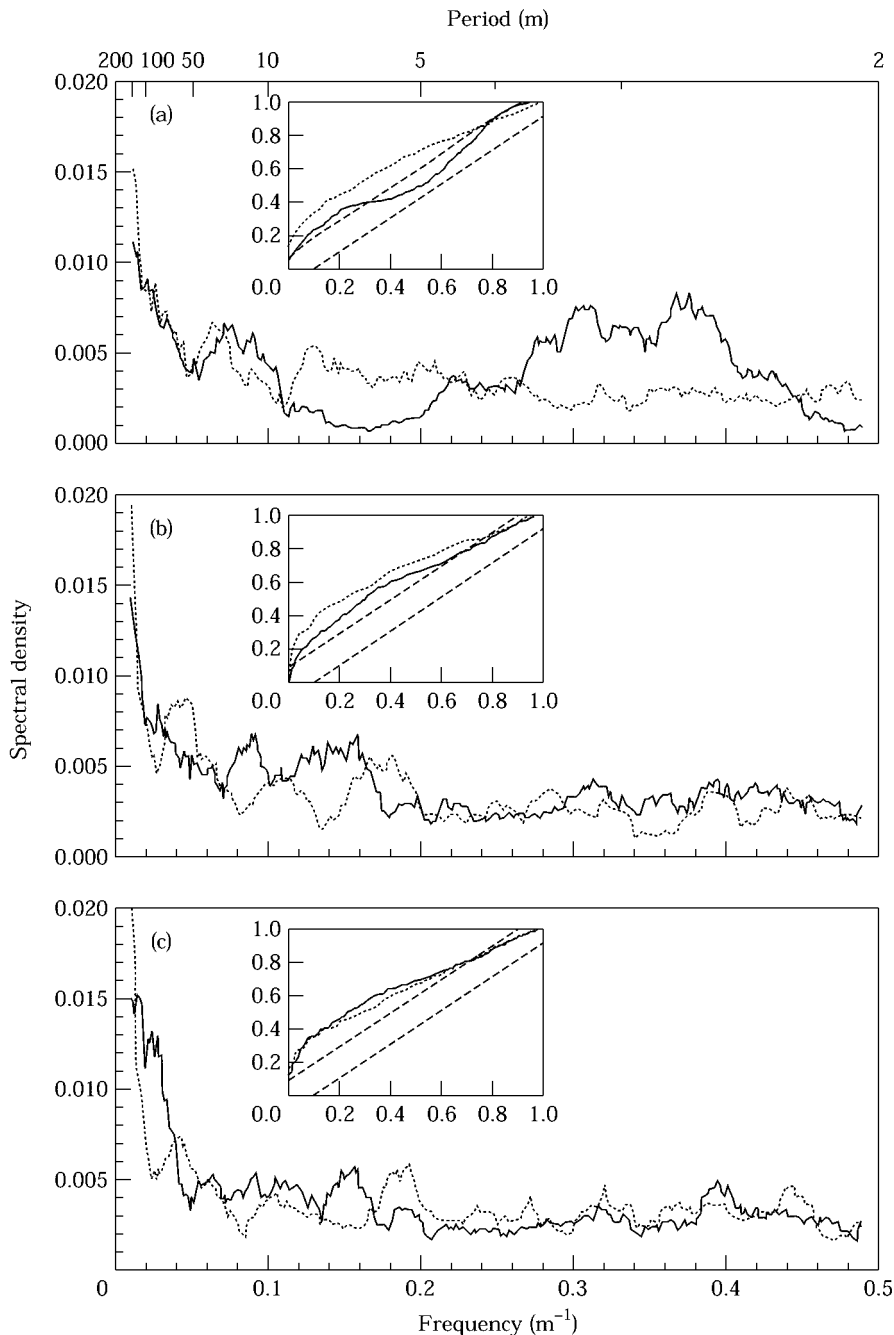
Figure 6. Spectral densities for termite casts found on (a) litter along control (———) and grazed (– – –) transects, (b) total plants along control (———) and grazed (– – –) transects, and (c) preferred plants ((———) = *Aristida* spp.; (– – –) = *E. pulchellum*) along both control and grazed 900 m transects. The values of spectral density represent the proportion of the total spatial variation across spatial scales (period, m). Note that the frequency (m^{-1}) is the inverse of the period (m). Insets show cumulative distributions of spectral densities and 95% confidence intervals derived from the Kolmogorov–Smirnov test statistic (all are significantly different at $p < 0.01$).

showed no spatial autocorrelation of termite cast densities at sample lags ≥ 30 m (Fig. 2). Instead, much of the spatial dependence in termite activity appears to be at finer scales (< 10 m; Fig. 2; see also Crist, 1998). Fine-scale dependence in termite activity is associated with litter availability on or beneath individual plants. The relative importance of termite patchiness at the scale of the individual plant, however, diminishes with livestock grazing (Fig. 6). A loss of fine-scale patchiness in termity activity associated with plants might therefore correspond to changes in termite colony size, foraging activity, or space use.

