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Original article

Unraveling landscapes with phytogenic mounds (nebkhas): An exploration of spatial pattern

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ABSTRACT

Phytogenic mounds (nebkhas) often are symptoms of desertification in arid regions. Interactions among nebkhas and between nebkhas and their environment are however poorly examined. To this end, three main hypotheses of nebkha pattern formation were evaluated in this study. These state that nebkha patterns are either shaped by: (i) biologically induced recruitment inhibiting zones, (ii) biologically induced recruitment encouraging zones, or (iii) by the spatial distribution of abiotic factors which are not biologically driven. Contrasting nebkha landscapes were examined: a highly dense New Mexican mesquite (*Prosopis glandulosa*) and snakeweed (*Gutierrezia sarothrae* and *Gutierrezia microcephala*) ecosystem, and a low-density mixed *Tamarix aphylla* and *Calligonum comosum* field in central Libya. Spatial second-order statistics of strategically chosen nebkha subpatterns were compared with those of null models in which observed patches were spatially randomized without overlap. Null model deviations were assessed with goodness-of-fit tests, and interpreted in terms of hypothesized mechanisms of nebkha pattern formation. Our results suggest that biologically induced recruitment inhibiting zones surround adult mesquite nebkhas. The configuration of *Calligonum* and *Tamarix* nebkhas may be driven by spatial dynamics of abiotic microsites which are not caused by nebkha interactions. Hence we conclude that both biotic and abiotic drivers can shape nebkha spatial patterns.

1. Introduction

Nebkhas are vegetated mounds originating from cumulative deposition of wind- and waterborne sediment around burial-tolerant host plants (Batanouny, 2001). Since, nebkha landscapes require unconsolidated transportable sediment, they are often found in deserts. A majority of authors argue that recently established nebkhas are symptoms of land degradation and aridification (Du et al., 2010; Gile, 1975; Rango et al., 2000; Tengberg, 1995; Wang et al., 2008). Indeed, a decrease in environmental resources (e.g. aridification under climate change) or an increase in disturbance (e.g. grazing pressure), may induce vegetation loss, and thereby promote sediment erosion, and subsequently favor burial-tolerant (i.e. nebkha initiators) over burial-intolerant plant species (Havstad et al., 2000). Land degradation and aridification have several definitions (Ravi et al., 2010) of which most have negative connotations, suggesting their symptoms (i.e. nebkhas) are undesirable too. However, nebkhas can have positive aspects: (i) They can act as biodiversity agents by nursing herbaceous species which, under the same climatic conditions, would not survive unsheltered (Brown and Porembski, 1997); (ii) They also trap airborne sediment (Bendali et al., 1990; Gibbens et al., 2005; Zhang et al., 2011), hereby impeding desert expansion; (iii) Nebkhas enrich soil with nutrients (Reyes-Reyes et al., 2002), although it is not yet clear whether these are locally reallocated, or are brought newly into the ecosystem (Du et al., 2010); (iv) Nebkha landscapes may also increase total soil water content with respect to bare landscapes. Indeed, higher infiltration rates are often observed within vegetated patches as compared to surrounding barren soil (Martinez-Meza and Whitford, 1996), where freshly fallen water is more prone to evaporation, especially in deserts (Glover et al., 1962); (v) Nebkha fields are probably intermediate between grasslands and sandy barren states, and in this respect, they might be useful in land restoration (El-Bana et al., 2003).

Spatial patterns of vegetation patches have already been extensively examined, especially in arid lands (e.g. Haase et al., 1996; Gilad et al., 2007). However, few studies examined nebkhas in a spatial statistical manner. Goslee et al. (2003) did analyze New Mexican

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mesquite nebkha patterns with Ripley's K function, but they focused on inter-nebkha scales larger than 25 m. This study as well wants to verify whether local interactions play a role in resulting patch configurations. Therefore smaller inter-nebkha scales were also included. We propose three alternative hypotheses which could explain spatial configurations of observed nebkhas. A first hypothesis states that adult nebkhas either deplete resources from, or release allelopathic substances in their near surroundings, hereby inducing local zones around nebkhas which inhibit seedling and juvenile recruitment. These zones should be reflected into the pattern when patch density is sufficiently high: younger vegetation patches should appear repulsed from adult nebkhas. A second hypothesis presumes that adult nebkhas enhance vegetation patch recruitment in their spatial proximity, either by distance-restricted seed dispersal, or by improving resources near their canopies (Schlesinger and Pilmanis, 1998). These two processes could lead young vegetation patches appear to be clustered around adult nebkhas. A last hypothesis postulates that nebkha landscapes are driven by spatial heterogeneities of resources or stresses which are not caused by nebkha interactions. Such heterogeneities could govern local success rates of recruitment, hence as well introducing clusters of young patches. These clusters should be located near adult patches when the aforementioned heterogeneities do not change position during the time frame in which the landscape was formed. However, when microsites do change position over time (e.g. due to changing sand depths), clusters of young patches could lay independent from adult patches.

We analyzed spatial nebkha patterns based on air and spaceborne images from two different areas (New Mexico, USA and Libya). The main objective was to identify whether biotic or abiotic drivers underlie observed nebkha patterns. To this end, nebkha patterns were examined on their spatial configuration with second-order spatial statistics. Results were interpreted in terms of hypotheses on nebkha pattern formation, as mentioned above.

2. Methods

Several nebkha fields mentioned in peer reviewed articles were screened for use in this study (Appendix A). Of those, only the field described by Langford (2000), located in the Mesilla basin about 13 km to the north of the US-Mexico border (31° 55′ 33″ North, 106° 54′ 7″ West), was finally withheld. This landscape is dominated by the nebkha host plant species *Prosopis glandulosa* (mesquite) (Ed Fredrickson, personal communication), while interspaces are predominated by two small persistent bushes *Gutierrezia sarothrae* (broom snakeweed) and *Gutierrezia microcephala* (snakeweed) (Brandon Bestelmeyer, personal communication). Both *Gutierrezia* species will further be simply addressed as snakeweed. Literature shows that the northern Chihuahuan desert evolved from grassland to a nebkha ecosystem during the second half of the 19th century (Gibbens et al., 2005). This transition was induced by a change in land use (more livestock) and enhanced by a series of drought incidents. Since mesquite and snakeweed are unpalatable to livestock, they were less affected by increased grazing pressure, which explains their current dominance (McDaniel and Ross, 2002). Seed pods and seeds of mesquite are however highly palatable for livestock, rodents and other wildlife. The latter often act as vectors of long-distance seed dispersal via fecal deposition of viable seeds (Brown and Archer, 1988; Kramp et al., 1998). According to Langford (2000), mesquite nebkha diameters can extent to 40 m, while Sterling et al. (2000) observed that snakeweed patch diameters can reach about 1 m in New Mexican snakeweed populations. Airborne imagery of this landscape, produced on June 13, 2010 was obtained from Google Earth (GE) (Appendix B). The exact resolution of the image source was not provided. However, after close inspection, isolated patches with areas of at least 0.09 m^2 could clearly be identified as perennial vegetation patches. All patches with areas smaller than this value were omitted to exclude possible annuals. Fortin and Dale (2005) stated that a study site's spatial extent should be large enough to fully capture all ecological processes under study, but not too large as to introduce unwanted large-scale heterogeneity. With the latter taken into account, two separate study sites were delineated from this nebkha field. In the first, both snakeweed and mesquite were examined in a 90 m × 90 m sized area (Fig. 1a). In the second study site, only mesquite patches were studied by excluding snakeweeds from analysis in a 250 m × 250 m plot (Fig. 1b). Snakeweeds were assumed excluded by eliminating patches with diameters smaller than 1.6 m. Indeed, this threshold size goes together with distinct patch textures and is higher than maximum observed snakeweed sizes in literature (i.e. about 1 m, as mentioned above). Moreover, ranked patch sizes of combined snakeweed and mesquite patches form a bilinear curve with a breakpoint at 1.6 m diameter (see Appendix C), which additionally supports this choice of threshold size. A number of small mesquite patches might be removed when eliminating patches below 1.6 m in Fig. 1b. However, this does not strongly affect the conclusions drawn from this analysis, as the size range of mesquite will only be slightly reduced.

A second withheld nebkha landscape (27° 14′ 40″ North, 14° 36′ 0″ East) is located in central Libya (Fig. 1c). This study site can be easily found on Google Maps. It is very close to Tamanhint city (near Sabha) and its small airfield. There is only 1 km between the study site and the edges of Tamanhint city. A 2006 field visit revealed *Tamarix aphylla* and *Calligonum comosum* as the most dominating host species present (all individuals of these species formed nebkhas in this region). This study site belongs to a protected area, and therefore is without livestock grazing. The majority of *Tamarix aphylla* nebkhas were larger than *Calligonum comosum* nebkhas (only very few of them had sizes falling in the size range of *Calligonum comosum*). Both *Tamarix aphylla* and *Calligonum comosum* are typical wind dispersers and their seeds may end up far from parent plants (Danin, 1996; Di Tomaso, 1998). An image of a 700 m × 700 m nebkha field of which the source image was produced on July 25, 2006 with IKONOS (a spaceborne sensor with 0.8 m resolution) was acquired from GE. Since no exact size ranges were recorded on the field, and because both species could not be distinguished on the image, size ranges were estimated from literature: *Calligonum comosum* patches have been reported not having diameters larger than 3.5 m (Koller, 1956) while typical *Tamarix aphylla* diameters have been assumed between 5 and 15 m (Hayes et al., 2009). Libyan study site patches, smaller and larger than 3.5 m, were therefore respectively assumed to be *Calligonum* and *Tamarix* nebkhas. In this way, a number of *Tamarix* juveniles smaller than 3.5 m might have been wrongfully labeled as *Calligonum*. However, based on the 2006 field observations, we assume this number negligibly small.

Spatio-temporal information was implicitly assumed by considering larger patches older than smaller patches in a single species pattern, as was already observed for mesquite nebkhas by Gadzia and Ludwig (1983). Patch ages are considered ordinal, not absolute. This size–age relationship was used to divide observed patterns into two subpatterns which correspond to distinct classes of patch age. Hereto, for each single species pattern, a threshold size (TS) was chosen to divide the pattern's total fractional cover into half. Such derived subpatterns were addressed as SP_S and SP_L, respectively comprising small and large vegetation patches. SP_S and SP_L thus each represent half of the total fractional cover of the single species pattern. Pattern divisions are in this way less dependent on image resolution compared to divisions based on more common central tendencies (e.g. the mean or median patch size). The latter is especially true when patch size distributions are negatively skewed, as commonly reported in literature for vegetation patches (Kéfi et al., 2007; Scanlon et al., 2007).