Termites responded to broad-scale changes in the availability of surface litter, as evidenced by the decrease in litter cover and densities of termite casts found in the grazed transect (Figs 1 and 2). Along the same bajada, Nash & Whitford (1995) observed a strong negative relationship between termite abundance and soil organic matter which, in turn, suggests that termites regulate broad-scale patterns of soil organic matter. Soil micro-organisms may compete with termites for organic matter, however, to produce a negative association between termite abundance and soil carbon or microbial biomass (Holt, 1996). None the less, removal of soil carbon by termites could still preclude microbial decomposition of organic matter and therefore limit soil microbial biomass. In either case, the broad-scale relationships between termite distribution and soil organic matter or microbial biomass will clearly be altered by livestock grazing because of a decreased litter availability and the redistribution of organic matter into fecal pats.

Subterranean termites are an important part of decomposition and nutrient cycling in desert ecosystems (Johnson & Whitford, 1975; Santos & Whitford, 1981; Elkins & Whitford, 1982; Whitford *et al.*, 1982; Silva *et al.*, 1985), yet there is little information about termite spatial distribution (Nash & Whitford, 1995) or how it is affected by livestock grazing. Termite use of plants centers on *Aristida* spp. in ungrazed areas and on *E. pulchellum* in grazed areas. The litter produced by these plants are likely hot spots of termite activity as well, as our observations during sampling suggested that termite casts were primarily on litter beneath *Aristida* spp. in the control transect and on *E. pulchellum* litter in the grazed transect. *Aristida* spp. are palatable to livestock (Holechek *et al.*, 1994) but *E. pulchellum* is not preferred for grazing (Stubbendieck *et al.*, 1992). This would explain the greater termite use of *Aristida* spp. on the control transect where *Aristida* spp. were more abundant. Silva *et al.* (1985) showed that termites remove $> 50\%$ of the *E. pulchellum* litter in 1 year. Our findings on termite use of *E. pulchellum* and the similarity in the spatial pattern of termite casts on *E. pulchellum* and in litter also suggest a coupling of termite activity and fluff grass litter in grazed desert grassland.

The loss of fine-scale heterogeneity of soil organic matter and nutrients in a semi-arid grassland is an important feature of desertification (Schlesinger *et al.*, 1990, 1996). In grazed areas, a decreased litter production results in less organic matter in the inter-plant spaces and the cycling of plant nutrients is therefore progressively confined to the zone beneath plants. This process, coupled with shrub invasion, leads to the development of 'islands of fertility' which characterize desert shrublands (Schlesinger *et al.*, 1990). MacKay *et al.* (1987) found that termites have only a minor role in the litter decomposition of creosote bush, which is the dominant plant in Chihuahuan Desert shrublands. Our findings also suggest that grazing results in reduced levels of termite activity and a loss of fine-scale patchiness as organic matter becomes redistributed into more widely spaced 'resource islands'. Further studies of termite distribution and abundance are needed to determine whether the roles of termites as keystone decomposers will diminish with continued livestock grazing and increased shrub encroachment in desert grasslands.

References

Bock, C.E. & Bock, J.H. (1993). Cover of perennial grasses in southeastern Arizona in relation to livestock grazing. *Conservation Biology*, 7: 371–377.

Buffington, L.C. & Herbel, C.H. (1965). Vegetational changes on a semidesert grassland range from 1858 to 1963. *Ecological Monographs*, 35: 39–164.

Crist, T.O. (1998). The spatial distribution of termites in shortgrass steppe: a geostatistical approach. *Oecologia*, 114: 410–416.

Davis, J.C. (1986). *Statistics and Data Analysis in Geology* (2nd Edn). New York: John Wiley & Sons, Inc. 500 pp.

Diggle, P.J. (1990). *Time Series: a biostatistical introduction*. New York, NY: Oxford University Press. 257 pp.

Elkins, N.Z. & Whitford, W.G. (1982). The role of microarthropods and nematodes in decomposition in a semi-arid ecosystem. *Oecologia*, 55: 303–310.

Haverty, M.I., Nutting, W.L. & LaFage, J.P. (1975). Density of colonies and spatial distribution of foraging territories of the desert subterranean termite, *Heterotermes aureus* (Snyder). *Environmental Entomology*, 4: 104–109.

Holechek, J.L., Tembo, A., Daniel, A., Fusco, M.J. & Cardenas, J. (1994). Long-term grazing influences on Chihuahuan Desert rangeland. *Southwestern Naturalist*, 39: 342–349.

Holt, J.A. (1996). Mound-building termites and soil microbial biomass: an interaction influencing termite abundance. *Insectes Sociaux*, 43: 427–434.

Johnson, R.A. (1992). Soil texture as an influence on the distribution of the desert seed-harvester ants *Pogonomyrmex rugosus* and *Messor pergandei*. *Oecologia*, 89: 118–124.

Johnson, K.A. & Whitford, W.G. (1975). Foraging ecology and relative importance of subterranean termites in Chihuahuan Desert ecosystems. *Environmental Entomology*, 4: 66–70.

Ludwig, J.A. & Cornelius, J.M. (1987). Locating discontinuities along ecological gradients. *Ecology*, 68: 448–450.

MacKay, W.P., Blizzard, J.H., Miller, J.J. & Whitford, W.G. (1985). Analysis of above-ground gallery construction by the subterranean termite (*Gnathamitermes tubiformans*) (Isoptera: Termitidae). *Environmental Entomology*, 14: 470–474.

MacKay, W.P., Silva, S., Loring, S.J. & Whitford, W.G. (1987). The role of subterranean termites in the decomposition of above ground creosotebush litter. *Sociobiology*, 13: 235–239.

Manly, B.F.J. (1991). *Randomization and Monte Carlo Methods in Biology*. New York, NY: Chapman and Hall. 281 pp.

Nash, M.N. & Whitford, W.G. (1995). Subterranean termites: regulators of soil organic matter in the Chihuahuan Desert. *Biology & Fertility of Soils*, 19: 15–18.

Nutting, W.L. & Jones, S.C. (1990). Methods for studying the ecology of subterranean termites. *Sociobiology*, 17: 167–189.

Nutting, W.L., Haverty, M.I. & LaFage, J.P. (1987). Physical and chemical alteration of soil by two subterranean termite species in Sonoran Desert grassland. *Journal of Arid Environments*, 12: 233–239.

Santos, P.F. & Whitford, W.G. (1981). The effects of microarthropods on litter decomposition in Chihuahuan Desert ecosystem. *Ecology*, 62: 654–663.

Schlesinger, W.H., Reynolds, J.F., Cunningham, G.L., Huenneke, L.F., Jarrell, W.M., Virginia, R.A. & Whitford, W.G. (1990). Biological feedbacks in global desertification. *Science*, 247: 1043–1948.

Schlesinger, W.H., Raikes, J.A., Hartley, A.E. & Cross, A.F. (1996). On the spatial pattern of soil nutrients in desert ecosystems. *Ecology*, 77: 364–374.

Silva, S., MacKay, W.P. & Whitford, W.G. (1985). The relative contributions of termites and microarthropods to *E. pulchellum* litter disappearance in the Chihuahuan Desert. *Oecologia*, 67: 31–34.

Sokal, R.R. & Rohlf, F.J. (1981). *Biometry* (2nd Edn). New York: W.H. Freeman & Co. 859 pp.

Stubbendieck, J., Hatch, H.L. & Butterfield, C.H. (1992). *North American Range Plants* (4th Edn). University of Nebraska Press: Lincoln. 722 pp.

SYSTAT 1992. *Statistics*, version 5.2 edition. Evanston, IL: SYSTAT.

Turner, S.J., O'Neill, R.V., Conley, W., Conley, M.R. & Humphries, H.C. (1991). Pattern and scale: statistics for landscape ecology. In: Turner, M.G. & Gardner, R.H. (Eds), *Quantitative Methods in Landscape Ecology*, pp. 17–49. New York, NY: Springer-Verlag. 536 pp.

Ueckert, D.N., Bodine, M.C. & Spears, B.M. (1976). Population density and biomass of the desert termite *Gnathamitermes tubiformans* (Isoptera: Termitidae) in a shortgrass prairie: relationship to temperature and moisture. *Ecology*, 57: 1273–1280.

Whitford, W.G. (1996). The importance of biodiversity of soil biota in arid ecosystems. *Biodiversity and Conservation*, 5: 185–195.

Whitford, W.G., Steinberger, Y. & Ettershank, G. (1982). Contributions of subterranean termites to the ''economy'' of Chihuahuan Desert ecosystems. *Oecologia*, 55: 298–302.

Whitford, W.G., Forbes, G.S. & Kerley, G.W.E. (1995). Diversity, spatial variability, and functional roles of invertebrates in desert grassland ecosystems. In: McClaran, M. & Van Devender, T.R. (Eds), *The Desert Grassland*, pp. 152–195. Tucson, AZ: University of Arizona Press. 346 pp.

Wierenga, P.J., Hendrick, J.M.H., Nash, M.H., Ludwig, J. & Daugherty, L.A. (1987). Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. *Journal of Arid Environments*, 13: 53–63.